



The role of time delays in a non-autonomous host–parasitoid model of slug biocontrol with nematodes

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Abstract

Motivated by the difficulty in designing efficacious biocontrol strategies for dominant, agriculturally damaging slug species using naturally occurring parasitic nematodes, we investigate theory for the significant impact of stage structured delays on a non-autonomous host–parasitoid system. Initially, we mathematically strengthen existing stability results for a general class of autonomous system with delays at different trophic levels using analytical and numerical continuation methods. These results are employed to guide theoretical analyses of the effect of delays in a particular, seasonally forced, host–parasitoid system that can model aspects of slug–nematode biocontrol dynamics. Significantly, the model reveals a log-dose response consistent with experiments, and suggests that the optimal timing and frequency of applications is highly dependent on the form of the control required. We find that short-term high-level as well as less dramatic but sustained control are both possible by varying the timing of application. Moreover, we establish that resonance can occur between application and slug life-cycle frequencies inducing potentially undesirable large amplitude fluctuations in slug numbers. Finally, we assess the practicality of planning a crop protection response in the field.

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1. Introduction

Slugs are devastating agricultural and horticultural pests, causing damage to crops at all

stages of their growth. *Deroceras reticulatum* is a species of global economic importance (accounts for approximately 70% of slugs in UK, Glen and Bohan, 2003; Lovatt and Black, 1920; Quick, 1960; Dell, 1964; Altena and Smith, 1975; South, 1992). However, the often irregular dynamics of these slugs are not well understood, and contrasts with more regular and generally less abundant species.

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Slugs predators are mostly opportunistic and few in number (Wilson et al., 1994a; birds, hedgehogs, etc.). The exceptions to this are carabid beetles, especially *Pterostichus melanarius* (Bohan et al., 2000; Digweed, 1993; Symondson et al., 2002), although they too do not restrict their predation to slugs (Pollett and Desender, 1986a,b; Sunderland, 1975). Beetles may not always be present, and their direct effects on slug populations are still under investigation (Symondson et al., 2002).

Prevalent control strategies for slugs rely on methio-carb or metaldehyde pellets, often used pre-emptively. Most chemical treatments, however, are indiscriminate and can kill other species, especially natural slug predators; it has been shown that following such treatments the recovery time of carabid beetles is much longer than the target species (Purvis and Bannon, 1992). Although it is desirable (and essential in organic farming) to employ alternative methods of control, market garden techniques such as barriers or traps are not suitable for large scale agriculture.

The parasitic nematode *Phasmarhabditis hermaphrodita* killed all tested varieties of UK slug (Wilson et al., 1993a) and pest snails (Coupland, 1995). Infection occurs via the slug's mantle, and death results due to toxins released by nematode gut bacteria (Wilson et al., 1995a). Infected slugs stop feeding within 0.6 weeks and move underground before dying, which occurs within 1–3 weeks (Glen et al., 2000). Since nematodes are specialised parasites, their presence does not affect other species, including slug predators (Wilson et al., 1993b, 1994b; although see Morand and Gonzalez, 1997). In particular, they do not have a significant impact on endangered snail species (Wilson et al., 1993a), although they are capable of killing some water snails. Similar varieties of nematode infect other species of slug the world over (Charwat and Davies, 1999; Morand and Barker, 1995). Although shown to be more effective against slugs than chemical treatments (Wilson et al., 1994a), nematodes are currently too expensive to be used in conventional commercial farming. It is thus necessary for the nematode treatment to be applied efficaciously – strategically placed at the correct concentration and in a timely fashion. Many timescales are involved in slug–nematode dynamics and it is not obvious which are important. Using a modelling approach, this paper aims to elucidate the role of these timescales by revealing important mechanisms for stability and

overstability. In particular, we shall address whether the combination of seasonality, slug delay (9 months between eggs and egg-laying) and nematode delay can account for some of the variability in slug and nematode numbers.

Schley and Bees (2003) developed and explored several models for slug biomass and population size. Here, we shall employ the model robustness results to formulate a non-autonomous delay differential equation model of the slug–nematode interaction, taking into account the recent studies of Shirley et al. (2001) and Symondson et al. (2002), and incorporating both seasonal fluctuations and stage structure. Alternative model forms should also be noted, such as the discrete model based on slug egg production with overlapping generations, Schley and Bees (2002), which splits the year up into several in-season and extra-season batches. However, we found that this system does not easily lend itself to the full spectrum of timescales identified in experimental studies of biocontrol. The delay differential system best captures the short lifespan characteristics and rapidly varying densities of the nematodes as well as the slug dynamics with longer timescales.

Recent theoretical attention has focused on the effect of delays at various trophic levels and their stabilizing and/or destabilizing influences, in autonomous host–parasitoid/pathogen systems (see for example Briggs et al., 1999). We shall see that these systems have much in common with the autonomous slug–nematode system. Hastings (1984) considered stability implications of time delays at different trophic levels in an autonomous model exhibiting equilibria associated with either extinction or coexistence, concluding that parasitoid delays are more critical than host delays. In a similar approach, Murdoch et al. (1987) indicated that an invulnerable age class (e.g. time delay in the recruitment of adults or juveniles) had a stabilizing role in host–parasitoid dynamics, which they further linked to the lack of local extinctions in some bio-control arenas. Briggs and Godfray (1995) considered a more general system, but also autonomous and in the absence of a carrying capacity (see their Appendix C), and derived a characteristic equation from which to determine local stability of the coexistence equilibrium, whence they numerically obtained stability results. Simulations revealed the existence of sub- and multi-generational cycles (see also Briggs et al., 1999).

They conclude that equilibria are generally stabilized (and Lotka–Volterra cycles destabilized) by models in which the hosts have age-structure, especially when juveniles are susceptible, and destabilized by parasitoid/pathogen age-structure.

Initially we adopt these approaches for a model which includes a carrying capacity and, furthermore, obtain explicit analytical results for the stability of equilibria for particular cases of host and parasitoid delays. We develop these results with the application of continuation methods, thus providing a framework from which we can study the more realistic non-autonomous system. In order to theoretically investigate the mechanisms involved in realistic biological control strategies it is essential to consider seasonal variations in life-cycle factors, and the discrete timing of nematode applications. These non-autonomous features can express a wealth of additional behaviour beyond the underlying trends revealed by the study of autonomous systems (e.g. Wiegand and Wissel, 1994).

In the next section, we construct the full non-autonomous slug–nematode system, and, in the following section, summarize the analysis of the associated autonomous system with delays, which reveals basic solution trends and may also be directly applicable to controlled environments (such as greenhouses). In later sections we numerically address the dynamics of the full delayed non-autonomous system using a combination of independently derived field and laboratory data and, finally, assess strategies for effective biocontrol. Treatment programmes are investigated to either maximise the reduction in host numbers with a limited supply of parasitoids or control the host life cycle and so contain outbreaks. In particular, we consider treatment timing, application frequency and host (slug) damage response strategies.

