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Inaccessibility of Reinforcement Increases Persistence and Signaling Behavior in the Fox Squirrel (*Sciurus niger*)

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Under natural conditions, wild animals encounter situations where previously rewarded actions do not lead to reinforcement. In the laboratory, a surprising omission of reinforcement induces behavioral and emotional responses described as frustration. Frustration can lead to aggressive behaviors and to the persistence of noneffective responses, but it may also lead to new behavioral responses to a problem, a potential adaptation. We assessed the responses to inaccessible reinforcement in free-ranging fox squirrels (*Sciurus niger*). We trained squirrels to open a box to obtain food reinforcement, a piece of walnut. After 9 training trials, squirrels were tested in 1 of 4 conditions: a control condition with the expected reward, an alternative reinforcement (a piece of dried corn), an empty box, or a locked box. We measured the presence of signals suggesting arousal (e.g., tail flags and tail twitches) and found that squirrels performed fewer of these behaviors in the control condition and increased certain behaviors (tail flags, biting box) in the locked box condition, compared to other experimental conditions. When faced with nonreinforcement, that is, frustration, squirrels increased the number of interactions with the apparatus and spent more time interacting with the apparatus. This study of frustration responses in a free-ranging animal extends the conclusions of captive studies to the field and demonstrates that fox squirrels show short-term negatively valenced responses to the inaccessibility, omission, and change of reinforcement.

Keywords: emotional valence, signaling behaviors, frustration, tail flag, *Sciuridae*

Since Charles Darwin's first treatment of the subject of animal emotions (in 1872), basic emotional responses in nonhuman animals (hereafter, animals) have been studied in great detail, particularly discrete emotions such as fear and panic (Darwin, 1872; Mendl & Paul, 2004; Panksepp, 2004; Paul, Harding, & Mendl, 2005; but see LeDoux, 2012). One such emotional response is frustration, the response to the omission of an expected reward, which is often also described as a behavioral state (Lawson, 1965). Affect, or emotional experience, can be described in relation to an individual's level of arousal and valenced state and to the maximization of reward and minimizing of punishment (Paul et al., 2005). Within this context, frustration has been described as a high-arousal, negative state (Mendl, Burman, & Paul, 2010).

Several studies indicate that the surprising omission of reinforcement, such as during the extinction process, leads to behaviors suggesting a negatively valenced emotional experience (Azrin, Hutchinson, & Hake, 1966; Papini & Dudley, 1997). Frustration responses may occur when reinforcements are inaccessible (Finch, 1942) or are changed in size or type, to something less desirable to the subject (Papini & Dudley, 1997). Frustration may also be a response to an insoluble problem (Maier, 1958), or when any reinforcing experience is inaccessible, such as interactions with a potential mate or rival (e.g., Legrand, 1978; Whalen, 1961). Frustration appears to be universal among mammals, and has been observed in other animals, such as pigeons (Azrin et al., 1966) and fish (Vindas et al., 2012, 2014). Frustration responses include behaviors that are not immediately or exclusively goal-directed such as aggression, and stereotypies, or fixations on highly available responses (Finch, 1942). Frustration may lead an animal to try alternative responses to those that previously solved the problem or led to reinforcement (Amsel, 1992; Broom & Johnson, 1993; Lawson, 1965; Maier, 1958).

The frustration-aggression hypothesis suggests that aggression in response to a frustrating task may be a displacement behavior that is either cathartic or reinforcing (Berkowitz, 1989; Lawson, 1965). Laboratory pigeons (*Columba livia*) directed aggression toward a restrained conspecific when reinforcements were extinguished (Azrin et al., 1966), and leghorn hens (*Gallus domesticus*) increased aggression toward a cohoused conspecific when food was visible but not physically accessible (Duncan & Wood-Gush, 1971; Haskell, Coerse, & Forkman, 2000). Common chimpanzees (*Pan troglodytes*) kicked and hit the walls of their cages when denied access to expected reinforcement (Finch, 1942). Squirrel

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monkeys (*Saimiri sciureus*) shaped to press a bar for pellets on a continuous reinforcement schedule began biting on an available rubber hose when extinction was introduced (Hutchinson, Azrin, & Hunt, 1968). These findings suggest that the aggressive behavior is not specifically caused by the presence of a conspecific, but by the frustrating task. Removal of reinforcement has been shown to cause other behaviors that indicate high arousal or negative valence, such as increased vocalizations and repetitive behaviors in chimps (Finch, 1942), increased startle response in laboratory rats (*Rattus norvegicus*) in an operant chamber (Daly & McCroskery, 1973), and increased angry vocalizations and facial expressions in human infants (Stifter & Grant, 1993).

Inaccessibility of reinforcement may lead to changes in behavior that are not aggressive or negatively valenced, such as increased variability in behaviors offered and persistence in responding (Antonitis, 1951; Skinner, 1938). An important question is how frustration contributes to learning and behavior change. Aggression, persistence, and expression of new behaviors may all serve a function in solving novel problems. During a frustrating task, new behaviors could be elicited, animals could select successful new responses, and eliminate unsuccessful responses from behaviors offered in the presence of a stimulus (Wong, 1977). Goal persistence may increase the likelihood of solving a problem, particularly when new responses are tried (e.g., Benson-Amram & Holekamp, 2012; Wong, 1977). However, sensitivity to the level of a presented challenge or threat could allow an animal to modulate and adjust responses accordingly. This sensitivity could both aid survival and conserve energy for wild animals. Here, we studied the responses of a wild, free-ranging animal to a frustrating task and examined how these responses changed as the level of potential frustration was changed.

