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An ounce of prevention: Quantifying the effects of non-lethal tools on wolf behavior

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ABSTRACT

Human-carnivore conflict is presently on the rise as human populations continue to grow and carnivore conservation efforts gain precedence. The behaviors exhibited by carnivores that cause conflict are often learned; therefore, reducing learning potential through the use of non-lethal tools is important for coexistence. In this study we measured how prior experience (i.e., conditioning) influenced the motivation and persistence of captive wolves (*Canis lupus*) seeking a food reward by quantifying latency to first behavior and duration of behavior for two behavior groups: investigative and work behaviors. Latency to first behavior was faster in conditioned wolves for both investigative (11 times faster; $P = 0.0491$) and work (4 times faster; $P = 0.0112$) behaviors, indicating prior experience motivated wolves to overcome neophobic behaviors and facilitated learning to access rewards more quickly. We found little difference in duration for both investigative ($P = 0.3194$) and work behaviors ($P = 0.7016$), indicating conditioned and non-conditioned wolves will spend similar amounts of time trying to obtain a reward once a behavior is initiated. When wolves were unable to attain food rewards, we found that the duration of both investigative ($P = 0.0631$) and work ($P = 0.0609$) behavior declined over the course of three weeks for both non-conditioned (37.3% and 92.6% decline in investigative behaviors and work behaviors, respectively) and conditioned (59.5% and 88.2% decline in investigative behaviors and work behaviors, respectively) wolves, indicating decreased persistence with the application of a secure prevention measure. Overall, our results indicate that the use of non-lethal tools that prevent animals from attaining anthropogenic food can effectively curb learning in carnivores and help reduce human-carnivore conflict.

1. Introduction

Conflict between people and carnivores is an ancient issue (Breitenmoser, 1998; Fascione et al., 2004) that occurs when carnivores prey upon livestock, utilize anthropogenic resources, or threaten human health and safety (Bangs and Shivik, 2001; Woodroffe et al., 2005; Olson et al., 2015). Recent increases in human-carnivore conflict throughout the world (e.g., Mech, 1995; Fascione et al., 2004; Woodroffe et al., 2005; Baruch-Mordo et al., 2008; Poessel et al., 2016) result from continuously expanding human populations and/or successful predator conservation efforts. For example, coyotes (*Canis latrans*) have expanded their range throughout North America and successfully occupy urban areas (Gehrt et al., 2009; Poessel et al., 2016), while wolves (*Canis lupus*) and brown bears (*Ursus arctos*) have growing

populations in the U.S. and Europe (Musiani and Paquet, 2004; Kendall et al., 2009; Chapron et al., 2014). Reducing conflict while simultaneously maintaining carnivore populations has thus become an important management priority and understanding carnivore behavior is a critical endeavor in this effort.

1.1. Understanding the role of learning in conflict

Often carnivores learn behaviors that allow them to access human resources and cause conflict (Linnell et al., 1999). For example, Mazur and Seher (2008) demonstrated the importance of learning between mothers and offspring in the perpetual raiding of campgrounds in Yosemite and Sequoia National Parks (California, USA) by black bears. Woodroffe and Frank (2005) implied that African lions needed to learn

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new behaviors to access livestock protected at night in bomas (e.g., loitering outside bomas and waiting for panicked livestock to breakout, jumping boma walls) and that development of more effective bomas thwarted this learning process for many lions. In both examples, once individuals learned to overcome novelty (i.e., campgrounds for black bears, bomas for lions) then stopping them from further conflict using non-lethal means (e.g., Shivik, 2006) became more difficult.

As a means of adaptation, learning provides animals with the ability to adjust to changes in their habitat and exploit novel resources (Davey, 1989). The influence of learning on adaptation (and ultimately on an animal's fitness) is supported by recent discoveries in neuroscience that demonstrate how seeking behaviors activate a global appetitive state and facilitate reward based learning (Alcaro and Panksepp, 2011). In the exploration of novel objects, seeking behaviors facilitate associative learning, with food rewards enhancing the effect of learned associations (Alcaro and Panksepp, 2011). Acquisition of information through exploration is further balanced by cost-benefit assessment, where low-cost sampling (i.e., investigation) may be advantageous (Mettke-Hofmann et al., 2006; Reader, 2015) albeit restrained by neophobia (Stöwe et al., 2006). Conversely, experience with a given object or circumstance through repeated exposure can modify exploration and allow quicker access to potential benefits (Mettke-Hofmann et al., 2006).

