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Does *Porcellio scaber* (Isopoda: Oniscidea) gain from coprophagy?

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Abstract

In feeding experiments, leaf litter of different tree species and isopod feces derived from these leaf litter materials were offered to the common woodlouse, *Porcellio scaber*. Consumption indices were used to elucidate the nutritional significance of coprophagy. Consumption rates of *P. scaber* clearly differed between feeding assays with alder (*Alnus glutinosa*) litter and those with isopod feces derived from alder. Differences between feeding assays depended on microbial activity of the food sources when oak (*Quercus robur*) litter or isopod feces derived from oak were offered. Further, microbiota increased the digestibility of oak material, but did not change digestibility of alder litter and reduced digestibility of feces derived from alder. Thus, the significance of litter- or feces-colonizing microbiota decreased with increasing nutritive value of the leaf litter. Inoculated feces derived from oak provided better growth than any other oak-derived food. In contrast, isopods grew better on alder litter than on alder-derived feces. In sum, we found little evidence to support the notion that *P. scaber* gains from coprophagy. We reject the hypothesis that coprophagy meets a need for nutrients that, due to digestive incapabilities, cannot be satisfied by feeding on leaf litter alone. The hypothesis that microbial colonizers render feces attractive as a source of microbial enzymes or nutrients is only partly corroborated. *P. scaber* gains from coprophagy through microbial activity or biomass only if leaf litter quality is low.

Keywords: Coprophagy; Saprophagy; Microbiota; Woodlice; Nutrition

1. Introduction

Coprophagy has frequently been described in terrestrial isopods (Isopoda: Oniscidea; Wieser, 1968; Dallinger and Wieser, 1977; Hassall and Rushton, 1982, 1985; Gunnarsson and Tunlid, 1986; Hassall et al., 1987; Ullrich et al., 1991; Szlávecz and Pobozsny, 1995; Szlávecz and Maiorana, 1998). Coprophagy may be an essential aspect of nutritional biology in isopods due to (1) a need for copper (and other nutrients) that cannot be satisfied by feeding on leaf litter alone, due to the incapability of extracting the required nutrient from plant tissue (Wieser, 1968; Dallinger and Wieser, 1977; Debry and Lebrun, 1979) or of absorbing nutrients released in the posterior hindgut (Dallinger and Wieser, 1977; Wieser, 1978, 1984; Zimmer, 1999). (2) On the other hand, microbial colonizers may render feces attractive as a source of microbial enzymes for the breakdown of recalcitrant compounds or of easily digestible or essential nutrients (Hassall and Rushton, 1982; Carefoot, 1984a,b; Ullrich et al., 1991).

According to Hopkin and Martin (1984), coprophagy by isopods occurs rarely in the field, due to difficulties in finding feces beneath the leaf litter layer, and Hassall and Rushton (1982) estimated that coprophagy accounted for less than 8% of total consumption under natural conditions. However, given that microbially inoculated feces are 'hot spots' of microbial activity (Ullrich et al., 1991), olfactory orientation along gradients of air-borne microbial metabolites (Zimmer et al., 1996) may eventually lead the foraging isopod to such hot spots. Thus, it is still unclear whether or not coprophagy is significant in the field (Carefoot, 1993). Further, although coprophagy may occur in the laboratory, its 'exact role in nutrition is still debated' (Carefoot, 1993; Zimmer and Topp, 1998). While Wieser (1966) reported that populations of *Porcellio scaber* went extinct when access to feces was denied in the laboratory, this observation was not confirmed by other investigators (White, 1968; Coughtrey et al., 1980; Hassall and Rushton, 1982, 1985; Hopkin and Martin, 1984). Recently, Szlávecz and Maiorana (1998) failed to confirm marked nutritive benefits from coprophagy to *P. scaber*, in the laboratory.

