

The population dynamic consequences of phenological asynchrony between parasitoids and their hosts

H.C.J. GODFRAY*, M.P. HASSELL* and R.D. HOLT*†

*Department of Biology and NERC Centre for Population Biology, Imperial College at Silwood Park, Ascot, Berkshire SL5 7PY, UK; and †Museum of Natural History, Department of Systematics and Ecology, University of Kansas, Lawrence, Kansas 66045, USA

Summary

1. Populations of hosts and parasitoids with discrete generations frequently show imperfect phenological synchronization resulting in some hosts experiencing reduced or even no risk of parasitism.
2. The population dynamic consequences of phenological asynchrony are explored by modelling within-generation dynamics by a set of delay-differential equations.
3. Phenological asynchrony can stabilize an otherwise unstable interaction. The influence of the interaction between phenological asynchrony and other stabilizing forces on the stability and equilibrium population densities of hosts and parasitoids is studied.
3. Preliminary results indicate that annual fluctuations in the synchrony between host and parasitoid populations can have a major effect on the persistence of the interaction.

Key-words: parasitoid, phenology, population dynamics, life histories.

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Introduction

The population dynamics of insect host–parasitoid interactions with discrete generations have received considerable attention (Hassell 1978). In recent years, a particular focus on study has been the potential for various forms of heterogeneity to promote the persistence of the interacting populations. This stabilizing heterogeneity can be conveniently expressed in terms of the degree of variation in the risk of parasitism between individual hosts within the population, and it can arise in many ways; for instance, by spatial variation in levels of parasitism (e.g. Chesson & Murdoch 1986; Hassell *et al.* 1991; Pacala & Hassell 1991) or by differences in the ability of hosts to resist parasitoid attack (Hassell & Anderson 1984; Godfray & Hassell 1990). In particular, most interest has focused on heterogeneity arising from the distribution of hosts and parasitoids in patchy environments, and there are now many examples where percentage parasitism has been recorded in relation to host density per patch (see Lessells 1985; Stiling 1987; Walde & Murdoch 1988 for recent reviews). These patterns have been classified as either density dependent, inversely density dependent or density independent, any of which can promote population persistence if they result in sufficient variation in the risk of parasitism between host individuals (Hassell 1984;

Chesson & Murdoch 1986; Pacala, Hassell & May 1990; Hassell *et al.* 1991).

Considering the enormous interest in spatial heterogeneity, it is surprising that little attention has been paid to heterogeneity arising from temporal asynchronies between the timing of the susceptible stage(s) of the host on the one hand and the foraging adult parasitoids on the other. The first suggestion that phenological mismatches may stabilize host–parasitoid interactions appears to have been made by Varley & Gradwell (1958). A decade later, Hassell (1969), working on the interaction between the winter moth (*Operophtera brumata*) and the tachinid fly parasitoid, *Cyzenis albicans*, and Griffiths (1969) who studied the parasitoids of European pine sawfly (*Neodiprion sertifer*), both noted temporal asynchrony in the field and suggested modifications of simple host–parasitoid models that might describe this phenomenon (see Appendix). In an important study, prompted by the observation of asynchrony between the spruce tortricid *Epinotia tedella* and its parasitoid *Pimpla dubuis*, Münster-Swendsen & Nachman (1978) constructed a simulation model of a host–parasitoid interaction and demonstrated that a realistic form of temporal asynchrony alone could stabilize an otherwise unstable interaction.

Our goal here is to extend this work by developing a relatively simple model of a seasonal host–parasitoid interaction. We construct our model as

a system of difference and differential equations, rather than use a simulation framework, in order to use a minimum number of parameters, and so that we can obtain some of the best understood models of host-parasitoid interactions as limiting case. The ability to obtain limiting cases markedly simplifies the interpretation of more complicated models which have to be solved by numerical techniques. We study the interaction of temporal asynchrony with other stabilizing features of host-parasitoid interactions that result in a reduction of parasitoid efficiency with increasing parasitoid density. We also begin to study the influence of temporal asynchrony that fluctuates from year to year.

Phenological asynchrony is likely to be a frequent feature of natural host-parasitoid interactions. Some species of parasitoids may not be able to search for hosts at times of the year when hosts are present, perhaps because the climate is too wet, too dry, too hot or too cold. Asynchrony may also occur if parasitoids introduced into new areas for biological control are imperfectly adapted to their new environment. The Argentine stem weevil (*Listronotus bonariensis*), for example, appears to have been introduced into New Zealand from a single site in South America. Populations of weevils throughout the latitudinal range of New Zealand have the same diapause strategies, which results in needlessly early diapause in the North Island (Goldson & Emberson 1980). A parasitoid of the weevil, the parthenogenetic braconid *Microctonus hyperodae*, has been collected from a number of sites in South America and different strains show different diapause strategies (Goldson & McNeil 1992). Questions of phenological matching are important in predicting which strain will most effectively control the pest. More speculatively, global climate change may disrupt the temporal match of hosts and parasitoids if temperature change differentially affects the development of hosts and parasitoids (Hassell, Godfray & Comins 1992).

