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Simulating the long-term dynamics of slug populations: a process-based modelling approach for pest control

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Summary

1. An individual-based simulation model was developed to investigate the long-term dynamics of slug populations using the field slug *Deroceras reticulatum* as the test species.

2. The model consisted of two components: a model to provide meteorological data and simulate crop growth; and a model to simulate slug life histories. The patterns of slug population dynamics produced by the model matched the characteristic bivoltine life cycle of *D. reticulatum* observed in field studies.

3. A sensitivity analysis showed that the output of the model was significantly influenced by soil moisture, air temperature and leaf area index. These three environmental factors relate directly to important features in the biology of slugs. Of the life-history variables used as inputs to the model, growth rate, environmental mortality and the mortality of sexually mature slugs had a significant effect on the population dynamics predicted by the model.

4. The model output was compared with the observed dynamics of slug populations collected in the field. Predicted slug dynamics and observed slug numbers showed a high degree of fidelity.

5. The simulation model was used to investigate the effects of varying the timing of control methods used to combat slug damage to crops. This result suggested that there is a 'window of opportunity', immediately post-harvest, when slug control is likely to have a significant effect on both the current slug population and the slug numbers in the following spring.

6. Modelling approaches that link crop growth and population dynamics of pests have potential in assessing their agricultural impacts and in evaluating alternative strategies for their management.

Key-words: *Deroceras reticulatum*, population prediction, sensitivity analysis, slug control.

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Introduction

Slugs are important pests of agricultural crops in moist temperate climates (Stephenson & Bardner 1976; Port & Port 1986), and the damage they cause is a persistent problem in agriculture. In the UK, *Deroceras reticulatum* Müller (Mollusca: Limacidae) is the main molluscan pest of cereal crops (Fleming 1989), causing about £4 million in damage each year in wheat alone (figure updated from Port & Port 1986); but slugs are also a major pest in nearly all arable and horticultural crops around the world (Godan & Gruber 1983). The damage that slugs cause can be sufficient to warrant substantial investment in control, mainly pesticides (an additional £10 million in molluscicides alone; Garthwaite & Thomas 1996) but crop husbandry (Edwards 1977; Barratt, Byers & Bierlein 1994), predators such as ground beetles (Symondson 1989), and parasites such as the nematode *Phasmarhabditis* (Glen *et al.* 1996) have also been considered.

There has been considerable interest in attempting to identify the most effective time to apply control measures to obtain the maximum reduction in slug populations. For most farmers and growers this means identifying the season or the stage in the cropping cycle

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when control will be most effective. From the point of view of pest management, timing needs to be linked to optimal phases in the population cycle of the pest.

For all terrestrial molluscs, water balance is a determinant of population processes, and to slugs, the most important characteristics of the environment are soil moisture and temperature (Young & Port 1989; Young, Port & Green 1993). Like all ectotherms, growth rate and mortality are greatly affected by temperature (South 1982), and Carrick (1942) showed that moisture and temperature play a pivotal role in the reproduction and survival of slugs and their eggs. Dehydrated slugs exhibit behavioural alterations (primarily shelter-seeking and huddling; Cook 1981; Prior 1989) to minimize water losses, and thus the presence of shelters (cracks in soil, stones, leafy foliage, etc.) in a landscape can have a significant effect on dehydration rate and survival. The presence of shelters also affects daily activity (Hommay, Lorvalec & Jacky 1998) and will have impacts on crop damage.

The effects of environment and control methods on the long-term population dynamics of slug populations are poorly understood: it is a complex, multivariable problem, and one that is most amenable to modelling.

Models that predict slug activity in the short term (Young *et al*. 1991) have shown that molluscicide usage can be reduced by using such models to optimize control methods (Young, Port & Green 1993). These types of statistical models can be very useful in making predictions in the short term, but lack the power of simulation models for more long-term predictions, as they take no account of the processes occurring in slug populations.

Simulation modelling of pest populations can be a powerful tool in investigating the management of pest species, and has been used for a variety of pests, e.g. the strawberry bud weevil *Anthonomus signatus* (Bostanian *et al*. 1999), the almond moth *Cadra cautella* (Throne, Hagstrum & Nawrot 1998), the cereal aphid *Sitobion avenae* (Freier, Triltsch & Rossberg 1996) and the bostrichid *Prostephanus truncatus* (Meikle *et al*. 1998). The approach has not been used to investigate the population dynamics of slugs and their control.

Individual-based modelling is a technique that involves the simulation of life-history processes of individual organisms in the modelled population. The main advantage of this approach is that it allows simulation of stochastic processes at the level of the individual. Such stochastic models also have an advantage over deterministic models, in that they simulate the dynamic processes of the organism's biology. Indeed, the failure of deterministic models for pest control generally has been attributed to a failure to include important aspects of behaviour and biology that affect levels of damage (Rossing & Heong 1997).