Adult tree squirrels occupy overlapping home ranges (Gorman & Roland, 1989; Pack, Mosby, & Siegel, 1967) and thus face continual competitive social interactions over food and other resources. They communicate with visual signals, olfactory cues, and vocalizations (Taylor, 1977). Signals utilized in aggressive interactions or during distress, fright, or threat include piloerection, tail fluffing, tail twitching, tail flagging, foot stamping, and tooth chattering (Bakken, 1959; McCloskey & Shaw, 1977; Steele & Koprowski, 2001; Taylor, 1966). Squirrels use their tails for several communicative purposes, directing rapid, stiff jerks at other squirrels. More flexible waving, or flagging of the tail is typically directed at more serious disturbances including aggressive interactions with other squirrels (Horwich, 1972), as well as predators or other intruders (Bakken, 1959; Taylor, 1966).

The goal of our study was to determine if fox squirrels give visible and measureable signals (such as tail flagging) associated with aggressive, agitated, or otherwise negatively valenced states, in response to a frustration-inducing task. Tail signals are easily measured, and, if correlated with induced frustration, these signals could provide insight into the emotional or valenced states of animals. These signals may also reflect the animal's knowledge state about their environment. We based our task on previous findings that both the removal and substitution of reward was frustrating (Finch, 1942) and that not being able to complete a task to obtain reinforcement was more frustrating than completing the task but not receiving reinforcement (Haslerud, 1938).

We trained squirrels to open a box to receive reinforcement and later tested them under four different conditions: control (receive

food as expected), alternative (open box to find a different reinforcement than expected), empty (open box to find no food), and locked (the box is locked with the reinforcement inside and cannot be opened). We anticipated that the task where the apparatus was locked would lead to the highest levels of frustration-related behaviors such as increased signaling and new types of interactions with the box. We also predicted that an empty box would be more frustrating than a box that contained an unexpected, less preferred reinforcement. Finally, if valenced states can be induced experimentally at different levels, and measured in the field, we predicted that the control condition would lead to the fewest changes in behavior.

Method

Participants

This research project was approved under a protocol submitted to the Animal Care and Use Committee of the University of California, Berkeley. Participants were 22 free-ranging adult fox squirrels on the University of California, Berkeley, campus. The introduced fox squirrel is a well-established resident species on the campus, whose habituation to human observation allows detailed studies of memory and decision-making processes under seminatural conditions (Jacobs & Shiflett, 1999; Preston & Jacobs, 2009; Waisman & Jacobs, 2008). Squirrels were individually marked with Nyanzol-D (American Color and Chemical Corporation, Charlotte, NC), by spraying the dye at the squirrels from a syringe while they were feeding. All marked squirrels were photographed, and their data were logged in a database.

Some squirrels participated in multiple conditions in the study, with three squirrels participating in all four conditions, five participating in three conditions, six participating in two conditions, and the remaining eight participating in just one condition. We used a predesignated counterbalanced Latin square design to reduce order effects. At least 1 week passed between any repeated test sessions for an individual squirrel. Participation in multiple conditions was reliant upon being able to locate and recruit squirrels on successive testing dates.

Experimental Setup

We tested squirrels between 10:00 and 16:00, May through July 2011. Experiments were conducted on a small folding table (82 cm × 82 cm × 72 cm high). The table was placed next to a tree in a wooded location on the University of California, Berkeley, campus. Placing the table next to a tree ensured that squirrels approached the apparatus from the same angle and started each trial in approximately the same location on the table. A piece of black nonskid mat (22 cm × 42 cm) was placed on the table next to the tree to facilitate accessing the table for the squirrels. A piece of white foam core board (73.5 cm × 102 cm) was placed on a folding easel as a backdrop for filming and to reduce visual distraction during trials. All sessions were recorded using a Canon FS300 camcorder (Canon, Lake Success, NY) mounted on a standard tripod.

The apparatus was a small black acrylic box (10.5 cm × 7.5 cm × 7.5 cm high) with a hinged lid and a locking mechanism that allowed the box to be screwed shut without changing the visual

appearance of the box (see Figure 1). The box was centered on the table, 10 cm from the far end, approximately 72 cm from where the table was aligned with the tree. Reinforcements were chopped walnut pieces (approximate weight 0.5 g and 1 cm × 1 cm in size) or a single dried kernel of corn. The two foods vary in calories and nutrients, with corn having fewer calories, fat, protein, calcium, and magnesium than walnuts (United States Department of Agriculture, 2012).

Procedure

We shaped squirrels to open the apparatus by training them to eat nuts on the table and then from the open box. The hinged lid of the box was then gradually closed so that the squirrel had to manipulate the lid to access the nut. For most squirrels shaping took less than 5 min. Because tree squirrels can live over 10 years in the wild (Koprowski, Roseberry, & Klimstra, 1988), some squirrels may have had previous experience with a similar apparatus for unrelated experiments on spatial orientation (e.g., Waisman & Jacobs, 2008). Squirrels were shaped to open the box on different days than the experimental sessions. Training, test, and posttest trials happened sequentially on the same day. If we tested squirrels in more than one condition, we ensured that tests in different conditions were separated by at least 1 week. Squirrels that were tested in multiple conditions were reexamined on subsequent sessions to ensure that they were still able to open the box, by giving reinforcements in the box with the lid partially closed before testing.

