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Coexistence of multiple parasitoids on a single host due to differences in parasitoid phenology

E. Hackett-Jones · C. Cobbold · A. White

Abstract There are many well-documented cases in which multiple parasitoids can coexist on a single host species. We examine a theoretical framework to assess whether parasitoid coexistence can be explained through differences in timing of parasitoid oviposition and parasitoid emergence. This study explicitly includes the phenology of host and parasitoid development and explores how this mechanism affects the population dynamics. Coexistence of the host with two parasitoids requires a balance between parasitoid fecundity and survival and occurs most readily if one parasitoid attacks earlier but emerges later than the other parasitoid. The host density can either be decreased or increased when a second coexisting parasitoid is introduced into the system. However, there always exists a single parasitoid type that is most effective at depressing the host density, although this type may not be successful due to parasitoid competition. The coexistence of multiple parasitoids also affects the population dynamics. For instance, population oscillations can be removed by the introduction of a second parasitoid. In general, subtle differences in parasitoid phenology can give rise to different outcomes in a host–multiparasitoid system, and this may offer some insight into why establishing criteria for the 'ideal' biological control agent has been so challenging.

Keywords Parasitoid coexistence ·
Mathematical model · Biological control

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Introduction

There are many examples where a single insect host suffers attack from a range of parasitoid species (Godfray et al. 1994; Hawkins 1994; Memmott et al. 1994). Well documented cases include the forest tent caterpillar (*Malacosoma disstria* Hübner), the winter moth (*Operophtera brumata* L.) and the California Red Scale, all of which support several parasitoids (Roland 1994; Parry 1995; Borer et al. 2003). In these natural systems, the coexisting parasitoids differ considerably in their life history traits. In particular, oviposition of the parasitoid on the host may occur over several host stages (from now on referred to as the *attack window*). Each parasitoid species may target different host stages, and the duration of the attack window may also vary among parasitoid species. Furthermore, the length of time needed for the completion of parasitoid development in the host may also vary, leading to differing parasitoid *emergence times*. For example, for the parasitoids supported by the forest tent caterpillar, the wasp, *Aleiodes malacosomatus*, emerges between the third and fourth larval instar, and the fly, *Arachnidomyia aldrichi*, emerges from the pupal stage

(Parry 1994). We aim to develop a theoretical framework to determine whether differences in timing of parasitoid oviposition and emergence can explain the coexistence of parasitoids on a single host species.

Theories explaining the coexistence of two parasitoids on a single host have most commonly required mechanisms that represent resource partitioning or niche separation between parasitoids. This has been included implicitly by assuming that the distribution of parasitoids is aggregated (May and Hassell 1981; Hogarth and Diamond 1984; Klopfer and Ives 1997). When parasitoids are sufficiently aggregated, intraspecific competition within parasitoid species counters interspecific effects and promotes coexistence (as in classical theory on species coexistence (MacArthur and Levins 1967)). Explicit spatial structure can also lead to coexistence (Comins and Hassell 1996). In this case, the authors considered a two-parasitoid–one-host model in a two-dimensional array with dispersal between patches and random searching within a patch. This promoted parasitoid coexistence at a metapopulation level. Coexistence occurred most readily when one parasitoid had high mobility between patches and the other a high attack rate within patches. This leads to a self-organising niche separation between parasitoids. Explicit partitioning of the host habitat and parasitoid habitat preference can also lead to coexistence (Snyder et al. 2005). Influenced by results from laboratory systems (Porter and Hawkins 2003a), the addition of spatial heterogeneity to refuge models has been shown to promote parasitoid coexistence (Hochberg and Hawkins 1992, 1993; Hawkins et al. 1993; Porter and Hawkins 2003b).

Mechanisms that partition the resource due to differences in the timing of parasitoid attack have also been shown to allow coexistence. Intraguild predation and (facultative) hyperparasitism can promote coexistence, provided the advantage of the additional resource for the predator or hyperparasite is countered by a loss of attack efficiency or reduction in attack window length (Briggs et al. 1993; Snyder et al. 2005). If the parasitoids attack different life stages and there is sufficient variability in the duration of host development times, then coexistence is promoted as the host's population is 'effectively' composed of a mixture of host types (Briggs et al. 1993).

The timing of parasitoid attack has also been shown to have important consequences for the population dynamics of density-dependent host–parasitoid systems (May and Hassell 1981; Cobbold et al., submitted) since parasitoid emergence time is correlated with the proportion of host density-dependence that is experienced by the parasitoid. In the study of Cobbold et al. (submitted), parasitoid emergence could occur at any point in the host lifecycle and therefore the parasitoid could experience any fraction of the host density-dependence. Emergence time can significantly affect the severity of host outbreaks and both the amplitude and period of the host–parasitoid cycles. This mechanism was suggested to explain the difference in population dynamics observed between field sites in the forest tent caterpillar system. We wish to investigate whether this mechanism can also promote the coexistence of multiple parasitoids.

In this study, we will develop a framework that represents differences in attack period and emergence time between parasitoids. The representation of host development is implicitly linked to the emergence time of the parasitoid, rather than explicitly considering separate host stages (Briggs et al. 1993). Our approach also differs from those considered previously in that it is non-spatial and considers random parasitoid searching and so does not invoke implicit niche separation through parasitoid aggregation (compare to Pederson and Mills 2004). The approach also considers the entire range of possibilities in parasitoid attack windows (and so does not invoke a hierarchy or ordering of parasitoid attack). We focus on comparing the conditions that lead to the dominance of a single parasitoid and the coexistence of parasitoids. Our aim is to lay bare the effects of parasitoid timing, in terms of differences in attack period and parasitoid emergence between the two competing parasitoids. We assume both parasitoids are endoparasitoids, requiring an unparasitised host for successful development, or that the larvae of earlier attacking parasitoids always out-compete those of the later parasitoid. By ignoring antagonistic interacting parasitoids such as hyperparasites and cleptoparasites, we isolate phenology as a mechanism for coexistence.

This paper is organised as follows. In the 'Host–multiple-parasitoid model' section, the model for one host and multiple parasitoids is introduced. This is derived from a continuum model which is presented in Appendix A. Coexistence of two parasitoid species is considered in the 'Results' section for different arrangements of attack period and emergence, and for a variety of underlying dynamics (equilibrium, and cycles or chaos). Finally, in the 'Discussion' section, the characteristics that promote parasitoid coexistence are discussed in relation to natural systems.

Host–multiple-parasitoid model

We extend a 'classical' Nicholson–Bailey approach (Nicholson and Bailey 1935) to include phenology which allows parasitism to occur before, during or after

a period of host density-dependent competition. Parasitised hosts are assumed to undergo the same competition for resources as unparasitised hosts; therefore, a later-emerging parasitoid incurs additional mortality via this competition. We wish to consider a host under attack by multiple parasitoids, and these parasitoids will differ in their attack window, emergence time and searching efficiency. We describe the model framework for a single host H and two parasitoids, P and Q, and later explain the generalisation to n parasitoids.

