

INCREASED TURN ALTERNATION BY WOODLICE (*Porcellio scaber*) IN RESPONSE TO A PREDATORY SPIDER, *Dysdera crocata*

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ABSTRACT: The common garden woodlouse (*Porcellio scaber*) is known to alternate turns (correcting behaviour), but the function of this behaviour is only poorly understood. We investigated Hughes' (1967) hypothesis that this behaviour enables woodlice to escape efficiently from unfavourable environmental conditions by considering the effect of contact with a predator, a potentially unfavourable environmental condition that has not been investigated previously. In experiments, woodlice alternated turns more frequently after contact with a known predator of woodlice (*Dysdera crocata*) than after contact with cotton wool or a nonpredatory arthropod (housefly, *Musca domestica*).

Many animals (Hughes, 1989) are known to alternate turns when they encounter obstacles: i.e., successive turns tend to be in opposite directions ("correcting behaviour"). Correcting behaviour has been shown in vertebrates and invertebrates, the latter including centipedes (Schäfer, 1972), earwigs (Schäfer, 1982) and woodlice (Hughes, 1967). Although the function of this behaviour is not well understood, Hughes (1967) suggested that one function of alternating turns by *Porcellio scaber*, the common garden woodlouse, might be to ensure efficient, direct movement away from biologically unfavourable conditions. Thus, by alternating turns upon encountering obstacles, an individual animal can move more efficiently away from a given area than would be possible as a result of a series of random turns. In support of this hypothesis, Hughes (1967, 1978) showed that *P. scaber* alternated turns more consistently when deprived of food or desiccated, than when well fed or kept in moist conditions.

Data are needed to ascertain whether other unfavourable conditions,

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in addition to food and water shortage, influence the rate at which woodlice alternate turns. In the present paper, we show that contact with *Dysdera crocata*, a spider which preys on woodlice, influences *P. scaber*'s correcting behaviour.

MATERIALS AND METHODS

Animals

Porcellio scaber is a well-known cosmopolitan terrestrial isopod. Being a crustacean, it is restricted to damp environments such as beneath stones or rotting vegetation. The vertebrate predators of *P. scaber* include birds, mice, shrews, hedgehogs, lizards, toads, frogs, and newts (Gorvett, 1956). However, *P. scaber*'s most significant predators are probably spiders (Bristowe, 1947). *Dysdera crocata*, the spider we used in the present study, is known to be a particularly important predator of *P. scaber* in nature (Bristowe, 1941; Cooke, 1965; Sunderland & Sutton, 1980). For controls, we used common houseflies, *Musca domestica*, and balls of cotton wool.

P. scaber and *D. crocata* were both collected from suburban Christchurch gardens, then cultured in the laboratory using standard methodology (Jackson & Pollard, 1982). Houseflies also were cultured in the laboratory. The size of animals in tests was standardized: adult *Dysdera crocata* (body length: c. 12 mm), adult *Musca domestica* (c. 8 mm), and large adult and juvenile *Porcellio scaber* (c. 10 mm).

Apparatus

Hughes (1967) tested woodlice in transparent Perspex mazes. Our test apparatus (Figs. 1-3) was a modification of Hughes' maze, the primary difference being that we provided a starting chamber (diameter 25 mm, height 55 mm) in which the stimulus animal (spider or fly) could be restrained and into which the woodlouse was placed.

The maze was set on a white paper base on a table and illuminated evenly by two fluorescent ceiling lights (65 watts) 1.6 m overhead. There was an opening in the starting chamber (Fig. 1) through which the woodlice could exit into an alley (40 mm × 8 mm × 8 mm) leading to a forced right turn (Fig. 2). From here, a woodlouse could then travel down a ramp and confront an initial T junction (point C, Fig. 2). The design of the maze required the woodlouse next to make another three "decision turns" before reaching an end point (Fig. 3). The woodlouse's eventual end point could therefore be the result of either three, two, one or no alternating turns following the initial forced turn at point C (Fig. 3). Therefore, each woodlouse's end point could be expressed as one of four fractions (i.e., 0/3, 1/3, 2/3, 3/3) indicating rate of alternation following

