

## Some dynamical consequences of parasitoid diapause

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Parasitoid diapause usually serves to synchronize parasitoids with host populations that are undergoing diapause, to avoid some period of unsuitable conditions. Non-synchronizing diapause can occur, however, in a number of situations. For example, a fraction of the diapausing parasitoids may stay dormant for a number of seasons. Parasitoids attacking each generation of a multivoltine host may enter a “bank” of diapausing individuals that will emerge at the beginning of the next season. Finally, parasitoid diapause initiation may be driven by density-dependent processes. I examine the effect of these three scenarios on the stability of Nicholson–Bailey type models. I show that in general, non-synchronizing parasitoids can potentially have a strong destabilizing influence on parasitoid–host dynamics.

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During diapause, an individual enters a dormant or quiescent state where normal activity and development is halted (Denlinger 2002). This state is often associated with seasonal environments and is usually interpreted to be an adaptation that increases an individual's probability of survival over some predictable period of intolerable environmental conditions. Normal triggers for the onset of diapause reflect this: these include low temperatures or moisture levels, and short-day photo-period regimes (Danks 1987, Denlinger 2002).

In insect parasitoid–host systems, the onset of parasitoid diapause is often triggered by either the onset of host diapause or by environmental cues similar to those that induce diapause in the host (Danks 1987, Godfray 1994). This has the effect of maintaining the synchronization between hosts and parasitoids that characterizes such systems (Hanski 1988). When both hosts and parasitoids undergo diapause and break synchronously, dynamical interactions between host and parasitoid populations should not be affected.

There are some circumstances when host and parasitoid diapause may not be closely coupled, which may in

turn have some potential effects on system dynamics. For example, parasitoids of tropical, non-diapausing fruit flies evidently enter long-term diapause (spanning several host generations), possibly as a strategy to avoid periods of low availability of host larval feeding sites (Aluja et al. 1998). Variable duration parasitoid diapause (lasting several years) can also occur in temperate systems and has been interpreted to be a bet-hedging strategy (Cohen 1966, Levins 1969, Hanski 1988, Hanski and Ståhls 1990). In multivoltine host systems, a portion of each parasitoid generation within a given season may enter diapause, essentially contributing individuals to a dormant “bank” that will emerge simultaneously at the beginning of the next season and attack the first host generation (Brodeur and McNeil 1989). Finally, parasitoid dormancy may be initiated by essentially density-dependent processes. Selection of sub-optimal hosts by parasitoids occurs more frequently under conditions of high parasitoid density relative to host availability (Roitberg et al. 1992, Godfray 1994) and parasitoid offspring developing under such circumstances show a greater propensity to enter diapause (Danks 1987,

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Hanski 1988, Brodeur and McNeil 1989). Presumably, this last allows a portion of the next adult generation to avoid a period of intense competition for hosts.

In the preceding scenarios, diapause can disrupt the synchronization between hosts and parasitoids to a greater or lesser extent. Loss of synchronization itself may have profound effects on the dynamics of such systems, acting either to stabilize or destabilize, depending on parameters (Adler 1993, Godfray et al. 1994). Additionally, diapause may further affect dynamics in a number of different ways, depending on the triggering mechanism for diapause and its duration. When a portion of the parasitoid population enters extended diapause, the density of individual parasitoids at any given time becomes more reflective of conditions extant at some number of host generations in the past. In other words, the time lag inherent in host-parasitoid systems can become greatly exacerbated, with attendant potential for reduced stability in the system. Multigenerational “banking” may have similar effects, as this also introduces a time-lag where parasitoid numbers attacking the first host generation of a season, to some degree reflect conditions attendant throughout the preceding season, rather than those during the final host generation. Such banking can also weaken the force of mortality on the host population as the season progresses, by reducing the number parasitoid individuals that would otherwise be present. Finally, density-dependent parasitoid diapause may have a stabilizing influence in a manner similar to other density-dependent processes (Taylor 1988, 1997) inasmuch as it acts to reduce host mortality in direct response to reduced numbers of available hosts.

I examine here the effect of non-synchronizing diapause in parasitoids on system dynamics under three scenarios. First, where the host is univoltine and a parasitoid’s progeny may enter diapause that persists for a variable number of host generations (i.e. extended diapause). Second, where the host is multivoltine and the proportion of progeny that enter diapause increases as the season progresses, but all dormant parasitoids emerge at the beginning of the first host generation of the season (i.e. ‘banking’). Finally, I model the situation where the host is continuously breeding, but its parasitoid’s progeny can enter a one-generation diapause under conditions of high parasitoid density, relative to host density (i.e. density-dependence).

