Parasitism and generation cycles in a salt-marsh planthopper

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Summary

1. In warm climates many insects exhibit discrete generations, in the absence of obvious factors that could synchronize their age structure. It has been hypothesized that parasitoid wasps might be responsible for these oscillations in the host age structure, known as generation cycles.

2. We examine the role of the parasitoid *Anagrus delicatus* in the dynamics of the salt-marsh planthopper *Prokelisia marginata*. In particular, we evaluate the hypothesis that *Anagrus* contributes to the formation of generation cycles in the hopper, in the subtropical climate of Florida.

3. Two kinds of evidence are presented. First, we construct continuous-time models of the system that incorporate what is known about *Anagrus* foraging behaviour, the life cycles of host and parasitoid, and their movements. We then examine the behaviour of these models to determine if *Anagrus* has the potential to induce generation cycles. We also show how spatial variation in the risk of parasitism can generate 'pseudo-interference' in our continuous-time framework. Secondly, we examine the temporal pattern of host and parasitoid abundance, and parasitism rates in the field. If *Anagrus* were contributing to the formation of generation cycles, we would expect to see a characteristic pattern of abundance and mortality from parasitism.

4. Both our modelling and empirical results suggest that *Anagrus* contributes to generation cycles in *Prokelisia*. *Anagrus* has the theoretical prerequisites for generation cycles to occur and in the field generates a cyclic pattern of parasitism that would help induce generation cycles in the planthopper.

5. The existence of an adult host stage that is invulnerable to parasitism strongly influences the stability of our models. Without this stage *Anagrus* cannot fully stabilize the system, even if the risk of parasitism varies greatly from patch to patch.

Key-words: *Anagrus delicatus*, generation cycles, host–parasitoid dynamics, planthopper, stability.

Journal of Animal Ecology (1994) **63**, 912–920

Introduction

Theoretical studies have identified many factors that can potentially influence the dynamics of host–parasitoid systems. In discrete-time systems with non-overlapping generations, these include interference among searching parasitoids, spatial differences in host vulnerability and parasitoid foraging behaviour, i.e. parasitoid aggregation (Bailey, Nicholson & Williams 1962; Hassell & Varley 1969; Hassell & May 1973, 1974; May 1978; Chesson & Murdoch 1986; Hassell *et al.* 1991; Ives 1992a). These factors have a similar stabilizing effect on host–parasitoid dynamics, because they all act to generate density dependence in the parasitoid population.

In continuous-time systems with overlapping generations, however, the theoretical results are harder to categorize. Recent models have examined the effect of parasitoid aggregation on stability within this framework (Murdoch & Stewart-Oaten 1989; Godfray & Pacala 1992; Ives 1992b; Murdoch *et al.* 1992). In contrast with discrete-time models, in which parasitoid aggregation is often stabilizing, aggregation in continuous-time systems may be stabilizing, destabilizing or may not influence the dynamics at all, depending on the type of aggregation and other details

of the model. One factor contributing to these disparate results is the movement of hosts between patches, a feature of many continuous-time models. These results suggest that to understand the dynamics of real continuous-time systems, it will be necessary to develop models that consider both the degree of host movement in the system and parasitoid foraging behaviour.

Further complications can arise in continuous-time models that include age structure. Hastings (1984) and Murdoch *et al.* (1987) divided the host and parasitoid life cycles into juvenile and adult stages, and found that if either stage was invulnerable to parasitism this helped stabilize the system, especially if the adult host was invulnerable. Godfray & Hassell (1987, 1989) showed that asynchrony in the life cycles of the host and parasitoid can destabilize the system in a unique way, producing oscillations in the age structure of the host population with a period of one generation (i.e. 'generation cycles'). They conjecture that this phenomenon is responsible for the discrete generations seen in many tropical biological control systems, where no obvious environmental factors exist to synchronize host generations. Three ingredients were necessary for generation cycles to occur in their models: (i) a parasitoid life cycle approximately 0·5 or 1·5 times that of the host; (ii) a short adult host life span; and (iii) some form of density dependence in the parasitoid population, i.e. an instantaneous rate of parasitism that is nonlinear in parasitoid density. Their models further assume that the parasitoid attacks a single juvenile stage of the host, while the adult hosts and other juvenile stages are invulnerable. Generation cycles have also been found in models where only the adult stage is vulnerable to parasitism, and in this case no density dependence in the parasitoid is needed (Hastings 1984; Murdoch *et al.* 1987).

Here, we examine the role of the parasitoid *Anagrus delicatus* Dozier (Hymenoptera: Mymaridae) in the population dynamics of the salt-marsh planthopper, *Prokelisia marginata* (Van Duzee) (Homoptera: Delphacidae). In particular, we evaluate the hypothesis that *Anagrus* contributes to the formation of generation cycles in populations of this insect, in the subtropical climate of Florida. Two kinds of evidence will be presented. First, we construct continuous-time models of the system that incorporate what is known about the foraging behaviour of *Anagrus*, the life cycles of *Anagrus* and *Prokelisia*, and their movements. We then examine the behaviour of these models to determine if *Anagrus* has the potential to induce generation cycles in the hopper. We also show how spatial variation in the risk of parasitism can generate 'pseudo-interference' in our continuous-time framework, similar to that observed in discrete-time models (Free, Beddington & Lawton 1977), given specific assumptions about host and parasitoid movement.

