Ecotoxicology **5**, 35–45 (1996)

Pesticide uptake and locomotor behaviour in the woodlouse: an experimental study employing video tracking and ^{14}C-labelling

MARK BAYLEY and ERIK BAATRUP*

Institute of Biological Sciences, Department of Zoology, University of Aarhus, Building 135, DK-8000 Aarhus C, Denmark

The toxicity of soil pesticide residues to target and non-target organisms depends on the amount of chemical absorbed by the organism. One of the principle factors governing chemical uptake is the amount of chemical encountered by the animal and, hence, the area of soil contacted. This in turn, depends on the locomotor behaviour of the animal. In the present study, the relationship between the uptake of soil residues of an organophosphate insecticide and locomotor behaviour was examined, employing ^{14}C-labelled dimethoate and computer-aided video tracking. Groups of male woodlice, *Porcellio scaber* (Isopoda), walked freely for 22 h on a soil substrate treated with three application rates of the pesticide. A strong correlation was found between pesticide uptake and path length, mean velocity and time spent in locomotor activity, which is consistent with previously reported modelling studies. Our data suggest a linear relationship for all locomotor parameters except for path length at the highest application rate, where uptake was best described by an inverse exponential relationship. All doses induced hyperactivity in terms of time spent in locomotor activity. However, when compared with a untreated control group, the most pronounced effects were displayed at the lowest dose where path length, mean velocity and turning rate were also significantly different. The number of shifts between locomotor active and inactive periods in the experimental period increased with increasing application rate.

Keywords: woodlouse; pesticide uptake; locomotor behaviour; ^{14}C-labelled dimethoate; behavioural toxicology.

Introduction

The toxicity of xenobiotics to target and non-target organisms depends on the amount present in the environment, the proportion available to the biota and, ultimately, to the amount actually encountered and absorbed by the organism. Harris (1971) suggested that the observed increase in toxicity of pesticides at elevated temperatures is, in part, caused by an increased locomotor activity. Salt and Ford (1984) developed a stochastic model of insecticide pick-up by larvae from plant surfaces, in which locomotor behaviour played a central role. In a sensitivity analysis of this model, Jepson *et al*. (1990) showed that a simple hazard index based on walking velocity, contact area with the surface and tolerance to a pesticide, correctly predicted the ranked susceptibilities of several

*To whom correspondence should be addressed.

Coleoptera to residual deposits. Jagers op Akkerhuis and Hamers (1992) modelled an inverse exponential increase in the body content of deltamethrin in the linyphiid spider, *Oedothorax apicatus* (Blackwall), with increasing distance walked. While simulation modelling is a fast and cost-effective method of analysing the effects of changing complex environmental variables, it depends on reliable experimental data at the input stage, in validation and in further development. Also, whenever financially and technically possible, experimental evidence is preferable to simulation studies. To our knowledge, experimental documentation of the relationship between locomotor behaviour and pesticide uptake over a prolonged period is not yet available.

The development of computer-automated video-tracking systems has enabled the detailed quantitative examination of the components of locomotor behaviour of small surface active invertebrates under laboratory and semi-field conditions. The woodlouse was chosen as a model organism representing the soil primary consumer community. It is a widespread and often numerous inhabitant of the leaf litter layer (Walton 1987) and is a primary consumer alongside the millipedes and earthworms (Sutton 1980) in, for example, woodland, hedgerows and orchards. Using the tracking system previously described by Baatrup and Bayley (1993a), the locomotor behaviour of male woodlice, *P. scaber* Latr. (Isopoda), was monitored before and during exposure to soil residues of ^{14}C-labelled dimethoate, an organophosphate pesticide. The relationship between the locomotor behaviour and uptake of ^{14}C-labelled dimethoate from a soil surface was studied at three application rates corresponding to 140, 280, and 560 g ha^{-1}. The doses applied in this study were sublethal, the lowest application rate corresponding to approximately one-tenth of the LD_{20} (96 h). Further the changes in locomotor behaviour resulting from exposure to these pesticide residues were quantified.

