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Prey preference and consumption by some non-specialist harvestman species (Arachnida: Opiliones)

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Summary

Only a few studies of harvestman prey have dealt with food preference, consumption rate and the value of different food types. This study seeks to clarify these aspects in the non-specialist harvestmen *Rilaena triangularis*, *Oligolophus tridens* and *Nemastoma lugubre*. Food quality was tested with adult *R. triangularis*, while all three species were used in food preference experiments. The harvestmen were offered eight food types: earthworm, slug, plum, turkey meat, *Drosophila melanogaster* (Diptera), *Sitobion avenae* (Aphidoidea), *Sinella curviseta* (Collembola) and *Folsomia candida* (Collembola). In the food quality experiment, consumption rate and effects on animal fitness were examined. In the preference experiment, feeding observations and consumption measurements were used to indicate preference. In general there was little agreement between preference, amounts consumed and food value. *Drosophila melanogaster* and turkey meat were high quality foods, but associated with high consumption rate of the former and low consumption rate of the latter. Slugs, earthworms, aphids and plum were low-quality foods, though *O. tridens* and *N. lugubre* ate surprisingly high amounts of plum. The low quality of slugs is due to pre-ingestive effects, that of earthworms to post-ingestive effects, while the value of *S. avenae* was limited by both. There is a general similarity between harvestmen and other generalist predators in the value of different food types.

Introduction

Harvestmen employ many different foraging strategies; they are predators, scavengers and frugivores. While a few species are specialised predators on molluscs (Nyffeler & Symondson, 2001), most are generalist feeders. There are many examples in the literature of harvestman food: they catch and kill a variety of small invertebrates, e.g. springtails, aphids and flies (Sankey & Savory, 1974); they are also scavengers of dead animals, both invertebrates, e.g. ants and beetles (Sankey & Savory, 1974) and earthworms (Halaj & Cady, 2000), and vertebrates, e.g. small rodents and birds (Sankey, 1949). There are also reports of harvestmen eating vegetable matter, e.g. scraping grass stalks (Todd, 1950), eating fruit (Halaj & Cady, 2000; Machado & Pizo, 2000) or other non-animal material, e.g. the gills of fungi (Sankey & Savory, 1974). They may obtain water from fruit in the form of juice (Todd, 1950), or lipids and carbohydrates from nuts or fruits (Wickham, 1918; Machado & Pizo, 2000).

The preference for specific food types among non-specialist harvestmen has been debated. Early statements that harvestmen only eat vegetable matter (refs in Edgar, 1971) are obviously erroneous. On the contrary, some later reports explicitly state that harvestmen reject vegetable and fungal material (Adams, 1984) or that their faeces contain such small amounts of plant remains that they could merely stem from the stomach content of the prey (Phillipson, 1960). However, recent observations indicate that harvestmen may eat more fruit than previously suspected. In one study fruit and other plant materials constituted 18% of the observed food items (Halaj & Cady, 2000). Machado & Pizo (2000) found that harvestmen exploited fallen fruit in tropical forests to a great extent. In the laboratory harvestmen will accept a variety of food types, e.g. banana, cooked vegetables, ham (Gnaspini, 1996), dried eggs, wholemeal flour, and yeast (Todd, 1949). Gnaspini (1996) concluded that harvestmen "seem to be largely omnivorous, with preference for animal matter".

All these observations on the food choice of harvestmen may give us a good picture of what they eat. However, they tell us little about what food types are really important: which food types are of good quality to

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harvestmen? How do their diets affect the fitness of harvestmen? Do different harvestman species prefer the same kinds of food? The aim of this study was to investigate to what extent harvestmen eat a variety of food types, how the diets affect their fitness, and to test if the value of the food is reflected in the preferences. We examined these questions by means of a food quality experiment and a preference experiment. The food quality experiment was performed on *Rilaena triangularis* (Herbst) (Phalangiidae), and comprised different food types. When food quality is evaluated it is important to measure simultaneously both the amount of food eaten and a fitness parameter. Therefore, food consumption was measured and body mass gain and survival were chosen as fitness parameters. Three harvestman species, *R. triangularis*, *Oligolophus tridens* (C. L. Koch) (Phalangiidae) and *Nemastoma lugubre* (O. F. Müller) (Nemastomatidae), all generalist feeders, were used in the preference experiment. The harvestmen were individually offered eight food types and the preference was indicated by observations of feeding and measurement of consumption. The food types for the experiment were chosen to represent the main types of food that harvestmen are often observed to eat and the different types of foraging strategies: dead vertebrates (scavenging): minced turkey meat; fruit (frugivory): plum; and small invertebrates (scavenging and predation): earthworm, slug, fruit fly, aphid, and two species of springtails. The invertebrates were selected to represent a wide range of invertebrate groups and potential crop pests. Some harvestmen are specialised snail/slug feeders, so it was therefore of interest to test the quality of slugs for generalist harvestmen.

Methods

The harvestmen

Rilaena triangularis is widespread in northern and central Europe and the Balkans (Martens, 1978) and has also been introduced to North America (Bragg & Holmberg, 1974). In Denmark it is dispersed all over the country in a variety of habitats. It is most abundant in woodlands, but can also be found at roadsides and near houses. The harvestman has a body length of 6–7 mm (females) and the second leg is 30 mm long (Martens, 1978). The life cycle is annual and the harvestmen overwinter as juveniles. The young harvestmen emerge in spring (in Denmark, March). The first adults can be found from mid April, and oviposition takes place in June–July (Meinertz, 1964). Prey records for *R. triangularis* include: Diptera, Hymenoptera and Isopoda (Immel, 1955; Parisot, 1962; Sunderland & Sutton, 1980). For the food quality experiment, mature *R. triangularis* females were collected in a small deciduous forest near Århus, Denmark, in June 2003. For the preference experiment, juvenile *R. triangularis* were collected in a forest at Møn, Denmark, in late April 2004.