Secondly, we examine the temporal pattern of host and parasitoid abundance, and parasitism rates, observed in populations of *Prokelisia* and *Anagrus* in the field. If *Anagrus* were contributing to the formation of generation cycles in this system, we would expect to see a characteristic cyclic pattern of host and parasitoid abundance, with peaks of adult parasitoid density occurring halfway between peaks of host density (Godfray & Hassell 1987, 1989). We would also expect to see cyclic changes in host mortality due to parasitism, corresponding with peaks and troughs in adult parasitoid density.

NATURAL HISTORY

The planthopper *Prokelisia marginata* is a common herbivore in the salt-marshes along the Gulf Coast of Florida, where it feeds exclusively on the cordgrass *Spartina alterniflora* Loisel (Denno & Grissell 1979). The life cycle of the hopper is divided into an egg stage, five nymphal instars and a short-lived adult stage. In the subtropical climate of the Gulf Coast reproduction takes place throughout the year, with a minimum generation time of 5–6 weeks in summer (Stiling *et al.* 1991). Although all stages of the hopper can be found at any time and season, *Prokelisia* populations typically show distinct generation cycles. Prokelisia lays its eggs within leaves of *Spartina*, where they are attacked by *Anagrus* (Stiling & Strong 1982a). The juvenile parasitoid takes about 4 weeks to complete development, while the adult is very short-lived, about two days in the laboratory (Cronin & Strong 1990a). As a result, the life cycle of *Anagrus* is poorly synchronized with its host, with *Anagrus* taking roughly 28 days to develop from egg to adult, while the hopper takes 42 days, at 25 °C. Given these life-history traits, a continuous-time framework is the most appropriate one for this system.

ANAGRUS FORAGING BEHAVIOUR

Several aspects of *Anagrus* foraging could potentially affect the dynamics of the system, and are important in formulating the models. Behavioural observations suggest that *Anagrus* has a simple foraging strategy, searching for the same time within a host patch (a *Spartina* leaf containing hopper eggs) regardless of host density (Cronin & Strong 1993a). *Anagrus* also has a Type I functional response, over the range of host densities commonly seen in the field. In agreement with these findings, parasitism rates are spatially density-independent in the field (Stiling & Strong 1982a,b; Strong 1989; Cronin & Strong 1990b). In isolation, these results imply that a simple random search model could adequately describe *Anagrus* foraging behaviour.

Evidence exists for two mechanisms that could potentially generate density-dependence in the parasitoid population, however, and so influence the dynamics of the system. The first is a very heterogeneous (but density-independent) spatial pattern

of parasitism, that suggests the risk of parasitism varies greatly across host patches (Fig. 1). Such heterogeneity could mean there is a highly skewed distribution of parasitoids across host patches (Murdoch *et al.* 1984; Hassell *et al.* 1991), or alternatively, that patches differ in their vulnerability to parasitoid attack (Bailey *et al.* 1962). In a discrete-time framework either mechanism would help stabilize host–parasitoid dynamics, because they generate 'pseudo-interference' in the parasitoid population (Free *et al.* 1977). In another paper (Reeve, Cronin & Strong 1994), we quantify variation in the risk of parasitism in the *Prokelisia–Anagrus* system using the statistical methods of Pacala & Hassell (1991). Using a gamma distribution with shape parameter k to model the distribution of risk across host patches, we estimated k for 29 weekly samples of 92 *Spartina* leaves from an archipelago of small islands (for further details on the sampling procedure see Strong 1989). The median value of k across the 29 weeks of the study was 0·479, indicating a highly heterogeneous and skewed distribution of risk. Additional information suggests the source of this heterogeneity is not parasitoid aggregation, however, because *Anagrus* has a nearly homogeneous distribution across host patches (see below). Instead, parasitism rates may differ across natural *Spartina* leaves because of other factors that affect their vulnerability to parasitism, such as tidal inundation (Stiling & Strong 1982b).

There is also evidence for direct interference among searching *Anagrus*, a second mechanism that could generate density dependence in the parasitoid population. This was detected in a field experiment which exposed laboratory-generated host patches (*Spartina* leaves infested with hopper eggs) to parasitism in the field, at a site in Oyster Bay, Florida (Cronin & Strong 1990b, 1993a,b). Ambient *Anagrus* densities were censused at the same time by applying sticky patches of Tanglefoot (The Tanglefoot Co., Grand Rapids, Michigan) to leaves along the same transect as the experimental host patches. The experiment was repeated on 20 different dates. Analysis of this data set
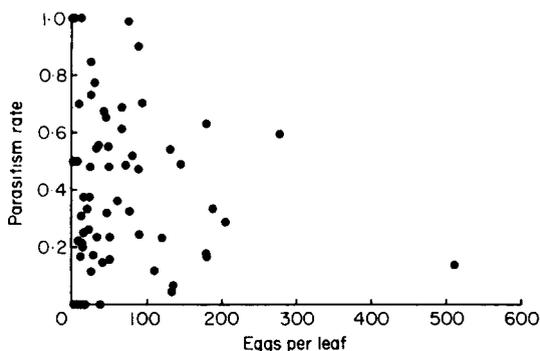
using the method of Hassell & Varley (1969) revealed a significant interference relationship ($m = 0·587$; see Fig. 2). What is the source of this interference? It is unlikely to be 'pseudo-interference', because there was little heterogeneity in parasitism rates across the experimental patches, nor were *Anagrus* aggregated across the sticky *Spartina* leaves (Reeve *et al.* 1994). Instead, laboratory observations suggest that direct interference occurs among parasitoids searching the same host patch (Cronin & Strong 1993b).