The present study aims to determine the nutritive

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significance of coprophagy in the common woodlouse, *P. scaber*. We focus on the above-mentioned hypotheses and derived predictions. (1) If the isopods' need for nutrients cannot be satisfied by feeding on leaf litter alone, due to some digestive incapabilities, isopods will benefit from coprophagy, no matter whether or not feces are microbially colonized. Further, the nutritional value of feces will be expected to be always higher than that of the leaf litter from which the feces are derived, but the nutritive gain from coprophagy will depend on the digestibility of the leaf litter. (2) If feces serve as a source of microbial enzymes or essential nutrients isopods will benefit from coprophagy exclusively in case of dense microbial colonization, but not if feeding on feces with low microbial biomass or activity. (3) If there is no nutritive gain from coprophagy, isopods will not perform better (or even less well) when feeding on feces than when feeding on leaf litter. We test these hypotheses on the adaptive significance of coprophagous behavior comparing the above predictions with the results of feeding experiments with *P. scaber* feeding on leaf litter or feces (representing the 'gut passage' of food that serves as factor in ANOVA) after experimental reduction of, or inoculation with, microbiota (factor 'microbiota'). We also use leaf litter of different tree species to elucidate the significance of the initial 'material' on isopod performance when feeding on leaf litter or feces derived from these different leaf litter materials.

2. Materials and methods

2.1. Isopods

Isopods (*P. scaber* Latreille 1804) were collected in the vicinity of Cologne, Germany. Prior to the experiments, isopods were collectively maintained at 15 °C, 16 h L:8 h D, in translucent plastic boxes, the bottoms of which were covered with plaster of Paris, and fed with mixed deciduous leaf litter.

During the experiments, isopods ($N = 24$/treatment) were kept in small Petri dishes, each containing only one isopod, the food source and a wetted piece of terra cotta for maintaining high humidity. Petri dishes were stored in plastic boxes, the bottoms of which were covered with wetted filter paper. Dishes were stored at 15 °C, 16 h L:8 h D.

Only pre-adult individuals with a live mass of 10–20 mg were used for feeding trials to obtain high consumption and growth rates (Wieser, 1965; Striganova and Kondeva, 1980). The experiments lasted 14 d which made the gravimetrical detection of growth possible, but reduced the probability of molting events that would have affected consumption and mass gain. Those isopods that underwent molt during the experiment were omitted from analyses. To compensate for oscillations in live mass, due to changes in body water content, isopods were weighed daily, and changes in live mass during the experiment were obtained through linear regression analyses of live mass vs. time.

From these values and the data for mass loss (dry mass) of the food, and the dry mass of daily collected feces, we calculated consumption indices of Waldbauer (1968): relative consumption rate (RCR = (mg food ingested)/(day × g animal)), approximate digestibility (AD, i.e. % mass loss of ingested food due to digestion and absorption = 100 × (mg food ingested − mg food egested)/(mg ingested food)), and relative growth rate (RGR = (mg dry mass change)/(day × g animal)). Each food source was offered in amounts that were likely to be reduced by about 80% during feeding experiments (Schmidt and Reese, 1986). Besides providing optimal accuracy of consumption data (Schmidt and Reese, 1986), these amounts prevented physiological adaptation to food shortage (Hubbel et al., 1965). Initial dry mass of food sources was estimated through wet mass:dry mass ratios ($N = 15$).

2.2. Food sources

Leaf litter of oak (*Quercus robur* L.) and alder (*Alnus glutinosa* (L.) Gaertn.) were served as food materials in feeding experiments. For pre-experimental storage, microbial activity of freshly fallen leaf litter was reduced by air-drying (Zimmer and Topp, 1997). Air-dried leaf litter was either re-wetted or microbially inoculated before being offered as food with low or high microbial activity, respectively. For re-wetting, air-dried leaf litter was stored (21 d at 20 °C) between autoclaved wet sheets of filter paper that were replaced every day. For microbial inoculation, air-dried leaf litter was packed in gauze bags (100 μm mesh size) and placed in a pool of freshly collected leaf litter to be inoculated by native leaf litter-colonizing microbiota for 21 d at 20 °C (Zimmer and Topp, 1997). In contrast to microbial inoculation through aqueous suspensions of densely colonized leaf litter, this technique not only alters microbial activity and/or biomass, but also mimics microbial conditioning of freshly fallen leaf litter in the field by changing physicochemical characteristics of the substrate.

