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Coprofagia em detritívoros: direcionamento metodológico para estudos de taxas alimentares em isópodos terrestres (Crustacea, Isopoda, Oniscidea)

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RESUMO

Os isópodos terrestres consomem fezes tanto em condições de laboratório quanto na natureza. Esse comportamento ainda não é bem compreendido e pode estar relacionado com o consumo de cobre, de enzimas recalcitrantes ou também com o consumo de microrganismos. A coprofagia é evitada em experimentos sobre taxas alimentares mesmo que não se saiba quais são os seus efeitos. Por isso, o objetivo deste trabalho foi verificar os efeitos da coprofagia na taxa de consumo, de crescimento e na digestibilidade dos isópodos a fim de sugerir o melhor desenho experimental para futuros estudos sobre taxas alimentares. Para isso, utilizamos três espécies de isópodos representando grupos eco-morfológicos diferentes, *Atlantoscia floridana* (corredor), *Balloniscus glaber* (aderente) e *Armadillidium vulgare* (rolador), e duas espécies de folhas, *Machaerium stipitatum* e *Lithraea brasiliensis* com alto e baixo teor de nitrogênio, respectivamente. Os experimentos tiveram duração de sete dias. Utilizamos tratamentos com acesso às fezes, retirada manual das fezes e rede como uma barreira para que os isópodos não acessassem as fezes. Não encontramos diferença significativa para nenhuma espécie de isópodo com nenhuma folha para a taxa de consumo e para a digestibilidade. A taxa de crescimento (biomassa) apresentou maior variação na espécie *A. floridana*, com diferença significativa para o tratamento rede com a folha *M. stipitatum*. Essa diferença pode estar relacionada ao curto período de tempo dos experimentos e também à suscetibilidade desta espécie às variações ambientais. A sobrevivência acumulada não apresentou diferença significativa entre os tratamentos. Com esses resultados, sugerimos o tratamento acesso para calcular as taxas de consumo e crescimento por este não necessitar evitar a coprofagia. Para cálculos de digestibilidade, sugerimos o tratamento retirada porque este apresenta valores mais acurados já que evita a coprofagia e a decomposição microbiana. O tratamento rede não é aconselhável para animais pequenos, já que os animais podem ultrapassar a rede e ter acesso às fezes e também afastar-se do alimento. Entretanto, esse tratamento pode ser uma boa alternativa para evitar a interferência do gesso no peso das fezes dos animais maiores como *B. glaber* e *A. vulgare* que são mais resistentes à flutuação da umidade da unidade.

Palavras-chave: taxa de consumo; taxa de crescimento; digestibilidade; tatuzinhos.

Artigo a ser submetido à revista Nauplius

Coprophagy in detritivores: methodological design for feeding rates studies in terrestrial isopods (Crustacea, Isopoda, Oniscidea)

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RUNNING HEAD: Effects of coprophagy on feeding rates

ABSTRACT

Isopods consume feces in laboratory conditions although it is not known if coprophagy affects feeding rates. Here, we investigate the effects of coprophagy on consumption and growth (biomass) rates and on assimilation efficiency in order to suggest the best methodological design. We used three species of isopods representing different eco-morphological groups and leaves with low and high nitrogen content. We tested three treatments: (1) free access to feces; (2) periodically removal of feces and (3) net acting as a barrier to the pellets. We did not find any significant difference in any isopod or leaf species for consumption rate. Assimilation efficiency did not differ significantly for any species either. Growth rate was significantly different for the species *Atlantoscia floridana* with the leaf *Machaerium stipitatum* and it may be due to the short duration of experiments and the isopod's susceptibility to environmental changes. With our results, we suggest treatment

access in order to study consumption and growth rates because it does not require any special material nor extra time. For assimilation, we suggest treatment removal because it provides more accurate values. More delicate species such as *A. floridana* require larger sample number and/or longer experiment duration in order to analyze the data.

Key words: assimilation efficiency; consumption rate; growth rate; woodlice.