The host lifecycle is partitioned according to the order of parasitoid attack (Fig. 1). The host–multiple-parasitoid model can be derived from a continuum analogue involving a system of ordinary differential equations. These equations are solved across a host

generation and each round of parasitoid attack (Fig. 1) can be considered separately by applying relevant boundary conditions. The final densities obtained at the end of one host generation are then discretised to give the model Eqs. 1–3. This procedure is shown explicitly in Appendix A. As indicated in Eqs. 1–3, each term in the model has a very simple interpretation in terms of the probability that P or Q parasitises the host in a given round. Note that the equations apply for any combination of P–Q attack since the ordering determines the terms, t_{1stF}, t_{2ndS} which act to turn on or off particular rounds (e.g. if P attacks later than Q then $t_{2ndS} = t_{ps}$ and the probability that P finds a host in round 1 (R1) is zero). The discrete time host–multiple-parasitoid model is as follows.

$$H_{n+1} = = e^r e^{-g H_n T_{dd}} H_n e^{-a_p(t_{pf}-t_{ps})P_n} e^{-a_q(t_{qf}-t_{qs})Q_n} \tag{1}$$

$$P_{n+1} = e^{-g H_n T_{dd}\alpha_p} H_n \left(\underbrace{(1 - e^{-a_p(t_{2ndS}-t_{ps})P_n})}_{\substack{\text{Prob. P finds} \\ \text{host in R1}}} + \underbrace{e^{-a_p(t_{2ndS}-t_{ps})P_n - a_q(t_{2ndS}-t_{qs})Q_n}}_{\substack{\text{Prob. the host is NOT} \\ \text{parsitised in R1}}} \frac{a_p P_n}{a_p P_n + a_q Q_n} \underbrace{\left(1 - e^{-(t_{1stF}-t_{2ndS})(a_p P_n + a_q Q_n)}\right)}_{\substack{\text{Prob. P finds} \\ \text{host in R2}}} \right.$$

$$\left. + \underbrace{e^{-a_p(t_{2ndS}-t_{ps})P_n - a_q(t_{2ndS}-t_{qs})Q_n}}_{\substack{\text{Prob. the host is NOT} \\ \text{parasitised in R1}}} \underbrace{e^{-(t_{1stF}-t_{2ndS})(a_p P_n + a_q Q_n)}}_{\substack{\text{Prob. the host is NOT} \\ \text{parasitised in R2}}} \underbrace{\left(1 - e^{-a_p P_n(t_{pf}-t_{1stF})}\right)}_{\substack{\text{Prob. P finds} \\ \text{host in R3.}}} \right) \tag{2}$$

$$Q_{n+1} = e^{-g H_n T_{dd}\alpha_q} H_n \left(\underbrace{(1 - e^{-a_q(t_{2ndS}-t_{qs})Q_n})}_{\substack{\text{Prob. Q finds} \\ \text{host in R1}}} + \underbrace{e^{-a_p(t_{2ndS}-t_{ps})P_n - a_q(t_{2ndS}-t_{qs})Q_n}}_{\substack{\text{Prob. the host is NOT} \\ \text{parsitised in R1}}} \frac{a_q Q_n}{a_p P_n + a_q Q_n} \underbrace{\left(1 - e^{-(t_{1stF}-t_{2ndS})(a_p P_n + a_q Q_n)}\right)}_{\substack{\text{Prob. Q finds} \\ \text{host in R2}}} \right.$$

$$\left. + \underbrace{e^{-a_p(t_{2ndS}-t_{ps})P_n - a_q(t_{2ndS}-t_{qs})Q_n}}_{\substack{\text{Prob. the host is NOT} \\ \text{parasitised in R1}}} \underbrace{e^{-(t_{1stF}-t_{2ndS})(a_p P_n + a_q Q_n)}}_{\substack{\text{Prob. the host is NOT} \\ \text{parasitised in R2}}} \underbrace{\left(1 - e^{-a_q Q_n(t_{qf}-t_{1stF})}\right)}_{\substack{\text{Prob. Q finds} \\ \text{host in R3.}}} \right) \tag{3}$$

Here, e^r represents the per capita growth rate of the host in the absence of host density-dependence; the term $e^{-g H_n T_{dd}}$ represents Ricker type density-dependence over a period T_{dd}; the parameters α_p, α_q are the fraction of the host density–dependence experienced by parasitoids P and Q, respectively, and a_p, a_q are the corresponding parasitoid searching efficiencies. The other terms are defined in Fig. 1, Table 1 and in Appendix A.

The model and its population dynamics can be understood further by considering the case when we set

$Q_n = 0$. We then obtain a host–single-parasitoid model represented by the following equations:

$$H_{n+1} = e^r e^{-g H_n T_{dd}} H_n e^{-a_p T_p P_n} \tag{4}$$

$$P_{n+1} = e^{-g H_n T_{dd}\alpha_p} H_n (1 - e^{-a_p T_p P_n}) . \tag{5}$$

This model resembles the classical Nicholson–Bailey host–parasitoid model in which parasitoid searching is assumed to be a random process (Nicholson
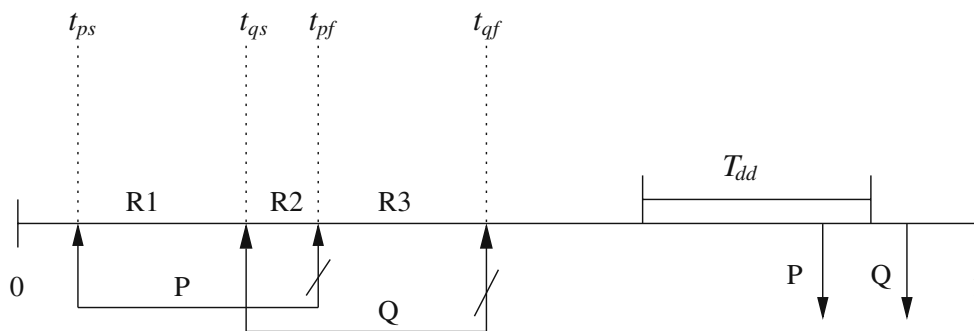
Fig. 1 Illustration of the parasitoid attack and emergence during one host generation. Parasitoid P (Q) commences host attack at time t_{ps} (t_{qs}) and finishes oviposition and searching by time t_{pf} (t_{qf}). The total attack period is divided into 'rounds' (*R1*, *R2*, etc.) where different numbers of parasitoids attack the host— e.g. in round 1 (*R1*), only parasitoid *P* is attacking the host. The emergence time of each parasitoid is indicated by the *downward arrows*. Host density-dependence operates for a time length T_{dd} during the host generation. Parasitoid *P* experiences a fraction $\alpha_p < 1$ of the host density-dependence as it emerges before the end of host density-dependence period, whereas *Q* emerges after the density-dependence period and therefore experiences a fraction $\alpha_q = 1$. The ordering of parasitoid attack and emergence and the host density-dependence position and length is only illustrative and the model applies for any combination of these events

and Bailey 1935) but additionally includes host density-dependence (as in Beddington et al. 1975) and assumes that parasitised hosts may experience host density-dependence prior to parasitoid emergence (as in Cobbold et al. 2005, submitted). This model has been shown to closely match experimental data for the forest tent caterpillar (Cobbold et al., submitted).

