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Gut Passage, Respiratory Rate and Assimilation Efficiency of three Millipedes from a Deciduous Wood in the Alps

(Julidae, Diplopoda)

by

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Abstract: Adult females of *Ophyiulus pilosus, Ommatoiulus sabulosus* and *Allaiulus fulviceps* were collected from the upper litter layer of a mixed oak wood in Stams (Tyrol, Austria), kept in petri dishes on agar and supplied with one year old oak litter. Gut passage, respiratory rate and assimilation efficiency were investigated at 15°C. The gut passage time varies between 2 - 5 (with food) and 11 - 12 (without food) hours depending on the food supply. *O. pilosus* indicates the highest respiratory rate (61.2 µl O_2 gfw^{-1} hr^{-1}, 15°C), *O. sabulosus* the lowest (42.2). Differences in oxygen consumption and defaecation rates between the three species are significant. The mean assimilation rates (%) are quite similar (*A. fulviceps:* 33.7, *O. sabulosus:* 36.6, *O. pilosus:* 30).

1. Introduction:

Millipedes play an important role in leaf litter decomposition. In an inneralpine mixed oak wood in Stams (Tyrol, Austria) millipedes occur in numbers up to 1128 ind./m^2. With a dominance of 11,6 % and a very low fluctuation rate (maximal/minimal abundance) of 2,3 they are the most important saprovores after lumbricids in this ecosystem (MEYER et al. 1984). Three species are regularly found in the upper litter layer; *Ommatoiulus sabulosus* (LINNÉ), *Allaiulus fulviceps* (LATZEL) and *Ophyiulus pilosus* (NEWPORT). Gut passage, respiratory rate and assimilation efficiency were studied to detect possible differences between these three species.

2. Material and Methods

2.1. Animals

All animals used for the experiments were sampled in a mixed oak wood in Stams, Austria from March 1988 to January 1989. They were kept in petri dishes (Ø 9 cm), filled with agar (1%) at 15° C. They were regularly fed with one year old oak litter, which can be found throughout the year, and thus must be regarded as the main food source for saprovores in this ecosystem, especially after the virtual disappearance of other leaf types which are more attractive for decomposer organisms. In all cases adult females were used for the experiments.

2.2. Gut Passage

Gut passage was studied with a photographic method. Every hour one photograph of the animal was taken. On these pictures the number of faeces could be counted. To detect possible differences in gut passage time with food or without food, the experiment was divided into two parts: The animals were first starved for 24 hours and then supplied with food. The time until the first appearance of faeces was regarded as the gut passage time. In the second part of the experiment the food was removed, in this case the gut passage time was considered the duration until the last faeces were produced. The experiment lasted for 48 hours (one day with food, one day without). The experimental vessels were petri dishes filled with agar. To prevent the animals from burying, the agar surface was

covered with nylon gauze. Pieces of a polyvinyl tube were placed in the vessel to increase the complexity of the habitat. The food consisted of one year old oak litter.

All experimental vessels were installed in an incubator (Fig. 1) to maintain a constant temperature of 15° C. A timer (T) controlled the camera (C). To prevent reflections on the top of the petri dishes (P) two flashlights (F) were placed beneath the vessels. The light passed through a sheet of frosted glass (G), which made the illumination more even. A neon tube (L) was used to control the diurnal periodicity (light from 6 a.m. to 6 p.m.).

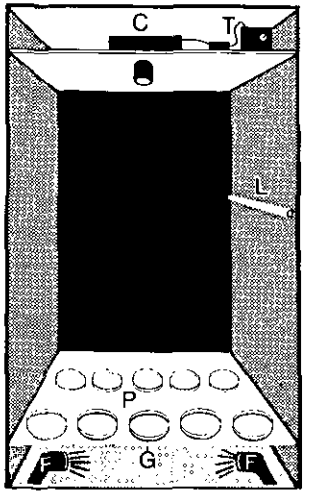

Fig. 1: Experimental design to study gut passage: **C** camera, **T** timer, **L** neon tube, **P** petri dishes, **G** sheet of frosted glass, **F** flash light.

2.3. Respiration

Oxygen consumption of single specimens was measured with a Gilson differential respirometer at 15° C. KOH was used as a CO_2 absorbent, moistened filter paper was placed on the bottom of the vessel to keep the necessary humidity. No food was given to avoid bacterial respiration. Measurements were carried out every two hours from 8.30 a.m. to 8.30 p.m. Immediately after the experiment the fresh weight of the animals was determined. The values for oxygen consumption were converted to standard conditions (0° C and 760 torr).

