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24 Abstract

25

26 We showed that *Folsomia candida* (a blind soil-dwelling Collembola) was able to shift from
27 non-directional (random or search strategy) to directional (target-oriented) movements at short
28 distance of food. We measured departure from linearity and access (or not) to food by the springtail
29 according to distance to the target position. Video-records and image analysis were used to obtain
30 numerical data at 0.2 sec interval. The probability of food capture within 10 min (maximum duration
31 of the experiment) was negatively related to distance. Two patterns can be observed along successful
32 trajectories in our experimental conditions (22°C, ambient light, still air), non-directional movement
33 being followed by directional movement when the animals approach food at 25 mm.

34

35 *Keywords:* Soil invertebrates; directional movement; food capture

36

37 Text

38

39 More has to be learned about the way soil invertebrates reach a target food or other favoured
40 place without spending too much energy. While directional movements can be expected to waste less
41 energy and time than random movements they need sophisticated sensory and nervous equipment
42 (Applebaum and Heifetz, 1999). Between random and directional movements a third category consists
43 of efficient 'search strategy', using looping behaviour (Bell, 1991). Bengtsson et al. (2004) and
44 Wiktorsson et al. (2004) studied the small-scale movement of springtails in environments without food
45 as attractant. Westerberg et al. (2008) showed that the presence of food decreased the time spent to
46 move and modified looping behaviour. It was demonstrated that chemical cues are used by
47 Collembola for attraction or avoidance, but experiments were made either by transporting odours via
48 air currents in olfactometers (Hedlund et al., 1995) or using odour-conditioned places (Sadaka-Laulan
49 et al., 1998; Nilsson and Bengtsson, 2004). It can be expected that (i) blind or eye-reduced soil-
50 dwelling species will use rather odours as clues, contrary to aboveground species which use visual
51 cues to move over long distances (Hågvar, 1995), and that (ii) this is possible only at short distance if

52 only brownian motion (diffusion) transports olfactory molecules. Salmon and Ponge (2001) showed
53 that the odour of earthworm excreta attracted the soil-dwelling *Heteromurus nitidus* at 1 cm distance,
54 which is far below the range of higher insects (Laubertie et al., 2006). By studying the movement of
55 animals deposited at varied distances from a food source we expect to find (i) a negative relationship
56 between distance and success of food capture, and (ii) a shift from non-oriented (random or 'search
57 strategy') to directional movements when food is perceived.

58

59 *Folsomia candida* Willem 1902 was used because of its insensitivity to light, which was
60 verified beforehand: intolerance or attraction to light might interfere with the direction of movement
61 (Salmon and Ponge, 1998). The trajectory was studied by video-tracking naive animals in short-time
62 experiments (< 10 min). Experiments were performed without soil in order to avoid any heterogeneity
63 of the substrate and to follow individual animals continuously through an optical system. For that
64 purpose the arena was made of a fine black cotton cloth which was thoroughly rinsed under tap water
65 before each experimental run, thus avoiding pheromone deposition (Verhoef et al., 1977). The absence
66 of air turbulence was provided by placing a glass cylinder 14 cm diameter and 30 cm height above the
67 cotton cloth, which delimited the arena. The temperature was $22\pm 1^\circ\text{C}$ and the light was ambient light,
68 to which *F. candida* was insensitive, as ascertained by preliminary experiments.

69

70 The animals were reared for several years on fine quartz sand moistened with tap water and
71 were fed ad libitum with dried powdered cowdung. They also ate their excrements, which formed a
72 thick layer covering the sand. This layer, made of an intimate mixture of cowdung debris and faeces,
73 was used as attractant food in the experiments, *Folsomia candida* being pheromone-conditioned
74 (Leonard and Bradbury, 1984). Animals (adults and sub-adults) were fed *ad libitum* until experiment.
75 Food (~ 1 mg) was placed as a mound at the centre of the arena, 3-5 minutes before each experimental
76 run, and was covered with a short piece of white cloth of similar area (~ 0.25 cm²) for the need of
77 image analysis. For each video-recorded run, one naive animal was introduced with a syringe at an
78 uncontrolled distance from the side of the white cloth, varying from 1 to 50 mm (Fig. 1), and its
79 movement was recorded with a Sony[®] DSR-PD100AP camera mounted on an adjustable support and

80 connected to a personal computer, starting from the time the animal was deposited in the arena. On
81 each run, which ended when food was encountered and movement ceased (the animal was no longer
82 visible under the white cloth) or at 10 min, white animals were followed on the black background by
83 image analysis using Simulink[®] software. At each 0.2 sec interval visual data were transformed into X
84 and Y values for further calculations by Excel[®] software. For the need of calculation, the path
85 followed by the animal within each 0.2 sec interval was assimilated to a straight line. By avoiding
86 vibrations and shocks care was taken that no avoidance jump using the furcula occurred during the
87 experiment. At each time of recording, the length of the trajectory followed by an animal from start
88 was calculated by summing up 0.2 sec segments. This allowed us to compare the distance remaining to
89 travel to the distance in straight line to food. An efficiency index of movement (E.I.) was calculated by
90 dividing the length of the trajectory by the straight line joining start and end of movement record.

