



Comparison of Exploratory Behavior of Two Different Animal Species: Woodlice (*Armadillidium vulgare*) and Rats (*Rattus norvegicus*)

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Exploratory behavior is a commonly used instrument for studying animal behavior in the laboratory, usually using rodents. The goal of the present study was to investigate the exploratory behavior of woodlice (*Armadillidium vulgare*) and compare it to the behavior of rats (*Rattus norvegicus*). For this, we used two common rat laboratory models: the square open-field and another inspired by the rat Light/Dark box. In a first test, rats were submitted to a square open-field; woodlice were also submitted to an open-field adapted to their size. In a second test, rats were submitted to a Light/Dark box, and the woodlice were submitted to a Dry/Moist box designed to be equivalent to the rat apparatus but adapted to woodlice size. Results of the first test showed both rats and woodlice explored the square open-fields in similar ways, both in terms of frequencies of entries in the areas and in terms of the time spent in them. Subjects of both species occupied the corners more than the areas close to the walls and the latter more than the central areas. Results of the second test showed a striking resemblance: Both species spent more time in the safe areas (dark or moist) and less time in the aversive areas (light or dry). Given this similarity, woodlice could be used as laboratory animals for behavioral studies with advantages: They occupy little room in the animal facilities, are easy to catch in many places around university campuses, and cost very little to be fed.

Keywords: *Armadillidium vulgare*, exploratory behavior, *Rattus norvegicus*, species comparison, thigmotaxis

Animals living free in nature display a large amount of behaviors when they are awake. They frequently exhibit behaviors that are analogous when considering the end result. For example, a leopard preying on a gazelle and a spider preying on a fly (e.g., *Frigga sp.*, of the *Salticidae* family) both have to search, find, and attack the prey before consuming it. Another example is the sexual displays exhibited by a diversity of animals, like mammals, birds, reptiles, amphibians, fish, and even insects. All these displays have in common the exhibition, certain physical or behavioral characteristics that allow or facilitate mating. Exploratory behavior is another instance in which many different species present analogous behaviors adequate to their environment, size, and diet, for example, the exploratory behavior necessary to locate food (Collier & Johnson, 1990).

Exploratory behavior is a well studied topic using laboratory rodents, mainly rats and mice. Montgomery (1950, 1955) investigated whether a novel environment evokes both the fear and exploratory drives. Reynolds (1962) approached the concepts of curiosity and novelty-seeking in the study of exploratory behavior. Blanchard et al. (1974) studied defensive reactions and exploratory behavior in rats. File (1985) reviewed the effects of drugs that decrease fear/anxiety on exploratory behavior. Laboratory studies of exploratory behavior have generally used the open-field (Hall, 1934; Hall & Ballechey, 1932) or the elevated plus-maze (Handley & Mithani, 1984). The open-field was reviewed by Walsh and Cummins (1976) and by Kraeuter et al. (2019). It was first reported in the early 1930s (Hall, 1934; Hall & Ballechey, 1932) and has been used to investigate exploratory behavior in a variety of species beyond rats and mice: ferrets (Ehrlich & Burns, 1958), cats and domestic fowls (Candland & Nagy, 1969; Kozak et al., 2019), dogs (Bergeron, 2019; Martinek & Lat, 1969), and gerbils (Oldham & Morlock, 1970). In all these instances, the behavior of the different species had common elements that characterize the apparatus.

In the previous cases, a variety of species have been studied. Likewise, it would be interesting to compare exploratory behavior of species farther apart in evolutionary history. One such species is the woodlice, a terrestrial crustacean. Woodlice (also called sow bugs, pill bugs, and slaters) are terrestrial isopods (class of *Crustacea*, sub-order *Isopoda*) of the family *Oniscidea*, which have invaded terrestrial habitats from aquatic environments and have even colonized deserts. Their body surface is covered by setae, scales, glands, and sometimes ornaments in various shapes (Holdich, 1984). Their main habitat is under mulch, fallen leaves, branches or logs, and rocks. Woodlice are nocturnal and require humid conditions during the day and may be found with other species, such as millipedes and earthworms (Capinera, 2001). Most woodlice spend the daytime hours hiding under stones, logs, and under other damp places (Cloudsley-Thompson, 1952). Humidity is an important factor in the survival of terrestrial isopods since low levels of it can lead to desiccation and death. Terrestrial isopods can detect the increase in humidity that occurs at night, and they also respond to light, by avoiding it, and to the absence of light (and accompanying increase in humidity) by leaving their hiding places at night to mate and search for food (Cloudsley-Thompson, 1952).