2.4. Assimilation

The following formula was used for assimilation investigations:

$$A = C - F$$

(A = assimilation, C = consumption, F = defaecation).

In this study assimilation was investigated with a gravimetric method. The animals were kept in agar dishes with filter paper on the surface in order to avoid feeding from the agar. One year old oak litter was cut into pieces, mixed to exclude possible differences between single leaves and finally dried at 60° C for 24 hours. Each specimen was kept in a single petri dish and provided with one gram of oak litter (dry weight). Every day faecal pellets were collected and dried to prevent weight changes due to microbial activity. After eight days the experiment was stopped. The remaining leaves, which had not been eaten, and the collected faeces were weighed.

3. Results

3.1 Gut Passage:

3.1.1 Gut Passage Time:

Figure 2. (a - c) shows the gut passage time in specimens supplied with food. It varies between two hours (*A. fulviceps*) and five hours (the other two species). Without food, gut passage time lasts

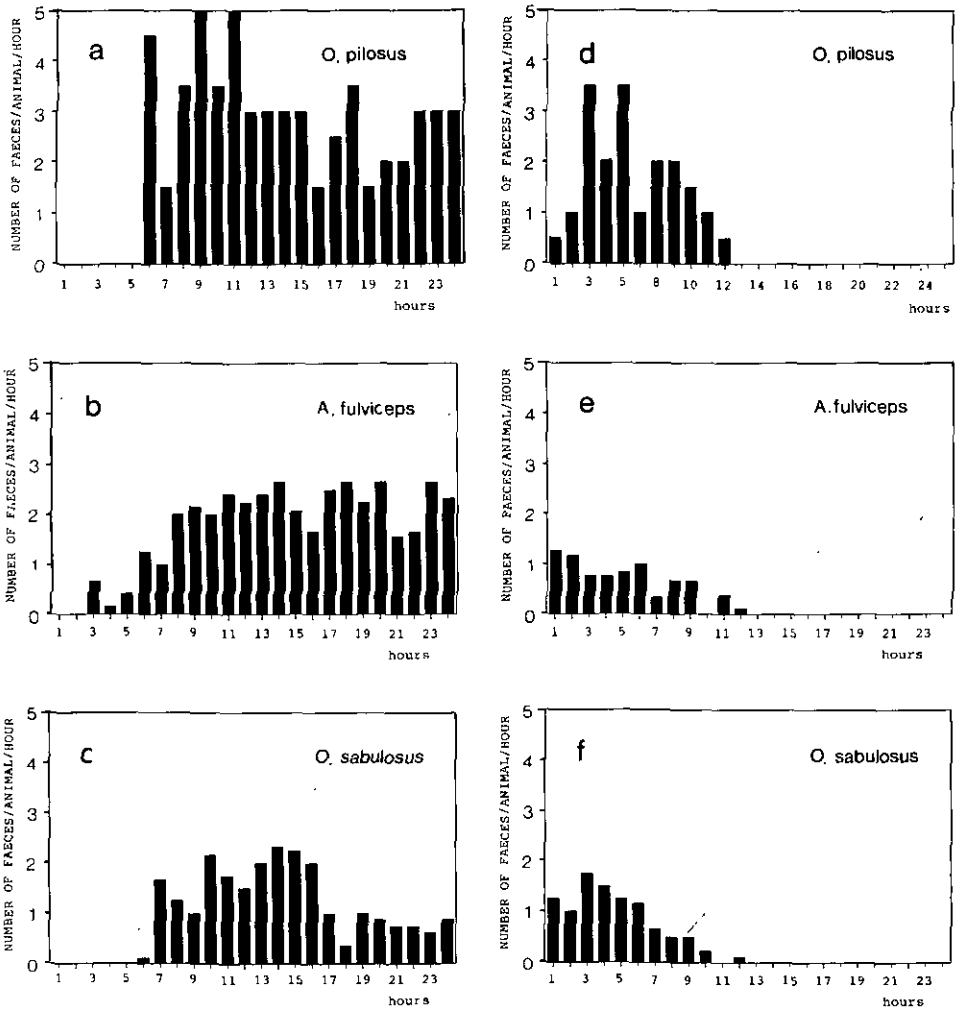

Fig. 2: Gut passage time in three millipede species. The columns represent mean numbers of faeces produced per animal and per hour. a - c with food supply after 24 hours starvation, d - f after removing the food.

