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Food passage time in a tropical millipede, *Doratogonus uncinatus* (Diplopoda, Spirostreptida, Spirostreptidae) from Zimbabwe

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Abstract
In the present study, passage time of different food types in a southern African millipede was investigated and the proportion of the gut containing food was measured in the laboratory in December 2000. Food type did not affect food passage time in millipedes ($p>0.05$). The gut is always full (100%) when millipedes are active on the surface. The results support the notion that millipedes, as detritivores, do not adjust food passage time even when the food type/quality changed, as happens when they are active during the rainfall season.

Keywords: Litter, detritivores, pellet, transit, time

1. Introduction

Millipedes are characterised by high ingestion rates, low assimilation efficiencies and high throughput rates [1, 2]. Plant litter, on which millipedes subsist mainly is of poor quality [3, 4, 5, 6, 7, 8] and is composed mainly of cellulose [9] which presents a digestive challenge to the simple and undifferentiated digestive system of millipedes [3]. Although plant litter is abundant, millipedes also feed on living plants [2, 4], soil [5-7, 10, 11], fungi, dead animals and faecal material [3, 4], algae, seeds and fruits [12] and lichens, moss and pollen [8]. Laboratory observations demonstrated that millipedes feed on different types and proportions of food items depending on availability [11].

Food passage time in millipedes is poorly known and there is a paucity of data on the influence of food type in comparable invertebrate taxa. Although transit times have been reported in termites [13] and earthworms [14], the only known record of passage time in millipedes was reported in three temperate species [9]. Given that adaptive feeding and digestive strategies enhance efficient extraction of energy and nutrients from food items, associated defaecatory adjustments could also occur. Ingestion and defaecatory adjustments in response to food supply were reported in freshwater pulmonates [15]. However, it is unknown whether millipedes employ similar strategies depending on food quality and/or availability.

Despite being abundant and having large bodies, little is known about food passage time in tropical millipedes. As such, the present study aimed to provide basic data and highlight the importance of millipedes as detritivores in the tropics. The laboratory study compared gut passage times of prepared food items. The hypothesis that different food types will have different transit times in *Doratogonus uncinatus* (Attems 1914) was tested. In addition, this study answered the following questions:

1. What proportion of the gut contains food at any time?
2. Does passage time change after starvation?

2. Materials and Methods

2.1 Sampling site

Surface active mature females and males of *D. uncinatus* (Attems 1914), soil, *Combretum erythrophyllum* (Burch.) Sond. leaf litter and *Uapaca kirkiana* Müell. Arg fruits were collected during the 2000 wet season in Miombo woodland at Mazowe Dam (17° 31′ S, 30° 59′ E), 20 km north of Harare, Zimbabwe. The soils at Mazowe Dam are derived from mafic rocks and they are rich in ferromagnesian minerals [6]. *Doratogonus uncinatus* is widespread in Zimbabwe, Malawi and Mozambique, adult are between 100 mm and 145 mm long, and they have a maximum body diameter of 12 mm [17, 18].

2.2 Sample collection and dissection

A sample of 320 millipedes was collected by hand along two parallel 100 m x 2 m transects for 30 minutes. To determine the proportion of gut containing food, millipedes (n=60) from the sample were killed immediately by drowning in 70% ethanol. In order to measure gut length and the proportion filled with food these millipedes were dissected in the laboratory. Later in the laboratory, millipedes fed prepared food were also dissected. The gut was exposed by cutting through the lateral sides of the exoskeleton along the line of ozopores from the anal valve to the head after which the dorsal exoskeleton was lifted off. After removing the gut the length and the proportion containing food were measured using a 30 cm ruler. Further samples of 20 millipedes were taken monthly from the same site until the end of the rainfall season and dissected as above.

2.3 Laboratory experiments and statistical analyses

The remaining millipedes (n=160) were used in food passage experiments. Food was prepared in the laboratory using ground fruits, leaf litter, maize meal and soil. Ground maize grain was used because in the field maize grains were eaten when they were encountered. The soil was ashed at 650 °C in a muffle furnace for 24 hours. Ripe fruits and leaf litter were dried at 70 °C for 24 hours before grinding (particle size < 2 mm) and mixing (1:1 by mass) with ashed soil. To 5 g of each of the food types, 50 yellow non-digestible brush bristles (approximately 1 mm long) were added as markers. The food was moistened by adding 4 ml of distilled water to each food dish. Earlier, a preliminary investigation demonstrated that the brush bristles did not affect transit time of the food.