In the context of mediating human-carnivore conflict, seeking and exploration are fundamental behaviors for survival, but also result in carnivores exploiting anthropogenic resources that lead to conflict. Because learning plays an important role in honing future preferences (Heinrich, 1995) and the perpetuation of behavior, it is logical to conclude that preventing carnivores from attaining food rewards (i.e., gaining experience) in situations that lead to conflict should suppress innate seeking behaviors and therefore reduce conflict. This idea about the importance of learning and prevention of conflict is captured in the colloquial phrase, 'an ounce of prevention is worth a pound of cure'. Measures to prevent carnivore conflict can be implemented using a variety of non-lethal tools (e.g., Shivik et al., 2003; Shivik, 2006) but are often employed in reaction to conflict (i.e., after learning has occurred), potentially diminishing their impact given tools must completely discourage or prevent future attempts. Given the importance of prevention in conflict mitigation (Woodroffe et al., 2005), understanding the mechanisms of effective prevention methods and gaining knowledge of underlying carnivore behaviors and learning is essential.

1.2. Objectives

In this study our goal was to elucidate how experience and learning influenced subsequent motivation to overcome neophobic behaviors. We did this by studying captive wolves in a controlled experiment where conditioned wolves had previous experience and learning opportunity surrounding the acquisition of a reward, and non-conditioned wolves had no previous experience or opportunity to learn. We measured both exploratory (i.e., investigative) behaviors and behaviors that demonstrated concerted effort to access a food reward (i.e., work). We assessed the time to first investigative and work behaviors and the duration of these behaviors to understand how prior experience influenced learning and motivation to overcome neophobic behaviors between our two groups of wolves.

2. Methods

2.1. Study area and subjects

Our study was conducted at the Wildlife Science Center, a captive wildlife research center near Forest Lake, MN, USA during the winter of 2004–2005. Wolves were housed in pens containing between one and seven individuals. We randomly selected pens as either control (i.e., non-conditioned) or treatment (i.e., conditioned) groups; pens containing single wolves were excluded due to differential object

Table 1

Pen numbers, the number of wolves housed in each pen, and the randomly assigned treatment for each pen. We excluded pens 10 and 12 given different object exploration behaviors can be expected in single animals vs groups of animals (Moretti et al., 2015).

Pen	Num Wolves	Treatment
1C	2	Control
2T	2	Treatment
3C	2	Control
4T	5	Treatment
5T	5	Treatment
6C	2	Control
7C	3	Control
8T	7	Treatment
9T	4	Treatment
10T	1	Treatment
11C	2	Control
12T	1	Treatment
13C	3	Control
15C	2	Control

exploration behavior exhibited by animals in alone vs pair or pack conditions (Moretti et al., 2015). We identified five pens for conditioning with two, four, five, five, and seven individuals and seven non-conditioned pens, five with two individuals and two with three individuals (Table 1). All wolves were adults or sub-adults and fed on a normal schedule throughout the duration of the study. Our study protocol was approved by the National Wildlife Research Center Animal Care and Use Committee under study protocol QA 928.

2.2. Experiment

To conduct our experiment we chained a clear plastic screw-top cylindrical canister to a fixed post along the perimeter of each pen (Fig. 1). We drilled holes into the bottom of each canister to allow scent, but not food, to be released from the canister. We placed a video camera (Sony CCD-TR517 Hi8 8 mm Handyman Video Camcorder, Minato, Tokyo, Japan) directly outside the pen about 2.5 feet above ground level and aimed to capture the area surrounding the canister. All animals were conditioned to the camera and an empty canister with closed lid for 2 h a day, 5 days a week, for 2 weeks. After initial camera and canister conditioning, we then food conditioned our selected treatment pens by placing two pounds of sled dog food in the open canister with its lid off so wolves attained a food reward from the canister. This sled dog food was an uncommon but highly prized component of the wolves' diet. Food conditioning trials also occurred 2 h a day, 5 days a week, for 2 weeks. During the food conditioning period, we placed empty canisters with closed lids in non-conditioned (i.e., control) pens for the same duration. Following the food conditioning period, we conducted three trials over the course of 3 weeks, with each trial about 8 h in duration and roughly 1 week apart. We left canisters in pens for the entirety of the study period; however, food rewards were removed from canisters when each 8 h trial was complete. For each trial we placed 2 pounds of sled dog food in each conditioned and non-conditioned pen's canister and secured the lid to ensure that wolves did not attain a reward at any time during the three trials. We video recorded each trial in its entirety with a brief pause mid trial to switch camera tapes. We expected that conditioned wolves would respond to food conditioning and therefore be less wary and more persistent in obtaining reward from canisters in our experimental trials. We expected reduced wariness (i.e., neophobia) and increased persistence to manifest as a measure of investigative and work behaviors directed towards canisters in two ways: 1) as quicker demonstration of first behavior over the course of our trials (i.e., latency to first behavior); 2) as increased time and effort exploring and seeking reward (duration of behavior).



