

A DISCRETE SLUG POPULATION MODEL DETERMINED BY EGG PRODUCTION

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ABSTRACT

Slugs are significant pests in agriculture (as well as a nuisance to gardeners), and it is therefore important to understand their population dynamics for the construction of efficient and effective control measures. Differential equation models of slug populations require the inclusion of large (variable) temporal delays, and strong seasonal forcing results in a non-autonomous system. This renders such models open to only a limited amount of rigorous analysis. In this paper, we derive a novel batch model based purely upon the quantity of eggs produced at different times of the year. This model is open to considerable reduction; from the resulting two variable discrete-time system it is possible to reconstruct the dynamics of the full population across the year and give conditions for extinction or global stability and persistence. Furthermore, the steady state temporal population distribution displays qualitatively different behaviour with only small changes in the survival probability of slugs. The model demonstrates how small variations in the favourability of different years may result in widely different slug population fluctuations between consecutive years, and is in good agreement with field data.

Keywords: slugs, extinction, global stability, seasonal variation.

1. Introduction

Terrestrial slugs (*Gastropoda*) are common in all temperate climates, and individual as well as different species have adapted to a variety of environments. Several species are agricultural and horticultural pests, and an estimated £4-11million is spent each year on chemical treatments by farmers in the United Kingdom alone. Alternatives, such as using naturally occurring parasitic nematodes as organic bio-control agents, are also available and have been shown to be effective [18,3]. These have the advantage of not affecting the environment and other organisms, as well as providing protection for longer periods when appropriately applied [19]. At present, however, these methods are too expensive to be commercially viable for conventional farming.

This paper is a first step towards a mathematical understanding of the dynamics

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of slugs, and ultimately their interaction with other (especially control) species, with the aim of producing cost effective strategies for the deployment of biological controls. Regardless of which method is used to control slugs in agriculture, a clearer understanding of when significant variations in population numbers are likely to occur would be of value. Large fluctuations in slug populations are observed in field data [6], compared to relatively small (or unobserved) changes in surrounding factors that are generally considered to be of importance. It is necessary to try to understand both the underlying dynamics of this behaviour and to be able to predict, with some measure of certainty, future populations.

A major pest slug is *Deroceras reticulatum* [16], and it is this species we shall have in mind when biological assumptions are made. In addition to most of western Europe, *D. reticulatum* is considered indigenous to the western Palaearctic region [16], and has been introduced to most parts of the world [10], such as Australia [1] and even sub-antarctic islands [4]. After its (accidental) introduction it has frequently become a serious pest; indeed, almost all pest slugs in the USA are introduced species [9]. *D. reticulatum* is considered a serious pest and of economic importance [16], perhaps exacerbated by its choice of food. It is a well established species, being recorded as such in Massachusetts by 1843, and reaching Colorado (1890), California and Oregon (1891) shortly thereafter. The majority of slug damage in UK agriculture is caused by *D. reticulatum*, estimated at approximately 70% [2]. For a comprehensive description of the life-cycle of this species under various conditions see [13,14,15,16,17] and references therein.

Previous models [11,12] have modelled the dynamics of adult slug biomass (a significant factor when determining crop damage), although time delays and essential seasonal fluctuations in this system inhibit analytical approaches. In this paper, we develop a model based purely upon the quantity of eggs produced at different times of the “reproductive season.” By considering the survival of emergent slugs it is therefore possible to evaluate the total number of slugs of different ages (and hence mass) present at any given time of the year, and thus reconstruct the full population dynamics. It is also possible to collapse the system down to two dimensions and obtain analytical results; here we are interested in the key mechanisms of the population dynamics and not quantitative predictors. Realistic seasonal variations may be included through the model parameters, and although analytical results are far more complex their derivation remains feasible.

In the following section we shall construct the model and explain the notation. Section 3 introduces the “collapsed” model and Section 4 gives our main analytical results concerning conditions for extinction or persistence. In Section 5 we relate these results to the population distribution across the year, and consider variations in favourability between years in Section 6. Section 7 is concerned with the application of controls, especially the best time of year for these to be used. Alternative model formulations are discussed in Section 8, and the implications of results discussed in Section 9.

2. Egg batch model

Consider the slug eggs laid during the main breeding season. The season may be divided into six-weekly intervals, since this is approximately how long eggs take to hatch and leads to a simpler modelling approach. Slugs are therefore divided into separate “batches,” corresponding to eggs laid in the same time interval. After the eggs (E) have been laid, they spend three time intervals as juveniles (J) before becoming mature individuals (M) capable of laying eggs.

Slugs such as *D. reticulatum* are hermaphrodite whose male reproductive system is developed before the female part. They are incapable of self fertilisation, and during reproduction young individuals often act as “males”, while larger individuals act as egg producing “females”. The sexual role of these young juveniles (J) is not, however, considered as either necessary or significant, since mature adults (M and A) may also take on the role of “males” in the absence of smaller slugs. The fertilisation of other individuals is relatively inexpensive, in terms of both time and energy, in comparison to the production of eggs.

Juveniles are considered too small to survive winter if they have not reached the mature stage by the end of the season. Mature slugs, on the other hand, are considered as capable of overwintering and return the next year as older adults (A). They continue to lay eggs during the following year, but are then considered to old (exhausted) to survive a second winter. Most eggs hatch the following time interval, although those laid at the end of the season take longer to hatch [7], and these are then classed as lying dormant until the following season (becoming members of the first “batch”). Here we have allowed only the last egg batch to overwinter, although similar results are obtained if we allow the last two batches to overwinter (see Section 8).

It has been shown that adults may survive quite cold conditions [5], their numbers are sharply reduced when night frost is present without snow cover [15]. Eggs are less susceptible to winter conditions, but again benefit from snow cover in very cold temperatures [5]. Young slugs appear the most susceptible, and reductions in overall population numbers have been attributed to their demise [8].

The full dynamics of the model are portrayed in Fig. 1. There are six main egg batches covering the active period of the year for slugs and one adult batch representing slugs that survive the winter. The developmental stage of each batch is shown, where the suffix denotes the batch number (the time interval of the year when it was laid). The number of eggs produced (ρ), survival probability during each time interval (σ) and for the winter (μ) may vary with time or for different batches. Survival at different times is clearly important since it determines our full population from the egg population.

Fig. 1 near here (see end).

We denote the number of individuals in batch i (i.e. eggs laid in time interval i) in year t by B_i^t ($i = 1, 2, \dots, 6$), and the adults who have overwintered from the previous season by B_0^t . As individuals progress through the season they have a

probability σ_i of surviving interval i , while the probability of surviving the winter is μ_6 or $\tilde{\mu}_i$ ($i = 1, 2$) for eggs in batch 6 or mature slugs in batches 1 and 2 respectively. The number of eggs laid by each mature batches during each time interval is denoted by ρ_k (or $\tilde{\rho}_k$), where the subscript distinguishes the varying rates of egg production both between different size/age slugs in different batches, and due to the time of year (see Figure 1 for details).

Our model may thus be written as:

$$\begin{aligned}
B_0^t &= (\tilde{\mu}_1 \sigma_1 B_1^{t-1} + \tilde{\mu}_2 B_2^{t-1}) \sigma_5 \sigma_4 \sigma_3 \sigma_2, \\
B_1^t &= \rho_1 B_0^t + \mu_6 B_6^{t-1}, \\
B_2^t &= \rho_2 \sigma_1 B_0^t, \\
B_3^t &= \rho_3 \sigma_2 \sigma_1 B_0^t, \\
B_4^t &= \rho_4 \sigma_3 \sigma_2 \sigma_1 B_0^t, \\
B_5^t &= \rho_5 \sigma_4 \sigma_3 \sigma_2 \sigma_1 B_0^t + \tilde{\rho}_7 \sigma_4 \sigma_3 \sigma_2 \sigma_1 B_1^t, \\
B_6^t &= \rho_6 \sigma_5 \sigma_4 \sigma_3 \sigma_2 \sigma_1 B_0^t + \tilde{\rho}_8 \sigma_5 \sigma_4 \sigma_3 \sigma_2 \sigma_1 B_1^t + \rho_9 \sigma_5 \sigma_4 \sigma_3 \sigma_2 B_2^t,
\end{aligned} \tag{2.1}$$

where tilde denotes a parameter which is not constant (see below). Clearly, if all the parameters are constant, then we have a linear system with the trivial outcome of either extinction or unbounded growth. Self limitation is considered to occur through resource limitation at critical times of the year, although we have attempted to include only minimal limitations, maintaining the maximum freedom while keeping populations bounded.

