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Nilsson, Elna; Bengtsson, Göran

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Elna Nilsson and Göran Bengtsson

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We used video-tracking of individuals of a Collembola, *Protaphorura armata*, on a clay surface in a petri dish to analyse their movement pattern in an environment with attractive and repellent cues. An area with dead conspecifics was repellent whilst live conspecifics made the area attractive. An area which had been occupied for 24 hours by the predatory mite, *Hypoaspis aculeifer*, was avoided only if the mite had preyed upon *P. armata* before it was placed in the area. *P. armata* lost their looping behaviour, moved faster and more straightened out (decreased turning rate) in the presence of attractive or repellent odours. The resulting net squared displacement was faster than in the control and best described as a correlated random walk. Our results emphasise the importance of considering varying movement pattern in response to environmental cues when predicting dispersal and spatial distribution of an animal.

E. Nilsson and G. Bengtsson, Dept of Ecology, Lund Univ., Sölvegatan 37, SE-223 62 Lund, Sweden (elna.nilsson@ekol.lu.se).

A prey can recognise a predator directly by visual, auditory and olfactorial cues or indirectly from e.g. the odour of alarmed, injured and dead conspecifics. Such odours are sometimes called alarm pheromones (Purrington et al. 1991), and sometimes injury-released chemical cues (Wisenden et al. 1999), endogenously produced repellents (Rollo et al. 1995), or necromones (Rollo et al. 1994). It is often not known whether the odour is an "intentional signal", such as a pheromone, or a metabolite, in e.g. the hemolymph.

Soil animals use chemical cues to recognise conspecifics, food, and predators at a distance and to adjust their distribution and movement in relation to those sources. This requires well developed chemical senses, as in the free-living nematode *Caenorhabditis elegans*, which can detect hundreds of compounds (Troemel 1999). Sexual and aggregation pheromones link conspecifics in the soil and are present in nematodes (Bone and Shorey 1978) and collembolans (Verhoef et al. 1977, Joosse and Koelman 1979, Leonard and Bradbury 1984). Collembola and nematodes are also able to detect and choose among different food odours (Bengtsson et

al. 1988, Bengtsson et al. 1991, Anderson et al. 1997a). However, chemical communication is virtually unknown in soil compared to aquatic and above-ground environments. Perception of chemical cues from a predator (kairomones) has not been observed in soil-living prey, and alarm signals are known only in soil-living mites (Diaz et al. 2000) and collembolans (Purrington et al. 1991, Messer et al. 1999).

Prey respond to predator cues by hiding, reducing their locomotory activity, by defence or escape behaviour (Dicke and Grostal 2001). Prey detected by visual or auditory cues can benefit from hiding or freezing their movement. This strategy seems less useful for springtails, which are detected by chemical cues by certain predators (Schlegel and Bauer 1994), unless they are able to hide their odour. The option would then be defence or escape. Collembola with a furca can jump away from their predators, but some soil-living species have a reduced spring organ and defend themselves by secreting a fluid which is repellent to certain predators (Usher and Balogun 1966, Dettner et al. 1996). The escape may be triggered by alarm signals from conspecifics and lead to

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a changed movement pattern. The activity or speed of the movement has been used to characterise predator escape in arthropod preys (Dicke and Grostal 2001), but the turning behaviour could also be affected. A prey can use different movement patterns, e.g. a straight line or a zigzag-line, to escape a predator. Some prey can even adjust their movement to the speed of the predator or to the distance to the predator (Furuichi 2002).

The main predators of Collembola are probably other arthropods, and soil-living predatory mites can survive and breed successfully on Collembola as the only prey (Krogh 1995). The aim of this study was to elucidate a below-ground prey response by determining if and how the collembolan species *Protaphorura armata* can detect and avoid a predator. We expected the blind and soil-living *P. armata* to use its olfactorial sense in recognition of a predator, either by direct or indirect cues. Interferences from other odour sources in their natural habitat than those tested were excluded by assaying the behaviour on a plane surface without soil. We used a video-recording equipment to follow individuals on the plane surface where half of the area was treated with possible repellents, viz. predators, dead conspecifics, or known attractants, i.e. live conspecifics (Joosse and Koelman 1979). Since *P. armata* tends to increase its migration rate in response to both attractive, e.g. food odour (Bengtsson et al. 1994a), and repellent forces, e.g. high metal concentration in soil (Sjögren 1997), we expected a changed movement pattern both in response to cues from live conspecifics and predators.

