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REPORT

Periodic travelling waves in cyclic predator–prey systems

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Abstract

Predation is an established cause of cycling in prey species. Here, the ability of predation to explain periodic travelling waves in prey populations, which have recently been found in a number of spatiotemporal field studies, is examined. The nature of periodic waves in these systems, and the way in which they can be generated by the invasion of predators into a prey population is discussed. A theoretical calculation that predicts, as a function of two parameter ratios, whether such an invasion will lead to a stable periodic travelling wave that would be observed in practice is presented - the alternative outcome is spatiotemporal chaos. The calculation also predicts quantitative details of the periodic waves, such as speed and amplitude. The results give new insights into the types of predator-prey systems in which one would expect to see periodic travelling waves following an invasion by predators.

Keywords

Periodic waves, population cycles, predator–prey, spatial synchrony.

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INTRODUCTION

Predator–prey systems have an intrinsic tendency to cycle. This was one of the first predictions from mathematical modelling in ecology (Lotka 1925; Volterra 1926), and has subsequently been confirmed by a large volume of theoretical modelling (May 1981; Nisbet & Gurney 1982), and by a number of experimental studies (Korpimaki & Norrdahl 1998; Turchin *et al.* 1999; Klemola *et al.* 2000). However, the spatial synchrony of these population cycles is much less well understood, and is currently an active area of study. An important recent contribution to this debate has been the identification of periodic travelling waves in the dynamics of cyclic field voles (*Microtus agrestis*) (Ranta & Kaitala 1997; Lambin *et al.* 1998). This development is made possible by new statistical methods, together with extensive spatiotemporal data sets (reviewed by Bjørnstad *et al.* 1999). The ecological mechanisms underlying these periodic waves remain unclear, but one hypothesis has been that the waves arise from interactions with weasels (*Mustela nivalis*), a small rodent specialist predator (Lambin *et al.* 1998). Mathematical models are a key resource in the understanding of such phenomena. Here, I present a detailed discussion of periodic travelling wave behaviour in a simple mathematical model for predator–prey interactions. The work is not specifically oriented towards the vole–weasel interaction; rather, it is deliberately general, aiming to highlight the behaviour that arises simply as a consequence of basic predator–prey dynamics. I will show that mathematical analysis of travelling waves enables specific ecological predictions to be made.

The term "periodic travelling wave" means that equally spaced peaks in population density are moving through space. Thus, if one were monitoring the population at a particular location, one would see a cycle in population levels, as peaks and troughs alternately occurred. A key point is that the occurrence of moving peaks and troughs does not imply a large-scale movement of individuals in the population. A useful aid in understanding this is the "Mexican wave", familiar in sports stadiums. There, one sees a moving wave, but nothing is physically moving in space. Periodic travelling waves in ecology are a little different because there is typically local movement of individuals, but despite this, when averaged over time, there is no net movement of the population in space. Thus, periodic travelling waves imply large-scale spatial synchrony of population cycles, but without large-scale spatial movement.

To enable a more detailed discussion of periodic travelling waves, I will use a mathematical model of predator–prey interaction. The majority of theoretical work on spatial synchrony has used models of "coupled map lattice" type (Hassell *et al.* 1991; Bascompte & Solé 1998; Savill & Hogeweg 1999) in which population dynamics are followed on a series of separate but coupled patches. This type of model is an efficient simulation tool, but underlying mathematical theory is rather limited. For example, I am not aware of any mathematical results on periodic waves in coupled map lattice models. For this reason, I will illustrate my discussion using a model of "reaction-diffusion" type, which has much stronger mathematical underpinning. Reaction–diffusion models have a long history in theoretical ecology (Skellam 1951; Holmes *et al.* 1994), and assume continuous time population dynamics together with unbiased local dispersal. The specific model I consider is

$$\boxed{\text{predators}} \quad dp/dt = \delta \overbrace{\frac{\partial^2 p}{\partial x^2}}^{\textit{dispersal}} + \overbrace{apf(kh)}^{\textit{benefit from predation}} - \overbrace{bp}^{\textit{death}} \qquad (1a)$$

$$\boxed{\text{prey}} \quad dh/dt = \delta \underbrace{\frac{\partial^2 h}{\partial x^2}}_{\textit{dispersal}} + \underbrace{rh(1 - h/h_0)}_{\textit{intrinsic birth death}} - \underbrace{cpf(kh)}_{\textit{death}}. \qquad (1b)$$

