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Modelling the within-field recovery of carabid beetles following their suppression by exposure to an insecticide

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A simple random-movement diffusion model was used to simulate the recovery of ground beetles following their suppression by exposure to the organophosphorus insecticide dimethoate in a field of winter wheat at flowering. The output from the model was compared to a linear model of the recovery process that was derived from field collected data and also to published data on the daily rates of movement of ground beetles. The diffusion model gave the best fit to the field collected data at beetle movement rates that were similar to published values. The results of our approach show how the recovery process may be simulated on a computer in addition to demonstrating how the recovery of ground beetles may be mediated by their random movement.

1. Introduction

There is extensive evidence that insecticide applications to arable crops in the UK can cause depletions in their indigenous non-target terrestrial arthropod fauna (Vickerman & Sunderland 1977, Powell *et al*. 1985, Cole *et al*. 1986, Vickerman *et al*. 1987, Thacker & Jepson 1990). These depletions, which have been studied most extensively in the arthropod families Carabidae, Linyphiidae and Staphylinidae, are always temporary, with recovery occurring within the growing season when the experimental design utilises within-field untreated control plots.

For species which are primarily cursorial, the sources from which the recovery of arthropods can occur include these within-field control plots as well as surrounding untreated fields (Thacker & Jepson 1990). In the case of ground beetles, field experiments have shown that the recovery process is mediated primarily by the movement of individuals into treated plots from within-field untreated control plots (Jepson & Thacker 1990, Thacker & Jepson 1993, Duffield & Aebischer 1994). Indeed, Jepson (1989), in an analysis of ground beetle recovery, was able to demonstrate a significant linear correlation between the duration of the treatment effect and the scale on which the experiment was carried out. For this group of arthropods then, the within-season recovery process is illusory in the sense that it results from a redistribution of the extant population across the field rather than from a return to pre-treatment population levels.

The implications of these results, at least in the short term, are threefold. Firstly, the larger the treated area, the longer the time will be to population recovery (Jepson 1989). Secondly, where trials are carried out using whole fields as treatment replicates we might expect that recovery times for carabid beetles would be even longer. Data from the UK (Burn 1992, Vickerman 1992) and France (Basedow 1990) have both demonstrated that this is the case. Thirdly, if the depletion of these non-target species causes a decrease in the level of predatory activity within treated fields, then there might also be a knock-on effect on pest populations. For example, pest species would be expected to build up more rapidly in areas of comparatively lower predatory activity (Duffield & Aebischer 1994), all other factors being equal.

Since 'real-world' insecticide applications do not involve the use of within-field control plots it would be useful to know: (1) whether the recovery process is mediated by the random diffusion of ground beetles back into areas in which their populations have been depleted or whether it is mediated by a directed colonisation process, and (2) whether landscape features such as hedgerows represent a barrier to ground beetle movement. If hedgerows are a barrier to movement then the recovery of indigenous predatory activity in whole fields could be severely curtailed.

In this paper we present the results of research that was carried out to address the first of these last two points. Using a simple linear model derived from field-collected data (Thacker & Jepson 1993) an analytical simulation of the recovery process is compared to a second model that is based on the random movement of individuals. Sensitivity analyses of the second model identified which parameters in this model were the most sensitive to change and which set of parameters gave the best fit to the field collected, data-based, model. The biological realism of these parameters is used to validate the model. The results are discussed in relation to the movement of ground beetles between treated and untreated areas and in relation to toxicity testing and field trials in general.

2. Materials and methods

2.1. Algorithm development

The computer algorithm (available upon request from the authors), written in turbo pascal, comprised three sections; a linear model of recovery based upon published field collected data (Jepson & Thacker 1990, Thacker & Jepson 1993), a stochastic model of random movement, and a statistical comparison of the two models. The algorithm simulated the recovery of ground beetles in a wheat field which had been divided into four equal plots where two diagonally opposed plots had had their beetle populations completed suppressed.