The distribution of *Oligophus tridens* covers Iceland, the British Isles, northern and central Europe (Martens, 1978) and there is also a report from North America (Bell, 1974). The species is abundant in Denmark, and can be found in a variety of biotopes, especially in woodlands and fallow fields. The females have a body length of 5–6.5 mm (Sankey & Savory, 1974) and the second leg is 17 mm long (Martens, 1978). The life cycle is annual and the harvestmen overwinter in the egg stage. Hatchlings emerge in spring and mature in July–August in Denmark (Meinertz, 1964). Prey records for *O. tridens* include: Coleoptera (Chrysomelidae), Collembola, Diptera (Phoridae and Muscidae), Homoptera (Aphidae, Psyllidae, Delphacidae and Jassidae), Lepidoptera (larvae), Diplopoda, Acari, Araneae, Opiliones, Isopoda, Oligochaeta (Enchytraeidae), Gastropoda, plant matter, nutty seeds, dead vertebrates, and bird droppings (Bristowe, 1949; Sankey, 1949; Todd, 1950). Female *O. tridens* were collected in a meadow near Århus, Denmark, in mid October 2003.

Nemastoma lugubre is widespread in central and eastern Europe, including southern Sweden, Norway and southern Finland (Martens, 1978). It can be found in most habitats with high humidity, e.g. woodlands and moors, beneath moss, pieces of wood and fallen leaves. The body length is 1.6–1.8 mm (males) and 2.1–2.7 mm (females), and the second leg is 6 mm long (Martens, 1978). Mature individuals can be found all year round, and juveniles from July to September (Meinertz, 1962). Prey records for *N. lugubre* include: Collembola, Diptera, Homoptera, Psocoptera, Myriapoda, Acari, Araneae, Isopoda, Oligochaeta, Gastropoda, fungi (Rimsky-Korsakow, 1924; Parisot, 1962; Sunderland & Sutton, 1980; Adams, 1984). Mature *N. lugubre*, both males and females, were collected in a forest at Møn, Denmark, in late April 2004.

In all experiments, the harvestmen were kept in clear plastic containers with a lid (11 × 11 cm, height 6 cm). The water source was a piece of moist filter paper, wetted by a water-filled glass tube with a cotton plug. In the food quality experiment the harvestmen were kept at a constant temperature of 17 °C and a photoperiod of 16L: 8D. The preference experiment was carried out at 15 °C and with a photoperiod of 10L: 14D for *O. tridens*, and 14L: 10D for *N. lugubre* and *R. triangularis*, which corresponded to the day lengths in nature at the times of experimentation.

Food types

Eight food types were used in the experiments. All food types were presented to the harvestmen in the preference experiment, but the two species of springtails were not included in the food quality experiment as they were not available at that time. The food types were: earthworm (mainly *Lumbricus terrestris* Linnaeus), slug (*Deroceras reticulatum* (Müller)), plum, fruit fly (*Drosophila melanogaster* (Meigen)), aphid (*Sitobion avenae* (Fabricius)), minced turkey meat, and two species of springtails (*Sinella curviseta* Brook and *Folsomia candida* (Willem)). The earthworms and slugs were collected in the field. The plum and turkey meat were bought in a store. *Drosophila melanogaster*, *S. curviseta*, *F. candida* and *S. avenae* were from laboratory cultures. Wild-type fruit flies were reared on instant *Drosophila* medium (Formula 4–24, Carolina Biological Supply, Burlington, NC) mixed with crushed dog food (Techni-Cal Adult®, Martin Pet Foods, Ontario, Canada) in the proportion 100: 54.5 g. The dog-food enrichment ensured a high nutritional quality of the flies. Compared with fruit flies raised on the plain medium, which are inadequate for bringing a wolf spider through the full development, the enriched fruit flies increase growth and survival and allow development to maturity (Mayntz & Toft, 2001); they have also been reported to support a high level of egg production in a carabid beetle (Bilde *et al.*, 2000). The aphids were reared on wheat seedlings of mixed cultivars. *Folsomia candida* was reared on baker's yeast, and *S. curviseta* on baker's yeast and *Drosophila* medium. In order to prevent prey behaviour from influencing the results and ensure that only nutritional aspects of the food would be included, the prey were freeze-killed, and large prey (earthworm, slug and plum) were cut into small pieces for easier handling by the harvestmen. The food presented had also been dried in a vacuum oven at 50 °C for a minimum of two days, in order to prevent moulding during the experiment and also to prevent evaporation from making consumption measurements inaccurate. Despite these efforts, the consumption estimates were negative in a few cases, where the harvestmen apparently did not eat anything. In such cases consumption was recorded as 0. The harvestmen were expected to accept the dried food based on a laboratory study of four harvestman species (*Leiobunum* spp.), which showed that they ate dried carabid beetles and grasshoppers without hesitation and apparently survived well on this diet (Edgar, 1971).