Material and methods

Organisms used

Specimens of the Collembola *Protaphorura armata* (Tullberg) were extracted from a soil of a deciduous forest near Lund (Sweden) and kept in darkness in petri dishes (90 mm in diameter) with a bottom of moistened plaster of paris and activated charcoal. They were continuously fed with the fungus *Verticillum bulbillosum* (W. Gams and Malla). Individuals chosen for the experiment were 1–1.5 mm long, corresponding to an age of more than 70 days (Bengtsson et al. 1983). The predatory mite, *H. aculeifer* (Canestrini), was delivered in a mixture of peat and vermiculite (BioProduction, Denmark), in which they were kept until used (less than one week) without adding any food. The delivering company assured that the mites had no former experience of *P. armata* as prey, but what they had been fed during breeding was a trade secret.

Experimental set-up

Observations of the movement pattern were made on petri dishes (90 mm in diameter) half-filled with clay (Skromberga clay Hb20; 45% quartz, 5% chlorite, 50% illite), dyed black by adding Fe_3O_4 (8:1). The clay surface was replaced between each set of observations so that odour from a previous individual should not affect the movement pattern of the next one.

Treatments

The petri dish was divided into two equally large areas, and in each treatment one side of the petri dish (the test area) was prepared in the different ways described below and the other left untreated. A control treatment had both sides of the petri dish untreated. When the test area was conditioned with live animals, viz. treatment 1, 2, 4, 9 and 10 below, a piece of carton hindered the mites and collembolans from moving into the control area.

Response to a predator

A response to one or more of the following three treatments would indicate an ability of *P. armata* to detect a predator by direct chemical cues.

1)   Five predators, *H. aculeifer*, spent 24 h in the area and were removed before the movement of *P. armata* was recorded.
2)   Five predators, *H. aculeifer*, were put in a petri dish with a bottom of moistened plaster of paris and activated charcoal and fed with *P. armata* for one week before used as in (1).
3)   Five predators, *H. aculeifer*, were killed in the test area and the content of the bodies was smeared on the surface with a brush.

Response to dead conspecifics and dead individuals of another Collembola species

The following treatments were added to test (i) the ability of *P. armata* to detect dead conspecifics by chemical cues (treatment four and five), (ii) the persistence and volatility of the cues (treatment six and seven) and (iii) the response to dead individuals of another Collembola species (treatment eight).

4)   Five predators and five *P. armata* were placed in the test area. After 24 h, any surviving *P. armata* (very rare) and the predators were removed.
5)   Three *P. armata* were killed in the test area and the content of the bodies was smeared on its surface with a brush.

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6) The area was prepared as in (5) but the dish was left with the lid on for 24 h before recording to test the persistence of the effect in (5).
7) Three *P. armata* were killed on the part of the glass lid that covered the test area, and the content of the bodies was smeared on its surface with a brush. If an effect was found in (4) and repeated in this treatment, the cue would be considered volatile.
8) Five *Folsomia candida* (Willem) (Collembola) were killed in the test area and the content of the bodies was smeared on the surface with a brush.

Response to stressed and undisturbed conspecifics

A response to treatment nine would indicate that stressed *P. armata* releases an alarm signal. A treatment with live and undisturbed individuals (treatment ten) was included as a reference in a comparison of the movement pattern in treatments with dead and stressed conspecifics.

9) Three *P. armata* were disturbed by repeatedly touching them with a brush in the test area for five minutes without damaging their bodies. They were removed before recording.
10) Three *P. armata* were allowed to move in the test area for 24 h and removed before recording.