Fig. 1. One clear plastic canister, with holes drilled into the base to allow for scent to pass through, was chained to the fenceline in each pen for the duration of the experiment. During our conditioning phase, control wolves were conditioned to empty canisters and treatment wolves were conditioned to receive a food reward from canisters. In our experimental trials, a food reward was placed into canisters for both control and treatment pens with a lid (black screw top, not pictured) securely attached so that wolves could not obtain the reward.

2.3. Data analysis

To quantify behavior from video footage we used the Noldus Observer XT (2013, Wageningen, The Netherlands) event logging software. We created a coding scheme to capture all tangible behaviors wolves displayed that were associated with investigation of the canister or direct effort to open it and scored each video continuously, recording both the latency to first behavior and the duration of each behavior. While distinct behaviors such as sniffing or chewing an object are relative to a suite of behaviors which can vary significantly amongst individuals (Benson-Amram et al., 2013) and can be difficult to classify (MacNulty et al., 2007), a general categorization of behavior units can provide more holistic insight. We thus categorized all behaviors into two behavioral groups: investigative and work (Table 2). Investigative behaviors capture initial exploration of an object including base level sensory and spatial exploration through sniffing, licking, scratching and nudging. Work behaviors transcend base level exploration and demonstrated concerted effort towards gaining reward associated with an object, including pawing, chewing, tugging and pinning behaviors. We defined a behavior as work when the behavior focused directly on the canister, with tugging defined as a wolf picking up the canister with its mouth to pull on the chain attachment and pinning as placing one or both paws on the canister to hold it in place, usually to aid in more effective chewing. Each pen was considered a distinct sample unit and behaviors were scored on a per pen basis. Given the social nature of wolves we did not consider individual variation within pens, rather controlled for the number of wolves using statistical measures as described below.

Table 2

An ethogram of behaviors directed towards investigation of or direct effort towards sealed canister containing reward.

Behavior	Description
Investigative Behaviors	
Sniffing	Basic olfactory investigation; nostrils flared, nose directed at object; either in contact or within one body length from canister
Scratching	Digging earth surrounding can; claws scraping the dirt or snow; either in contact or within one body length from canister
Licking	Tongue contact with canister; either prolonged licking or short, probing test licks
Nudging	Use of nose to poke or push canister; short, quick movements where wolf either lunges at or repeatedly pushes canister with nose
Work Behaviors	
Pawing	Use of front paw(s) to swat at canister in an attempt to penetrate surface or set canister into motion
Chewing	Gnawing motion with teeth (either carnassial teeth/canines or incisors) on canister used in attempt to open canister
Tugging	Placing chain or chain attachment point to canister in mouth and backing up until canister is taut on its chain, then using entire body to pull back with force
Pinning	Use of one or both paws to immobilize canister in either a crouched or standing position; usually performed to stabilize for better chewing

Latency to the first behavior exhibited in each group was calculated as the time elapsed from the start of the trial to the time at which the first behavior in the respective category was performed. Given each pen contained multiple animals, we calculated latency as a measure of the first behavior exhibited by an individual in the pen. We scored the start of the trial as the moment the baited canister left the hands of the technician and the end of the trial as either when sled dog food was removed from the canister or the camera was turned off. For wolves that did not exhibit work behaviors across the span of the trial we assigned the total duration of the trial (~8 h) as the time of latency to first work behavior. We used latency to first approach as a measure of how quickly wolves approached and interacted with the container and expected that conditioned pens would more quickly approach canisters for both investigative and work behaviors. We used the duration of behaviors to assess the amount of effort and interest directed towards gaining the reward in the canisters for both investigative and work behaviors. We expected that food conditioned wolves would spend more time with the canisters than non-conditioned wolves, particularly for work behaviors. In addition, given the three trials occurred in succession over 3 weeks, we expected to see a temporal effect between trials, with the greatest duration of behaviors exhibited in Trial 1 followed by a subsequent tapered decrease in duration over the following two trials.