Food quality experiment

Only mature female *R. triangularis* were used in this experiment. The harvestmen were standardised before the experiment began: first they were fed to satiation on blow-fly pupae (Calliphoridae) for three days and then starved for two days. There were six treatment groups: earthworm, slug, plum, *D. melanogaster*, *S. avenae*, and turkey meat. The duration of the experiment was 13 days, with four feeding periods. The harvestmen were weighed on the first day (Sartorius electronic balance MC5: 0.001 mg accuracy) and divided into six treatment groups with roughly the same mean body mass. Some of the harvestmen laid eggs during the experiment and were therefore discarded from the analysis; replication therefore varied between 10 and 14 per treatment. Mortality was the number of dead harvestmen at the end of the experiment. A 10–20 mg portion of the dried treatment food was weighed out and 10 μl water was added to soften it. The food portions were offered to the harvestmen after soaking for a few minutes. The harvestmen were given three days to feed, then the remaining food was collected, the harvestmen were weighed, and new food portions were added. The food remains were dried in the vacuum oven, weighed and consumption calculated.

Preference experiment

The preference experiment was performed with *R. triangularis* (juveniles), *O. tridens* (mature females), and *N. lugubre* (mature males and females). The harvestmen were starved for 4–5 days under experimental conditions, before preference and food consumption were measured. The starvation served to increase hunger and thus make preferences more apparent. Food consumption was determined over three days. The harvestmen were weighed on the first day (Sartorius electronic balance MC5: 0.001 mg accuracy). Every harvestman was offered eight different food types. The food portions (3–10 mg depending on the size of the animal) were weighed out on small glass plates and 10 μl of water was added to each portion. The food portions were soaked for a few minutes and the glass plates were then gently placed in the container with the harvestman. The behaviour of the harvestmen was observed for the next five hours, in the first hour every 15 minutes, later every 30 minutes. It was noted if the harvestman ate from one of the food types. The harvestman would either sit on the glass plate and eat directly from the lump of food, or it would carry some of the food around in its chelicerae. It was not recorded as feeding if the harvestman just wandered over the glass plates containing the food. None of the *N. lugubre* harvestmen was observed to eat the food during the first five hours after feeding, so it was not possible to make preference observations for this species. *Nemastoma lugubre* is mostly active by night (Hillyard & Sankey, 1989) and feeding probably took place only after dark, but this was difficult to observe because of the small size of the animals. After three days the harvestmen were weighed again and the food remains were collected and dried in the vacuum oven. Pieces of food carried away from the plates could be identified by their colour and surface structure. The dried food remains were weighed and consumption calculated.

Statistical analysis

Survival of the harvestmen was analysed by means of a binomial test. The body mass changes and total consumption were tested with one-way analysis of variance (ANOVA), and body mass change was further tested with a one-sample t-test. The data complied with the requirements of variance homogeneity. However, the sample sizes were small in some of the diet groups because of high mortality. As treatments were planned, Student's t-tests were used for post-hoc comparisons after the analysis of variance. Food utilisation was analysed by analysis of covariance (ANCOVA) with diet as factor, body mass change as dependent variable and total consumption as covariate. The growth curves were compared using multivariate analysis of variance (MANOVA) with repeated measures, with time as the repeated factor. The time * diet interaction term was used to detect differences in growth over time between the diets. Animals that died before the end of the experiment were excluded from this analysis, resulting in

Diets	Living	Dead	
Earthworm	3	11	b
Slug	5	7	b
Plum	9	2	a
Drosophila melanogaster	9	2	a
Sitobion avenae	9	1	a
Turkey meat	13	1	a

Table 1: Number of living and dead *Rilaena triangularis* at the end of the food quality experiment. Diets with same letters are homogeneous regarding survival (binomial test).

a low number of replicates in some of the diet groups. Bonferroni adjustments due to multiple tests were not applied (cf. Moran, 2003) because the prey types were chosen based on prior assumptions and the relatively high number of prey types would itself make it difficult to obtain significance.

Preference was presented visually by means of graphs showing the cumulative number of observations of harvestmen eating a food type at subsequent observations. The consumption was analysed by ANOVA if homogeneity of variance was achieved or by Welch ANOVA if the criteria of variance homogeneity could not be met by any transformation. Student's t-tests were used to locate the differences between individual diets.

All statistical analyses were performed with JMP 5.0 for Windows (SAS Institute).

Results

Food quality experiment

Survival of the harvestmen differed between the six treatments (Table 1). The binomial test revealed that the harvestmen from the turkey meat, *S. avenae*, *D. melanogaster*, and plum treatments had a high survival. The harvestmen from the slug and earthworm treatments had a lower survival.