## The basic model

I use a modification of the Nicholson and Bailey (1935) model, which includes density-dependent competition among hosts and parasitoid aggregation (May 1978, Taylor 1997), as well as parasitoid dormancy. To do this, I add a third equation to the basic model to describe the dynamics of the pool of dormant parasitoids.

$$\begin{aligned}
 H_{t+1} &= H_t^{r(1-\frac{H_t}{K})} \left(1 + \frac{AP_t}{k}\right)^{-k} \\
 P_{t+1} &= H_t \left(1 - \left(1 + \frac{AP_t}{k}\right)^{-k}\right) (1-c) + D_t(b) \\
 D_{t+1} &= D_t(1-b) + H_t \left(1 - \left(1 + \frac{AP_t}{k}\right)^{-k}\right) (c)
 \end{aligned} \tag{1}$$

Here,  $H_t$ ,  $P_t$  and  $D_t$  are the host, active parasitoid and dormant parasitoid populations, respectively. The probability that a parasitoid offspring will go into dormancy,  $c$ , and the probability that a dormant parasitoid will break diapause,  $b$ , is determined by the specific scenario (below). The intrinsic rate of increase for the host population is  $r$ ,  $K$  is its carrying capacity,  $A$  is the parasitoid lifetime area of discovery and  $k$  is the aggregation term for the negative binomial distribution. This last term has the effect of increasing the probability of host escape from parasitism (i.e. high aggregation of parasitoids) with lower values. The actual form of the dormancy equation depends on the scenario.

## Variation in duration of diapause

In this scenario each generation of parasitoid progeny are all assigned dormancy “fates”, where the duration of each individuals term of dormancy is defined at birth to be of a specific duration. To accomplish this, I made the dormant term of Eq. 1 into a vector,  $D$ , whose elements,  $d_i$ , are the number of parasitoid individuals in the dormant pool that are presently one, two, three, etc. seasons away from breaking diapause. The vector elements are updated each season, such that;

$$d_{i,t+1} = d_{i+1,t} + H_t \left(1 - \left(1 + \frac{AP_t}{k}\right)^{-k}\right) \left(\frac{\mu^i}{i!} e^{-\mu}\right) \tag{2}$$

Here an element  $d_i$  at time  $t+1$  is comprised of already-dormant individuals at time  $t$  that were previously one time-step further from breaking dormancy,  $d_{i+1,t}$ , and the sub-set of current parasitoid offspring that go into a dormancy period of duration,  $i$ . Distribution of each generation of parasitoid offspring among vector elements was accomplished by using the Poisson formula with a predetermined “average duration” of dormancy,  $\mu$ . One convenient aspect of this approach is that it avoids problems associated with simply assigning Markov probabilities to the processes of entering and leaving the dormant pool. Also, the proportion of the parasitoid population that does not enter dormancy is automatically defined as those individuals assigned a dormancy period of 0 seasons. Thus, in this scenario, the parasitoid term in Eq. 1 changes to;

$$P_{t+1} = H_t \left( 1 - \left( 1 + \frac{AP_t}{k} \right)^{-k} \right) (e^{-\mu}) + d_{1t} \quad (3)$$

Here, the zero term of the Poisson ( $e^{-\mu}$ ) gives that proportion of offspring that do not go into dormancy at all, but instead emerge as active parasitoids in the next generation and  $d_{1t}$  are those dormant individuals that are scheduled to come out of dormancy at time  $t+1$  (i.e. will become  $d_0$ ). In this version of the model, low values of  $\mu$  produce relatively few offspring that enter dormancy, whereas high values result in a large proportion of parasitoid offspring entering long-lasting dormancy.