For each session, we identified a uniquely marked squirrel to participate, and we lured it onto the testing table by calling and gesturing with a hand (a movement many campus squirrels associate with being offered food). We kept the testing area free of other squirrels by feeding them peanuts away from the table and adjacent tree.

All squirrels were next given nine training trials where they opened the box to obtain a small piece of walnut; previous studies have found 10 deliveries of food to be sufficient to elicit frustration

responses in pigeons during extinction (Azrin et al., 1966). Because our test subjects were free-ranging, we chose this number of trials to maximize participation without losing subjects due to distraction or satiation. Each training trial ended when the squirrel finished eating the walnut piece. Between each trial, the experimenter took a step toward the testing table, which typically caused the squirrel to leave the table and return to the tree. The next trial began when the squirrel returned to the table from the tree, which most squirrels did of their own accord or after brief gesturing by the experimenter.

On the tenth trial, each squirrel was tested in one of four conditions. In the control condition ($n = 11$), the squirrel opened the box for a walnut piece, as they had done in the nine training trials. In the alternative condition ($n = 14$), instead of a walnut piece, the box contained one piece of dried corn. In the empty condition ($n = 10$), there was no reinforcement in the box when opened by the squirrels. In the locked condition ($n = 12$), the box was locked on the test trial with the walnut piece inside to control for odor cues. Due to the lock, the box could not be opened and the reinforcement could not be obtained. On the test trial, regardless of experimental condition, all squirrels were allowed to stay on the table until they jumped or climbed off of their own volition.

After the test trial, squirrels were given one additional trial, identical to the training trial with one piece of walnut in an unlocked box, to determine if the experimental condition had any residual effect on their response to the box. We conducted 33 posttest trial sessions. Fourteen squirrels did not return for the posttest trial: four (36.4%) that had participated in the control condition, three (21.4%) that had participated in alternative, one from empty (10%), and six (50%) from locked, leaving 33 squirrels that participated in the posttest trials (control: $n = 7$; alternative: $n = 11$; empty: $n = 9$; locked: $n = 6$).

All videos of the sessions were coded using The Observer XT (Noldus, Leesburg, VA), a video coding and analysis software that allows playback of videos at several different speeds, while manually coding. Coders were blind to the experimental condition, although it was determinable within a few seconds of the squirrel's interaction with the box if the box was locked. Five coders were trained on a subset of up to four videos, which constituted 8.8% of the total trial videos. Overall interrater agreement on behaviors between pairs of coders ranged from Cohen's kappa (κ) of 0.61 to 0.90. Overall kappas were highest for tail movement behaviors (mean $\kappa = 0.88$, 95% confidence interval [CI] [0.76, 1.00] across 249 occurrences) and time variables related to time spent on the experimental table (mean $\kappa = 0.93$, 95% CI [0.80, 1.06] across 57 occurrences) than for interactions with the box (mean $\kappa = .70$, 95% CI [0.46, 0.93] across 334 occurrences). This level of agreement is considered moderate to strong (Haidet, Tate, Divirgilio-Thomas, Kolanowski, & Happ, 2009; Landis & Koch, 1977).

We recorded two types of dependent variables: durations and latencies of behaviors (time, in seconds), and the presence or absence of behaviors in counts. The timing measures were the latency to touch the box from the time the squirrel first stepped on the testing table, time spent interacting with the box on the training and test trials, and time spent on the table.

We recorded the total number of tail movements, both tail twitches and flags. For the purposes of this study, we adapted an ethogram of tail movements utilized in a recent study of gray squirrels (McRae, 2012; McRae & Green, 2014). Movements were

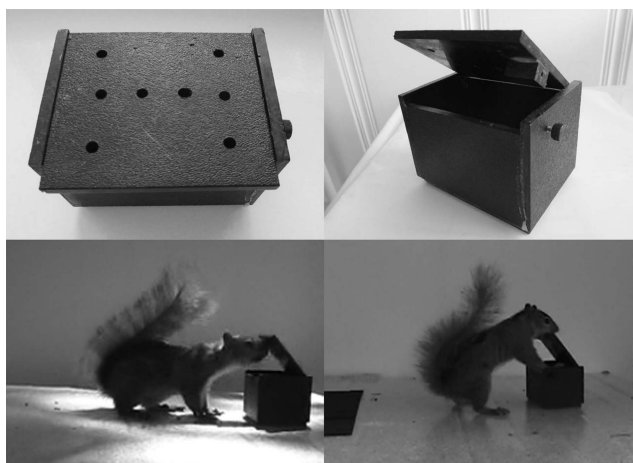


Figure 1. The apparatus used in all experimental sessions, upper left-hand corner is a top view, and upper right-hand side shows the side view and locking mechanism. Lower photos are video stills depicting squirrels opening the box with a nose push (L) and with teeth (R).

counted individually as starting and stopping when the tail returned to the baseline resting position. As seen in Figure 2, tail twitches were defined as controlled movements of less than 45°, with the tail held mostly parallel to the ground. Tail flags involved S-shaped rapid whipping movements of the tail in arcs greater than 45°, with large conspicuous movements. We also recorded other behaviors that indicated arousal or agitation, including foot stomping, tooth chattering, and freezing (Bakken, 1959; McCloskey & Shaw, 1977; Steele & Koprowski, 2001; Taylor, 1966). We noted the frequency of nine different types of interactions with the box. These were sniffing (any orientation to the box, with the nose closest to and touching or almost touching the box), biting (oral contact with teeth closed onto a surface of the box once), chewing (multiple bites on the box), dragging (pulling the box with teeth), lifting (box is moved vertically off the surface of the table with the teeth), flipping (the box is knocked over so that another surface is touching the table), exploring (moving to the opposite side of the box to interact with it), touching (with the paws), and pushing (moving the box laterally with the body). These behaviors were chosen in part based on an ethogram from a previous study of animals interacting with puzzle feeders (Benson-Amram & Holekamp, 2012). We also noted the method each squirrel used to open the box (by biting with teeth, nose bumping, or paws) Any time that the squirrel spent eating a food item was not included in the analyses of the behaviors of interest.

