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The Effect of Owl Feces on Rat Operant Responding: Can Rats Recognize a Conspecific-Eating Predator?

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Exposure to canid or felid odor has often been reported to elicit distinctive anti-predator behaviors in laboratory mice and rats (e.g., Apfelbach et al., 2015a), including avoidance and suppression of operant responding. Recent research has also shown that rabbits (Prada et al., 2018) and dwarf hamsters (Apfelbach et al., 2015b) differentially respond to the presence of conspecifics in their predator's feces or urine. The present study examined whether laboratory rats had the ability to recognize conspecifics in a predator's diet through their feces. Rat (*Rattus norvegicus*) subjects were exposed to great horned owl feces after a meal of conspecifics (rats) or heterospecifics (rabbit and squirrel) in an operant conditioning chamber. Response rates decreased during the first minute of operant sessions when predator odor was present, but the same effect was produced by perfume, and whole-session response rates were unaffected by owl feces (regardless of owl diet), perfume, or coyote urine. Our findings suggest that rats may show no fear toward owl feces regardless of what the owl ate. However, because coyote urine also did not suppress operant responding, another interpretation of the current results could be that rats' responsiveness to predator odor is a small or inconsistent effect, and failures to replicate such findings are not often reported.

Keywords: predator odor, suppression of operant responding, anti-predator behavior

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Introduction

Chemical cues from predator skin, fur, feces, urine, or anal secretions have repeatedly been shown to elicit anti-predator behavior in rats and other prey species. Anti-predator behavior, as described by Apfelbach et al. (2005a), may include inhibition of locomotion, suppression of non-defensive behaviors (e.g., foraging, feeding, & grooming), and retreat towards one's habitat or secure locations when possible. In prey species, Trimethylthiazoline (TMT), a derivative of red fox (*Vulpes vulpes*) feces, is a substance commonly often used to elicit fear and anti-predator behavior (e.g., Apfelbach et al., 2015b; Endres et al., 2005; Fendt & Endres, 2009; Wallace & Rosen, 2000).

Extreme immobility, or freezing, is a common behavioral response to TMT (Blanchard et al., 2003b, Endres & Fendt, 2009; Storsberg et al., 2018; Wallace & Rosen, 2000; Rampin et al., 2018; McGregor et al., 2002). Similarly, foraging suppression by predator stimuli has been demonstrated in both laboratory (Endres et al., 2005) and field (Bytheway et al., 2013) settings. However, other studies failed to find such foraging suppression in field studies (Bramley & Waas, 2001; Orrock et al., 2004; Stryjek et al., 2003). Suppression of grooming behavior has also been recorded due to exposure to cat fur and TMT, but also to aversive—but not fear-inducing—odors (butyric acid, isoamyl acetate) (McGregor et al., 2002; Morrow et al., 2002).

Another common anti-predator behavior, particularly for TMT exposure, is avoidance (Endres & Fendt, 2009; Storsberg et al., 2018; Wallace & Rosen, 2000). It should be noted that aversive olfactory stimuli unrelated to predators, such as butyric acid, also elicit avoidance behavior. However, avoidance of aversive olfactory stimuli differs from predator-stimuli aversion in that it is not associated with increased anxiety (Blanchard et al., 2003a). Anxiety caused by predator odors has been studied through administering anxiolytic drugs (i.e., benzodiazepines) after exposure to odors (e.g., Berton et al., 1998; McGregor et al., 2002). Additional support that predator stimuli elicit emotionality in the form of anxiety is rapid context conditioning seen through extinction trials after exposure to predator stimuli (Blanchard et al., 2003a; Blanchard et al., 2003b; McGregor et al., 2002; Staples & McGregor, 2006).