The symbols p and h denote predator and prey densities, which depend on space x and time t; a, b, c, r, h_0, k and δ are positive parameters. The function $f(.)$ represents the prey consumption rate per predator, as a fraction of the maximal consumption rate, c. This will he an increasing saturating function of the prey density: the constant k reflects how quickly the consumption rate saturates as prey density increases. Parameters a and r denote maximal per capita predator and prey birth rates; for predators, that is the birth rate when the prey density is very high, while for prey it is the birth rate at very low prey density. The per capita predator death rate is denoted by b, and h_0 is the prey carrying capacity. To facilitate calculations later in the paper, I assume that the two populations have the same dispersal coefficient, δ – all of my results apply more generally provided the predator and prey dispersal rates are fairly similar.

The model (1) has been very well studied for a number of different forms for $f(.)$ (e.g. May 1981; Nisbet &; Gurney 1982). A key property of the model is that for appropriate parameters, when there is no variation in space, the population dynamics are cyclic, with oscillations in predator and prey densities. When spatial variation is allowed, periodic travelling waves are then possible, and standard mathematical results can be applied. Most importantly, these show that there is a family of possible periodic travelling waves (Kopell & Howard 1973). This family contains a periodic wave solution for each value of the wave speed above a critical minimum value; as the wave speed becomes large, so does the spatial wavelength, and the amplitude approaches that of the spatially homogeneous population cycle.

WAVES GENERATED BY INVASION

The occurrence of a family of periodic travelling waves has an important consequence: even if one knew all of the parameter values in a particular case, one still could not predict the details of a periodic travelling wave occurring in practice. This is because different mechanisms of periodic wave generation may cause different members of the periodic wave family to develop. Therefore, one cannot study the generation of periodic travelling waves as a general topic; rather, it is necessary to focus on the periodic waves generated by a particular type of ecological event, corresponding mathematically to particular initial conditions. For predator–prey interactions, I am aware of only one type of ecological event that has been shown to generate periodic waves: the invasion of a predator population into prey.

Ecological invasions have been an important research topic in recent years [see the books by Shigesada & Kawasaki (1997) and Williamson (1996) for review], but in almost all cases, both experiments and field data have focussed on the taxonomy of the invader, rather than its interaction with existing species. Theoretical work by myself and others on cyclic predator–prey systems predicts that, while the rate of invasion is determined by predator characteristics only, the cyclic nature of the interaction with prey leads to either periodic travelling waves or spatiotemporal chaos behind invasion (Sherratt *et al.* 1995, 1997; Petrovskii & Malchow 1999; Ashwin *et al.* 2000; see also Pascual 1993). An example of periodic wave formation is given in Figure 1(a), which simulates behaviour when a small group of predators are introduced into a prey population. The predator population grows and invades surrounding prey, with this invasion generating periodic travelling waves moving in the opposite direction to the invasion, at a faster speed. In order to make a detailed assessment about whether this mechanism could be responsible for the periodic waves seen in recent field data (Lambin *et al.* 1998; Ranta & Kaitala 1997), it is necessary to predict quantitatively how the speed and amplitude of the periodic waves behind invasion depend on parameter values; this is the subject of the next section of the paper.

For some parameters, invasion generates spatiotemporal chaos – highly disordered oscillations, rather than the simple, periodic oscillations in a periodic travelling wave; an example of this is illustrated in Figure 1(b). I have shown previously that, from a mathematical viewpoint, these chaotic oscillations occur when the mechanism of periodic wave generation selects a wave that is unstable. From the ecological viewpoint, this implies that the calculation of periodic wave speed and amplitude (from which the stability of the wave can be deduced) is