Each of the models was based upon a 26×26 grid of elements where each element represented an area of a field crop that was 10×10m. Within each element the population density of the ground beetle population was recorded as an integer value from zero to eight. This integer value, which was displayed as a colour in the model, was analogous to a percentage recovery level. A value of zero indicated a population that had recovered by 0–10% of it's original level while a value of eight indicated a population that had recovered by 80–100%.

2.1.1. *Linear model of recovery*

The linear model of recovery was based upon field collected data (Jepson & Thacker 1990) from an experiment identical in design to the modelled recovery process. This experiment produced a significant regression of the time to recovery for ground beetles in days (y), at any given point, against distance in metres (x) from the nearest untreated control plot:

$$y = 7.287 + 0.1154x \quad \text{(Jepson \&Thacker 1990).}$$

Using this equation the recovery of the ground beetle population in the two suppressed plots of the field was simulated. At any instant in time the model produced a density map outlining the level of recovery attained within the plots.

2.1.2. *Random model of recovery*

The starting conditions for this model were identical to those in the linear model however, while the former model was not sequential this model was, i.e. the state of the model at time 't' was dependent upon the state of the model at time 't–1'. Within the model movement of ground beetles was random and could occur in a north, south, east or west direction. The magnitude of movement was also determined randomly while the probability of movement occurring and the minimum and maximum distance moved were input for each run of the model. The model did not allow for interaction between elements and therefore contained no density dependent effects. As with the linear model, as time progressed the model produced a density map outlining the level of recovery in all elements across the field.

2.2. Model comparisons

The two models of recovery were compared using an analysis of their percentage similarity and by using a statistical regression analyses. Percentage similarity was calculated by comparing the population density levels within each element in both models. This value was then totalled, subtracted from the maximum total difference, divided by the maximum total difference and multiplied by 100 to give a percentage. The comparative regression analyses were carried out with regression models of the recovery process (derived from the random movement model) and with the linear regression model derived from field collected data. In the random movement model when over 50% of the points at any distance from the untreated area were recorded as recovered a point was plotted on a comparison graph. Once a minimum of 5 points had been plotted the equation of the line through those points was then calculated and this line compared to the original recovery model equation. This comparison was based upon the relationship between the residual sum-of-squares for a single line plotted from all data points and the sum of the residual sum-of-squares for the two lines fitted separately (Bailey 1979). The resulting F-ratio was taken as a measure of the statistical similarity between the two models.

2.3. Sensitivity analysis and validation of model 2

In order to determine which of the parameters in the random movement model had the greatest effect upon its output and to find out which combination of parameters gave the best fit to the linear model of recovery the random model was run under a series of different conditions. Movement probability was varied through the series 10%, 20%, ..., 100%, the minimum distance moved was varied through the series 10 m, 20 m, ..., 100 m, and the maximum distance moved was varied through the series 20 m, 30 m, ..., 200 m. For any given combination of input parameters the model was run 10 times over a 40 day time interval. The mean F-ratio (of the 10 runs) was taken as the best statistical value indicating the degree of similarity of the models. In total the model was run 10 000 times over an eight day period.

3. Results

Fig. 1–3 show sample output from the two models at 1, 10 and 20 days after the start of a simulation with a movement probability of 100% and a movement range of 0–70 metres. The linear model based on field collected data is labelled 'Thacker 1989' and the model based on random movement is labelled 'Dixon 1989'. The figures show the change in the shading of the elements in the depleted areas as recovery in those areas takes place. On the right hand side of the output are the percentage similarity and the regression model comparison.