The analysis of total consumption showed that there were significant differences between the six diets in the amounts eaten (overall ANOVA, $n=48$, $F_{5,\ 42}=4.2731$, $p=0.0031$, Fig. 1). *Drosophila melanogaster* was eaten in the highest amounts, slugs in the lowest, and the remaining four diets in intermediate amounts (see horizontal bars above Fig. 1 for statistical differences). The body mass changes of the harvestmen at the end of the experiment also showed clear differences between the six diets (overall ANOVA, $n=48$, $F_{5,\ 42}=7.8424$, $p<0.0001$, Fig. 1). On two of the diets the harvestmen gained weight (one-sample t-test, *D. melanogaster*: $p=0.02$ and turkey meat: $p=0.04$). Plum and *S. avenae* resulted in a reduced body mass (one-sample t-test, plum: $p=0.0007$; *S. avenae*: $p=0.02$). The body mass change of harvestmen from slug and earthworm treatments was also negative, though not significantly different from 0; the number of animals in these treatments was low because of high mortality. The regression lines for the six diet groups had the same slope (ANCOVA, $n=48$, $F_5=0.7312$, $p=0.61$), but the intercepts differed significantly (ANCOVA, $n=48$, $F_5=6.4314$, $p=0.0002$). Contrasts (see vertical bars to the right of Fig. 1) showed that body mass change on turkey meat and fruit flies was significantly higher than on *S. avenae*, earthworm and plum. Moreover, body mass change in the plum treatment was significantly lower than in the slug, *S. avenae*, turkey meat, and *D. melanogaster* treatments. In accordance with these results the repeated measures MANOVA on body masses showed a significant overall time * diet interaction (MANOVA, $n=48$, Wilk's $\lambda=0.2701$, $F=3.1529$, NumDF=20, DenDF=130.3, $p<0.0001$). Contrast analyses indicated a separation between the same two groups of diets (*D. melanogaster* and turkey meat vs. slug, earthworm, *S. avenae* and plum).

Preference experiment

The preference curves for *R. triangularis* show that the harvestmen were observed to eat *D. melanogaster* more often than the other food types (Fig. 2A). The springtails, earthworm and slug were eaten to some extent, but the aphid, turkey meat and plum were only observed being eaten in a few cases at the beginning of the experiment. The preference curves for *O. tridens* show that this harvestman was observed to eat *F. candida* and *S. avenae* more often than the other food types (Fig. 2B). Turkey meat was observed to be eaten to an intermediate extent and *D. melanogaster*, plum, slug and earthworm were the least observed. *Oligolophus tridens* was never observed to eat *S. curviseta*. The degree of preference for *D. melanogaster* can also be seen in the analysis of consumption, which showed that there was a significant difference in the amounts eaten between the eight diets for the two phalangiid species (*R. triangularis*: overall ANOVA, $n=15$, $F_{7,\ 112}=12.6992$, $P<0.0001$, Fig. 3A; *O. tridens*: $n=16$, $F_{7,\ 120}=43.7165$, $p<0.0001$, Fig. 3B). Both species ate *D. melanogaster* in large amounts,

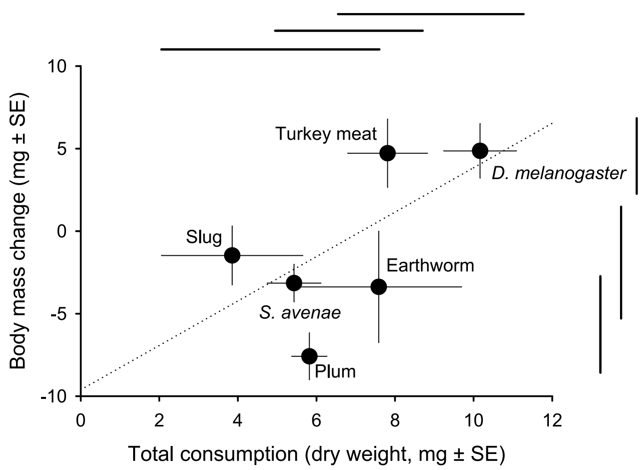

Fig. 1: Total consumption (dry weight in mg, mean ± SE) versus body mass change (mg, mean ± SE) in adult female *Rilaena triangularis* from six diet treatments. Horizontal bars (above figure) connect treatments that are not significantly different with respect to total consumption; vertical bars (to right) connect treatments that are not significantly different with respect to body mass change (ANOVA and Student's t-tests). The dotted regression line is a common line, based on all data points. The slopes of the regression line for each treatment were not significantly different (not shown).

turkey meat only a little, and other food types in intermediate amounts. Consumption by *N. lugubre* also showed significant differences in the amounts eaten (overall Welch ANOVA, $n=18$, $F=18.9116$, NumDF$=$ 7, DenDF$=55.067$, $p<0.0001$, Fig. 3C) and differed from the other species in that plum was eaten in the greatest amounts and that *D. melanogaster* was not highly preferred.

Discussion

The overall conclusion from the results of the food quality experiment regarding body mass change and survival in *Rilaena triangularis* is that the diets separate into a high-quality group (turkey meat and *D. melanogaster*) and a low-quality group (*S. avenae*, earthworm, slug and plum). The results of the preference experiment only partly reflect this. The inconsistency is only partly due to the different species or developmental stages used in the two experiments. The main reason must be that neither consumption rate nor frequency of observed feeding correctly reflects food quality. For prey that is eaten, the animal may gain a large body mass by eating only a small amount if it is of a high quality. With prey of lower nutritional quality the animal may compensate by eating a larger amount without getting better fitness, because the prey has an insufficient composition of nutrients (Toft, 1996; Marcussen *et al*., 1999). In the first experiment the harvestmen ate similar amounts of earthworm and turkey meat but the result was much higher growth for turkey meat than for earthworm. Thus, the low consumption rate of turkey meat by all three species in the second experiment need not be an indication of low quality. Rather, the animals may have fulfilled their specific demand for protein after eating just a small amount. The same argument may be used when plum is compared with the other food types. The harvestmen fed plum lost more body mass than those fed other diets, although plum was eaten in the same amounts as slug, *S. avenae*, earthworm and turkey meat. These results (Fig. 1) indicate the existence of post-ingestive effects for plum, *S. avenae* and earthworm, either through reduced assimilation of the food or reduced utilisation of the nutrients assimilated (cf. Horton & Redak, 1993).