Material and methods

The animals used in this study were removed from a 1 year old woodlouse culture kept at 20 ± 1 °C and 58 ± 5% RH with a 16L : 8D lighting cycle. In total 60 adult male *P. scaber* were used in the present study. The woodlice had body lengths of 8–10 mm and fresh weights of 64.8 mg (±14.6 SD). The age of the woodlice was unknown but animals were selected at the intermoult stage after the criteria given by Steel (1982).

Test arena

The woodlice locomotor activity measurements were made in 150 mm diameter milled polyoxymethylene (POM) bowls containing 416 g sandy loam soil (dry weight after 24 h at 100 °C) sieved through a 2 mm mesh. The soil composition was organic matter 1.7%, clay 11%, silt 13%, sand 48% and course sand 27% with a pH_{H_2O} of 5.8. The soil surface of the arena was made level by adding 120 ml distilled water to the dry soil and allowing this mixture to dry in the arenas overnight. During experimentation the soil in the arenas was kept at approximately 74% of field water holding capacity by means of a cotton wick connecting the arena soil to a subjacent water bath (Bayley 1995). The 25 mm high oblique sides of the arenas were coated with Fluon (polytetrafluoroethylene, Imperial Chemical Industries Ltd, UK), to prevent the woodlice from escaping from the test arenas. Locomotion was monitored in dark conditions, obtained by inserting a combination of primary red and dark blue filters (Lee filters, Berkey Technical, Denmark) in front of four fluorescence tubes. This combination of filters excluded wavelengths shorter than 720 nm and reduced the illumination of the arenas to 0.25 lux in the visible spectrum. In order to maintain a constant physical environment and to minimize disturbances, the experimental room was devoted exclusively to the woodlice culture and activity measurements.

Radioactive dimethoate solution

The amounts of pesticide absorbed by the animals were measured by liquid scintillation counting using ^{14}C-labelled dimethoate. Before each experiment, 100 ml radioactive dimethoate solution, containing 18.5 kBq ml^{-1} and either 27.2, 54.3 or 108.6 μg dimethoate per millilitre (depending on application rate) was freshly prepared. The 'cold' dimethoate stock solution was supplied by CHEMINOVA AGRO a/s, Denmark. The radioactive dimethoate stock solution (radioactive concentration 37 MBq ml^{-1}, specific activity 2.07 GBq mmol^{-1}), which was ^{14}C-labelled at the carboxy-amide position, was obtained from ISOTOPCHIM s.a.r.1, France.

Experimental procedure

One day before measuring locomotor behaviour, the woodlice were weighed and tagged with silver paint (EDDING 780 silver paint marker) on pereionites 2–5 and placed in individual aluminium trays containing 1 cm of the experimental soil. Three hours before tracking, animals were placed individually in each of the six arenas. The locomotor activity was then measured under dark conditions for 22 h (12.00am–10.00am), after which the animals were returned to their aluminium trays between 10.00am and 12.00am while 10 ml of the radioactive dimethoate solution was poured over the surface of the arena. This volume of liquid formed a thin layer over the entire surface of the arenas, which slowly sank to approximately 10 mm below the soil surface over the following 2 h. At this time animals were returned to their experimental arenas and tracked for a further 22 h. Three residual doses of dimethoate, corresponding to 140, 280 and 560 g ha^{-1}, respectively, were tested with 15 animals at each dose and 15 animals in a control group exposed to water only. All three doses were sublethal. The lowest dose of 140 g ha^{-1} was a factor of ten below the LD_{20} (96 h) estimated in a small-scale pilot experiment to determine the residual toxicity of dimethoate under these experimental conditions.

