FORAGING BEHAVIOUR OF ARMADILLIDIUM VULGARE (ISOPODA: ONISCIDEA) IN HETEROGENEOUS ENVIRONMENTS

by

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Summary

Foraging behaviour of *Armadillidium vulgare* was observed in laboratory arenas in which the spatial distribution of patches of high quality food (powdered dicotyledonous leaf litter) was varied within a background of low quality food (powdered grass leaf litter). The hypotheses that the foraging behaviour and foraging path of *A. vulgare* would be influenced by food quality and the patchiness of high quality food resources were tested.

More time was spent in high quality food patches than in low quality food backgrounds than expected by chance in all heterogeneity treatments, but an increasingly higher percentage of time was spent in low quality food as the high quality food became more clumped in space. More time was spent searching, but less time was spent feeding in low quality food backgrounds than in high quality food patches in all the treatments. Walking speed was found to be lower in high quality food patches than in low quality food backgrounds and this was not affected by treatment. Turning frequency and turning angle were found to be higher in high quality food patches than in low quality backgrounds. Turning frequency in low quality food backgrounds decreased as the high quality food became more clumped in space, whereas turning angle in high quality food patches significantly increased in the patchy, but then decreased again in the clumped treatment.

The effects of varying the spatial heterogeneity of high quality foods on the trade-off between costs of searching and intake benefits for saprophages are discussed in relation to predictions from optimal foraging theory for circumstances when intake rate maximisation is affected by the constraint of limited nutrients.

Keywords: optimal foraging, resource patchiness, food quality, terrestrial isopods, woodlice.

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Introduction

The fitness of an animal is affected by both the quality and quantity of its diet. For some animals maximizing the energetic gain from foraging is often constrained by the requirements for one or more essential nutrients (Stephens & Krebs, 1986; Bjorndal, 1989), most commonly nitrogen (White, 1993). There may be a trade-off between searching for foods high in nitrogen content and feeding on foods containing the most readily digested energy (Crawley, 1983).

Optimal foraging theory predicts that individuals will evolve foraging strategies that maximize net energy gain, subject to constraints of nutrient limitation, through trade-offs between the costs of searching for more profitable patches and benefits of immediate feeding (MacArthur & Pianka, 1966; Emlen, 1966; Krebs *et al.*, 1983). Both theoretical and empirical studies have shown that the behaviour of many predators and herbivores follow optimal foraging predictions (Hughes, 1993; Wanink & Zwarts, 1996; Seed & Hughes, 1997; Goldberg *et al.*, 1999). The trade-off between costs of searching and intake gains is not only strongly influenced by the spatial distribution of food resources (Pyke, 1984; Hassall, 1996; Wallis De Vries *et al.*, 1999) but also for herbivores by the quality of their food (Crawley, 1983).

Food quality is now widely recognized to affect foraging decisions of saprophages (Cadish & Giller, 1997) but almost nothing is known about how decomposers are affected by spatial heterogeneity in quality of nutritional resources. Grassland isopods are constrained by the nitrogen content of food (Rushton & Hassall, 1983; Hassall & Rushton, 1984). The terrestrial isopod *Armadillidium vulgare* both grows and survives better on a diet of dead dicotyledonous leaves than when fed only monocotyledonous material (Rushton & Hassall, 1983), so as both growth and survivorship are closely correlated with fitness, dead dicotyledonous food is by definition a higher quality food than dead monocotyledonous food (Crawley, 1983).

To investigate the effect of spatial heterogeneity in food quality on *A. vulgare* the difference in quality of the experimental foods needs to be confirmed and was studied by monitoring growth rates of *A. vulgare* on diets of two foods, differing in nitrogen content. The high quality food was naturally senesced leaves from the umbellifer alexanders *Smyrnium olusatrum* L. and the low quality food consisted of dead leaves from the grass *Festuca ovina*.