The purpose of this study was to investigate the population dynamics of *D. reticulatum*, through the development of an individual-based model that simulates changes in slug numbers in relation to changes in the environment and control. We compared the output of the models with field data. We used sensitivity analysis on the model to generate hypotheses regarding which factors drive slug population dynamics, with which to direct future empirical research. We used the model to investigate the relationship between slug activity and the effectiveness of control measures.

Methods

THE SIMULATION MODEL

Overall structure

The simulation model has two components. The first is a slug simulation model, the second is an environmental model that generates crop and weather data for input into the slug simulation model.

Slug population simulation

A flow chart for the slug population model is given in Fig. 1. This was an individual-based model with the weight and age of each slug as the state variables. The model interrogated each slug at each time step to determine stochastically the life history of the individual slug. All life history 'decisions' were made on a weekly basis using a probabilistic approach, each individual having a particular chance that it will hatch (assuming it was an egg), mature (assuming it was a juvenile), grow or reproduce (based on age) and die (based on a measure of environmental stress).

Each week, weather and crop variables were input from the environmental model outlined below. Assuming that the slug was alive, the next step was to determine whether the individual was an egg or not. In any given week the chance that eggs will hatch was determined stochastically, based on its current physiological age.

If the individual slug was not an egg, then it was either active or inactive. When weather conditions are inclement to slug activity, they shelter below the soil surface (Dainton 1954a) and they were considered inactive when in this state. The model assumes that temperature and soil moisture were the most important factor in controlling activity, and slugs became inactive if the mean daily temperature was less than 2 °C and/or the soil moisture was less than 25% (Young & Port 1989). Active slugs either grew or reproduced, according to their state of maturity.

The chance of a slug maturing increased with the physiological age of the slug. Growth in *D. reticulatum* occurs in two phases (Abeloos 1944; South 1989); phase I is the rapid-growing juvenile phase and is strongly temperature-dependent (South 1982). Slugs in phase I did not reproduce, but upon reaching sexual maturity (at which point most slugs weighed 125–200 mg) slugs entered phase II growth, which is independent of environmental temperature. Mature slugs were assumed either to grow or reproduce at each time step. Reproduction in this context was defined as laying eggs, and thus was the province of older

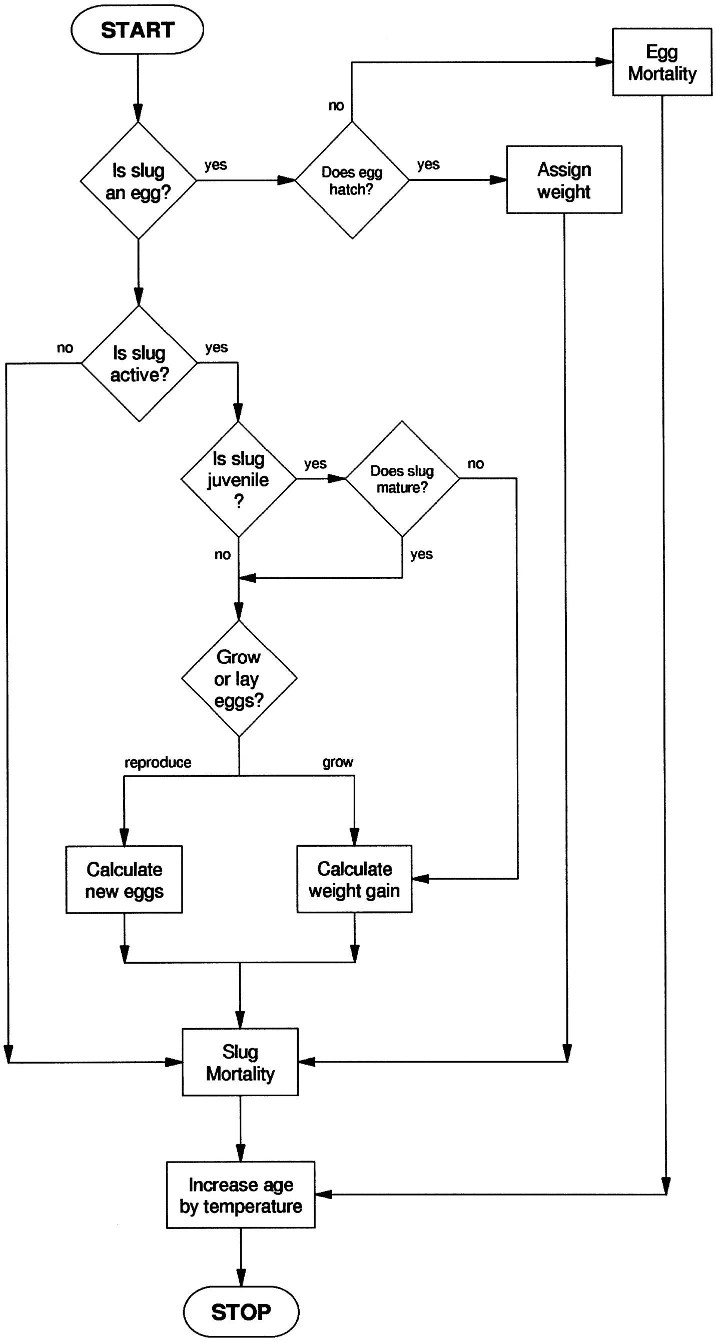

Fig. 1. A flow diagram of the slug population model. An explanation is given in the text.

slugs, which were assumed to be physiologically female. The probability that an individual slug grows (as opposed to reproducing) in any given week was assumed to be unity for phase I slugs, and for phase II slugs decreased linearly with slug weight to a value of 0·1. This resulted in a pattern where large slugs (which have large energy reserves available for egg production) devote more effort to reproduction as opposed to growth.