Feces for feeding experiments were derived from isopods, collectively maintained in translucent plastic boxes (15 °C, 16 h L:8 h D), feeding exclusively on oak or alder litter. Feces were collected daily and air-dried prior to storage. Feces were either re-wetted before being offered as food with low microbial activity, or were microbially inoculated in the same pool as the leaf litter (see above).

Air-drying does not sterilize leaf litter, but may result in short-term increase of microbial activity (Scheu and Parkinson, 1994; Pulleman and Tietema, 1999) and only a slight reduction in microbial biomass. However, microbial inoculation of air-dried leaf litter in a pool of freshly collected leaf litter (Zimmer and Topp, 1997; this study) does not only promote microbe-induced changes in the leaf litter (Table 1), but also increases microbial activity and density, as compared

Table 1
Characteristics of experimental food sources (based on dry mass). Data are mean ± SD ($N = 10$); superscript letters (f–i) indicate differences between materials and gut passages, and due to microbial inoculation (Bonferroni-corrected t tests, $\alpha = 0.05$)

	Alnus glutinosa				*Quercus robur*			
Material stage	Litter		Feces		Litter		Feces	
Microbial inoculation	NO	YES	NO	YES	NO	YES	NO	YES
PH level	5.4 ± 0.2^{f}	5.6 ± 0.3^{f}	5.6 ± 0.2^{f}	5.7 ± 0.4^{f}	6.2 ± 0.3^{g}	5.1 ± 0.3^{h}	5.8 ± 0.3^{f}	5.6 ± 0.2^{f}
Microbial density[a] (10^{10} cells g^{-1})	0.9 ± 0.2^{f}	4.2 ± 0.3^{g}	1.9 ± 0.4^{h}	3.8 ± 0.4^{g}	0.4 ± 0.1^{f}	3.7 ± 0.2^{g}	1.2 ± 0.3^{fh}	4.0 ± 0.5^{g}
Cellulolytic activity[b] (μg glucose $(g\ h)^{-1}$)	9 ± 3^{f}	60 ± 5^{g}	18 ± 3^{h}	49 ± 4^{g}	3 ± 1^{i}	35 ± 4^{j}	3 ± 1^{h}	11 ± 2^{f}
Water content[c] (%)	79 ± 3^{f}	48 ± 2^{g}	72 ± 3^{f}	66 ± 2^{h}	74 ± 4^{fi}	50 ± 3^{g}	76 ± 2^{f}	70 ± 1^{fi}
Phenolics[d] (mg g^{-1})	14 ± 3^{f}	5 ± 1^{g}	15 ± 3^{f}	4 ± 1^{g}	18 ± 3^{f}	4 ± 1^{g}	5 ± 1^{h}	3 ± 1^{i}
C:N ratio[e]	25 ± 1^{f}	16 ± 2^{g}	14 ± 3^{g}	13 ± 3^{g}	32 ± 3^{h}	29 ± 3^{fh}	22 ± 2^{f}	18 ± 2^{fg}

[a] DAPI-staining; Hobbie et al. (1977).
[b] As described in Skambracks and Zimmer (1999).
[c] Gravimetrically.
[d] As described in Zimmer (1997).
[e] N: Kjeldahl method; C: total organic carbon analyzer.

to the air-dried and re-wetted material (Zimmer and Topp, 1997; this study: Table 1). Therefore, we consider air-dried and re-wetted food material to have a lower microbial activity and biomass than material that has been subsequently inoculated with leaf litter-colonizing microbiota.

Food sources were characterized in terms of pH value (measured in supernatant 3 M KCl after homogenization), microbial density (Hobbie et al., 1977) and cellulase activity (Skambracks and Zimmer, 1999), water content (gravimetrically), phenol content (Folin-Ciocalteu assay, as described in Zimmer (1997)), and the C:N ratio (N: Kjeldahl method; C: total organic carbon analyzer, Ströhlein, Kaarst, Germany). Differences between the eight food sources of our feeding experiments are indicated in Table 1. In ANOVA analyses, we considered three factors of food sources, namely the food material (alder vs. oak), the gut passage of the food (litter vs. feces), and microbiota (re-wetted food with low microbial activity and density vs. inoculated food with high microbial activity and density).