INTRODUCTION

Terrestrial isopods consume feces in laboratory conditions as well as in the wild (Szlávecz and Pobozny, 1995). However, there are discussions related to the nutritional significance of this behavior to the animals (Zimmer, 2002). Copper and calcium are two important elements for isopods as terrestrial animals have difficulties in assimilating sufficient amounts of these elements. Copper is an essential part of hemocyanin (Weiser, 1968) and calcium is a major part of the composition of the cuticle. Calcium assimilation does not depend on coprophagy (Coughtrey *et al.*, 1980) but this behavior may be related to the need to fulfill the copper demand since isopods are unable to extract it from plant tissue because of their low copper content (Weiser, 1966; Weiser, 1968; Zimmer, 2002). However, Hassall and Rushton (1982) suggest that copper balance is not the reason coprophagy has evolved. It may be instead related to other nutrients that are not sufficiently ingested by litter consumption (Wieser, 1968) or as a source of microorganisms' enzymes that aid in the breakdown of recalcitrant compounds and also as the consumption of microorganisms as food source (Hassall and Rushton, 1982; Carefoot, 1984). These explanations are not mutually exclusive and we cannot explain the coprophagous behavior yet.

In order to deal with this behavior in lab experiments, the feces are removed periodically from the units in laboratory experiments regarding feeding rates of terrestrial isopods in order to avoid coprophagy interference. The consumption of feces is avoided by the use of nets that serve as a barrier so the animal cannot access the feces (Loureiro *et al.* 2006; Wood *et al.*, 2012), or by manual removal every one or two days using tweezers (Wood and Zimmer, 2014). Nonetheless, both methods demand time and/or material.

The effects of coprophagy vary with the physiology of the isopod species, with the leaves offered as food and with the developmental stage of the individuals (Zimmer, 2002); however, Szlavecz and Maiorana (1998) and Kautz *et al.* (2002) could not find clear evidence of nutritive benefits of the coprophagous behavior to *Porcellio scaber* Latreille, 1804 and, so far, it has not been established if coprophagy affects the feeding rates of terrestrial isopods. We wonder if the effort to spend time removing the pellets manually or using nets to avoid coprophagy is worth and/or necessary. Thus, the aim of this article is to investigate if coprophagy influences feeding rates of terrestrial isopods using three different species. We investigated the effects in the growth and consumption rates and assimilation efficiency of isopods using high and low quality leaves (higher and lower quantity of nitrogen, respectively) (Zimmer, 2008), in order to suggest the best methodological design to researches about feeding rates. We hypothesize that we would find: (1) no significant difference for consumption, but higher values in treatments where coprophagy is avoided, (2) no significant difference for assimilation, but higher rates in access, medium in net and lower in removal, and (3) no significant difference for growth.

MATERIAL AND METHODS

Isopods and Leaves

For the experiments, we used three terrestrial isopod species: (1) *Atlantoscia floridana* (Van Name, 1940) (Philosciidae) representing the ecomorphological group of runners, (2) *Balloniscus glaber* Araujo and Zardo, 1995 (Balloniscidae) representing the clinger group and

(3) *Armadillidium vulgare* (Latreille, 1804) (Armadillidiidae) as a roller representative. We used species representing these ecomorphological groups (*sensu* Schmalfuss, 1984) because the runners, clingers and rollers cluster most part of the biodiversity of isopods. Moreover, these ecomorphological groups have different morphologies and life strategies that are correlated with their environment and behavior. The species will be further regarded by the genus name to avoid confusion. The animals were collected at Morro Santana, Porto Alegre, Rio Grande do Sul (04'11.3"S 51°07'19.2"W). We only used intermolt animals and ovigerous females were excluded from the study since reproduction and molt are processes that are known to interfere in the consumption of food. The mean weight was 0.0052 g for *Atlantoscia*, 0.0243 g for *Balloniscus* and 0.0735 g for *Armadillidium*.

Leaf litter was also collected from the same locations of the animals and leaves of the two abundant species *Lithraea brasiliensis* Marchand (Anacardiaceae) (lower nitrogen content) and *Machaerium stipitatum* (DC.) Vogel (Fabaceae) (higher nitrogen content) (c.f. Quadros *et al.*, 2014) were sorted out, cut and kept in refrigeration (-5° C) until the start of the experiment. Before the experiments, leaves were dried at 40º C for 48 h before and after the experiments to weight the material. These leaves were selected based their abundance and importance to isopods in the collection location (Quadros *et al.*, 2014). At the end of the experiment, the feces were dried at 60º C for 48 h.