The reproductive effort of a slug was assumed to be determined by body mass; although there is no supporting evidence for this assumption, it seems reasonable that large slugs will invest more in a reproductive event than smaller slugs. Fewer eggs were laid in dry conditions than in wet ones (Carrick 1942).

Survival was also modelled at the level of the individual. There was a ‘background’ mortality rate that produced a type III survivorship curve (Pearl 1928), i.e. a very high juvenile mortality which drops off exponentially with age. This was simulated using two age-specific parameters, juvenile mortality (which was generally high) and adult mortality (which was generally low). Mortality was also imposed on slugs through adverse environmental constraints. Low moisture content, high temperature, low food availability and lack of shelters all imposed additional mortality on slug populations through a single variable called environmental mortality. This variable essentially expressed the suitability of the environment to slug biology.

Table 1. The seven environmental variables and 12 life-history variables together with the ranges used to assess the sensitivity of the population dynamics model

Variable	Range modelled	Source of life-history data
Leaf area index	3 (rye grass) 4 (oilseed rape) 5+ (wheat)	Kiniry *et al.* (1995)
Soil moisture content	0–30%	Field capacity for heavy soil (FitzPatrick 1980)
Temperature	–5–25 °C	A.G. Young (unpublished data)
Activity	0–7 days	Derived from thresholds in Young *et al.* (1991)
Probability of hatching	0–1	50% chance of hatching at the average incubation period of a slug egg (data from South 1989)
Probability of maturation	0–1	50% chance of hatching at the average juvenile period of a slug (data from South 1989)
Probability of a reproductive event	0–1	–
Growth index (gradient of temperature-dependent growth rate)	0–2	South (1982), Abeloos (1944)
Number of eggs in an egg mass	2–40	A.G. Young (unpublished data)
Number of egg masses	0–7	Carrick (1942)
Egg mortality due to moisture extremes	0–1	Carrick (1942)
Egg mortality due to temperature extremes	0·05–1·0	Carrick (1942)
Environmental slug mortality	0–1	Rollo (1983)
Mortality in juvenile slugs	0–0·95	Reconstructed from Pearl & Miner (1935)
Mortality in adult slugs	0–0·95	
Mortality due to slug control on nights of high activity	0–1·0	–

Data for growth rates were derived from South (1982) and Prior (1983), fecundity from Carrick (1942) and South (1982), and survivorship information from Pearl & Miner (1935). The life-history variables used in the slug simulation model are shown in Table 1.

Environmental simulation

The environmental simulation model generated stochastically a set of weather and crop parameters appropriate to the location and time of year.

Daily estimates of temperature were simulated using the regression method of Johnson & Parsons (1985), who considered daily air temperature to be a sine function of the Julian day (1 January = 1, 2 January = 2, etc.) and developed a regression equation to account for the seasonal change in temperature. Stochastic variation in the temperature was included by drawing a Gaussian deviate from a skewed normal distribution based on a set of weather data collected in Northumberland. This resulted in a simulated temperature appropriate to the time of year. Solar radiation was calculated in a similar fashion.

The surface soil moisture for any given day was calculated using a method modified from Walker (1974). Gains in soil moisture were due to precipitation, which was modelled according to the methods outlined in Arnold *et al.* (1990). The probability of a rainfall event was based on a Markov chain model (Sharpley & Williams 1990), where the probability of rain on a particular day is dependent on whether it rained the previous day. The amount of precipitation, given that rain occurs, is drawn from a skewed normal distribution based on monthly averages derived from data collected in Northumberland. Losses in soil moisture were from three sources: evaporation from the soil surface, transpiration from plants, and percolation through the soil layer. As soil moisture in agricultural land is generally below the field capacity of the soil, percolation was considered to be negligible (Arnold *et al.* 1990). Evapotranspiration was calculated according to Ritchie's (1972) method, which has solar radiation and air temperature as inputs. The model that calculates soil moisture can be used for all types of soils for which the field capacity, bulk density and albedo are known.

The crop growth component of the model was adapted from EPIC (Erosion/Productivity Impact Calculator) (Sharpley & Williams 1990). This model is capable of simulating a wide range of crops through the accumulation of heat units from planting date to harvest date, up to a maximum calculated for each crop from empirical data. Perennial crops can be simulated by conserving root systems throughout the year. Output of the model takes the form of leaf area index and biomass for the crop (both total and above-ground biomass). Crop parameters for winter wheat, spring wheat, oilseed rape and grassland for this model were obtained from Kiniry *et al.* (1995). The crop growth simulation requires inputs in the form of daily temperature, solar radiation and soil moisture, all of which were provided by the weather simulation.