The model Eqs. 4–5 exhibits two non-trivial equilibria: host persistence in the absence of the parasitoid and stable coexistence (Fig. 2). Beyond the boundary for stable coexistence, the population dynamics for the host and parasitoid exhibit quasi-periodic stable cycles, chaos or parasitoid extinction.

The two-parasitoid model (Eqs. 1–3) can easily be generalised to *N* parasitoids. However, the equations become cumbersome if we consider the most general arrangement of parasitoid attack windows. Therefore, we will not write down the equations for more than

two parasitoids. Note that when all attack windows are equal, the equations for *N* parasitoids are quite simple and are given in Appendix B.

The host–multiple-parasitoid model framework captures a range of common parasitoid strategies, for instance, scenarios where the two attack windows are disjoint, and therefore, one parasitoid acts first, followed by the other. Other scenarios described by the model include cases where *P* and *Q* act together on the same developmental stage, with one parasitoid species always being the superior competitor and eliminating the larvae of the other species in the case of multiparasitism. In cases where the attack windows overlap completely, competition for the host is decided based on which parasitoid is most likely to find the host. A simple scaling argument can show that the parameter *a*, which we normally refer to as the searching efficiency of the parasitoid, can implicitly include a bias parameter representing the advantage of an intraguild predator

Table 1 The definition of the parameters used in the model Eqs. 1–3, together with their baseline values or range of values (in square brackets) used in this study (Figs. 2–5)

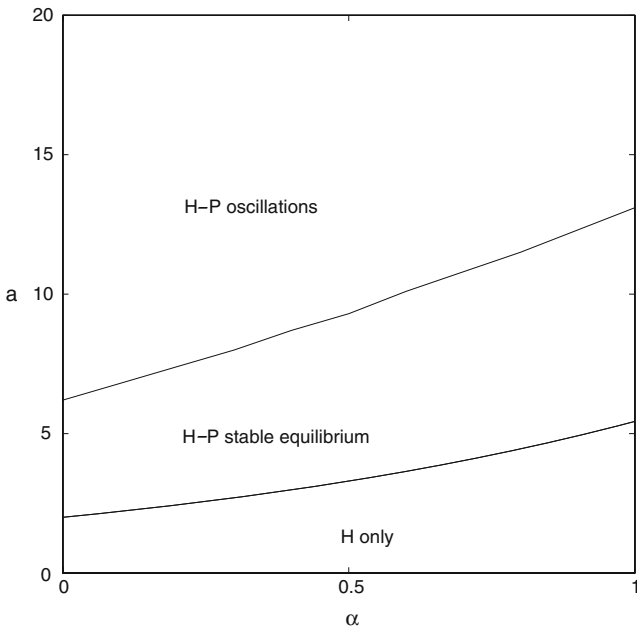| Parameter	Description	Baseline value
t_{ps} (t_{qs})	Time $P(Q)$ **starts** attacking and searching for host	[0, 0.25]
t_{pf} (t_{qf})	Time $P(Q)$ **finishes** attacking	[0.25, 0.625]
$T_p = t_{pf} - t_{ps}$ (T_q)	Length of P(Q) attack window	[0.125, 0.375]
$t_{1stF} = \min(t_{qf}, t_{pf})$	The earliest attack end time	
$t_{2ndS} = \max(t_{qs}, t_{ps})$	The latest attack start time	
T_{dd}	Length of host density–dependent (HDD) period	0.5
g	Strength of density–dependence	1
e^r	Per capita growth rate of hosts	e^1
$\alpha_{p(q)}$	Fraction of HDD experienced by P(Q)	[0, 1]
$a_{p(q)}$	Searching efficiency of P(Q)	[3, 20]

Fig. 2 The a vs α parameter space for the H–P model, with density Q set to zero. All parameter values are given in Table 1. Changing the attack window length from the current value of $T_p = 0.25$ simply scales the a axis

(competitive advantage in the case of multi-parasitism) (*cf.* Snyder et al. 2005).

Results

We examine the conditions under which one parasitoid species may out-compete the other and where two parasitoids can coexist. This is investigated for both equilibrium and non-equilibrium underlying population dynamics. To determine which parasitoid species will succeed, we calculate the invasion exponent (fitness), $s_P(Q)$, for Q to invade an established (resident) H–P system at its dynamical attractor. The fitness is the linearised exponential growth rate of the invading parasitoid in the environment set by the host and the resident parasitoid. If Q's fitness satisfies $s_P(Q) > 0$, then Q can invade the H–P system and increase its density. The invasion of P where Q is the resident parasitoid can be determined by considering $s_Q(P)$. Coexistence of P and Q will be possible when both $s_P(Q) > 0$ and $s_Q(P) > 0$.

The fitness expression for Q, $s_P(Q)$, is computed as follows: First, we calculate

$$M_n = \left. \frac{\partial Q_{n+1}}{\partial Q_n} \right|_{Q_n=0}. \tag{6}$$

Using Eq. 3, this gives

$$
M_n = \frac{a_q H_n}{a_p P_n} e^{-g H_n \alpha_q T_{dd}} e^{-a_p P_n (t_{2ndS} - t_{ps})}
$$
$$
\times \Big\{ a_p P_n (t_{2ndS} - t_{qs}) e^{a_p P_n (t_{2ndS} - t_{ps})} + 1
$$
$$
- e^{-a_p P_n (t_{1stF} - t_{2ndS})} \left(1 - a_p P_n (t_{qf} - t_{1stF}) \right) \Big\}. \tag{7}
$$

If the H–P system were at equilibrium, then H_n and P_n could be replaced by their equilibrium values H^* and P^*. Then, $M_n = M^*$ would become time-independent and $s_P(Q) = \ln(M^*)$. It is rarely possible to compute the fitness algebraically when the underlying population dynamics are non-equilibrium, and so we determine the largest Lyapunov exponent, which equates to fitness (Metz et al. 1992), using numerical techniques. This method allows the calculation to proceed regardless of whether the underlying dynamics are at equilibrium or not. The fitness in terms of the largest Lyapunov exponent is defined as follows,

$$
s_P(Q) = \lim_{n \to \infty} \frac{1}{n} \ln(M_{n-1} \cdot M_{n-2} \cdot \ldots M_1 \cdot M_0), \tag{8}
$$

where M_n is as defined in Eq. 7, which includes terms for H_n and P_n which are successive terms for the resident host and parasitoid on their dynamic attractor. To compute the fitness of P when Q is the resident, $s_Q(P)$, requires only that all P and Q terms are swapped in Eqs. 7 and 8. (In numerical procedures, taking the limit to infinity is not possible and we take the limit over a large number of generations at the resident attractor.)

Equilibrium dynamics

We first consider the outcome of competition between the parasitoid species when parameters are chosen to maintain equilibrium underlying population dynamics. The parameters for P are fixed (a_p, α_p) and those for Q are varied (α_q, a_q) and the sign of $s_P(Q)$ and $s_Q(P)$ is determined at each point in parameter space. This details the regions in parameter space where one parasitoid can out-compete the other or where coexistence is possible. This procedure is repeated for a range of combinations of attack windows (Fig. 3a–i).