Only batch 1 and 2 overwinter as adult slugs competing for food, and so we consider the winter survival probability as being inversely proportional to the total overwintering population:

$$\tilde{\mu}_i = \frac{\beta \mu_i}{\sigma_5 \sigma_4 \sigma_3 \sigma_2 \sigma_1 B_1^t + \sigma_5 \sigma_4 \sigma_3 \sigma_2 B_2^t + \beta}, \quad i = 1, 2, \tag{2.2}$$

where β is some absolute maximum for the number of individuals who could survive. The largest batch to hatch is B_1 , resulting from both dormant eggs and those laid by overwintering adults. Although we expect sufficient resources so that overcrowding will not significantly effect survival, it may impinge on the growth - and hence maturation rate - of individuals. The proportion of the batch likely to attain egg laying ability will therefore decrease with the size of the batch, which may be incorporated by scaling the expected number of eggs produced by B_1 later in the season as follows:

$$\tilde{\rho}_i = \frac{\alpha \rho_i}{B_1^t + \alpha}, \quad i = 7, 8. \tag{2.3}$$

Here α is again some absolute maximum for the number of individuals who are likely to mature to egg laying size during the season. We assume that all individuals will attain maturity by the end of the season (and hence survive the winter, returning as egg laying adults at the start of the next season), since the initially smaller individuals will have conserved extra energy not expended on egg production. Later batches are relatively free from such competition (and any consequential delay in

maturation) due to the lower number of individuals, and because their initial growth occurs later in the season when there is a relative abundance of resources.

Note that ρ, μ, σ (and, hence, α and β) are all positive. Furthermore, since they are survival probabilities, $\mu, \sigma \leq 1$.

3. Reduced model

For notational simplicity we assume from this point on that

$$\sigma_i \equiv \sigma, \quad \mu_i \equiv \mu \quad \text{and} \quad \rho_i \equiv \rho, \quad (3.1)$$

for all i . What follows is technically possible without this assumption, but the analysis is messy and merely obscures the results.

Define x_t and y_t by

$$x_t = \mu B_6^t \quad \text{and} \quad y_t = \frac{\rho \beta \mu \sigma^4 (\sigma B_1^t + B_2^t)}{\sigma^4 (\sigma B_1^t + B_2^t) + \beta}. \quad (3.2)$$

Then the system (2.1) may be written as

$$\begin{aligned} B_0^{t+1} &= \frac{1}{\rho} y_t, \\ B_1^{t+1} &= y_t + x_t, \\ B_2^{t+1} &= \sigma y_t, \\ B_3^{t+1} &= \sigma^2 y_t, \\ B_4^{t+1} &= \sigma^3 y_t, \\ B_5^{t+1} &= \sigma^4 \left(y_t + \rho \frac{\alpha (y_t + x_t)}{y_t + x_t + \alpha} \right), \\ B_6^{t+1} &= \sigma^5 \left(y_t + \rho \frac{\alpha (y_t + x_t)}{y_t + x_t + \alpha} + \rho y_t \right). \end{aligned} \quad (3.3)$$

By substituting (3.3) into (3.2) we may derive the system of difference equations

$$\begin{aligned} x_{t+1} &= \mu (1 + \rho) \sigma^5 y_t + \mu \rho \sigma^5 \frac{\alpha (x_t + y_t)}{x_t + y_t + \alpha} \\ y_{t+1} &= \mu \rho \sigma^5 \frac{\beta (x_t + 2y_t)}{\sigma^5 (x_t + 2y_t) + \beta}. \end{aligned} \quad (3.4)$$

Note that x and y in (3.2) are (positive) functions of B_1, B_2, B_6 alone, so that initial conditions for the system (3.4) only require these values to be given. Moreover, if we can find x_t and y_t , we have totally determined the system (3.3) and hence the population distribution.

4. Global stability and extinction

We define the parameters

$$a = \mu \sigma^5 (1 + \rho), \quad b = \frac{\beta}{\sigma^5} \quad \text{and} \quad c = \mu \sigma^5 \rho \quad (4.1)$$

for convenience, and henceforth consider the system

$$\begin{aligned}x_{t+1} &= \frac{\alpha c (x_t + y_t)}{x_t + y_t + \alpha} + ay_t, \\y_{t+1} &= \frac{bc (x_t + 2y_t)}{(x_t + 2y_t) + b},\end{aligned}\tag{4.2}$$

with strictly positive initial conditions

$$x_0, y_0 > 0.\tag{4.3}$$

Theorem 1 Consider the system (4.2) with initial conditions (4.3).

(i) Solutions remain positive and bounded; explicitly,

$$0 < x_t < \mu\sigma^5\rho(\alpha + \mu(1 + \rho)\beta) \quad \text{and} \quad 0 < y_t < \mu\rho\beta.\tag{4.4}$$

for all $t \geq 2$.

(ii) If

$$\mu\sigma^5\rho(3 + \mu\sigma^5) > 1\tag{4.5}$$

then $\lim_{t \rightarrow \infty} (x_t, y_t) = (x^*, y^*)$, where (x^*, y^*) is the unique positive solution of

$$x^* = c \frac{\alpha (x^* + y^*)}{x^* + y^* + \alpha} + ay^*, \quad y^* = \frac{bc (x^* + 2y^*)}{(x^* + 2y^*) + b}.\tag{4.6}$$

(iii) If inequality (4.5) does not hold then $\lim_{t \rightarrow \infty} (x_t, y_t) = (0, 0)$.

The proof of Theorem 1 is sketched below; less mathematically inclined readers may wish to go straight to Section 5 .

Proof. (i) It is trivial to show that if $(x_t, y_t) > 0$ then $(x_{t+1}, y_{t+1}) > 0$, from which it follows by induction that $(x_t, y_t) > 0$ for all t given (4.3).

It follows from (4.2) that

$$y_{t+1} = \frac{bc (x_t + 2y_t)}{(x_t + 2y_t) + b} < bc \quad \forall x_t, y_t \in (0, \infty),\tag{4.7}$$

so that $y_t < bc$ for all $t \geq 1$. Similarly

$$x_{t+1} < ay_t + c\alpha \quad \forall x_t, y_t \in (0, \infty),$$

giving $x_t < abc + c\alpha$ for all $t \geq 2$.

Consider the solution $y_*(x_t)$ of $y_{t+1} = y_t$, which satisfies the equation

$$2y_*^2(x_t) + (x_t + b(1 - 2c))y_*(x_t) - bcx_t = 0.\tag{4.8}$$

Since $bc > 0$ there exists a unique positive real root $y_*(x_t)$ for each x_t .

Lemma 1 $y_*(x_t)$ is concave for $x_t \geq 0$. Explicitly, it is strictly monotonically increasing (with decreasing gradient) from 0 if $2c < 1$ and from $b(2c-1)/2$ otherwise, and is bounded above by bc for $t \geq 1$.

Proof. We first note that $y^*(0) = 0$ or $b(2c-1)/2$ only. Differentiating (4.8) implicitly and solving we obtain

$$\frac{dy_*(x_t)}{dx_t} = \frac{bc - y_*(x_t)}{4y_*(x_t) + (x_t + b(1-c))} = \frac{bc - y_*(x_t)}{\sqrt{(x_t - b(c-1))^2 + 8bcx_t}}.$$

It follows from condition (4.7) that $\frac{dy_*(x_t)}{dx_t} > 0 \forall t \geq 1$. By differentiating again it is simple to show that the second derivative of $y_*(x_t)$ (with respect to x_t) remains strictly negative for all $x_t > 0$. \square .

By a similar argument we may establish that there exists a unique positive real root $x_*(y_t)$ of $x_{t+1} = x_t$ and that

Lemma 2 $x_*(y_t)$ is concave for $y_t \geq 0$. Explicitly, it is strictly monotonically increasing (with decreasing gradient) from 0 if $c < 1$ and from $(c-1)\alpha$ otherwise, and is bounded above by $abc + c\alpha$ for $t \geq 2$.

Proof. This is immediate from calculating the derivative $\frac{dx_*(y_t)}{dy_t}$, applying (4.2) and noting that $y < bc$ for $t \geq 1$. \square .