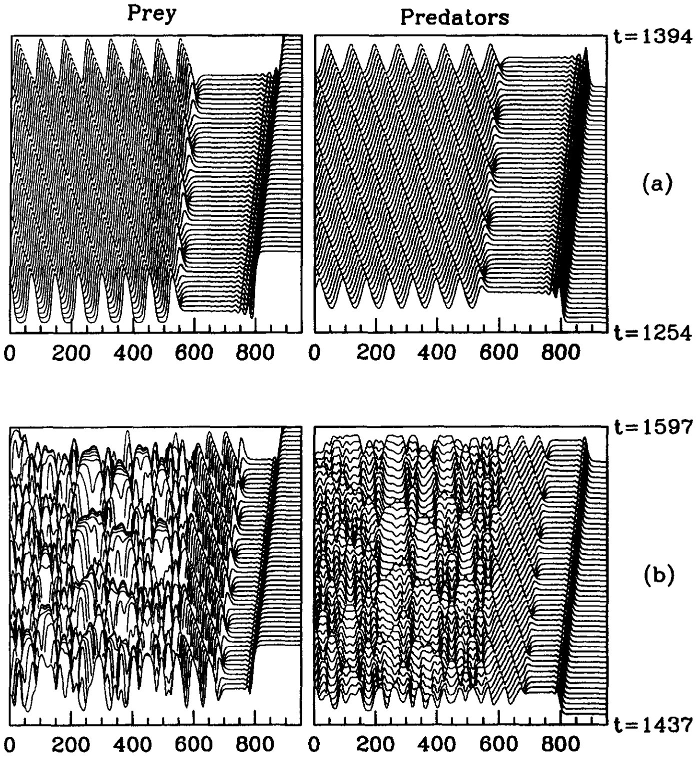


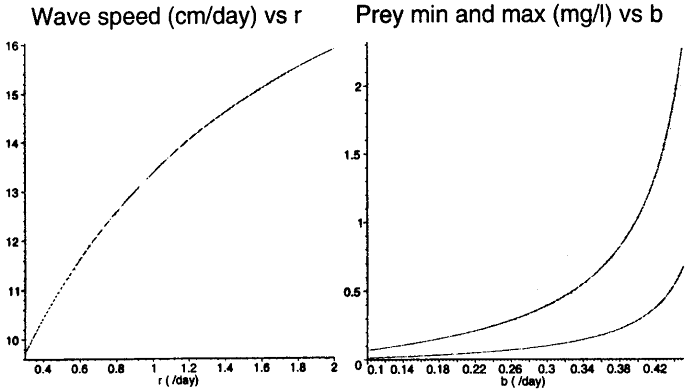
Figure 1 An illustration of the behaviour generated by the invasion of predators into prey in cyclic populations. The changes in prey and predator densities with space and time are illustrated for two sets of parameter values: there is a receding wave front of prey, and a corresponding advancing wave front of predators, behind which there is a periodic travelling wave in (a), and spatiotemporal chaos in (b). Note that in (b), a small band of periodic waves is visible just behind the invasion front: this is the unstable member of the periodic wave family that is selected by the invasion, and which destabilises to give chaos. Model simulations predict that one of these two types of behaviour is seen whenever invasion occurs in a cyclic predator–prey system. The plots show numerical solutions of the dimensionless model equations (A.3), with $f(\xi) = \xi/(1+\xi)$, and (a) $A = 3$, $B = 4$, $C = 3$; (b) $A = 1.2$, $B = 1.2$, $C = 13$. The equations were solved using the method of lines and Gears method, with initial conditions corresponding to a prey-only state everywhere, except at $x = 0$, where there is a small non-zero predator density.

important for understanding qualitative as well as quantitative behaviour.

PREDICTING THE PERIODIC TRAVELLING WAVE

A cyclic predator–prey system represented by the model (1) has a family of possible periodic travelling waves, with different members of the family having different speeds and amplitudes. The invasion of predators into a prey population leads to the formation of one particular travelling wave from this family – the same wave is generated even if environmental heterogeneity is included (Kay & Sherratt 2000). In order to make predictions in any detail for particular predator–prey systems, it is essential to know which of the waves is generated, as a function of parameter values. I have previously given a mathematical solution of this wave selection problem (Sherratt 1998). Application of this to the predator–prey model (1) involves some long calculations, which are described in the Appendix. The calculations can be done most easily using computer algebra, and a worksheet for use with the package maple is available at the Web address http://www.ma.hw.ac.uk/~jas/predprey_worksheet.html. This worksheet performs all the calculations described in the Appendix and automatically draws the graphs illustrated below.