3. Results

3.1. Food sources

As indicated in Table 1, characteristics of the food sources depended on both the leaf litter material (alder vs. oak) and the gut passage of the food (litter vs. feces), as well as on microbial conditioning (air-dried and re-wetted vs. inoculated). Leaf litter of alder with low microbial activity exhibited lower pH values than oak litter, but the opposite was true for inoculated leaf litter. Similarly, the water content of leaf litter differed between the air-dried and re-wetted varieties (i.e. alder vs. oak), but not after microbial conditioning. The C:N ratio was lower in alder litter than in oak litter, with a stronger decrease of this value through microbial inoculation in alder litter than in oak litter.

Feces derived from both leaf litter materials did not differ with respect to pH, no matter whether air-dried and re-wetted or inoculated feces were compared. Except for air-dried and re-wetted feces derived from alder litter, feces contained more water and less phenolics than the corresponding leaf litter variety. Further, the C:N ratio of alder material decreased during the gut passage. Material derived from both alder and oak exhibited lower C:N ratios after microbial conditioning than the air-dried and re-wetted material.

Besides changing physicochemical characteristics of the food material, inoculation by native leaf litter-colonizing microbiota resulted in a significant increase in cellulolytic activity, serving as a measure of microbial activity, and in microbial density. These increases were about four- to sixfold for alder litter and even tenfold for oak litter. Microbial activity and density increased by about 4 on feces. When comparing isopod feeding and performance on different food sources, changes in both physicochemical and microbial characteristics of the food sources must be taken into account.

3.2. Isopod performance

Differences in consumption rates of *P. scaber* (RCR: Fig. 1) depended on all three tested factors (ANOVA: Table 2). Of these, the leaf litter species (material) contributed most to the explanation of variance; except for inoculated leaf litter, alder material was consumed at significantly higher rates than oak material. The gut passage influenced consumption in that RCR was lower on inoculated feces than on inoculated leaf litter, but leaf litter and feces with low microbial biomass and activity were consumed at similar rates. The effect of microbial conditioning (microbiota) was manifested in higher consumption rates of inoculated oak material, but microbiota had no effect on consumption of alder material. From these

Table 2
Analyses of variance (ANOVA), explaining the variance in consumption (RCR), digestibility (AD) and growth (RGR) of *Porcellio scaber* by the factors material, gut passage and microbiota

		Consumption			Digestibility			Growth		
	df	SS	*F*	*P*	SS	*F*	*P*	SS	*F*	*P*
Material	2	6,560,853	518.1	<0.001	65,603	189.6	<0.001	929	53.1	<0.001
Gut passage	1	598,085	94.5	<0.001	2525	14.6	<0.001	163	18.6	<0.001
Microbiota	1	311,205	49.2	<0.001	1080	6.2	0.014	25	2.9	0.090
Material × gut passage	1	20,390	3.2	0.075	1594	9.2	0.003	146	16.7	<0.001
Material × microbiota	1	285,507	45.1	<0.001	9189	53.1	<0.001	14	1.6	0.206
Gut passage × microbiota	1	309,165	48.8	<0.001	5959	34.4	<0.001	4	0.5	0.496
Material × gut passage × microbiota	1	45,279	7.2	0.008	97	0.6	0.456	52	6.0	0.016
Error	134	848,395			23,183			1172		
Total	142	8,978,880			109,230			2507		

results, it is obvious that the effects of each tested factor depended on the status of the other factors (interactions in ANOVA: Table 2); in particular the effects of microbiota appeared to be affected by the material and the gut passage.