We may now prove the following

Lemma 3 A unique positive solution of (4.6) exists if and only if condition (4.5) holds.

Proof. By the intermediate value theorem it is clear that $y_*(x)$ and $x_*(y)$ will intersect (in the positive quadrant of the (x, y) plane) once unless the curve $y_*(x)$ remains below $x_*(y)$ for all $x, y > 0$. Necessary and sufficient conditions for this (since $x_*(y)$ and $y_*(x)$ are concave) are that $x_*(y)$ and $y_*(x)$ both pass through the origin, and $\left. \frac{dy_*(x)}{dx} \right|_{(0,0)} < \left. \frac{dy(x_*)}{dx_*} \right|_{(0,0)}$. After some algebra these become (the first by Lemmas 1 and 2):

$$2c < 1 \text{ and } \frac{1-c}{a+c} > \frac{c}{1-2c}. \quad (4.9)$$

Condition (4.5) may be rewritten as

$$(1-c)(1-2c) < c(a+c). \quad (4.10)$$

To satisfy the first of (4.9) we require $c < \frac{1}{2}$, under which (4.10) rearranges to give the converse of the second of (4.9). Condition (4.5) therefore implies the existence of a point of intersection. If (4.5) does not hold then $a \geq c$ implies $c \leq \frac{1}{3} < \frac{1}{2}$ and it quickly follows that the second of (4.9) will also hold. When $\mu\sigma^5\rho(3 + \mu\sigma^5) = 1$ we have intersection at the origin, so that we require (4.5) to be a strict inequality. A single point of intersection of the curves implies a unique solution to (4.6). \square .

For convergence, consider $t \geq 2$ so that $y_t < bc$, $x_t < abc + c\alpha$. Assume first that there exist positive equilibria $x^*(y_t)$ and $y^*(x_t)$. We note that

$$y_{t+1} - y_t = \frac{-2y_t^2 + (x_t + b(1-2c))y_t + bcx_t}{x_t + 2y_t + b} > 0 \text{ iff } y_t < y_*(x_t),$$

since $y_*(x_t)$ is the solution of (4.8). Furthermore, if $y_t > y_*(x_t)$ then

$$y_{t+1} = \frac{bc(x_t + 2y_t)}{(x_t + 2y_t) + b} > \frac{bc(x_t + 2y_*(x_t))}{(x_t + 2y_*(x_t)) + b} = y_*(x_t)$$

so that

$$\begin{aligned} y_t > y_*(x_t) &\Rightarrow y_t > y_{t+1} > y_*(x_t), \\ y_t < y_*(x_t) &\Rightarrow y_t < y_{t+1} < y_*(x_t). \end{aligned} \quad (4.11)$$

Similarly,

$$\begin{aligned} x_t > x_*(y_t) &\Rightarrow x_t > x_{t+1} > x_*(y_t), \\ x_t < x_*(y_t) &\Rightarrow x_t < x_{t+1} < x_*(y_t). \end{aligned} \quad (4.12)$$

We may now prove the final set of lemmas to complete Theorem 1.

For each $t \geq 0$, consider the four regions

$$\begin{aligned} \mathcal{I} &= \{(x_t, y_t) : y_t \geq y_*(x_t), x_t \geq x_*(y_t)\}, \\ \mathcal{II} &= \{(x_t, y_t) : y_t > y_*(x_t), x_t < x_*(y_t)\}, \\ \mathcal{III} &= \{(x_t, y_t) : y_t \leq y_*(x_t), x_t \leq x_*(y_t)\}, \\ \mathcal{IV} &= \{(x_t, y_t) : y_t < y_*(x_t), x_t > x_*(y_t)\}, \end{aligned}$$

within the bounds given by (4.4). In what follows we need only consider bounded initial conditions since (x_t, y_t) is in one of the four regions for all $t \geq 2$ by (i).

Lemma 4 *If (4.5) holds then there exists $\epsilon > 0$ such that for every $T > 0$ there exists $t_\epsilon > T$ such that $x_{t_\epsilon} + y_{t_\epsilon} \geq \epsilon$.*

Proof. For a contradiction assume that given $\epsilon > 0$ there exists $T > 0$ such that $x_{t_\epsilon} + y_{t_\epsilon} < \epsilon$ for all $t > T$. We linearise (4.2) about the origin, giving

$$\begin{pmatrix} x_{t+1} \\ y_{t+1} \end{pmatrix} = \begin{pmatrix} c & a+c \\ c & 2c \end{pmatrix} \begin{pmatrix} x_t \\ y_t \end{pmatrix}.$$

Linear stability is determined by roots of the the characteristic equation

$$C(\lambda) = \lambda^2 - 3c\lambda + c(c-a),$$

which satisfies $C \rightarrow +\infty$, $\lambda \rightarrow \infty$. Now,

$$C(1) = c^2 - (3+a)c + 1 = 1 - \mu\sigma^5\rho(3 + \mu\sigma^5) < 0$$

by (4.5), so that there exists a real root $\lambda_c > 1$ of $C(\lambda)$ and, hence, the origin is an unstable equilibrium. Thus (x_t, y_t) cannot tend to $(0, 0)$ for all solutions with initial conditions of the form (4.3). \square .

Lemma 5 *If (4.5) holds then any solution with initial conditions (x_t, y_t) such that $(x_t - x_*(y_t))(y_t - y_*(x_t)) > 0$ converges monotonically to (x^*, y^*) .*

Proof. We show the proof for $(x_t, y_t) \in \mathcal{I}$; the proof for region \mathcal{III} is similar.

It is clear by (4.11), (4.12) that any solution with initial conditions inside either region \mathcal{I} or \mathcal{III} will remain in that respective region for all time, since

$$\begin{aligned} (x_t, y_t) \in \mathcal{I} &\Rightarrow \begin{aligned} x_t &\geq x_*(y_t) &\Rightarrow x_t &\geq x_{t+1} &\geq x_*(y_t) \\ y_t &\geq y_*(x_t) &\Rightarrow y_t &\geq y_{t+1} &\geq y_*(x_t) \end{aligned} \\ &\Rightarrow \begin{aligned} y_*(x_t) &\geq y_*(x_{t+1}) &\Rightarrow x_{t+1} &\geq x_*(y_{t+1}) \\ x_*(y_t) &\geq x_*(y_{t+1}) &\Rightarrow y_{t+1} &\geq y_*(x_{t+1}) \end{aligned} \Rightarrow (x_{t+1}, y_{t+1}) \in \mathcal{I} \end{aligned}$$

Since $x_*(y_t)$ and $y_*(x_t)$ are monotonic increasing with a unique positive intersection (x^*, y^*) , it follows that

$$\begin{aligned} x_t &> x_*(y_t), & \Rightarrow & y_*(x_t) > y^*, \\ y_t &> y_*(x_t), & \Rightarrow & x_*(y_t) > x^*, \end{aligned} \quad \forall t \geq t_3. \quad (4.13)$$

To show this, consider the set

$$\{(x, y) : x_*(y) \leq x < abc + \alpha c, y_*(x) \leq y < bc; x + y \geq \epsilon\},$$

with x_* and y_* as in Lemmas 1 and 2. Without loss of generality we can choose $\epsilon > 0$ small enough so that (x^*, y^*) is in this set. Define x_{min} as the minimum value of x within the set, which we know exists since x_* and y_* are bounded below. Since y_* is monotonic increasing in x , the minimum value of y within the set is

$$y_{min} = y_*(x_{min}). \quad (4.14)$$

Similarly

$$x_{min} = x_*(y_{min}). \quad (4.15)$$

Since (x^*, y^*) is the unique positive intersection point of x_* and y_* , solving (4.14) and (4.15) simultaneously implies

$$x_{min} = x^*, \quad y_{min} = y^*,$$

and the proof of (4.13) is complete.

Therefore, by (4.11), (4.12) and the above we have

$$x_t > x_{t+1} > x_*(y_t) > x^* \quad \text{and} \quad y_t > y_{t+1} > y_*(x_t) > y^*,$$

for all $t \geq t_3$. The sequences $\{x_t\}_3^\infty, \{y_t\}_3^\infty$ are, therefore, monotonic decreasing and bounded below, and thus converge to some limit. By Lemma 3 and 4 the unique solution to which (x_t, y_t) converges is (x^*, y^*) , given by (4.6). \square .

