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Predator odor exposure increases food-carrying behavior in rats

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HIGHLIGHTS

- Foraging prey species trade-off energy gain against predation risk avoidance.
- Rats eat smaller food pellets at the food source but carry larger ones to the nest.
- Presentation of fox urine next to a food source increases food-carrying behavior.
- That suggests that food-carrying behavior is a pre-encounter defensive response.

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ABSTRACT

To cover their energy demands, prey animals are forced to search for food. However, during foraging they also expose themselves to the risk of becoming the prey of predators. Consequently, in order to increase their fitness foraging animals have to trade-off efficiency of foraging against the avoidance of predation risk. For example, the decision on whether a found food piece should be eaten at the food source or whether it should be carried to a protective site such as the nest (food-carrying behavior), is strongly dependent on different incentive factors (e.g., hunger level, food size, distance to the nest). It has been shown that food-carrying behavior increases the more risky the foraging situation becomes. Since predator odors are clearly fear-inducing in rats, we ask here whether the detection of predator odors in close proximity to the food source modulates food-carrying behavior. In the present study, the food-carrying behavior of rats for six different food pellet sizes was measured in a "low risk" and a "high risk" testing condition by presenting water or a fox urine sample, respectively, next to the food source. For both testing conditions, food-carrying behavior of rats increased with increasing food pellet weight. Importantly, the proportion of food-carrying rats was significantly higher during exposure to fox urine ("high risk") than when rats were tested with the water control ("low risk"). Taken together, these results demonstrate that food-carrying behavior of rats is increased by the detection of a predator odor. Our data also support the idea that such food-carrying behavior can be considered as a pre-encounter defensive response.

1. Introduction

Wild rats have to leave their protective nests to search for food in order to cover their energy demands. However, being outside the nest foraging is also connected to the risk of being detected and attacked by a predator. Both foraging and predation risk avoidance are clearly essential for the survival of all prey species. However, in nature, maximization of feeding efficiency while simultaneously minimizing predation risk is impossible [15,16]. Consequently, prey animals try to optimize the trade-off between foraging behavior and risk avoidance [15,16,23].

Upon encountering a food source, rats face a so called "food-handling conflict", where they have to decide on whether to eat a piece of food at the food source or to pick it up and to transport it to the safe nest (food-carrying behavior) to eat it there [14–16,19]. Eating food where it was found directly reduces hunger, whereas carrying food allows eating to occur in a safe place, although carrying food wastes time and requires energy for transportation. [15]. Such decisions on where to eat are known to be dependent on different incentive factors [14,19,23]. For instance, it has been shown that sated rats carry more food to the nest, while hungry rats eat more food at the food source indicating that the feeding status modifies food-carrying behavior [22]. If hunger alters the food-handling decision in favor of immediate food intake to maximize feeding efficiency, then foraging rats should likewise increase food-carrying behavior when the foraging situation becomes more risky. In most field and laboratory studies investigating food-carrying behavior in rodents, predation risk was defined as a function

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of the time spent away from a protective cover [14,16,19]. The lack of protective cover, however, represents only one possibility of danger and not the imminence of a direct threat. To increase the aversiveness of a foraging situation, Onuki & Makino [23] tested food-carrying behavior of rats while presenting a conditioned fear stimulus as a risk-approaching signal. Presentation of this conditioned stimulus increased food-carrying behavior.

In contrast to stimuli with acquired fear properties, there are also stimuli that innately induce fear in prey animals [11,17,27]. Being primarily olfactory oriented, rats, as most other rodent species, can recognize predation threats in their environment by detecting predatory olfactory cues [12]. Such odors connected to a selective disadvantage for the releaser while being beneficial for the perceiving animal (of another species) are termed kairomones [13,25]. Predator odors can induce an array of different anti-predatory responses (reviewed in [1,5,37]). For example, using an open-field or the olfactory hole-board test, we previously reported robust avoidance behavior of laboratory rats in response to urine samples from predators (e.g., fox, bobcat, puma) [11,23,39,40]. In addition, predator odors have been proven to be effective repellents protecting forestry and agricultural areas from feeding-related damage [3,20,24]. Whether predator odors during foraging can modulate food-carrying behavior in rats has not been investigated so far.

Therefore, the aim of the present study was to examine whether the presentation of predator odors increases food-carrying behavior in laboratory rats. Animals were first trained to travel along an alley to find a food source at the end of the alley. Since food-carrying behavior has been shown to be also dependent on the food size and/or weight [16,23], food pellets of different sizes and weights were used. Food-carrying behavior was measured under the following two conditions: (1) in a "low risk" testing condition when a water sample was presented next to the food source and (2) in a "high risk" testing condition by presenting a fox urine sample next to the food source.