There are many studies on woodlice, usually covering biological aspects, mainly ecology (Bugs et al., 2014; Hassall & Dangerfield, 1990; Moreau & Rigaud, 2000; Paris, 1963) but very few studies investigating their behavior in laboratory controlled conditions (e.g., Moriyama et al., 2016). More specifically, do woodlice behave in similar ways as other animals studied in laboratory conditions? The main goal of the present work was to study the exploratory behavior of woodlice in laboratory controlled conditions.

Experiment 1 – Comparative Study of Exploratory Behavior in an Open-Field

The goal of the present experiment was to study woodlice exploratory behavior. Because our previous experience involved studying rat exploratory behavior (Bonuti et al., 2020; Bonuti & Morato, 2018), we decided to study woodlice behavior in a similar way. One simple model to study exploratory behavior is the open-field (for a review, see Walsh & Cummins, 1976). A wide variety of animals are studied using this model: crustaceans (Kohler et al., 2018), domestic cockroaches (Salazar et al., 2018), larval (Schnörr et al., 2012 and adult zebrafish (Blaser & Rosenberg, 2012), earthworms (Doolittle, 1972), some lizards (Maximino et al., 2014), mice (Simon et al, 1993), rats (Grossen & Kelly, 1972), and humans (Walz et al., 2016). It seemed appropriate to investigate woodlice exploratory behavior using this model. The present experiment aimed at investigating woodlice submitted to an open-field. We also studied rats in an open-field to see whether there are similarities in behavior.

Method

Subjects

Twenty male woodlice (*Armadillidium vulgare*, approximately 50 mg) were used. They were captured in the campus of the University of São Paulo at Ribeirão Preto, Brazil, 30 days before beginning the experiments and were kept in a polypropylene box (40 × 25 × 7 cm) with a 2-cm layer of washed sand and four wood blocks (10 × 5 × 1.5 cm) under which the isopods could hide. The box was kept in a room with a large window to the outside, which allowed daylight in and a natural light/dark cycle. This room also had air-conditioning and artificial lights from 8 a.m. to 5 p.m. Temperature was never higher than 28° C. A bottle full of water with a small hole in the bottom provided a continuous flow of water to maintain the sand humidity. Humidity was visually inspected in the sand and under the wood blocks. The isopods were fed TetraFin Goldfish Flakes (Tetra Holding, United States) and tortoise commercial chow (Alcon, Brazil) ad libitum.

Fifteen 60-day old male Wistar rats (*Rattus norvegicus*, approximately 220 g) were also used for comparison. They were control rats used in a study published elsewhere (Rico et al., 2019) and were used only in one behavioral experiment in which the rats were first tested in the open-field. The rats were housed in groups of five in polypropylene cages (41 × 34 × 17 cm) with rat chow (Nuvilab, Brazil) and tap water ad libitum. The animal room was maintained in a 12-h light/dark cycle (lights on at 7:00 a.m.) with the temperature kept between 24 and 27°C. Cleaning of the cages was performed three times a week, and dust-free wood shavings were used as bedding.

All testing was performed between 7:30 and 11:30 a.m. All experimental procedures with rats were carried out in accordance with the Guidelines of the Brazilian Society for Neuroscience and Behavior recommendations for animal care and with the APA ethical guidelines. Woodlice were treated likewise.

Apparatus

Square open-fields were used for both species. The woodlice were tested in a 10 × 10 × 5 cm black Plexiglas open-field lined with white cardboard. The cardboard was replaced after testing three woodlice. The rats were tested in a 120 × 120 × 40 cm open-field with dark wooden walls and floor lined with dark brown opaque Formica. After each test the floor was cleaned with a 5% alcohol solution and dried with a cloth.

Procedure

All behavioral tests were recorded by a video camera placed above the apparatuses and connected to a video recorder. Videos were subsequently analyzed by a trained observer. Behaviors were scored with the X-PlorRat software (Tejada et al., 2018). To record where the behaviors occurred, the open-field floor image was divided into squares on a transparent plastic mask placed over the computer screen: 25 2-cm squares for the woodlice open-field and 36 20-cm squares for the rat open-field.