Treatments

We used three treatments for the experiments: 1) free access to the feces; 2) daily manual removal of the feces, kept refrigerated until the end of experiments and 3) net to avoid the access to the feces, kept in the experimental unit (Fig. 1). Before and after the experiments, the animals were fed with carrots so that the feces had a different coloration (Fig. 1D), so only the plant material consumed during the experiments were analyzed (Wood *et al.*, 2012). The units contained one previously weighed animal and one food source type.

The experiment lasted 7 days and the units were monitored every one or two days. At the end of the experiments, the feces and the food left were oven-dried at 60º C and 40º C, respectively, for 48 h. We maintained a control unit with only the food source for the same period of time in order to discount the leaf mass lost due to autogenic changes.

Data Analysis

During the experiments, the animals were weighed every one or two day and the initial and final weights were estimated through linear regression equation for each animal to discount the mass change due to water fluctuation. Assimilation was not analyzed statistically for *Atlantoscia* due to interference of plaster, which altered the weight of the feces and we considered assimilation of 100% when there was no feces in the units. Results are presented as indexes but analyzed by Covariance Analysis (ANCOVA) as proposed by Raubenheimer and Simpson, 1992. All statistical analyses as well as normality tests were conducted using SPSS software 18. Treatments were compared for each animal species and food source.

Consumption rate, assimilation efficiency and growth rate were calculated for each experimental unit as proposed by Waldbauer (1968). Consumption rate is presented as mg of consumed food by g of animal per day and it was calculated as follows: CR = $[(m_{if} - m_{af}) - m_c]/ m_{isop}$*day, where: CR = consumption rate (mg food/g isopod^{-1}*day^{-1}); m_{if} = initial food mass (mg DW); mf_{ff} = final food mass (mg DW); m_c = percentage of lost mass in control leaves; m_{isop} = mean isopod mass (g FW); DW = dry weight; FW = fresh weight. Assimilation was expressed as percentage of consumed food that was not egested, calculated as: A: $(m_{cf} – m_p)$ *100/ m_{cf}, where: A = assimilation (%); m_{cf} = mass of consumed food (mg DW); m_p= pellet feces mass (mg DW). Growth rate was expressed in g of animal per day, calculated as: GR = $(m_{isopf}-m_{isopi})/ t * m_{isop}$, where: GR = growth rate; m_{isopf} = final isopod mass (g FW); m_{isopi} = initial isopod mass (g FW); t = time (days); m_{isop} = mean isopod mass (g FW).

Consumption was analyzed as consumed food using experiment duration and initial isopod mass as covariates. Assimilation was analyzed as pellets weight with experiment duration, consumed food and initial isopod mass as covariates. Growth was analyzed as final isopod mass and covariates were experiment duration, initial isopod mass and consumed food. Treatments were compared for each animal species and food source.

Pearson correlation was used to determine association between cumulative survivorship and time for each animal species. Analysis of covariance was used to compare regressions among treatments within isopod species and among species. As there was no difference, we performed the analyses using units of both leaves in order to increase sample number.