2. Modelling slug–nematode dynamics

2.1. Mature slug biomass

Schley and Bees (2003) proposed the following delay differential equation model for mature slug biomass (henceforth, assumed measured in *mg*), $S(t)$, in the absence of predation or parasitism (which they classified as type Ii):

$$\frac{dS(t)}{dt} = \rho(t - \tau(t))S(t - \tau(t)) - \mu(t)S(t) - \frac{S^2(t)}{K(t)}, \quad (1)$$

where $\rho(t)$ (>0) represents the slug reproduction rate, and is the rate of production of mature slug biomass (*mg*) from eggs through juveniles to adults, per *mg* of biomass. Individual slug growth is distinct from reproduction and is incorporated in the parameter $\mu(t)$ = (death – growth), the slug biomass net decay rate. The delay $\tau(t)$ (>0) is the time span from when the eggs are laid until the hatched slugs reach (egg laying) maturity and $K(t)$ (>0) represents the limitation placed upon the population size by the environment, and is related to the carrying capacity $C = K(\rho - \mu)$. (Although C appears naturally for autonomous systems, it does not have the same interpretation for non-autonomous delay systems, as in general $S(t - \tau(t)) \neq S(t)$.) The most natural unit of time, t , for slug dynamics is weeks (*wk*; for convenience 1 year \equiv 52 *wk*), although all simulations employ time steps of 1 h. The juvenile populations are implicitly modelled and their dynamics have been absorbed into the (delayed) reproduction rate $\rho(t - \tau(t))$ (see Schley and Bees, 2003, for details), with the assumption that the relatively mobile mature slugs (South, 1982; Shirley et al., 2001) do not compete directly with juveniles for resources.

Beyond this approach, Schley and Bees (2003) investigated a range of models for adult and/or juvenile populations of slugs (as well as for slug number) and concluded that the adult biomass model provided a range of representative solution behaviour. Furthermore, they noted that in the absence of predation the other representations can be obtained from this model by suitably scaling the forcing functions and parameters (by consistently scaling/absorbing time dependent terms). In all models the temporal delay terms were found to have a qualitative effect on the dynamics, both for equilibrium and transient solutions. Schley and Bees (2003) further argued that for a simple ODE model it is more important to keep track of slug biomass than slug numbers due to the large range of slug sizes, and slug-size related crop consumption and possible nematode discharge (Gwynn, 2000).

In this paper, in order to develop simple models of slug biocontrol we shall adopt the adult slug biomass model for the reasons discussed above and

shall develop it for slug–nematode interactions. The results discussed in this paper can be adapted for other slug models in this genera, if the need arises.

2.2. Nematode parasitism

As the nematode population relies solely on the slug population, we require a second equation for the number of free nematodes, $N(t)$ – those living in the soil and not in slugs. Slug infection results in the removal of healthy adult slugs from the population $S(t)$, since infected individuals no longer reproduce or feed/compete. Infected slugs are not explicitly modelled as they generally move underground to die (Glen et al., 2000). Rather, we implicitly model the time lag between infection and the certain addition to the free nematode population. Following reproduction in and consumption of the cadaver by nematodes, infection ultimately results in an increase in the free nematode population (Wilson et al., 1993a). Glen et al. (2000) showed that the probability of infection was nematode concentration dependent, so that we amend the right hand side of Eq. (1) by adding the term

$$-c(t)N(t)S(t), \quad (2)$$

where $c(t) > 0$ is the contact rate between slugs and nematodes.

It is reasonable to assume that all but a negligible amount of nematode reproduction occurs within the slug (Gwynn, 2000). The emergence rate of free nematodes is thus proportional to the amount of slug biomass infected a time $t - \sigma(t)$ ago, given by

$$+p(t)c(t - \sigma(t))N(t - \sigma(t))S(t - \sigma(t)),$$

where $p(t) (>0)$ is the nematode reproduction rate (per mg slug biomass), and $\sigma(t) (>0)$ is the time from infection until free nematodes emerge. Furthermore, we require a natural nematode mortality, which we assume to be linear of the form

$$-v(t)N(t),$$

where $v(t) (>0)$ is the nematodes' natural death rate.

Unifying all of the above, we obtain the non-autonomous slug–nematode system

$$\begin{aligned} \frac{dS(t)}{dt} &= \rho(t - \tau(t))S(t - \tau(t)) - \mu(t)S(t) - \frac{S^2(t)}{K(t)} \\ &\quad - c(t)N(t)S(t), \\ \frac{dN(t)}{dt} &= p(t)c(t - \sigma(t))N(t - \sigma(t))S(t - \sigma(t)) \\ &\quad - v(t)N(t). \end{aligned} \quad (3)$$

We can cast this model in a more general host–parasitoid form, for which $S(t)$ represents the mature hosts and $N(t)$ the number of parasitoids, $\rho(t) (>0)$ is the host reproduction rate, $\mu(t)$ is the host net decay rate, $K(t) (>0)$ is an environmental limitation on mature hosts, which here do not compete for food resources with a juvenile class, $\tau(t) (>0)$ is the host maturation delay, $c(t) > 0$ is the contact rate between host and parasitoids, $p(t) (>0)$ is the parasitoid reproduction rate (per unit host), $\sigma(t) (>0)$ is the time from infection until the parasitoids emerge and $v(t) (>0)$ is the parasitoids' natural death rate. Note that if $S(t)$ represents number then $\mu(t) = \text{death} > 0$, whereas if $S(t)$ represents biomass then $\mu(t)$ can be negative at certain times. The full system is a non-autonomous extension of Murdoch et al. (1987) and Model 1 of Briggs and Godfray (1995) with the inclusion of an environmental carrying capacity. This model may be set in the context of invulnerable juveniles, which are modelled implicitly. For the slug–nematode system, juvenile slugs move much less distance (South, 1982; Shirley et al., 2001) than the significantly larger, possibly sexually motivated, adult slugs (>100 mg). It seems reasonable to assume that the juveniles are then less likely to come into contact with the nematodes and so are relatively invulnerable. Such a description is consistent with the adult slug biomass model and useful in that the supporting data for non-autonomous events are most readily available for this scenario (see Schley and Bees, 2003).

3. Autonomous host–parasitoid delay dynamics

In this section we neglect the time dependence of model parameters, with application to controlled environments such as regulated greenhouses or poly-tunnels, which have constant levels of temperature and humidity, and relatively few predators. It is instructive to analyse the possible parameter regions through which the non-autonomous model may pass, in order

to help predict the behaviour of the full system. This section aims to set the scene and to reinforce and extend analyses of similar systems, although it may be skipped in favour of later sections on the non-autonomous slug–nematode dynamics and agricultural biocontrol strategies.

3.1. Non-dimensionalization and steady states

To reduce the number of free parameters, we non-dimensionalize by setting

$$\begin{aligned} \tilde{t} &= \rho t, & \tilde{\tau} &= \rho \tau, & \tilde{\sigma} &= \rho \sigma, & \tilde{\mu} &= \frac{\mu}{\rho}, & \tilde{\nu} &= \frac{\nu}{\rho}, \\ \tilde{p} &= cKp, & \tilde{S}(\tilde{t}) &= \frac{S(\tilde{t}/\rho)}{\rho K} = \frac{S(t)}{\rho K}, \\ \tilde{N}(\tilde{t}) &= \frac{cN(\tilde{t}/\rho)}{\rho} = \frac{cN(t)}{\rho}. \end{aligned}$$

On dropping tildes, the model becomes

$$\begin{aligned} \frac{dS(t)}{dt} &= S(t - \tau) - \mu S(t) - S^2(t) - N(t)S(t), \\ \frac{dN(t)}{dt} &= pN(t - \sigma)S(t - \sigma) - \nu N(t). \end{aligned} \tag{4}$$

The nullclines of Eq. (4) are $\{S = 0, N = 1 - \mu - S\}$ and $\{N = 0, S = \nu/p\}$, which at most give three steady states $E^* = (S^*, N^*)$ given in Table 1 (extinction, exclusion and co-existence). Note that the co-existent host population is lower than in the absence of parasitoids, since $\mu < \mu_* = 1 - \nu/p$ implies $\nu/p < 1 - \mu$. For the case of no delays ($\tau = \sigma = 0$), stability results are tabulated in Table 1. In the next sections we shall consider the local stability of the equilibria E_0 , E_1 and E_2 , under various delay conditions. To elicit analytical results, four cases will be addressed: $\tau > 0, \sigma = 0; \tau = 0, \sigma > 0; \tau = \sigma > 0; \tau \neq \sigma$.