For *A. vulgare* in a heterogeneous grassland, a behavioural trade-off between foraging and sheltering results in a demographic trade-off between growth and survivorship rates respectively, the balance of which is determined by the patchy distribution of dicotyledonous plant leaf litter (Hassall, 1996). Animals exploiting patchy environments are known to modify their search path according to the quality of each patch (Gunn, 1937; Frankel & Gunn, 1961; Smith, 1974). Animals can modify their search path in a number of ways including modifying turning angle, frequency of turn alternation and walking speed (Stillman & Sutherland, 1990). This will consequently have effects on the amount of time an animal spends searching for high quality food and the amount of time it spends feeding on it.

We hypothesize that foraging behaviour of *A. vulgare* is affected by both food quality and the patchiness of high quality food resources. In this paper we therefore test the hypotheses that *A. vulgare* will alter its search path according to the quality of each patch in the grassland, and when high quality food is more clumped in space, so harder to find, it will spend less time feeding on it because it takes more time to find it. Experiments were designed to assess effects of spatial heterogeneity on foraging behaviour with treatments varying in the extent to which high quality food patches were clumped in space within a low quality food background. This represents in a simplified way the variety in the patchiness of these food types in heterogeneous grasslands (Hassall, 1996; Tuck, 2001).

Methods

Effect of food quality on growth

Growth chambers consisted of 170 × 115 × 55 mm transparent plastic boxes with lids containing a sloping base of plaster of Paris, sloping from a height of 30 mm at one end of the base to 10 mm at the other end, with 100 ml of water added to a foam rubber reservoir in the deeper end to maintain a humidity gradient along the length of the box. 50 ml of sand was placed over the base in the drier half of the box for shelter and an excess of 5.00 g of powdered food was placed on the plaster of Paris in the other half. One treatment contained *S. olusatrum* and the other *F. ovina*. There were five replicates of each treatment, each replicate box containing five individuals of differing sizes, over a comparable range in each box, so that specimens could be identified individually. The experiment was run at 15°C (12 h light, 12 h dark). Food was replaced with the same amount after two weeks to reduce mould and dead individuals replaced by similar sized specimens. Individuals were weighed at the beginning, if they were replacements and after 30 days.

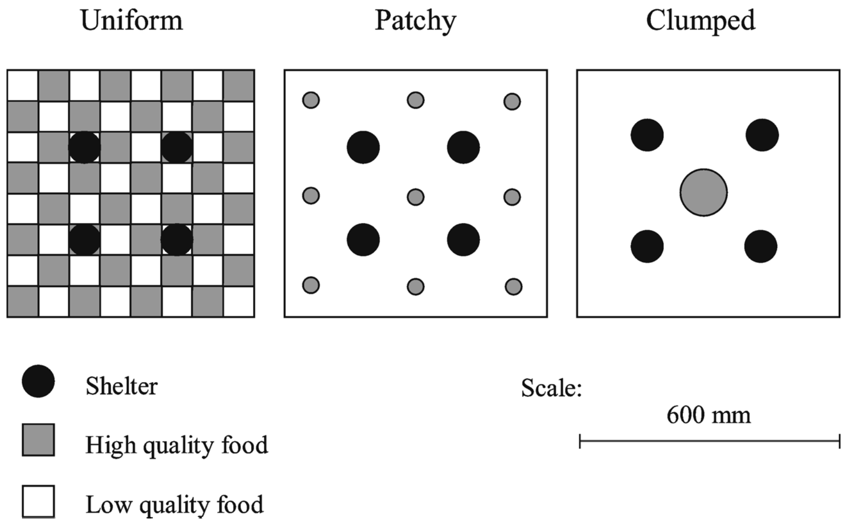

Fig. 1. Design of experiment to investigate effects of spatial heterogeneity of high quality food on the foraging behaviour of *Armadillidium vulgare*.

Effects of spatial heterogeneity in food on foraging behaviour

Experimental arenas 600 × 600 × 80 mm were made from plastic gravel trays lined with 20 mm of plaster of Paris and covered with 620 × 620 mm perspex airtight lids resting on foam rubber draft excluder fixed to the top of the tray walls to prevent animals escaping. The patchiness of a constant excess amount of high quality food, 1.90 g of powdered *S. olusatrum*, was altered in a low quality background of 9.60 g of powdered dead *F. ovina*. Foods were placed directly on the plaster of Paris in three treatments (Fig. 1): uniform, high quality food placed in alternate 75 × 75 mm squares with low quality food distributed in alternate squares; patchy, with the same quantity of high quality food restricted to nine 30 mm diameter patches; and clumped, with high quality food in one large 90 mm diameter patch. These arrangements of high quality food are within the range of patchiness of dicotyledonous plants observed in the field (Tuck, 2001).