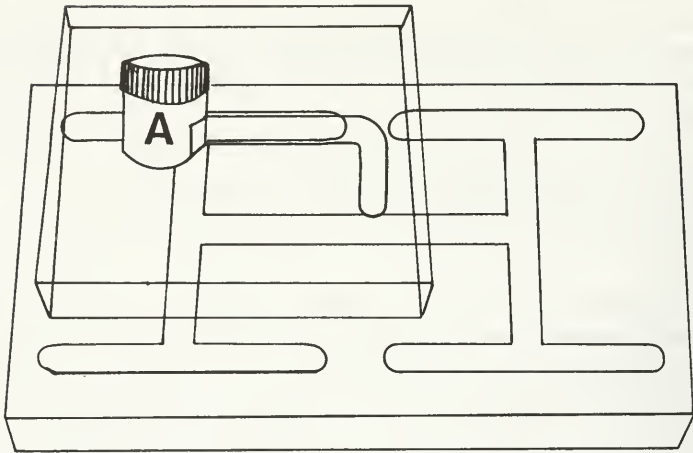


FIGURE 1. Drawing of test apparatus. Woodlouse placed in starting chamber (A) before allowed to enter maze (below).

contact with the stimulus animal in the starting chamber. Data were analysed using the Kruskal-Wallis one-way ANOVA, with Bonferroni adjustments for subsequent simultaneous comparisons (Rice, 1989).

Procedure

In an experimental test, a woodlouse was put in the starting chamber with a *Dysdera crocata* ("spider"). In a control test, a woodlouse was

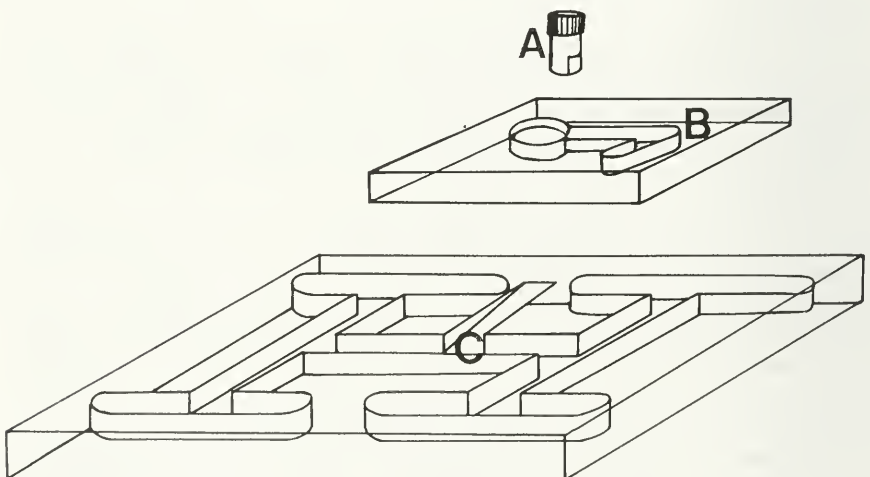


FIGURE 2. Exploded diagram of test apparatus. Woodlouse moves from starting chamber (A) to 8×8 mm alley which leads to forced right turn (B) and down ramp to initial T junction (C). From here woodlouse is free to walk through maze to an end point.

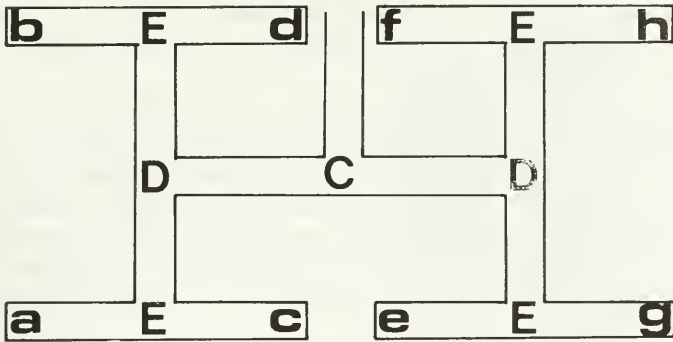


FIGURE 3. Floor plan of maze. At bottom of ramp, woodlouse is confronted by initial T junction (C) where it also has choice of turns at points labelled D and E. From E, woodlouse can proceed to one of eight possible end points (a, b, c, d, e, f, g, or h). Finishing point of woodlouse recorded as $a = 2/3$, $b = 1/3$, $c = 1/3$, $d = 0$, $e = 1/3$, $f = 1/3$, $g = 3/3$, or $h = 2/3$.

put in the starting chamber with either a ball of cotton wool or a *Musca domestica* ("fly").