Subjects of both species were tested individually. Each subject was gently placed in the center of the apparatus and allowed to freely explore for 10 min. The behaviors recorded were time spent (1) in the center, (2) close to the walls, and (3) in the corners and (4) the number of crossed squares.

Data Analysis

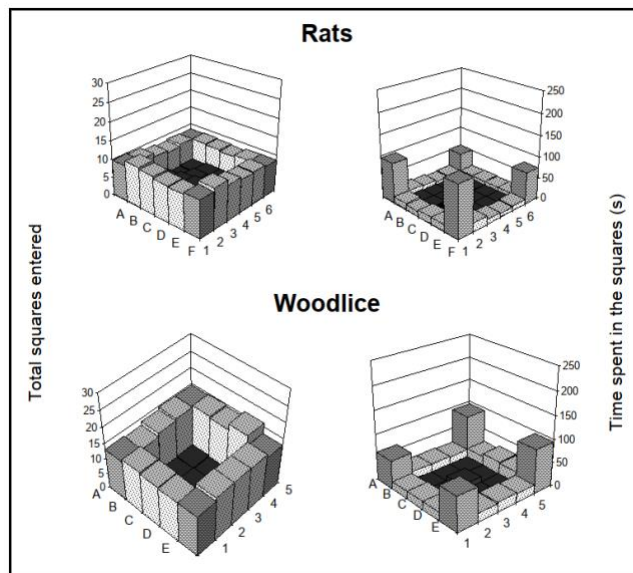
Data are reported as means ± S.E.M. and analyzed by two-factor analysis of variance (ANOVA) with species (*Rattus* × *Armadillidium*) as one condition and areas (corners × walls × center) as the other, and followed, whenever appropriate, by the Duncan all pairwise multiple comparison procedure. The number of squares crossed by rats and woodlice was analyzed using an independent-samples Student’s *t*-test. In all cases, a significance level of *p* < 0.05 was used.

Results

Figure 1 is a schematic representation of the two open-fields used and shows how the two species explored the environment. It shows a similar pattern of exploration by the two species. The total-entries data (left in the figure) show a strong preference for moving close to the walls. However, subjects from both species tended to remain longer in the corners (right in the figure).

Figure 1

Schematic Representation of the Divisions of the Open-Fields and the Patterns of Use of the Space

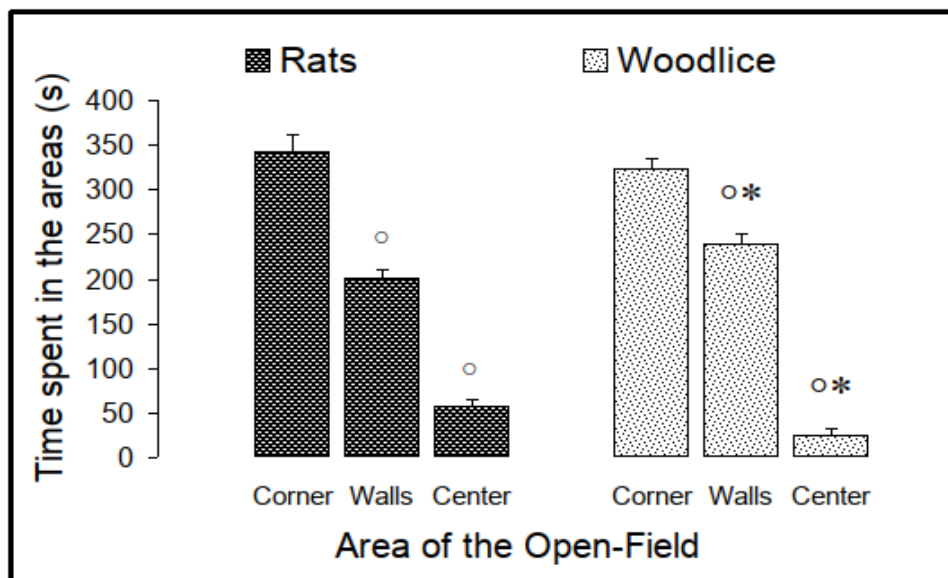


Note. Black columns refer to the center of the open-field; dark gray columns, corners; and, light gray columns, close to the walls.