The amount and patchiness of shelter was kept constant. The four shelters consisted of a 50 mm diameter petri dish half filled with plaster of Paris (containing 8 ml of water) filled to the brim with 10 ml of sand (with 3 ml of water added) to provide a refuge into which individuals could burrow during moulting, with a 52 mm diameter wooden circle with dowelling to support the centre (soaked in water) stuck into the sand. The edges of the shelters were 100 mm from the edge of the patchy and clumped food patches. To create a high relative humidity 200 ml of water was poured evenly on the plaster of Paris base in each arena before the start of each experiment. The observations were carried out in a dark room illuminated with a red light at approximately 20°C.

Ten medium sized (with headwidths of 0.8-1.1 mm) and ten large isopods (with head-widths of 1.4-2.0 mm) were given individual identities with 'Tipp-Ex' marks in different patterns on the pereion and placed in an arena. This density of 56 isopods m^{-2} is comparable to densities found in the field (Hassall & Dangerfield, 1997). Isopods were acclimatized with

12 h light at night time and 12 h dark during the day for one week before the experiment so that nocturnal foraging behaviour could be observed during the day. Experimental animals were acclimatized to the arena for 24 h before observations were made.

The detailed movements of 10 individual isopods selected in a random sequence were traced using an overhead projector pen on an acetate sheet for 15 minutes each, one after the other. All their movements and behavioural traits: time spent searching, turning frequency, turn angle, walking speed and time spent feeding in high and low quality food patches were recorded. Time spent searching was counted as time spent walking at any speed or in any direction whilst probing the surface with their antennae. Turning was counted as any turn that was made which was 10° or greater and feeding was identified by movement of the mouthparts and head. This procedure was carried out for each treatment.

Data were analysed using two-way ANOVAs to find significant effects of food quality on the different aspects of foraging behaviour and for significant interactions between food quality and the patchiness of the treatment. For each aspect of foraging behaviour t-tests were carried out within each heterogeneity treatment to compare high and low quality food.

To analyse for significant effects of the spatial heterogeneity of high quality food on the different aspects of foraging behaviour in both high and low quality food types one-way ANOVAs were used. *Post-hoc* tests were also carried out for each aspect of foraging behaviour in both types of food.

Results

Effects of food quality on growth

The relative growth rate of *A. vulgare* (5.7 ± 0.5 μg mg^{-1} day^{-1}) was significantly higher ($t = 3.585$, df $= 8$, $p = 0.007$) when fed a diet of exclusively *S. olusatrum* leaf litter than when fed a diet of only *F. ovina* leaf litter (1.9 ± 0.9 μg mg^{-1} day^{-1}).

Effects of food quality on foraging behaviour

In each treatment the amount of time spent in low and high quality food patches differed from the expected amount of time spent in each type of food patch by chance considering the area covered by each type of food, although this was only significant for the patchy treatment (Table 1). In each treatment less time was spent in the low quality food backgrounds and more time in the high quality food patches than expected by chance.

Of the total time spent in a food type the mean percentage of time spent searching was significantly higher in the low quality food background than in high quality food patches in both uniform and patchy treatments (Fig. 2a).

TABLE 1. *Time out of 15 minutes spent in low and high quality patches with increasing patchiness of high quality food*

	Time in different treatments (minutes)											
	Uniform				Patchy				Clumped			
	O	TV	*t*	*p*	O	TV	*t*	*p*	O	TV	*t*	*p*
Low quality food background	4.59	7.5	−1.761	0.112	10.83	14.735	−3.866	0.004*	13.74	14.735	−0.822	0.432
High quality food patches	10.41	7.5	1.761	0.112	4.17	0.265	3.866	0.004*	1.26	0.265	0.822	0.432

For all t values df = 9. O, observed; TV, test value, the expected time on basis of area covered by patches. *, where $p < 0.05$.