The lowest F-ratio's, at each movement probability levels tested, are given in Table 1. The table shows that as movement probability declined, the lowest F-ratios (obtained from the model comparisons) were given by an increase in the range of distances over which movement could occur. For example, with a movement probability of 30% the lowest F-ratio (and therefore the best comparison between the linear and random movement models) was obtained with a distance spread of 10–110 metres. In comparison, with a movement probability of 100%, the F-ratio was the lowest with a minimum movement distance of 10 metres and a maximum of 60 metres, i.e. an average rate of movement of 35 metres per day. Table 2 shows sample output of the calculated F-ratio's over the movement probability 30–100% and distance range 10–110 m. The figure clearly shows that as the movement probability increases the range giving the best fit (lowest F-ratio) decreased. This trend was recorded for all distance ranges.

4. Discussion

With a movement probability of 100% the random movement model indicated that an average ground beetle movement rate of 35 metres/day could account for the recovery pattern observed in the field. A comparison of this data value with others from the published literature is given in Table 3. The estimates of movement rates in Table 3 vary from less than one to tens of metres per day depending on the species considered. Although the present work considered ground beetles as an amorphous group, the samples that were collected were dominated by *Pterostichus melanarius* (Illiger) and a value of 35 metres/day is therefore not considered to be unrealistic. We conclude, therefore, that the recovery of ground beetle populations in plots in which their

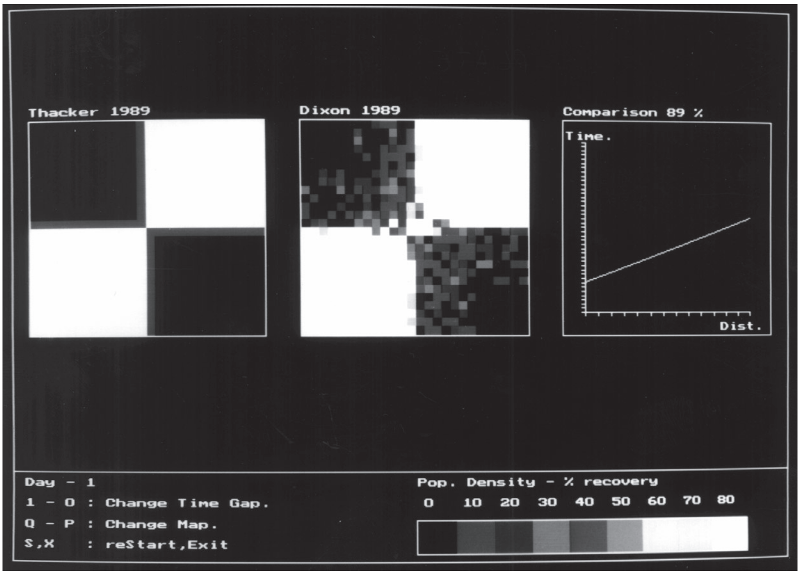

Fig. 1. Output from the two models of the recovery process at day 1. The scale (bottom-left) displays the population density as a percentage recovery value. The linear equation on the right headed 'Comparison' shows the model that was used for the recovery process that is being simulated in the in the model headed 'Thacker 1989'. The random movement model is shown as the central simulation.