The environmental variables used as inputs into the slug simulation are given in Table 1.

SENSITIVITY ANALYSIS

The sensitivity of the population dynamics model to input parameters was investigated by analysing the total population size of simulated slug populations over 8 months to variations in the model inputs. A Latin hypercube sampling strategy following the methods of Vose (1996) was used to select input parameters for the model from the known or estimated ranges of the different variables in the model. Latin hypercube sampling uses stratified sampling without replacement to select suites of input parameters from known distributions of those variables. In practical terms, the probability distribution for each variable is split up into *n* intervals of equal probability, where *n* is the number of sets/suites of input variables selected (in this case, $n = 1000$). The creation of input variables for the simulation model run proceeds as follows. A random number is used to select an interval and a further random number determines the position, and hence the value, for the input variable for inclusion in the set. Once selected, an interval cannot be used again.

The aim was to provide a range of input values for each variable that could potentially occur under field conditions. In other words the model was run a sufficiently large number of times to encompass all of the potential range of conditions that occur naturally rather than simply worst and best case scenarios (*sensu* Bart 1995). Sixteen parameters were considered; the details are shown in Table 1.

In all cases there were insufficient data available to identify the distribution function for each parameter. Furthermore, there were no data available to assess the extent to which each of the life-history parameters were correlated with the others. A uniform distribution was assumed for each variable, with upper and lower limits derived from the literature, and all variables were assumed to vary independently of each other. The range of each parameter from which samples were taken is given in Table 1. In effect, the use of uniform distributions for all of the input variables without intercorrelations leads to an overestimate of the size of the likely universe of possible values that each life-history parameter could take, as it is likely to lead to the selection of values for parameters that are near the extremes of their distributions more frequently than would be expected in reality. In addition, by not including intercorrelations it means that the probable range in parameter values modelled will also be larger than that occurring in reality. On the other hand, it also ensures that all potential values (within the known range of observed behaviours for each variable) are sampled. In other words, while we know that the hyperspace of possible values for each parameter in the model will be larger than reality, we know that reality lies somewhere in that space and not outside it (Rushton *et al.* 2000).

The sensitivity analysis was performed twice, the first time without slug control. The second analysis simulated the populations with additional control mortality applied each week to all active slugs.

A thousand sets of the input parameters were selected and the model was then run for 8 months for each set with a starter population obtained from field data. For each model run the number of slugs in the population and the total numbers of juvenile and sexually mature individuals were output at the end of the 8 months. The total population size was then correlated with the input variables and partial correlation coefficients were calculated to assess the impact of the individual life-history parameters on the dynamics of the population as simulated by the model.

COMPARING MODEL OUTPUT WITH OBSERVED SLUG DYNAMICS

The model output was compared with observed slug dynamics using data collected in the field. Monthly samples of slug populations were collected from six sites in Northumberland using defined area traps (Byers, Barratt & Calvin 1989). The longest time series in this data set was for 16 months from a set-aside field at the study site. This field had been grass meadow for over 10 years, and was on a south-facing slope. The data collected from this site in July 1997 were used as input data for the model, which then simulated 15 months of slug population dynamics. The weather data collected from the field site were used instead of the weather simulation model. It was necessary to estimate the number and age of slug eggs in the initial sample, as these data were not collected from the field. This was done by simulating a slug population from January until July, and adding all the eggs in the simulated population to the input data with the real slug population. All of these eggs would have been laid by slugs that had matured over winter and had been sexually active in late spring–early summer. The same process was used to produce two shorter simulations of 12 months each for a winter wheat field (data collected from September 1997 until August 1998) and an oilseed rape field (data collected November 1997 to October 1998).

Field collection of slugs with defined area traps records only a proportion of the population; however, over the 2 weeks of trapping it is assumed that all of the active slugs in that area are collected. The simulation model predicts the total slug population, so it was necessary to adjust the simulated population size by a measure of activity. The weekly simulated population sizes were multiplied by the proportion of days in the week that the slugs were predicted to be active, according to the criteria of Young *et al.* (1991). This was done to simulate the approximate number of active slugs in the predicted population.

TIMING OF SLUG CONTROL

The simulation model was also run multiple times with added mortality in September, October, November, December or January. This added mortality was deemed only to affect active slugs, and therefore simulated the effects of most control methods (molluscicides, invertebrate predators such as carabids, etc.).