Competitive exclusion

If the attack window length of parasitoid Q is small compared to that of P, then Q fails to invade for almost all parameter combinations (Fig. 3a–c where $T_q = 0.5 T_p$). Here, the number of hosts parasitised by P is high compared to Q, and this difference cannot be readily overcome by Q gaining access to the hosts
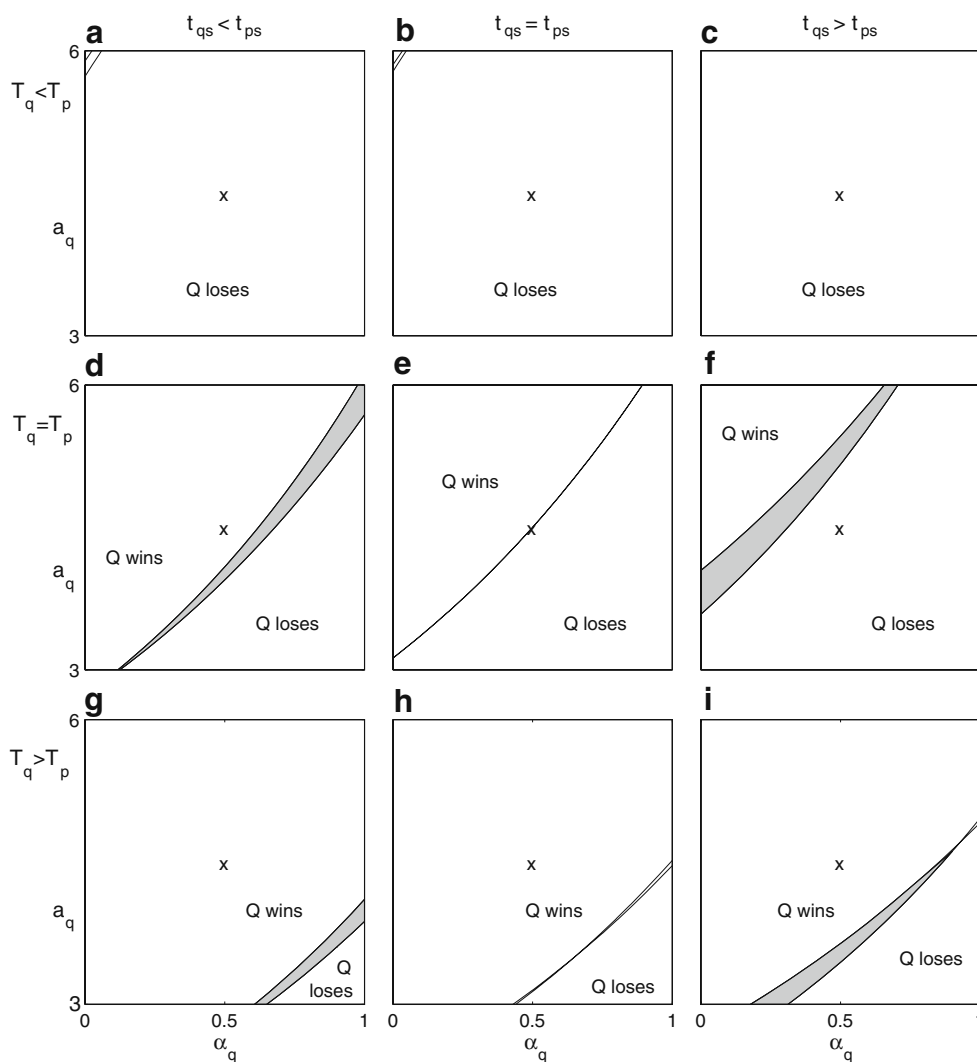
Fig. 3 Plots of the sign structure of fitness functions $s_P(Q)$ and $s_Q(P)$. P's parameters are fixed at $\alpha_p = 0.5$, $a_p = 4.5$ and denoted by the *cross* in each diagram. We compute the sign of $s_P(Q)$ and $s_Q(P)$ as Q's parameters vary across the ranges $\alpha_q \in [0, 1]$ and $a_q \in [3, 6]$. The parameter space is partitioned into the region where 'Q loses' against the fixed parasitoid P (i.e. $s_P(Q) < 0$ and $s_Q(P) > 0$ and the parasitoid P with $(\alpha_p, a_p) = (0.5, 4.5)$ will exclude Q for any choice of parameters in these regions), the region where 'Q wins' against the fixed parasitoid P (i.e. $s_P(Q) > 0$ and $s_Q(P) < 0$ and any choice of (α_q, a_q) in this region will result in Q out-competing P) and the *shaded region* in which there is coexistence of P and Q (i.e. $s_P(Q) > 0$ and $s_Q(P) > 0$). Moving from left to right in this figure corresponds to increasing Q's attack start time relative to P's. Moving from top to bottom corresponds to increasing Q's attack length, T_q, relative to P's. $T_p = 0.25$ in all plots, while in **a–c** $T_q = 0.125$, **d–f** $T_q = 0.25$ and **g–i** $T_q = 0.375$, and in **a**, **d** and **g** $t_{ps} = 0.25$, $t_{qs} = 0$ and **b**, **e** and **h** $t_{ps} = 0.125$, $t_{qs} = 0.125$ (**c**, **f**, **i**) $t_{ps} = 0$, $t_{qs} = 0.25$. All other parameters are defined in Table 1

before P, by increasing survival of hosts parasitised by Q through early emergence, or by increasing the searching efficiency of Q.

If the attack window lengths are the same, then the parasitoid that attacks first has an advantage and can exclude the other parasitoid even if it has a slight disadvantage, such as emerging from the host later or having a lower searching efficiency (Fig. 3d–f). For the later attacking parasitoid to 'win' requires that it has a suitable advantage in terms of earlier emergence from the host and/or a higher searching efficiency.

Figure 3d, f represents a decrease in the length of time that P and Q spend in direct competition for hosts compared to Fig. 3e and reflects the fact that successful parasitoid invasions require a balance between early emergence, and thus, avoidance of host intraspecific competition, and the avoidance of parasitoid interspecific competition.

If the attack window length of parasitoid Q is large compared to that of P, then Q can invade regardless of whether it attacks before or after P and for a large region of parameter space where Q has a disadvantage

in terms of emergence and searching efficiency (see Fig. 3(g–i) where $T_q = 1.5T_p$). Parasitoid Q can still be excluded by P, but this requires that P has a significant advantage in emergence and searching efficiency.

In summary, the length of the attack window and parasitoid searching efficiency determine parasitoid fecundity, and emergence time determines parasitoid survival. It is the balance of these processes that allows for a given parasitoid to persist. Fecundity can be increased by reducing the period over which two parasitoids are in competition (overlap of the two attack windows), but this effect is less pronounced than the effect of differences in the attack window length and emergence time.