Methods

Let us imagine a host that is attacked by a specific parasitoid species. At the beginning of the season, all hosts are in a non-susceptible stage and all parasitoids are in a non-searching stage. For narrative simplicity we shall assume that at this time hosts are eggs and only become susceptible to parasitism when they hatch, and parasitoids are pupae and begin to search for hosts as soon as they emerge. Hosts are susceptible to attack until they pupate and parasitoids search until they die. The model, however, is fully general, and the susceptible host stage and the parasitoid searching stage may occupy any portion of the respective life cycles of the two species.

Our modelling strategy is to produce the simplest possible description of the host-parasitoid system

that includes the key features to be investigated. Thus, we deliberately leave out much important biology to get as clear as possible a picture of the effects of phenology. We now describe the model and present a 'canonical parameter set': a set of biologically defensible parameter values that provide the starting point for the analysis. Time is measured in days and we arbitrarily define day 0 as the beginning of the season.

The model consists of two parts: a within-generation component that describes the dynamics of emergence, maturation and parasitism, and a between-generation component that relates the numbers of surviving and parasitized hosts at the end of one season to the numbers at the beginning of the next. The between-generation component is particularly simple. Each parasitized host is assumed to give rise to one parasitoid in the following season, and it is assumed that each surviving host reproduces to give rise to two hosts in the following generation. Thus, the net host rate of increase (λ) is two so that, at an equilibrium, and in the absence of any other mortality factors, parasitoids must destroy 50% of all hosts.

The within-generation component is more complex. A verbal description is given in this section while the formal equations are relegated to the appendix. Hosts begin to hatch and parasitoids to emerge at times τ_H and τ_p , respectively; the rate of entry into the next stages is at first slow, but then accelerates (Fig. 1a). Two parameters, δ_H and δ_p , describe the temporal distribution of host and parasitoid life cycles, respectively: high values signify that most hosts hatch together or that most parasitoids emerge together. Hosts are susceptible to parasitism for a period W , after which they pupate and can no longer be attacked. Parasitoids may die at a rate $\mu(t)$, although here we assume for the most part complete survival during the season, $\mu(t) = 0$. For the canonical parameter set we assume that parasitoids begin to emerge on day 5, but that hosts do not begin to hatch until day 25. Hatching and emergence is completed in about 20 days (as in Fig. 2a where $\delta_H = \delta_p = 0.001$). The window of host susceptibility (W) is 10 days.

In order to describe parasitism we first define $H(t, \tau)$ and $P(t, \tau)$ as the numbers of susceptible hosts and searching parasitoids alive at time t in generation τ (for simplicity, we henceforth shall drop the second parameter, τ). The rate of loss of hosts due to parasitism is $H(t)f[P(t), H(t)]$ where $f[P(t), H(t)]$, describes the instantaneous risk of parasitism. The simplest form of $f[P(t), H(t)]$ assumes a linear function of the number of parasitoids [$f[\bullet] = aP(t)$] where a is a constant normally called the attack rate (Fig. 1b; line a), as in the neutrally stable Lotka-Volterra model or the oscillatorily unstable Nicholson-Bailey model (Lotka 1925; Volterra 1926; Nicholson & Bailey 1935). The local instability in

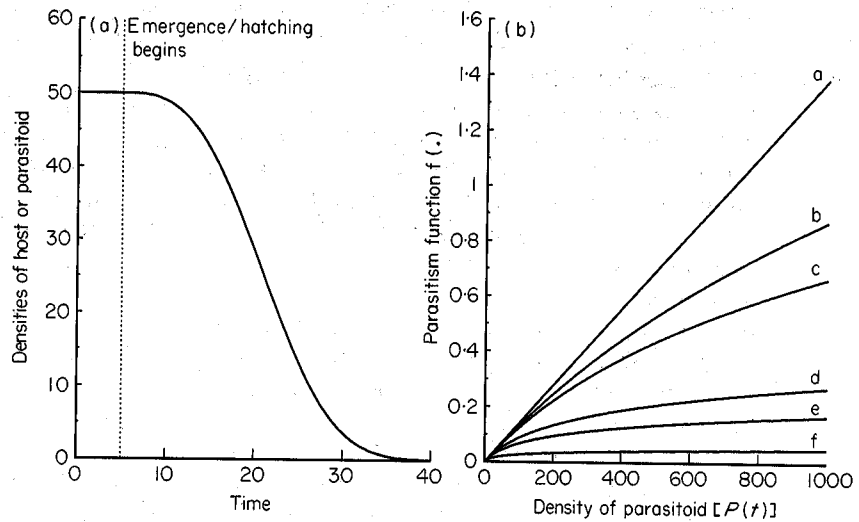


Fig. 1. (a) The shape of the host hatching and parasitoid emergence distributions. The curve shows the change in density of either host eggs or parasitoid pupae when $\delta_p = \delta_H = 5 \times 10^{-4}$. (b) The effect of parasitoid density on the parasitism function $f[P(t), H(t)]$. As described in the text, the extent of density dependence is inversely proportional to the parameter k : (a) $k = \infty$; (b) $k = 1$; (c) $k = 0.5$; (d) $k = 0.1$; (e) $k = 0.05$; (f) $k = 0.01$. The attack parameter $a = 0.00139$.