Lemma 6 *If (4.5) holds then all solutions (x_t, y_t) converge to (x^*, y^*) .*

Proof. First assume that there exists a solution which does not leave \mathcal{II} for all $t \geq t_c$ for some $t_c \geq 0$. By (4.12) and part (i) we have that $\{x_t\}_{t_0}^\infty$ is a monotonic increasing sequence bounded above by $abc + \alpha c$, and by (4.11) and part (i) that $\{y_t\}_{t_0}^\infty$ is a monotonic decreasing sequence bounded below by 0. Therefore, both sequences converge, by uniqueness, to (x^*, y^*) . Similarly, it may be shown that any solution which remains in region \mathcal{IV} will also converge to the equilibrium. Note that we do not claim that such solutions exist, only that any solutions which remain in \mathcal{II} (or \mathcal{IV}) converge.

Since all solutions which enter \mathcal{I} or \mathcal{III} remain there (and converge, by Lemma 5), it only remains to consider solutions which alternate between \mathcal{II} and \mathcal{IV} for all time. Consider the time t_0 at which such a solution first enters \mathcal{II} . We need to consider three cases, although the method of proof in each case is similar.

Case 1: Assume that

$$x_{t_0} < x^*, \quad y_{t_0} < y^*. \quad (4.16)$$

Given the monotonicity properties of x_* and y_* defined in Lemmas 1 and 2, it immediately follows that

$$(x, y) \in \mathcal{II} \cap \{(x, y) : x < x^*, y < y^*\} \Rightarrow x < x_*(y_*(x)) < x^*. \quad (4.17)$$

It is simple to show this graphically, and follows from the fact that the curve $y_*(x)$ is above the curve x^* (w.r.t. x) in this region. Since $(x_{t_0}, y_{t_0}) \in \mathcal{II}$, we have

$$x_{t_0} < x_{t_0+1} < x_*(y_{t_0}), \quad y_{t_0} > y_{t_0+1} > y_*(x_{t_0})$$

Define t^0 as the next time the solution enters \mathcal{IV} , so that

$$(x_t, y_t) \in B_0 = [x_{t_0}, x_*(y_{t_0})] \times [y_*(x_{t_0}), y_{t_0}]$$

for all $t_0 \leq t \leq t^0$.

Let t_1 be the first return to \mathcal{II} . Since $(x_t, y_t) \in \mathcal{IV}$ for $t^0 \leq t < t_1$ by definition,

$$x_t < x_{t^0} < x_*(y_{t_0}),$$

and

$$x_t > x_*(y_*(x_{t_0})) > x_{t_0}$$

using (4.17). Similarly, we may show that $y_*(x_{t_0}) < y_t < y_{t_0}$ for $t^0 \leq t < t_1$, which combine to give

$$(x_t, y_t) \in B_0, \quad \text{for all } t_0 \leq t < t_1.$$

It can be shown by induction that if t_i are the times the solution re-enters \mathcal{II} , then

$$(x_t, y_t) \in B_i, \quad \text{for all } t_i \leq t < t_{i+1},$$

where B_i is the box defined by:

$$B_i = [x_{t_i}, x_*(y_{t_i})] \times [y_*(x_{t_i}), y_{t_i}]. \quad (4.18)$$

We will prove convergence of the solution to the equilibrium by showing the convergence of the series of boxes $\{B_i\}$ to the point (x^*, y^*) . Since the diagonal to (x_{t_i}, y_{t_i}) of B_i is the point $(x_*(y_{t_i}), y_*(x_{t_i}))$, we can generate a new box such that

$$(x_{t_{i+1}}, y_{t_{i+1}}) \in [x_*(y_*(x_{t_i})), x_*(y_{t_i})] \times [y_*(x_{t_i}), y_*(x_*(y_{t_i}))]. \quad (4.19)$$

We first show that if (x_{t_i}, y_{t_i}) satisfies (4.17), then $(x_{t_{i+1}}, y_{t_{i+1}})$ does too. Since $(x_{t_{i+1}}, y_{t_{i+1}}) \in \mathcal{II}$ by definition,

$$x_{t_{i+1}} < x_*(y_{t_{i+1}}). \quad (4.20)$$

The monotonicity of x_* , together with $y_{t_{i+1}} < y_*(x_*(y_{t_i}))$ by (4.19) implies that

$$x_*(y_{t_{i+1}}) < x_*(y_*(x_*(y_{t_i}))). \quad (4.21)$$

Since

$$y_{t_i} < y^* \Rightarrow x_*(y_*(x_*(y_{t_i}))) < x_*(y_*(x_*(y^*))) = x^*, \quad (4.22)$$

we see that (4.17) implies, using (4.20), (4.21) and (4.22), that

$$x_{t_{i+1}} < x^* \quad (4.23)$$

also. We can similarly show that $y_{t_{i+1}} < y^*$.

Since (x_{t_0}, y_{t_0}) satisfy (4.16), and hence (4.17), we have shown by induction that (x_{t_i}, y_{t_i}) satisfy (4.17) for all i . This states that

$$x_{t_i} < x_*(y_*(x_{t_i}))$$

which, together with

$$x_*(y_*(x_{t_i})) < x_{t_{i+1}}$$

by (4.19), implies that the sequence $\{x_{t_i}\}_{i=0}^{\infty}$ is monotonic increasing.

The sequence is bounded above since all points satisfy (4.17) and, therefore, converges to some limit x_l . It follows that $\{y_*(x_{t_i})\}$ is also monotonic increasing and bounded above (by y^*) and converges to some limit y_l . The limits must satisfy

$$x_*(y_*(x_l)) = x_l,$$

which has the solutions $x_l = x^*$ or $x_l = 0$. The latter is clearly not valid since $x_0 > 0$. Similarly, we may show that y_{t_i} converges to y^* (and hence $(x_*(y_{t_i})) \rightarrow x_*$). The lower and upper bounds of our boxes B_i thus converge monotonically to the point (x^*, y^*) . Since for every i there exists a t_i such that for all $t \geq t_i$, $(x_t, y_t) \in \bigcup_{j \geq i} B_j$, convergence for the series (x_t, y_t) is proven.

Case 2: Assume that the solution (x_t, y_t) satisfies $x_{t_0} > x^*$, $y_{t_0} > y^*$, where t_0 is the time it first enters region \mathcal{II} . The proof is identical, but with monotonically decreasing bounds on B_i .

Case 3: Assume that $x_{t_0} < x^*$, $y_{t_0} > y^*$. We again consider the return times t_1, t_2, \dots for which the solution re-enters region \mathcal{II} . More specifically, we may consider only those solutions whose return paths satisfy

$$x_{t_i} < x^*, \quad y_{t_i} > y^*, \quad i \geq 0,$$

since otherwise the solution enters one of the regions considered in *Case 1* and *2* above and convergence is already proven.

Therefore we consider solutions which satisfy

$$(x_{t_i}, y_{t_i}) \in \mathcal{II} \cap \{(x_{t_i}, y_{t_i}) : x_{t_i} < x^*, y_{t_i} > y^*\}, \quad i \geq 0, \quad (4.24)$$

and show that convergence occurs through strictly nested boxes B_i . In an analogous fashion to (4.17), we can derive the property

$$(x, y) \in \mathcal{II} \cap \{(x, y) : x < x^*, y > y^*\} \Rightarrow \begin{aligned} x &< x_*(y_*(x)) < x^*, \\ y &> y_*(x_*(y)) > y^*. \end{aligned} \quad (4.25)$$

It follows from observing that

$$(x_{t_{i+1}}, y_{t_{i+1}}) \in [x_*(y_*(x_{t_i})), x_*(y_{t_i})] \times [y_*(x_{t_i}, y_*(x_*(y_{t_i})))],$$

that $\{x_{t_i}\}_{i=0}^\infty$ is monotonic increasing, since

$$x_{t_{i+1}} > x_*(y_*(x_{t_i})) > x_{t_i}$$

by (4.25). Similarly we may show that $\{y_{t_i}\}_{i=0}^\infty$ is monotonic decreasing.

The sequences $\{x_{t_i}\}_{i=0}^\infty$ and $\{y_{t_i}\}_{i=0}^\infty$ are bounded above and below respectively by (4.24), so that each converge to some limit. By uniqueness, the limits are x^* and y^* . The interim time steps may be included using boxes B_i by a similar argument to that used above, completing the proof that $(x_t, y_t) \rightarrow (x^*, y^*)$, $t \rightarrow \infty$ for *Case 3*.