91

92 The examination of the whole set of records (118) showed that about one third of animals (35)
93 reached the food in the course of their wandering. Systematic search using looping behaviour, as
94 described by Bengtsson et al. (2004), was not observed, although paths followed by animals could be
95 crossed several times in the course of a single run. Successful food capture was negatively influenced
96 by the distance at which the animals were placed at the start of the experiment, the rate of food capture
97 decreasing from 65% at less than 1 cm to zero beyond 4 cm (Fig. 1). Logistic regression was
98 performed with Addinsoft XLSTAT[®], using food capture (0 = failure, 1 = success) as dependent
99 variable and distance to food at run start as independent variable. It showed that the probability of food
100 capture (within 10 min) was negatively influenced by the initial distance between the animal and the
101 target food ($P < 0.0001$). The efficiency of movement, as expressed by E.F., was 12.1 (± 2.4 S.E.) in
102 case of failure vs 4.5 (± 0.8 S.E.) in case of success of food capture (Kolmogorov-Smirnov test,
103 $P < 0.0001$).

104

105 The trajectory followed by an animal was studied when it reached food within the maximum
106 duration (10 min) of the experiment (35 runs). The latter distance decreases in the course of the
107 experiment, while the former increases or decreases according to the kind of behaviour of the animal.

108 As an example, Figure 2 displays the characteristic patterns exhibited by an animal that reached food
109 in the course of the experiment. Two patterns can be distinguished, a first pattern corresponding to
110 wandering around the original position of the animal (random movement or ‘search strategy’), and a
111 second pattern where and when the animal approaches food continuously. Although the second pattern
112 is represented by a straight line on Figure 2, the actual 2D-movement may be curvilinear (data not
113 shown). The straight distance to food below which the linear part was observed along the curve
114 measures the distance at which movement was directional. The average value was calculated to be
115 25.2 mm (± 1.4 mm S.E.). Given that the passage from the first to the second pattern of movement was
116 not exhibited at the same time for the whole set of animals tested, and because the rate of locomotion
117 strongly differed from an animal to another and within the same individual record, it was judged
118 impossible to incorporate time in a predictive model.

119

120 Within the limits of our study we confirm that olfactory signals are detected by soil
121 invertebrates over only a few centimetres, as already observed by Salmon and Ponge (2001) in *H.*
122 *nitidus* when attracted to earthworm odour. Here our method allows us to estimate it being ~2.5 cm in
123 *F. candida*, i.e. 1.5 cm longer than in earthworm-attracted *H. nitidus*. The examination of the whole
124 set of successful trajectories (35) showed that the movement of an animal placed in the vicinity of a
125 food source starts with non-directional movements (as exemplified by the zigzag part of the curve on
126 Fig. 2) followed by directional movements (as exemplified by the final ‘straight line’ on Fig. 2). *F.*
127 *candida* being insensitive to light, visual inspection of the environment can be discarded as an
128 explanatory factor, but we cannot rule out that other factors than odour could contribute to reveal the
129 presence of food, such as temperature gradients issuing from microbial respiratory metabolism.