Corn and Walnut Preference Test

To further determine if the squirrels' behavioral responses to the alternative condition of the experiment could be due to the corn being less desirable than walnuts to the squirrels, we performed a preference test on eight adult squirrels. Each squirrel was presented with the same apparatus used in the aforementioned experiment. On each trial, the box contained five walnut pieces and five dried corn pieces of comparable size. The box was gently shaken to combine the food items, and the closed box was placed in front of the squirrel, at a distance of approximately 30 cm away. The squirrel opened the box, and their first food choice was noted. The eaten food item (corn or walnut piece) was replaced, and the next trial was initiated by placing the closed box in front of the squirrel. Six squirrels completed 20 trials, one squirrel completed 14 trials, and one squirrel completed only eight trials.

Statistical Analysis

All data were analyzed using R 3.2.1 (R Foundation for Statistical Computing, Vienna, Austria) and JMP Pro12.0 (SAS Insti-

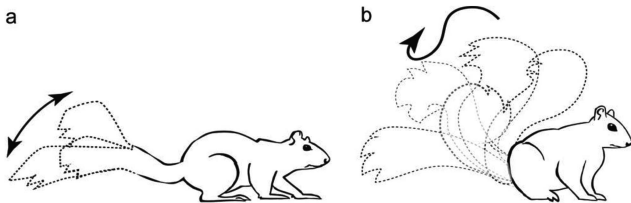


Figure 2. Illustration of tail twitches and tail flags. (a) Tail twitches were defined as smaller tail movements of less than 45°, with the tail held mostly parallel to the ground. (b) Tail flags were defined as large, S-shaped, rapid-whipping movements of the tail in an arc greater than 45°.

tute, Cary, NC). Because the data involved repeated measures, missing data points and nonnormal distributions, we used mixed models whenever possible (Bolker et al., 2009). All mixed models used the control condition as the baseline for comparison.

Unless otherwise noted, generalized linear mixed models (GLMMs) with a Poisson distribution were used to examine outcome variables that were integer-valued counts of events (number of tail movements, number of different interactions with box), using the “lme4” and “lmerTest” packages in R (Bates, Maechler, Bolker, & Walker, 2015a, 2015b; Kuznetsova, Brockhoff, & Christensen, 2015). Pairwise post hoc comparisons were performed using the “phia” package in R (De Rosario-Martinez, 2015).

For continuous variables (trial time, latency, rates of tail movements), least squares mixed models with Tukey's post hoc pairwise comparisons were assessed using JMP. Positively skewed continuous data were log transformed for analysis and the alpha level for all analyses was set at 0.05 unless otherwise noted. Subject identity was entered as a nominal, random effect in all analyses to account for repeated measures.

Results

Time Variables

Training trials. Trial time was defined from the moment all four of a squirrel's paws touched the surface of the table until the squirrel obtained the reinforcement from the apparatus. Training trials averaged 5.70 s (95% CI [5.38, 6.02]) and the intertrial intervals (ITIs) averaged 9.69 s (95% CI [8.20, 11.19]). There was no effect of condition on trial time, $F(3, 399.5) = 0.60, p = .61$, adjusted $R^2 = .23$. There was a main effect of trial number, $F(8, 376.4) = 2.25, p = .024$, adjusted $R^2 = .25$, with a Tukey's honest significant difference post hoc test indicating that the first trial showed a marginal difference from trial seven ($p = .043$) and a nonstatistically significant tendency to be longer than all other trials. The mean latency to contact the box across all training trials was 1.83 s (95% CI [1.68, 1.99]). There was no effect of condition, or trial number on latency to contact the box (all $p > .48$).

Interaction with the box was defined as any time the squirrel was touching or sniffing the box. Squirrels spent an average of 3.63 s interacting with the box (95% CI [3.41, 3.85]) which averaged 65.8% of total trial time. The proportion of total trial time spent interacting with the box was arcsin transformed for analysis. There were no effects of condition or trial on proportion of trial time spent interacting with the box (all $p > .22$).

Test trials. The average ITI between the last training trial and the test trial was 11.99 s (95% CI [5.57, 18.42]). There were no differences between conditions on trial time, although there was a tendency for trials in control to be shorter than those in alternative, $F(3, 35.6) = 2.54, p = .07$, adjusted $R^2 = .40$. There were no differences in latency to approach the box, $F(3, 32.5) = 0.91, p = .44$, adjusted $R^2 = .15$. There was an effect of condition on proportion of trial time spent interacting with the box, $F(3, 29.6) = 3.48, p = .028$, adjusted $R^2 = .37$. A Tukey's honest significant difference post hoc test indicated that the smallest proportion of trial time was spent in the alternative condition, $t(28.79) = 3.08, p = .005, d = 1.29$, and this proportion was significantly different from the locked condition. See Table 1 for means.