Table 1
The steady states of Eq. (4), conditions for their existence and stability results in the absence of delays

Steady state $E^* = (S^*, N^*)$	Exists if and only if	$\tau = \sigma = 0$: stable if and only if
$E_0 = (0, 0)$		$1 < \mu$
$E_1 = (1 - \mu, 0)$	$\mu < 1$	$\mu_* < \mu < 1$
$E_2 = \left(\frac{\nu}{p}, 1 - \mu - \frac{\nu}{p}\right)$	$\mu < \mu_* = 1 - \frac{\nu}{p}$	$\mu < \mu_*$

3.2. Host maturation delay without parasitoid reproduction delay ($\tau > 0; \sigma = 0$)

One might wish to assume that the delay σ be neglected as it is typically smaller than the host maturation delay τ . However, we show in Appendix A that the local stability criteria for all three of the above steady states do not alter in this case. We note that it is not possible for a delay of the above form to induce stability in the system, since delay induced bifurcations occur through complex conjugate roots crossing the imaginary axis and the undelayed unstable system has positive real roots.

However, even when the positive equilibrium is found to be linearly stable, the stability results are local results and stable periodic solutions can still exist.

3.3. Parasitoid reproduction delay without host maturation delay ($\tau = 0; \sigma > 0$)

Although it may be unrealistic to neglect the host maturation delay, it is instructive to analyse stability if we do so. Once again, the stability criteria for E_0 and E_1 do not alter in the presence of this delay. However, we show in Appendix A that E_2 can be destabilized by a sufficiently large delay.

3.4. Linear analysis for multiple delays ($\tau > 0; \sigma > 0$)

When the host maturation delay τ and the parasitoid reproduction delay σ are both present, new dynamics are introduced. It is straightforward to show that the stability criteria for E_0 and E_1 remain unaltered, and so we consider only the coexistence steady state E_2 (requiring $\mu < \mu_*$). Multiple delays are, in general, complicated to analyse, and although it is possible to analyse the stability of the equilibria when the delays are integer multiples of each other, they are inherently dependent on the majority of the parameters and tend not to result in explicit stability criteria. It is for this reason that we first consider a simple case, and then use numerical continuation techniques to extend the results. This provides an analytical skeleton from which to build solutions to the characteristic equation, without resorting solely to numerical computations. Thus we may illustrate how the presence of a delay in host maturation can stabilize the coexistent state when the

parasitoid reproduction delay is present. This effect is proportional to the magnitude of the maturation delay.

When the delays are equal such that $\tau = \sigma$ the resulting characteristic equation can be analysed as in Appendix A. There is a critical value $\mu_\tau (< \mu_*)$ of μ above which bifurcations may not occur, and below which instability sets in for sufficiently large σ . Numerical results suggest that this is approximately μ_0 for small ν , but for larger values of ν this critical value is strongly dependent on all of the parameters.

For independent delays ($\tau \neq \sigma$) and by employing the above results, we may determine $\sigma_0(\mu, \nu, p)$, the value of σ at which bifurcation occurs for $\tau = 0$, and the critical root $\lambda = i\omega_\sigma$ of the characteristic equation (8). Using the frequency ω_σ as a free parameter, the solutions $\sigma(\tau)$ ($\tau > 0$) of (8) can then be computed for any given (μ, ν, p) (e.g. using the continuation software AUTO; <http://indy.cs.concordia.ca/auto/>). Fig. 1 shows the case (0.5, 0.1, 6), but other values are similar (when such bifurcations occur). It is found that the stable range of values $[0, \sigma_c)$ of the parasitoid delay, where σ_c is the

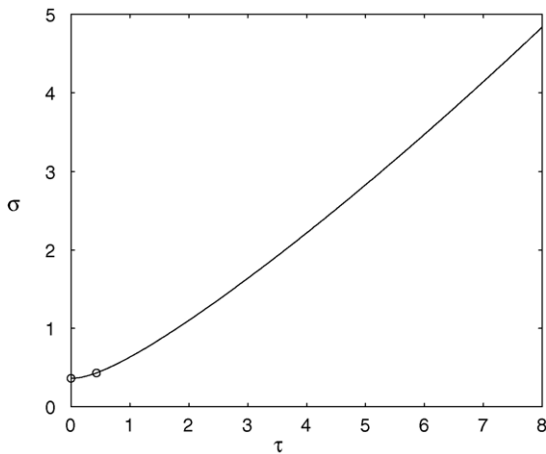


Fig. 1. The stability boundary for the coexistent steady state with respect to the two delays, τ and σ , when $p = 6$, $\nu = 0.1$ and $\mu = 0.5$. Destabilization only (and always) occurs with increasing σ for any τ ; for fixed σ we may always (re)stabilize the equilibrium by increasing τ sufficiently. The curve is calculated by continuing solutions (τ, σ) which satisfy (8) for $\lambda = i\omega_\sigma$, where ω_σ is a free parameter. Note that the curve intersects the vertical axis at $\sigma = \sigma_0$, since $\tau = 0$. From the text we have that $\sigma_0(0.5, 0.1, 6) = 0.364$ for which $\omega = \omega_\sigma = 0.216$ from Eq. (10). These values may be used as the initial conditions for numerical continuation. In addition, the points $(0, \sigma_0)$ and $(\sigma_\tau, \sigma_\tau)$ given in the text are marked with circles (here $\sigma_\tau = 0.435$). The curve $\sigma_c(\tau)$ passes through these points as required.

bifurcation value with respect to σ , increases monotonically with the host delay τ , and that this relationship becomes linear for large τ . In the above example, the line $\sigma_c = 1.06\tau - 8.69$ is a good approximation for $\tau > 30$.

Since $\sigma_0 \leq \sigma_c$, we have shown that the addition of the second delay can stabilize the equilibrium. Analytically, we have shown that the delays in the model can have destabilizing as well as stabilizing effects. Notably we have demonstrated that the parasitoid reproduction delay would need to be of the same or larger order as the host maturation delay to destabilize the equilibria, in line with previous numerical results reported in the literature for similar models without a carrying capacity (e.g. Briggs and Godfray, 1995). In practice, however, $\tau \gg \sigma$ and we would not expect such behaviour. We must emphasize that delays can also result in periodic solutions, so that stable steady solutions may only be locally (not globally) stable, and that for convergence, solutions may be required to originate sufficiently close to the desired steady solution.

3.5. Slug biocontrol strategies (autonomous model)

For ease of interpretation we return to the dimensional parameters in this section. We shall assume that a delay induced instability does not occur (τ is sufficiently large compared to σ), so that there is always exactly one locally stable equilibrium (see Table 2).

With reference to the above analysis we shall consider biocontrol strategies for the two equilibria when

Table 2

Autonomous model with delays ($\tau \gg \sigma$): expected behaviour of slug and nematode populations in terms of the original parameters

Parameter range	Outcome	Convergence ^a to (S^*, N^*)
$K(\rho - \mu) < 0$	Extinction	$(0, 0)$
$0 < K(\rho - \mu) < \frac{\nu}{cp}$	Exclusion ^b	$(K(\rho - \mu), 0)$
$\frac{\nu}{cp} < K(\rho - \mu)$	Coexistence	$\left(\frac{\nu}{cp}, \frac{1}{cK} \left(K(\rho - \mu) - \frac{\nu}{cp}\right)\right)^c$

^a Only linear stability has been proven, although numerical results suggest that the convergence results are globally valid.

^b Only slugs persist.