^{14}C analysis procedure

Following exposure to dimethoate, the woodlice were washed for 10 s in each of four consecutive distilled water baths in order to remove excess dimethoate from the surface without extraction from within the animal (dimethoate solubility in water at 21 °C is 25 g l^{-1}). The animals were then dried on filter paper and placed in 8 mm diameter polythene embedding capsules (TAAB Laboratories Equipment Ltd., UK) where they were cut into small pieces using scalpel blades. The blade was rinsed with 100 μl 65% nitric acid into a capsule for digestion of the animal. After a digestion period of 24 h, the capsule was placed in a glass scintillation tube and 10 ml Opti-fluor scintillation cocktail (Packard Inc.) and 1 ml 0.1 M sodium hydroxide were added. Finally, the tube was sealed, shaken vigorously and left for approximately 1 h before ^{14}C activity was measured in a Packard 2200 CA Tri-Carb liquid scintillation analyser with an automatic efficiency tracing DPM software. The whole-body burden of dimethoate and its metabolites in the animal was calculated by comparing its counting rate with the counting rate of standard samples with a known dimethoate content. Standards were prepared by mixing 50 μl of the appropriate radioactive dimethoate solution and 50 μl of 65% nitric acid in the polythene embedding capsules. ^{14}C background levels were determined using the control animals.

Automated video tracking

The locomotor activity of the woodlice was recorded using the GIPSTRA (Image House a/s, Denmark) computer-centred video-tracking system previously described in Baatrup and Bayley (1993a,b) and Bayley (1995). Briefly, this system identifies moving objects by their size and specific colour or grey level in successive digitized images. The identification of the woodlice was based on the contrast between the silver tag and the background. The position of the centroid, calculated from all pixels fulfilling the grey-level contrast criteria in a small area around the animal, was recorded as the *x,y*-position of the woodlouse. In the present study, the system was configured to collate the time series of Cartesian coordinates of six animals in six separate arenas, once every second during the recording periods of 22 h.

Data analysis

The analysis of the time series of *x,y*-coordinates created by GIPSTRA was handled by did the mean velocity. None of the other locomotor parameters measured, such as the number of moves or turning parameters, showed any correlation with uptake (Table 1). At the two lower application rates (140 and 280 g ha^{-1}), the available data points suggest a linear correlation between pesticide uptake and distance walked. However, at the highest dose (560 g ha^{-1}), the best fit appears to be the curve (Fig. 1) following the inverse exponential function:

$$C = K_1 \cdot (1 - \exp(-K_2 \cdot L)) + C_0$$

where C is the concentration of dimethoate in the animal after walking L m. In this equation K_1 is a steady state constant, K_2 a rate constant and C_0 is the concentration obtained by a stationary animal on treated soil. The results indicate that a stationary animal would absorb some chemical, however, further measurements at the low end of the distance walked scale are required to determine the *y*-axis intercept.

The rate of dimethoate uptake increased with increasing residual application rate. This can be seen in the increasing slopes of the regression lines with increasing application rates (Fig. 1 and Table 2). It is noteworthy that these uptake rates (slopes) were not directly related to the pesticide application rates. Thus, while the application rates were evenly spaced (by a factor of two), the uptake rate at the intermediate dose is depressed for all three locomotor parameters (Fig. 1).

Residual application rate/behavioural response

In addition to demonstrating the relationship between locomotion and pesticide uptake, the measurements also provide information on the different effects of the three application rates on woodlouse locomotor behaviour. When comparing the 22 h exposure period with the preceding 22 h control period, the unexposed control animals showed a considerable decrease in locomotor activity. These woodlice allocated less time to locomotion, reduced mean velocity and thereby path length and increased their turning rate (Fig. 2). The greatest deviation from this pattern was seen in the group of woodlice exposed to the lowest dimethoate application rate. Thus, these animals allocated more

Table 1. Spearman's rank correlation coefficient r_s significance level between locomotor parameters and dimethoate body concentration in woodlice (nanogrammes of dimethoate a.i. per milligramme of live weight)

Dimethoate application rate (g ha^{-1})	140	280	560
Time in locomotor activity, r_s	0.768	0.736	0.821
$p <$ value	0.002	0.010	0.002
Mean velocity, r_s	0.686	0.614	0.739
$p <$ value	0.010	0.050	0.010
Path, r_s	0.804	0.761	0.818
$p <$ value	0.002	0.002	0.002
Number of moves, r_s	−0.025	−0.418	0.05
Turn rate per millimetre, r_s	−0.564	−0.532	−0.682
Turn rate per second, r_s	−0.146	−0.114	0.071

r_s varies from −1 to 1, where 1 indicates complete concordance between variables and −1 indicates absolute disconcordance. There is no significant correlation where *p*-values are omitted.