Posttest trials. The average ITI between the test trial and the posttest trial was 27.16 s (95% CI [17.18, 37.14]). There were no significant differences between the test conditions on posttest trial time, latency to approach the box, or percent of time spent interacting with the box (all $p > .63$).

Signaling Behaviors

Training trials. The number of total tail twitches and flags made by an individual squirrel during each training trial ranged from zero to nine (average across all training trials: twitches $M = 0.44$, 95% CI [0.37, 0.52]; flags $M = 0.46$, 95% CI [0.36, 0.57]). Although there was an effect of condition on tail twitches, with a higher average of tail twitches displayed in the alternative condition ($M = 0.57$, 95% CI [.40, .74], range 0–6, median = 0) relative to the control condition ($M = 0.27$, 95% CI [.16, .38], range 0–3, median = 0) the differences were small in actual counts. There was no effect of trial number on the number of tail twitches. There was no effect of condition or trial number on the number of tail flags (all $p > .34$). There were not enough instances of tooth chattering, foot stomping or freezing observed to include in statistical analysis. See Table 2 for results of GLMMs.

Test trials. The total number of tail twitches by an individual during the test trial ranged from zero to 21 ($M = 3.06$, 95% CI [1.64, 4.48]), and the number of tail flags ranged from 0 to 28 ($M = 2.87$, 95% CI [1.01, 4.73]). There were statistical differences between conditions on tail twitching and tail flagging behaviors. The control condition elicited fewer tail twitches than all other conditions, rate per second: $\chi^2(3) = 8.84$, $p = .032$. There were no differences in number of tail twitches between conditions alternative, empty, and locked. The control condition elicited fewer tail flags than all other conditions, rate per second: $\chi^2(3) = 7.33$, $p = .062$. A post hoc comparison with a Holm correction showed that the locked condition led to more tail flags than alternative, $\chi^2(1) = 13.59$, $p < .001$. See Table 1 for means. See Table 2 for results of GLMMs of count data.

Posttest trials. There were no differences between conditions on tail flags or twitches (see Figure 3).

Types of Interactions With the Apparatus

Training trials. Squirrels pushed the box open with their nose ($M = 1.07$, 95% CI [1.02, 1.13]) and lowered their head into the box at least once per training trial to obtain the nut ($M = 1.52$, 95% CI [1.44, 1.59]). Other behaviors were observed less frequently on

average (sniff box, $M = 0.52$, 95% CI [0.45, 0.60]; bite box, $M = 0.40$, 95% CI [0.34, 0.47]; lift box with teeth, $M = 0.14$, 95% CI [0.11, 0.18]; dragging box with teeth, $M = 0.03$, 95% CI [0.01, 0.05]; explore other side of box, $M = 0.01$, 95% CI [0.00, 0.03]; other, $M = 0.11$, 95% CI [0.08, 0.14]).

Test trials. There were statistical differences between conditions for number of times biting the box, lifting the box with the teeth, and pushing on the box lid with the nose. The control condition elicited less biting than the alternative and locked conditions. Post hoc comparisons with a Holm correction showed that the locked condition also elicited more biting than alternative, $\chi^2(1) = 11.55$, $p = .003$, and empty, $\chi^2(1) = 10.75$, $p = .004$, conditions. The locked condition elicited more lifting of the box with the teeth than all other conditions: alternative: $\chi^2(1) = 17.07$, $p < .001$; empty, $\chi^2(1) = 11.83$, $p = .003$. The locked condition elicited more nose pushes than all other conditions (control: $Z = 5.86$, $p < .001$); alternative, $\chi^2(1) = 39.63$, $p < .001$; empty, $\chi^2(1) = 27.91$, $p < .001$. There were insufficient data to analyze differences between conditions for dragging, flipping or chewing the box, or exploring other sides of the box. See Table 2 for summary of GLMMs.

Posttest trials. There were no differences based on condition in the mean number of types of interactions that squirrels directed to the box during the posttest trial (all $p > .36$; Figures 3 and 4).

Changes in Interactions With the Apparatus

We compared the total number of interactions and number of different types of interaction behaviors on the training (using means across all training trials), test and posttest trials to see if squirrels would engage in new behaviors when frustrated. Only the squirrels that had all three types of trials were included in the comparisons. Kruskal–Wallis tests were performed to compare the number and types of interactions with the apparatus across the three trial types and by condition. There was no effect of condition, number of total interactions: $\chi^2(3) = 1.26$, $p = .74$; number of types of interactions: $\chi^2(3) = 4.22$, $p = .24$, but there was an effect of trial type, total interactions: $\chi^2(2) = 52.33$, $p < .001$; types of interactions: $\chi^2(2) = 38.22$, $p < .001$. Pairwise Wilcoxon's rank sum tests found differences between all trial types on both measures, with squirrels showing the largest number of total and different types of interactions with the box on the test trial compared to the other trial types, and the fewest interactions with the box on the posttest trial compared to test and training

Table 1
Means and 95% Confidence Intervals for Apparatus Interactions and Signaling Behaviors During Test Trials