The key results of this calculation are formulae for the amplitude and speed of the periodic travelling waves generated by invasion, as a function of parameters. Examples of this are illustrated in Figure 2, for case of the interaction between the zooplankton *Daphnia pulex* and the phytoplankton *Chlamydomonas reinhardii*; Nisbet *et al.* (1991) performed a detailed parameter estimation of the model (1) for this case. I should stress that there is, to the best of my knowledge, no data showing periodic waves in plankton systems: I choose this system simply because it is a rare example of a cyclic predator–prey system that has been parameterised in detail. In Figure 2(a), the variation in wave speed with *r*, the phytoplankton birth rate is plotted; Figure 2(b) shows the amplitude of the prey periodic wave as a function of the predator death rate *b*. Previous studies of periodic wave behaviour in ecological systems have mostly been qualitative, with occasional quantitative simulations for single parameter sets. My calculation enables detailed quantitative predictions to be made, for the first time. One particularly important consequence of this is that one can predict whether invasion will result in stable periodic waves, or spatiotemporal chaos (which develops from an unstable wave). This involves calculating the wave amplitude, and then using standard results on stability–amplitude relationships



(a) (b)

Figure 2 Predicted variations in (a) wave speed and (b) prey amplitude, for the periodic travelling waves generated by invasion of the predator *Daphnia pulex* into the prey population *Chlamydomonas reinhardii*. Some of these waves are stable and would be observed in practice, others are unstable, so that the observed behaviour would be spatiotemporal chaos. The calculation is as described in the Appendix. Parameter values are as estimated by Nisbet *et al.* (1991) except for those being varied: $a = 0.5$ day^{-1} $b = 0.14$ day^{-1} $c = 1.0$ day^{-1} $k = 6.1$ l mg^{-1} $r = 1.0$ day^{-1}. The values of h_0 and δ are not given by Nisbet *et al.* (1991). I take $\delta = 10^{-4}$cm^{2}s^{-1}, based on estimates for other plankton species (Kessler 1985; Bees & Hill 1998). The parameter h_0 must be above a critical minimum value for the population to be cyclic [see the Appendix and Nisbet *et al.* (1991)], and I take h_0 to be 10% above this minimum value (arbitrarily: Nisbet *et al.* (1991) regard h_0 as a free parameter). Increasing/decreasing h_0 causes the wave speed to decrease/increase, while the prey amplitude increases/decreases. Following Nisbet *et al.* (1991), the assumed form for the functional response is $f(\xi) = \xi/(1 = \xi)$.

(Kopell & Howard 1973); details are in the Appendix. This shows that one can predict whether periodic waves or chaos will be generated by the invasion of predators into prey, from two parameter ratios: r/a and a/b. These are the ratio of prey and predator birth rates, and the ratio of predator birth and death rates, respectively. Here the birth rates required are the maximum possible levels, that would be achieved when resources are abudent (this is the definition of parameters r and a); these will of course be much higher than the actual birth rates in the field.