Some millipedes (n=40) were fed *ad libitum* in the laboratory on the four food types (without the marker) in order to determine the proportion of gut containing food after 24 hours. The specimens were dissected and gut measurements were done as above.

Some millipedes were starved by keeping them in a glass holding tank (length 80 cm, width 50 cm, height 30 cm) without food for three and 21 days. Water was provided in two dishes (diameter 9 cm, depth 1.5 cm) placed 40 cm apart and replenished daily. Any pellets that were produced during the starvation period were immediately removed to prevent coprophagy. Empty guts were confirmed after dissection of 10 millipedes after 3 days of starvation.

In order to determine transit times, four food types (fruit only, fruit-soil, litter-soil and maize meal-soil) were used. To determine transit time for each food type in the millipedes that had not been starved (n=15), four glass tanks (length 80 cm, width 50 cm, height 30 cm) were set up each containing five feeding dishes filled with 5 g of the same food type with marker. To allow adjustments to prepared food, millipedes were fed unmarked food for 24 hours before being given marked food. The feeding dishes were randomly placed in the tanks but not in contact with the walls to allow free movement of millipedes. Five millipedes of known sex were put in each tank. Each millipede was uniquely marked with a letter or symbol on its dorsal surface using a gold pen so that individuals could be monitored. The same was done with starved millipedes. The number of millipedes put in each tank was based on the observed density of surface active millipedes at Mazowe Dam. The times between feeding and production of a faecal pellet containing a marker were recorded for each millipede. Feeding was taken as the movement of mandibles on the food. All experiments were conducted at 25 °C and observed for 24 hours. Each faecal pellet was dropped in a petri-dish half-filled with distilled water and searched for markers. The pellets crumbled in the water making the markers visible. After the study millipedes that had been used in the experiments were returned to the site from where they had been collected.

2.4 Statistical Analysis

An analysis of variance and pairwise comparisons of passage times of the different food types were performed using SPSS (version 21).

3. Results

Guts of millipedes (n=60) that were dissected immediately after collection and millipedes (n=60) collected monthly during the rainfall season were always full (100%) of food. Laboratory observations after millipedes fed *ad libitum* on different food types showed that the gut was 95 to 100% full when specimens were dissected. There was no food mixing in the gut, that is, different food types in the gut appeared in distinct bands according to the order in which they were ingested.

Food passage in *D. uncinatus* was between 6 and 19 hours long. Food passage time was not significantly different among the food types (Table 1). There was no difference in food passage time between starved and un-starved millipedes feeding on leaf litter and maize meal; and between males and females when they are fed the same food type ($p>0.05$). However, the passage time was shorter when the fruit-soil mixture was provided after starvation ($p<0.01$) (Table 1 and 2). Passage time was significantly different between millipedes that were starved for 21 days and fed fruit-soil, and millipedes that were starved for 3 days and fed fruit-soil ($p<0.05$), and millipedes that were not starved and fed fruit-soil ($p<0.01$). Passage time was also significantly different between millipedes that were not starved and fed fruit-soil mixture, and those fed fruit only ($p<0.01$).

Table 1: Pairwise comparisons of food transit times in *D. uncinatus* starved for 3 days (st3) and 21 days (st21) and in un-starved (nst) specimens fed fruit-soil (Fnst, Fst3, Fst21), leaf-soil (Lst3, Lnst), maize-soil (Mnst) and fruit not mixed with soil (Fnstsf).

	Mnst	Lst3	Lnst	Fst21	Fst3	Fnstsf
Fnst	ns	ns	ns	0.01	ns	0.01
Fnstsf	ns	ns	ns	ns	ns	
Fst3	ns	ns	ns	0.05		
Fst21	ns	ns	ns			
Lnst	ns	ns				
Lst3	ns					

ns = not significant

Table 2: Transit times (hr) of different food types in *D. uncinatus* after no starvation (nst), starvation (st) for 3 and 21 days (st3 and st21) and when soil (sf) was not added to organic matter.