130

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177 **Figure captions**

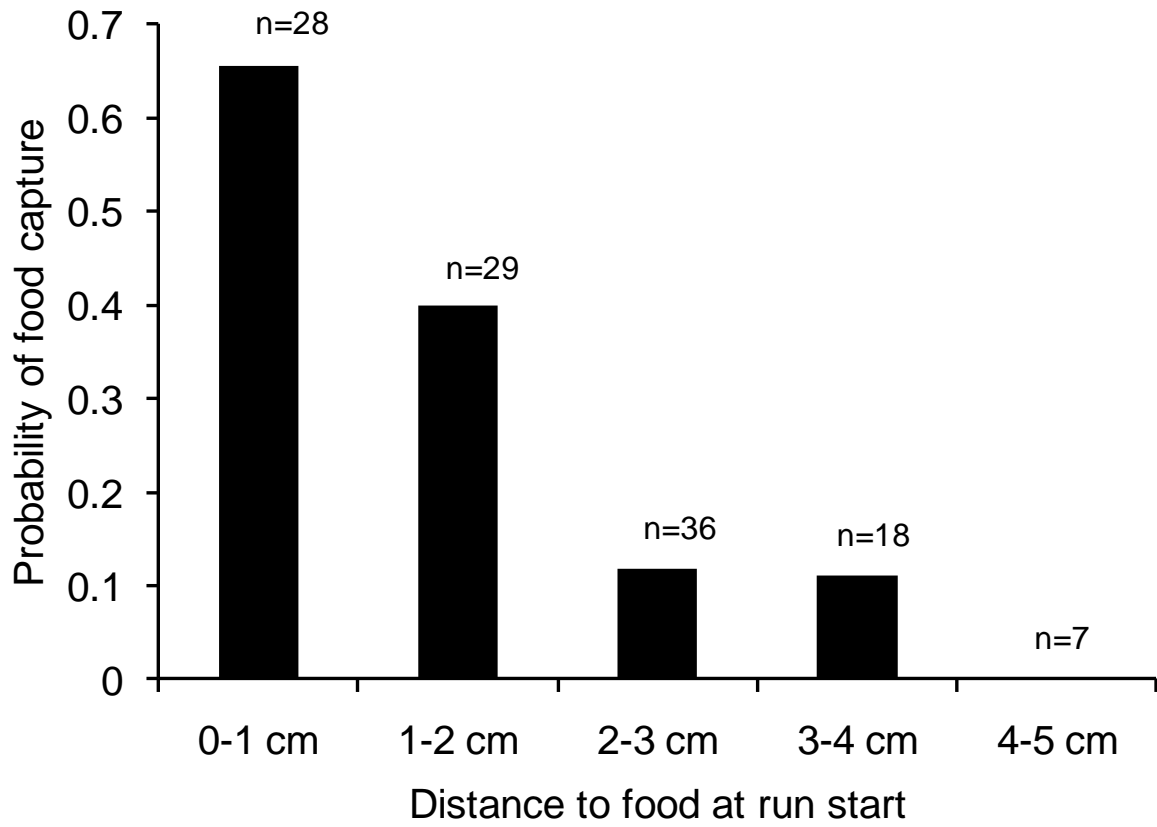
178

179 **Figure 1.** The influence of distance to food at run start (abscissa) on the probability of food capture
180 within experimental time (ordinate). Distances were classified in five groups (n = number of
181 runs)

182

183 **Figure 2.** Graphical representation of the distance remaining to travel along a given trajectory
184 according to straight distance to food (an individual run is shown here as example). The zigzag
185 part of the curve (non-directional movement) is followed by a linear part (directional
186 movement)

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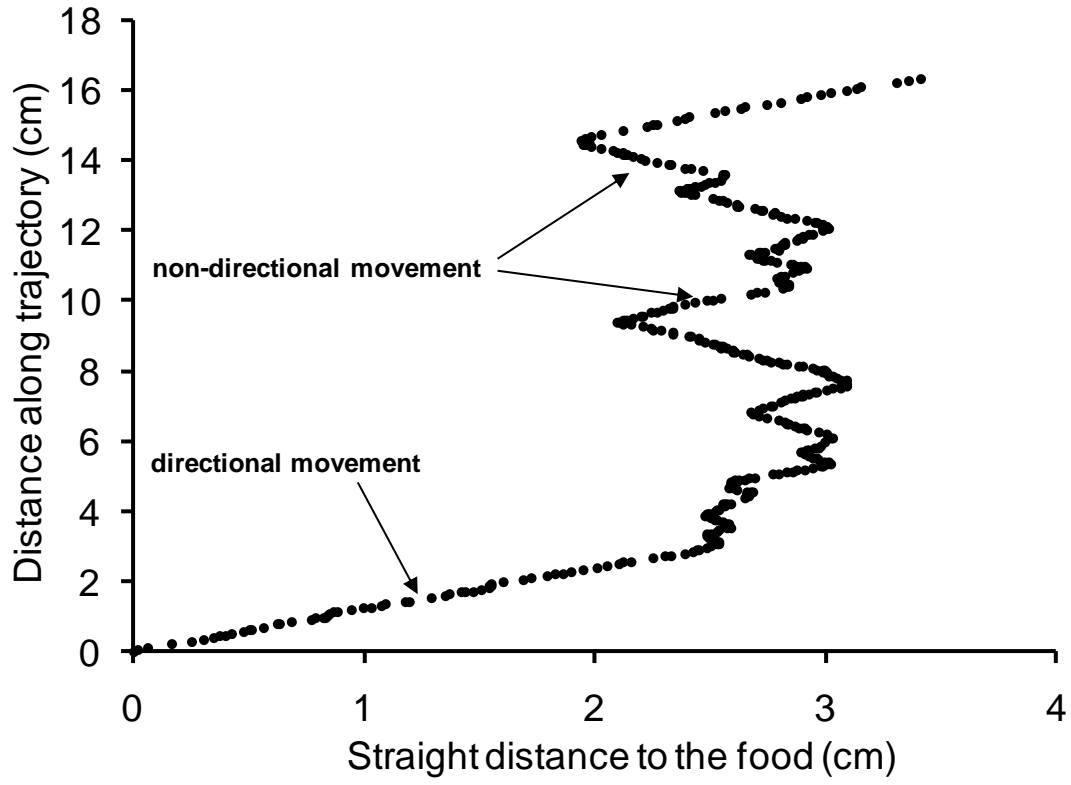


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189

190 Fig. 1

191



192

193

194 Fig. 2