Figure 3 shows the predicted behaviour as a function of these two ratios, for a particular functional response $f(.)$: different functional responses give slightly different parameter regions, but with the same general form. For the *Daphnia pulex* – *Chlamydonomas reinhardii* interaction, Nisbet *et al.* (1991) estimated $r/a = 2.0$ and $a/b = 3.6$, implying that invasion will generate spatiotemporal chaos. These ratios can also be calculated for the interaction between field voles (*Microtus agrestis*) and weasels (*Mustela nivalis*), even though there is insufficient data to parameterise the whole model in this case. Recall that maximum possible birth rates are required. When prey are abundent, female weasels can have two litters in each breeding season, with an average of six young per litter (King 1989). Moreover, the early-born females (three on average) can breed themselves within the same season. Thus each female can have up to 30 offspring, giving a maximum per capita productivity of 15 per year (King 1989). The birth rate a is then given by $e^a = 15 \Rightarrow a = 2.7$ year^{-1}. For field voles, 6 litters could be expected in optimal conditions, with an average litter size of 5 (Dyczkowski & Yalden 1998); again, early-born females can breed themselves, giving a maximum possible per capita annual productivity of 27.5 $(=\frac{1}{2}\ (6 \times 5 + 2.5 \times 2 \times 5))$. Thus $e^r = 27.5 \Rightarrow r = 3.3$ year^{-1}, and $r/a = 1.2$. Annual mortality for weasels is 77.5% (King 1989), so that $e^{-b} = 0.225$, giving $b = 1.5$ year^{-1} and $a/b = 1.8$. Again, these ratios correspond to a point outside the parameter region giving stable periodic waves (see Figure 3), suggesting that the invasion of a field vole population by weasels would generate spatiotemporal chaos, not periodic travelling waves. As a third example, I consider the interaction of snowshoe hare (*Lepus americanus*) and lynx (*Lynx canadensis*) in the North American boreal forest. This was an early example of cyclic populations, from the famous Hudson Bay Company data (see Murray 1989). Recent experiments suggest that the cycles involve a third trophic level (Krebs *et al.* 1995) and that additional predators are important (Stenseth *et al.* 1997); nevertheless, this is a useful case to consider in view of the large attention given to it in the literature. Moreover, the population cycles do exhibit large scale spatial synchrony (Smith 1983), though whether or not this involves periodic waves remains unclear. Parameters for this case have been estimated previously (Tanner 1975; Mowat *et al.* 1996): maximal per capita productivities for hare and lynx are about 4.5 and 2 per year, with 75% annual survival for lynx, giving $a/b = 2.4$ and $r/a = 2.2$. These imply stable periodic travelling waves following invasion of a hare population by lynx.

DISCUSSION

The temporal oscillations implicit in a cyclic predator–prey system mean that periodic travelling waves are a possible form of spatial synchronisation; this mathematical result has been known for nearly 30 years (Kopell & Howard 1973). More recently, it has been shown that this type of synchronisation is actually one of two possible behaviours when the predators invade a prey population, with the other being spatiotemporal chaos (Sherratt *et al.* 1997). Here, I have shown how one can calculate which of these two behaviours will occur, as a function of parameter values. For a given functional response $f(.)$, the distinction depends on only two parameter ratios, which can be estimated for many specific predator–prey systems. A case of particular interest is the weasel–field vole interaction, which has been suggested as a possible explanation for the periodic waves seen in cyclic field vole populations in the Kielder forest (Lambin *et al.* 1998). My results suggest that invasion of a field vole population by weasels will generate spatiotemporal chaos, not periodic waves. This is due predominantly to the high maximal productivity of the weasel *Mustela nivalis*: a key implication of Figure 3 is that stable periodic waves following invasion require the predators to be much less productive than their prey. Since periodic waves do occur in field vole populations, two possible explanations remain. Firstly, the interaction with weasels may have generated the observed periodic waves, but via a process other than predator invasion – although no such process has been suggested to the best of my knowledge. Secondly, the periodic waves may have been generated by a mechanism other than the interaction with weasels, for example by parasites, which are established as the cause of population cycles in red grouse (*Lagopus lagopus scoticus*) (Hudson *et al.* 1998).

As with any theoretical predation, there are a number of potentially important ecological features that have been excluded from the modelling. Weasels are estimated to comprise only about a third of total predation on voles (Dyczkowski & Yalden 1998), with the remainder due mainly to foxes and raptors; the model assumes that these other predators are present at constant density, and changes in their densities may be significant (for discussions of other vole predators, see O'Mahony *et al.* 1999; Lambin *et al.* 2000; Petty *et al.* 2000). In addition, seasonality of breeding and the specific form of functional response are factors that would be required in a more detailed, specific model.