The ball of cotton wool was c. 10 mm in diameter. Tests using balls of cotton wool were controls for the effect on woodlice of encounters simply with objects comparable in size to *D. crocata*. Flies are nonpredatory arthropods similar in size to *D. crocata*. Wings were removed from flies so that, like the spiders, the flies could move about in the starting chamber by walking but not by flying. Tests using flies were controls for the effect on woodlice of encounters simply with animals comparable in size to *D. crocata*. By comparing data from tests using *D. crocata* to data

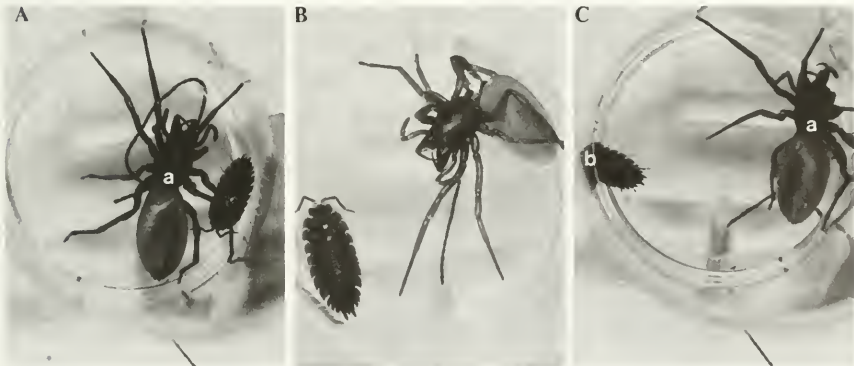


FIGURE 4. View into starting chamber where stimulus (in this instance, spider) contacts woodlouse. A: stimulus secured by cotton thread (a) with sufficient slack to allow interaction with woodlouse. Exit closed (b). B: thread (a) tightened, pulling spider up against side of starting chamber, thereby ending interaction before woodlouse can be attacked. C: starting chamber rotated to open exit hole (b) and allow woodlouse to enter maze.

from controls, we could ascertain whether increased rates of alternating turns was a response by woodlice specifically to the encounters with the predator.

The spider or fly was first immobilised with carbon dioxide. Next, a cotton thread (Fig. 4A) was tied around the spider (between its cephalothorax and abdomen) or fly (between its thorax and abdomen). The other end of the thread was then held by hand at a length which allowed the stimulus animal sufficient slack to move throughout the starting chamber but insufficient to permit escape from it. Each spider and fly was used repeatedly in multiple tests. However, each woodlouse was tested only once.

The woodlouse to be tested was carefully pushed into a glass vial with an artist's brush, then gently dropped into the starting chamber. The lid was then placed on the chamber to start a test.

In a successful test, the woodlouse was contacted by the spider (Fig. 4A), fly, or cotton wool. As soon as this happened, we tightened the thread to draw the spider, fly, or cotton wool tight against the side of the chamber opposite the exit hole (Fig. 4B). Next, the exit hole was opened to provide the woodlouse access to the maze (Fig. 4C). Once in the maze, the woodlouse could run freely and its end point was recorded (Fig. 3).

If a woodlouse failed to reach an end point within 2 min after contacting the spider, fly, or cotton wool, or if at any time the woodlouse backtracked, the test was aborted. Fortunately such events occurred in fewer than 10% of the trials. Between trials, the maze was wiped off, first with ether, then with distilled water, after which it was wiped dry with clean cotton wool. Following each trial, the paper base under the maze was replaced.

For each of the three treatments, there were 100 trials. The starting chamber was occupied by: treatment 1) a tethered spider (to test for the effect of the predator); treatment 2) a tethered ball of cotton wool (a control for the effect of spider-size objects); or treatment 3) a tethered fly (a control for the effect of spider-size nonpredatory arthropods).