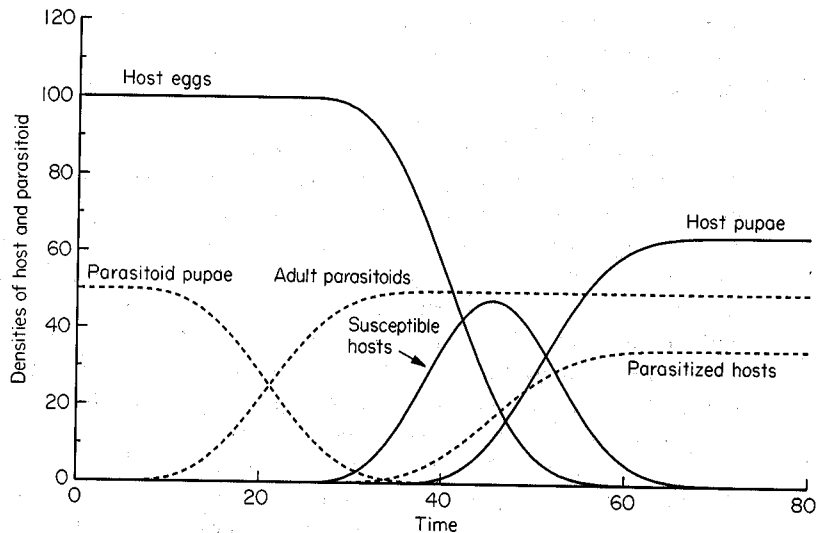


Fig. 2. An example of the changes in host and parasitoid life-history stages within one generation. The curves were drawn using the canonical parameter set in Table 1 and with $\tau_p = 5$ and $k = 0.05$. The initial densities of hosts and parasitoids were set at 100 and 50, respectively.

these models is due to the lack of any density dependence in the risk function $f[P(t), H(t)]$. In this study, we assume that the risk of parasitism rises with the number of searching parasitoids, but at a decelerating rate (Fig. 1b), which thus introduces density dependence into the parasitism function. Such density dependence might arise in a number of ways: some hosts may be in a physical or probabilistic refuge, a fraction of hosts may be able to defend themselves physiologically from parasitism or there may be interference among parasitoids at high density. We do not specify the cause of the parasitoid density dependence, but assume it is of the form shown in Fig. 1b. The amount of density dependence is indexed by a parameter k (with dimension 1/time) and the model converges to $f[\bullet] = aP(t)$ (no density

dependence) as $k \rightarrow \infty$. This particular function has been chosen because it allows the model to converge under certain conditions to a discrete generation model whose dynamics are very well understood (see Appendix). In the canonical parameter set we assume $k = 0.05$, and that a single parasitoid can search about 1/1000 of one unit of the environment in a day $a = 0.00139$ (the exact figure was chosen to give convenient equilibrium densities in the limit $k \rightarrow \infty$). Finally, we assume that an individual parasitoid has a maximum attack rate, perhaps set by a maximum rate of egg maturation or by the time needed to attack and parasitize a host. The reciprocal of the maximum number of hosts that can be attacked in a day is the parameter θ which, for simplicity, we shall refer to as the handling time

(Holling 1959). For the canonical parameter set, we also assume that parasitoids can attack up to 30 hosts per day.

An example of the within-generation dynamics using the canonical parameter set is shown in Fig. 2. To explore the dynamic consequences of changes in phenology, we now assume that parasitoids begin to emerge at different times relative to the host, as shown in Fig. 3, at the same time varying the amounts of density dependence in the parasitism function. The following situations were explored in two series of simulations.

Series 1. Using the canonical parameter set, with the time of first parasitoid emergence (τ_p) and density dependence k allowed to vary.

Series 2. As Series 1, except the hosts are now susceptible for a longer period of time ($W = 25$), and host and parasitoid emergence is more synchronous ($\delta_p = \delta_H = 5 \times 10^{-3}$) (Fig. 4). The two parameters, a and k , are also adjusted so that aW and kW are kept constant.

Details of the stimulation methods and stability criteria are given in the appendix.