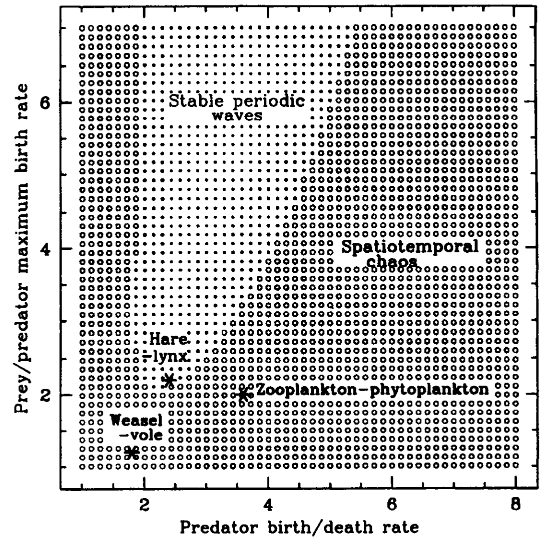


Figure 3 The predicted parameter regions in which invasion of prey by predators generates either periodic travelling waves or spatiotemporal chaos. The distinction between the two behaviours depends on two dimensionless parameter ratios: the maximum possible birth rate for prey divided by that for predators, and the maximal predator birth rate divided by the predator death rate. Estimated ratios for three specific predator–prey systems are plotted: the *Daphnia pulex–Chlamydomonas reinhardii* interaction; the interaction between weasels (*Mustela nivalis*) and field voles (*Microtus agrestis*); and the snowshoe hare (*Lepus americanus*)–lynx (*Lynx canadensis*) system. The calculation of the parameter regions is as described in the Appendix, and depends on the assumed form for the functional response $f(.)$; the case shown is for $f(\xi) = \xi/(1 = \xi)$. Changing the functional response alters the precise location of the boundary between the two behaviours, but the overall form remains the same.

In the context of other predator–prey systems, the calculation that I have performed gives important information about the types of predator–prey system in which invasion would be expected to generate periodic waves. Moreover, the quantitative predictions on wave speed and amplitude provide specific tests for predator–prey invasion as a cause of periodic travelling waves.

APPENDIX

In this Appendix, I summarise the mathematical calculation that determines the periodic travelling wave solution generated by the invasion of predators into a prey population. It is this calculation that leads to predictions such as Figure 2, which shows the speed and amplitude of periodic waves as a function of parameters, and Figure 3, which illustrates the parameter region in which stable periodic oscillations, rather than spatiotemporal chaos, are generated behind invasion.

The equations (1) have a spatially homogeneous oscillatory solution (mathematically, a limit cycle in the reaction kinetics) provided the parameter k is sufficiently large. As k is increased from a small value, the oscillations appear at a critical value of k, known as a Hopf bifurcation point. The standard mathematical theory of "normal forms" implies that when k is close to this critical value, the model equation (1) can be reduced to equations of "λ–ω" type by a series of changes of variable. These λ–ω equations have the form

$$\frac{\partial u}{\partial t} = \frac{\partial^2 u}{\partial x^2} + \lambda_0 u - \omega_0 v - (\lambda_1 u + \omega_1 u)(u^2 + v^2) \qquad \text{(A.1a)}$$

$$\frac{\partial v}{\partial t} = \frac{\partial^2 v}{\partial x^2} + \omega_0 u + \lambda_0 v + (\omega_1 u - \lambda_1 v)(u^2 + v^2)\cdot \qquad \text{(A.1b)}$$

Previously, I have calculated the behaviour behind invasion in general oscillatory systems, as a function of λ_0, λ_1, ω_0 and ω_1. In order to apply these results to the predator–prey model (1), it is necessary to calculate λ_0, λ_1, ω_0 and ω_1 in terms of the parameters in (1). This is known as a "reduction to normal form". The theory underlying this calculation is described in most books on normal form theory, but the practical implementation in not explained in detail, and thus I will summarise it here; note that there is an alternative method for deriving normal forms, using perturbation theory (Yu 1998), which can be used as an independent check on the results. Some of the steps in my calculation involve complex algebra that is most efficiently done using a computer algebra package such as maple; an example of a maple worksheet that performs the entire calculation automatically is available at http://www.ma.hw.ac.uk/~jas/predprey_worksheet.html. The worksheet also generates automatically a plot of the parameter domain for periodic travelling waves, of the type shown in Figure 3.