Coexistence

The largest region of coexistence occurs when the parasitoid attack windows are of similar length (Fig. 3d–f). To achieve coexistence, the parasitoids must start their attack of the host at different times, and the largest regions of coexistence occur when the attack windows do not overlap (Fig. 3d, f). For coexistence to occur, the advantage gained by attacking the host first must be bought at a cost of emerging later and/or of a reduction in searching efficiency. Thus, coexistence is possible through the balance of parasitoid and host competition, and a biological interpretation of how the coexistence process operates is as follows. The parasitoid that attacks first has higher fecundity due to the initial absence of interspecific competition for the host. However, the survival of this parasitoid is reduced due to mortality caused by host density-dependence associated with late parasitoid emergence. In contrast, the parasitoid that attacks later produces fewer offspring, but they have higher survival since they emerge from the host earlier.
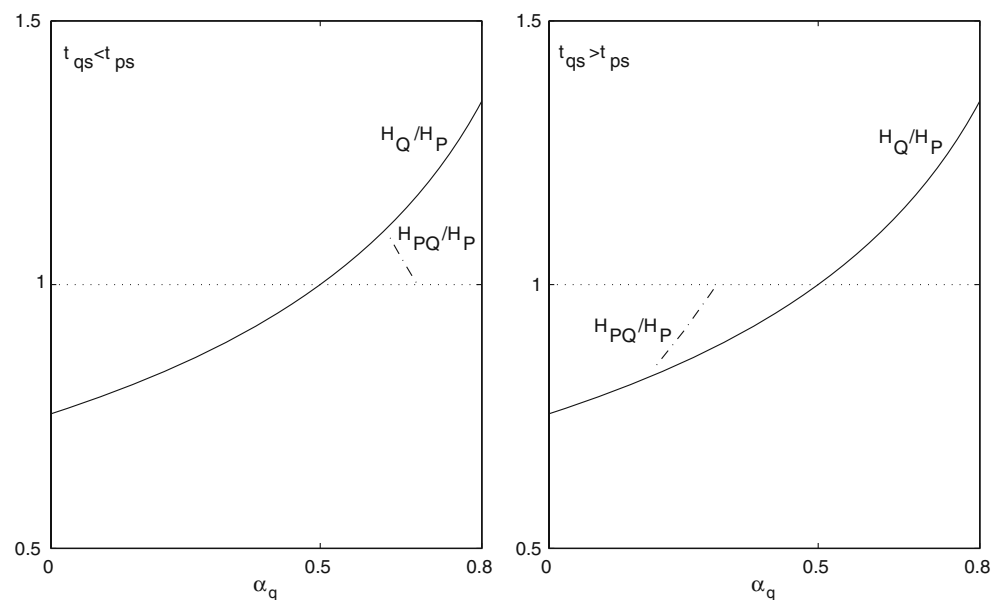
Depression of host levels

One of the practical questions ecologists are interested in is whether the introduction of parasitoid P, Q or both P and Q results in the most significant depression of host density. Multiple parasitoid introductions are common in field settings, and our model can address whether parasitic timing is an important consideration when making multiple parasitoid introductions.

In Fig. 4, we plot the ratio H_Q/H_P and H_{P+Q}/H_P, which is the host density in the H–Q and H–P–Q systems, respectively, relative to the host density in the H–P system. The attack windows for P and Q are equal in length but non-overlapping (the same attack window setup as in Fig. 3d, f). For single-parasitoid–host interactions, it is the parasitoid that emerges first that can suppress host density by the largest amount. This implies that there are circumstances where one parasitoid may competitively exclude the other even though it is less effective at suppressing host density. This occurs when the advantages of early host attack outweigh those of late host emergence.

In regions where parasitoid coexistence occurs, the combined effect on host suppression can be beneficial if introducing an earlier emerging parasitoid to an established host–parasitoid system but costly if introducing a later emerging parasitoid. Therefore, although the coexistence of parasitoids may suppress the host compared to some single parasitoid types, a single type that is optimal for suppressing host density can always be

Fig. 4 Host density ratios H_Q/H_P (*solid line*) and H_{PQ}/H_P (*dot-dashed line*). H_Q is the host density for the H-Q system and H_{PQ} is the host density when both P and Q are coexist. P's parameters are fixed to $\alpha_p = 0.5$ and $a_p = 4.5$. Q's searching efficiency is fixed to $a_q = 4.5$, while α_q varies along the x axis (thus, we examine the results along a horizontal line at $a_q = 4.5$ in Fig. 3d, f)

found. That is, one of the parasitoids in a coexisting pair would suppress host density better than the pair (the other one would be worse).

Analogous findings occur if we consider the effect that variation in parasitoid searching efficiency has on host density suppression. In particular, we can simply substitute 'early emergence' for 'higher searching efficiency' in the results above.

Non-equilibrium conditions

We consider the regions of parasitoid competitive exclusion and parasitoid coexistence when the system exhibits non-equilibrium population dynamics. This is achieved by increasing the value of the parasitoid attack rate and thereby crossing the H–P stability boundary to enter the region of non-equilibrium dynamics (Fig. 2). In Fig. 5a, the region where Q excludes P and part of the coexistence region exhibit non-equilibrium popu-

lation dynamics in the H–Q system. The explanations for when exclusion or coexistence occur are analogous to the findings under equilibrium conditions (Fig. 3f), although the invasion lines have moved away from the resident's (P's) parameter set. This means exclusion and coexistence require the two parasitoids to be more dissimilar than under equilibrium conditions.

When the attack rate parameters are adjusted further such that the entire parameter space exhibits non-equilibrium dynamics, the P and Q invasion boundaries cross and there is no longer any possibility of coexistence (Fig. 5b). In the regions between the invasion boundaries, there is a single parasitoid winner which is contingent on initial conditions. Thus, as the likelihood of non-equilibrium population dynamics increases, the chance of parasitoid coexistence decreases and can disappear.

The resultant population dynamics can also be modified depending on the outcome of the parasitoid
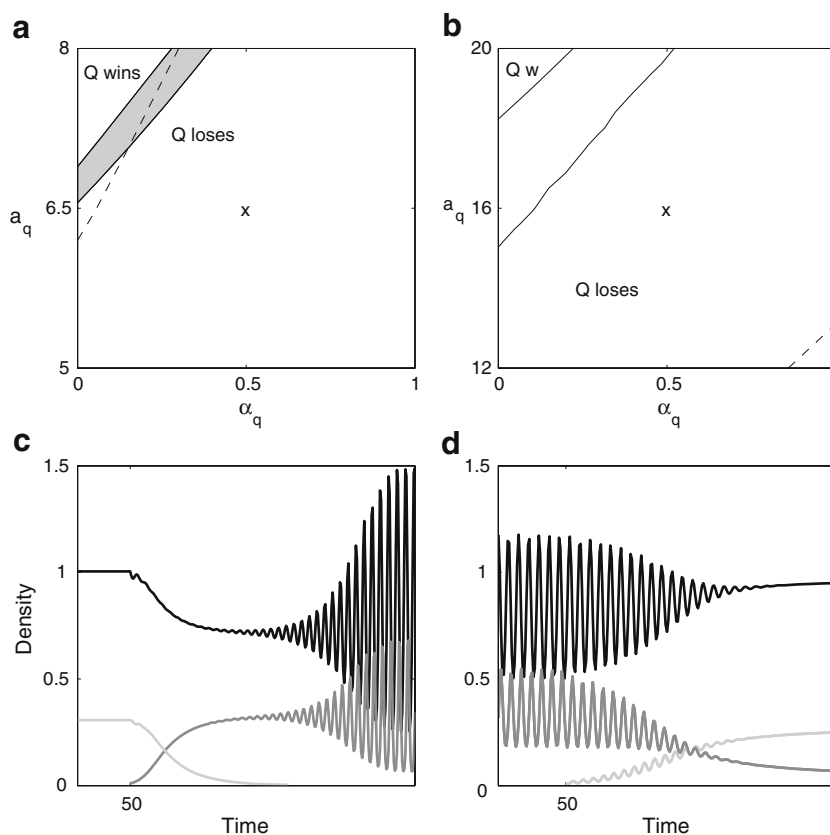