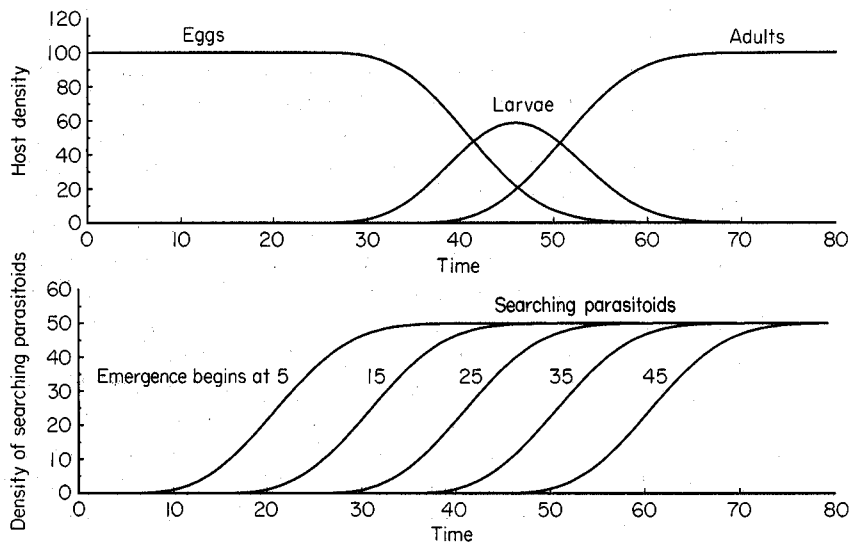


Fig. 3. The top panel shows the numbers of the three host stages over the season in the absence of parasitism (100 hosts at the beginning of the season) and using the canonical parameter set (with $\tau_p = 5$ and $k = 0.05$). The bottom panel shows the temporal distribution of searching parasitoids when emergence starts on days 5, 15, 25, 35 and 45.

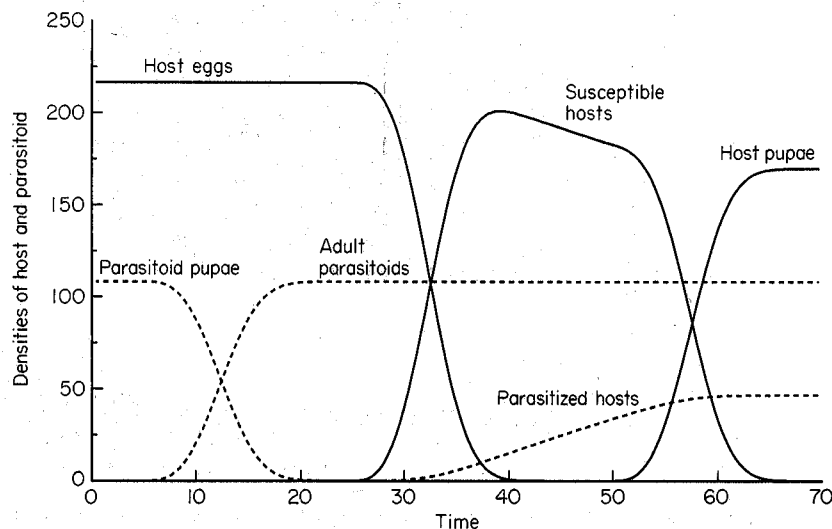


Fig. 4. An example of the within generation dynamics with the parameter values used in the second series of simulations (see text; $\tau_p = 5$, $k = 0.02$). Host hatching and parasitoid emergence are now more concerted, and the window of host susceptibility is wider.

Results and discussion

The results of the Series 1 simulations are shown in Fig. 5. We consider first the stability properties of the system when parasitoids begin to emerge at day 5. As parasitoid density dependence increases (i.e. k gets smaller), the system is stable above a critical threshold ($k < 1/W$), but then becomes unstable again when density dependence gets very strong. The stability in this example is not due to any asynchronies in phenology since parasitoid emergence starting on day 5 is completed before the appearance of any individuals of the host stage (there is assumed to be no parasitoid mortality during the season). The stability boundaries are thus simply a result of the intrinsic density dependence in the parasitoid attack rates and the handling time. This can be confirmed from certain limiting cases of the model (see Appendix). Thus, when the number of searching parasitoids is constant throughout the period that susceptible hosts are present and when handling time is zero, the model reduces to a discrete generation model due to May (1978) which is stable whenever $k < 1/W$. As density dependence in the parasitism term (kW) increases in this model, the equilibrium population of hosts and parasitoids also increases. When host population are very large, they can only be regulated if individual parasitoids are able to attack many hosts. Under these circumstances, handling time is destabilizing and accounts for the loss of stability for small values of kW (Hassell & May 1973; Hassell 1978).

The stability boundaries at the far left of Fig. 5 thus represent the behaviour of the model in the absence of any temporal asynchrony. As parasitoid

emergence is delayed, the stability properties of the system change in a number of ways. Thus, when parasitoids begin to emerge between days 26 and 34, the system requires less density dependence in the parasitism term in order to be stable. Indeed, when the first emergence occurs between days 35 and 40, the system is stable without any density dependence in the parasitism term (Münster-Swendsen & Nachman 1978). When the first emergence is even later — between days 41 and 45 — the system once again can only be stable if the parasitism term contains enough density dependence. Finally, if parasitoids do not begin to emerge until day 46, the interaction can never be stable, irrespective of the level of the density dependence. In addition, the maximum density dependence that the system can tolerate and still be stable decreases as parasitoid emergence is delayed. Finally, apparently persistent population cycles are observed in a narrow region of parameter space (Fig. 5).