Note that we do not need to deal with region \mathcal{IV} separately, since any alternating solution is considered from the time it first enters \mathcal{II} . \square .

Lemma 7 *Assume that condition (4.5) does not hold. Then all solutions (x_t, y_t) converge to $(0, 0)$.*

Proof. The proof of this is similar to that above and is not shown here. In this case we have a unique steady state at $(0, 0)$. The case of equality in (4.5) results in convergence to an equilibrium which is the origin and therefore also gives extinction. \square .

The proof of our theorem is complete. \square .

It may be noted that although environmental limitations (parameterised by α and β) affect the size of the population, they do not determine persistence, unless one considers stochastic effects at low population levels. Criterion for extinction are of the intuitive form $\rho < \rho_c$ (see Section 7 for details).

5. Temporal population distribution

Given initial conditions (B_1^0, B_2^0, B_6^0) we may determine the dynamics of the system through (4.2), and the long term behaviour by Theorem 1. The number of eggs laid in each interval of the year is then given by (3.3), from which it is possible to determine the slug population throughout the year. Explicitly, if S_i^t is the total number of slugs (J, M and A but not E) at interval i in year t , then

$$S_i^t = \sigma^{i-1} B_0^t + \sum_{j=1}^{i-1} \sigma^{i-j} B_j^t, \quad i = 1, \dots, 6. \quad (5.1)$$

(where we have considered the simplification (3.1) for notational convenience). Furthermore, we may calculate the post-season population (mature slugs about to overwinter) by:

$$S_7^t = \sigma^4 (\sigma B_1^t + B_2^t), \quad (5.2)$$

so that the adult slug population that survives the winter is given by

$$S_1^{t+1} = B_0^{t+1} = \frac{\mu\beta S_7^t}{S_7^t + \beta}.$$

Note that S_i^t ($i = 1, \dots, 7$) are also functions of x and y only. We define $S(t, i) = S_i^t$ as the annual population distribution.

It is interesting to note that while the solution (x^*, y^*) may simply be a globally attractive positive equilibrium, the temporal population distributions generated by it may exhibit a variety of behaviours depending upon the favourability of the year. Clearly $S(t, i)$ converges to a globally stable periodic solution, but the annual distribution may exhibit one or two maxima and either grow or decay over the year. Examples of different temporal population distributions are given in Fig. 2. These are the steady state solutions (i, S_i^*) which result from the convergence of (x_t, y_t) to (x^*, y^*) . The variation in temporal population distribution can be brought about by a small change in the survival probability σ . In other words, we may witness markedly different behaviour in the temporal population distribution simply because of small annual variations in the prevailing environmental factors. We are primarily interested in the steady state temporal distribution of the population, not transient effects. The results shown are therefore of the equilibrium distribution, to which all solutions rapidly converge.

These results compare favourably with available field data [6,15], where the population exhibits both monotonic and multi-peak distributions in a given year, including very sharp increases and decreases in the population. Increasing the number of peaks in our model to a number greater than two requires σ to vary within the season ($\sigma_i \neq \sigma$ for some i). This is discussed in section 6.

Fig. 2 near here (see end).

6. Parameter variation

6.1. Seasonal

Although analysis is only shown for the case (3.1) for simplicity, qualitatively similar results are obtainable for general parameters which do not remain constant throughout the year. Thus for example, we might expect the survival probabilities of individuals in spring (σ_1) to be greater than at the height of summer (σ_4).

We again find that the system either attains a stable steady temporal population distribution or results in extinction. In addition, however, the possible stable annual distributions (as shown in Fig. 2 for the above model) are extended, with a greater number of maxima possible during the year, as sometimes observed in the data [6].

6.2. *Between seasons*

In temperate climates there are significant variations in climatic conditions between different years, and these will influence the population dynamics (such as survival and how many eggs survive per laying adult). We therefore consider variations in the model parameters, based upon the effects of the average annual rain fall and temperature in consecutive years. Fig. 3 shows the resultant population for a ten year period, with relatively small variations in the model parameters between years (but not within seasons), based on basic biological assumptions. For example, egg production is reduced when the temperature is too high or too low (for more details on these aspects of the biology of *D. reticulatum* see [13,14,15,16]; for appropriate modelling approaches see [11]). We do not, of course, have a convergent solution (except the possibility of extinction), since in each individual year solutions will be converging to a (generally) different steady temporal population distribution.

Fig. 3 near here (see end).

7. Effect of treatment

Necessary and sufficient conditions for extinction of the population are given in Theorem 1, although it should be noted that the positive equilibrium (x^*, y^*) approaches the origin arbitrarily closely as equality is approached. If we define

$$\delta = \mu\sigma^5 \quad (7.1)$$

as the limiting annual survival probability (for large populations), then extinction will occur, by (4.5), if and only if $\rho < \rho_c$, where

$$\rho_c = \frac{1}{\delta(\delta + 3)}, \quad (7.2)$$

which we may alternatively express as $\delta \leq \delta_c$ where

$$\delta_c = \frac{\sqrt{9 + (4/\rho)} - 3}{2} > 0.$$

This means that the population would become extinct if the annual survival probability dropped (and stayed for sufficient time) below some critical value. This value is determined by, and monotonically decreasing with respect to, the egg production ρ .

The extinction rate is given by $\epsilon = |1 - \lambda_c|$, where λ_c is the principle eigenvalue at the origin. Explicitly, the characteristic equation given by linearising the continuous version of (4.2) about $(0, 0)$ is

$$\lambda^2 - 3c\lambda - c(a - c) = 0,$$

with largest eigenvalue

$$\lambda_c = \frac{\delta\rho}{2} \left(\sqrt{9 + (4/\rho)} + 3 \right) = \frac{\delta}{\delta_c},$$

giving

$$\epsilon = 1 - \frac{\delta}{\delta_c}, \quad (\delta < \delta_c).$$

In this section we consider the effect of applying some protective treatment (biological or chemical) to crops, designed to reduce the survival rate of slugs. Untreated populations would generally be expected to have a survival rate $\delta > \delta_c$, that is, under normal conditions they do not go extinct. We consider reducing the survival rate in any given time interval i where treatment takes place by a factor τ_i , that is,

$$\begin{aligned} \sigma_i &\rightarrow \tau_i \sigma_i, \\ \mu_i &\rightarrow \tau_i \mu_i, \end{aligned} \quad 0 \leq \tau_i \leq 1, \quad (i = 1, \dots, 6) \quad (7.3)$$

where $\tau_i = 1$ is obviously equivalent to no treatment in interval i .

If we assume that treatment affects slugs and eggs equally, then it immediately follows that the annual survival rate following treatments will be given by $\delta_\tau = \delta \tau_1 \tau_2 \tau_3 \tau_4 \tau_5 \tau_6$ ($\leq \delta$). If $\delta_\tau < \delta_c$ then the treatment is sufficient to eliminate the population.

Most treatments, however, are aimed at slugs, and do not directly affect eggs. We therefore need to consider the case where the survival rate in a time interval in which treatment is applied is reduced to the form (7.3) for hatched slugs only, and remains unchanged for newly laid batches. We will refer to treatments implemented at the end of each time interval i as reducing the proportion of slugs in each batch that survive to the next interval by a factor τ_i . The survival of eggs laid in that interval are not affected, nor the rate at which they are laid.

To do this we need to consider a more general form of the model (3.4), namely the system of difference equations

$$\begin{aligned} x_{t+1} &= \frac{\alpha v (x_t + y_t)}{x_t + y_t + \alpha} + u y_t, \\ y_{t+1} &= \frac{w b (x_t + \gamma y_t)}{(x_t + \gamma y_t) + B}, \end{aligned} \quad u, v, w, \gamma > 0. \quad (7.4)$$

Parameter values for the untreated system (3.4) and the case when treatments are applied at various times are given in table 1, but the following theorem holds for all $u, v, w, \gamma, B > 0$.

Theorem 2 *The solution $(0, 0)$ of system (7.4) is globally attractive if and only if*

$$v + \gamma w \leq 2 \quad \text{and} \quad (v + \gamma w) + w(u + v(1 - \gamma)) \leq 1. \quad (7.5)$$

The proof is similar to that of section 4 and the analysis is not given here.

Note that in the absence of treatment, criteria reduce to the converse of (4.5).