While TMT is commonly used, some research suggests other odor stimuli may elicit higher levels of anti-predator behavior. A study by Staples and McGregor (2006) found that rats exposed to cat integumentary odors (i.e., those from skin or fur) exhibited more defensive behaviors compared to controls and the TMT group. A study by Blanchard et al. (2003b) examined the behavioral effects of a wooden block left in a cat's bed, feces, and urine. Blanchard and colleagues (2003b) found that cat feces and integumentary odor caused similar levels of anti-predator behavior in the realms of avoidance and freezing, but urine did not differ from controls. Additionally, cat feces and urine appeared to be a weaker unconditioned stimulus than the fur-scented block when both types of stimuli were paired with an unscented wooden block conditioned stimulus. Blanchard and colleagues interpreted this finding as due to the fact that cats tend to urinate and defecate

away from where they spend most of their time. Therefore, the odor from a cat's fur and/or skin would be a better predictor of a cat's actual presence compared to urine and feces in nature.

Another way to identify which odors predict the most immediate predation threat is through chemical analysis of the predator's diet through their feces or urine. Berton and colleagues (1998) found that mice behaved differently to cat feces from a carnivorous diet versus a vegetarian diet. While mice exposed to feces from cats fed either a carnivorous or vegetarian diet decreased foraging and food consumption, those in the carnivorous diet condition returned to their nests more often (Berton et al., 1998).

Instead of identifying carnivorous predators from feces, some prey animals appear able to discriminate between conspecifics and heterospecifics in predator feces. Cox et al. (2010) conducted a study to analyze whether odors from predators fed a diet of conspecifics could be used for pest control on prey species. Both goats (*Capra hircus*) and kangaroos (*Macropus giganteus*) ate less from a food trough when tiger feces were present, and the amount they consumed depended on whether the tiger feces contained conspecifics or heterospecifics (Cox et al., 2010). Predator-naïve dwarf hamsters (*Phodopus campbelli*) preferred the Y-Maze arm with ferret urine after a meal of mice over the arm with ferret urine after a meal of hamsters (Apfelbach et al., 2015^v). Additionally, in a field study, wild European rabbits (*Oryctolagus cuniculus*) avoided areas sprayed with a solution of ferret feces after a rabbit meal, and preferred areas sprayed with ferret feces after a meal of beef (Prada et al., 2018).

The aim of the present study was to evaluate laboratory rat behavior when exposed to great horned owl feces, and to determine whether laboratory rats can recognize conspecifics in owl feces. To our knowledge, owl feces have not yet been used to elicit fear in laboratory rats; however, a study by Guo et al. (2002) found that plateau zokors (*Eospalax baileyi*), a Chinese rodent, suppressed foraging behavior when exposed to eagle owl feces. Rats were exposed to owl feces from an owl previously fed either rats or other animals (squirrels and rabbits), perfume, and coyote urine while lever-pressing for food reinforcers in an operant chamber. We hypothesized that response rates would decrease in the presence of coyote urine and owl feces, particularly from an owl previously fed rats.

Method

Subjects

Adult male rats (*Rattus norvegicus*; $N = 12$) were used as subjects. Half of them ($n = 6$) were approximately 18-month-old Wistar rats (Simonsen Laboratories, Gilroy, CA), and remaining subjects ($n = 6$) were approximately 7-month-old Sprague-Dawley rats (Charles River Laboratories, Wilmington, MA) to analyze potential differences between strains. All Wistar rats were previously trained by students as part of a *Learning and Behavior Laboratory* course, either to lever press in an operant chamber or on a reinforced alternation task in a T-Maze. Due to handling by students, Wistar rat subjects were likely exposed to other odorants (e.g., deodorants, colognes/

perfumes, trace odor from students' pet). Sprague-Dawley subjects were experimentally naïve and had not been used in any past studies or academic courses. All rats were housed in pairs or groups up to 4 in two plastic cages (41cm x 21cm x 20cm; Allentown Caging, Allentown, NJ) connected by acrylonitrile butadiene styrene (ABS) pipe (7.75cm diameter). Pine shavings and shredded paper were used as bedding. Subjects had *ad libitum* access to Mazuri® Rodent Pellets (PMI Nutrition International, LLC, Brentwood, MO) and tap water. The subjects' colony room had a 12h light-dark cycle (lights on from 19:00-7:00) and was climate controlled (72-74°F; 20-21% humidity). Subjects were returned to their pairs/groups after training and test sessions. Experimental procedures were approved by the university Institutional Animal Care and Use Committee (IACUC IRBNet Protocol #1620128).