We analyzed data using linear mixed models with Kenward-Roger approximation for degrees of freedom and the pen number as a random effect using the lme4 and lmerTest packages in R Studio (Bates et al., 2015; Team, 2015; Kuznetsova et al., 2016). We could not meet the assumption of equal variance for these models given large variation

across our small sample size and thus ran models using log transformations of all data. We performed four different tests on our investigation and work data sets, using latency and duration as response variables and testing for the effects of trial, treatment, and the interaction of trial and treatment. Given latency was calculated as the moment the first wolf within a pen exhibited an investigative or work behavior, we did not anticipate that the number of wolves would influence latency results. To confirm this belief and check for unforeseen effects of the number of wolves in each pen, we performed tests on latency data with models that both included and excluded the number of wolves as a covariate. Models that included the number of wolves as a covariate did not influence latency results between our treatments for investigative ($df = 1$, $F = 1.411$, $P = 0.2656$) or work ($df = 1$, $F = 0.1579$, $P = 0.7017$) behaviors and were therefore excluded from our results. For duration tests we included the number of wolves in each pen as a covariate to control for any effects of varying pack sizes. In visual inspections of duration data we controlled for number of wolves by dividing total duration by the number of wolves in each pen.

3. Results

3.1. Latency to first behavior

As predicted we found strong evidence that conditioned wolves had shorter latency to first investigative ($P = 0.0491$) and work behaviors ($P = 0.0112$) than non-conditioned wolves (Table 3); however, it is important to note that in Trial 1 we removed one non-conditioned pen from our latency results due to missing start sequence footage because of faulty equipment. Latency to first investigative behavior was almost 11 times faster in conditioned wolves ($n = 5$, mean 15.2 s, SE 6.4) than in non-conditioned wolves ($n = 7$, mean 165.9 s, SE 83.5) (Fig. 2a). Latency to first work behavior in conditioned wolves ($n = 5$, mean 3,318 s, SE 2,086.4) was nearly four times faster than in non-conditioned wolves ($n = 7$, mean 13,260 s, SE 2576.2) (Fig. 2b). Latency to first work behavior exhibited by conditioned wolves occurred in the first 30 s in three of the five conditioned pens in Trial 1 (Fig. 2b). Wolves in three non-conditioned pens and one conditioned pen did not exhibit work behaviors throughout the entirety of Trial 1 (Fig. 2b). In Trial 2, all conditioned wolves exhibited work behaviors during the trial period and one non-conditioned pen of wolves exhibited no work behaviors. In Trial 3, wolves in one conditioned pen and two non-conditioned pens did not exhibit work behaviors during the trial period (Fig. 2b). Of the non-conditioned wolves that did not exhibit work behaviors, one pen (1C) did not exhibit work behaviors across all three trials, approaching the canister with investigative behaviors only (Fig. 2b). For both investigative and work behaviors there was notable variation in latency across wolves, treatments, and behavior groups (Figs. 1a, 2b) and we found no indication that this variation was related

Table 3

Linear mixed model test statistics for latency and duration of work and investigative behaviors in captive wolves. Duration models included the number of wolves as a covariate.

	Model	df	F value	p value
Latency to First Investigative Behavior	Treatment	1	5.0173	0.0491
	Trial	2	2.8074	0.0854
Latency to First Work Behavior	Treatment* <i>Trial</i>	2	0.0346	0.9661
	Treatment	1	9.6662	0.0112
Duration of Investigative Behaviors	Trial	2	0.3674	0.6973
	Treatment* <i>Trial</i>	2	2.1788	0.1403
Duration of Work Behavior	Num Wolves + Treatment	1	1.1223	0.3194
	Num Wolves + Trial	2	3.3056	0.0631
Duration of Work Behavior	Num Wolves + Treatment* <i>Trial</i>	2	0.7261	0.4991
	Num Wolves + Treatment	1	0.1579	0.7016
Duration of Work Behavior	Num Wolves + Trial	2	3.3404	0.0609
	Num Wolves + Treatment* <i>Trial</i>	2	0.4601	0.6392

to the number of wolves in each pen. Our model results were suggestive of an effect between trial and latency to first investigative behavior ($P = 0.0854$, Table 3) although visual inspection of our untransformed data does not reveal a clear pattern in this finding (Fig. 2a). We did not observe an effect between trial and latency to first work behavior, nor did we observe an interaction effect between trail and treatment for investigative or work behaviors (Table 3).