^c Valid when delay induced instability does not occur. Otherwise, we expect coexistence with oscillations (periodic or quasi-periodic).

slugs are present (assuming that $\mu > \rho$ so that slug extinction does not occur). If slugs exist in the absence of nematodes, the parameters satisfy

$$\frac{v}{c\rho} > K(\rho - \mu) = S^*. \quad (5)$$

The most advantageous strategy is to reverse the inequality (5) so that we have coexistence, while rendering $v/c\rho$ (the new stable steady state slug population) as small as possible.

In practice it may be difficult to change p , which represents the number of free nematodes released from the body of an infected slug. Reducing the nematode mortality, v , should be possible in controlled environments (such as poly-tunnels) by maintaining a suitable temperature and climate, although this is also likely to benefit slugs. Warm damp conditions which improve the survival of the nematodes in the soil (reduce v) will also reduce μ , and so careful consideration will have to be given as to whether a reversal of inequality (5) may be attained. The final possibility for producing a reduced coexistent slug population is to increase c , the contact rate between slugs and nematodes. In practice, this will be dominated by how “active” nematodes are, which is strongly affected by extreme temperatures. Improvements on the infection rate of slugs might be achieved by increasing the homogeneity of the populations, such as through tillaging (while maintaining a moist exposed surface). However, breaking up the soil might also increase μ and reduce ρ , so that a switch may be harder to obtain, but if $v/c_{\text{new}}p < K(\rho_{\text{new}} - \mu_{\text{new}})$ then it immediately follows that $v/c_{\text{new}}p < K(\rho_{\text{old}} - \mu_{\text{old}})$, so that the slug population will be reduced. Tillaging would be beneficial if μ and ρ were increased and decreased, respectively, since this would still result in a reduction of the steady slug population $K(\rho - \mu)$, even if a persistent nematode population could not be established.

4. Non-autonomous slug–nematode dynamics

In this section, we explore explicit solution behaviour of the non-autonomous slug–nematode model. The motivation in doing so is two-fold. The functional dependence of most slug and nematode life-factors on the season is multifaceted and sometimes extreme, and we have access to data on this functional

dependence from many years of well-controlled laboratory and field experiments.

4.1. Parameters

For numerical simulations of the slug biomass population we have used the temporally varying parameters of Schley and Bees (2003), which were derived using the independently measured laboratory and field data of South (1982, 1989a) and Hunter and Symmonds (1971) as functions of temperature. Whilst it is clear that many environmental factors will influence slug dynamics, including moisture, the literature has concentrated on the effects of temperature in the laboratory and supports the view that temperature is the dominant factor in the life cycle of slugs (South 1989a, 1989b; Wareing and Bailey, 1985). We have taken this temperature data as “representative” and, furthermore, seek to disentangle effects by looking at average years as in Schley and Bees (2003). However, the results described here are not overly dependent on the parameters.

Choi et al. (2004) adopt a different approach by fitting a simple model of juvenile and adult slug dynamics with 8 free parameters to an initial data set of 20 data points from field data, which they then employ in a predictive fashion. One of the aims of their paper was to theoretically investigate the relative importance of temperature and rainfall on the slug dynamics, although due to a lack of data various functional forms were assumed. They conclude that temperature and rainfall affect different aspects of the slug lifecycle and, furthermore, that the parameters provided by the fitting process differ from laboratory experiments. In the absence of independent field data, we prefer to use the reproducible laboratory data as above (and some field data), whilst recognising that refinements could be made with more experimental data. With the representative seasonal data that we shall employ we shall look to isolate mechanisms rather than provide forecasts by fitting our model. (See Comins and Fletcher, 1988, on the virtues of using reliable laboratory data rather than “setting the parameters post hoc to produce realistic results”, and Feldman et al., 1981, for example, on the success of laboratory-derived models of beetles for field predictions.)

To calculate the nematode related parameters arising in this model, we first note that there should exist a background nematode population in the absence of

treatment (Wilson et al., 1994a), and so we expect the system to support a natural state of coexistence. The time until death of infected slugs depends on their degree of initial infection, and varies from 1 to 3 wk (Wilson et al., 1993a). As before, we assume that the level of initial infection is proportional to the current nematode density. We may then use the field data of Wilson et al. (1994a), for infection levels versus treatment doses, to calculate both the expected background level of nematodes and the contact rate between individuals. The number of newly infected individuals in 1 week is approximately cNS , where N is the total number of nematodes (treatment plus background level) and S is the current slug population. Fitting the data we find that $c = 6.4 \times 10^{-6}$ and the background level is $N_2^* \approx 9 \times 10^3$ nematodes, which equates to an infection load of 10% of slugs, in good agreement with field observations (Wilson et al., 1994a).

The per capita lifespan of *P. hermaphrodita* is approximately 2 wk (Wilson et al., 1993b; Gwynn, 2000). Since *P. hermaphrodita* is a specialised parasite and its life-cycle is closely linked to that of *D. reticulatum* (Glen and Wilson, 1997), it is not unreasonable to assume that $v(t)$ is proportional to the slug death rate with a mean determined by the laboratory data. It has been shown that nematodes may also survive in freezing temperatures, although they remain inactive. However, we will initially let the contact rate remain constant, so that $c(t) \equiv 6.39 \times 10^{-6}$ nematodes $^{-1}$ wk $^{-1}$, and shall consider the inactivity at extreme temperatures later on.

We estimate the number of active nematodes that emerge from infective cadaver as $p = 45$ nematodes mg $^{-1}$, based upon a lower threshold yield of 50 nematodes mg $^{-1}$ of culture medium recorded by Wilson et al. (1993b), approximately 90% of which were dauer larvae. A prerequisite for coexistence is that $S_1^* > S_2^*$, and we thus use the upper bound parameters for ρ and μ calculated in Schley and Bees (2003). Noting that $KcN_2^* = S_1^* - S_2^* = K(\rho - \mu) - v/pc$ we may use all of the above to solve for the expected value of K , giving $K \approx 3.5 \times 10^4$. The full non-autonomous model is detailed in Appendix B.

We note that there is limited evidence to suggest that highly infected slugs die sooner (Wilson et al., 1993a). Thus one might consider a state dependent delay such as $\sigma(N) = 3 - 2(N - \beta)/(\delta - \beta)$, where β is the back-

ground level of nematodes and δ is the dosage applied (to give a delay of between 1 and 3 wk). However, this leads to small quantitative rather than qualitative changes in dynamics and we disregard such a term in the current study.

4.2. Nematode treatments and log-dose response

Standard nematode treatments apply approximately 3×10^5 nematodes m $^{-2}$ (Glen and Wilson, 1997). Experiments have shown, however, that approximately 80% of nematodes applied to the soil are lost (Gwynn, 2000) and, therefore, we assume a “true” treatment dose of 6×10^4 nematodes m $^{-2}$ per application. The treatment is easily incorporated into the simulations with the addition of a periodic step function $F(\omega t)$ to the nematode growth rate, which quickly forces the population to the application level (see Appendix B).

Although nematode numbers decrease rapidly following their application, the model reveals that a secondary peak may be observed in their population shortly after the treatment time, as illustrated in Fig. 2. This is a result of the nematode reproduction delay, σ , between slugs being infected and the new dauer larvae emerging, and is a prediction that could be investigated in the field. The magnitude of this second peak depends

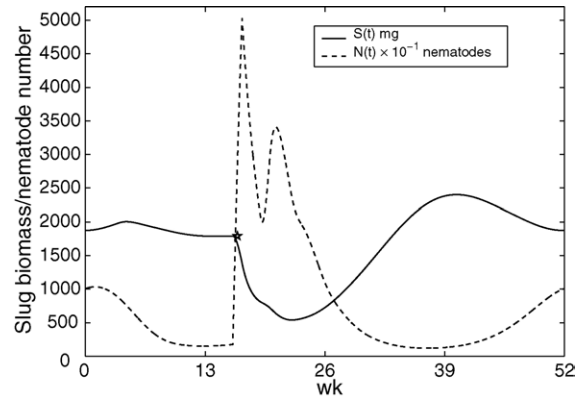


Fig. 2. The slug biomass level and nematode population (scaled for comparison) when treatment is applied annually in week 16 (marked with a \star) and there is variable nematode activity (see text). The large delay τ means that treatment not only affects the slug population at the time of application, but results in reduced recruitment later in the year (because of reduced egg laying now). This has knock-on effects on the nematode population, which requires the presence of slugs (in addition to a good contact, and thus infection, rate c) for reproduction.