Variables	Control	Alternative	Empty	Locked
Latency (s)	1.08 [.37, 1.78]	1.26 [.64, 1.88]	1.72 [.98, 2.46]	1.99 [1.32, 2.67]
Trial time (s)	42.70 [20.81, 64.60]	69.51 [50.18, 88.84]	58.35 [35.35, 81.35]	55.61 [34.68, 76.54]
Time interacting with box (s)	19.90 [5.58, 34.23]	21.99 [16.06, 27.92]	23.37 [9.72, 37.03]	29.53 [11.30, 47.75]
Proportion of trial time interacting with apparatus	.47 [.37, .57]	.34 [.25, .43]	.41 [.30, .52]	.53 [.43, .62]
Tail twitches	.64 [.11, 3.74]	4.86 [2.75, 8.57]	2.30 [.87, 6.11]	3.83 [1.92, 7.65]
Tail flags	.64 [.08, 4.88]	1.36 [.39, 4.67]	2.40 [.80, 7.21]	7.08 [3.95, 12.71]
Twitch rate	.79 [−.09, 1.67]	4.03 [1.17, 6.89]	1.72 [.22, 3.22]	4.65 [.56, 8.75]
Flag rate	1.31 [−.45, 3.07]	1.82 [−.19, 3.84]	1.67 [.03, 3.30]	5.78 [.57, 10.99]

Table 2
Summary of Generalized Linear Mixed Models Investigating Differences Between Experimental Conditions on Signaling and Apparatus Interaction Behaviors

Predictor	Estimate	95% CI of estimate	SE	Z	p
Training trials tail twitch					
Intercept	-1.35	[-1.94, -.76]	.30	-4.56	<.001
Alternative	.78	[.30, 1.26]	.24	3.18	.001
Empty	.64	[.12, 1.15]	.26	2.44	.015
Locked	.26	[-.30, .81]	.28	.91	.363
Trial Number	-.05	[-.10, .01]	.029	-1.65	.100
Training trials tail flags					
Intercept	-1.16	[-1.86, -.46]	.36	-3.24	.001
Alternative	.29	[-.21, .79]	.25	1.13	.260
Empty	.23	[-.35, .81]	.30	.76	.446
Locked	.07	[-.52, .67]	.30	.23	.814
Trial Number	-.03	[-.09, .02]	.03	-1.16	.245
Test tail twitch					
Intercept	-.85	[-1.81, .11]	.49	-1.73	.083
Alternative	1.69	[.88, 2.50]	.41	4.09	<.001
Empty	1.23	[.32, 2.13]	.46	2.66	.008
Locked	1.35	[.49, 2.21]	.44	3.09	.002
Test tail flags					
Intercept	-1.85	[-3.25, -.44]	.72	-2.57	.010
Alternative	1.59	[.39, 2.79]	.61	2.60	.009
Empty	2.22	[.97, 3.46]	.63	3.50	<.001
Locked	2.79	[1.58, 4.00]	.62	4.53	<.001
Test biting					
Intercept	-1.21	[-2.25, -.17]	.53	-2.28	.023
Alternative	1.20	[.1, 2.31]	.56	2.13	.033
Empty	.96	[-.24, 2.16]	.62	1.56	.120
Locked	2.24	[1.19, 3.30]	.54	4.16	<.001
Test lifting					
Intercept	-2.69	[-4.81, -.57]	1.08	-2.48	.013
Alternative	.33	[-2.09, 2.75]	1.24	.27	.791
Empty	.06	[-2.64, 2.76]	1.38	.04	.965
Locked	3.33	[1.22, 5.43]	1.07	3.10	.002
Test nose push					
Intercept	-.08	[-.72, .56]	.33	-.25	.803
Alternative	.05	[-.70, .81]	.39	.14	.892
Empty	.24	[-.55, 1.03]	.40	.60	.546
Locked	1.89	[1.26, 2.53]	.32	5.86	<.001

Note. CI = confidence interval.

trials. However, only one squirrel interacted with the box in a novel way during the test trial. See Figures 3 and 4.

Results Corn and Walnut Preference Test

All eight squirrels chose more walnut pieces than corn pieces (see Table 3 for individual performances of each squirrel). Of the 13 corn pieces that were chosen, the squirrels dropped five of them without eating them. Of 142 choices, 129 (90.8%) of them were for walnuts. Given an equal likelihood of choosing a walnut piece or a piece of corn on each trial, the probability of choosing 129 or more pieces of walnut per a binomial test is $p < .0001$, $\chi^2 = 88.34$. From these results, we find it reasonable to conclude that squirrels generally find walnut pieces preferable to dried corn pieces.

Discussion

Our study examined how the fox squirrel's behavioral responses and signaling behaviors changed under different levels of a task that induced frustration. To our knowledge, this is the first study of

experimentally induced frustration responses in a wild animal. By giving fox squirrels different types of frustrating experiences, we showed that the squirrels modulated their behavioral responses in relation to the accessibility of reinforcement. Squirrels increased signals indicating arousal, increased the time spent contacting the apparatus, and were more likely to contact the apparatus with their teeth when food was suddenly inaccessible. There was differentiation in signaling responses to the different experimental conditions. For example, the control condition elicited the fewest tail flags whereas the most tail flags were elicited by the locked condition. Tail twitching was high in all conditions, compared to the control condition. Thus the experimental conditions induced different patterns of tail twitching and tail flagging. Previous studies have also suggested that these two tail movements serve different signaling functions. Tail twitches may be generally directed at other squirrels, but tail flagging is typically seen during aggressive interactions, to deter predators, and in response to the alarm calls of other squirrels (Bakken, 1959; Horwich, 1972; Partan, Larco, & Owens, 2009; Taylor, 1966). In a recent study of