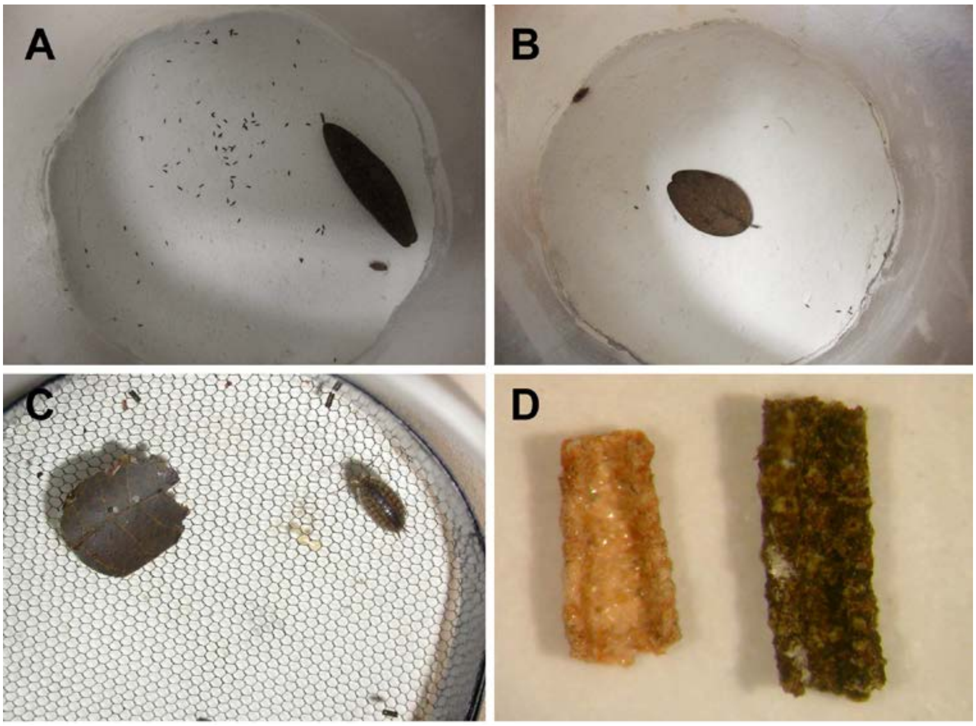

Figure 1. Experimental units for feeding rates tests with terrestrial isopods and fecal pellets from different food sources. A) Treatment access; coprophagy is allowed. B) Treatment removal; coprophagy and bacterial activity on feces are avoided. C) Treatment net; coprophagy is avoided and bacterial activity on feces allowed. D) Fecal pellet from carrot (left) and decomposing leaf (right) consumption.

RESULTS

We did not find significant difference in the mean size of the animals for *Balloniscus* and *Armadillidium* with any of the leaves and for *Atlantoscia* with *M. stipitatum*. The experiment with *Atlantoscia* and *L. brasiliensis* presented a significant difference in the mean size in treatment net. Animals were larger in this treatment because small animals would go through the net.

Consumption rates (Fig. 2) did not differ significantly for any of the animal species and for any of the leaves (Table 1). However, the consumption of *L. brasiliensis* was higher in all of the treatments for all isopod species.

Assimilation ranged from 11.3 to 64.4% for *Atlantoscia*, 24.9 to 51.6% for *Balloniscus* and 16.7 to 39.6% for *Armadillidium* (Fig. 3). Assimilation efficiency was not analyzed for *Atlantoscia* with the leaf *M. stipitatum* due to the low sample numbers available. The weight of the feces was altered due to consumption of plaster and also because plaster got stuck on the fecal pellets. No significant difference was detected for *Atlantoscia* with *L. brasiliensis*. We did not find significant difference for assimilation in *Balloniscus* and *Armadillidium* for any of the plant species (Table 1).

Growth rates were very close to zero for all isopod species (Fig 4). *Atlantoscia* presented the highest variations (Fig. 4A); however the only difference was on the species *Atlantoscia* with the leaf *M. stipitatum* between access and net treatments (Table 1). We performed a paired t-test to verify if there was a significant difference between initial and final weight, *i.e.*, if the growth rate was significantly different from zero. There was a significant difference for the treatment net ($t = -7.08$; $df = 11$; $p = 0.002$) but no difference for treatments access ($t = 0.67$; $df = 10$; $p = 0.519$) or removal ($t = -2.18$; $df = 10$; $p = 0.054$). We did not find significant difference on growth among treatments for *Balloniscus* nor *Armadillidium*, and values were very low and close to zero (Fig. 4B).

We found association between cumulative survivorship and time for each treatment of each isopod species (considering both leaves together) (Table 2). Survivorship was not significantly different among treatments within the same isopod species (*Atlantoscia*: $F_{2,32}$ = 2.28; p = 0.118; *Balloniscus*: $F_{2,32}$ = 0.22; p = 0.805; *Armadillidium*: $F_{2,32}$ = 1.36; p = 0.270). However, when considering all treatments together, survivorship was significantly different among isopod species ($F_{2,104}$ = 3.53; p = 0.033), with difference between *Balloniscus* (highest) and *Atlantoscia* (lowest) (p = 0.011).