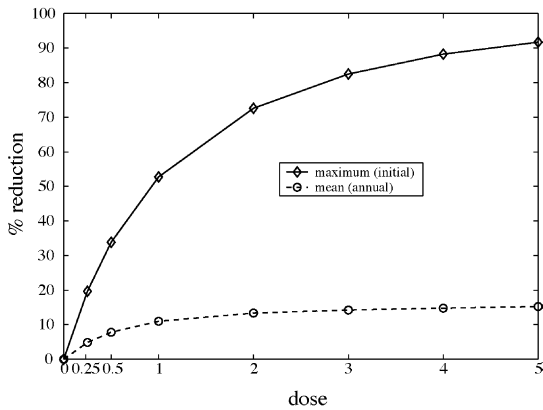


Fig. 3. The mean and minimum slug biomass present each year in relation to the dose strength of an annual nematode treatment. For clarity here, we have considered the autonomous model, with each parameter assigned its annual mean value. In each case, the minimum slug biomass was attained shortly after (and directly attributable to) the application of nematodes.

on the level of nematode activity c and indicates how nematode reproduction assists in treatment efficacy.

The calculation of background nematode levels (and the measured level of slug infection, Wilson et al., 1994a) suggests that a high level of slug “control” exists in the absence of treatments. Moreover, simulations of the autonomous system with delays (i.e. non-equilibrium dynamics) indicate that slug populations are maintained at roughly half the levels which they attain in a parasite-free environment.

The model predicts a log-dose slug response to increasing nematode dosage, which has previously been observed in experiments (Wilson et al., 1994a, 1995b). The reduction in slug biomass when nematodes are applied once per year ($\omega = 2\pi/52$) in a controlled environment is shown in Fig. 3. Note that there is a large difference in the initial response and the mean effect of treatment over a year.

4.3. Application efficacy

Even a single nematode treatment dose can have a long term effect on slug biomass populations. Repeated annual applications, however, bring about a greater overall reduction. Simulations show that the slug population has a recovery time of several years, an example of which is given in Fig. 4. The short-term control (tens of weeks) and form of oscillation are the most measur-

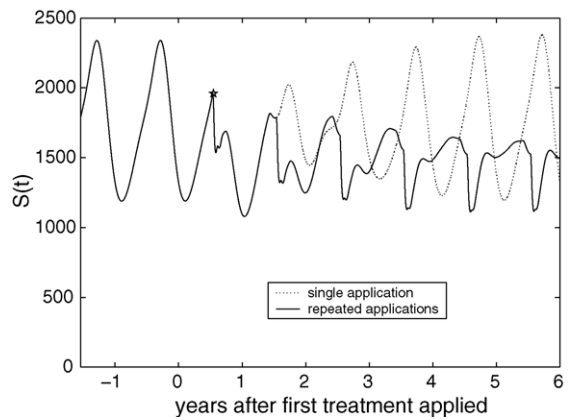


Fig. 4. Nematode treatments appear highly effective at producing and maintaining a low level slug population. A single treatment (dotted line) produces a significant reduction whose effects linger for 4–5 years. A significantly lower population level can be achieved (2–3 years) through annually repeated applications (solid line). In each case year zero represents the first year nematodes are applied, and treatments have been applied in week 28 (the first treatment is denoted by a *).

able features, as displayed in Fig. 2. It has been shown experimentally that treatments provide significant crop protection for at least 7 wk, but not after 27 wk (Wilson et al., 1994b, 1996).

If a nematode dose is applied just once per year, there is a quick transition to a controlled population that can have an annual mean which is 15% less than the untreated population (although this percentage depends on when the nematodes are applied, see below). In Fig. 4 we display the results when the nematodes are applied every year in week 28 (which generally admits the least variation, see below), forcing the slug population from a periodic solution with a large mean to one with a lower mean and smaller amplitude. It should be remembered that the periodic nature of these solutions is due to the deterministic periodic forcing and in practice we would expect yearly fluctuations to drive variations about these solutions. Importantly, Fig. 4 indicates that the long term advantage of repeated treatments is not immediately obvious at the time of application, and is due to the delays in the system.

4.4. Application timing

The reduction in annual mean slug population changes only slightly with the timing of a single annual

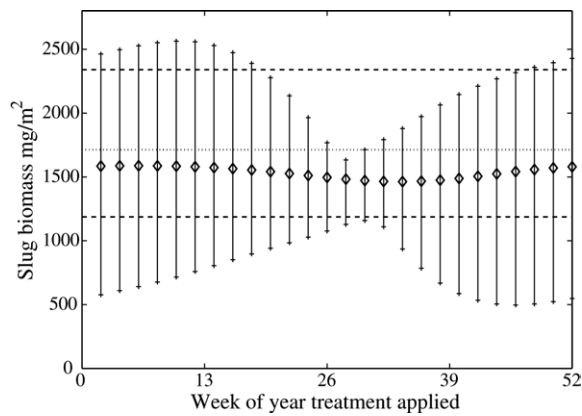


Fig. 5. The mean slug population (\diamond), and the minimum and maximum values it attains (+) in any 1 year, depending on the time at which the nematode treatment is applied. For comparison, the mean (dotted) and extreme (dashed) values of the untreated slug population (with only the background level of nematodes) has been marked.

nematode application (Fig. 5), but the amplitude varies markedly. A non-intuitive result occurs when applications outside of weeks 18–46 actually result in larger fluctuations (higher maxima!) than would normally be attained, and suggests that applications should be timed to coincide with vulnerable crop times. Some crops, however, may require sustained protection and it may be more desirable to maintain a non-fluctuating slug population.

4.5. Application frequency: resonance in controlled environments

Here we consider the separate issue of how frequently treatments should be applied in unforced (autonomous) model, whilst maintaining the net annual dose. We find that the mean slug population is not significantly affected, suggesting that if there is a cost involved in the application of the nematodes, then it is most efficient to apply the entire dose in one treatment. But one must also consider the amplitude of the population variations with regard to vulnerable crops. In particular, resonance with the natural slug dynamics causes large fluctuations as can be observed in Fig. 6, which shows the mean and range of the resultant slug population for the autonomous model in relation to the frequency of treatment.

If crops are vulnerable for only a short period of time, it may be desirable to apply the nematode treat-

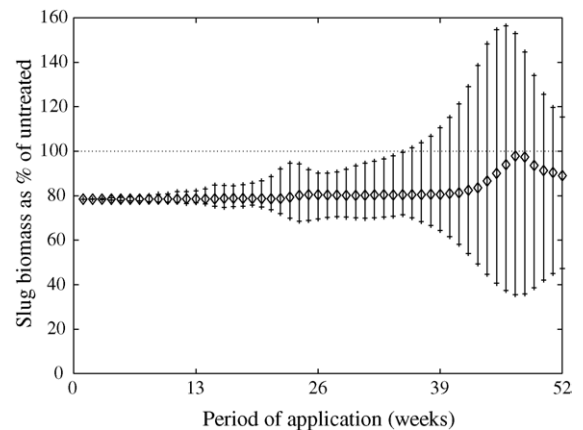


Fig. 6. For a constant annual quantity of nematodes, the mean (\diamond) slug biomass, given as a percentage of the average untreated population, in a controlled environment remains relatively unaffected by the frequency of nematode application. The fluctuations in the population do, however, change significantly; the maxima and minima (+) may be well above and below the normal range. There is a clear resonance with the delay $\tau + \sigma \approx 46.2$ and its sub-harmonics.

ment at the main resonant frequency (period of 46 wk) in order to obtain a few weeks of exceptionally low slug damage. In this case, the slugs crash to approximately 36% of the uncontrolled level, but peak at 156% later in the year. Results indicate that treatments must be applied with a period of no more than 35 wk if the population is to be maintained below its uncontrolled level for the whole year. The slug population fluctuates less as treatments become more frequent, due to the stabilizing effect on the nematode population.