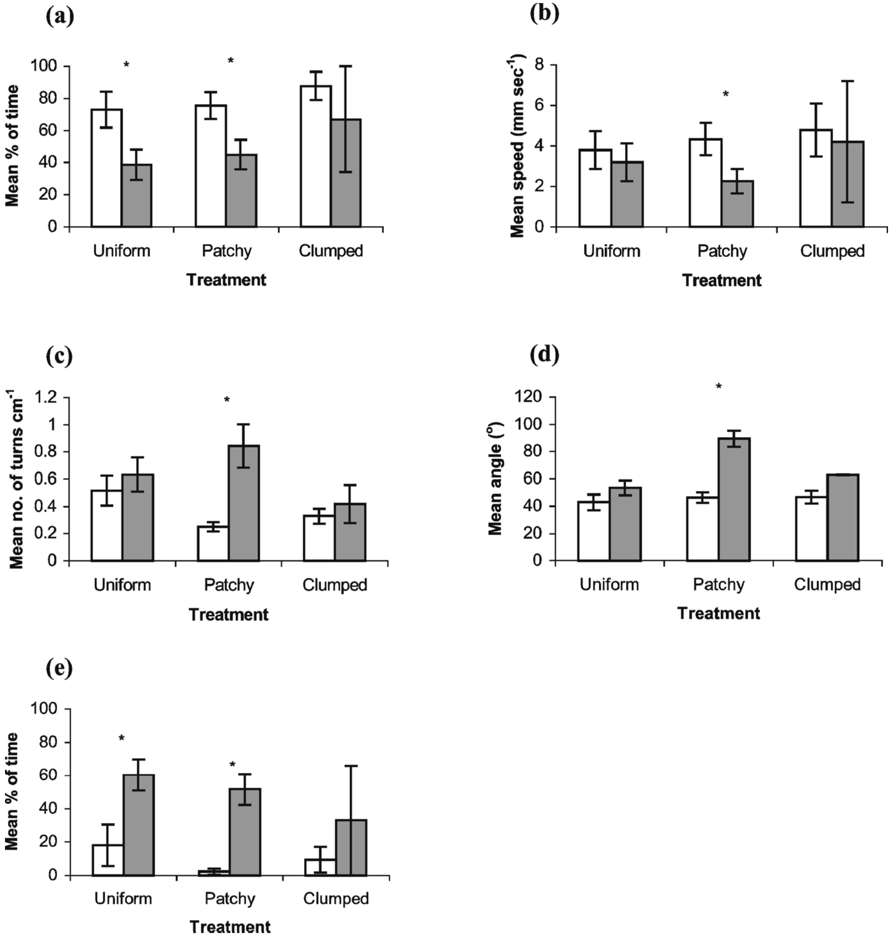

Fig. 2. Effects of □ low quality food *Festuca ovina* and ■ high quality food *Smyrnium olusatrum* on the foraging behaviour of *Armadillidium vulgare.* (a) Mean proportion of time in each of low and high quality food patches that was spent searching as the high quality food becomes more clumped (effect of food quality; $F_{1,41} = 6.691$, $p = 0.013$). (b) Mean walking speed in low and high quality food patches as the high quality food becomes more clumped. (c) Mean number of turns cm^{-1} in low and high quality food patches as the high quality food becomes more clumped (effect of food quality; $F_{1,41} = 5.984$, $p = 0.019$). (d) Mean turn angle in low and high quality food patches as the high quality food becomes more clumped (effect of food quality; $F_{1,41} = 19.777$, $p < 0.001$). (e) Mean proportion of time in each of low and high quality food patches that was spent feeding as the high quality food becomes more clumped (effect of food quality; $F_{1,41} = 19.771$, $p < 0.001$) (asterisks between pairs of bars mean that the values differ at $p < 0.05$), $N = 10$.

Isopods walked more slowly (Fig. 2b), turned more often (Fig. 2c) but at greater angles (Fig. 2d) in high quality food patches than in low quality ones, significantly so in the patchy treatment.