Table 1. Analysis of covariance for feeding rates of *Atlantoscia floridana*, *Balloniscus glaber* and *Armadillidium vulgare* fed on *Machaerium stipitatum* and *Lithraea brasiliensis*.

Isopod species	Food source	Consumption rate	Assimilation efficiency	Growth rate
Atlantoscia floridana	*M. stipitatum*	$F_{2,32}$ = 0.499; p = 0.612	- -	$F_{2,32}$ = 6.736; **p=0.004**
	L. brasiliensis	$F_{2,31}$ = 1.304; p = 0.286	$F_{2,16}$ = 0.034; p = 0.966	$F_{2,31}$ = 1.355; p = 0.273
Balloniscus glaber	*M. stipitatum*	$F_{2,38}$ = 0.089; p = 0.915	$F_{2,30}$ = 1.350; p = 0.275	$F_{2,38}$ = 0.833; p = 0.442
	L. brasiliensis	$F_{2,32}$ = 1.343; p = 0.275	$F_{2,23}$ = 2.607; p = 0.095	$F_{2,32}$ = 0.705; p = 0.502
Armadillidium vulgare	*M. stipitatum*	$F_{2,29}$ = 2.907; p = 0.071	$F_{2,28}$ = 0.170; p = 0.844	$F_{2,28}$ = 1.550; p = 0.230
	L. brasiliensis	$F_{2,34}$ = 1.594; p = 0.218	$F_{2,33}$ = 0.583; p = 0.564	$F_{2,33}$ = 1.813; p = 0.179

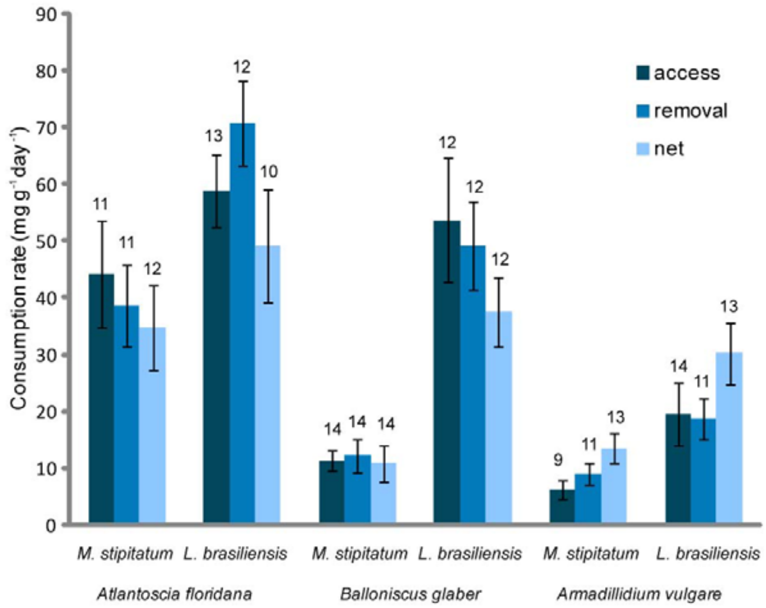

Figure 2. Consumption rates of three different isopod species with two different food sources in three different treatments (access, removal and net). The values are mean ± SE and the numbers on top indicate the sample number for each index.