4.6. Variable nematode activity

Although it is possible to calculate the mean value of the contact rate $c(t)$ (see above), little data is available on its likely variation. In the field, we would expect $c(t)$ to vary (like most other parameters in the non-autonomous model), reflecting how active nematodes are in seeking out and infecting slugs. To derive a time dependent contact rate, we follow the method used by Schley and Bees (2003) for slug life-cycle parameters. Firstly, we consider c as a function of temperature T ($^{\circ}\text{C}$), and then calculate the value of $c(t)$ by using the average (monthly) temperature in the UK. As for slugs

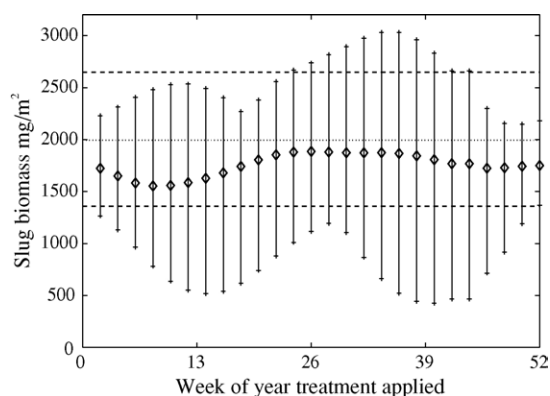


Fig. 7. As Fig. 5, but with variable nematode activity – and hence infection rate – $c(t)$ given by Eq. (13), as opposed to a constant contact rate ($c = 6.39 \times 10^{-6}$).

(South, 1989b; Wareing and Bailey, 1985), temperature is considered the most significant factor in the life cycle of nematodes (Wilson et al., 1993a; Gwynn, 2000). Finally, we fit a curve to these points (with the assumption that it has a period of 1 year or integer fraction thereof; Appendix B). The result, as expected, is almost zero activity during the winter months, peaks in spring and autumn and reduced activity during the summer.

A variable contact rate is less effective overall than a constant rate (with equal means), as slug populations tend to recover in times of nematode inactivity (Fig. 7). Surprisingly, winter applications provide reasonable protection, despite the low nematode activity, due to the low nematode death rate at this time. However, this prediction is unlikely to be valid during periods of sustained hard frost. The immediate reduction in slug numbers following an application at the start of the year is negligible but, under a regime of repeated annual applications, results in sustained control. An application later in the year can result in a dramatic drop in slug population (due to high nematode activity), but induces large oscillations.

Further research on the exact response of nematode activity to temperature would be extremely useful in order to more accurately calculate treatment times. These results strongly suggest that consideration should be given to the crop protection required both at the time of application and for the rest of the year.

5. Conclusions

The control of slugs is an issue of great importance in agriculture and horticulture. Recently parasitic nematodes have been used as an efficacious biocontrol measure, although some optimisation is necessary to help it become economically competitive with conventional chemical treatments.

In this paper, we have developed a realistic, uniform model for the dynamics of interacting slug and nematode populations in the presence of delays in slug and nematode maturation, and seasonal forcing. In particular, we have considered a system of two non-autonomous, delayed ODEs and have investigated both autonomous and non-autonomous aspects of the model. Such systems have previously been used to model parasitoid-invulnerable age classes. Here, juveniles have been assumed invulnerable due to their much reduced infection rates, attributed to their relative small size and lack of locomotion (including the absence of reproductive impulse), and the negligible movement of the parasitoid (nematode). One avenue of future research might assess the validity of effective juvenile invulnerability by explicitly, rather than implicitly, modelling juveniles in a spatial setting.

For the slug component of the model presented herein, Schley and Bees (2003) have shown how the autonomous model may be extended to model either mature populations, juveniles or a combination of both, with an appropriate rescaling of parameters and implicit modelling techniques. The choice of model setup would in practice necessarily be governed by the attributes of the supporting data.

As the slug–nematode model readily fits within the host–parasitoid framework, we have followed previous stability analyses of autonomous versions of such systems (Hastings, 1984; Murdoch et al., 1987; Briggs and Godfray, 1995). Furthermore, we show that the slug–nematode model, including a carrying capacity, is amenable to analytical techniques for special cases of the delay terms. In particular, we present an alternative method to direct numerical computation of the stability results: analytical calculations yield a skeleton of exact expressions upon which we build with continuation techniques.

The system of equations contains multiple delays, which are themselves time-dependent. The large delay

in host maturation proves to be sufficient to dampen the effects of the (potentially destabilizing) delay in parasitoid reproduction, resulting in local stability of steady states. Stability results have only been proven locally, although numerical results suggest that they are mostly global: the delays alone do not favour periodic or quasi-periodic solutions, for realistic values of the parameters (where typically host delay is greater than parasitoid delay) and in the absence of seasonal forcing terms.

Results confirm what one would expect intuitively, that improvements to the efficacy of parasitoids (nematodes) at any given time are best achieved by reducing their death rate and increasing their activity/contact rate with hosts (slugs). Unfortunately, most measures to aid the survival of nematodes (such as maintaining soil moisture) also benefit slugs. Favourably however, methods of improving contact, such as tillage, may be harmful to slugs.

The non-autonomous slug–nematode model (replicating the field environment) with seasonal forcing terms representing conditions for an “average” year, generally produces periodic solutions. We choose not to fit our model to data and instead derive representative seasonal forcing terms from independent, well-established laboratory data, and some field data, as in Schley and Bees (2003). There is some evidence to suggest that parameters derived from fitting models to field data may differ from the laboratory (Choi et al., 2004; as hinted at previously: South 1982, 1989a) although little independently measured data is yet available. We should keep this in mind for future studies. In practice, climatic variations between years will also play a role, although it is reasonable to expect this to generate solutions with an attractor close to the periodic solutions. Within-season variations prove to be very important, and we show that they strongly influence the effectiveness of potential control strategies. In this paper, we illustrate the lasting effect of nematode applications (under realistic environmental conditions); results indicate the advantage that can quickly accumulate through regular applications.

The model demonstrates a log-dose response, as observed both in bioassays and in the field (Wilson et al., 1994a, 1995a). Results derived from experimental data indicate that there is a significant background level of nematodes present in the field. Due to the log-dose

response this offers a relatively high level of natural control. Therefore, we suggest that the occasional application of nematodes is worthwhile in all farming systems – even those not intending to utilize them as the main control – to ensure that a natural background level of nematodes is present (also important for sterilized compost or where slugs have previously been absent).

Results indicate that the timing of nematode treatments is crucial, and can give different amounts of crop protection due to the seasonality of slug and nematode dynamics. At certain times of the year an application will provide short-term high-level protection, while at other times it results in a less dramatic but more sustained reduction in the slug biomass. Variability in nematode activity, which is temperature dependent, is also highly influential.