The time spent in the different areas of the open-fields is shown in Figure 2. Two-way ANOVA applied to the time spent in the different areas of the open-fields showed an effect of area, $F(2, 104) = 329.58, p < .01$, but not of species, $F(1, 104) = 0.18, p = .67$. ANOVA also showed an interaction between area and species, $F(2, 104) = 5.47, p = .01$. Duncan's all pairwise multiple comparison procedure showed both rats and woodlice spent more time in the corners than near the walls. It also shows that the both kinds of subjects spent more time close to the walls than in the center. Duncan's all pairwise multiple comparison procedure also showed that woodlice spent more time than the rats close to the walls but spent less time than the rats in the central area.

Figure 2

Time Spent in the Areas of the Open-Fields by Rats and Woodlice



Note. ° = Smaller than the previous areas. * = Different from the same area compared with the rats (Duncan's method, $p < .05$).

Discussion

Subjects of both species tended to explore the open-field in a similar way, as rats usually do, moving from one square to the next but avoiding the central area and remaining close to the walls. Another common characteristic is that both rats and woodlice remained in the corners much longer than in the other areas. More specifically, there were no differences in the time both rats and woodlice spent in the corners. However, woodlice spent more time close to the walls and less time in the center than did the rats. One possible explanation is that both species present strong thigmotactic responses. Thigmotaxis is exhibited by a wide variety of species serving as a self-protection mechanism: Remaining close to vertical or under horizontal surfaces helps animals to avoid predators (Grossen & Kelly, 1972). Examples of animals exhibiting thigmotactic responses include a great diversity of species: crustaceans (Kohler et al., 2018), domestic cockroaches (Salazar et al., 2018), larval (Schnörr et al., 2012) and adult zebrafish (Blaser & Rosenberg, 2012), earthworms (Doolittle, 1972), some lizards (Maximino et al., 2014), mice (Simon et al, 1993), rats (Grossen & Kelly, 1972), and humans (Walz et al., 2016). Thus, thigmotaxis may be a well preserved behavioral protection throughout evolution, an adequate hypothesis to explain the mechanism of woodlouse behavior in the open-field.

Experiment 2 – Comparative Study of Exploratory Behavior in a Two-Environment Apparatus with Different Degrees of Aversiveness

Experiment 1 showed woodlice behave in a very similar way as rats do in an open-field. The behavior of rats in an open-field is usually explained by two dimensions. On the one hand, the displacements of the animals are usually hypothesized as being motivated by a tendency to explore, curiosity, or search for an escape (Welker, 1957, 1959). On the other hand, behavior could be, at least partially, a result of fear and/or anxiety (Handley & Mithani, 1984). An attempt to investigate exploratory behavior apart from fear/anxiety in rats was the use of the light/dark box model (for a review, see Bourin & Hascoët, 2003). Basically, the apparatus used in this model consists of two adjacent equal-sized walled compartments, one of them well illuminated and the other in the dark. A division separating the two compartments has a small opening (usually in the middle of it) through which the rodent can go from one compartment to the other. A typical, untreated control rodent usually passes through the opening a few times, which is interpreted as exploration, and tend to remain much longer in the dark compartment, interpreted as fear/anxiety (Bourin & Hascoët, 2003). Most researchers generally record only the transitions from one compartment to the other and the time spent in the light and in the dark compartments.

In order to investigate whether the woodlice in the open-field were motivated only by exploration or by both exploration and fear/anxiety, we tried submitting the small crustaceans to a light/dark box model analogous to the rat apparatus. This pilot study showed the woodlice spent the same amount of time in both compartments, passing through the opening many times. Possibly the woodlice vision system, less complex than the rat vision, made the crustaceans insensitive to such an apparatus. Then, we considered that light is aversive to rats (Garcia et al., 2005, 2011; Morato & Castrechini, 1989), which prefer a dark environment, which in turn explains rats' behavior of remaining much longer in the less aversive compartment. Thus, we saw the need to investigate woodlice behavior in an apparatus with an aversive compartment and a safe compartment. The literature showed woodlice avoid dry places and spend much time in moist ones (Cloudsley-Thompson, 1952). So, the present experiment aimed at investigating woodlice submitted to the equivalent of the rat's light dark box: the dry/moist box. We also studied rats in a light/dark box to see whether there are similarities in behavior.