Fig. 5 Plots of the sign structure and examples of dynamics when the stability boundary in Fig. 2 are crossed by increasing the searching efficiency, a. The attack windows have $T_p = T_q = 0.25$ and $t_{ps} = 0, t_{qs} = 0.25$ as in Fig. 3f. In **a**, $a_q \in [5, 8]$ and $a_p = 6.5$. Non-equilibrium dynamics start to appear in the top left of the diagram but all coexistence is at equilibrium. In **b**, $a_q \in [12, 20]$ and $a_p = 16$. All dynamics are non-equilibrium. The

region between the invasion boundaries has $s_P(Q), s_Q(P) < 0$. Here, there will be a single parasitoid persisting with the host; whether this is P or Q is contingent on initial conditions. **c** and **d** are examples of dynamics occurring respectively in the 'Q wins' or 'coexistence' regions of **a**. *Dark grey* denotes parasitoid Q, *light grey* denotes P and *black* is used for the host. Parameters used are **c**: $\alpha_q = 0.1, a_q = 7.9$; **d** $\alpha_q = 0.1, a_q = 7$

interaction. When Q excludes P in Fig. 5a, the population dynamics become quasi-periodic (Fig. 5c). Thus, the introduction of a parasitoid may destabilise the population dynamics. In the coexistence region, the H–P–Q system exhibits equilibrium dynamics even though the H–Q system is not at equilibrium (Fig. 5d). Thus, the introduction of a parasitoid can be stabilising. Non-equilibrium dynamics of both P and Q in the coexistence region have not been observed for a wide range of parameter choices.

Discussion

Host–parasitoid systems are an interesting and perhaps puzzling example of multiple consumers coexisting on a single limiting resource. Classical competition theory would predict that this coexistence cannot occur (Chesson and Case 1986). However, temporal niches have been suggested as one explanation by which multiple specialist parasitoids can coexist with a single host. The focus of this paper has been to develop a discrete time model that explicitly includes the phenology of host and parasitoid development and explore this as a mechanism for coexistence.

Coexistence of the host with two parasitoids is possible in our model and requires a careful balance between parasitoid fecundity and survival. When the model dynamics converge to a stable equilibrium, the relative lengths of the parasitoid attack windows determine which parasitoid persists with the host. The parasitoid with the larger attack window generally out-competes the other parasitoid even if it is disadvantaged in terms of the start time of parasitoid attack and the emergence time of the parasitoid from the host. The increased fecundity associated with a longer period of time to locate and parasitise hosts commonly outweighs any cost incurred by late emergence (intraspecific competition between parasitised and unparasitised hosts) and late attack (extrinsic interspecific competition between parasitoids).

When the attack windows for the two parasitoids have the same length, the earlier attacker has the advantage in *interspecific* competition, while the early emerger has the advantage in *intraspecific* competition. The strength of these two effects determines which parasitoid wins in competition or if coexistence of the parasitoids can be established.

The largest regions of parameter space giving rise to multi-parasitoid coexistence occur when there is no overlap between the attack windows of the parasitoids. This suggests minimising interspecific competition is key for establishing coexistence. This is in agreement with the findings of Bonsall et al. (2002). Examples of this are found in parasitism of the oak galler in which the two primary parasitoids attacked galls of differing sizes (Plantard et al. 1996). Similarly, Amarasekare (2007) found that there is a partial temporal segregation between two parasitoids of harlequin bug (*Murgantia histrionica*) and this promoted multi-parasitoid coexistence. Our model only considers interspecific competition that is extrinsic, occurring as a result of the parasitoid's ability to locate the host. Intrinsic competition, as seen with hyperparasitism, has been ignored to focus explicitly on phenology. Intrinsic competition can be easily introduced into the model by including a removal term of $P(t)$ by $Q(t)$ and vice versa in the continuum model (Eqs. 10 and 11). Examples of intrinsic interspecific parasitoid competition occur with obligate and facultative hyperparasitism. Hyperparasitism has been explored as a mechanism for coexistence in host–multi-parasitoid systems by a number of groups, including Hochberg and Holt (1995) and Snyder et al. (2005). A topic for future work is to explore if hyperparasitism would have a super- or sub-additive effect on the region of coexistence found in the current model.

We find that coexistence due to phenology is most likely to occur when P and Q have equal attack lengths but attack the host at different times. This amounts to a temporal niche separation. The largest regions of coexistence occur when Q attacks after P and emerges earliest (or vice versa—Q attacks first but emerges last). This is somewhat counter-intuitive. It is possible to find coexistence for the 'intuitive' attack-emergence arrangement, but the parameters a and α must be more finely tuned (c.f. Fig. 3d and f). While the attack-emergence arrangement favoured by our model seems counter-intuitive, koinobiont parasitoids that lay their eggs in older hosts tend to develop faster and survive better as larvae and early attacking parasitoids take longer to develop (Murdoch et al. 1997). In a delay-differential equation model, Briggs et al. (1993) found coexistence of two parasitoids attacking different host stages was not possible with host stages of a fixed duration. Briggs et al. (1993) did not include the effects of intraspecific competition between hosts, suggesting this could also be important in promoting persistence of multiple parasitoids.

In our study, we have chosen to focus on a random distribution of parasitoid attack, allowing us to isolate phenology as a mechanism for coexistence. However, a growing body of evidence suggests that the distribution of parasitoid attacks are, in fact, clumped as a result of interference competition (see Amarasekare 2002 and references there in). Clumped parasitism gives rise to the negative binomial model for parasitism and has

been shown to stabilise host parasitoid dynamics. Both May and Hassell (1981) and Snyder et al. (2005) found that stabilising mechanisms broadened the regions of parasitoid coexistence. Consequently, we expect that clumped parasitism would increase the region of coexistence in our model. Other forms of parasitism such as type II functional responses have been shown to destabilise the Nicholson–Bailey model; hence, we do not expect them to enhance the region of parasitoid coexistence.