There are also indications of pre-ingestive effects limiting the consumption of slug, which was eaten in far lower amounts than *D. melanogaster* or turkey meat. The regression lines for these three prey have the same slope and intercept (not shown in Fig. 1), which means that the harvestmen get the same benefit per amount eaten. Their different food quality is therefore due to the different consumption capacity of the predator. The low intake of slug may be due to the prey being toxic or in other ways impeding digestion. A limited consumption capacity for *S. avenae* and plum is indicated but was not significantly different from that of turkey meat.

In spite of a generally higher than expected consumption of plum the experiments show that frugivory does not support growth in the species tested here. The harvestmen fed a pure plum diet lost body mass during

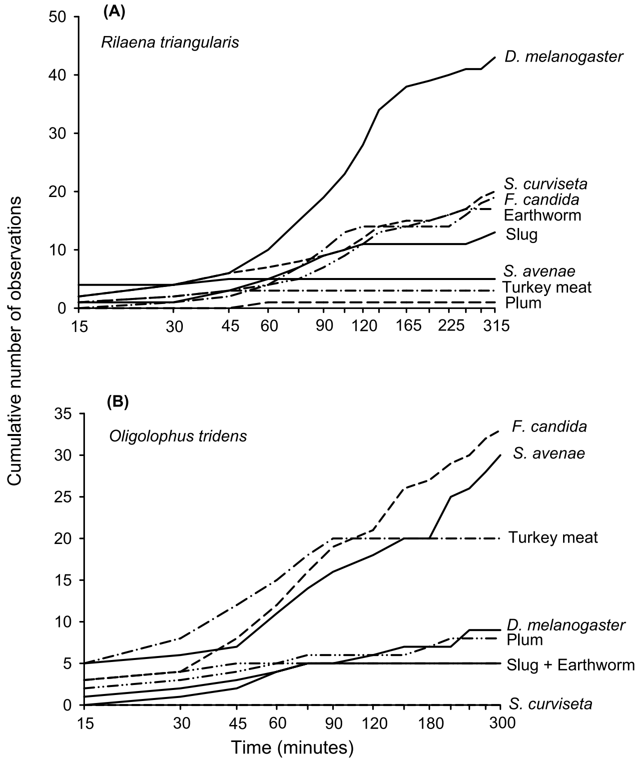

Fig. 2: Preference curves for (**A**) juvenile *Rilaena triangularis* and (**B**) adult female *Oligolophus tridens.* Time (minutes) on a logarithmic scale versus cumulative number of observations of harvestmen eating different food types.

the 13 days of the food quality experiment. When harvestmen have been observed to eat non-animal matter, it has often been in a very soft form, e.g. fallen fruit or the gills of fungi. Harvestmen have also been observed to drink the sugar water laid out by lepidopterists (Sankey, 1949). Fruits may be a source of both water and simple sugars, but little of the vegetable dry mass eaten seems to be usable. Harvestmen are very vulnerable to desiccation and they will try to drink if they are desiccating (Sankey & Savory, 1974). Possibly consumption of fruit will improve survival even if it has no effect on growth, and this might be the reason for harvestmen eating fruit in nature.

The low-quality diet *S. avenae* resulted in a significant decline of body mass. The weight loss suggests that something in the aphids prevented the harvestmen from utilising the available energy and nutrients. Bilde & Toft (2001) found *S. avenae* toxic to a spider; Allard & Yeargan (2005) found *Aphis glycines* to be toxic to *Phalangium opilio* (L.), and Hvam & Toft (2005) found *S. avenae* and *Rhopalosiphum padi* (L.) to be poor-quality food for *O. tridens*. Other studies of spiders and carabid beetles indicate that they are energy limited and draw on their body reserves when fed on pure aphid diets (Toft, 1995, 2005; Bilde & Toft, 1999). Similar effects seem to hold for the harvestmen tested here.

Plum, earthworms and slugs were not expected to contain any toxic elements but still gave low or no benefits to the harvestmen. Mortality was surprisingly high on some of the low-quality diets, especially slugs and earthworms. The experiment was relatively short (13 days), so the harvestmen were not expected to die from malnutrition in this short time. Water was added to the food so the harvestmen should be able to eat it, and drying of the food is not expected to be the cause of the high mortality. Unfortunately, the experiment did not include a starvation control which would be necessary to draw conclusions about prey toxicity (Toft & Wise, 1999a).

Earthworms have a high protein content (Lee, 1985), and this might indicate that earthworms are a high-quality prey for spiders and other generalist predators (Nyffeler *et al.*, 2001). In one study 47% of the harvestmen observed feeding were eating earthworms (Halaj & Cady, 2000) and Elpino-Campos *et al.* (2001) found normal reproductive activity in a gonyleptid harvestman when feeding on earthworms. Most harvestmen are not capable of killing an earthworm, so they probably only scavenge on their carcasses (Halaj & Cady, 2000). However, the suggestion that earthworms are high-quality food was not confirmed in this experiment. The harvestmen lost body mass when eating a pure earthworm diet and there was high mortality in this group (almost 80% died during the 13 days of the food quality experiment). Moreover, earthworms were not preferred as food, consumption was low, and there were few observations of harvestmen eating earthworms. Earthworms were also low-quality food for a generalist carabid beetle (Bilde & Toft, 2001).