A. vulgare spent a greater proportion of the total time that they were in a food type feeding when in high quality food patches than when in low quality food backgrounds in both uniform and patchy treatments (Fig. 2e).

Effects of spatial heterogeneity of high quality food on foraging behaviour

The proportion of time *A. vulgare* spent in an arena in the low quality food background increased significantly and time in the high quality patches decreased significantly as the high quality food became more clumped (Fig. 3a & b). Increased patchiness of high quality food resulted in $61.0 \pm 13.7\%$ less time spent in the clumped high quality patch than in uniform patches.

The turn frequency in the low quality background was lower in the patchy and clumped treatments than in the uniform treatment, significantly so in the patchy treatment (Fig. 3c). The mean turn angle in high quality patches was significantly higher in the patchy treatment than in the other two treatments (Fig. 3d).

There was no significant effect of the spatial heterogeneity of high quality food on the mean proportion of time in low or high quality food patches spent searching or feeding or on the mean walking speed in low or high quality food patches.

Discussion

It is evident that *Armadillidium vulgare* displays higher growth rates when fed a diet consisting solely of the umbellifer *Smyrnium olusatrum* litter compared to the grass *Festuca ovina* litter, which is likely to be a result of the significantly higher nitrogen content of *S. olusatrum* litter (Tuck, 2001). Rushton & Hassall (1983) also showed that survivorship and reproduction were significantly lower on a diet of *F. ovina* litter than when fed on litter from dicotyledonous plants with higher nitrogen contents, the wider significance of which was reviewed by Hassall & Rushton (1984). This experiment shows that *F. ovina* litter is a lower quality diet in that this isopod shows clear fitness costs when fed on it compared with when fed on *S. olusatrum*, which is therefore, by Crawley's (1983) definition, a higher quality food.

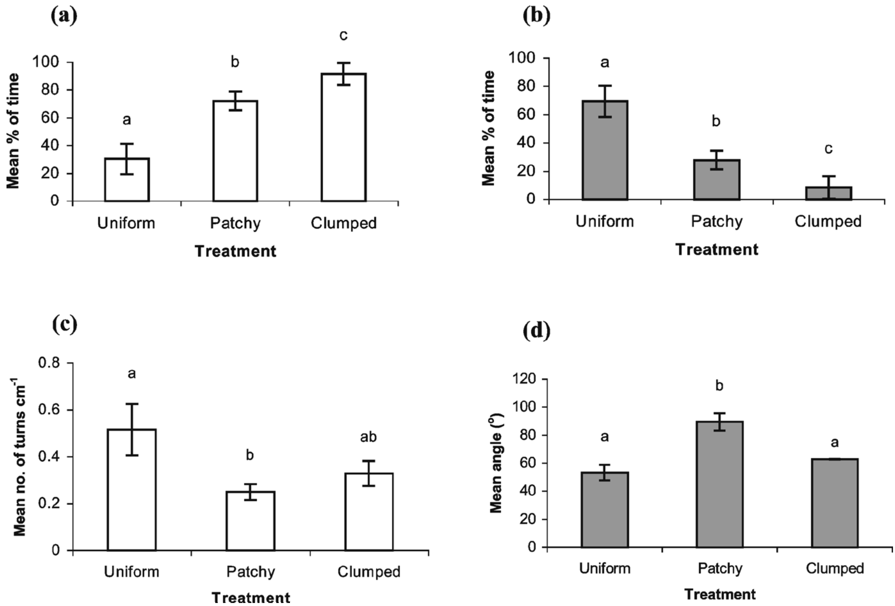

Fig. 3. Effects of spatial heterogeneity of ■ high quality food *Smyrnium olusatrum* in a □ low quality food *Festuca ovina* background on the foraging behaviour of *Armadillidium vulgare*. (a) Mean percentage of time spent in an arena in low quality food backgrounds as the high quality food becomes more clumped. (b) Mean percentage of time spent in an arena in high quality food patches as they become more clumped. (c) Mean number of turns cm^{-1} in low quality food backgrounds as the high quality food becomes more clumped (effect of treatment; $F_{2,24} = 4.013$, $p = 0.031$). (d) Mean turn angle in high quality food patches as they become more clumped (effect of treatment; $F_{2,17} = 10.841$, $p = 0.001$) (different letters for different bars mean that the values differ at $p < 0.05$), $N = 10$.