11 to 12 hours (Fig. 2 d - f). Hence the retention time for food in the gut varies between two and twelve hours depending on food supply. There are only minor differences between the three species.

3.1.2 Faeces Production:

The mean faeces production rates of the three investigated species are summarized in Table 1. *O. pilosus* produces 2.4 faeces per hour and per animal, *O. sabulosus* less than half (1.0) of it. *A. fulviceps* ranges in between. The values of the three investigated species differ significantly.

Table 1: Faeces production in three millipede species at 15° C. Mean numbers ($\bar{x} \pm SE$) of faeces produced per animal and per hour are given.

	[no. of faeces h^{-1} $animal^{-1}$] *) $\bar{x} \pm SE$		n
O. pilosus	2,4 ± 0,57	a	7
A. fulviceps	1,7 ± 0,35	b	7
O. sabulosus	1,0 ± 0,28	c	8

*) Values followed by different letters within a column are significantly different at $P \leq 0.01$ (t-test).

3.1.3. Rhythmics:

Although there was a change in illumination at 6 a.m. and at 6 p.m., no rhythmic in feeding or defaecation could be found.

3.2. Respiration:

Mean oxygen consumption rates for all three species are summarized in Tab. 2. *O. pilosus* indicates the highest respiratory rate (61.2 µl O_2 gfw^{-1} hr^{-1}), *O. sabulosus* the lowest (42.2). All values differ significantly at the $P\ 0.01 \leq$ level. Fig. 3 shows oxygen consumption for all three species during measurements from 8.30 a.m. to 8.30 p.m. There is a decrease in oxygen uptake over time, which was probably due to declining activity. The higher oxygen consumption of *O. pilosus* was not due to higher activity, because from the second measurement on (4 hours after starting of the experiment) all animals showed only accidental movements.

Table 2: Oxygen consumption in three species of millipedes at 15° C. Mean values ($\bar{x} \pm SE$) calculated from (n) measurements (8.30 a.m. to 8.30 p.m. each) are given.

	mean oxygen consumption *) [µl O_2 gfw^{-1} hr^{-1}] $\bar{x} \pm SE$		number of measurements n
O. pilosus	61,2 ± 2,80	a	76
A. fulviceps	50,8 ± 2,01	b	80
O. sabulosus	42,2 ± 1,56	c	90

*) Values followed by different letters within a column are significantly different at $P \leq 0.01$ (t-test).

3.3. Assimilation:

Assimilation efficiencies from this study and from literature are cited in Tab. 3. For all three investigated species the assimilation rates ($x \pm SE$) are quite similar (*A. fulviceps*: 33.7 ± 5.68 %, $n = 5$; *O. sabulosus*: 36.6 ± 0.9, $n = 4$; *O. pilosus*: 30 %), although the amount of food in the gut is different. In general different experimental conditions, especially the quality of food, influence the assimilation considerably. This can be seen best in the case of *G. marginata*, where values ranging from 5 % to 50 % have been reported. An assimilation efficiency of about 30 % seems to be normal for millipedes. It must be drawn into consideration that the cellulose content of leaf litter is about 50 % (dry weight), thus an assimilation efficiency higher than 50 % would indicate cellulose digestion (PETERSON & LUXTON 1982).

Table 3: Assimilation efficiencies of millipedes according to the present study and results from other authors.

Species	assimilation efficiency [%]	author
Allaiulus fulviceps (LATZEL)	11 - 43	present study
Amblyiulus continentalis ATTEMS	31 - 43	STRIGANOVA (1971)
Chromatoiulus projectus VERHOEFF	5 - 21	GERE (1956)
Cylindroiulus punctatus (LEACH)	14	KAYED (1978)
Enantiulus nanus (RIBAUT)	36 - 67	BOLLER (1986)
Glomeris hexasticha BRANDT	4 - 18	GERE (1956)
G. marginata (VILLERS)	36	ANDERSON & BIGNELL (1982)
G. marginata (VILLERS)	6 - 22	BOCOCK (1963)
G. marginata (VILLERS)	50	FRANZ & LEITENBERGER (1948)
G. marginata (VILLERS)	14	KAYED (1978)
G. marginata (VILLERS)	5	VAN DER DRIFT (1951)
Julus scandinavius LATZEL	30	KAYED (1978)
Leptoiulus noricus VERHOEFF	20 - 40	BOLLER (1986)
L. saltuvagus (VERHOEFF)	22 - 49	BOLLER (1986)
Narceus americanus (BEAUVOIS)	15	O'NEILL (1968)
N. annularis (RAFINESQUE)	10 - 18	SHAW (1970)
Ommatoiulus sabulosus (LINNE)	33 - 38	present study
Ophyiulus pilosus (NEWPORT)	30	-"-
O. pilosus (NEWPORT)	23 - 27	KAYED (1978)
Pachyiulus foetidissimus (MURALEWICZ)	37 - 39	STRIGANOVA (1971)