Digestibility of food (AD: Fig. 2) mainly depended on the offered material, but was also influenced by the gut passage of the food and by microbiota (ANOVA: Table 2). While air-dried and re-wetted alder material exhibited significantly higher digestibility than the respective oak material, we did not find differences in the digestibility of inoculated oak and alder material. As for consumption, the gut passage resulted in reduced digestibility of both inoculated oak and alder material, but leaf litter and feces with low microbial biomass and activity had the same digestibility. Thus, *P. scaber* did not gain from coprophagy in terms of digestibility of food, but obtained lower digestibility when being coprophagous. Microbiota increased the digestibility of oak material, but only weakly influenced the digestibility of alder material; in fact, inoculated feces derived from alder litter were less digestible than the respective feces with lower microbial

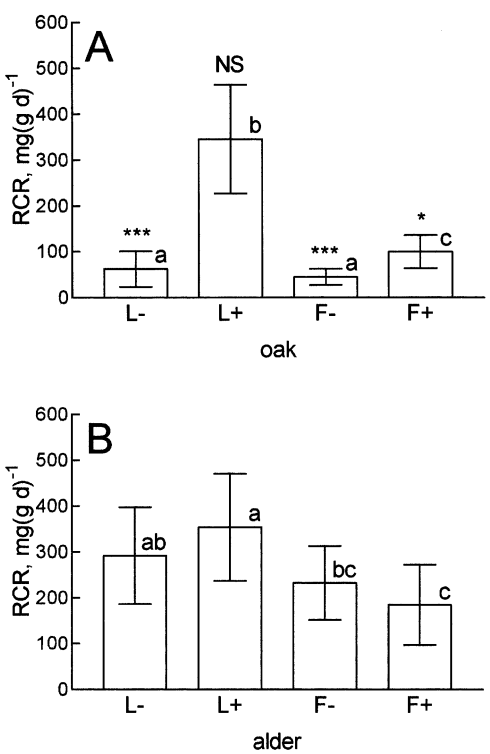

Fig. 1. Consumption (RCR) of different food sources derived from oak (A) or alder (B) by *Porcellio scaber*: (L) leaf litter; (F) feces; (−) re-wetted; (+) microbially inoculated. Bars show mean ± SD ($N = 24$). Different lower case letters indicate significant differences (Bonferroni-corrected *t* tests, $\alpha = 0.05$) between different food sources (L or F; − or +) derived from the same litter species (A, oak; B, alder). Asterisks in (A) indicate differences between corresponding food source treatments (L/F; −/+) of different leaf litter species (A, oak; B, alder; Bonferroni-corrected *t* tests, $\alpha = 0.05$; NS: not significant; *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$).

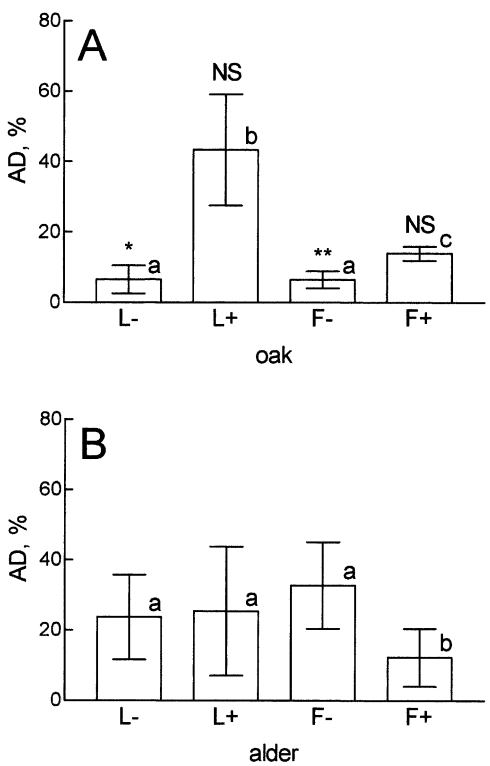

Fig. 2. Digestibility (AD) of different food sources derived from oak (A) or alder (B) for *Porcellio scaber*: (L) leaf litter; (F) feces; (−) re-wetted; (+) microbially inoculated. Data are presented as in Fig. 1.