Step 1: Nondimensionalisation

The first step is to simplify (1) by the standard process of nondimensionalisation. Substituting the rescalings

$$H = h/h_0 \quad P = p\cdot c/(rh_0) \quad T = rt \; A = a/b$$
$$B = r/a \; C = kh_0 \; X = x\sqrt{r/\delta} \qquad \text{(A.2)}$$

gives

$$\partial P/\partial T = \partial^2 P/\partial X^2 + P\,[A\,f(CH) - 1]/(A\cdot B) \quad \text{(A.3a)}$$
$$\partial H/\partial T = \partial^2 H/\partial X^2 + H\,(1 - H) - P\,f(CH). \quad \text{(A.3b)}$$

Step 2: Steady states and linear stability analysis

I assume that $f(.)$ is an increasing function, with $f(0)=0$ and $f(+\infty)=1$: this will be true for any realistic function form. (Recall that $f(.)$ represents the consumption rate of prey per predator, as a function of prey density.) Then (A.3) has zero and prey-only steady states, and in addition exactly one coexistence steady state (P_s,H_s), where

$$P_s = AH_s(1 - H_s) \qquad \text{and} \qquad H_s = f^{-1}(1/A)/C\cdot$$

Note that $A > 1$ is required for this steady state to exist – otherwise the death rate of the predators is too great for a predator population to be maintained. Standard linear stability analysis (see for example May 1981) shows that the population represented by (A.3) becomes cyclic when the parameter C is above the critical value C_0, given by the formula

$$C_0 = f^{-1}(1/A)[1 + \tfrac{1}{1-\Gamma}]\cdot$$

where $\Gamma = Af^{-1}(1/A)\,f\,(f^{-1}(1/A))$. The linear stability analysis itself implies that λ_0 is given by

$$\lambda_0 = (C - C_0)\frac{\partial}{\partial C}(Re(\varepsilon))\,|_{\,C=C_0} = \frac{(C-C_0)(1-\Gamma)^2}{f^{-1}(1/A)(2-\Gamma)}$$

where ε is the complex conjugate pair of eigenvalues at (P_s,H_s). Similarly ω_0 is given by $Im(\varepsilon)$ at $C=C_0$, which gives

$$\omega_0 = [\tfrac{\Gamma}{AB(2-\Gamma)}]^{1/2}.$$

Step 3: Converting linear part to normal form

Calculation of λ_1 and ω_1 is more involved. Standard theory implies that one can set $C \equiv C_0$, since corrections due to changes in C only enter higher order terms in the normal form (Guckenheimer & Holmes 1983). Fixing C at this value, the next step is to do a linear change of variables so that the linear part of the equations is in normal form. For (A.3), this is achieved by setting

$$\hat{p} = (P_s - P)/\sqrt{A(1 - 2H_s)/B} \qquad \text{and} \qquad \hat{h} = H - H_s$$

which gives the equations

$$\partial\hat{p}/\partial T = \partial^2\hat{p}\,/\partial X^2 - \omega_0\hat{h} + \mathcal{F}\,(\hat{p},\hat{h}) \qquad \text{(A.4a)}$$

$$\partial\hat{h}/\partial T = \partial^2\hat{h}\,/\partial X^2 + \omega_0\hat{p} + \mathcal{G}\,(\hat{p},\hat{h})\cdot \qquad \text{(A.4b)}$$

Here the functions $\mathcal{F}$ and $\mathcal{G}$ have complicated algebraic forms, but are easily calculated by a computer algebra package; a simple check on the calculation is possible because both functions should be zero with zero first derivatives at $\hat{p}=\hat{h}=0$.