Table 1 near here (see end).

Theorem 3 *The application of treatment will result in extinction if and only if*

$$\rho \leq \rho_\tau = \frac{1}{\delta \tau_3 \tau_4 \tau_5 (\tau_1 \tau_6 + \tau_2 + \tau_2 \tau_6 + \delta \tau_1 \tau_2^2 \tau_3 \tau_4 \tau_5 \tau_6)}. \quad (7.6)$$

Proof. We first show that the first condition of Theorem 2 is always satisfied by our parameters when the second is, and then simplify this stronger (second) condition to the form (7.6).

Lemma 8 *If u, v, w, γ, B are as in Table 1, then*

$$(v + \gamma w) + w(u + v(1 - \gamma)) \leq 1 \Rightarrow v + \gamma w \leq 2.$$

Proof. The case for no treatment is proven separately in Theorem 1, although it is a corollary of the following when $\tau_i = 1$ ($i = 1, \dots, 6$).

We may rewrite the above two conditions as $w < w_1, w < w_2$ respectively (since here $\gamma + u + v - \gamma v > 0$), where

$$w_1 = \frac{1 - v}{\gamma + u + v - \gamma v} \text{ and } w_2 = \frac{2 - v}{\gamma}.$$

Now

$$w_1 = \frac{1 - v}{\gamma + \delta\tau_1\tau_2\tau_3\tau_4\tau_5} < \frac{1 - v}{\gamma} < w_2,$$

so that $w < w_1 \Rightarrow w < w_2$ for all w . \square .

Substituting in our explicit parameters from Table 1, we have that

$$1 \geq v + \gamma w + w(u + v(1 - \gamma)) = \rho\delta\tau_3\tau_4\tau_5(\tau_1\tau_6 + \tau_2 + \tau_2\tau_6 + \delta\tau_1\tau_2^2\tau_3\tau_4\tau_5\tau_6),$$

which is equivalent to (7.6). \square .

We note that the threshold ρ_c given by (7.2) may be derived by considering $\tau_i = 1, i = 1, 2, \dots, 6$ in ρ_τ given by (7.6).

Theorem 4 *For a single application τ applied in only one time interval i :*

$$\tau_i = \tau, \tau_j = 1, \text{ for } j \neq i, j = 1, \dots, 6,$$

the corresponding extinction threshold ρ_{τ_i} satisfy:

- (i) $\rho_c < \rho_{\tau_1} < \rho_{\tau_6} < \rho_{\tau_2} < \rho_{\tau_3} = \rho_{\tau_4} = \rho_{\tau_5}, 0 < \tau < 1$;
- (ii) $\rho_{\tau_i} = \rho_c$ when $\tau = 1$.

Proof. By substituting each $i = 1, \dots, 6$ into (7.6) in turn, we derive:

$$\begin{aligned} \rho_{\tau_1} &= \frac{1}{\delta(2 + \tau(1 + \delta))}, \\ \rho_{\tau_2} &= \frac{1}{\delta(1 + \tau(2 + \delta\tau))}, \\ \rho_{\tau_k} &= \frac{1}{\delta\tau(3 + \delta\tau)}, \quad k = 3, 4, 5, \\ \rho_{\tau_6} &= \frac{1}{\delta(1 + \tau(2 + \delta))}, \end{aligned}$$

and (ii) is a direct consequence of considering $\lim_{\tau \rightarrow 1} \rho_{\tau_i}$. Part (i) follows from $\tau < 1$ so that

$$\begin{aligned} \frac{1}{\rho_c} - \frac{1}{\rho_{\tau_1}} &= \delta(3 + \tau) - \delta(2 + \tau + \delta\tau) = \delta(1 - \delta\tau) > 0 \Rightarrow \rho_c < \rho_{\tau_1}, \\ \frac{1}{\rho_{\tau_1}} - \frac{1}{\rho_{\tau_6}} &= \delta(2 + \tau + \delta\tau) - \delta(1 + 2\tau + \delta\tau) = \delta(1 - \tau) > 0 \Rightarrow \rho_{\tau_1} < \rho_{\tau_6}, \\ \frac{1}{\rho_{\tau_6}} - \frac{1}{\rho_{\tau_2}} &= \delta(1 + 2\tau + \delta\tau) - \delta(1 + 2\tau + \delta\tau^2) = \delta^2\tau(1 - \tau) > 0 \Rightarrow \rho_{\tau_6} < \rho_{\tau_2}, \\ \frac{1}{\rho_{\tau_2}} - \frac{1}{\rho_{\tau_3}} &= \delta(1 + 2\tau + \delta\tau^2) - \delta\tau(3 + \delta\tau) = \delta(1 - \tau) > 0 \Rightarrow \rho_{\tau_2} < \rho_{\tau_3}. \end{aligned}$$

□.

Corollary 1 *Complete elimination (i.e. $\tau = 0$) of slugs in a time interval i will result in extinction:*

- (i) *unconditionally for $i = 3, 4, 5$;*
- (ii) *for $\rho < 1/\delta$ for $i = 2, 6$;*
- (iii) *for $\rho < 1/2\delta$ for $i = 1$.*

Proof. This follows immediately by considering $\lim_{\tau \rightarrow 0} \rho_{\tau_i}$ ($i = 1, \dots, 6$). □.

The above theorems give a clear order of priority for the time intervals that should be selected for treatment, if the aim is for the long term elimination of slugs.

The total elimination of slugs is not sufficient to guarantee extinction, except in that part of the season after all maturing slugs have hatched but before overwintering eggs have been laid. At all other times the delay in reproduction due to egg development can result in the re-emergence of individuals. Since a reduction in the population, rather than extinction, is often the more likely outcome in the field, treatment regimes are often applied for short term crop protection, rather than overall population control. Results here however show that, since all batches B_i^t (and hence the population in each interval $S(t, i)$) are monotonic increasing in x_t and y_t , and x^* and y^* are monotonic decreasing in each τ_i , it is the latter strategy which will give better protection.

Treatments should therefore attempt to control the overall slug population, rather than simply dealing with the large numbers which appear at certain times of the year. The situation is obviously more complicated when there are significant variations in the parameters (both between years and within a season), or when annually repeated treatments have not been applied, so that in this case other short term strategies may be advantageous.

8. Alternative model formulations

The model considered in this paper is based on a strongly defined season for slug activity, with a harsh winter which eliminates a large proportion of the individuals. If we are considering the possibility of highly favourable seasons, it is natural to extend the model to the case where more individuals survive. As an example we have considered the case where many more eggs laid late in the season (and not just at the end) may lie dormant until the next season. Instead of individuals laid in time interval 5 hatching therefore, they remain eggs and survive the winter (with rate μ_5) to become part of Batch 1, similar to the eggs laid in Batch 6. Results are very similar, although for the special case (3.1) only a single peak per season is possible. Solutions again either attain a stable steady population distribution or extinction, and the analysis follows in the same way.

To extend the model further we could consider juveniles of all (or most) classes surviving the winter, allowing for a continuous population. At this point, however, the concept of a specific slug breeding season becomes invalid, and the analysis

developed here is no longer relevant. Thus, although the seasonal model allows for analytical progress not available to other models such as [11,12], the assumption required for its simplified formulation is a necessary one.

9. Discussion

In this paper we have constructed and analysed a simple model for slug populations, based on the predominant species *D. reticulatum*. By simply considering the number of eggs laid during each breeding season, a model has been developed that may be reduced to a set of two difference equations. Conditions are derived for extinction, or for the persistence of a stable steady temporal population distribution, including the effect of applying control strategies at different times of the year. Egg production is used to determine the whole population (based on survival rates) without further consideration of adult dynamics, with the additional advantage that the age distribution of the slug population is also known.

The observed behaviour is qualitatively similar to available field data [6], especially if one allows for the effect of minor variations in the favourability of individual years. It is significant that large variations in the size and dynamics of the population in different years may be caused by small variations in the parameters, due to slight changes in the temperature and rainfall (and thus ground humidity) between consecutive years. Thus these relatively small variations in climate may result in the large changes in the population dynamics observed in the field.

Results here are in agreement with those found in other types of model [11]. While the concept of a single season is at best only an approximation of the true dynamics, we feel it has allowed for analytical progress while remaining relevant to the original biological problem.