Video recording

The different treatment and movement observations were made in a temperature-controlled room ($20 \pm 0.5°C$). To avoid disturbing the animals with daylight, the video recordings were made in red light from four sources (red darkroom lamp 230 V Philips). One individual at a time was placed in the petri dish and tracked for 30 min. The petri dish was covered with a glass lid during recording in order to keep the environment moist and avoid disturbance, and each treatment was replicated ten times. The treatments were done in a random order and half of the control treatment replicates were tracked in the beginning of the whole experiment and the other half in the end. The image of the petri dish was captured by a monochrome video camera (Cohu 4710), and digitised by a framegrabber (VIGA+) connected to a personal computer. Image processing was performed by using EthoVision® (Noldus Information Technology, Wageningen, The Netherlands), which provides both object detection and data analysis. Detection of the animals was based on a grey scaling. One image per second was processed and resulted in a time series of X,Y-coordinates indicating the position of the animal.

Data analysis

Data analysis was carried out in three different ways; first, by using the built-in functionality of EthoVision®, second by transferring the data files with coordinates to SPSS (SPSS Inc.), and third by using the data to make 95% confidence interval of net squared displacement with the bootstrap method in Matlab (Mathworks). Resampling at a coarser scale was done to exclude body movement from side to side from data analysis as recommended by Turchin (1998). Hence, the time step between samples was 2 seconds. From EthoVision® we extracted the following parameters for each individual:

A) Total distance moved (cm) in control and test area.
B) Speed (mm/s), mean speed of all sampling intervals for an individual moving in the whole area.
C) Turning rate per distance (°/cm), mean of turning rates (independent of sign) between the movement vectors of two consecutive sampling intervals divided by the distance moved.
D) Relative turning angle (°/step), the signed angle between the movement vectors of two consecutive sampling intervals.
E) Step length (cm), the distance, measured from a straight line, moved by an individual between two consecutive samples.

Sampling at the edge of the petri dish was excluded from the calculations of parameters B–E.

The possibility that the moving distances in control and test area in the petri dish were equal was tested with a paired t-test. When the distance moved in the control area was significantly longer or shorter than that in the test area, the individuals of a treatment were considered repelled or attracted to the cues tested. The speed and turning rate per distance in the treated and control petri dish were compared with Mann-Whitney U-test. We only made planned comparisons, and no tests of differences between treatments were done.

SPSS was used to calculate the observed and predicted net squared displacement (cm^2). Net squared displacement was used to characterise the movement pattern of individuals in the different treatments but also to estimate the effect on the dispersal capability. Means of replicates were used but the net squared displacement was based on the observations until the first individual of a treatment reached the edge. We calculated predicted net squared displacement (R_n^2) as described in Appendix A. The corresponding diffusion rate was calculated from $D = m_2/(4 \times t)$ (Turchin 1998), where m_2 is the mean of the squared step lengths (Appendix A) and t is duration of a step (2 seconds in the test), using data from the control treatment. The distribution of step lengths and relative turning angles were used to calculate a 95% confidence interval for net squared displacement with the bootstrap method (Turchin 1998).

Results

Protaphorura armata used cues from a predator for avoidance only when the predator had prior experience of *P. armata* as a prey (Fig. 1A:1–4), without attempting to change the speed (Fig. 2:1–4) or turning rate (Fig. 3:1–4). Neither a predator inexperienced of collembolans as prey (Fig. 1A:1) nor one killing and eating *P. armata* in the petri dish (Fig. 1A:4) made the area repellent. The odour of dead conspecifics was strongly repellent (Fig. 1A:5–7), as opposed to the odour of dead collembolans of another species (Fig. 1A:8) or dead predators (Fig. 1A:3). Except for the treatment with a time-delay between the killing of conspecifics on the surface and recording them (Fig. 1B:6), repellence and attraction were only observed for the first ten to twenty minutes, whereafter the effect faded (Fig. 1B). There was a response in treatment six (Fig. 1A:6), where we waited for 24 hours after killing the conspecifics before recording an individual, suggesting that the active chemicals were present for at least 24 hours. If the repellent was still present after twenty minutes of recording the lack of response in Fig. 1(B) may be due to saturation of the

sensory system in the individuals, which leads to decreased sensitivity to a stimulus (reviewed by Dalton 2000). It is also possible that diffusion of volatiles from the odour source removed the concentration gradient used by individuals for orientation. The repellence effect of dead conspecifics increased the speed (Fig. 2:5–7) and decreased the turning rate (Fig. 3:5–7). As a result, the walking pattern became straightened out, and *P. armata* repelled by the odour of dead conspecifics had almost one order of magnitude larger net squared displacement than in absence of the odour (Fig. 4A).