Apparatus

Four MED Associates, Inc. operant conditioning chambers (31cm x 26cm x 23cm) were used. Within the chamber were two 5cm x 2cm retractable levers (Med Associates, St. Albans, VT; ENV-112CM), corresponding 100mA incandescent white stimulus lights (ENV-221M) 4cm above each lever, and a Med Associates pellet dispenser system (ENV-203-45). 45mg grain-flavored precision pellets (Bio-Serv®, Frenchtown, NJ) were used for reinforcement and were dispensed according to a computer with Med-PC IV 4.0 software. The white stimulus light above the active lever turned on at the beginning of both training and test sessions and turned off once the session finished. The chambers were located inside cabinets to minimize distractions; however, peep holes were present on the cabinet doors such that subjects could be removed if an odor became too distressing. No subjects were removed due to distress.

Odors. Two types of owl feces, bottled coyote urine, and a perfume were used as olfactory stimuli. Owl feces was categorized into either owl feces after a meal of conspecifics (rats), or owl feces after a meal of heterospecifics (rabbit and squirrel). Owl feces were obtained from a 24-year-old great horned owl (*Bubo virginianus*) through Bird TLC, a local rehabilitation center for injured wild birds (euthanized rats from our laboratory are regularly donated to Bird TLC and were utilized in the current project; however, no rats were euthanized specifically for this project). Feces samples were collected during routine cage cleanings in zip-seal plastic bags. After collection, feces samples were kept frozen and thawed immediately before use. Coyote urine (Harmon Deer Scents®, “Coyote Attractant”) was used as it has been found to cause fearful reactions such as avoidance, risk assessment, and freezing in laboratory rats (Maestras-Olguin et al., 2021; Fendt, 2006). Perfume (Aeropostale®, “Promise Me”) served as a control for novelty and was not expected to elicit fear. While this perfume has not specifically been used as a control, various studies have used novel non-predator odors alongside predator odors as a control for novelty, including one perfume (Downes & Shine, 1998) namely isoamyl acetate (a fruity, banana/pear scent) and/or butyric acid (a putrid and unpleasant scent) (Endres & Apfelbach, 2005; Rosen et al., 2006; Wallace & Rosen, 2000).

Procedure

Subjects were trained to lever press on a VI 7.5-second schedule of reinforcement. Each training session lasted 30 minutes, and subjects were trained once a day 4 to 6 days per week. Subjects continued training sessions until the number of responses within the session was deemed stable; stability was defined as five consecutive days in which total session responses did not exceed or fall below the range of responses for the previous 10 days. After response rates stabilized, subjects were placed in the operant chamber with one of the following four odors: owl feces after a meal of rat conspecifics, owl feces after a meal of heterospecifics, coyote urine, or perfume. The two types of owl feces are referred to as *Owl:Con* (feces after a meal of conspecifics) and *Owl:Het* (feces after a meal of heterospecifics). Odors were sprayed (perfume and coyote urine, approximately 0.1 ml) or spread onto a paper towel and placed in a tray directly under the steel bars which made up the floor of the operant chamber. Liquid odors (perfume and coyote urine) were administered with a common spray bottle, presenting approximately 0.1 ml per subject. Owl feces were weighed to 0.5 gram per subject. Each subject remained in the same operant chamber for all odor presentations.