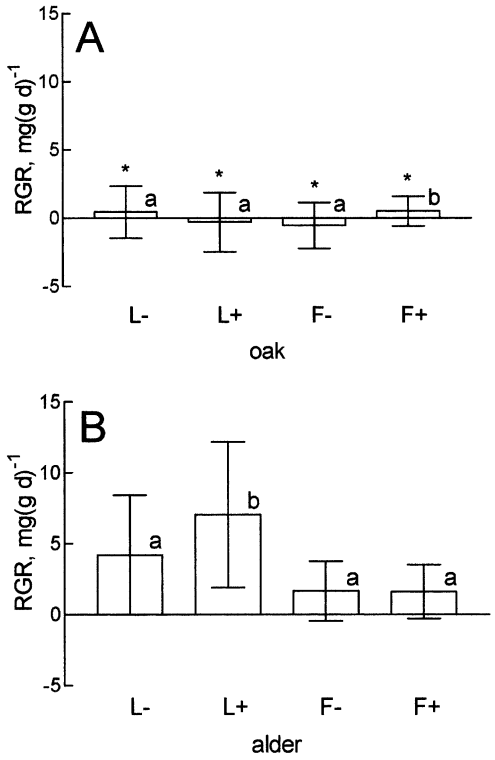

Fig. 3. Growth (RGR) of *Porcellio scaber* feeding upon different food sources derived from oak (A) or alder (B): (L) leaf litter; (F) feces; (−) re-wetted; (+) microbially inoculated. Data are presented as in Fig. 1.

biomass and activity. Similar to our results on consumption, the effect of each tested factor on digestibility depended on the status of each other factor (two-way interactions in ANOVA: Table 2).

Growth rates of *P. scaber* (RGR: Fig. 3) were affected by the food material and the gut passage, but not by microbiota (ANOVA: Table 2). For both leaf litter and feces, *P. scaber* grew significantly better on alder material than on oak material. Growth rates on oak material were highest, albeit still very low, when feeding on inoculated feces. When, however, feeding on alder material, isopods grew best on inoculated leaf litter. In sum, there was no gain from coprophagy in terms of growth when feeding on alder material, but microbial inoculation resulted in enhanced growth of coprophagous isopods on oak material. Thus, the effects of the gut passage and material depended on each other (two-way interaction in ANOVA: Table 2).

4. Discussion

In the present study, we found little evidence to support the hypothesis that *P. scaber* gains from coprophagy. Similar conclusions have been drawn previously for *P. scaber* (Szlávecz and Maiorana, 1998) as well as for the freshwater isopod, *Asellus aquaticus* (Asellota: Asellidae; Marcus et al., 1978). In *P. scaber*, no clear pattern of how food characteristics (material, gut passage, microbiota) affected feeding, digestion or growth were obvious.

In this context, we have to consider changes in physicochemical characteristics due to digestion during gut passage and due to microbial conditioning of leaf litter or feces (Table 1) that were not explicitly taken into account when analyzing the effects of ANOVA factors on isopod performance. These changes, however, reflect microbe-induced decomposition of leaf litter and feces in the field. Thus, we consider them natural side-effects of gut passage and substrate conditioning by microbiota that determine the significance of coprophagy.

The observed effects of the tree species the leaf litter and feces were derived from (material), of the gut passage of the food, and of microbial conditioning of the food material (microbiota) on isopod performance, as deduced from ANOVA, depended on each other. Hence, we cannot provide a simple solution to the problem which factors influence isopod performance. Further, the effects of the tested food parameters differed between the examined performance parameters (RCR, AD, RGR); consumption indices of Waldbauer (1968) did not correlate with each other, in the present study. The relation between consumption (RCR) and growth (RGR) clearly depends upon both the food's digestibility (AD) and its nutritive value that, in turn, need not necessarily correlate with each other. A particular food source may be easily digestible but low in, e.g., nitrogen or essential nutrients. Hence, the relation between digestibility of a given food source and growth of its consumers, too, depends on its nutritive value.