Table 2. Results of the sensitivity analysis (partial rank correlation). Columns 2–4 are the results for the sensitivity analysis performed in the absence of control, the last three columns are the results for the model run performed with additional mortality (an additional 0–100% mortality on nights of high activity).The degrees of freedom were 1 (numerator) and 981 (denominator – the number of replicates minus the number of variables). The critical value for the *F* distribution at (1, 984) degrees of freedom is approximately 7·88 for $P < 0{\cdot}001$ (indicated as + + + in the table) and 5·02 for $P < 0{\cdot}05$ (indicated as + +). The abbreviations are as follows: LAI, leaf area index; MC%, soil moisture content; temp, air temperature; activity, number of days spent active on the surface; probHatch, probability of hatching; probMat, probability of maturation; probLay, probability of a reproductive event; growthIndex, gradient of the temperature-dependent growth rate; avEggs, average number of eggs in an egg mass; eggMasses, average number of egg masses per reproductive event; waterMort, egg mortality due to moisture extremes; heatMort, egg mortality due to temperature extremes; suitMort, slug mortality due to environmental constraints; youngMort, juvenile slug mortality; oldMort, adult slug mortality; controlMort, mortality due to simulated slug control

	No control			Additional mortality		
Variable name	Partial correlation	*F*-statistic	Significance	Partial correlation	*F*-statistic	Significance
LAI	0·286	87·39	+ + +	0·162	26·36	+ + +
MC%	0·475	285·37	+ + +	0·313	106·71	+ + +
temp	0·455	255·85	+ + +	0·329	118·81	+ + +
activity	0·005	0·02	–	0·364	149·95	+ + +
probHatch	0·058	3·26	–	0·050	2·51	–
probMat	0·025	0·63	–	0·014	0·18	–
probLay	0·002	0·00	–	0·018	0·31	–
growthIndex	0·438	233·04	+ + +	0·306	101·30	+ + +
avEggs	0·003	0·01	–	0·023	0·51	–
eggMasses	0·007	0·04	–	0·040	1·60	–
waterMort	0·017	0·28	–	0·020	0·38	–
heatMort	0·033	1·10	–	0·064	4·07	–
suitMort	0·283	85·17	+ + +	0·152	23·13	+ + +
youngMort	0·046	2·08	–	0·033	1·07	–
oldMort	0·653	730·43	+ + +	0·499	324·66	+ + +
controlMort	0·008	0·06	–	0·080	6·39	+ +

Results

SENSITIVITY ANALYSES

The response variable for the sensitivity analysis was the total number of slugs in the population at the end of each 6-month simulation, and the predictor variables were the output of the Latin hypercube sampling.

The results of a partial rank correlation are summarized in Table 2. This table gives the *r*-values, *F*-statistic and significance level. Of the five environmental variables, leaf area index, soil moisture content and temperature were all highly significant in determining slug population size. Of the 12 life-history variables, growth rate, environmental mortality and adult mortality were also highly significant. In scenarios involving slug control, the number of nights spent active on the surface and the predicted slug numbers were also significant correlates with mortality rate of control measures.

COMPARING MODEL OUTPUT WITH OBSERVED SLUG DYNAMICS

The age structure of simulated slug populations can be seen in Fig. 2. The pattern observed matched that observed in other data sets (South 1989). The patterns of population sizes showed overlapping generations. The first generation had a peak of juveniles in autumn from eggs laid in mid-spring, which overwintered as immature adults, laying eggs again the following spring. The second generation arose from eggs laid in about November, which overwintered, hatched into a small population of juveniles in late spring, and then matured into egg-laying adults by the end of autumn. As can be seen from Fig. 2, the first of these generations was larger than the other (mainly due to losses of overwintering eggs in the second generation), thus adults were most abundant in spring whereas juveniles were more abundant in autumn than in spring.

The results of the comparison of the model with field data are shown in Figs 3 and 4. Figure 3 displays the result of a 15-month simulation of the set-aside field. As can be seen, there was good correlation between the active populations predicted by the simulation model and those observed in the field. Figure 4 shows the data for the two shorter simulations in winter wheat and oilseed rape.

To test the accuracy of the model in predicting slug populations, the weekly simulated slug numbers were converted into averages for each month. These averages were then compared with the monthly field data using Pearson's correlation.

All three simulations were significantly correlated with their corresponding field data (set-aside: $n = 13$, $r = 0{\cdot}756$, $P < 0{\cdot}005$; winter wheat: $n = 8$, $r = 0{\cdot}724$, $P < 0{\cdot}05$; oilseed rape: $n = 9$, $r = 0{\cdot}722$, $P < 0{\cdot}02$). This means that the pattern of peaks and troughs in the data were the same, and the magnitude of the changes in simulated slug populations was realistic.