Table 4: Synopsis of ecological parameters of *Ophyiulus pilosus*, *Ommatoiulus sabulosus* and *Allaiulus fulviceps*. All data from this study refer to adult females and 15° C.

	O. pilosus	*O. sabulosus*	*A. fulviceps*	data from:
Reproduction	semelparous	iteroparous	-	BLOWER (1985)
Life span	2 years	3-4 years	-	-"-
Defense strategy	run	coil	coil	this study
Mean live weight [mg]	129	190±14,83 n=4	201±15,47 n=5	-"-
Oxygen consumption [μl O_2 gfw^{-1} hr^{-1}]	61,2±2,80 n=76	42,2±1,56 n=90	50,8±2,01 n=80	-"-
Consumption [oak litter mg dw day^{-1} $animal^{-1}$]	13,3	20,1±1,87 n=4	14,6±1,45 n=5	-"-
Faeces production [mg dw day^{-1} $animal^{-1}$]	9,3	12,7±1,01 n=4	10,0±1,85 n=5	-"-
Assimilation efficiency %	30	36,6±0,9 n=4	33,7±5,68 n=5	-"-

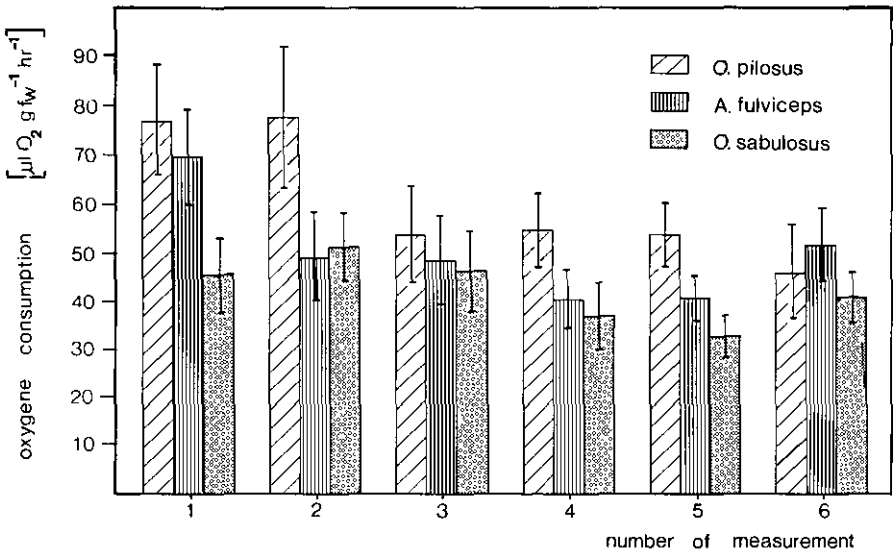

Fig. 3: Mean oxygen consumption (± SD) of three millipede species (adult females) at 15° C. Measurements from 8.30 a.m. to 8.30 p.m., reading every two hours.

4. Discussion:

Table 4 summarizes data and observations concerning life cycles, consumption rates, faeces production and assimilation efficiencies of the three investigated species. *O. sabulosus*, which is described as a wandering species extremely vagile moving over a wide range vertically and horizontally (BLOWER 1985), shows the lowest values for oxygen consumption in this study. This could be due to the fact, that the respiration experiments were carried out beyond the seasonal activity period. Moreover *O. sabulosus* was not caught in pitfall traps in the same wood (KURNIK & THALER 1985), whereas it is commonly found in warmer inneralpine habitats. The high respiratory rates for O. pilosus correspond to its behavior in the field. This species behaves according to its common name "snake millipede" and tries to flee when touched, the other two species show the typical millipede reaction and coil. Due to its restricted, inneralpine occurrence very little is still known about *A. fulviceps.*

5. Acknowledgements:

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