### Multivoltine hosts and parasitoid ‘banking’

In this version of the model, host populations go through a number of generations per season. Parasitoid progeny that enter dormancy at any time within the season all emerge and attack the first host generation at the beginning of the following season. To include this, I replace the constant  $c$ , in Eq. 1 with  $C(g)$ , where the proportion of parasitoids entering dormancy in a given generation is now a function of time within the season which is defined as;

$$C(g) = \left( \frac{g}{G} \right)^s \quad (4)$$

where a given host generation within a season,  $g$ , is divided by the total number of host generations per season,  $G$ , and raised to the exponent,  $s$ , where values of  $s$  greater than 1.0 result in most dormancy occurring later in the season and values less than 1.0 result in early onset of dormancy. Thus, in the strictly linear version of this equation ( $s=1.0$ ), the proportion of parasitoid progeny entering diapause after emerging from the second host generation of say, 5 host generations per season, would be 0.4. Finally, the parasitoid term in Eq. 1 becomes a conditional wherein the number of parasitoids present during the season are simply those that do not enter dormancy and the number present at the beginning of the season are all parasitoid progeny that entered dormancy during the previous season. Thus;

$$P_{t+1} = \begin{cases} H_t \left( 1 - \left( 1 + \frac{AP_t}{k} \right)^{-k} \right) (1 - C(g)), & g > 0 \\ D_{1t}, & g = 0 \end{cases} \quad (5)$$

### Density-dependence

In this final scenario the proportion of parasitoid progeny that enter dormancy (the  $c$  term in Eq. 1) is

replaced by a function  $C(P,H)$ , whose value is determined by using a negative exponential of the ratio of parasitoids to hosts.

$$C(P,H) = 1 - e^{-Q \frac{P}{H}} \quad (6)$$

In general, large numbers of parasitoids, relative to hosts, increase the proportion of parasitoid progeny that enter diapause. The strength of this density-dependence is determined by the value of  $Q$ , where high values result in a strong tendency to enter dormancy with only modest numbers of parasitoids, relative to available hosts.

### Sensitivity analyses

Model properties were assessed numerically for all scenarios. Here, I was interested in how the different dormancy scenarios affected the relationship between parasitoid aggregation and model stability. The version of the Nicholson–Bailey model that includes parasitoid aggregation has a useful property in that it shows an abrupt transition from stable to unstable dynamics when the aggregation term,  $k$ , takes on values greater than 1.0. This is useful for evaluating the effect of dormancy on system stability, since a switch from stable to unstable dynamics occurring at a value of  $k$  less than 1.0 indicates a generally destabilizing effect of dormancy and vice versa. Accordingly, I ran each scenario, varying the aggregation term,  $k$ , from 0.01 to 100. In most cases, the model ran with each set of parameters for 1,250 generations. The only exception to this was for the scenario with multivoltine hosts, where I increased the number of generational runs of the model to  $(1,000 \times G + 250)$  to compensate for any effects imposed by multiple host generations per season. For each value of  $k$ , I recorded the last 250 values for host population density  $H_t$  and used these values for either bifurcation plots or for evaluating the amplitude of any system oscillations (results). For each scenario, this procedure was repeated for a range of values of the intrinsic rate of increase ( $r$ ). I show here the general results values for values of  $r = 0.1, 0.5, 1.5$  and  $3.0$ . In all results shown, the carrying capacity,  $K$ , was maintained at a value of 500, as varying this parameter had no strong effect on the qualitative outcome of the model. Changing the lifetime area of discovery,  $A$ , generally had an effect on stability of the host–parasitoid interaction whereby low values would broaden the range of parameter space that produced stability. However, there were no strong interactions between changes in  $A$  and the dynamics of the different diapause scenarios. Consequently, I present only results where  $A$  was kept constant at a value of 0.2.

## Results

As expected, in the absence of any dormancy, host–parasitoid dynamics are stable when the aggregation term ( $k$ ) takes on a value of 1.0 or less (Fig. 1a). Increasing the value of  $k$  past 1.0, results in an abrupt transition from stability, first to chaotic dynamics, then with the system finally crashing due to parasitoid extinction as parasitoid attack approaches randomness at the highest values of  $k$  (Fig. 1a). This system behaviour becomes more complex at high intrinsic rates of host increase ( $r = 3.0$  and higher). Here, a chaotic pattern and period doubling reversal emerges as  $k$  increases from very low (i.e. highly aggregated parasitoid attack) to moderate values, finally stabilizing at moderate values and then becoming unstable in the familiar way as  $k$  exceeds a value of 1.0 (Fig. 2–4). A pool of dormant parasitoids imposes some changes on this basic pattern. Generally-speaking, all scenarios involving some kind of parasitoid dormancy show a restricted range of conditions within parameter space where we obtain stable dynamics. However each dormancy scenario has its particular effect on system dynamics.