The preference curves show differences in which food types *R. triangularis* and *O. tridens* were observed to eat. The high preference of *R. triangularis* for *D. melanogaster* was expected from its high food quality, but the preference of *O. tridens* for *F. candida* and *S. avenae* was not expected given the low quality of both prey types (Hvam & Toft, 2005). For *R. triangularis* the preferences were also reflected in the amounts eaten. For *O. tridens* the picture is more muddled, since the food with most feeding observations was not the type that was eaten in the greatest amounts. Generalist predators have no innate search images for their prey but must learn by experience which prey are high- or low-quality, respectively (Toft & Wise, 1999b; Toft, 2005). Therefore, when presented with a new prey type for the first time they will often manipulate it extensively. If the prey is palatable they will usually start eating it very soon, but less palatable prey is often manipulated for a long time even though little or nothing is eaten. Comparing the amounts of food eaten by *R. triangularis* and *O. tridens* (Fig. 3A–B), it is clear that they both ate more of *D. melanogaster* than the other food types. Plum, *S. curviseta* and *F. candida* also rank highly for both species. Of these only *S. curviseta* is high-quality prey (Hvam & Toft, 2005). For *N. lugubre* the pattern is slightly different, with plum as the most eaten food type, turkey meat as the least eaten, and all other food types intermediate. In nature this species is believed to eat mostly Collembola (Adams, 1984). It seems then that *O. tridens* and *R. triangularis* prefer *D. melanogaster*, *F. candida* and *S. curviseta*, confirming the statement by Adams (1984) that harvestmen prefer "small, soft bodied prey".

The results of the present experiments are consistent with earlier studies, which have classified the nutrient-enriched *D. melanogaster* as a high-quality prey for generalist predators, e.g. spiders (Toft, 1995; Mayntz & Toft, 2001), carabid beetles (Bilde *et al.*, 2000) and the harvestman *O. tridens* (Hvam & Toft, 2005). Its high quality as food coincides with a high consumption capacity. The springtail *S. curviseta* has also been classified as a high-quality prey (Vanacker *et al.*, 2004; Hvam

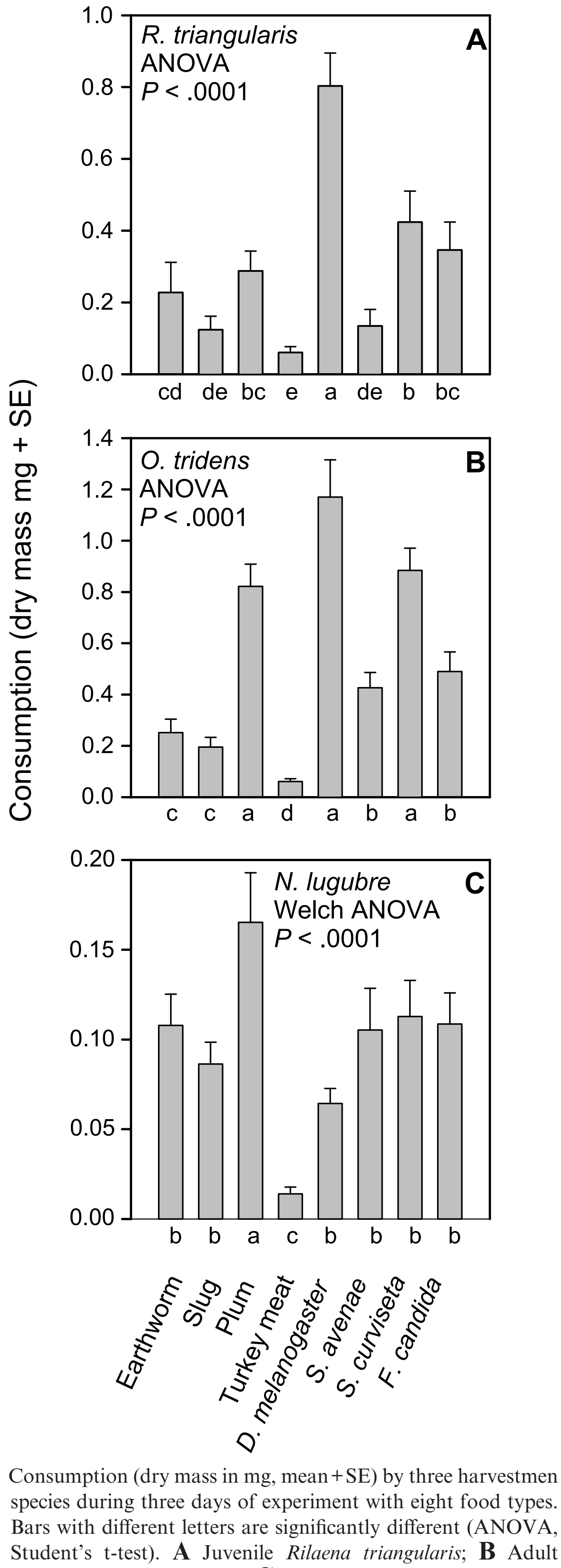

Fig. 3: Consumption (dry mass in mg, mean + SE) by three harvestmen species during three days of experiment with eight food types. Bars with different letters are significantly different (ANOVA, Student's t-test). **A** Juvenile *Rilaena triangularis*; **B** Adult female *Oligolophus tridens*; **C** Adult female and male *Nemastoma lugubre*.

& Toft, 2005) which also agrees with the high consumption capacity in all three species (Fig. 3).