When we examine the depression of host densities in the model, we find that early emergence time is important in reducing host densities. When one parasitoid is competitively excluded, this may lead to an increase in host densities if the weak competitor is the earlier emerging parasitoid. When coexistence of the two parasitoids occurs, the host depression is always less than can be achieved with a single parasitoid. We would expect that this may not be the case with the negative binomial model for parasitism. When parasitoid attack is clumped, host density-dependence effects are weak and parasitoids control the host level; thus, the effects of parasitoid emergence time are reduced. Multi-parasitoid models using the negative binomial description of parasitism have been used to study hyperparasitism (Hogarth and Diamond 1984; Hochberg 1996; Pederson and Mills 2004). In this context, multiple parasitism can increase host levels and, we hypothesise, could have a similar effect in our model. Thus, in the context of biological control of a host, pest species phenology is likely to be important in determining the outcome of parasitoid introduction.

Our results for parasitoid persistence continue to hold under non-equilibrium conditions. However, we do not find any parasitoid coexistence. The introduction of a second parasitoid into the system can, however, stabilise or destabilise the population dynamics, leading to the creation or destruction of large-scale host oscillations. The fact that oscillations can be stabilised by judicious introduction of another species may be useful in a field setting. A study of harlequin bug (*Murgantia histrionica*) found that interactions between its two coexisting specialist parasitoids (*Trissolcus murgantiae* and *Ooencyrtus johnsonii*) dampened host fluctuations as predicted by our theory (Amarasekare 2003).

Parasitoid phenology does have a role to play in determining the outcome of introducing multiple parasitoid species as biological control agents. In this context, the early emerging parasitoid depresses the host to the greater extent, but the attack window determines if this parasitoid wins in competition, so the early emerging parasitoid may not always be the parasitoid that persists with the host. Even in the case where

the early emerging parasitoid persists with the host and gives rise to the best average host-depression if the host-parasitoid dynamics are quasi-periodic, the host can undergo boom–bust dynamics which may violate the objectives of a biological control programme. Early emergence has a destabilising effect on dynamics (Cobbold et al., submitted). Subtle differences in parasitoid phenology can give rise to very different outcomes in a host–multi-parasitoid system, and this may offer some insight into why establishing criteria for the 'ideal' biological control agent has been so challenging.

In summary, our results indicate that parasitoid coexistence can be influenced by parasitic timing. However, temporal niches generated by differences in lifehistory strategy do not appear to be sufficient to explain the prevalence of host–multi-parasitoid systems found naturally. This leads naturally into the debate about how future studies may wish to extend the model formulation to examine whether additional mechanisms can increase the region of coexistence. We have previously discussed the role hyperparasitism may play in expanding the region of coexistence. Other factors, such as differentiating the mortality rates between parasitised and unparasitised hosts or differential parasitoid survivorship independent of host density due to the life history characteristics of the different parasitoids, may also allow for increased coexistence under the temporal framework considered in this study. These factors are of interest biologically and will form the basis of future investigations.

Appendix A: Deriving the host-multi-parasitoid model

In this section, a continuum analogy, involving a system of ordinary differential equations, is used to show how the model in Section 'Host–multiple-parasitoid model' for two parasitoids, P and Q, and one host, H, is obtained. For concreteness, we assume that the order of attack is exactly as shown in Fig. 1, and that density–dependence acts for the whole season, i.e. $T_{dd} = 1$. Other arrangements of attack window and choices of T_{dd} can be applied in a similar way.

The equations for the continuum model are

$$\frac{dH(t)}{dt} = - \overbrace{a_p H(t) P_n}^{\substack{\text{Host is parasitised} \\ \text{by parasitoid } P}} - \overbrace{a_q H(t) Q_n}^{\substack{\text{Host is parasitised} \\ \text{by parasitoid } Q}}$$

$$- \overbrace{g H_n H(t)}^{\substack{\text{Mortality due to} \\ \text{intraspecific competition}}} \qquad (9)$$

$$\frac{dP(t)}{dt} = a_p H(t) P_n - g H_n P(t) \tag{10}$$

$$\frac{dQ(t)}{dt} = a_q H(t) Q_n - g H_n Q(t) \tag{11}$$

Here, H_n, P_n and Q_n are constants which correspond to the density of hosts and adult parasitoids of type (P, Q) at the start of the season, which we take to be the density in year n. It is important to make clear that by $P(t)$ and $Q(t)$ we actually mean hosts parasitised by parasitoid P or Q. On the day the parasitoid emerges, the host is killed, so the parasitoid density instantaneously becomes equal to the parasitised host density. The equations above govern the most general situation when both P and Q are attacking the host. For periods where one (or both) of the parasitoids is not attacking, we should set the associated searching efficiency to zero. The host mortality term is due to intraspecific competition for resources. We assume that parasitised hosts compete in the same way as unparasitised hosts. Mortality depends on the density of hosts at the start of the season. One interpretation of this term is that hosts have reduced fitness if the parent generation was at a high density and experienced strong competition.

Solving Eq. 9 for $H(t)$, and then substituting into the equations for $P(t)$ and $Q(t)$, gives the following general solutions:

$$H(t) = c_1 e^{-(a_p P_n + a_q Q_n + g H_n)t} \tag{12}$$

$$P(t) = -\frac{a_p P_n}{a_p P_n + a_q Q_n} c_1 e^{-(a_p P_n + a_q Q_n + g H_n)t} + c_2 e^{-g H_n t} \tag{13}$$

$$Q(t) = -\frac{a_q Q_n}{a_p P_n + a_q Q_n} c_1 e^{-(a_p P_n + a_q Q_n + g H_n)t} + c_3 e^{-g H_n t}, \tag{14}$$

where c_1, c_2, c_3 are integration constants. We now apply the boundary conditions in each segment of the year indicated in Fig. 1 to work out $H(n+1)$, $P(n+1)$, $Q(n+1)$, i.e. the densities at the start of year $n+1$.

First, we consider the period $0 < t < t_{ps}$. The initial host density is $H(0) = H_n$. Since no parasitoid attacks the host in this period, we should set $a_p = a_q = 0$ in Eqs. 12–14 and the boundary conditions are $P(0) = P(t_{ps}) = 0$ and $Q(0) = Q(t_{ps}) = 0$. Therefore, at the end of the first period, we obtain

$$H(t_{ps}) = H_n e^{-g H_n t_{ps}}, \qquad P(t_{ps}) = 0, \qquad Q(t_{ps}) = 0. \tag{15}$$

These will be initial conditions for the solutions in the next time period.

We now consider round 1, namely, $t_{ps} < t < t_{qs}$. Since Q has not begun its attack, we set $a_q = 0$ in Eqs. 12–14. Our initial conditions are Eq. 15, which allow us to determine the constants as follows:

$$c_1 = H_n e^{a_p P_n t_{ps}}, \qquad c_2 = H_n, \qquad c_3 = 0.$$

Therefore, at the end of round 1, we have densities

$$H(t_{qs}) = H_n e^{-a_p P_n (t_{qs} - t_{ps})} e^{-g H_n t_{qs}}$$

$$P(t_{qs}) = H_n (1 - e^{-a_p P_n (t_{qs} - t_{ps})}) e^{-g H_n t_{qs}}$$

$$Q(t_{qs}) = 0. \tag{16}$$

These give the initial conditions for round 2.