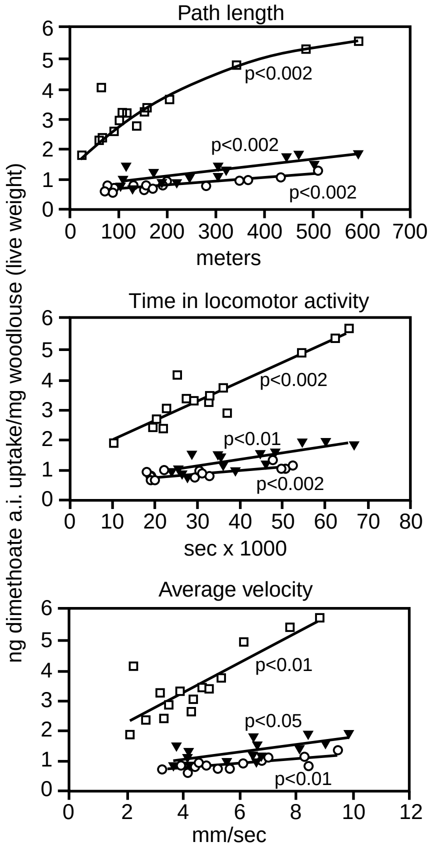

Fig. 1. The uptake of [14]C-labelled dimethoate as a function of path length, time in locomotor activity and mean velocity. Three application rates were tested: □ 560 g ha^{-1}, ▼ 240 g ha^{-1} and ○ 140 g ha^{-1}. *P* gives the probability that the parameters are not correlated. Uptake was strongly correlated to all three measures of locomotor activity. The correlation appears in most cases to be linear. However, with path length at the highest application rate, an inverse exponential relationship is suggested by the data. The uptake rate at the intermediate dose is depressed towards the lowest dose suggesting that bioavailability does not increase linearly with application rate.

Table 2. Uptake rate of dimethoate expressed in terms of three components of locomotor activity

Dimethoate application rate (g ha^{-1})	140	280	560
Uptake rate–path (ng a.i per gramme of live weight m^{-1})	1.18	1.90	6.1
Uptake rate–locomotor activity time (ng g^{-1} h^{-1})	43.9	81.0	231
Uptake rate–mean velocity (ng g^{-1} mm^{-1} s^{-1})	75.9	119	488

The values show the gradients of linear regression lines calculated between the woodlouse dimethoate content data and the locomotor behaviour parameters.

time to locomotion at a higher mean velocity, resulting in a longer distance walked and a reduction in turning rate (Fig. 2). This hyperactivity response was less pronounced in the two groups having received the two higher application rates. The time in locomotor activity was also significantly higher here than in the control group ($p < 0.01$), whereas this was not the case with respect to the mean velocity and path length.