3.2. Duration of behaviors

There was a decrease in the amount of both investigative ($P = 0.0631$) and work ($P = 0.0609$) behaviors for both conditioned and non-conditioned wolves between Trials 1 and 3 (Table 3); however, it is important to note that due to technical difficulties with some of our cameras that caused loss of continuous footage, we removed two non-conditioned pens and one treatment pen from the duration results in Trial 1 and two non-conditioned pens from Trial 2. Between Trial 1 and Trial 3 we documented a 37.3% and 59.5% reduction of investigative behaviors in non-conditioned and conditioned wolves, respectively (Fig. 3a). Between Trial 1 and Trial 3 we documented a 92.6% and 88.2% reduction of work behaviors in non-conditioned and conditioned wolves, respectively (Fig. 3b). Conditioned and non-conditioned wolves exhibited a similar amount of both investigative and work behaviors (Fig. 3a,b). Non-conditioned wolves spent only slightly more time investigating canisters ($n = 7$, mean 235.4 s, SE 46.9) than conditioned wolves ($n = 5$, mean 157.3 s, SE 33.3) and the duration of work behaviors exhibited by non-conditioned ($n = 7$, mean 57.4 s, SE 23.3) wolves was nearly identical to that exhibited by conditioned ($n = 5$, mean 62.3 s, SE 28.4) wolves. We did not observe an interaction effect between trail and treatment for investigative or work behaviors (Table 3).

4. Discussion

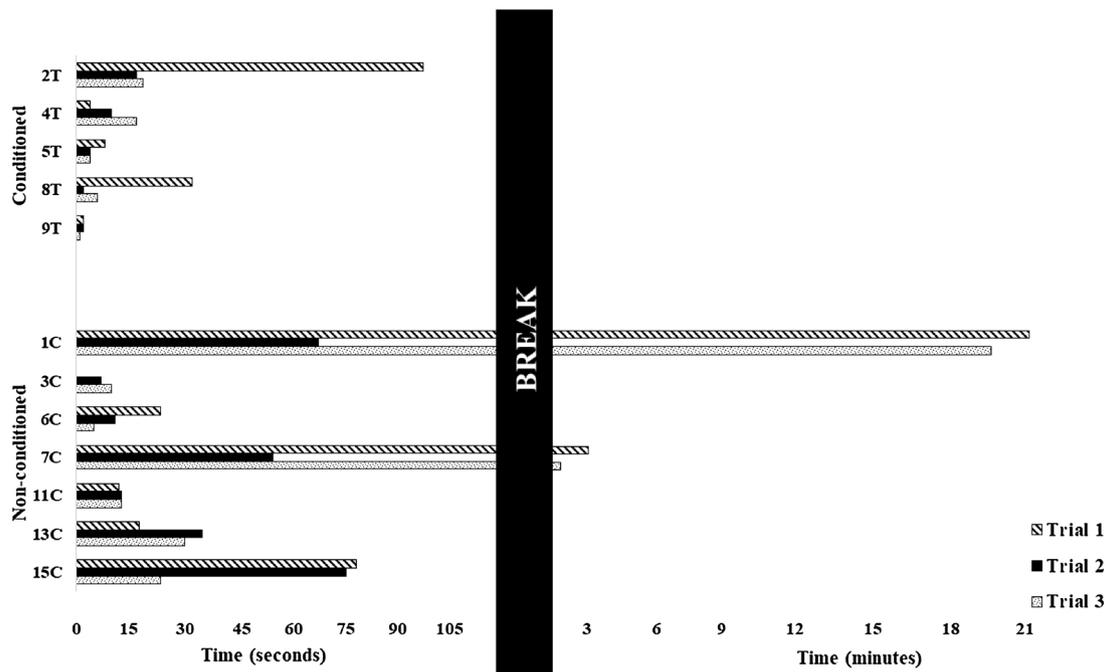
We demonstrated wolves that attained food rewards from an object (i.e., conditioned) showed greater proclivity for future exploration of that object and reduced neophobic behaviors. In particular, our results indicated that conditioned wolves were faster to initiate both investigative and work behaviors than non-conditioned animals. In addition, our results revealed that preventing access to food rewards resulted in decreases of investigative and work behaviors over time; though, surprisingly this decrease in effort did not differ between conditioned and non-conditioned animals. Our findings provide evidence that prevention measures are important for the non-lethal management of carnivores and reinforce a fundamental tenant of using non-lethal tools proactively before conflict occurs, as well as reactively when prevention measures can effectively exclude carnivores from attaining future rewards.

4.1. Latency to first behavior

Conditioned wolves in our study investigated canisters 11 times faster than non-conditioned wolves and initiated behavior to open canisters (i.e., work behavior) 4 times faster (Fig. 2a,b). Results from Trial 1 were particularly indicative of the effects of learning on latency to exert work behaviors (Fig. 2b). Of the six pens with non-conditioned wolves in Trial 1, three of the six pens exhibited no work behaviors over the course of the roughly 8 h long trial. In contrast, while the latency to first work behavior in conditioned animals varied across pens, all conditioned wolves exerted effort at some point during the first trial with three of the five pens exhibiting a work behavior in the first 30 s of the trial (Fig. 2b). In addition, the pattern of increased latency to first work behavior in non-conditioned wolves persisted across all three trials, indicating learning reduced neophobic behaviors and expedited future exploratory action in conditioned animals.

