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Defensive responses of Brandt's voles (*Lasiopodomys brandtii*) to stored cat feces

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HIGHLIGHTS

- Fresh cat feces induce highest behavioral, physiological, *c-fos* mRNA responses in Brandt's voles.
- Behavioral, endocrine and molecular responses are concurrent.
- Waning of all defensive responses happened with old predator feces.

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ABSTRACT

Predator odors are non-intrusive natural stressors of high ethological relevance. Animals are daily challenged with stressors of varying intensity and it is essential for their survival to respond to a wide range of threats. Behavioral and hormonal responses and changes in the level of medial hypothalamic *c-fos* mRNA were examined in Brandt's voles (*Lasiopodomys brandtii*) exposed to the feces of a domestic cat (*Felis catus*) stored for different periods. One hundred voles were tested in the defensive withdrawal apparatus. The voles showed an aversion to freshly collected cat feces, indicated by high levels of flight-related behaviors, increased freezing behavior, and more vigilant rearing compared to old feces. The serum levels of adrenocorticotropic hormone and corticosterone significantly increased when the voles were exposed to fresh cat feces. The level of *c-fos* mRNA in the medial hypothalamic region was highest in the individuals exposed to fresh cat feces. All of these behavioral, endocrine and *c-fos*-mRNA responses were lower when voles were subjected to older cat feces. We conclude that these responses depend on volatile chemical constituents of cat feces rather than their physical characteristics and that this accounts for the lower responses to feces stored for longer periods.

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1. Introduction

Predation is a strong selective force in the evolution of prey species [45]. Most animals must deal with predators during their lifetime and failure in this task may lead to their death. Consequently, prey species have developed adaptations at several levels (e.g., morphological, behavioral, physiological, molecular) to decrease the risk of being preyed upon [28]. A large number of field and laboratory studies have highlighted anti-predator defensive responses, including changes in behavior [35,42], hormone levels [28,40], and neuronal activation of specific regions of the brain [34]. Although anti-predator strategies are essential for survival, they may be costly. Cessation of regular feeding activities and increased investment in defensive strategies reduce energy income and may also interfere with mating behavior [33]. Hence, animals would be expected to modulate their anti-predator responses according to the perceived risk of predation [16,18].

In predator–prey interactions, early perception is the key step for prey animals to avoid being preyed on. The information that the prey animals are able to acquire from predators varies qualitatively and quantitatively with the type of cues presented. Therefore, it is important to know which stimuli or cues are better perceived by the prey animals: visual, auditory or chemical [15]. It has already been shown that chemical cues are of superior importance to others because they can provide comprehensive information to the prey regarding predation risk [22]. In particular, the strength of the chemical cue may provide information on the distance from the predator, the number of predators nearby [18], or what the predator has recently been feeding on [27].

The idea that prey animals assess and respond flexibly to different degrees of predation threat is known as the threat-sensitive predator avoidance hypothesis [16]. It predicts that prey animals use predator cues to evaluate danger and respond in a manner appropriate to the level of threat. This type of strategy minimizes the costs of mistakenly

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responding to predator activities and avoids interfering with foraging opportunities, territorial defense, or mate search when there is actually no risk [10]. Several studies have examined the threat-sensitive predator avoidance hypothesis by changing the concentrations of predator odors in aquatic organisms [17,41,26].

Brandt's vole (*Lasiopodomys brandtii*), a typical herbivorous rodent, mainly inhabits the grasslands of the Inner Mongolia Autonomous Region, China, as well as Mongolia and the Baikal region of Russia. The voles live in social groups and dig complex burrow systems with densities as high as 5616 holes/ha [48]. To test the threat-sensitive predator avoidance hypothesis in rodents, we used a novel approach in this study that mimicked a naturalistic situation when an animal is confronted with old feces of a predator. Brandt's voles were subjected to cat feces stored for different periods, and then we measured the changes of behavior, endocrine and *c-fos* gene expression. We hypothesized that the strongest anti-predator responses would occur at these three levels when the voles were confronted with fresh feces and that they would exhibit flexible graded responses with increased storage time. The data presented here expand our understanding for the ethology of predator odors and highlight their potential usefulness in damage control of the Brandt's voles.