Phytophages need to select a balanced diet, not just maximizing the rate of energy gain, but also obtaining the right balance of nutrients (Crawley, 1983; Behmer *et al.*, 2002). The need for a mixed diet for optimal nutritive gain for isopods has been shown (Rushton & Hassall, 1983; Hassall & Rushton, 1984), so it would be expected that *A. vulgare* would feed on both types of food offered in this experiment, as was found. *A. vulgare* in the field is confronted by a trade-off between maximizing intake rates by eating abundant widely distributed low quality graminaceous plant litter and minimizing the nutrient constraints by searching for higher quality less abundant and more heterogeneously distributed dicotyledonous litter. In these experiments where in two treatments the high quality food was more clumped there were increased costs of searching for a potentially more profitable food resource.

In these treatments it can therefore be predicted from optimal foraging theory that individuals would modify their foraging strategy in order to maximize their fitness (MacArthur & Pianka, 1966).

A. vulgare spent more time in high quality food patches than in low quality food backgrounds in each treatment than expected by chance (although the mechanism by which they detect this is not the subject of this study) confirming this preference for high quality food which could be predicted from the fitness benefits of higher growth rates when fed on this food. Of the time spent in high and low quality food patches *A. vulgare* spent more time searching when in low quality food backgrounds than in high quality patches. The time spent searching in low quality food backgrounds increased with increasing heterogeneity of the high quality food.

Animals exploiting patchy environments modify their search path according to the quality of each patch (Gunn, 1937; Frankel & Gunn, 1961; Smith, 1974; Pyke, 1984) which affects the costs of searching for high quality food. Many studies have shown that animals, including the terrestrial arthropod *Porcellio scaber* (Gunn, 1937), slow down in better patches (Pienkowski, 1983) and also turn more frequently, associated with greater turning angle (Stillman & Sutherland, 1990), causing the animal to stay in a good patch. Many insects and mites show increased turning behaviour after finding a food item (Hassell & Southwood, 1978). As high quality food becomes more heterogeneously distributed it can be predicted that *A. vulgare* would walk faster, turn less often and with lower angles in low quality food patches compared to in high quality food patches. *A. vulgare* was found to behave in this way when comparing its behaviour in the patchy treatment to that in the uniform treatment (the clumped treatment was not so clear as few animals made it into the patch).

The lower turning frequency, with lower turn angles, in the low quality food background would have resulted in the woodlice moving through the low quality food more directly, increasing the probability of them encountering a patch of higher quality food. The turning frequency in low quality food was less in the patchy and clumped treatments than in the uniform treatment possibly because the low quality food formed a background covering a larger area of the arena in the patchy and clumped treatments, so increasing the benefits of moving straight through the more extensive low quality food.

A. vulgare turned more frequently, through greater angles, in high quality food patches than in low quality food backgrounds. This was most significant in the patchy treatment which is likely to be because in this treatment the patches of high quality food were small (30 mm in diameter) so more frequent turning with greater angles would have resulted in individuals staying within the patches for longer. It is therefore possible that *A. vulgare* can detect the boundaries of high quality patches.

Within the time spent in high and low quality food patches the time spent feeding by *A. vulgare* was higher in high quality food patches than in low quality backgrounds. Therefore as the time spent in high quality food patches decreases as high quality food becomes more clumped in space it follows that individuals will spend less time feeding on high quality food the more clumped the high quality food. In heterogeneous grasslands where dicotyledonous plants are very heterogeneously distributed (Hassall, 1996; Tuck, 2001) this has clear implications for fitness.

This study illustrates the importance of food quality in influencing the foraging behaviour of this macro-decomposer. Furthermore it shows that these terrestrial isopods alter the component traits of their foraging behaviour in response to spatial heterogeneity of high quality food so as to maximize their probability of encountering high quality patches and the time they spend feeding within them.

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