In round 2, i.e. $t_{qs} < t < t_{pf}$, both P and Q are attacking. Using the initial conditions Eq. 16 at time t_{qs} in the solutions Eqs. 12–14, we find

$$c_1 = H_n e^{a_p P_n t_{ps} + a_q Q_n t_{qs}}$$

$$c_2 = H_n \left(1 - \frac{a_q Q_n}{a_p P_n + a_q Q_n} e^{-a_p P_n (t_{qs} - t_{ps})} \right)$$

$$c_3 = \frac{a_q Q_n}{a_p P_n + a_q Q_n} H_n e^{-a_p P_n (t_{qs} - t_{ps})}.$$

So, using these values for the constants, at the end of round 2, we have

$$H(t_{pf}) = H_n e^{-a_p P_n (t_{pf} - t_{ps})} e^{-a_q Q_n (t_{pf} - t_{qs})} e^{-g H_n t_{pf}}$$

$$P(t_{pf}) = H_n e^{-g H_n t_{pf}} \left(1 - \frac{1}{a_p P_n + a_q Q_n} e^{-a_p P_n (t_{qs} - t_{ps})} \right.$$
$$\left. \times \left(a_q Q_n + a_p P_n e^{-a_q Q_n (t_{pf} - t_{qs})} \right) \right)$$

$$Q(t_{pf}) = \frac{a_q Q_n}{a_p P_n + a_q Q_n} H_n e^{-g H_n t_{pf}}$$
$$\times \left(e^{-a_p P_n (t_{qs} - t_{ps})} - e^{-a_p P_n (t_{pf} - t_{ps}) - a_q Q_n (t_{pf} - t_{qs})} \right) \tag{17}$$

which become the initial conditions for the next round.

In round 3, $t_{pf} < t < t_{qf}$, P has stopped attacking, so we should set $a_p = 0$ in Eqs. 12–14. Using Eq. 17 as initial conditions, we obtain

$$c_1 = H_n e^{-a_p P_n (t_{pf} - t_{ps})} e^{a_q Q_n t_{qs}}$$

$$c_2 = H_n \left(1 - \frac{1}{a_p P_n + a_q Q_n} e^{-a_p P_n (t_{qs} - t_{ps})} \right.$$
$$\left. \times \left(a_q Q_n + a_p P_n e^{-a_q Q_n (t_{pf} - t_{qs})} \right) \right)$$

$$c_3 = \frac{H_n}{a_p P_n + a_q Q_n} \left(a_q Q_n e^{-a_p P_n (t_{qs} - t_{ps})} \right.$$
$$\left. + a_p P_n e^{-a_p P_n (t_{qs} - t_{ps}) - a_q Q_n (t_{pf} - t_{qs})} \right).$$

So by the end of round 3, the densities are

$$H(t_{qf}) = H_n e^{-a_p P_n(t_{pf}-t_{ps})} e^{-a_q Q_n(t_{qf}-t_{qs})} e^{-g H_n t_{qf}}$$

$$P(t_{qf}) = H_n e^{-g H_n t_{qf}} \left(1 - e^{-a_p P_n(t_{qs}-t_{ps})}\right)$$

$$+ H_n e^{-g H_n t_{qf}} e^{-a_p P_n(t_{qs}-t_{ps})} \frac{a_p P_n}{a_p P_n + a_q Q_n}$$

$$\times \left(1 - e^{-a_p P_n(t_{pf}-t_{qs}) - a_q Q_n(t_{pf}-t_{qs})}\right)$$

$$Q(t_{qf}) = H_n e^{-g H_n t_{qf}} e^{-a_p P_n(t_{qs}-t_{ps})} \frac{a_q Q_n}{a_p P_n + a_q Q_n}$$

$$\times \left(1 - e^{-(a_p P_n + a_q Q_n)(t_{pf}-t_{qs})}\right)$$

$$+ H_n e^{-g H_n t_{qf}} e^{-a_p P_n(t_{pf}-t_{ps}) - a_q Q_n(t_{pf}-t_{qs})}$$

$$\times \left(1 - e^{-a_q Q_n(t_{qf}-t_{pf})}\right) . \tag{18}$$

For $t > t_{qf}$, both parasitoids have finished attacking (ovipositing on) the hosts. Density-dependence continues to affect the parasitised host until the parasitoids emerge from the host at α_p, α_q. Unparasitised hosts continue to experience density-dependence for the remainder of the season. Therefore, the densities at $t = n + 1$ are

$$H(n+1) = H_n e^{-a_p P_n(t_{pf}-t_{ps}) - a_q Q_n(t_{qf}-t_{qs}) - g H_n}$$

$$P(n+1) = H_n e^{-g H_n \alpha_p}$$

$$\times \Bigg[\left(1 - e^{-a_p P_n(t_{qs}-t_{ps})}\right) + \frac{a_p P_n}{a_p P_n + a_q Q_n}$$

$$\times e^{-a_p P_n(t_{qs}-t_{ps})} \left(1 - e^{-(a_p P_n + a_q Q_n)(t_{pf}-t_{qs})}\right) \Bigg]$$

$$Q(n+1) = H_n e^{-g H_n \alpha_q}$$

$$\times \Bigg[\frac{a_p Q_n}{a_p P_n + a_q Q_n} e^{-a_p P_n(t_{qs}-t_{ps})}$$

$$\times \left(1 - e^{-(a_p P_n + a_q Q_n)(t_{pf}-t_{qs})}\right)$$

$$+ e^{-a_p P_n(t_{qs}-t_{ps})} e^{-(a_p P_n + a_q Q_n)(t_{pf}-t_{qs})}$$

$$\times \left(1 - e^{-a_q Q_n(t_{qf}-t_{pf})}\right) \Bigg] \tag{19}$$

To obtain the model in Section 'Host–multiple-parasitoid model', we assume that, just prior to the start of the next season, adult hosts reproduce with, on average, e^r offspring per host, which means we multiply the equation for H by e^r. In a more general setting where the density–dependent phase has length T_{dd}, we can obtain the corresponding model by scaling $g \to g T_{dd}$. (Note that in this model framework, density dependence always appears in the equations as an overall multiplicative factor.)

Appendix B: Host–*N*-parasitoid model for equal attack windows

In the special case when all attack windows are equal, the equations for N parasitoids, $P^{(i)}$, are described by the following equations:

$$H_{n+1} = H_n e^r e^{-g H_n T_{dd}} e^{-(t_f - t_s) \sum_i a_i P_n^{(i)}} \tag{20}$$

$$P_{n+1}^{(i)} = H_n e^{-\alpha_i g H_n T_{dd}} \frac{a_i P_n^{(i)}}{\sum_i a_i P_n^{(i)}} \left(1 - e^{-(t_f - t_s) \sum_i a_i P_n^{(i)}}\right), \tag{21}$$

where t_s, t_f are the start and finish times of the attack window and $i = 1, \ldots, N$. Each parasitoid species $P^{(i)}$ has an associated searching efficiency, a_i, and fraction of host density-dependence which it experiences, α_i.

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