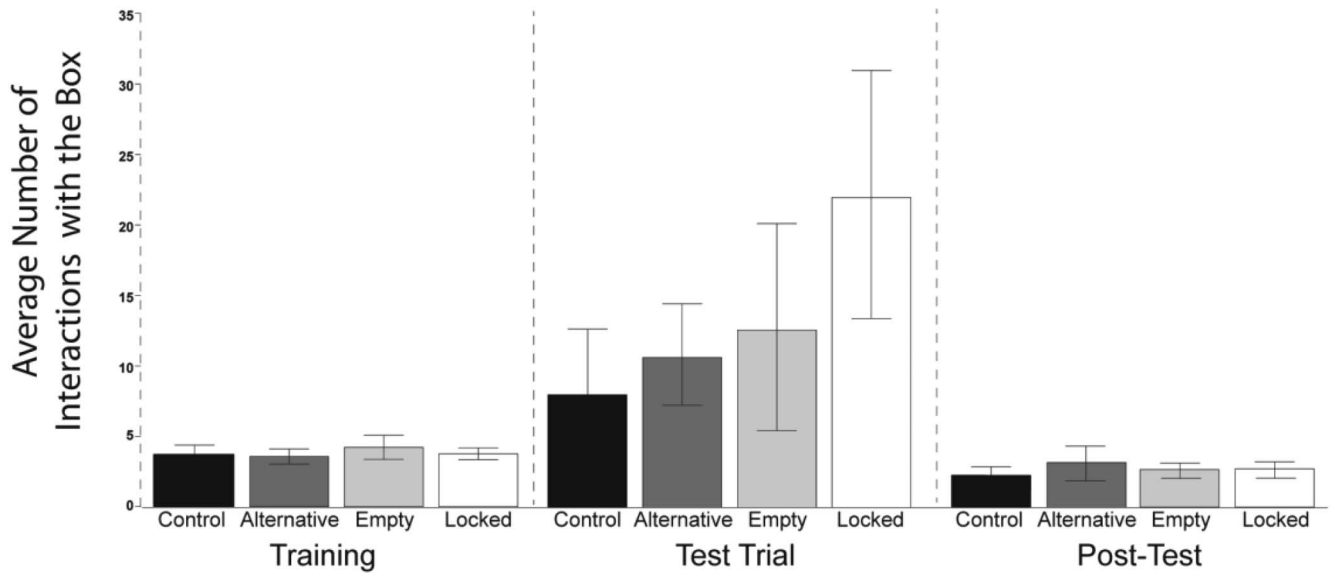


Figure 3. Means and 95% confidence intervals for number of interactions with the apparatus during training, the test trial, and the posttest trial. Squirrels increased interactions with the boxes during the test trial and decreased number of interactions in the posttest trial.

the responses of Eastern gray squirrels (*Sciurus carolinensis*) to ground and aerial predators, squirrels twitched their tails as a sign of general alarm regardless of predator type, but tail flagging was reserved for terrestrial threats (McRae, 2012; McRae & Green, 2014).

Tail movements have been identified as a response to frustration in other species, such as domestic cats (*Felis catus*) and elands (*Taurotragus oryx*; Hickman, 1979; Kiley-Worthington, 1976). Tail flagging in California ground squirrels (*Spermophilus beecheyi*) may be an indicator of arousal independent of commu-

nicative functions (Hennessy, Owings, Rowe, Coss, & Leger, 1981; Stankowich, 2008), as in our study. Our results show that tail twitches were a response to a more general state of arousal, but that tail flagging changed depending on the level of arousal. Tail flagging in fox squirrels may be both a communicative signal and an overt measure of valence or arousal, and could be a useful tool to study the dynamics of emotional arousal in mammals.

Squirrels spent a larger proportion of trial time interacting with the apparatus and had more total interactions with it when it was locked. Persistence in responding is a common response to frus-