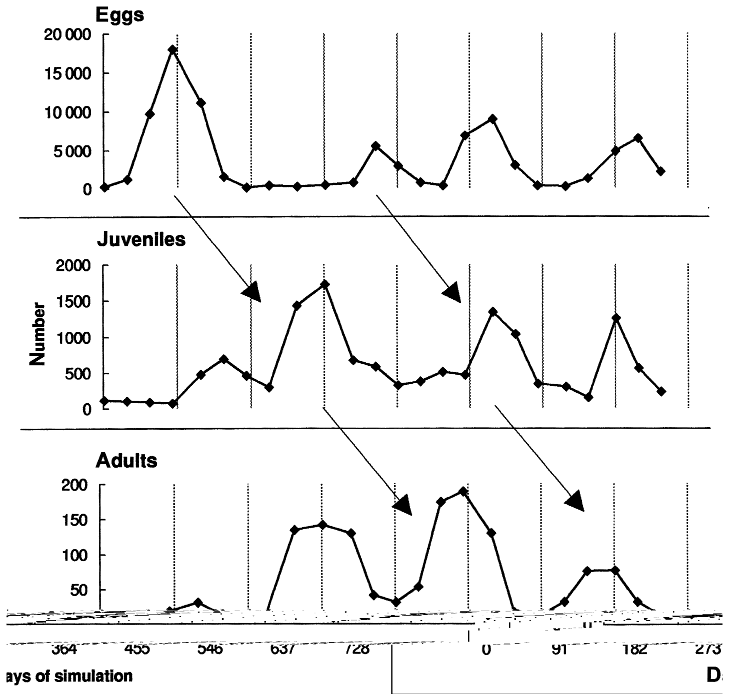

Fig. 2. The two generations of slugs over the course of a 2-year simulation. The arrows indicate the progression of the overlapping generations. Note the 10-fold difference in the *y*-axis of each graph.

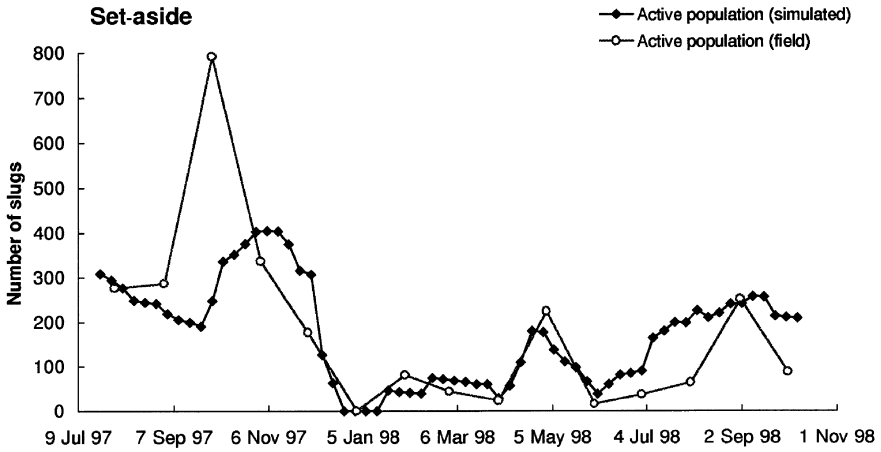

Fig. 3. The slug population simulated by the model using the recorded environmental data in a set-aside field between July 1997 and October 1998. Closed symbols represent simulated population sizes, open symbols actual population sizes.

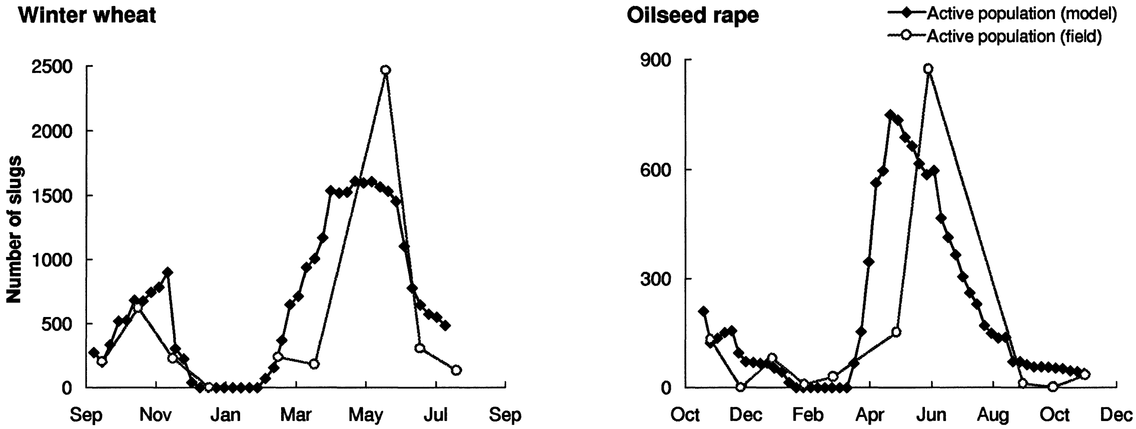

Fig. 4. The simulated population sizes in winter wheat and oilseed rape, along with the recorded environmental data for 1997 and 1998. Closed symbols represent simulated population sizes, open symbols actual population sizes.