Behavioral measurements are among a suite of methods that can be

A) Latency to First Investigative Behavior



B) Latency to First Work Behavior

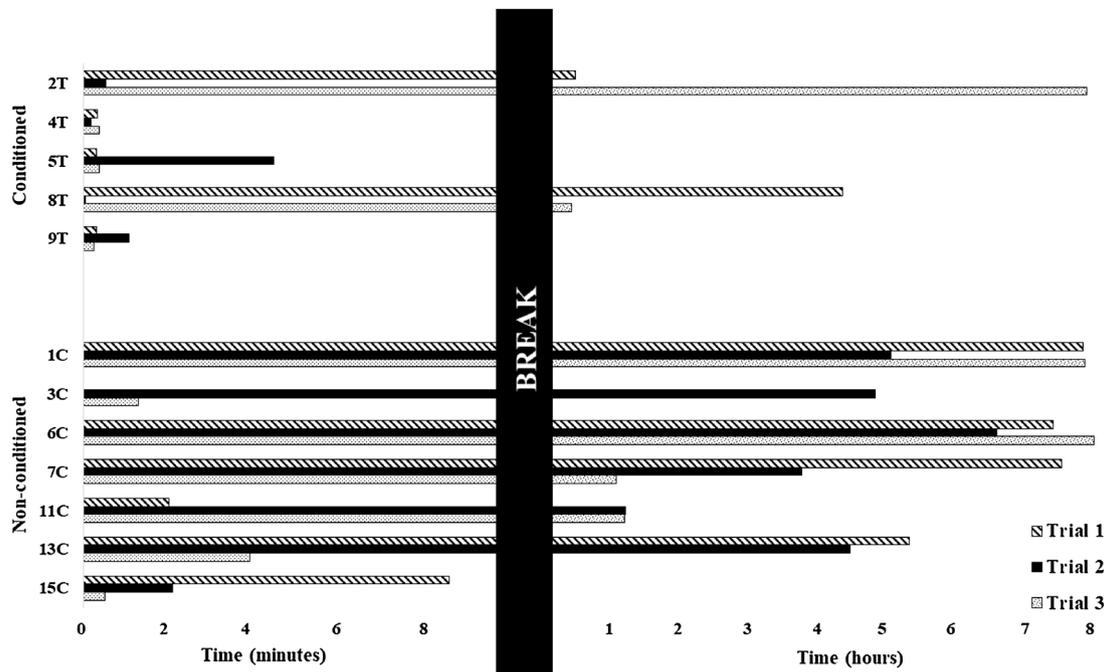
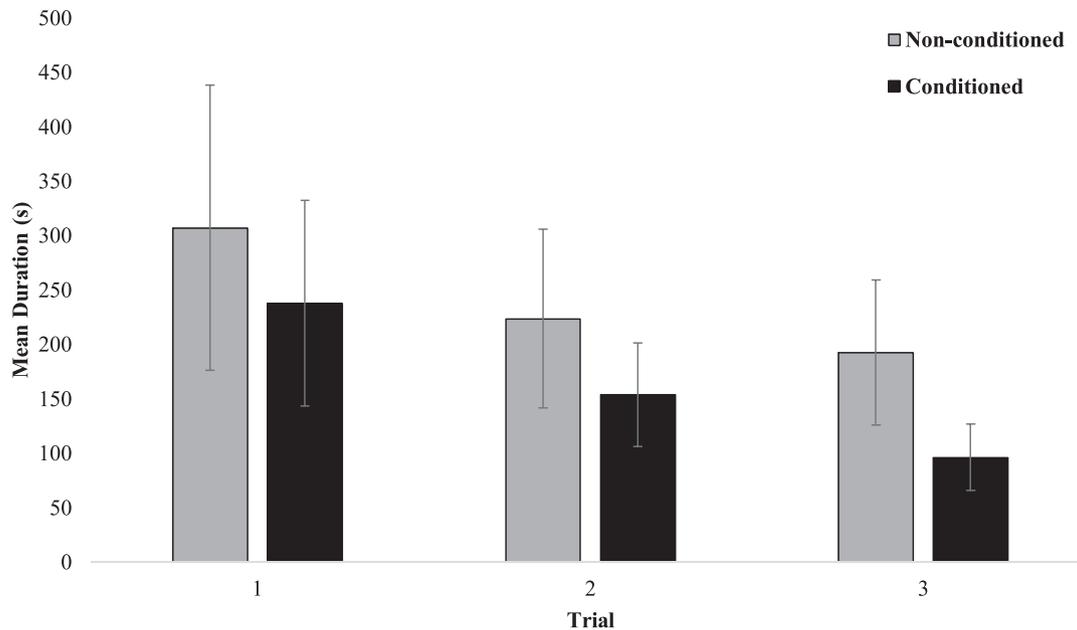