Subjects received one odor presentation a day for four days according to a Latin-Square design (i.e., three subjects received each possible order). Testing occurred in groups, such that the

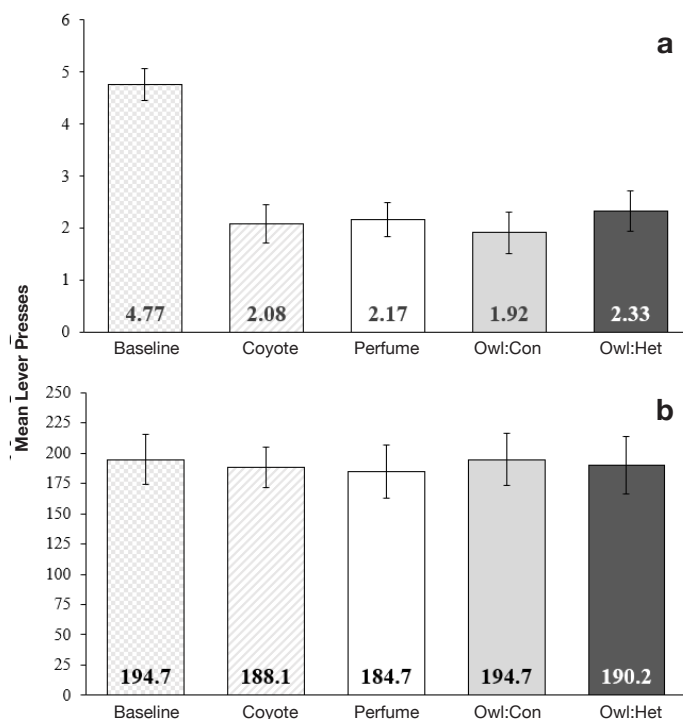


Figure 1. Panel a presents mean responses emitted by rats during the first minute of 30-minute operant sessions, and panel b presents the mean responses emitted across entire sessions. The baseline condition refers to the average of 5 days of stable responding with no odor present. Other odor conditions were owl feces after a meal of rat conspecifics (*Owl:Con*), owl feces after a meal of heterospecifics (rabbit or squirrel; *Owl:Het*), coyote urine (*Coyote*), and perfume (*Perfume*). Error bars indicate standard errors of the mean.

same odor was present in all active testing chambers at one time to prevent the possibility of subjects reacting to smells from neighboring chambers. When each group finished, subjects were returned to their home cages before odors were changed. To change the odor within a chamber, the tray containing the paper towel with odor was removed, cleaned with water and wiped dry, the scented paper towel was discarded and replaced with a paper towel containing the new odor.

Results

Mean responses across the first minute (panel a) as well as across entire 30-minute operant sessions (panel b) are presented in Figure 1. A 2×5 mixed design repeated measures ANOVA [rat strain (Wistar vs. Sprague-Dawley) \times odor (none/baseline, coyote urine, owl:con, owl:het, vs. perfume)] was conducted to determine if significant differences in total responses were present across entire 30-minute operant sessions. The effect of rat strain was not significant $F(1, 10) = 0.04, p = .85, \eta_p^2 = .004$. The effect of odor $F(4, 40) = 0.06, p = .99, \eta_p^2 = .006$, and the interaction between rat strain and odor were also not significant $F(4, 40) = 0.18, p = .95, \eta_p^2 = .02$.

Although none of the predator odor stimuli nor perfume suppressed operant responding across a 30-minute operant session, we considered the possibility that habituation to the odor may have occurred, so that the odors would have suppressed responding only early in the sessions. Therefore, a second 2×5 mixed design repeated measures ANOVA was conducted to determine if significant differences in responses were present during the first minute of operant sessions. The effect of odor $F(4, 40) = 3.73, p = .01, \eta_p^2 = .27$ was significant. The effect of rat strain approached, but did not reach, conventional statistical significance $F(1, 10) = 4.41, p = .06, \eta_p^2 = .31$. The interaction between rat strain and odor was not significant $F(4, 40) = 0.34, p = .85, \eta_p^2 = .03$. None of the odor conditions differed significantly from one another, according to paired-sample t tests (e.g., $t(12) = 0.63, p = .54$ for the largest mean difference between odor conditions during the first minute).

Discussion

In the current study, rats were presented with two types of owl feces (i.e., collected after the owl had consumed either a rat meal or a squirrel/rabbit meal), coyote urine, and perfume while responding in operant chambers for food reinforcers. None of the odors resulted in a significant decrease in the number of whole-session lever presses, and no predator odor suppressed response rates more than perfume during the first minute of operant sessions.