2. Materials and methods

2.1. Subjects

Subjects were experimentally naive male Sprague–Dawley rats, 2–3 months old at the start of testing. Rats were bred and reared at the local animal facility (original breeding stock: Taconic, Denmark). They were housed in groups of 5–6 rats in standard Macrolon Type IV cages (55 cm × 33 cm × 20 cm) in temperature – (22 ± 2 °C) and humidity – (50–55%) controlled rooms under a 12 h light/dark cycle (lights on at 6:00 am). Animals received water ad libitum and were maintained at about 85% of their free-feeding body weight by providing a limited amount of 12 g standard laboratory rodent chow (Sniff Spezialitäten GmbH, Soest, Germany) per rat per day. All experiments were conducted during the light phase between 8:00 am and 4:00 pm.

All experiments were carried out in accordance with the international ethical guidelines for the care and use of laboratory animals for experiments (2010/63/EU), and were approved by the local authorities (Landesverwaltungsamt Sachsen-Anhalt, Az. 42505–2-1172 UniMD).

2.2. Testing apparatus

Both training and testing took place in a straight alley with closed side walls made of gray polyvinyl chloride (Fig. 1). The apparatus consisted of a start box (31 cm × 31 cm × 30 cm) fitted with some fresh bedding materials and home cage bedding materials, and an alley (15 cm × 160 cm × 28 cm). Via a small opening (11 cm × 10 cm) in the start box, rats were allowed to enter freely both compartments of the testing apparatus. At the distal end of the alley was a 1 cm deep notch, which served as a food well. Beside the food well, a glass bowl (4 cm outer diameter, 2.5 cm height) was fixed. The experimental room was only dimly illuminated (start box: ~30 lx, alley at food well: ~100 lx) by an indirect light source. During testing, the rats' behaviors were observed by an experimenter, standing calmly next to the start box.

2.3. Food pellet preparation

During training, 25 mg casein pellets (Dustless Precision Pellets; Bio-Serv Inc., Frenchtown, New York, USA) were used. Food-carrying behavior was tested using casein pellets of six different weights and sizes (45 mg, 180 mg, 360 mg, 540 mg, 720 mg, 990 mg). The five larger pellet sizes were produced by compressing a corresponding amount of 45 mg food pellets in a self-made pill press. All pellets were stored dry and cool at ~4 °C until usage.

2.4. Behavioral testing procedure

2.4.1. Training

On the first day, rats were placed into the start box, first in groups, then individually to familiarize them for 10 min to the testing apparatus without any casein pellets presented. Over the next days, rats were trained to run along the alley till the food well, to get the casein pellet there, and to return to the start box. For this, a trace of 45 mg casein pellets was placed along the alley with at least 5 cm distance between two pellets. Once rats improved their performance, the trace of casein pellets

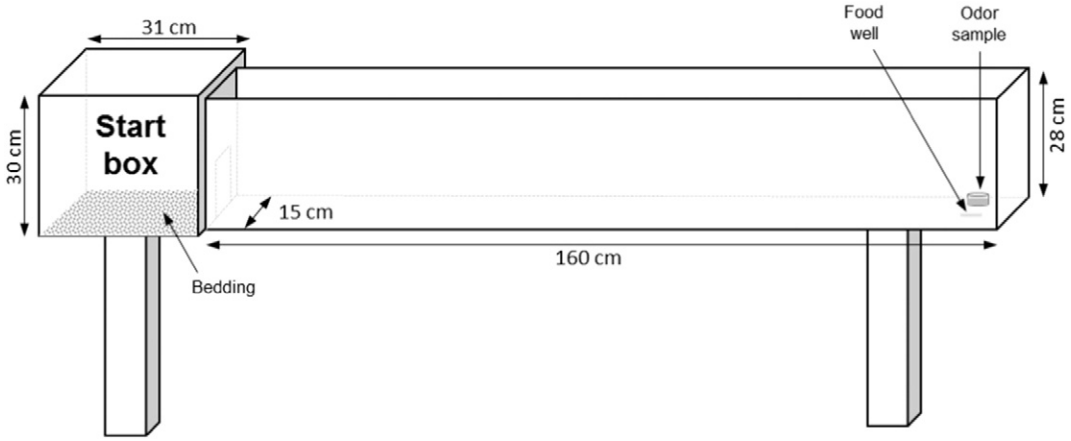

Fig. 1. Scheme of the straight alley testing apparatus consisting of the start box and the alley.