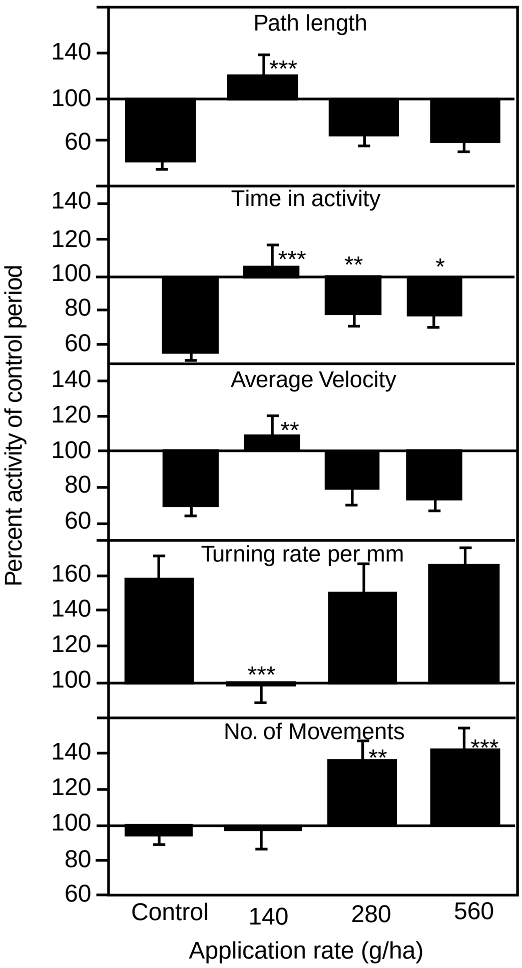

Fig. 2. The mean change in locomotor behaviour (presented as the percentage of the preceeding control period measurement) of woodlice exposed to three application rates of dimethoate and distilled water (controls). All three application rates caused significant hyperactivity in terms of time spent in locomotor activity, the effect being strongest at the lowest application rate, where path length, mean velocity and turning rate were also significantly different from the control animals. The number of movements, on the other hand, increased with application rate, which is interpreted as an indication of disruption of the locomotor pattern. Significance level between exposed groups and the control; (***) indicates $p < 0.001$, (**) $p < 0.01$ and (*) $p < 0.05$.

In contrast to the pattern described above, the number of moves made by woodlice increased with increasing residual application rate (Fig. 2). Thus, while the exposure of animals to the lowest application rate of 140 g ha^{-1} did not affect the number of moves made by the animals during the experimental period, increasing application rate caused a considerable and significant increase (Fig. 2).

Discussion

Computer-aided video tracking combined with a suitable quantitative measurement of xenobiotic within the animal allows detailed studies of the relationship between locomotor behaviour and the uptake of chemical compounds. Such information is valuable for understanding differences in the sensitivity of animal species to a particular compound and the variation in bioavailability of xenobiotics from different substrates. Also, such experimental data should be considered as prerequisite input parameters in mathematical simulation models. As stated by Wiles and Jepson (1993) it is neccessary to quantify the amount of pesticide actually picked up during a given exposure period to develop models that accurately predict mortality resulting from residual deposits. It would strengthen simulations if the locomotor component of the model was based on detailed and prolonged measurements, free of assumptions about the diel activity patterns of the insect, made at different temperatures and on various substrates. Also, since pesticide encountered by the animal depends on the contact area, which is determined by the stepping pattern and, hence, by the walking speed (Gray 1968), frequency distributions of velocities could be included. Most importantly, the stimulatory or inhibitory effects of pollutants on the locomotor activity (Baatrup and Bayley 1993b; Bayley 1995), which have a significant impact on the pesticide encountered and, hence, the uptake of xenobiotic by the animal, could be included in such models.

In the present study, computerized video tracking the liquid scintillation counting were used to relate the uptake of ^{14}C-labelled dimethoate to the locomotor behaviour in woodlice. The natural high variation of locomotor activity in male woodlice (Bayley 1995) allowed us to confine the experiment to a single 22 h exposure period. In species with a more homogenous locomotor activity level, exposure periods of increasing duration would, of course, be needed in order to draw the correlation curve. The presented whole-body concentrations of dimethoate in the woodlice are based on animal live weight. In many invertebrates this is a poor representation of animal size, but in the closely related species *P. spinicornis*, Bukhari and Alikhan (1985) showed a strong correlation between live and dry weight and between dry weight and body length.

The results show a strong correlation between pesticide uptake and the three linked components of locomotion: time in locomotor activity, mean velocity and path length. The strongest correlation was found for path length, which is also the locomotor component most directly related to the substrate area contacted by the animal and, hence, to pesticide encountered. At the highest application rate (560 g ha^{-1}), the best curve fit to the correlation between path length and uptake was represented by an inverse exponential function. Normally, this function describes the temporal uptake and depuration of a compound in a one-compartment model of constant size. In this case exposure time has been replaced by an activity parameter related to the quantity of pesticide encountered by the animal during experimentation. The inverse exponential function, determined in this experimental study, is equivalent to the relationship between uptake of deltamethrin and the distance walked by spiders as modelled by Jagers op Akkerhuis and Hamers (1992). Both cases indicate that there is a rapid initial uptake followed by a slower rate of entry until a theoretical equilibrium level is reached. Jagers op Akkerhuis and Hamers (1992) suggested that the distal parts of the animal functioned as small reservoirs and that uptake decreased as these reservoirs became saturated. Alternatively, the inverse exponential relationship may represent first-order uptake/depuration mechanisms or a temporal reduction in bioavailability of pesticide residues.