As *F. candida* is "small and soft bodied" one could expect that harvestmen would have a preference for this prey type and *O. tridens* was often observed to eat *F. candida*. However, several experiments have shown that *F. candida* is toxic to many generalist predators, resulting in low survival and growth (Toft & Wise, 1999a; Fisker & Toft, 2004; Hvam & Toft, 2005). Aphids are normally a low preference prey type for generalist predators, but *O. tridens* was often observed to eat *S. avenae*. Several experiments with generalist predators have demonstrated that aphids in pure diets are a low-quality prey (Bilde & Toft, 1994, 1999, 2001; Toft, 1995, 2005; Hvam & Toft, 2005). Survival was not affected in the present, relatively short experiments. Yet, long term experiments with juvenile generalist predators showed that mortality was high in wolf spiders (Toft, 1995), staphylinid beetles (Kyneb & Toft, 2004) and *O. tridens* (Hvam & Toft, 2005) fed pure aphid diets. Development was also affected in wolf spiders, which were unable to moult to the second instar (Toft, 1995). Seemingly contrary results have been obtained from experiments in potato fields, suggesting that harvestmen might be undervalued as predators of crop pests (Dixon & McKinlay, 1989). *Oligolophus tridens* was also the most efficient generalist predator in a microcosm study with different generalist predators and the aphid *Rhopalosiphum padi*, reducing aphid numbers by 97% compared with predator-free controls (Madsen *et al*., 2004). These two studies indicated that harvestmen might be of value for biological control of aphid outbreaks. The consumption of aphids was not high in the present preference experiment, although *S. avenae* were among the most frequently observed food items of *O. tridens*. In the light of our present results and those of Allard & Yeargan (2005) and Hvam & Toft (2005) it seems that harvestmen can, at most, play a small part in the combined effect of the generalist predator assemblage on aphid populations (Edwards *et al*., 1979; Symondson *et al*., 2002).

Based on the results presented, we conclude that the nutritionally most important feeding strategies for generalist harvestmen are predation on some kinds of small insects and scavenging on arthropod and vertebrate prey, whereas frugivory and scavenging/predation on molluscs, earthworms and some chemically protected insects also occur but are of little importance quantitatively.

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References

ADAMS, J. 1984: The habitat and feeding ecology of woodland harvestmen (Opiliones) in England. *Oikos* **42**: 361–370.

ALLARD, C. M. & YEARGAN, K. V. 2005: Effect of diet on development and reproduction of the harvestman *Phalangium opilio* (Opiliones: Phalangiidae). *Envir. Ent.* **34**: 6–13.

BELL, R. T. 1974: A European harvestman in North America (Phalangida, Phalangiidae). *Ent. News* **85**: 154.

BILDE, T. & TOFT, S. 1994: Prey preference and egg production of the carabid beetle *Agonum dorsale*. *Entomologia exp. appl.* **73**: 151–156.

BILDE, T. & TOFT, S. 1999: Prey consumption and fecundity of the carabid beetle *Calathus melanocephalus* on diets of three cereal aphids: high consumption rates of low-quality prey. *Pedobiologia* **43**: 422–429.

BILDE, T. & TOFT, S. 2001: Value of three cereal aphid species as food for a generalist predator. *Physiol. Ent.* **26**: 58–68.

BILDE, T., AXELSEN, J. A. & TOFT, S. 2000: The value of Collembola from agricultural soils as food for a generalist predator. *J. appl. Ecol.* **37**: 672–683.

BRAGG, P. D. & HOLMBERG, R. G. 1974: *Platybunus triangularis* and *Paroligolophus agrestis*: two phalangids introduced to North America (Arachnida, Opiliones). *J. Arachnol.* **2**: 127.

BRISTOWE, W. S. 1949: The distribution of harvestmen (Phalangida) in Great Britain and Ireland, with notes on their names, enemies and food. *J. Anim. Ecol.* **18**: 100–114.

DIXON, P. L. & MCKINLAY, R. G. 1989: Aphid predation by harvestmen in potato fields in Scotland. *J. Arachnol.* **17**: 253–255.

EDGAR, A. L. 1971: Studies on the biology and ecology of Michigan Phalangida (Opiliones). *Misc. Publs Mus. Zool. Univ. Mich.* **144**: 1–64.

EDWARDS, C. A., SUNDERLAND, K. D. & GEORGE, K. S. 1979: Studies on polyphagous predators of cereal aphids. *J. appl. Ecol.* **16**: 811–823.

ELPINO-CAMPOS, A., PEREIRA, W., DEL-CLARO, K. & MACHADO, G. 2001: Behavioural repertory and notes on natural history of the neotropical harvestman *Discocyrtus oliverioi* (Opiliones: Gonyleptidae). *Bull. Br. arachnol. Soc.* **12**: 144–150.

FISKER, E. N. & TOFT, S. 2004: Effects of chronic exposure to a toxic prey in a generalist predator. *Physiol. Ent.* **29**: 129–138.

GNASPINI, P. 1996: Population ecology of *Goniosoma spelaeum*, a cavernicolous harvestman from south-eastern Brazil (Arachnida: Opiliones: Gonyleptidae). *J. Zool., Lond.* **239**: 417–435.

HALAJ, J. & CADY, A. B. 2000: Diet composition and significance of earthworms as food of harvestmen (Arachnida: Opiliones). *Am. Midl. Nat.* **143**: 487–491.

HILLYARD, P. D. & SANKEY, J. H. P. 1989: Harvestmen (2nd edn). *Synopses Br. Fauna* (N.S.) **4**: 1–20.

HORTON, D. R. & REDAK, R. A. 1993: Further comments on analysis of covariance in insect dietary studies. *Entomologia exp. appl.* **69**: 263–275.