The odour of live conspecifics made the area attractive (Fig. 1A:10), but if the conspecifics were stressed in the petri dish as described, the area was neither attractive nor repellent (Fig. 1A:9). The tracks left by live undisturbed and stressed conspecifics had the power to raise the speed (Fig. 2:9) and decrease the turning rate per distance (Fig. 3:9). Their net squared displacement approximated a correlated random walk (Fig. 4B), characterised by absence of loops, high speed and slow turning rates. In contrast, the looping behaviour, higher turning rates, and lower speed in the control resulted in a more limited displacement, which was better predicted
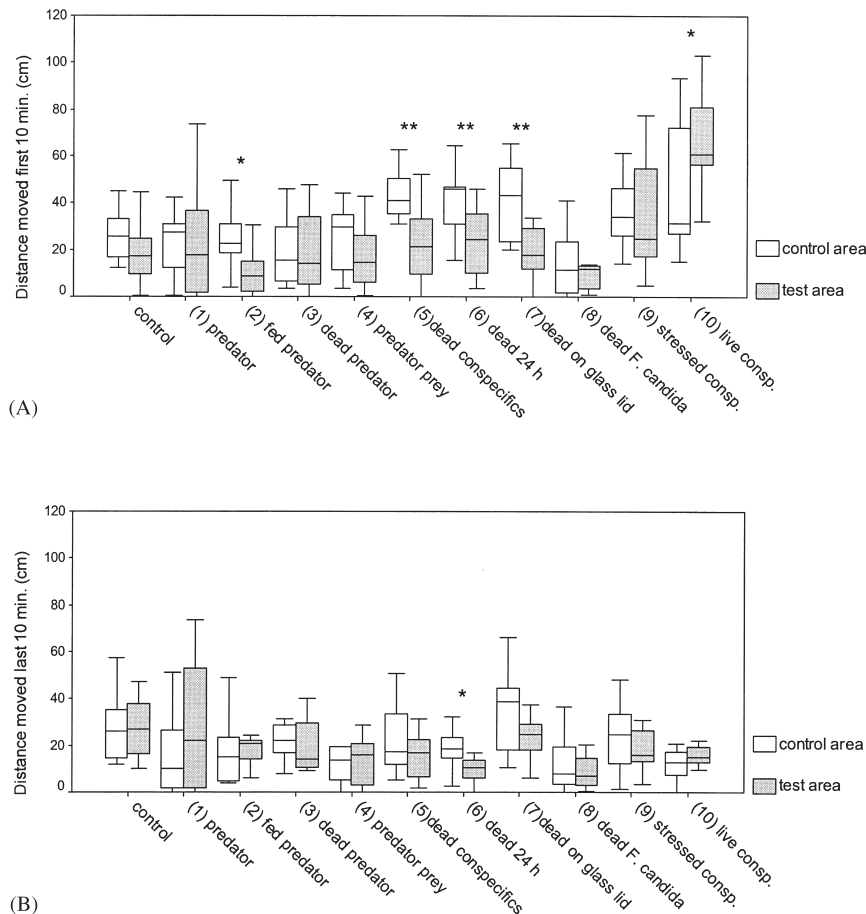

(A)

(B)

Fig. 1. Total distance (cm) moved by *P. armata* during (A) the first ten minutes of recordings (exception was the treatment with live conspecifics, where the individuals moved for twenty minutes), and (B) distance moved during the last 10 minutes of recordings in the control and test area. The test area of the petri dish was treated as indicated below the x-axis. The numbers in parentheses refer to the numbers assigned a treatment in the method section. The plot gives the 10th, 25th, 50th (median), 75th and 90th percentiles of the variable. There are significant differences in distance moved in control and test area in (A) in treatment (2) (t = 2.92, p = 0.014), (5) (t = 3.16, p = 0.009), (6) (t = 3.12, p = 0.011), (7) (t = 3.22, p = 0.008), and (10) (t = −2.31, p = 0.043). In (B) there are significant differences in treatment (6) (t = 2.39, p = 0.038). Significance levels are illustrated in the graph by asterisks, *: p ≤ 0.05 and **: p ≤ 0.01.