RESULTS AND DISCUSSION

Using the Kruskal-Wallis one-way ANOVA, the effect of treatments (Fig. 5) was found to be highly significant ($p < .001$), thus justifying subsequent use of post hoc comparisons between individual treatments. Woodlice made significantly more alternating turns after contact with a predatory spider than after contact with a fly ($p < .01$) or a ball of cotton wool ($p < .005$), but there was no significant difference in the alternation rates when contact with a fly was compared to contact with a ball of cotton wool. Therefore, the effects on woodlouse correcting behaviour that we observed in tests using *D. crocata* appear to be caused by specific

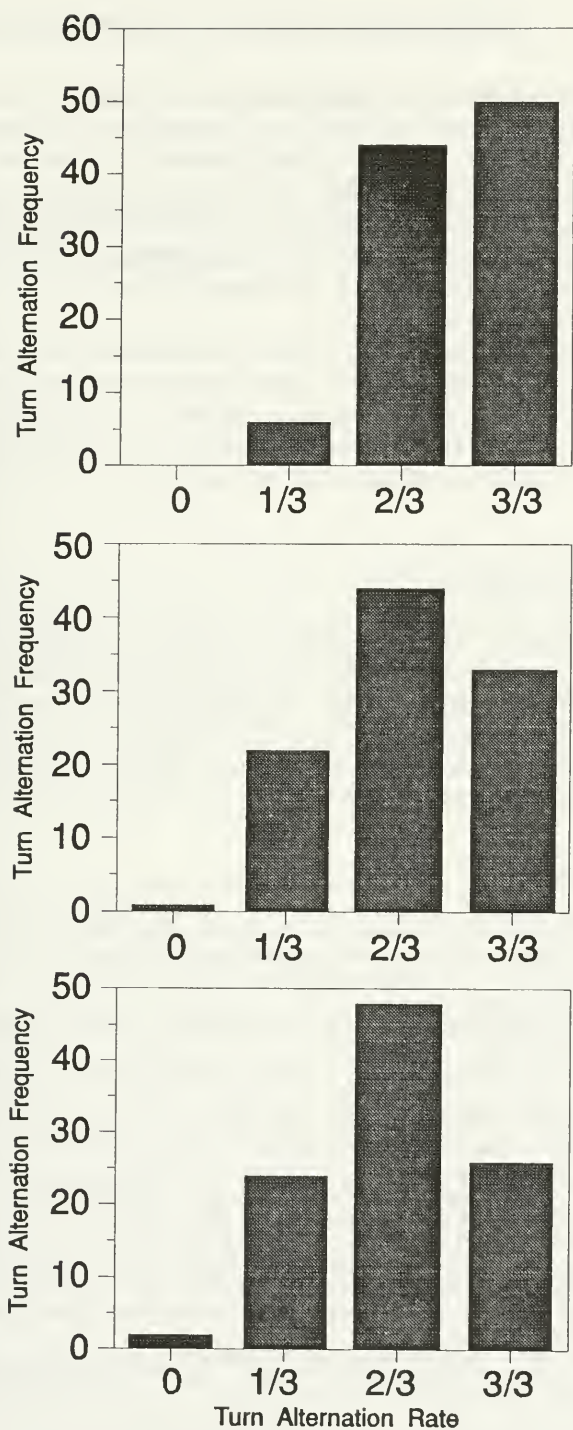


FIGURE 5. Results from testing *Porcellio scaber* with, from top, *Dysdera crocata* (A), *Musca domestica* (B), and cotton wool (C).

cues from this predator, not by generalised stimuli from inanimate objects or from animals of a size comparable to the predator. We do not know exactly what cues from *D. crocata* are important, but they are evidently something other than the predatory behaviour of the spider because we always pulled the spider back before it could attack the woodlice. We suggest that chemical cues from *D. crocata* are important because woodlice species are known to have well-developed abilities to discern chemical stimuli (Sutton, 1972).

Hughes (1967) proposed that correcting behaviour may function to facilitate efficient movement away from unfavourable conditions. The results of this study support Hughes' hypothesis by providing evidence that woodlice react to the presence of a predator (an unfavourable condition not previously investigated) by increasing their rates of alternating turns.

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