For the two lowest application rates, the available data suggest a linear correlation between the three components of locomotor activity and dimethoate accumulation. However, it cannot be excluded that a better representation of data in the lower range of activity would produce a similar inverse exponential relationship.

The amount of pesticide encountered by the animal depends on the animal's activity but also on the density of bioavailable molecules. If the amount of bioavailable pesticide was directly related to the application rate, a proportional increase in animal uptake with application rate would be expected. The much steeper gradient of the regression lines (Fig. 1) at the highest application rate suggests a non-linear increase in bioavailability with increasing application rates. Chemical analysis of the availability of dimethoate on the soil surface over the 22 h exposure period would be needed to confirm this.

The hyperactivity response to dimethoate poisoning was most pronounced in the group of woodlice exposed to the lowest application rate, where all the measured components of locomotor activity, except the number of moves made by exposed animals, were significantly different from the control group (Fig. 2). Organophosphate compounds have previously been reported to induce hyperactivity at sublethal doses in insects (Barker *et al*. 1980; Moosbeckhofer 1983). At the intermediate and high application rates, the animals still allocated more time to locomotion than the control animals, but the mean velocity and distance walked were not significantly different from control values. By further increasing the dose or by extending the time of exposure, a state of hypoactivity would undoubtedly precede paralysis and death. Several other neurotoxic agents elicit locomotor hyperactivity at low doses and hypoactivity at higher doses in mammals (Frantík and Horváth 1992). Hyperactivity is considered as the initial action of the chemical on the nervous system, caused by an impairment of normal neuronal excitability (Frantík and Horváth 1992).

The inverse relationship between the application rate and locomotor activity bears similarities with the hormesis hypothesis (Luckey 1968; Stebbing 1982), which predicts that low doses of a harmful substance will be stimulatory to the organism due to over-corrections of biosynthetic control mechanisms. This hypothesis is usually associated with growth or fecundity measurements and has been interpreted as beneficial to the organism, giving rise to increased fitness (Stebbing 1982; Parsons 1989; Morse and Zareh 1991). It is, however, questionable whether locomotor hyperactivity *per se* and the reduced turning rate can be considered beneficial to animals. Hyperactivity may disrupt feeding and increase vulnerability to predation (Laurence 1972; Little and Finger 1990) and thus violate inherent behavioural patterns. For instance, the positive dose–response relationship between application rate and movement frequency indicates that the animal's pattern of movements is increasingly disrupted with increasing pesticide application rates.

The strong correlation between locomotor activity and pesticide uptake implies that the most active animals will absorb the largest amounts of chemical during residual exposure. This puts the highly active non-target predatory animals at most risk of poisoning from this route of uptake. In addition, the stimulatory effect of small doses of dimethoate on locomotor activity further enhances the uptake of pesticide by the animal.

Acknowledgements

This study was funded by the Danish Environmental Research Programme and a PhD grant from the University of Aarhus. Our special thanks to Dr Jens Møller of Cheminova Agro a/s for supplying the ^{14}C-labelled dimethoate. The authors also gratefully thank Mr Nils Skyberg for his elegant software development.

References

Baatrup, E. and Bayley, M. (1993a) Quantitative analysis of spider locomotion employing computer-automated video tracking. *Physiol. Behav.* **54**, 83–90.

Baatrup, E. and Bayley, M. (1993b) Effects of the pyrethroid insecticide Cypermethrin on the locomotor activity of the wolf spider *Pardosa amentata*: quantitative analysis employing computer-automated video tracking. *Ecotoxicol. Environ. Saf.* **26**, 138–52.

Barker, R.J., Lehner, Y. and Kunzmann, M.R. (1980) Pesticides and honey bees: nectar and pollen contamination in alfalfa treated with dimethoate. *Arch. Environ. Contamin. Toxicol*. **9**, 125–33.

Bayley, M. (1995) Prolonged effects of the insecticide dimethoate on locomotor behaviour in the woodlouse, *Porcellio scaber* Latr. (Isopoda). *Ecotoxicol*. **4**, 1–12.