Step 4: Calculating λ_1 and ω_1

Once the equations are in the form (A.4), standard formulae can be used to find λ_1 and ω_1. Methods for deriving these formula are described in textbooks and some papers (Guckenheimer & Holmes 1983; Knobloch 1986), but I am not aware of a reference in which both formulae are given explicitly, and thus I repeat them here:

$$\lambda_1 = \tfrac{-1}{16}[\mathcal{F}_{\hat{p}\hat{p}\hat{p}} + \mathcal{F}_{\hat{p}\hat{h}\hat{h}} + \mathcal{G}_{\hat{p}\hat{p}\hat{h}} + \mathcal{G}_{\hat{h}\hat{h}\hat{h}}]+$$

$$\tfrac{1}{16\omega_0}[\mathcal{F}_{\hat{p}\hat{p}}\,\mathcal{G}_{\hat{p}\hat{p}}-\mathcal{F}_{\hat{h}\hat{h}}\,\mathcal{G}_{\hat{h}\hat{h}}-\mathcal{F}_{\hat{p}\hat{h}}\,(\mathcal{F}_{\hat{p}\hat{p}}+\mathcal{F}_{\hat{h}\hat{h}})+\mathcal{G}_{\hat{p}\hat{h}}\,(\mathcal{G}_{\hat{h}\hat{h}}+\mathcal{G}_{\hat{p}\hat{p}})]$$

$$\omega_1 = \tfrac{1}{16}[\mathcal{G}_{\hat{p}\hat{p}\hat{p}} + \mathcal{G}_{\hat{p}\hat{h}\hat{h}} - \mathcal{F}_{\hat{p}\hat{p}\hat{h}} - \mathcal{F}_{\hat{h}\hat{h}\hat{h}}]+$$

$$\tfrac{1}{48\omega_0}[\mathcal{F}_{\hat{p}\hat{p}}\,(\mathcal{G}_{\hat{p}\hat{h}} - \mathcal{F}_{\hat{h}\hat{h}}) + \mathcal{G}_{\hat{h}\hat{h}}(\mathcal{F}_{\hat{p}\hat{h}} - \mathcal{G}_{\hat{p}\hat{p}}) -$$

$$3\,\mathcal{F}_{\hat{h}\hat{h}}\,(\mathcal{G}_{\hat{p}\hat{h}} + \mathcal{F}_{\hat{h}\hat{h}}) - 3\mathcal{G}_{\hat{p}\hat{p}}\,(\mathcal{F}_{\hat{p}\hat{h}} + \mathcal{G}_{\hat{p}\hat{p}})$$

$$-2\,(\mathcal{F}_{\hat{p}\hat{p}} + \mathcal{F}_{\hat{h}\hat{h}} - \mathcal{G}_{\hat{p}\hat{h}})^2 - 2(\mathcal{G}_{\hat{p}\hat{p}} + \mathcal{G}_{\hat{h}\hat{h}} - \mathcal{F}_{\hat{p}\hat{h}})^2]$$

Here the subscripts $\hat{p}$ and $\hat{h}$ denote partial derivatives: thus for example $\mathcal{F}_{\hat{p}\hat{h}\hat{h}} \equiv \partial^3\mathcal{F}/\partial\hat{p}\partial\hat{h}^2$. These formulae are extremely laborious to use by hand, but a computer algebra package makes them easy to evaluate. Typically the results require considerable algebraic simplification, but this can be done automatically by computer algebra.

Using the results

The final result of these four stages are expressions for λ_0 λ_1 ω_0 and ω_1. Of these, λ_0 depends on A, B and C, but the other three are functions of A and B only. These expressions can easily be rewritten in terms of original model parameters using (A.2), and can then be used to determine properties of the periodic waves generated by invasion. In particular, the amplitude of the periodic waves is given by

$$R = \left[\tfrac{2\lambda_0}{\omega_1^2}\left(\sqrt{\lambda_1^2+\omega_1^2}-\lambda_1\right)\right]^{1/2} \qquad \text{(A.5)}$$

(Sherratt 1998), with the speed given by $(\omega_0+\omega_1 R^2)/(\lambda_0-\lambda_1 R^2)^{1/2}$. A key issue is whether the waves of this amplitude are stable: if not, the observed behaviour will be spatiotemporal chaos. A mathematical condition on R for stability was determined by Kopell & Howard (1973), and substituting (A.5) into their condition implies that the periodic waves generated by invasion will be stable if $\omega_1^2/\lambda_1^2 < 1.148$. Figure 3 is generated by substituting the expressions for ω_1 and λ_1 into this condition: the parameter ratios on the axes of Figure 3 are simply the dimensionless parameters A and B.

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