Method

Subjects

Twenty male woodlice (*Armadillidium vulgare*, approximately 50 mg) were used. The subjects had similar characteristics as described in Experiment 1. Fifteen 60-day-old male naïve Wistar rats (*Rattus norvegicus*, approximately 220 g) were also used for comparison. They were obtained from the animal house of the University of São Paulo at Ribeirão Preto 72 hr before the tests. The rats were housed in groups of five in polypropylene cages (41 × 34 × 17 cm) with rat chow (Nuvilab, Brazil) and tap water ad libitum. The animal room was maintained in a 12-h light/dark cycle (lights on at 7:00 a.m.) with the temperature kept between 24 and 27°C. Cleaning of the cages was performed three times a week, and dust-free wood shavings were used as bedding.

Apparatus

In a pilot study, we investigated a light-dark box adapted to the woodlice size, in which it was shown that the woodlice explored both sides equally. Then, we reasoned that what was necessary was an apparatus with two environments differing not in illumination but in some other property. It turned out that humidity is an important environmental factor for woodlice, and, so, instead of a light-dark box, we used a moist-dry box. It consisted of a transparent 10 × 5 × 5 cm Plexiglas box with two 5 × 5 cm divisions, one of which was lined with dry white cardboard and the other with a moist white cardboard. Nine drops of water were added to the moist cardboard in order to guarantee the same amount of humidity in every test. The light-dark box for the rats consisted of a rectangular 100 × 50 × 40 cm box, divided into two equal square compartments connected through a 10 × 10 cm opening allowing passage from one compartment to the other. The light compartment was lined with white opaque Formica, while the dark compartment was lined with black opaque Formica. The luminous intensity at the center of the light compartment was 90 lux and at the center of the dark compartment was 30 lux. As the lucimeter did not fit inside the woodlice apparatus, we obtained the luminous intensity placing it by the side of the box: 103 lux. Thus, both species had an aversive compartment (light or dry) and a safe compartment (dark or moist). The cardboard parts were replaced after testing three woodlice, and, for the rats, after each test, the floor was cleaned with a 5% alcohol solution and dried with a cloth.

Procedure

All behavioral tests of this experiment were recorded by a video camera placed above the apparatuses and connected to a video recorder. Videos were subsequently analyzed by a trained observer. Behaviors were scored with the X-PlorRat software (Tejada et al., 2018) recording (1) the number of transitions from one compartment to the other and (2) the total time spent in each compartment. Subjects of both species were tested individually. Each woodlice was gently placed in the center of the moist compartment and allowed to freely explore for 10 min. Each rat was gently placed in the center of the dark compartment and allowed to freely explore for 10 min.

Data Analysis

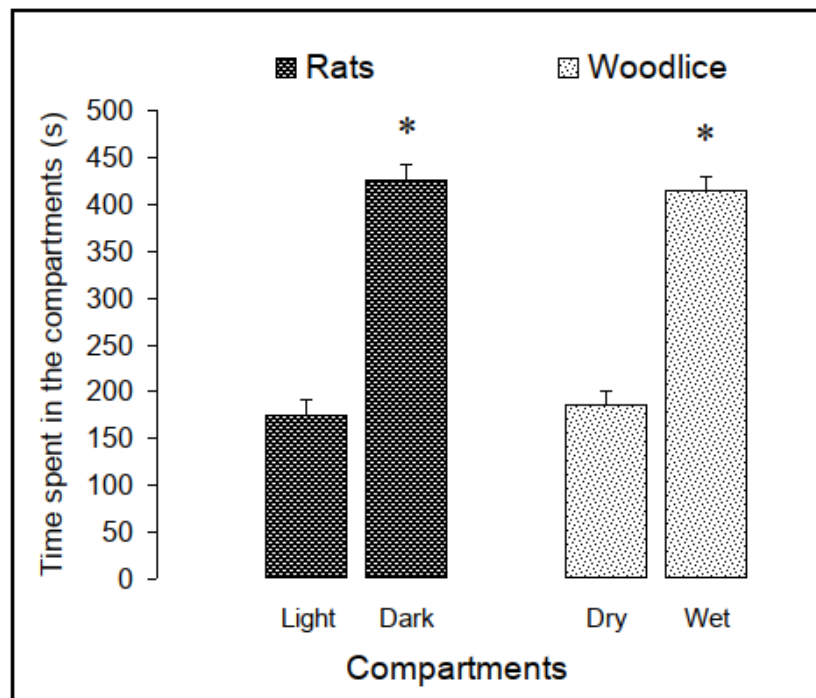
Data are reported as means \pm S.E.M. and analyzed by two-factor analysis of variance (ANOVA) with species (*Rattus* \times *Armadillidium*) as one condition and compartments as the other (moist/dark vs. dry/light) followed, whenever appropriate, by the Duncan all pairwise multiple comparison procedure. The number of transitions from one compartment to the other by rats and woodlice was analyzed by an independent-samples Student's *t*-test. In all cases, a significance level of $p < 0.05$ was used.