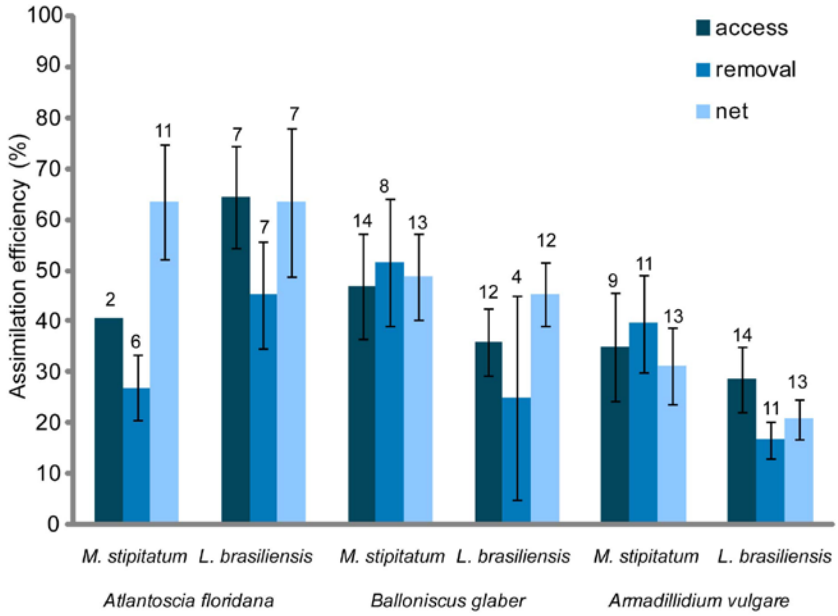

Figure 3. Assimilation efficiency of isopods fed on two different leaves in treatments access, removal and net. The values are mean ± SE and the numbers on top indicate the sample number for each index.

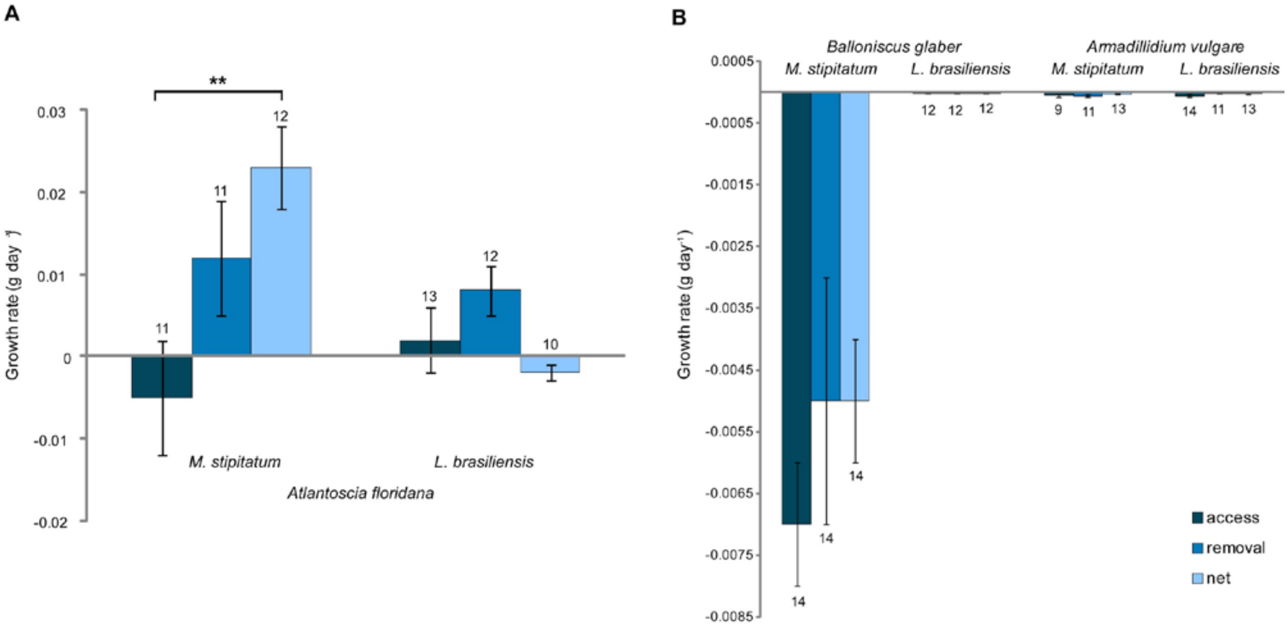

Figure 4. Growth rate of isopods in three different treatments. A. Growth rate of *Atlantoscia floridana*. B. Growth rate of *Balloniscus glaber* and *Armadillidium vulgare*. The values are mean ± SE and the numbers on top indicate the sample number for each index.

Table 2. Pearson correlation of cumulative survivorship and time of three isopod species in feeding experiments with treatments access, removal and net.