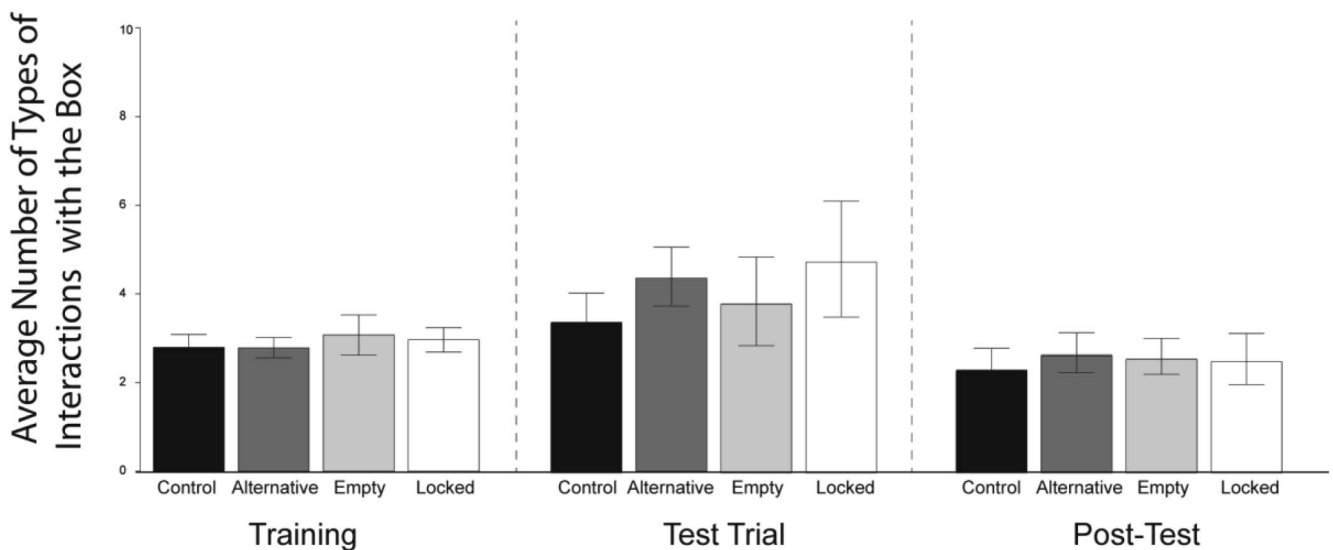


Figure 4. Means and 95% confidence intervals for number of different types of interactions with the apparatus during training, the test trial, and the posttest trial. Squirrels increased types of interactions with the boxes during the test trial and tended to decrease behaviors in the posttest trial.

Table 3
Individual Performances of Fox Squirrels and Binomial Probabilities for the Corn–Walnut Preference Test

Subject	Choices for walnut/total trials	Binomial probability
Flame	20/20	<.001
Leopard	7/8	.035
Moon	19/20	<.001
Clementine	12/14	.006
Streak	17/20	.001
Quinn	20/20	<.001
Aggie	18/20	<.001
Thunder	16/20	.005

tration (e.g., Antonitis, 1951; Skinner, 1938). Measures of persistence include time spent on a task, and different ways of attaining a goal (Wong, 1977). However, the squirrels spent a smaller proportion of trial time interacting with the apparatus during the test trial compared to the training trials. This is in part because the training trials were much shorter, but it could also be that squirrels were engaging in other behaviors (e.g., exploration) during test trials.

For innovation to occur, an animal must generate a novel response to a situation (Ramsey, Bastian, & van Schaik, 2007). An increase in variability in responses could improve the ability of an animal to solve a problem (Wong, 1979). A recent study assessing problem solving found that spotted hyenas (*Crocuta crocuta*) that employed a larger diversity of exploratory behaviors and demonstrated persistence were more successful in opening a puzzle box feeder (Benson-Amram & Holekamp, 2012). In meerkats (*Suricata suricatta*), exploratory behavior was helpful but not sufficient, as it was an individual's persistence in opening an apparatus that predicted its ability to obtain food rewards (Thornton & Samson, 2012).

Although squirrels showed an increase in types of interactions with the apparatus during the test trial, there was no effect of experimental condition. In comparison with training trials, the test trial elicited few novel behaviors. Instead, squirrels redeployed behaviors exhibited during training trials. We also found individual differences among participants, with some squirrels persisting in just one unsuccessful response and other squirrels trying several different responses during the test trial.

We did not find differences in latency to approach the box or number of tail movements based on condition in the posttest trial. This indicates that squirrels showed a quick recovery from the frustrating experience. However, this conclusion must be tempered by the fact that some squirrels from each condition (including the control condition) dropped out of the experimental session after the test trial. This is probably because test trials only ended when the squirrel left the table of its own volition, so that we could compare persistence across the four experimental conditions. However, staying on the table may have been perceived as an extinction of reinforcement to the squirrels in the control condition.

In general, animals show sensitivity to changes in reward, whether those changes involve an increase or decrease in value (Maxwell, Calef, Murray, Shepard, & Norville, 1976). Animals that are switched from a lower to higher valued food item show positive contrast effect, compared to animals that always receive

the higher valued item (e.g., Benefield, Oscós, & Ehrenfreund, 1974; Shanab, France, & Young, 1976). In our study, there was no condition where squirrels always received a lower valued reward, as would occur in a successive negative contrast study. This was in part due to the difficulty in getting this particular population of squirrels to eat the less preferred corn, despite the fact that corn is a palatable food, commonly used to feed and attract tree squirrels (Baumgartner, 1940; Sheperd & Swihart, 1995). Therefore, we tentatively conclude that the switch to a less preferred reinforcement led to changes in behavior, mainly an increase in the number of tail movements exhibited during the test trial. Similar changes in behavior to a degraded reinforcement have been observed in chimpanzees (Haslerud, 1938).

Frustration is a ubiquitous behavioral and emotional response, yet its adaptive significance remains little understood. Although posited as resulting from a negative state, frustration responses could have adaptive significance in the wild, where previously rewarded actions do not always lead to reinforcement. The behaviors we have described in this study could have adaptive properties: persistence and variability of responses could aid animals in problem-solving. Thus, frustration could be a useful instigator of novel behaviors. Likewise, aggressive responses could increase an animal's likelihood of removing an obstacle while decreasing the probability that a competitor, observing this interaction, would approach the resource.

To understand how cognition evolves, we need to understand how it functions in the wild. The present study suggests the kind of cognitive building blocks that might be necessary for innovative problem solving, as in our prior work on self-control in the same species (MacLean et al., 2012; MacLean et al., 2014). This work also raises questions about the potential role of emotional arousal and valence in the evolution of problem-solving, innovation, and learning. Future research to explore these questions in squirrels could use methods developed for carnivores where tasks allow for multiple solutions, and previously trained methods can be made unavailable while rewarding novel solutions (Benson-Amram & Holekamp, 2012; Benson-Amram, Dantzer, Stricker, Swanson, & Holekamp, 2016). In the meantime, our study highlights the potential of cognitive research in habituated urban wildlife.

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