Variation in the average duration of diapause ( $\mu$ ) had the least effect on the outcome of the basic model. Notwithstanding this, an interesting pattern emerged wherein a moderately large pool of dormant parasitoids ( $\mu = 0.10$ – $1.0$ ) operating at relatively high intrinsic rates

of increase, slightly increased the set of conditions that allowed stability (Fig. 1b, 2). However a very large pool of parasitoid progeny that expressed multi-season diapause ( $\mu = 1.0$ – $5.0$ ) constrained the range of conditions that allowed stable dynamics to relatively low values of  $k$  (Fig. 2). This last was most evident at relatively low host intrinsic rates of increase (Fig. 2).

Systems with multivoltine hosts were destabilized when the fraction of parasitoids that entered dormancy increased as the season progressed. Over the normally-stable range of parameter space, host numbers showed strong multiphase cycles where the number of phases was the product of number of host generations per season and the normal number of host phases (Fig. 1c). For example, when host populations complete 5 generations per season, a set of parameters that normally would produce a stable equilibrium would then produce five-phase cycles (Fig. 1c). An interesting departure from this general result (multivoltinism having a destabilizing effect) was that the normal transition point from stable to chaotic dynamics ( $k = 1.0$ ) was shifted right at lower intrinsic rates of increase and large numbers of host generations per season. Here, the system first entered multiphase cycles at values beyond the  $k = 1.0$  threshold, before transitioning to chaos, followed by extinction at much higher values of  $k$  (Fig. 3). Results for this scenario proved to be quite robust with respect to values of  $s$ , the exponential term in Eq. 4), that determined the relation-

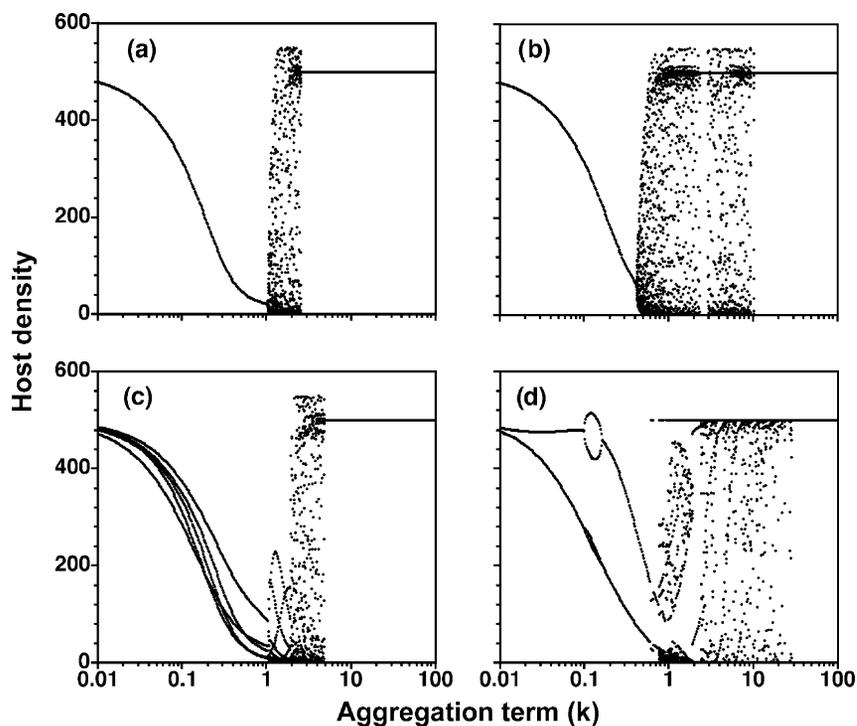


Fig. 1. Sample bifurcation plots showing the effects of diapause scenarios on system dynamics. All plots show the effect of changing values of  $k$  (aggregation) on system stability. In all plots  $r$  (host intrinsic rate of increase) = 1.5,  $A = 0.2$  and  $K$  (carrying capacity) is set at 500. Host numbers at 500 indicate extinction of the parasitoid population (i.e. at the right hand side of all plots). (a) The basic model with no parasitoid diapause; (b) Scenario where duration of diapause varies, with  $\mu = 5.0$ ; (c) Scenario with within-season “banking” with  $G$  (number of host generations/season) = 5; (d) Scenario with density-dependence with  $Q$  (density-dependent term) = 10.