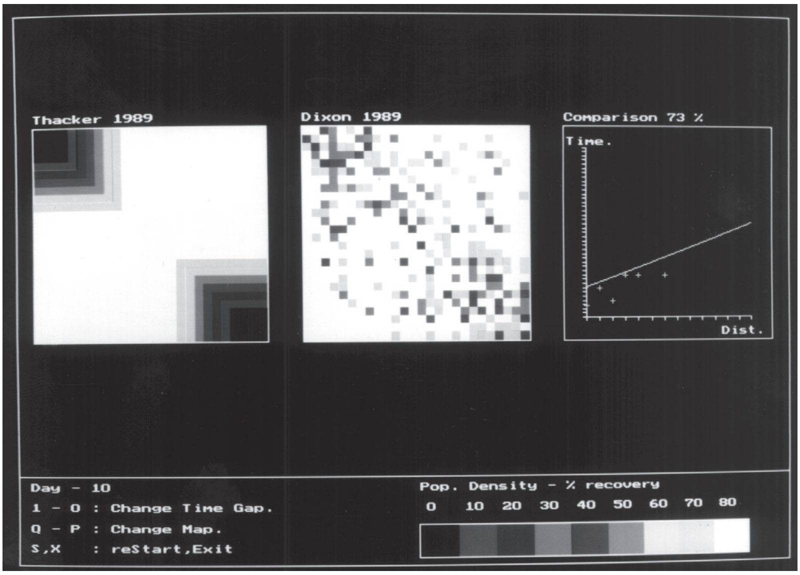

Fig. 2. Output from the two models of the recovery process at day 10. The comparison on the right hand side shows the points that are plotted as recovery occurs at different distances in the random movement model.

populations have been suppressed may occur due to the random movement of individuals from surrounding untreated plots.

This simple conclusion though should be tempered by the simplicity of the model. Many of the factors which are known to have an influence upon beetle movement were not included in the model. For example, Baars (1979) reported that the distances covered per day for the carabids *Pterostichus versicolor* (Sturm) and *Calathus melanocephalus* (L.) were dependent on both the ambient temperature and the level of rainfall. Further studies by Baars (1979) and Rijnsdorp (1980) showed that carabid movement could be partitioned into two types: random walk and directed movement depending on the level of satiation. Work by Mols (1987) supported this conclusion and suggested that the different types of move-

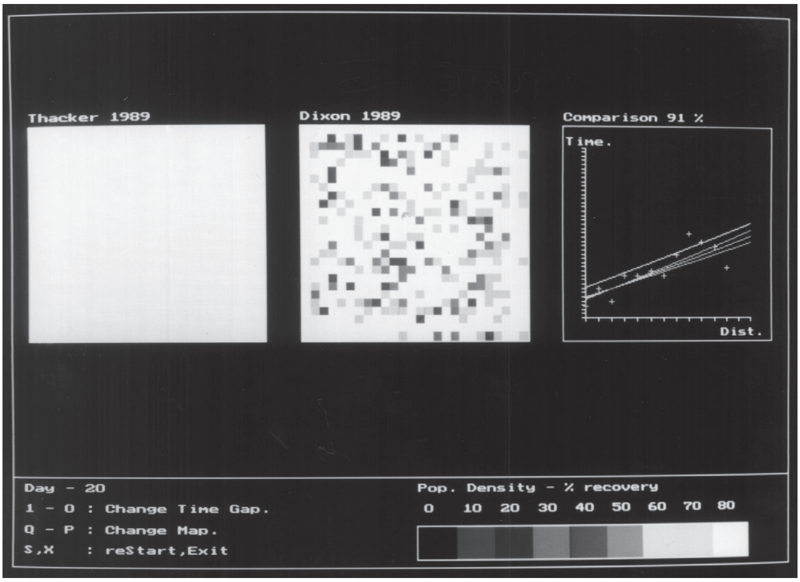

Fig. 3. Output from the two models of the recovery process at day 20. The comparison on the right hand side shows the linear models that are fitted to the points derived from the random movement model.

ment represented an adaption to different levels of prey clustering.

Despite the fact that many of the above factors were not simulated within the random movement model, however, does not negate the utility of our approach. The fact that field data show that beetles can move between different plots within fields and that it is possible to simulate this process with a simple computer model has a number of implications. For example, official protocols for field trials within the UK that are concerned with the effects of insecticides on beneficial arthropods in cereals recommend a minimum plot size of 1 ha for open field plots (Jepson 1993). Since these designs also use within-field control plots, it is likely that whatever the effects of the pesticide under evaluation, recovery mediated by reinvasion will occur within these experiments in a very short time period.

It is also likely that similar processes will mask any effects that are under evaluation within the UK in more substantial projects such as the SCARAB project (Cooper 1990). This UK Ministry of Agriculture, Fisheries and Food funded research programme is concerned with the effects of long term current pesticide use at the farm scale level. However, in this research single fields are split into halves which receive differing treatments. Perhaps unsurprisingly, to date there is no clear evidence for any substantial long term adverse effects (Çilgi & Frampton 1994).