Results

Like in the open-fields of Experiment 1, both species explored the apparatuses in a similar way. As judged by the number of transitions from one compartment to the other, the species explored the environment in similar ways (rat transitions: 12.73 ± 1.44 ; woodlice transitions: 11.00 ± 1.56), $t(43) = -0.71$, $p = .48$. Figure 3 shows the time spent in each compartment. Two-way ANOVA applied to the time spent in the compartments showed an effect of compartment, $F(1, 89) = 180.85$, $p < .01$, but not of species, $F(1, 89) = 0.00$, $p = 1.00$. The Duncan all pairwise method showed both species spent more time in the safe compartment (dark or moist) than in the aversive compartment (light or dry) and that there were no differences between species.

Figure 3

Time Spent in the Safe and Aversive Compartments by Rats and Woodlice



Note. * = Different from the aversive compartment. (Duncan's method, $p < .05$).

Discussion

The light/dark box is a common test for laboratory rodents in which a subject, by passing through a small opening, moves to and from a light compartment (usually white-walled) to a dark compartment (usually black-walled). Typically, a subject will pass through the opening a few times and remain longer in the dark compartment, a behavior that may be altered by drugs (Arrant et al., 2013; Bourin & Hascoët, 2003; Domonkos et al., 2017). Light is aversive to rats in novel environments (Garcia et al., 2005). Because a light/dark box for woodlice was not successful in our pilot study, the comparison was made with a dry/moist box. In order to compare, we interpreted the light compartment as aversive and the dark compartment as safe for the rats and studied the woodlice from the standpoint of humidity, a critical variable for these animals. The results showed a striking similarity of behaviors between the subjects of both species, indicating the preference for remaining longer in a safer environment and avoiding the more aversive one.

General Discussion

A general conclusion is that woodlice can be used in laboratory conditions, like their rodent counterparts. In the two rodent tests used, involving avoiding aversive conditions and seeking safer situations, woodlice behaved as the rats did. We can only suppose what motivated woodlice behavior in the two tests. Likewise, we also can only suppose what motivated rat behavior. Despite a large database of literature on laboratory rodent behavior, the best explanation of rat motivation remains theoretical. One explanation, suggested by Elwood and Appel (2009), argues that motivation can be inferred from behavior alterations seen after exposure to a stimulus situation, even in less complex animals, as in the hermit crabs these authors studied. We have used thigmotaxis as a plausible hypothesis to explain both rat and woodlice behavior based on the evolutionary notion: “same problem, same solution,” despite differences in their nervous systems. Also, this would indicate thigmotaxis as the conservation of a behavior strategy useful for survival of a variety of species (see Discussion, Experiment 1).

However, further studies are necessary to ascertain up to what point woodlice exploratory behavior is similar to rat exploratory behavior and whether the same hypotheses will be able to explain behavior, as we propose thigmotaxis may. For example, initial pilot data on drug effects suggest that exploratory behavior changed similarly to drug administration for both rats and woodlice. Beyond these limitations, further studies are also necessary to ascertain whether woodlice raised in captivity will behave in the same way as wild captured woodlice.

In spite of the limitations mentioned above, woodlice may constitute a very handy and useful laboratory animal. They can be used to compare similarities with rat behavior, mainly in studies involving exploratory behavior. Woodlice could also be studied to ascertain whether they have the same learning characteristics as other less complex animals. Finally, woodlice are very easy to maintain, easy to catch in many common places, occupy little space in animal facilities, and cost very little to be fed.

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