Fig. 2. The mean speed of *P. armata* (mm/s) in the different treatments during the first ten minutes of recordings. Symbols and abbreviations as in Fig. 1. There are significant differences between the speed in the control and treatment (5) (Z = − 2.70, p = 0.007), (6) (Z = − 2.27, p = 0.023), (7) (Z = − 2.47, p = 0.013), (8) (Z = − 2.24, p = 0.025), (9) (Z = − 3.403, p = 0.001) and (10) (Z = − 2.91, p = 0.004). Significance levels are illustrated in the graph by asterisks, *: p ≤ 0.05 , **: p ≤ 0.01 and ***: p ≤ 0.001.
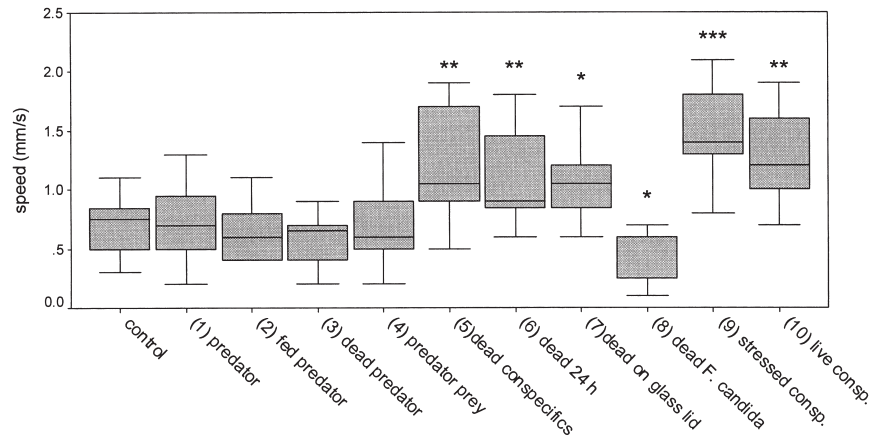
by a random walk (Fig. 4C). The diffusion rate calculated from a random walk in the control was 407 cm²/day.

Discussion

The demonstration of the ability of *P. armata* to recognise and respond to living and dead conspecifics by attraction and avoidance is an acknowledgement of earlier observations of the importance of odour cues in discriminating among food sources (Bengtsson et al. 1991) and detecting conspecifics (Joosse and Koelman 1979). The findings add further evidence to the understanding of chemical communication as a major factor influencing spatial distribution of Collembola.

The ability to recognise dead conspecifics is known from ants and bees, which quickly find and remove a dead body from the nest (Howard and Tschinkel 1976, Visscher 1983). This cleaning is thought to prevent

vector born diseases from being transmitted in the population. Other reactions, such as reduction of the movement of larvae of a mayfly (*Siphlonurus* sp.) in presence of volatile compounds from injured conspecifics (Huryn and Chivers 1999), and a movement to areas with lower predation risk in thrips (*Frankliniella occidentalis*) exposed to odours from predators eating conspecifics (Venzon et al. 2000), are interpreted as predator avoidance. A species that is preyed upon by a few specialist predators may be able to recognise them from their odour, while a prey with a variety of generalist predators, such as many springtails (Foster 1970, Ernsting and Joosse 1974, Johnson and Wellington 1980, Schlegel and Bauer 1994), would require an elaborate perception system to recognise each of them. Selection would likely favour a more general recognition system, e.g. based on the odour of injured or dead conspecifics (Grostal and Dicke 2000). It is also possible that a prey can detect a predator faster by perception of the odour of injured conspecifics since that cue could precede the