In conclusion, the results of the modelling approach described in this paper indicate that ground beetle recovery following suppression in conventional field trials' designs may be mediated by random movement. These results have implications for all field experiments in which this group of insects is monitored. For the future, further research is now needed on the significance of hedgerows and other landscape features as barriers to insects movement, both in the long-term and in the short-term. Although preliminary experiments concerning this aspect of

Table 1. The relationship between movement probability and the distance range giving the best *F*-ratio in the comparison between the regression lines of the linear movement and the random movement models. All the *F*-ratios's were calculated from analyses involving regression lines with a minimum of 11 data points.

Movement probability (%)	Distance range (m)	*F*-ratio
30	10–110	0.706
40	10–100	0.107
50	10–90	0.120
60	10–80	0.166
70	10–80	0.600
80	10–70	0.378
90	10–60	0.506
100	10–60	0.288

Table 2. The effects of changing the movement probability and movement range upon the statistical comparison (*F*-ratio) between the regression lines of recovery derived from the field experiment-based model and from the random movement model. The degrees of freedom for the comparison were 2, 20, and at the 1% and 5% significance levels the ratios are 5.85 and 3.49, respectively. All *F*-ratios below these values therefore indicate that, for that set of parameters, the random movement model represented a good simulation of the field behaviour of the ground beetle population. These latter ratios are in boldface within the table.

Movement	Movement Probability (%)							
Range (m)	30	40	50	60	70	80	90	100
10–20	14.06	16.80	13.58	11.41	14.81	15.21	16.44	19.97
10–30	14.06	16.80	13.58	11.41	14.81	15.21	16.44	19.97
10–40	14.06	16.80	13.58	11.41	14.49	16.79	15.22	12.81
10– 50	13.35	12.43	14.57	13.51	11.43	8.26	**5.64**	**3.14**
10–60	14.06	14.27	13.37	6.62	**2.91**	**1.00**	**0.51**	**0.29**
10–70	12.93	12.37	**4.11**	**2.14**	**0.43**	**0.38**	**1.07**	**2.19**
10–80	12.69	**4.40**	**1.01**	**0.17**	**0.60**	**2.11**	**3.04**	**5.46**
10–90	6.58	**1.11**	**0.12**	**0.70**	**2.87**	**4.12**	5.86	8.10
10–100	**2.46**	**0.11**	**1.04**	**3.07**	**5.34**	7.56	9.17	11.13
10–110	**0.71**	**0.40**	**2.14**	**5.67**	6.39	9.60	11.33	13.95

Table 3. Estimates of carabid beetle rates of movement obtained from the literature over the last 30 years.

Species	Speed	Habitat	Reference
T. quadristriatus	0.05–0.4 m/day	field	(1)
B. lampros	0.15–10 m/day	field	(1)
*P. melanariu*s	3–15 m/day	field	(2)
C. cancellatus	12–15 m/day	field	(2)
P. cupreus	up to 30 m/day	field	(2)
C. problematicus	70–77 m/day	open	(2)
C. granulatus	3.2–16.2 m/day	cereal field	(3)
P. niger	0.6–20.7 m/hour	cereal field	(4)
P. melanarius	0.3–17 m/hour	cereal field	(4)
H. rufipes	1.0–8.7 m/hour	cereal field	(4)
Medium-large species	5–20 m/day	n/a	(5)

(1) Mitchell (1963), (2) Thiele (1977), (3) Mascanzoni & Wallin (1986), (4) Wallin & Ekbom (1988), (5) Luff (1989).

agro-ecology have already been undertaken by some researchers (Duelli *et al*. 1990, Frampton *et al*. 1995, Mauremootoo *et al*. 1995), a great deal more detailed research is required if informed decisions are to be made regarding invertebrate survival in what are becoming increasingly fragmented habitats.

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