Since the reduction in the mean annual slug biomass is fairly constant, regardless of when treatments are applied, the timing of applications should be dependent on the form of crop protection required. This is especially significant in controlled (autonomous) environments where resonance with the natural period of the slug life cycle can induce large amplitude fluctuations, although the mean slug biomass remains relatively unaffected by the frequency of applications (constant net dose). Note, however, that this type of resonance may have less of a role if the system is strongly driven by environmental forcing. If the annual mean of the slug population is the most important factor then it is most economical and efficient to use a single application of nematodes, in both controlled and seasonally varying environments. All these considerations may be applied to other similar host–parasitoid systems.

Future work should consider the importance of spatial distribution upon the dynamics, as well as age or mass structure. For instance, the spatial dependence of the reproductive behaviour of slugs and nematodes suggests the possible formation of patterns and travelling waves. Recently, Choi et al. (in press) have investigated spatial effects on the life cycle of slugs using an individual based model approach incorporating size-dependent motility and time delays, which has proved useful for forecasting. Such an approach may also be useful in describing mass structure and spatial aspects of slug–nematode dynamics.

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Appendix A

$$\tau > 0; \sigma = 0$$

Setting $(S(t), N(t)) = E^* + (s(t), n(t))$ in (4) and linearizing with respect to $s(t)$ and $n(t)$, we look for solutions of the form $(s(t), n(t))^T \propto e^{\lambda t}$, to obtain the characteristic equation

$$\begin{aligned} &\lambda^2 + (\mu + \nu + N^* + (2 - p)S^*)\lambda + \nu\mu + \nu N^* \\ &\quad + S^*(2\nu - 2pS^* + p(1 - \mu)) \\ &= -(-\lambda + pS^* - \nu)e^{-\lambda\tau}. \end{aligned} \tag{6}$$

The stability analysis is carried out in three parts. Firstly, we require stability in the absence of delay ($\tau = 0$; see previous section). Secondly, we confirm that the characteristic equation is retarded (in the sense of Marshall et al., 1992) so that stability is maintained for infinitesimally small positive delays. Finally, we consider whether the delay can induce instability, by looking for roots of the form $\lambda = i\omega$ crossing the imaginary axis. If such roots are possible for some τ , then $\Omega = \omega^2 > 0$ must satisfy $W_\tau(\Omega) = 0$, where

$$\begin{aligned} W_\tau(\Omega) = &\Omega^2 + [\mu^2 + \nu^2 - 1 + (p^2 + 4)S^{*2} \\ &+ 2(2\mu - \nu p)S^* + 2(2 - p)N^*S^* + N^{*2} \\ &+ 2\mu N^*]\Omega + 4p^2S^{*4} + 4p(\mu p - 2\nu)S^{*3} \\ &+ (4\nu^2 - p^2 - 8\mu\nu p + \mu^2\nu^2)S^{*2} \\ &+ 2\nu(2\mu\nu + p - \mu^2 p)S^* + \nu^2 N^{*2} \\ &+ 2\mu\nu^2 N^* + (\mu^2 - 1)\nu^2 - 4\nu p N^* S^{*2} \\ &+ 2\nu(2\nu - \mu p)N^* S^*, \end{aligned} \tag{7}$$

obtained by multiplying Eq. (6) by its complex conjugate.

For E_0 the characteristic Eq. (7) has roots $-\nu$ and $1 - \mu^2$, which are both real and negative under the condition for stability in the absence of delays ($\mu > 1$). Hence, destabilization of E_0 due to the delay, τ , does not occur.

In the absence of delays we require $\mu_* < \mu < 1$ for E_1 to exist and be stable, for which Eq. (7) has roots $-(\nu - p(1 - \mu))^2$ and $-(1 - \mu)(3 - \mu)$, which are both real and negative. Again, destabilization with respect to the delay, τ , does not occur.

For $E_2, (S^*, N^*) = (\nu/p, 1 - \mu - \nu/p)$, we require $\mu < \mu_*$ for existence and stability in the absence of delays. We note that since $W_\tau(\Omega)$ is a quadratic which is bounded below, and that $W_\tau(0) > 0$ (which is clear by substituting for S^* and N^* explicitly), Eq. (7) can have a positive root if and only if it attains a minimum at $\Omega = \Omega_{\min} > 0$ such that $W_\tau(\Omega_{\min}) < 0$. Since

$$\Omega_{\min} = -\frac{\nu}{2p^2}((1 + 2p)\nu + 2p - 2p^2(1 - \mu)),$$

we thus require that

$$\mu < \mu_{\min}^\tau, \quad \text{where } \mu_{\min}^\tau = \frac{2p^2 - 2p(1 + \nu) - \nu}{2p^2} (< \mu_*),$$

and, after some algebra, that

$$\mu > \mu_W, \quad \text{where } \mu_W = \frac{4p^2 - 2p(1 + 2\nu) - \nu}{4p^2}.$$

We note, however, that $\mu_W > \mu_{\min}^\tau$, so that both conditions can never be satisfied simultaneously.

$$\tau = 0; \sigma > 0$$

The characteristic equation is

$$\begin{aligned} &\lambda^2 + (\nu + \mu - 1 + 2S^* + N^*)\lambda + 2\nu S^* + \nu N^* \\ &\quad - \nu(1 - \mu) = -(-pS^*\lambda - 2S^* + \mu - 1)e^{-\lambda\sigma}. \end{aligned} \tag{8}$$

The stability is determined in a similar manner as in Appendix A, whereby the roots $\lambda = i\omega$ must satisfy

$$\begin{aligned}
 W_\sigma(\Omega) &= 0, \text{ where } \sigma \text{ is to be determined, } \Omega = \omega^2 \text{ and} \\
 W_\sigma(\Omega) &= \Omega^2 + ((4 - p^2)S^{*2} + N^{*2} + 4(\mu - 1)S^* \\
 &\quad + 4N^*S^* + 2(\mu - 1)N^* + v^2 + (\mu - 1)^2) \\
 &\quad \times \Omega - 4p^2S^{*4} + 4p^2(1 - \mu)S^{*3} \\
 &\quad + p^2 \left(4\frac{v^2}{p^2} - (1 - \mu)^2 \right) S^{*2} \\
 &\quad + 4v(\mu - 1)S^* + v^2N^{*2} + 2v^2(\mu - 1)N^* \\
 &\quad + 4v^2N^*S^* - v^2(1 - \mu)^2. \tag{9}
 \end{aligned}$$

For $(S^*, N^*) = (v/p, 1 - \mu - v/p)$, we require $\mu < \mu_*$ for E_2 to exist and be stable in the absence of delays. For this equilibrium, Eq. (9) becomes

$$\begin{aligned}
 \Omega^2 + \frac{v^2}{p^2}\Omega + \frac{v^2}{p^2}(-3v^2 + 4(p - 1)v - p^2(1 - \mu)^2) \\
 = 0. \tag{10}
 \end{aligned}$$

By Descartes rule of signs (or alternatively by noting that $\Omega_{\min} = -v^2/2p^2 < 0$), we have one or zero positive real roots Ω , depending on the sign of $W_\sigma(0)$. For the existence of a positive real root we require

$$3v^2 - 4(p - 1)v + p^2(1 - \mu)^2 > 0,$$

which is satisfied if and only if

$$\mu < 1 - \frac{3v}{p} \quad \text{or} \quad \mu > \mu_*.$$

Since the second inequality is inconsistent with the above criteria, we note that there exists a single positive root Ω_σ , and corresponding value of $\lambda = i\omega_\sigma = i\sqrt{\Omega_\sigma}$, if and only if

$$0 < \mu < \mu_0 (< \mu_*), \tag{11}$$

where $\mu_0 = 1 - 3v/p$. Furthermore, Eq. (8), dictates that

$$\begin{aligned}
 \tan(\omega_\sigma\sigma) \\
 = \frac{\omega_\sigma(\omega_\sigma^2 p^2 + v((p + 2)v + (\mu - 1)(p + 1)p))}{\omega_\sigma^2((\mu - v - 1)p + v)p - v^2((\mu - 1)p + 2v)}. \tag{12}
 \end{aligned}$$