HVAM, A. & TOFT, S. 2005: Effects of prey quality on the life history of a harvestman. *J. Arachnol.* **33**: 582–590.

IMMEL, V. 1955: Einige Bemerkungen zur Biologie von *Platybunus bucephalus* (Opiliones, Eupnoi). *Zool. Jb.* (Syst.) **83**: 475–484.

KYNEB, A. & TOFT, S. 2004: Quality of two aphid species (*Rhopalosiphum padi* and *Sitobion avenae*) as food for the staphylinid generalist predator *Tachyporus hypnorum*. *J. appl. Ent.* **128**: 658–663.

LEE, K. E. 1985: *Earthworms. Their ecology and relationships with soils and land use*. Academic Press, Australia.

MACHADO, G. & PIZO, M. A. 2000: The use of fruits by the neotropical harvestman *Neosadocus variabilis* (Opiliones, Laniatores, Gonyleptiae). *J. Arachnol.* **28**: 357–360.

MADSEN, M., TERKILDSEN, S. & TOFT, S. 2004: Microcosm studies on control of aphids by generalist arthropod predators: effects of alternative prey. *BioControl* **49**: 483–504.

MARCUSSEN, B. M., AXELSEN, J. A. & TOFT, S. 1999: The value of two Collembola species as food for a linyphiid spider. *Entomologia exp. appl.* **92**: 29–36.

MARTENS, J. 1978: Weberknechte, Opiliones. *Tierwelt Dtl.* **64**: 1–464.

MAYNTZ, D. & TOFT, S. 2001: Nutrient composition of the prey's diet affects growth and survivorship of a generalist predator. *Oecologia* **127**: 207–213.

MEINERTZ, N. T. 1962: Mosskorpioner og mejere. *Danm. Fauna* **67**: 1–193.

MEINERTZ, N. T. 1964: Der Jahreszyklus der Dänischen Opilioniden. *Vidensk. Meddr dansk naturh. Foren.* **126**: 450–464.

MORAN, M. D. 2003: Arguments for rejecting the sequential Bonferroni in ecological studies. *Oikos* **100**: 403–405.

NYFFELER, M., MOOR, H. & FOELIX, R. F. 2001: Spiders feeding on earthworms. *J. Arachnol.* **29**: 119–124.

NYFFELER, M. & SYMONDSON, W. O. C. 2001: Spiders and harvestmen as gastropod predators. *Ecol. Ent.* **26**: 617–628.

PARISOT, C. 1962: Étude de quelques opilions de Lorraine. *Vie Milieu* **13**: 179–197.

PHILLIPSON, J. 1960: A contribution to the feeding biology of *Mitopus morio* (F) (Phalangida). *J. Anim. Ecol.* **29**: 35–43.

RIMSKY-KORSAKOW, A. P. 1924: Die Kugelhaare von *Nemastoma lugubre* Mull. *Zool. Anz.* **60**: 1–16.

SANKEY, J. H. P. 1949. Observations on food, enemies and parasites of British harvest-spiders (Arachnida, Opiliones). *Entomologist's mon. Mag.* **85**: 246–247.

SANKEY, J. H. P. & SAVORY, T. H. 1974: British harvestmen. *Synopses Br. Fauna* **4**: 1–76.

SUNDERLAND, K. D. & SUTTON, S. L. 1980: A serological study of arthropod predation on woodlice in a dune grassland ecosystem. *J. Anim. Ecol.* **49**: 987–1004.

SYMONDSON, W. O. C., SUNDERLAND, K. D. & GREENSTONE, M. H. 2002: Can generalist predators be effective biocontrol agents? *A. Rev. Ent.* **47**: 561–594.

TODD, V. 1949: The habits and ecology of the British harvestmen (Arachnida, Opiliones), with special reference to those of the Oxford District. *J. Anim. Ecol.* **63**: 209–229.

TODD, V. 1950: Prey of harvestmen (Arachnida, Opiliones). *Entomologist's mon. Mag.* **86**: 252–254.

TOFT, S. 1995: Value of the aphid *Rhopalosiphum padi* as food for cereal spiders. *J. appl. Ecol.* **32**: 552–560.

TOFT, S. 1996: Indicators of prey quality for arthropod predators. *In* K. Booij & L. den Nijs (eds), *Arthropod natural enemies in arable land. II. Survival, reproduction and enhancement*: 107–116. Århus: Aarhus University Press.

TOFT, S. 2005: The quality of aphids as food for generalist predators: implications for natural control of aphids. *Eur. J. Ent.* **102**: 371–383.

TOFT, S. & WISE, D. H. 1999a: Growth, development, and survival of a generalist predator fed single- and mixed-species diets of different quality. *Oecologia* **119**: 191–197.

TOFT, S. & WISE, D. H. 1999b: Behavioral and ecophysiological responses of a generalist predator fed single- and mixed-species diets of different quality. *Oecologia* **119**: 198–207.

VANACKER, D., DEROOSE, K., NIEUWENHUYSE, L. van, VANDOMME, V., VANDEN BORRE, J. & MAELFAIT, J.-P. 2004: The springtail *Sinella curviseta*: the most suitable prey for rearing dwarf spiders. *In* D. V. Logunov & D. Penney (eds), *European Arachnology 2003*: 333–342. Moscow: KMK Scientific Press Ltd.

WICKHAM, H. F. 1918: Feeding habits of a harvest spider (Phalangida). *Ent. News* **29**: 115.