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References

- [1] Altena, C.O. van R.& Smith, J.B. : Notes on introduced slugs of the families Limacidae and Milacidae in Australia, with two new records. *Journal of the Malacological Society of Australia* **3** (1975) 63-80.
- [2] Bohan, D. Personal communication.

- [3] Coupland, J.B. Susceptibility of helcid snails to isolates of the nematode *Phasmarhabditis hermaphrodita* from southern France. *Journal of Invertebrate Pathology* **66** (1995) 207-208
- [4] Dell, R.K. Land snails from sub-Antarctic islands. *Transcripts of the Royal Society of New Zealand (Zoology)* **4** (1964) 167-173.
- [5] Dmitrieva, E.F. Population dynamics, growth, feeding and reproduction of field slug *Deroceras reticulatum* in Leningrad Oblast. *Zoological Zhurnal* **48** (1969) 802-810.
- [6] Glen, D.M., Bohan, D. & co-workers, unpublished data (Long Ashton Research Station, IACR, UK).
- [7] Hunter, P.J. & Symonds, B.V. The leap-frogging slug. *Nature* **229** (1971) 349
- [8] Kennard, A.S. The holcene non-marine Mollusca of England. *Proceedings of the Malacological Society of London*, **16** (1923) 241-259.
- [9] Lovatt, A.L. & Black, A.B. The grey garden slug. *Oregon Agriculture Experimental Station Bulletin* **170** (1920) 1-43.
- [10] Quick, H.E. British slugs (Pulmonata: Testacellidae, Arionidae, Limacidae. *Bulletin of British Museum (Natural History), Zoological Series* **6** (1960) 106-226.
- [11] Schley, D. & Bees, M.A. Differential modelling of the population biomass dynamics of the agricultural pest slug *Deroceras reticulatum*. *Ecological Modelling* (submitted).
- [12] Schley, D. & Bees, M.A. The self-restrained slug. (In preparation).
- [13] South, A. A comparison of the life cycles of *Deroceras Reticulatum* (Müller) and *Arion Intermedius* Normand (Pulmonata: Stylommatophora) at different temperatures under laboratory conditions. *Journal of Molluscan Studies* **48** (1982) 233-244.
- [14] South, A. A comparison of the life cycles of the slugs *Deroceras Reticulatum* (Müller) and *Arion Intermedius* Normand on permanent pasture. *Journal of Molluscan Studies* **55** (1989a) 9-22.
- [15] South, A. The effect of weather and other factors on the number of slugs on permanent pasture. In *Slugs and Snails in World Agriculture* (ed. I. Herderson), British Crop Protection Council, Thornton Heath, (1989b) p355-360.
- [16] South, A. *Terrestrial Slugs*. (Chapman & Hall, London, 1992).
- [17] Wareing, D.R. & Bailey, S.E.R. The effects of steady and cycling temperatures on the activity of the slug *Deroceras Reticulatum*. *Journal of Molluscan Studies* **51** (1984) 257-266.
- [18] Wilson, M.J., Glen, D.M. & George, S.K. The rhabditid nematode *Phasmarhabditis hermaphrodita* as a potential biological control agent for slugs. *Biocontrol Science and Technology* **3** (1993) 513-521.
- [19] Wilson, M.J., Glen, D.M., George, S.K., Pearce, J.D. & Wiltshire, C.W. Biological control of slugs in winter wheat using the rhabditid nematode *Phasmarhabditis hermaphrodita*. *Annals of Applied Biology* **125** (1994) 377-390

Tables

	Untreated	Treatment τ_i in interval i .
u	$\delta(\rho + 1)$	$\delta\tau_1(\tau_2 + \rho)\tau_3\tau_4\tau_5$
v	$\delta\rho$	$\delta\rho\tau_2\tau_3\tau_4\tau_5$
w	$\delta\rho$	$\delta\rho\tau_2\tau_3\tau_4\tau_5\tau_6$
γ	2	$1 + \tau_1/\tau_2$
B	β/σ^5	$\beta/(\sigma^5\tau_2\tau_3\tau_4\tau_5)$

Table 1. The model parameters for system (7.4) for treatment applied at different times of the year, with the untreated system is included for comparison. Note that applications in time intervals 3, 4 and 5 all have identical effect, and that when $\tau_i = 1$ ($i = 1, \dots, 6$), all parameters are equivalent to no treatment being applied.

Figure Legends

Fig. 1. Eggs E_i laid in time interval i hatch into juveniles J_i which may eventually develop into mature slugs M_i , and overwinter to become older adults A_0 (suffix 0 denotes that individuals were laid and hatched in a previous year). An adult in A_0 lays ρ_i eggs in interval i , while mature slugs (M) lay at a different rate, reflecting their different size which may be affected by overcrowding (see text). Throughout the season, individuals of all states survive the time interval i with rate σ_i . Adults (A) and juveniles (J) do not survive the winter (being too old and too young respectively), but mature slugs (M) or dormant eggs (E) from batches i survive with rate $\tilde{\mu}_i$ or μ_i respectively.

Fig. 2. Examples of the steady state distribution (given by Theorem 1) of (5.1), (5.2) for different values of the survival probabilities $0 \leq \sigma, \mu \leq 1$. Small changes in the favourability of the season result in qualitatively different behaviour (here $\mu, \sigma = 0.7 \pm 0.2$).

Fig. 3. The total slug population $S(i, t)$ varying with time, where the model parameters are allowed to vary slightly with the climatic conditions. Here we have considered the effect of average annual rainfall and temperature (in Britain) for the period 1991-1997 inclusive. Explicitly, we have $\sigma = 0.5 + 0.4f^{\text{rain}}$, $\mu = 0.5 + 0.2f^{\text{temp}}$, $\alpha = 1 \times 10^4$, $\beta = 3 \times 10^4$, $\rho = 0 + 5f^{\text{rain}}f^{\text{temp}}$ where the functions f^{rain} and f^{temp} are normalized linear functions of the form $(h - h_{\min})/(h_{\max} - h_{\min})$.