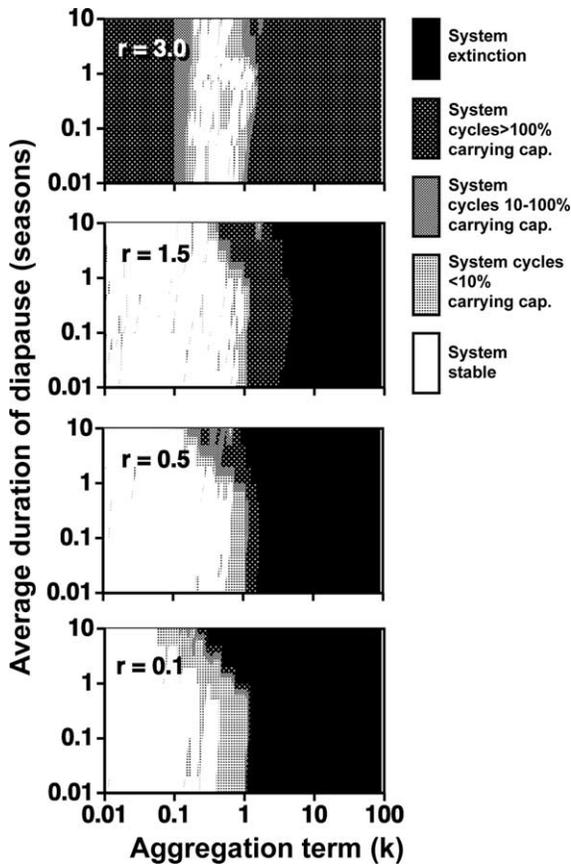


Fig. 2. Effect of variation in the average duration of diapause on system dynamics. All plots show the effect of changing values of  $k$  (aggregation),  $\mu$  (average duration of diapause) and  $r$  (intrinsic rate of increase) on system stability, categorized by the amplitude of system oscillations. Areas of plots with the darkest shading indicate parameter sets that produced greatest instability, with the darkest shading indicating system extinction. In all runs, carrying capacity ( $K$ ) equalled 500 and  $A = 0.2$ .

ship between time in season and proportion of offspring entering diapause. Low values of  $s$  had the effect of increasing the amplitude of the phase cycles, but not the number of phases or the transition point along the  $k$  continuum that produced unstable dynamics. In a similar manner, values of  $s$  higher than 1.0 decreased the amplitude of multiphase cycles.

Density-dependent diapause usually also strongly destabilized the interaction between parasitoids and their hosts. At the highest host intrinsic rates of increase, strong density-dependent diapause ( $Q = 10$ ) resulted in an increase in the range of parameter combinations that resulted in chaotic dynamics or an extinction of either the parasitoid or host population (Fig. 4). Even at relatively low intrinsic rates of increase ( $r = 1.5$ ), strong density dependence produced simple phase cycles (two or four-phase) under parameter combinations that normally produced a strong equilibrium (Fig. 1d, 4). Finally, density-dependent diapause did have a strong