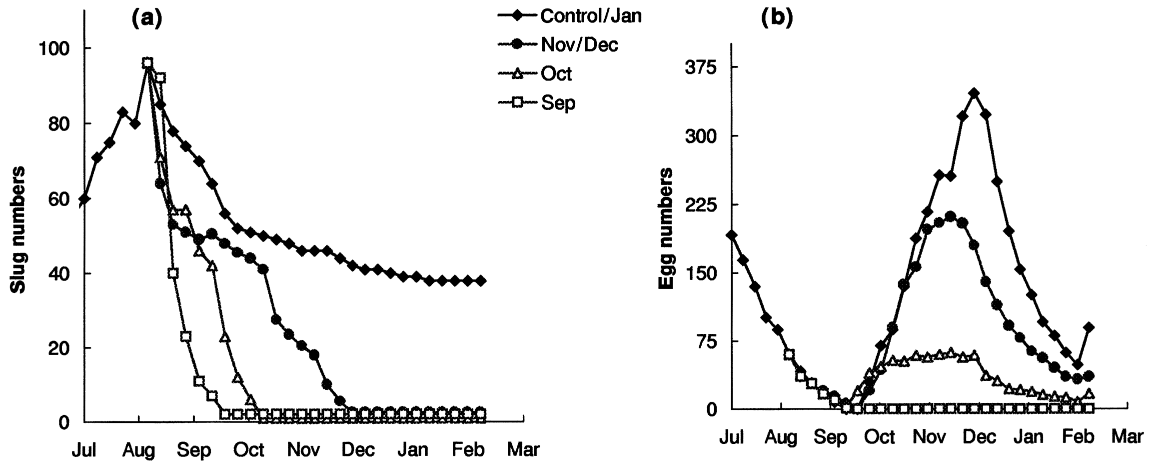

Fig. 5. A comparison of slug population size with different timings of additional mortality factors. (a) Total slug numbers; (b) egg numbers.

TIMING OF CONTROL

The effect of different timings of molluscicide treatment can be seen Fig. 5. The control/January treatment had the highest final population size, and the September treatment had the lowest final population size.

The impact of slug control on population size was likely to be greatest in September (Fig. 5a). Environmental conditions were nearly always suitable for slug activity at this time. More importantly, control at this time significantly restricted egg production (Fig. 5b) in the autumn population. The decline in egg numbers seen in Fig. 5b was due to both winter mortality and reduced egg laying. Slug control applied in November or December was predicted to still leave eggs laid by adult slugs in September, which mature by the next spring. Control in September, on the other hand, prevented the formation of an 'egg bank', which had a significant effect on the number of slugs in the following spring.

As this simulated control affected only active slugs, the January application was not significantly different from the control, where no additional mortality was applied. Slugs were predicted to be only very rarely active during January, when it was too cold for them.

Discussion

Invertebrates impact on humans through their effects on crops and diseases. Clearly, predicting pest activity in crops must be one of the most practical applications of population dynamics modelling. Population models of pests have been produced; similarly, plant growth models have been used extensively to predict how crops will grow and the yields they will produce, and these are used routinely (Kiniry *et al.* 1995; Wallinga *et al.* 1999). However, there have been few attempts to link crop growth and pest modelling. We investigated the potential for combining tested models of crop growth and weather simulation with a model to simulate slug population dynamics.

Simulation models have a number of problems associated with them. 'Models are constructions of knowledge and caricatures of reality' (Beissinger & Westphal 1998). So how good is our caricature and how accurate is our knowledge? Considering the caricature first, to what extent are the processes modelled accurate? In this model, each environmental variable was applied separately to the slug's life history, with no potential for interaction. There was no consideration for density-dependent fecundity. The slug control applied was of a generic nature, simply applying an additional mortality to active adult slugs; it therefore did not mimic the effects of parasites, predators or crop husbandry. As far as the accuracy of our knowledge goes, some basic facts about the biology of slugs are not known, despite their importance in world agriculture systems. In order to assess the model's response to the assumptions that we have been forced to make, we need to consider how sensitive it is to its inputs and whether it will produce outputs that are biologically meaningful.

The sensitivity analysis indicated that the environmental factors of soil moisture, air temperature and leaf area index significantly affect the size of simulated populations. Slugs are ectothermic and apparently poorly adapted to life on land, having a great reliance on water. They dehydrate very quickly in dry conditions (Dainton 1954a,b; Prior *et al.* 1983; Prior 1989) and are often forced into inactivity by such conditions (Hess & Prior 1985). Their behaviour is tightly controlled by environmental conditions (Waite 1987), often being forced to exhibit 'constrained' behaviour such as rehydration before 'unconstrained' behaviours such as foraging, eating or mating can occur (Rollo *et al.* 1983; Banta, Welsford & Prior 1990). It is perhaps no surprise that this reliance on maintaining their water balance explains why these three environmental factors were found to be so important in the sensitivity analysis. Temperature and leaf area index both affect soil moisture, which in turn affects mortality. As slugs are exothermic, temperature also impacts directly upon growth rate, incubation period and time to sexual maturity. The life-history variables that have the most effect upon slug population dynamics were their growth rate, background mortality (primarily due to moisture and temperature) and the mortality of sexually active slugs.