Thus, for each μ, v, p satisfying Eq. (11) and corresponding ω_σ , there exist an infinite number of positive

σ satisfying Eq. (12). Only the first is of real biological interest, and represents the value of the delay at which the coexistent steady state solution bifurcates to instability. We denote this value by $\sigma_0 = \sigma_0(\mu, v, p)$. Hence, we have demonstrated that there exists a region of parameter space in which there are no stable equilibria.

$$\tau = \sigma$$

When the delay in both host and parasitoid reproduction is given by a single value σ , the characteristic equation determining the stability of E_2 is given by

$$C(\lambda) = \sum_{k=0}^2 c_k(\lambda) e^{-\lambda k \sigma},$$

where

$$c_0(\lambda) = \lambda^2 + \left(\frac{v}{p} + 1 + v \right) + \frac{v}{p}(v + p),$$

$$c_1(\lambda) = -(1 + v)\lambda - 2\frac{v^2}{p} - v(\mu + 1), \quad c_2(\lambda) = v.$$

We introduce the notation

$$c_0^1(\lambda) = c_0(\lambda)c_0(-\lambda) - c_2(\lambda)c_2(-\lambda),$$

$$c_1^1(\lambda) = c_1(\lambda)c_0(-\lambda) - c_2(\lambda)c_1(-\lambda),$$

and

$$c_0^2(\lambda) = c_0^1(\lambda)c_0^1(-\lambda) - c_1^1(\lambda)c_1^1(-\lambda),$$

and let $W(\Omega) = c_0^2(i\omega)$, where $\Omega = \omega^2$. Hence, each positive root, Ω , of W will determine a possible root, $\lambda = i\omega$, of the characteristic equation for a σ to be determined. It is not immediately clear whether such roots will exist, since W is a positive quartic in Ω and $W(0) > 0$ for $\mu < \mu_*$, although in practice examples may easily be found for sufficiently small μ .

For each such $\omega = \sqrt{\Omega}$, the characteristic equation implies that

$$e^{-i\omega\sigma} = \frac{c_0^1(i\omega)}{c_1^1(i\omega)},$$

so that bifurcation occurs when $\sigma = \sigma_\tau(\mu, \nu, p)$, where σ_τ is the smallest positive σ which satisfies

$$\tan(\sigma\omega) = -\frac{\omega(p^2(\nu + 1)\omega^2 + \nu[\mu p(\nu + p(\nu + 1)) - p^2(\nu + 1) + \nu(\nu + 2)p + 2\nu^2])}{\omega^2 p[-\nu\mu p + (\nu + \nu^2 + 1)p + \nu(1 - \nu)] + \nu^3(p + 2\nu + \mu p)}.$$

As an example consider the case $p = 6$ and $\nu = 1/10$, so that E_2 exists (and is stable in the absence of delays) if and only if $0 < \mu < 59/60$. In the presence of only a nematode reproduction delay (i.e. $\tau = 0$), we have stability for $\mu > \mu_0 = 19/20$, and instability if $\sigma > \sigma_0(\mu)$ otherwise. For example, when $\mu = 19/40$, bifurcation to instability occurs when $\sigma_\tau = 0.345$ (with $\omega = 0.221$).

Appendix B

The full non-autonomous model used in numerical experiments is given by

$$\begin{aligned} \frac{dS(t)}{dt} &= \rho(t - \tau(t))S(t - \tau(t)) - \mu(t)S(t) - \frac{S^2(t)}{K(t)} \\ &\quad - c(t)N(t)S(t), \\ \frac{dN(t)}{dt} &= p(t)c(t - \sigma(t))N(t - \sigma(t))S(t - \sigma(t)) \\ &\quad - \nu(t)N(t) + F(\omega t), \end{aligned}$$

where $\omega = 2\pi/52$ and

$$\begin{aligned} \rho(t) &= r(t) \times e_s = 0.3149(29.32 - 7.99 \sin(\omega t + 7.51) \\ &\quad + 2.88 \sin(2\omega t - 8.50)) \times 10^{-2} \text{ wk}^{-1}, \end{aligned}$$

$$\tau(t) = 43.17 + 3.93 \sin(\omega t - 2.05) \text{ wk},$$

$$\begin{aligned} \mu(t) &= (17.59 + 8.43 \sin(\omega t + 4.21) \\ &\quad + 1.63 \sin(2\omega t + 6.44) - 28.30 \\ &\quad - 1.53 \sin(\omega t + 4.66) \\ &\quad - 1.35 \sin(2\omega t + 1.03)) \times 10^{-3} \text{ wk}^{-1}, \end{aligned}$$

$$K(t) \equiv 3.48 \times 10^4 \text{ mg wk},$$

$$\begin{aligned} \nu(t) &= (5.00 + 2.40 \sin(\omega t + 4.21) \\ &\quad + 0.05 \sin(2\omega t + 6.45)) \times 10^{-1} \text{ wk}^{-1}, \end{aligned}$$

$$p(t) \equiv 45 \text{ nematodes},$$

$$\sigma(t) \equiv 3 \text{ wk}.$$

More details can be found in Schley and Bees (2003). ν is fitted by assuming nematode death follows the same annual cycle as slug death, because it is a dedicated parasite, and then scaled to give the expected mortality rate of nematodes under ideal conditions (Gwynn, 2000).

When the contact rate is allowed to vary we establish from the biological data the following relationships. *P. hermaphrodita* is thought to be active between 5 and 20 °C (Wilson et al., 1994b; Gwynn, 2000), and we assume a symmetric distribution in the absence of other data. Taking $c = 0$ when $T = 0$ and 25 °C and an estimated 1% of peak activity when $T = 5, 20$ °C, we fit

$$c(T) = a \sin^b \left(\frac{\pi}{25} T \right),$$

whereby we find that $b = 8.67$. Applying monthly temperatures $T(t)$ to this generates discrete values of $c(t)$ to which we fit a smooth curve. This is then scaled to give it the expected mean ($c = 6.39 \times 10^{-6}$), which gives

$$\begin{aligned} c(t) &= (6.39 - 2.50 \sin(\omega t + 1.15) \\ &\quad + 3.87 \sin(2\omega t + 3.68)) \\ &\quad \times 10^{-6} \text{ nematodes}^{-1} \text{ wk}^{-1}. \end{aligned} \tag{13}$$

If variable contact rates are not used, we fix $c(t) = 6.39 \times 10^{-6} \text{ nematodes}^{-1} \text{ wk}^{-1}$.

The nematode application function (for one annual treatment) is given by:

$$\begin{aligned} F(\omega t) &= 6 \times 10^4 \sum_{n=0}^{\infty} \mathcal{X}_{[\mathcal{T}+(2\pi/\omega)n, (\mathcal{T}+1)+(2\pi/\omega)n]}(t) \\ &\quad \text{nematodes wk}^{-1}, \end{aligned}$$

where

$$\mathcal{X}_{\mathcal{I}}(t) = \begin{cases} 1, & t \in \mathcal{I}, \\ 0, & t \notin \mathcal{I}, \end{cases}$$

and \mathcal{T} is the first week of application. Unless otherwise indicated, simulation data are based on the last 5 years of a 30 year run, using time steps of 1 h. In all cases nematodes were not applied in the first 10 years to allow a periodic treatment-free solution to fully develop ($\mathcal{T} \geq 520$ wk).

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