Isopod species	Treatment	F	p	R
Atlantoscia floridana	Access	$F_{1,11} = 32.30$	< 0.001	0.87
	Removal	$F_{1,11} = 14.54$	0.003	0.77
	Net	$F_{1,11} = 57.93$	<0.001	0.92
Balloniscus glaber	Access	$F_{1,11} = 12.71$	0.005	0.75
	Removal	$F_{1,11} = 15.70$	0.003	0.78
	Net	$F_{1,11} = 19.05$	0.001	0.81
Armadillidium vulgare	Access	$F_{1,11} = 6.08$	0.033	0.61
	Removal	$F_{1,11} = 20.53$	0.001	0.82
	Net	$F_{1,11} = 97,53$	<0.001	0.95

DISCUSSION

Our results suggest that coprophagy does not affect consumption rates significantly since no difference was observed in any of the leaves tested for any isopod in this paper. Moreover, the consumption of the lower nitrogen content leaf *L. brasiliensis* was higher for all three isopod species analyzed. This possibly happened because the animal needs to consume more food the meet the nutrient demand in the low quality leaves. This was similar to food preference results found by Quadros *et al.* (2014) that isopods prefer *L. brasiliensis* over *M. stipitatum*. They suggest this difference may be related to terpenes and alkaloids present in *M. stipitatum* that could be offsetting the high nitrogen content.

Assimilation efficiency varied greatly among isopod species, leaf type and also among treatments. One explanation is the low sample number in some treatments due to consumption of plaster which altered the mass of the feces and plaster glued to the fecal pellets. It happened for *Atlantoscia* and *Balloniscus* species and the units where this happened where not included in the analysis. Assimilation did not show statistical difference for *Armadillidium* in any of the leaves tested, suggesting that any of the treatments can be used.

However, in projects where the main question is to verify assimilation efficiency, we suggest treatment **removal**. This treatment shows more accurate values of assimilation because it minimizes both coprophagy and bacterial activity. Even though treatment net also prevents coprophagy, there are two problems with this approach: (1) it does not prevent from bacterial activity and (2) animals may go through the net and get trapped in the bottom of the unit depending on their body size. If the animals are trapped in the bottom, the feces will then be the only available food source, possibly increasing coprophagy while preventing leaf consumption.

Regarding growth rates, our results suggest that any treatment can be used. We found significant difference for *Atlantoscia* with *M. stipitatum* but not for *L. brasiliensis* leaf or any of the other two isopod species. This difference could be related to the short duration of the experiments, which hinders statistical analysis of growth. *Atlantoscia* has a thinner and more delicate cuticle (Wood *et al.*, 2017) and their populations are more susceptible to environmental changes (Quadros and Araujo, 2007) and water fluctuation. Thus, long experiments should be performed in order to elucidate the effects of coprophagy on growth rate.

CONCLUSIONS

Based on our findings, we propose the following:

1) For consumption and growth rate, any treatment can be used. Therefore, we suggest the treatment **access** because this method does not require any special material and/or time.
2) For assimilation efficiency, any treatment is effective. However, treatment **removal** shows more accurate values of assimilation efficiency, being indicated for studies with this purpose.
3) For smaller animals such as *Atlantoscia* (~1 mm of cephalothorax width, *c.f.* Araujo and Bond-Buckup 2004), we suggest avoiding treatment net because they can get stuck in the bottom of the unit if they go through the net. This will prevent the animals to consume the leaf and possibly increase coprophagy. Mesh size could not be smaller because the pellets still must fall to the bottom of the unit.
4) Animals more susceptible to environmental fluctuations such as *Atlantoscia* demand a larger sample number or longer experiment duration.
5) Plaster is important to maintain humidity in the units. Treatment **net** can be an alternative to prevent larger animals to consume plaster, since they are not on the plaster surface.

6) Feeding carrots to the animals prior and after experiments is a good way to sort out fecal pellets from the prior food source and the food source being studied. When isopods consume carrots, the feces have an orange coloration that is easily distinguishable.
7) Linear regression is an appropriate approach to remove the influence of water quantity in the animal weight.
8) Analysis of Covariance (ANCOVA) is the more appropriate form to statistically analyze feeding rates because it is more accurate than Analysis of Variance (ANOVA). For growth rate in *Atlantoscia* with *M. stipitatum*, we found $p = 0.004$, whereas we found one significance degree higher than in ANOVA ($p = 0.015$).

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