2. Material and methods

2.1. Animals

Our experiments were conducted in the Laboratory of Animal Behavior, College of Bioscience and Biotechnology, Yangzhou University, Yangzhou, Jiangsu, China, between September and December 2012. The wild Brandt's voles were trapped using live-capture cage traps (YZ-LA: Shanghai Sinokil Environmental Service Co., Ltd., Shanghai, China) in the grassland of Inner Mongolia, transported to Laboratory of Animal Behavior, Yangzhou, and housed in plastic-bottomed wire cages (15 × 22 × 18 cm) in male/female pairs. The individuals of first generation (G_1) were weaned on the 21st day after birth and housed in a large cage (45 × 30 × 20 cm) with 12 same gender individuals in each cage. Then two or three same-gender individuals were housed in small cage (15 × 22 × 18 cm) when they were at the age of 60 days. Animals were provided with water and fed ad libitum with commercial diet supplied by Science and Technology Co. Ltd. Anritsu, Nanjing, Jiangsu, China. Wood shavings were used as bedding materials and changed every two weeks. Cages were washed every four weeks. Animals were kept on a constant 16L:8D light cycle (light on 6:00 am) at 21–23 °C. 50 male and 50 female individuals of first generations (three-month-old, 40–70 g weight) were used in this study.

2.2. Odor and animal grouping

Feces of a one-year-old domestic male cat (*Felis catus*) were collected and used for the experiment. The cat was captured on the Wenhui campus of Yangzhou University and housed in a wire cage (120 × 40 × 30 cm high) with a wire-mesh bottom and provided with water and food ad libitum. The cat was kept on a meat diet during the whole period of feces collection. The cat cage was monitored every 2 h and as soon as feces were found they were collected and immediately stored at −70 °C. The 100 voles were randomly allocated to 5 groups of 20 (10 males and 10 females in each). The five groups are referred to as: the Control group (Distilled water group); the First Day group, the Second Day group, the Fourth Day group, and the Eighth Day group (see Procedures section below).

2.3. Testing apparatus

The testing apparatus (75 cm × 37 cm × 40 cm) is shown in Fig. 1. An opaque Plexiglas® wall divided the box into two compartments. The 'testing arena' consisted of a rectangular area (60 cm × 37 cm × 40 cm) divided into 12 smaller areas marked with black lines. The second compartment, termed the 'hide box', was constructed from black Plexiglas®. A small square hole (6 cm × 6 cm) in the front wall of the hide box was just wide enough for the tested vole to enter the arena. The testing apparatus was mounted with two video cameras; one was situated on a tripod directly above the center of the apparatus and the other on the side wall of the testing arena for better recording and scoring of behaviors. Voles were transferred from the housing room to the testing room by a familiar person. A computer was connected to the cameras and located outside the testing room for live viewing and recording the session.

2.4. Procedures

All procedures were conducted between 9:00 am and 2:00 pm and all voles were handled identically for five days prior to the start of the experiment. Handling included weighing voles, holding them for 1 min, releasing them into cages, and then transporting them to the room in which testing was to be carried out without placing them in the test apparatus. Voles were always handled with protective rubber gloves and metal forceps. The test procedure was divided into two phases: familiarization and testing sessions. At the start of the experiment, each vole received a familiarization session on two consecutive days before the experiment, during which they were placed in a test apparatus for 10 min with no odor present. Voles in the Control group were tested for 10 min with distilled water. Collected cat feces were

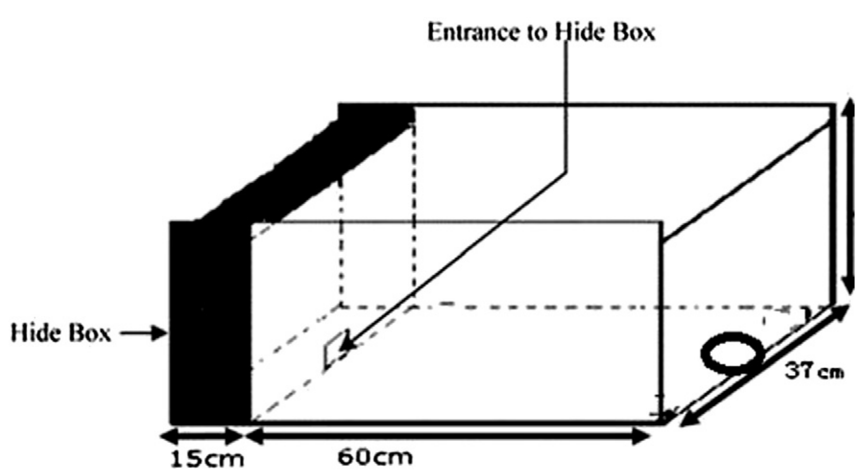

Fig. 1. Defensive withdrawal apparatus.

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