For figures see end

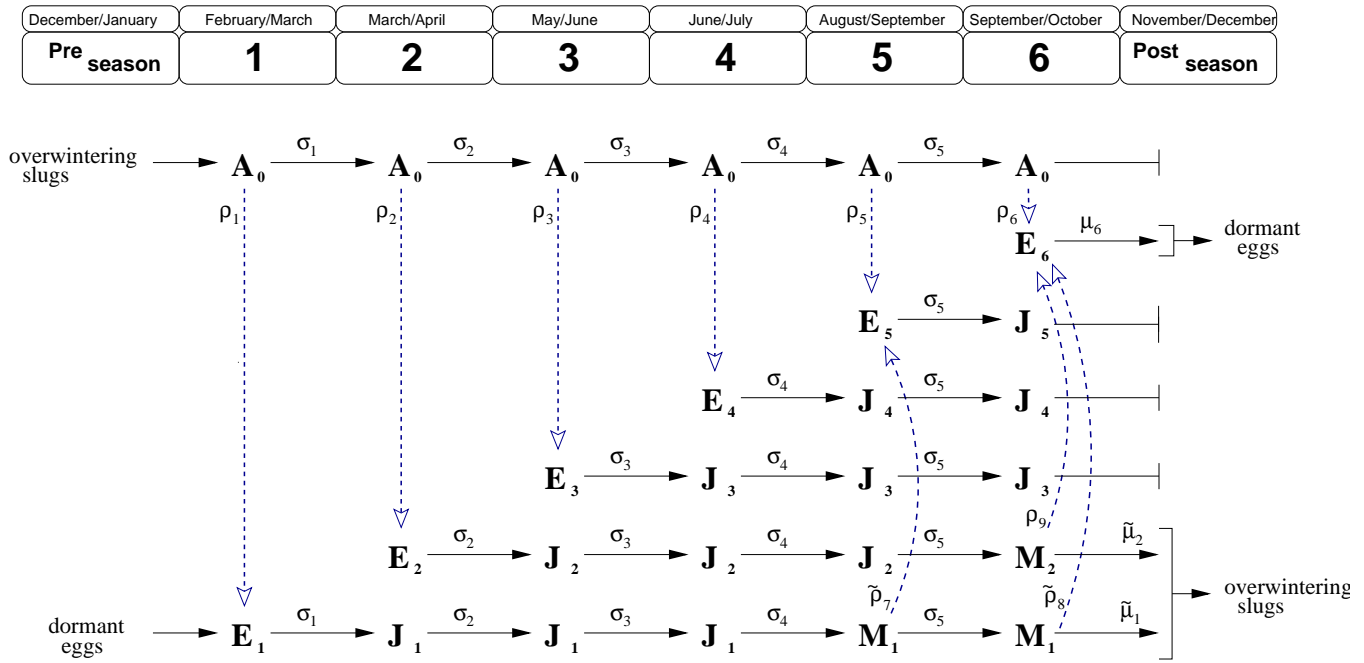
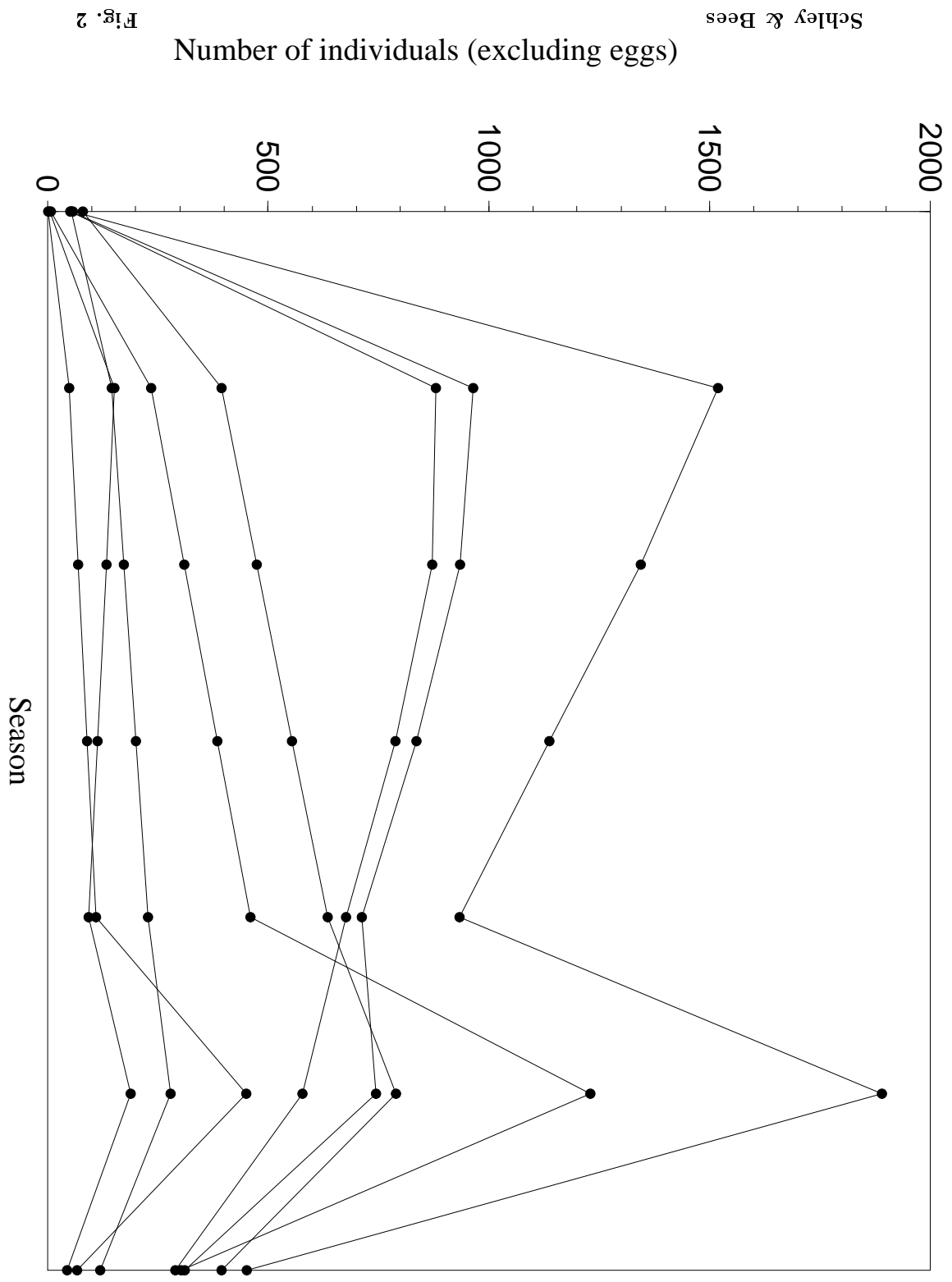


Fig. 1



Schley & Bees

Fig. 2

Number of individuals (excluding eggs)

Season

Schley & Bees

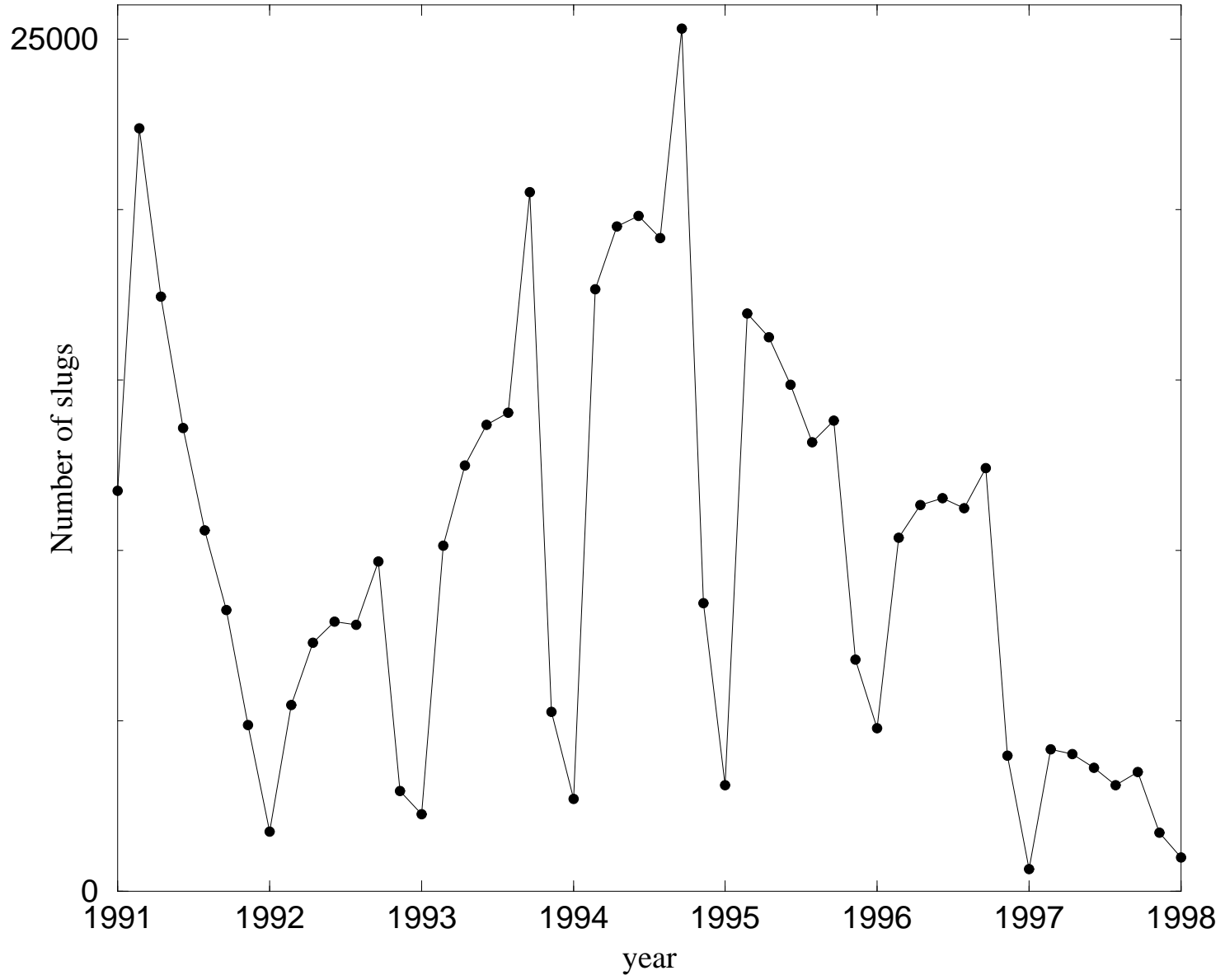


Fig. 3