While a significant decrease in responding was observed during the first minute of operant sessions, this decrease did not differ as a function of which odor was presented to subjects. Perfume, which would not be expected to elicit any specific anti-predator behaviors like freezing, suppressed responding similarly (and slightly more on average) as all predator odors. Taken together, our analyses of whole-session versus first-minute responses suggest

that while all odors initially appeared distracting, no predator odor suppressed operant responding more than perfume. The failures of the owl feces to suppress responding could be taken to mean that owl feces, which to our knowledge had not previously been tested, simply do not elicit anti-predator behavior in rats. However, the failure of coyote urine to suppress responding is more surprising, given that Fendt (2006) reported that coyote urine elicited avoidance behaviors in rats and Maestas-Olguin et al. (2021) found that coyote urine specifically induced freezing in rats. While previous investigations of coyote urine's effect on rat behavior did not expose subjects in operant conditioning chambers, they did document freezing, which is the mechanism by which fearful stimuli lower operant response rates in rats (Endres et al., 2005).

Another potential reason for our failure to document an effect may involve the fact that the current subjects were domesticated rats, many of which were accustomed to human handling.

Domesticated rats living in laboratory environments may lack survival instincts in foraging situations. One study by Stryjek, Modlinska, and Pisula (2012) demonstrated that Wistar rats were less neophobic than Warsaw-Wild-Captive-Pisula-Stryjek (WWCPS) rats. When presented with a baited live trap, Wistar rats were caught much faster ($M = 4.5$ minutes) versus WWCPS rats ($M = 2900$ minutes). Wistar rats almost immediately entered the trap, whereas WWCPS rats explored the trap from the outside before carefully exploring the inside in a defensive "stretch attend" (i.e., crouching low to the ground with neck extended to enable quick retreat) position. This finding was interpreted as evidence that neophobia, which once instinctively drove rats from eating unknown foods or familiar foods in a novel context, has all but been eliminated in a stable environment where foraging is no longer needed.

Additional differences between wild and laboratory rats were found by Storsberg and colleagues (2018). While both Lister Hooded (LH) and WWCPS rats increased freezing behavior with TMT exposure; LH rats exhibited a greater number of freezing instances, whereas WWCPS rats exhibited longer durations of freezing. Additionally, only the WWCPS rats had an increase in corticosterone levels when presented with TMT.

Responses to TMT may also differ across rat strains. A study by Rosen, West, and Donley (2006) found that Wistar rats were less responsive to TMT in comparison to Long-Evans (LE) and Sprague-Dawley (SD) rats. TMT induced avoidance in all strains, but only LE and SD rats froze in the presence of TMT. These findings suggest that Wistar rats find TMT repugnant rather than fear-inducing. However, many previous studies of predator odor effects on rats have been conducted with laboratory rat strains identical to those used in the presented experiments (e.g., Sprague-Dawley rats; Endres et al., 2005). Additionally, some studies with wild rodent populations have failed to find an effect of predator odor (Bramley & Waas, 2001; Orrock et al., 2004; Storsberg et al., 2018; Stryjek et al., 2018).

A limitation that warrants consideration is that the current subjects were not only domesticated, but in the case of the Wistar subjects, accustomed to being handled by multiple students. While it is unlikely that any of these students exposed the subjects to owl

or coyote odors, it is quite likely that the rats were exposed to odors from pet cats and dogs. Therefore, the Wistar rats may have been habituated to at least certain predator odors before data collection began. However, this cannot be said about the Sprague-Dawley subjects, who were experimentally naive.

Another interpretation of the current results could be that rats' responsiveness to predator odor is a small or inconsistent effect, and failures to replicate are not often reported. It is possible that responsiveness to predator odor is variable between subjects, which may contribute to replication failures in small sample size studies including but not limited to the current research. As a well-known Robert Rosenthal quote states, "journals are filled with the 5% of the studies that show Type 1 errors, while the file drawers back at the lab are filled with the 95% of the studies that show nonsignificant results" (1979, p. 638).

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