Delays in parasitoid emergence are another means by which heterogeneity in the risk of parasitism can be generated; those hosts that emerge early in the season experience a reduction in or even the complete absence of parasitoid attack. Early season hosts are in an absolute or partial temporal refuge, which is responsible for the increase in stability. As with spatial refuges, an increase in the size of a temporal refuge results in larger population densities (Fig. 6), a pattern also noted by Münster-Swendsen & Nachman (1978). When handling time is non-zero, very high host population densities cannot be regulated by parasitoids and this accounts for (i) the reduction in the maximum amount of density dependence that the system can tolerate, and (ii) the

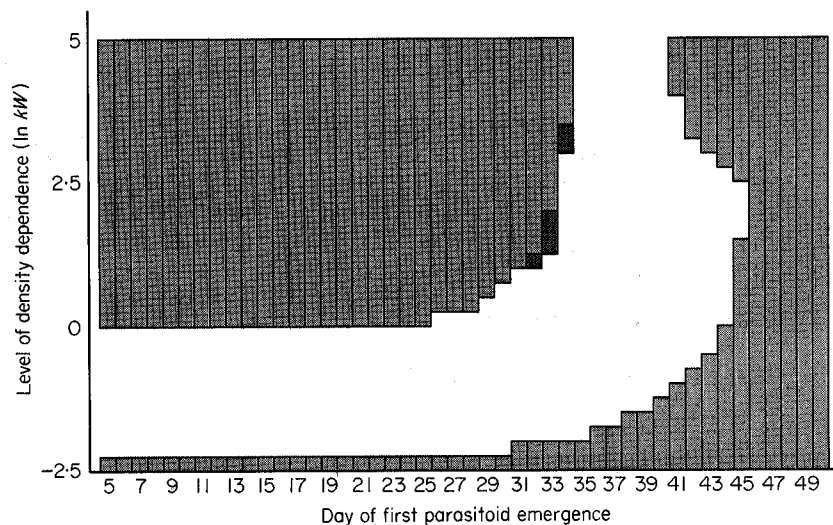


Fig. 5. Stability analysis from the first set of simulations (Series 1). Stability boundaries are displayed in a space with axes representing the data of parasitoid emergence (τ_p) and the logarithm of the product of the severity of density dependence and the parasitism window (k). White areas represent regions of parameter space where the system is asymptotically local stable and light grey areas regions of instability. The small dark grey regions represent model runs where the system showed cycling behaviour after 1000 generations.

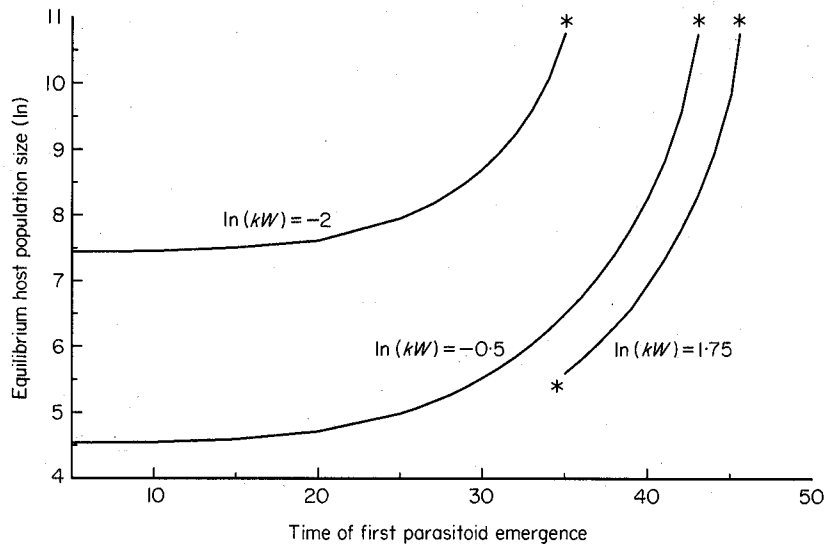


Fig. 6. Equilibrium host densities (before reproduction) in stable regions of the parameter space of Fig. 5. Host density increases as the density dependence grows stronger (smaller k), the parasitism window shorter (smaller W), or the temporal refuges grow larger (later parasitoid emergence). The stars indicate points where the equilibria become unstable.

instability of systems with little or no density dependence when parasitoid emergence begins between 41 and 45 days. Finally, when parasitoid emergence does not begin until day 46, so many hosts are in a refuge that no matter how effective the parasitoid is, it can never reduce the hosts sufficiently for regulation to occur.

Host-parasitoid models have been analysed in which a fixed proportion of hosts each year are protected from parasitism (proportional refuge models). As described in the appendix, the proportional refuge model can be derived as a limiting case of the present model if parasitoid emergence is synchronous and host hatching occurs over a long period of time relative to the length of the susceptible window. When only a small fraction of the population is in a

refuge, this model predicts limit cycles in host and parasitoid populations (Hassell & May 1988). Limit cycles are also found in the present model, but only for very narrow regions of parameter space (Fig. 5).