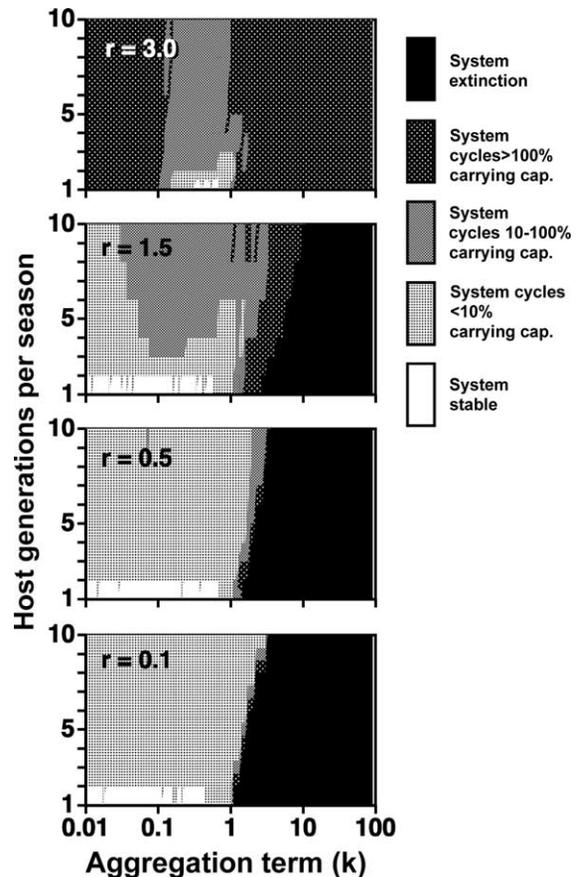


Fig. 3. Effect of within-season "banking" on system dynamics. All plots show the effect of changing values of  $k$  (aggregation), the number of host generations per season ( $G$  in Eq. 4), and  $r$  (intrinsic rate of increase) on system stability, categorized by the amplitude of system oscillations. Note here that a single host generation per season corresponds to the basic model with no parasitoid diapause. Areas of plots with the darkest shading indicate parameter sets that produced greatest instability, with the darkest shading indicating system extinction. In all runs, carrying capacity ( $K$ ) = 500 and  $A = 0.2$ .

stabilizing effect on host-parasitoid dynamics under a restricted range of conditions. Although the system never completely achieved an equilibrium, very low-amplitude cycles occurred at very low intrinsic rates of increase ( $r = 0.10$ – $0.50$ ) under conditions of strong density-dependence ( $Q = 5$ – $20$ , Fig. 4).

## Discussion

The theoretical dynamics of host parasitoid systems have been thoroughly explored with respect to community and spatial effects on the stability of these systems (Pacala 1990, Hassell et al. 1991, Adler 1993, Wilson et al. 1996, Olson et al. 2000, French and Travis 2001). The dynamical properties of May's (1978) model, which includes aggregation and a host carrying capacity, are

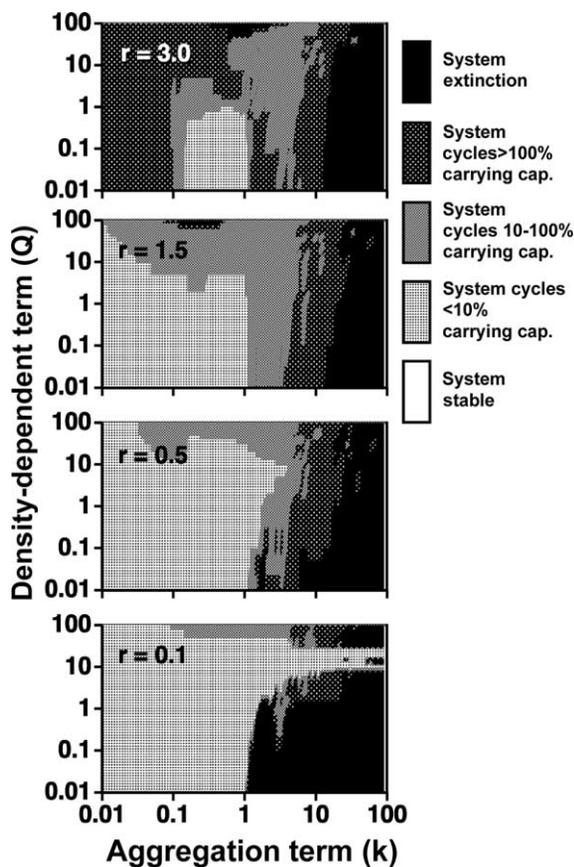


Fig. 4. Effect of variation in the strength of density-dependent diapause on system dynamics. All plots show the effect of changing values of  $k$  (aggregation),  $Q$  (strength of density-dependence) and  $r$  (intrinsic rate of increase) on system stability, categorized by the amplitude of system oscillations. Areas of plots with the darkest shading indicate parameter sets that produced greatest instability, with the darkest shading indicating system extinction. In all runs, carrying capacity ( $K$ ) equalled 500 and  $A = 0.2$ .

well-known and therefore provides a useful benchmark for elucidating the effects of dormancy on these systems. Typically, May's (1978) model exhibits an abrupt transition from stable to oscillatory dynamics as the value of the aggregation term,  $k$ , increases to values greater than 1.0. Here, the inclusion of non-synchronizing diapause changed the location of this transition point, either making the range of values of  $k$  that conferred stability broader or narrower, depending on the parameters employed. However, with some exceptions, the general effect was to decrease the transition from stable to unstable dynamics to values of  $k$  far less than 1.0, especially under conditions of high intrinsic rates of increase.