Fig. 2. Latency to first investigative (A) and work (B) behaviors for captive wolves seeking reward from a sealed canister over the course of three trials. Latency was measured as the time to first observed investigative and work behavior, starting from the time the canister (with newly inserted food reward) left the hands of the technician. We inserted a break at the 120 s (investigative behaviors; A) and 10 min (work behaviors; B) marks to highlight differences in latency given large variation among pens. Conditioned wolves were quicker to both investigate and work than non-conditioned wolves.

used to discern motivation in animals (Griffin and Guez, 2014) and latency to first behavior provided us with a metric to evaluate how prior experience influenced learning, where motivation to overcome neophobic behaviors increased with experience and could thus be associated with reduced approach latencies (Mettker-Hofmann et al., 2006). Exploration is consistently linked to problem solving (Reader, 2015), and as Day et al. (2003) demonstrated in extractive foraging task

experiments using three genera of small neotropical primates of the family Callitrichidae, latency to first contact predicted the latency to first success at solving a given task. Benson-Amram and Holekamp (2012) found that in both wild and captive hyenas, those that took longer to approach a puzzle box apparatus were less likely to solve the puzzle. Under such a framework, we assert that non-lethal tools can thus mediate a carnivore’s ability to explore and shape their experience

A) Duration of Investigative Behaviors



B) Duration of Work Behaviors

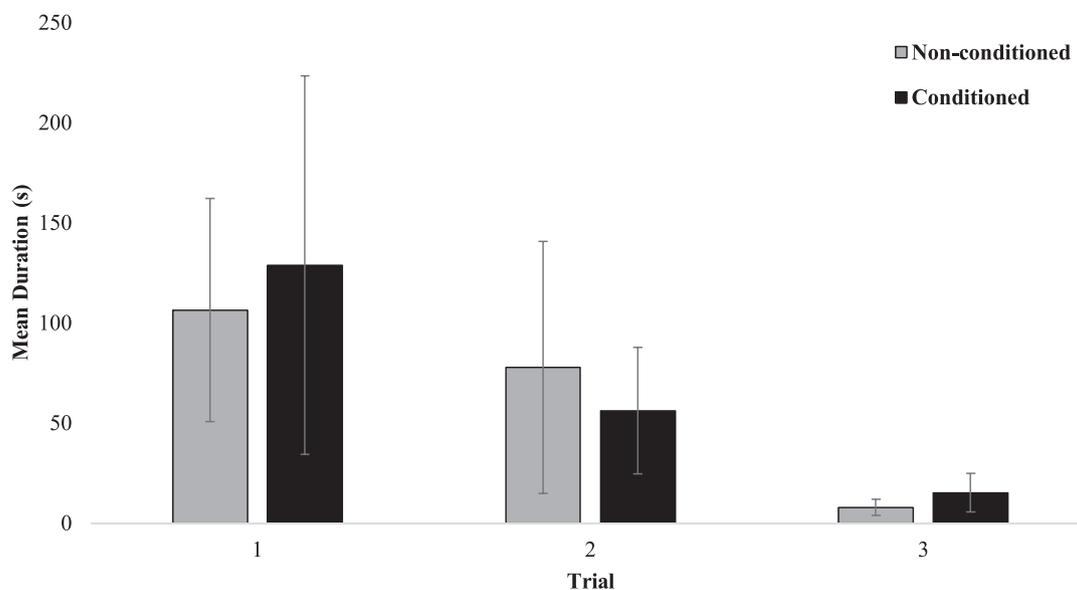


Fig. 3. Mean duration of investigative (A) and work (B) behaviors for wolves attempting to gain reward with associated standard error. Mean duration was controlled for the number of wolves in each pen. The duration of both investigative and work behaviors was similar between conditioned and non-conditioned wolves; however, we observed a trial effect for both behaviors, indicating use of secure prevention measures may decrease the prevalence of both behaviors with time.

with anthropogenic food sources by reducing learning opportunity, and therefore the possibility for successful conflict provoking behaviors.