The results of the second set of simulations are shown in Fig. 7. Although the details vary, the overall picture is broadly similar. The only significant qualitative difference is that the region in which the system is stable as $k \rightarrow \infty$ is much reduced. The reason for this is that the parasitoid population is more synchronized and, in consequence, the temporal refuge more clearly defined: hosts tend to be subjected either to no parasitism or parasitism by the whole parasitoid population. This increases the area of parameter space in which the host can escape regulation by the parasitoid.

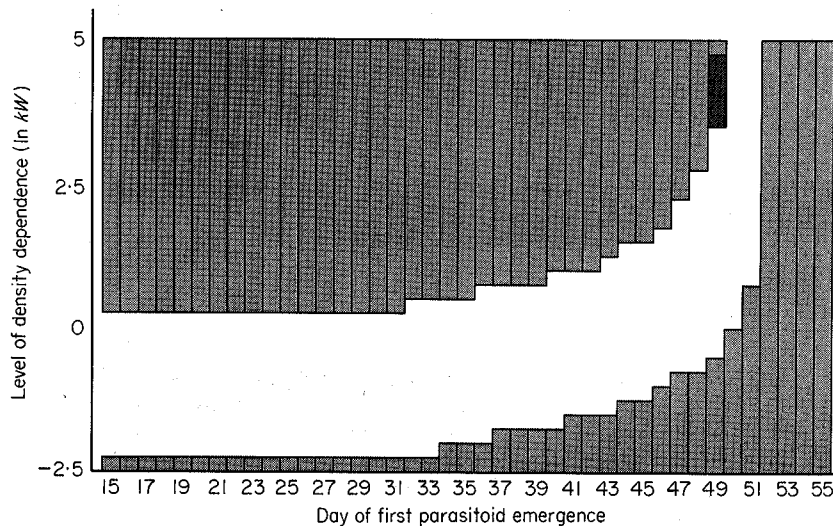


Fig. 7. Stability analysis from the second set of simulations (Series 2). As in Fig. 5, the white areas denote the stable regions, the light grey areas the unstable regions, and the dark grey areas regions of stable limit cycles.

The emergence patterns of hosts and parasitoids are likely to vary from year to year. As a first attempt to study the dynamic consequences of variable emergence times, a series of simulations have been run in which years of late parasitoid emergence alternate with years in which parasitoids emerged early. The system would be stable were the parasitoids always to emerge late, and unstable if they always emerge early. The same parameter combinations have been used as in the first set of simulations and $k = 5.5$ [$\ln(kW) = 4$] also assumed. In years when parasitoids emerged early, the date of first emergence was day 25, while in 'late years', the date of first emergence was day 37 (these parameter combinations can be located in Fig. 5). A simulation was adjudged persistent if the densities of the component populations remained within the bounds 10^{-3} – 10^5 for 500 generations.

Occasional early years had a marked destabilizing influence. No simulations persisted if early years occurred at a frequency greater than 1 in 20. If early years occurred exactly every 20 years, the system did persist, but persistence was generally not found if early years occurred randomly with an average frequency of 1 in 20. Only when early years occurred at a frequency of 1 in 25 or less was persistence the most frequent outcome.

Why are years in which parasitoids emerge early so destabilizing? Were emergence always late, parasitoids would be relatively common at equilibrium (with a temporal refuge, only part of the host population is susceptible to attack, and parasitoids have to be common in order to locate and parasitise sufficient hosts to balance host reproduction). If all parasitoids then emerge early, the complete host population is exposed to a relatively large number of searching insects and is considerably reduced. The few hosts that survive to reproduce produce only a small generation the next year, some of which are in temporal refuges. Consequently, the parasitoid population crashes to very low levels and would in nature probably become extinct. The host population then increases rapidly in the absence of regulation.

Conclusions

In this study, we have analysed a host–parasitoid model incorporating variable degrees of synchrony between hosts and searching parasitoids. Such asynchrony introduces a partial refuge effect in which some hosts, by virtue of their timing, are relatively less at risk from parasitism than others. Indeed, the familiar proportional refuge model (Hassell 1969, 1978) can be derived as a limiting case of the present model if parasitoid emergence is fully synchronous, but host hatching occurs over a long period of time relative to the length of the window of susceptibility to parasitism. When only a small fraction of the host population is protected, the proportional refuge model predicts limit cycles in the populations (Hassell & May 1988). Such limit cycles are also found in the present model, but only for very narrow regions of parameter space. A further limiting case occurs when there are constant numbers of searching parasitoids during the susceptible host stage and when handling time is zero; the model now corresponds exactly to the discrete-generation model of May (1978).