Fig. 3. Turning rate per distance (°/mm) of *P. armata* in the different treatments during the first ten minutes of recordings. Symbols and abbreviations as in Fig. 1. There are significant differences between the turning rate per distance in the control and treatment (5) (Z = − 3.41, p = 0.001), (6) (Z = − 2.89, p = 0.004), (7) (Z = − 3.00, p = 0.003), (9) (Z = − 3.94, p < 0.001) and (10) (Z = − 3.57, p < 0.001). Significance levels are illustrated in the graph by asterisks, **: p ≤ 0.01 and ***: p ≤ 0.001.
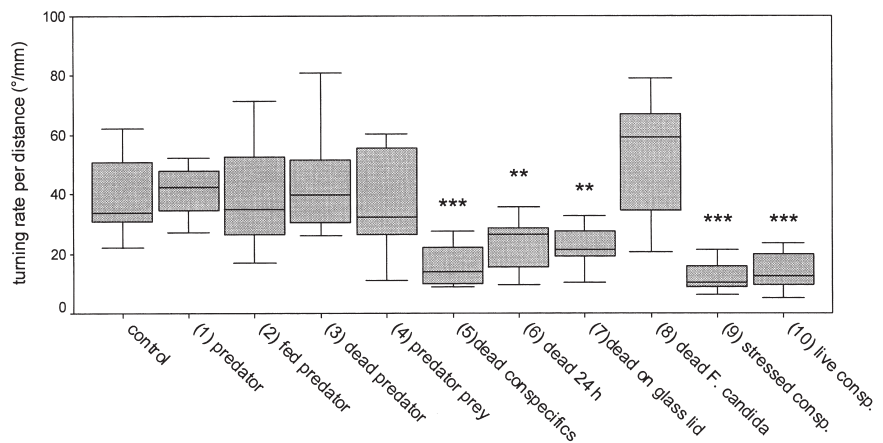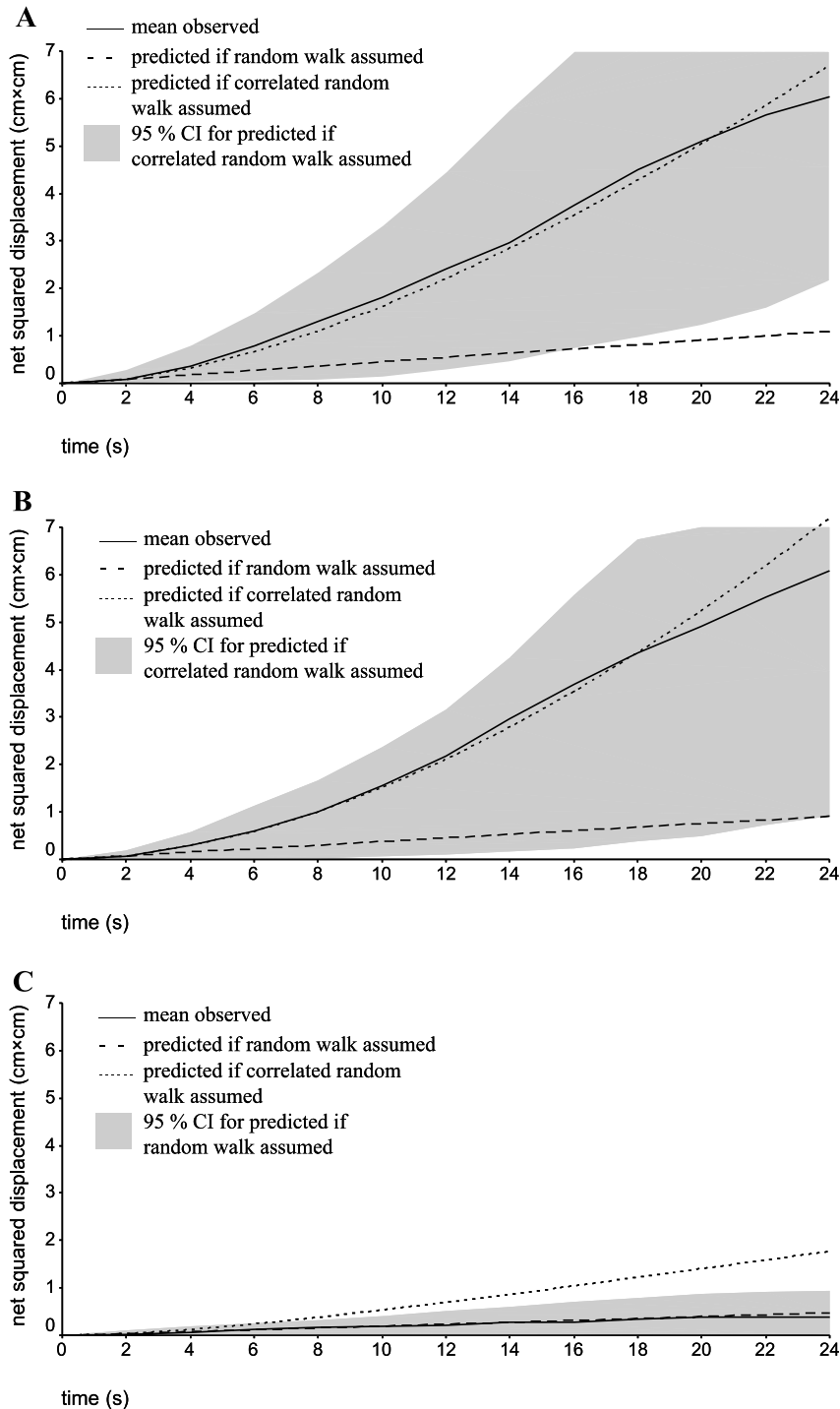
Fig. 4. Observed and predicted net squared displacement (cm^2) on petri dishes treated with (A) repelling odour, i.e. conspecifics killed in the test area (treatment 5), (B) attracting odour, i.e. live conspecifics moving in the test area prior to recording (treatment 10), and (C) on control petri dish, i.e. untreated test area. The shaded area represents the 95% confidence interval of the predicted displacement.