4.2. Duration of behaviors

We expected the duration of behaviors to provide us with a second measure of motivation where we predicted conditioned wolves to exhibit a greater amount of work behaviors as a result of previous experience and non-conditioned wolves to exhibit a greater amount of investigative behaviors as they explored the canister as a potential food source. Interestingly and counter to our predictions, we observed little difference in the duration of work and investigative behaviors between

our two groups of wolves, although visual inspection of investigative behaviors (Fig. 3a) suggests that non-conditioned animals may spend more time investigating objects than conditioned animals. Similar duration of behaviors between groups could be a result of working with captive animals who often have excess energy available, are less neophobic, have more experience with man-made objects, and have more undisturbed time to problem solve (Benson-Amram et al., 2013; Forss et al., 2015). However, the fact that we documented differences in motivation to overcome neophobic behaviors with prior experience (i.e., latency to first behavior) with captive animals indicated that the similarity in duration of investigative and work behavior could be a result of biological realism (e.g., Groothuis and Taborsky, 2015).

We assessed the duration of behaviors across a 3-week span (i.e., three trials) and noted a distinct decline in the amount of time wolves spent engaged with the canister between each subsequent trial, where the application of a prevention measure reduced investigative behaviors by 49.2% and 59.6% and work behaviors by 92.8% and 87.7% in non-conditioned and conditioned animals, respectively (Fig. 3a,b). The persistence of a behavior (or lack thereof) can here be used as another way to quantify motivation and the degree to which animals engage with the object they are exploring (Griffin and Guez, 2014). While the ecological relevance of behavioral persistence is often unique to the species of interest (Griffin and Guez, 2014) our results suggest a stark decrease of persistence with the application of a prevention measure. This finding aligns with evidence that performance of learned behaviors reinforced through conditioning will generally become extinct when the behavior is no longer reinforced (Bouton, 1994). For example, Thraillkill et al. (2016) found that in experimental trials using rats to study the extinction of behaviors in working dogs, a key component of behavior extinction was the number of nonreinforced trials. It is important to recognize however, that the persistence of a behavior is contingent on factors such as the animal's hunger or thirst states, and satiation can limit the extent to which an animal might pursue a food source (Schultz, 2006).

4.3. Management implications

Our findings support the idea that increased experience from learning reduced neophobic behavior in captive wolves and expedited future exploratory action, a notion particularly important in the context of managing “problem individuals” (i.e., individuals in a carnivore population that are more likely to attack livestock or otherwise cause conflict) (Linnell et al., 1999). How problem individuals develop is poorly understood but it is likely that reward based learning plays an important role. For example, Harper et al. (2005) found that learning was a likely cause of increased depredation by wolves in Minnesota. Karlsson and Johansson (2010) found the risk of repeated predation on previously depredated farms was 55 times higher than non-depredated farms and the risk was highest directly after an initial attack. Our data indicates that the primary result of learning was that conditioned wolves indeed gained the experience necessary to rapidly initiate future exploration of that object, which is conceptually similar to the findings of Harper et al. (2005) and Karlsson and Johansson (2010). However, in our study once wolves initiated contact with canisters, conditioned and non-conditioned animals spent similar effort trying to attain the food inside.

Together, these results imply that the primary advantage of keeping carnivores from attaining anthropogenic food rewards is that it reduces the likelihood of initiating the exploration of unfamiliar objects but not necessarily the effort expended investigating and working to attain a reward once a behavior has been initiated. Our results demonstrate the importance of using non-lethal measures preventatively to take advantage of neophobia and curtail learning and the subsequent development of behaviors to reduce conflict. While we found evidence supporting the preventive use of non-lethal tools, the results of this study should be interpreted with caution given the lack of balance in our treatments and small sample sizes. We recommend future studies *a priori* exclude using single animals (when studying a social species) from their study and intentionally balance the number of animals in pens using methods such as ranking and systematic treatment assignment.

The continued development and improvement of non-lethal tools in predator management is crucial to address concerns around livestock depredation, human health and safety, and the conservation of large carnivores (Breck and Meier, 2004; Shivik, 2006). Equally important however, is the proper use of non-lethal tools, particularly deploying tools in a proactive fashion so that carnivores never have a chance of learning to overcome novel prey and other novel anthropogenic food sources in novel environments. If learning has occurred and

management involves problem individuals, the use of non-lethal means becomes more difficult but not impossible. Given the observed temporal decay of behaviors over the course of our study, we provide evidence that the implementation of non-lethal tools could still be an effective strategy if managers are effective at preventing further food rewards. However, it is important to recognize that where learning has previously occurred, the extinction of a behavior is not synonymous with unlearning the behavior (Bouton, 1994) and therefore prevention measures must be continuously and actively employed to deter conflict behavior.

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