Our studies have confirmed Münster-Swendsen & Nachman's (1978) finding that temporal asynchrony alone can stabilise an otherwise unstable Nicholson-Bailey host–parasitoid model. Moreover, we have shown how temporal asynchrony, density-dependence in the efficiency of parasitism, and the host functional response interact together to influence the stability and characteristic abundance of a host–parasitoid system. On a more general note, we have developed a flexible, age-structured model of a host–parasitoid interaction that should also be useful in studying other problems in host–parasitoid dynamics; for example, the question of the stabilizing influence of density dependent aggregation when parasitoids travel between patches within a generation (Murdoch & Stewart-Oaten 1989; Godfray & Pacala 1992). Finally, our initial studies suggest that annual variation in the degree of phenological asynchrony may be an important destabilizing factor, although we stress that further work, ideally tied to

Table 1. The parameters of the model and the 'canonical values' assumed in the first series of simulations

Parameter	Description	Canonical value
λ	Fecundity	2
a	Attack rate	0.00139
k	Severity of parasitoid density dependence	Allowed to vary
θ	Reciprocal of maximum number of attacks per day	1/30
W	Length of susceptible host stage	10
$\mu(t)$	Mortality rate of adult parasitoids at time t	0
τ_p	Time first parasitoid emerges	Allowed to vary
τ_H	Time first host hatches	25
δ_p	Variance in parasitoid emergence	5×10^{-4}
δ_H	Variance in host hatching	5×10^{-4}

specific host-parasitoid systems, is required to substantiate this conclusion. This finding is potentially concerning if, as widely believed (see Schneider 1993), the main consequence of global climate change is increased environmental variability.

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Appendix

WITHIN-GENERATION MODEL

The within-generation model is described by a set of seven differential equations, some of which include time delays, plus two further equations which describe parasitoid and host emergence (Table A1). Host eggs begin to hatch at time τ_H (equation A1)

and the rate of hatching (Δ_H) accelerates over time (equation A8). The numbers of susceptible larvae increase as eggs hatch, but decrease as hosts are parasitized or pupate (equation A2). The accumulation of parasitized host is described by equation A6 and of those hosts that escape parasitism by equation A3. To calculate the numbers of hosts that pupate, it is necessary to know the probability that a host survives through the susceptible period

Table A1. Details of the within-generation model described in the text

Variable	Model	
Host eggs [$H_e(t)$]	$H'_e(t) = -\Delta_H(t)H_e(t)$	eqn A1
Host larvae [$H(t)$]	$H'(t) = \Delta_H(t)H_e(t) - H(t)f[P(t), H(t)] - M(t)$	eqn A2
Host pupae [$H_p(t)$]	$H'_p(t) = M(t)$	eqn A3
Parasitoid pupae [$P_p(t)$]	$P'_p(t) = -\Delta_p(t)P_p(t)$	eqn A4
Parasitoid adults [$P(t)$]	$P'(t) = \Delta_p(t)P_p(t) - \mu(t)P(t)$	eqn A5
Parasitized hosts [$P_h(t)$]	$P'_h(t) = H(t)f[P(t), H(t)]$	eqn A6
Host survival [$S(t)$]	$S'(t) = M(t)\{f[P(t - W), H(t - W)] - f[P(t), H(t)]\}$	eqn A7
Host emergence [Δ_H]	$\Delta_H(t) = 0$	$t \leq \tau_H$ eqn A8
	$\Delta_H(t) = \delta_H(t - \tau_H)^2$	$t > \tau_H$
Parasitoid emergence (Δ_p)	$\Delta_p(t) = 0$	$t \leq \tau_p$ eqn A9
	$\Delta_p(t) = \delta_p(t - \tau_p)^2$	$t > \tau_p$
where	$M(t) = \Delta_H(t - W)H_e(t - W)S(t)$	

Initial values: at the beginning of the season ($t=0$), the number of host eggs and parasitoid pupae are specified by the between-generation model. All other variables are set at zero except $S(t)|_{t=0} = 1$.

(W). This probability, $S(t)$, itself changes with time equation A7. Parasitoids begin to emerge from the pupal stage at time τ_p equation A4 and the rate of emergence (Δ_p) also accelerates over time equation A9. The numbers of searching parasitoids increase as adults emerge from pupae and decrease as parasitoids die equation A5. Finally, the instantaneous risk of parasitism is

$$f[P(t), H(t)] = k \ln \left(1 + \frac{aP(t)}{k[1 + a\theta H(t)]} \right), \text{ eqn A10}$$

where a is the attack constant, θ is handling time, and k is a measure of the strength of density dependence (see Fig. 2b). This expression for parasitism has been used by Godfray & Hassell (1989) and Gordon *et al.* (1991).

The use of delay-differential models to study age-structured insect populations has been pioneered by Gurney, Nisbet and colleagues (e.g. Gurney, Nisbet & Lawton 1983; Nisbet & Gurney 1983; Blythe, Nisbet & Gurney 1984; Gurney & Nisbet 1985), and has been used to study host-parasitoid dynamics in continuous time by Murdoch *et al.* (1987), Godfray & Hassell (1989), Godfray & Chan (1990) and Gordon *et al.* (1991). The numbers of parasitized hosts and host pupae at the end of the season are obtained by numerically solving equations A1–A10 with the initial values given in Table A1. Our results were obtained using a numerical integration program derived from the SOLVER program (Bence *et al.* 1986). We terminated a run if overwintering host or parasitoid densities fell below 10^{-3} or exceeded 10^5 .