Validation is 'a demonstration that a model within its domain of applicability possesses a satisfactory range of accuracy consistent with the intended application of the model' (Rykiel 1996). While there is some debate as to whether models can be validated (Bart 1995), most people consider that a comparison of the simulation with an independently collected set of field data forms a method of 'validating' models.

At the general level, the results of the simulation model show that the characteristic bivoltine pattern of *D. reticulatum*, often observed in the field (Judge 1972), emerges. Two distinct but overlapping generations are seen in the simulated populations, a feature of *Deroceras* populations recorded by Hunter & Symonds (1971) as 'leap-frogging' populations. However, it is important to note that *D. reticulatum* of most age classes may be found at any time of year (Haynes, Rushton & Port 1996), and this feature is also seen in some of the simulated populations.

No statistical difference was demonstrated between the model output and data collected in the field. The field population in a set-aside crop had peaks of slug numbers in September 1997 and 1998, and another in May 1998. These two peaks in slug numbers resulted from the influx of juvenile slugs into the population as eggs hatched, indicating that *D. reticulatum* achieved two overlapping generations per year, one overwintering as eggs (which hatch in spring) and another overwintering as juveniles, which lay eggs in spring that hatch in autumn (cf. South 1989). These same characteristics were seen in the simulation model.

The model did not simulate accurately the timing of the peak in slug numbers observed in September 1997, probably because the status of the egg bank in the field situation was unknown and had to be estimated. None the less, the peak of juvenile slugs was still present in the simulated data but occurred a fortnight too late and at half the expected numbers. This may reflect the inaccurate population data used to start off the simulation rather than a fault of the model formulation. The simulation model was designed to predict the pattern of the dynamics of slug populations, not mimic the actual numbers of slugs observed in the field, and there is little doubt from these results and the results of the correlation that it achieves this objective.

A similar pattern was found in the winter wheat field, although the populations reached much greater densities in this crop. The presence of abundant palatable food in the autumn (newly sown grain) probably contributed to the large numbers of juveniles appearing in May–June 1998. It was certainly a large egg bank that promoted large population sizes in the model. The oilseed rape field had a different pattern of slug population dynamics; the field data had no pronounced peak in numbers in the autumn of 1997, and the population had a single peak in the summer of 1998. This suggests that only a single generation of *D. reticulatum* was achieved in this crop. The input data for the model (i.e. the field data for September 1997) reflected this univoltine pattern, containing a predominance of subadult slugs. It could be that a peak in slug numbers occurred earlier in the year, or alternatively there may have been no overwintering population of eggs in 1997–98 and the peak in the summer of 1998 resulted solely from eggs laid by the preceding year's juveniles. The latter was the case in the simulated population: all of the simulated slugs in 1998 hatched from eggs laid in 1998.

So, we have some evidence to suggest that the model simulates slug populations reasonably well in two crop types that are known to generate different responses in slug populations. We believe that this model could help target future investigation into slug population dynamics by identifying those processes that have significant effects upon the life histories of slugs.

First, the direct effects of available water on slug mortality have not been investigated extensively, and this has been shown here to be a key factor in driving population dynamics. Soil moisture itself, and two factors that influence soil moisture (temperature and leaf area index), had significant effects on the numbers of slugs in the sensitivity analysis. The life-history variable driving environmental mortality of slug populations was also revealed to be significant.

Secondly, the effects of growth rate were discovered to be important in determining simulated slug numbers. This was assumed to be temperature-dependent, but a large amount of variability in slug growth rates has been demonstrated (Prior 1983) even in individuals from the same clutch reared at the same temperature. The sensitivity analysis of the model suggests that more work needs to be done to discover the factors influencing individual growth rate (particularly in the field) as it is likely to influence slug population dynamics.

Does the model have any practical value in slug population control? The model may have some utility in planning control strategies. The analysis given above deals with molluscicides, which require careful timing, and the results indicate that timing of control may be critical. They cannot be applied to the crop effectively during the summer months before harvest, which is when the largest numbers of (juvenile) slugs were found. The first opportunity for pellet application is immediately following harvest, which coincides with the maturation of juvenile slugs into egg-laying adults. There then follows a narrow window for control, while the weather remains suitable for slug activity and while there are adult slugs around before they die due to the cold weather. This is the only opportunity for effective slug control until the next spring, when the eggs hatch and the overwintering juveniles mature (Hammond, Smith & Beck 1996). If slug control is applied too late, then the simulation model suggests that it will be a great deal less effective, because the current generation of slugs will have already commenced egg laying, which affects the spring population. Late slug control also has less effect on the current generation of slugs as most of the population will be inactive, and therefore not exposed to the control methods.

It should be noted that this model currently applies to only one species of slug. Although slug populations in arable fields tend to be dominated by *D. reticulatum*, there are usually many different species present at the same time. These other species may have different responses to environmental factors, and therefore complicate decisions about the timing of slug control. None the less, this study reveals that insights into slug control can be gained through process-based modelling.

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