Bukhari, M.A. and Alikhan, M.A. (1985) Calorific value and ash content in relation to body length and dry weight of *Porcellio spinicornis* Say (Isopoda, Porcellionidae). *Crustaceana* **49**, 290–8.

Diem, K. and Seldrup, J. (1982) *Geigy Scientific Tables Vol.II. Introduction to Statistics, Statistical Tables, Mathematical Formulae*, eighth edition. Basle: Ciba-Geigy.

Elliot, J.M. (1993) *Some Methods for the Statistical Analysis of Samples of Benthic Invertebrates*, second edition. Ambleside, Cumbria: Freshwater Biological Association.

Frantík, E. and Horváth, M. (1992) Integration of behavioural and neurophysiological approaches in neurotoxicology. *Toxicol. Lett*. **64/65**, 225–9.

Gray, J. (1968) *Animal locomotion* London: Weidenfeld and Nicolson.

Harris, C.R. (1971) Influence of temperature on the biological activity of insecticides in soil. *J. Econ. Entomol*. **64**, 1044–9.

Jagers op Akkerhuis, G.A.J.M. and Hamers, T.H.M. (1992) Substrate-dependent bioavailability of deltamethrin for the epigeal spider *Oedothorax apicatus* (Blackwall) (Araneae, Erigonidae). *Pestic. Sci*. **36**, 59–68.

Jepson, P.C., Chaudhry, A.G., Salt, D.W., Ford, M.G., Efe, E. and Chowdhury, A.B.M.N.U. (1990) A reductionist approach towards short-term hazard analysis for terrestrial invertebrates exposed to pesticides. *Funct. Ecol.* **4**, 339–47.

Laurence, G.C. (1972) Comparative swimming abilities of fed and starved largemouth bass (*Micropterus salmoides*). *J. Fish Biol*. **4**, 73–8.

Little, E.E. and Finger, S.E. (1990) Swimming behavior as an indicator of sublethal toxicity in fish. *Environ. Toxicol. Chem*. **9**, 13–19.

Luckey, T.D. (1968) Insect hormoligosis. *J. Econ. Entomol*. **61**, 7–12.

Moosbeckhofer, R. (1983) Laboruntersuchungen über den einfluß von diazinon, carbofuran und chlorvinfos auf die laufaktivität von *Poecilus cupreus* L. (Col., Carabidae). *Z. Angew. Ent.* **95**, 15–21.

Morse, J.G. and Zareh, N. (1991) Pesticide-induced hormoligosis of citrus thrips (Thysanoptera: Thripidae) fecundity. *J. Econ. Entomol.* **84**, 1169–74.

Parsons, P.A. (1989) Acetaldehyde utilization in *Drosophila*: an example of hormesis. *Biol. J. Linn. Soc.* **37**, 183–9.

Salt, D.W. and Ford, M.G. (1984) The kinetics of insecticide action. Part III: the use of stochastic modelling to investigate the pick-up of insecticides from ULV-treated surfaces by larvae of *Spodoptera littoralis* Boisd. *Pestic. Sci.* **15**, 382–410.

Stebbing, A.R.D. (1982) Hormesis – the stimulation of growth by low levels of inhibitors. *Sci. Tot. Environ*. **22**, 213–34.

Steel, C.G.H. (1982) Stages of the intermoult cycle in the isopod *Oniscus asellus* and their relation to biphasic cuticle sectretion. *Can. J. Zool.* **60**, 429–37.

Sutton, S.L. (1980) *Woodlice*. Oxford: Pergamon Press.

Walton, K.C. (1987) Factors determining amounts of fluoride in woodlice *Oniscus asellus* and *Porcellio scaber*, litter and soil near an aluminium reduction plant. *Environ. Pollut.* **46**, 1–9.

Wiles, J.A. and Jepson, P.C. (1993) An index of the intrinsic susceptibility of non-target invertebrates to residual deposits of pesticides. In Eijsackers, H., Heimbach, F. and Donker, M. eds. *Ecotoxicology of soil organisms* pp 287–302. Chelsea, USA: Lewis Publishers.