odour of a predator (e.g. from predator feces, Grostal and Dicke 2000).

The phenomenon of prey perception limited to odour of predators that have eaten prey conspecifics is known

from other studies (Chivers et al. 1996, Laurila et al. 1997, Grostal and Dicke 2000, Venzon et al. 2000). The effect can be due to a general recognition of carnivores, which are known to excrete specific protein metabolites

(Nolte et al. 1994), or a recognition of predators that smell from prey alarm substances (Howe and Harris 1978). The latter explanation seems more applicable to the recognition of *H. aculeifer* by *P. armata* since the odour of the unfed predator was ignored by the prey but the odour after one week of feeding on *P. armata* was avoided. The feeding of the mite with collembolans for 24 hours before the movement assay may have been too short to leave sufficiently strong traces of alarm substances or predator excretions to be perceived by the prey. It is also possible that the absence of a net response to the predator and prey treated area after 24 hours came from a conflict between attraction to the tracks of conspecifics before they were eaten and avoidance of the tracks of the fed predator and dead conspecifics.

Attraction and repulsion mostly changed the movement pattern of *P. armata*, but in two treatments, i.e. when the test area was treated with stressed individuals and with dead *F. candida*, the change of speed was not connected with attraction or repulsion. The short conditioning time of the area with stressed individuals (5 min) may explain this result and if we would have been able to condition the area with stressed individuals for the same time as with live and dead individuals attraction or repellence may have occurred. The decelerated speed on petri dishes with odour of dead *F. candida* could correspond to the arresting behaviour in an olfactometer prepared with food odours (Bengtsson et al. 1991). However, if the odour of dead animals in general was recognised as a possible food source by *P. armata*, a lower speed should also have followed the application of dead predators to the petri dish.

The observation of increased movement speed of *P. armata* triggered by attractive or repellent forces has an analogue in soil (Bengtsson et al. 1994a), in which attractive food sources increased the dispersal rate by more than four times, high population density by two times. *P. armata* also move with enhanced velocity in a soil gradient of metal concentrations (Bengtsson et al. 1994b). Similarly, nematodes increase their speed in response to food odour in the soil (Young et al. 1998) and substitute loops with a more directed walk in presence of attractive odours (Anderson et al. 1997a). These results taken together give confidence to the qualitative extrapolation of the observations on the influence of odour on the walking behaviour of *P. armata* on a plane surface to the soil environment. The three dimensional pore size and fracture distribution in a soil call for scaling translation in extrapolations since the diffusion coefficient calculated from our data, 407 cm^2/day, was much higher than that estimated for a soil, 0.5–8 cm^2/day (Bengtsson et al. 2001).