LIMITING CASES

Some of the classic discrete-generation models of host-parasitoid dynamics can be obtained as limiting cases of equations A1–A10. Suppose that all parasitoids emerge before any hosts enter the susceptible stage ($\tau_p \ll \tau_H$) and that no parasitoids die over the period hosts are susceptible to attack ($[\mu(t) = 0]$).

Furthermore, assume that individual parasitoids are capable of attacking enough hosts per day that $\theta \rightarrow 0$. Finally, denote H_0 and P_0 as the total number of hosts and parasitoids at the beginning of the season.

Under these assumptions, the risk of parasitism experienced by all hosts is constant, $f[\bullet] = k \ln(1 + aP_0/k)$. The probability of an individual surviving parasitism is

$$\exp \int_{t-W}^t -k \ln \left(1 + \frac{aP_0}{k} \right) dt = \left(1 + \frac{aP_0}{k} \right)^{-kW}. \text{ eqn A11}$$

The number of hosts surviving parasitism can be written

$$\text{Hosts surviving} = H_0 \left[\left(1 + \frac{\hat{a}P_0}{\hat{k}} \right)^{-\hat{k}} \right] \text{ eqn A12}$$

where $\hat{a} = aW$ and $\hat{k} = kW$ (and is, thus, dimensionless). The expression in square brackets, the probability of escaping parasitism, is the zero term of the negative binomial distribution. May (1978) used the negative binomial distribution to describe parasitoid aggregation in a discrete generation model that has been widely discussed and analysed (e.g. May & Hassell 1981; Hassell, Waage & May 1983; Chesson & Murdoch 1986). The model is stable for all $\hat{k} < 1$ and unstable otherwise. Equilibrium population densities increase as \hat{k} decreases. As $\hat{k} \rightarrow \infty$, May's model reduces to the Nicholson Bailey model ($f[\bullet] = \hat{a}P_0$). May's model is most often used to describe parasitoid aggregation in certain host patches, independent of host density (Chesson & Murdoch 1986; Hassell *et al.* 1991). We stress that our biological justification for equation A10 is that it provides a good description of parasitoid density-dependence; it is not intended as a specific model of aggregation, though aggregation may be one mechanism contributing to the density-dependence.

In understanding the model analysed here, it is useful to derive a second limiting case. Assume no

density dependence ($k \rightarrow \infty$) and that while hosts hatch from their eggs over a very long period (δ_H small), most parasitoids emerge simultaneously (δ_P large). If parasitoid emergence begins after hosts have started to hatch, the host population can be divided into those that experience parasitism and those that escape: if host hatching is sufficiently protracted the small number of individuals whose susceptible period spans parasitoid emergence can be ignored. Let α be the fraction of hosts that hatch, grow and pupate before parasitoid emergence. The number of hosts escaping parasitism is $\alpha H_0 + (1 - \alpha)H_0 e^{aP_0}$ and the number of parasitised hosts $(1 - \alpha)H_0(1 - e^{-aP_0})$.

We have now derived the proportional refuge model (Bailey, Nicholson & Williams 1962, Maynard Smith 1974; Hassell 1978) which Varley & Gradwell (1958) and Hassell (1969) suggested might describe some aspects of phenological asynchrony. The stability properties of this model are well known. If a small proportion of the population is in a refuge, the system shows stable limit cycles; as the proportion in the refuge increases, the system first becomes stable and then unstable. Instability occurs because the parasitoid does not have access to enough of the host population to prevent exponential growth. When net fecundity equals two, the stable region of parameter space occurs when between one-third and one-half of the population is in a refuge. As fecundity increases, the band of stability narrows, and the onset of instability occurs with smaller refuges.

One of the first attempts to study quantitatively the effects of host and parasitoid phenology was by Griffith (1969). He suggested that the following formula (based on Griffith & Holling, 1969) might be used in a discrete-time model for the number of hosts attacked

$$\text{Hosts surviving} = H_0 \left[\left(1 + \frac{T_c a P_0}{k(1 + a\theta H_0)} \right)^{-k} \right].$$

eqn A13

We have rearranged the equation given by Griffith, and also substituted the symbols used in this paper, to emphasize the similarities in our approaches. The only new parameter is T_c which represents the time the host and parasitoid populations are in contact; an increase in host-parasitoid asynchrony acts to reduce T_c . We have not been able to derive this equation from a mechanistic within-generation model. The chief problem is that all hosts are exposed to parasitism, however, great the discrepancy in host and parasitoid phenologies; the only effect of the discrepancy is to reduce the searching efficiency of the parasitoids. Griffiths does not perform a formal stability analysis, but simulates the model over 30 generations and calculates equilibrium population densities. The main effects he observes can be understood chiefly as a consequence of changing the attack constant (a).

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