Food type	n	Mean passage time (hr) ± SD
Fruit-soil (nst)	21	17.33 ± 3.68
Fruit only (nstsf)	18	6.17 ± 4.45
Fruit-soil (st3)	19	15.79 ± 3.33
Fruit-soil (st21)	23	11.09 ± 1.44
Leaf-soil (nst)	16	18.18 ± 2.83
Leaf -soil (st3)	17	17.29 ± 2.73
Maize-soil (nst)	20	19.05 ± 1.64

4. Discussion

Millipedes do not carry an empty or a partially filled gut, as demonstrated after dissecting fresh specimens from the field, thus indicating regular food ingestion. Because millipedes are detritivores, regular feeding and a full gut ensure constant supply of energy and nutrients from an abundant but nutritionally poor diet of plant litter. An alternative adaptive digestive strategy could be longer retention of food in the gut. Although longer retention of food has been reported in a pulmonate [15], it is unlikely that millipedes adjust transit time because they have a simple and undifferentiated gut [3]. These present results corroborate Calow [3] who reported that tropical millipedes have high ingestion rates and short retention. Short retention reduces the costs of carrying food from which the millipedes are unlikely to get significantly more energy or nutrients by increasing retention time. Short transit times in *D. uncinatus* mean that large volumes of food litter are processed in a short time to ensure that enough energy is obtained from food of poor quality.

Although the fruit-soil mixture was perhaps easier to process, transit time did not differ from the other food mixtures. In the field, nutritionally rich and easier to breakdown food, such as fruits, is likely to be available for short periods, thus it is encountered rarely. Hence, natural selection would favour strategies that efficiently process the abundant food, in this case, plant litter. When millipedes were fed fruit without soil, transit time became shorter (mean 6 hours), probably because ripe fruit (which contains simple sugars) is processed easily than, for example, leaf litter which contains cellulose. According to Sufi and Kaputo [19], *U. kirkiana* fruits contain 4.1% glucose, 2.7% fructose, 1.5% sucrose and other simple sugars. However, the shorter passage time for fruit may not be an indication that millipedes can adjust retention times, but rather supports the notion that food type could influence transit time depending on the characteristics of the material.

According to Cammen [20], ingestion rates may vary in response to previous feeding history of the animal in aquatic detritivores, for example, starved animals increased ingestion rates when food became available. Similar observations have not been reported in terrestrial invertebrates. In the present study starvation seemed to influence transit time only when nutritionally rich and easier to process food (in this case fruit) is abundant, an unlikely scenario in the field. Food of poor quality (leaf litter and maize meal) did not have similar effects on transit time irrespective of whether the millipedes had been starved or not, probably because they are of poor quality and difficult to digest. This is consistent with the known characteristics of detritivores in terrestrial habitats in which detritus is processed rapidly.

Given that food availability and quality in the field differ during surface activity of millipedes, passage time may be variable depending on the characteristics of items ingested. As such, the present study may be simplistic because millipedes are polyphagous [3] and the proportion of the different food items ingested is variable. Therefore, these results may not give a complete picture of possible variation in passage time because the millipedes were studied under unnatural conditions. Although there appears to be food precedence in millipede gut, ingesting different food types and in different proportions may influence passage time. Given that the proportion of soil in the faecal pellet varies within a season (Mwabvu *per. obs.*) passage time may also vary because soil facilitates high throughput rates in millipedes [3]. However, based on the results in this study, soil may not influence throughput rates when the food ingested is easier to digest. These aspects, including food preference, require further investigation.

Based on the short passage times recorded and the full gut observed in *D. uncinatus*, these data are consistent with detritivory. The results are comparable with the transit times of between 2 and 12 hours reported for three smaller temperate millipedes [9], termites [13] and earthworms [14].

5. Conclusion

The present results highlight the important role of millipedes in breaking down organic material. In addition to their large body size, the high throughput rates or short passage times of food in *D. uncinatus* further supports the notion that millipedes — together with termites and earthworms — are key detritivores in tropical ecosystems.

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