The food material strongly affected consumption, digestibility and growth, but no consistent pattern of how isopod performance depended on the food material arose from our data. In all cases but inoculated leaf litter, alder material was consumed at higher rates than oak material. Assuming a higher nutritive value of alder than of oak (Zimmer and Topp, 1997, 2000, and references therein), this result confirms the compensatory consumption of low-quality food (Dallinger and Wieser, 1977; Rushton and Hassall, 1983; Cruz-Rivera and Hay, 2000) only when the low quality of oak litter had been increased through microbial conditioning. Growth of *P. scaber* was always higher on alder material, but digestibility of alder material was only higher than that of oak material when material with low microbial activity and biomass ('re-wetted') was fed, stressing the proposed nutritive significance of microbiota (Coughtrey et al., 1980; Gunnarsson and Tunlid, 1986; Ullrich et al., 1991; Zimmer and Topp, 1997, 2000; Zimmer, 1999).

Coprophagous behavior (gut passage) affected consumption rates, digestibility and growth, but only in case of inoculated food sources. This result is clearly contrary to our predictions that feces will be of higher nutritional value than leaf litter, independent of feces-colonizing microbiota, if coprophagy is due to digestive incapabilities when feeding on leaf litter alone. On the other hand, this result stresses the

significance of feces-colonizing microbiota, but in fact, coprophagy on inoculated feces lowered isopod performance in all cases but growth on oak material.

Microbiota strongly affected consumption and digestibility. They, further, mediated the effects of the food material and the gut passage on growth of *P. scaber* and, thus, had indirect effects on isopod performance. Microbial activity and/or biomass increased the digestibility of food, so that there were no differences between inoculated materials from oak and alder. With respect to consumption, the effect of microbial inoculation was stronger in case of oak material than in case of alder material (see above). In a previous study, the addition of cultured bacteria to feces increased the survival rate of coprophagous *Oniscus asellus* as compared to isopods feeding on sterile feces (Ullrich et al., 1991). This result is in coincidence with the present increase of digestibility and growth on inoculated vs. re-wetted oak-derived feces, but contrary to the reduced digestibility of alder-derived feces after microbial inoculation. Thus, in contrast to our predictions, we did not find a promoting effect of microbial activity and/or biomass in general.

In sum, there is no consistent evidence that *P. scaber* benefits from coprophagy. This result is clearly contrary to our predictions derived from the hypothesis (1) that coprophagy meets the isopods' need for nutrients that cannot be satisfied by feeding on leaf litter alone (Wieser, 1968, 1978, 1984; Dallinger and Wieser, 1977; Debry and Lebrun, 1979; Zimmer, 1999). In fact, consumption and digestibility of (inoculated) feces were lower than of leaf litter. The little gain from coprophagy we observed with respect to growth depended on microbial inoculation of the feces, corroborating the hypothesis (2) that microbial colonizers increase the nutritive value of feces by providing a source of microbial enzymes or nutrients (Hassall and Rushton, 1982; Carefoot, 1984a,b; Ullrich et al., 1991). Since growth was positively affected, but not digestibility (that was actually lower on oak-derived feces than on litter), we propose that rather nutrients than enzymes are involved here (Zimmer and Topp, 1998), but further experimental evidence is needed to unambiguously decide upon this issue.

Microbiota increased digestibility of and growth on oak-derived feces, but not on alder-derived feces. Since alder litter provided better isopod performance than oak litter, the effects of feces-colonizing microbiota appear to depend on the leaf litter. In coincidence, *P. scaber* gained from coprophagy through microbial activity and/or biomass only if the initial leaf litter quality was low. Based on this, we propose that the influence of feces-colonizing microbiota on the gain from coprophagy decreases with increasing nutritive value of the leaf litter the feces are derived from.

Still, the significance of coprophagy in the field remains unclear (Carefoot, 1993). Although foraging isopods may encounter densely inoculated feces beneath the litter layer (Zimmer et al., 1996; Hopkin and Martin, 1984; Hassall and Rushton, 1982), we can only speculate on the effects of coprophagy on decomposition processes. The present results suggest that being coprophagous will only pay, if the available leaf litter is of low nutritive value (see above). If this holds true for the field, the contribution of coprophagy to decomposition processes will be significant only in advanced stages of litter decay, when easily digestible compounds have already been removed. Clearly, experimental evidence from the field is needed in this regard.

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