Parasitoid–host dynamics show a greater potential for instability than do other exploiter–victim interactions because of the inherent time-lag built into these discrete-time systems. Indeed, several explorations of continuous-

time predator–prey systems show that instability is not an inevitable consequence of system time-lags (Hastings 1983, Holt 1984). For example, Hastings (1983) showed that the presence of invulnerable stages in the prey population could produce stable dynamics as long as time delays did not correspond with the period of the predator–prey system: a condition that cannot be met in a discrete-time system. In my system, the addition of a persistent pool of diapausing parasitoids evidently exacerbates the destabilizing effect of time-lags in many circumstances. This effect is counterintuitive, because one might suppose that extended diapause would act to dampen out large population fluctuations and stabilize an unstable interaction. Such an effect has been reported for both single-species populations in stochastic environments (Takahashi 1977) and competing populations (Warner and Chesson 1985). In fact, moderately long diapause (when  $\mu = 0.5$ ) does extend the range of parameters that allow stable dynamics to a small extent (Fig. 1b, 2) and this may be due to the “storage” effect (Warner and Chesson 1985). However, any buffering effect evidently becomes swamped by the destabilizing effect of the extreme time lag: a consequence of having a large fraction of the parasitoid population in long-term diapause.

System destabilization by long-term diapause may in and of itself promote the increase of individuals that exhibit long-term diapause within a population. Holt (1996) has pointed out that the fitness of a disperser strategy in a metapopulation will be the arithmetic average of fitnesses across patches, whereas the fitness of non-dispersers will be the geometric average over time of fitnesses within a patch. When fitness varies, the arithmetic average is always higher than the geometric average. Thus, a dispersing strategy will enjoy higher fitness than a non-dispersing strategy as long as local patches are unsynchronized and exhibit chaotic local dynamics. The temporal dispersal which results from long-term diapause may confer the same fitness benefits to stragglers that employ such extended dormancy, since the fitness of a temporal dispersing strategy will be similar to that of a spatial dispersing strategy.

Multivoltine host dynamics were always at least slightly destabilized by seasonally-triggered diapause induction in parasitoids. The “banking” effect prevented host populations from attaining an equilibrium for two reasons. Most obviously, an enlarged cohort of emergent parasitoids at the beginning of a season tended to suppress host numbers far below the equilibrium point. Less obviously, sequestration of an increasing fraction of the parasitoid population over the season progressively reduced mortality and allowed an increasing fraction of the host population to reproduce. This resulted in the production the generational phase cycles exhibited by multivoltine hosts (Fig. 1c). It should be noted however that even though banking resulted in loss

of a stable equilibrium over a large range of parameters, parameter sets that resulted in complete system extinction were also reduced. Thus, the banking effect also contributed to a certain degree towards system persistence. This probably occurred because banking acted to partially decouple parasitoid–host dynamics and established a partial temporal refuge to hosts, preventing extinction, in a manner similar to Adler’s (1993) spatial model.

Density-dependent feedback processes expressed via intraspecific aggression (Taylor 1988, 1997), sex allocation (Comins and Wellings 1985) and dispersal (French and Travis 2001) have been shown to act as strong stabilizing forces in model parasitoid–host systems. In this study, density-dependent diapause imposed a strongly stabilizing influence on systems only when host replacement rates were kept very low. In contrast, density-dependent diapause has a strong destabilizing effect on host–parasitoid dynamics when the range of intrinsic rates of increase approached values that characterize most host insect systems. Why should this be so? In the above examples, strong density-dependence had the effect of directly reducing the mortality rate imposed by parasitoids when host availability was low. However, density-dependent diapause reduces mortality at the cost of increasing the mortality imposed upon the succeeding generation. Finally, chaotic dynamics can result in single-species population models under a combination of overcompensating density-dependence and high intrinsic rates of increase (May 1976). Arguably, some aspects of both factors are present in this instance.

A final note. It is the extensive use of parasitoids in classical biological control that has generated much of the interest in these systems over the years. One aim of this pest management technique is to establish stable host–parasitoid systems that will result in long-term suppression of pest (i.e. host) populations below some economic threshold (Hochberg and Hawkins 1994, Quicke 1997). It may be useful to include information about diapause mechanisms in parasitoids when screening candidates for introduction, if a component of diapause is non-synchronizing and is therefore likely to contribute to unstable dynamics.

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