The random walk model predicted the net squared displacement of individuals in the untreated petri dish (Fig. 4C), even if the assumptions of evenly distributed turning angles were not met. *Protaphorura armata* moves with a bias towards smaller turning angles, but the looping behaviour gives a displacement in agreement with a random walk model. Although this experimental set-up was not optimal for dispersal studies because of the short distance to the edge of the petri dish, the introduction of a chemically heterogeneous environment with attractive and repellent sources apparently decreased looping, reduced the turning angles, increased the speed and made a correlated random walk model a better choice of description of the movement pattern. It is possible that either model can be used to predict dispersal, for example by adding chemotaxis to the random walk model or looping behaviour and chemotaxis to the correlated random walk, but the extent of autocorrelation both in turning angles and speed must first be addressed. A random walk model with both looping behaviour and chemotaxis was used to describe nematode movement (Anderson et al. 1997b), and Holmes et al. (1994) added attraction/repulsion between conspecifics to a random walk. A model with a conspecific interaction term, with attraction and repellence depending on the distance between individuals, gives a better prediction of dispersal of *P. armata* in soil than a pure random walk (Bengtsson et al. 2001).

Varying movement pattern in a heterogeneous environment can be used to explain and predict the spatial distribution of animals (Turchin 1991, Boughton 2000). If the response by *P. armata* in this experiment can be taken as a general repellence and attraction response, the movement will be higher in areas with detectable cues and lower in areas without. The latter may be rare why the movement pattern observed during attraction and repellence would be common. That means that *P. armata* may have a high movement activity between attracting patches but not within, whereas a soil with a high frequency of patches with repellent cues may support a high emigration rate from the area.

Hypoaspis aculeifer is attracted to the preferred food of another fungivorous Collembola but not to the prey itself (Hall and Hedlund 1999). Thus, both Collembola and their predators can be attracted by fungal odour. However, our results suggest that fungal patches may repel *P. armata* as their predators assemble there and catch prey. The recognition of generalist predators by death odour may moderate top-down control of soil food webs and make prey with that ability less dependent on variations in predator density than prey without. The indirect olfactorial predator recognition and subsequent faster movement in *P. armata* may also have implications for their spatial distribution in soil and mobilisation of nutrients by grazing. It is possible that the predator memory effect clears away *P. armata* from certain patches and adds to the heterogeneity of their distribution and helps to explain e.g. the insensitivity of primary production to removal of top predators in decomposer food webs (Laakso and Setälä 1999).

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Appendix A

A.1. Calculation of predicted net squared displacement

We used the following equations to calculate predicted net squared displacement (R_n^2):

(i) for a random walk: $R_n^2 = nm_2$, where n is the number of moves taken (one move lasted for two seconds in the tests), and m_2 is the mean of the squared step lengths calculated as: $m_2 = (1/k)\Sigma_{i=1}^{k} l_i^2$, where l_i is the i:th step length and k is the number of steps.

(ii) for a correlated random walk:

$$R_n^2 = nm_2 + 2m_1^2 \frac{\psi}{1-\psi}\left(n - \frac{1-\psi^n}{1-\psi}\right)$$

(Kareiva and Shigesada 1983), where m_1 is the mean of the step lengths calculated as $m_1 = (1/k)\Sigma_{i=1}^{k} l_i$, and ψ is the mean cosine value of turning angles, θ, calculated as $\psi = (1/s)\Sigma_{i=1}^{s}\cos\theta_i$, where s is the number of turning angles (s = k − 1).

A random walk assumes no autocorrelation in any movement parameter. This should give an even distribution of turning angles, i.e. changing direction by 180° is as likely as turning 30°, and the R_n^2 will give the same value for a random walk and a correlated random walk, since ψ will be zero. In a correlated random walk, the direction of a step is not independent of the direction of the former step; there is an autocorrelation in step movement direction, resulting in a non-even distribution of turning angles. For most animals, the movement pattern is more straightened out than is predicted by a random walk, typically with the turning angles distributed around zero and with a higher probability for smaller than larger turning angles. This results in a positive ψ making the second term in the correlated random walk equation positive. If the movement is assumed to follow a random walk, the net squared displacement will be underestimated. However, the correlated random walk expression does not allow autocorrelation in any other movement parameter than step movement direction. If the speed increases, the step length increases, which will result in a larger net squared displacement, regardless of assumptions on autocorrelations.