Models

In the following we formulate and examine the dynamics of two models of the *Prokelisia–Anagrus* system. Both are cast in terms of delay-differential equations, using the procedures in Murdoch *et al.* (1987) and Godfray & Hassell (1989). Model A incorporates heterogeneity in the risk of parasitism as a potential source of density dependence in the parasitoid, while Model B uses direct interference.

MODEL A

As reviewed above, there is a significant level of heterogeneity in parasitism rates across natural host patches in the *Prokelisia–Anagrus* system. This result suggests that the risk of parasitism varies quite strongly from patch to patch, although the exact mechanism is unknown. We can model this situation by defining a variable θ, the relative risk of parasitism, which amalgamates all factors which generate spatial variation in the risk of parasitism (Chesson & Murdoch 1986). These factors would include any spatial differences in the vulnerability of hosts to parasitism and any parasitoid aggregation which did occur. The absolute risk of parasitism for a given patch is then defined as $aP\theta$, where a and P are the mean attack rate and mean parasitoid density averaged across all patches (Chesson & Murdoch 1986). We assume that θ has gamma distribution with mean 1 and shape parameter k, and that θ is independent of host density
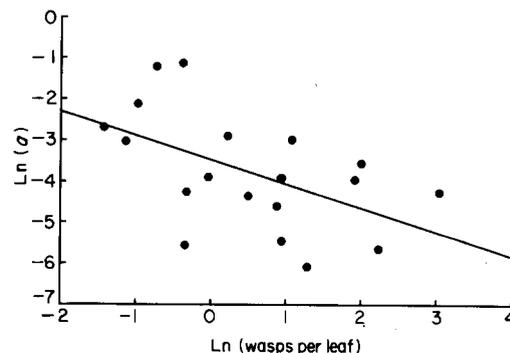

Fig. 1. Parasitism rate vs. host density (*Prokelisia* eggs per leaf), in a weekly sample of 92 *Spartina* leaves taken from an archipelago of four small islands in Oyster Bay, Florida. For further details see Strong (1989).

Fig. 2. Attack rate (a) vs. parasitoid density (female *Anagrus* wasps per sticky leaf), across 20 replicates of an experiment which exposed laboratory-generated host patches to parasitism in the field.

in a patch. These assumptions seem reasonable given our empirical results.

In a discrete-time system with non-overlapping generations, this definition of θ leads to the Bailey *et al.* (1962) model, or the negative-binomial model (May 1978). What is needed is an equivalent model for the *Prokelisia–Anagrus* system, which operates in continuous-time, and also incorporates the age structure of the organisms. An initial solution to this problem was developed by Murdoch & Stewart-Oaten (1989), who found in their particular modelling framework that variation in θ had no effect on stability. This solution has been criticized on the basis that it implies a significant degree of the host movement from patch to patch (Godfray & Pacala 1992; Ives 1992b; but see Murdoch *et al.* 1992), which does not occur in many host–parasitoid systems. In our model, we assume that the host stage of the hopper (the egg) is sessile, remaining in a single patch throughout its development, and that during development its value of θ remains the same. In contrast with the egg stage, however, we assume that both adult hosts and adult parasitoids move across many patches in their lifetime. These assumptions are consistent with what is known about movement in this system. Adult *Anagrus* have been observed to move rapidly from patch to patch in laboratory arenas (Cronin & Strong 1993a) and, indeed, this high rate of movement may explain why their densities are relatively homogeneous in space. While adult hoppers are less mobile than *Anagrus*, most moving less than a meter per day (Roderick 1987; J. D. Reeve, unpublished data), they live longer than *Anagrus* and can potentially visit many *Spartina* leaves during their lifetime.

Consider now the fate of hopper eggs laid at time t-T_E, where T_E is the egg development time. If they are laid in a patch whose relative risk is θ, then the probability they will survive parasitism and hatch at time t is given by

$$S(t) = \exp\left(-\int_{t-T_E}^{t} aP(x)\theta dx\right). \qquad \text{eqn 1}$$

This equation reflects the assumption that eggs remain in the same patch throughout development, because θ is constant through time. For the total egg population, the probability of surviving parasitism is the expected value of S, where the expectation is taken over the distribution of θ. We have:

$$E[S(t)] = \left(1 + \frac{a\int_{t-T_E}^{t} P(x)dx}{k}\right)^{-k}. \qquad \text{eqn 2}$$

This is exactly the probability of surviving parasitism in the Bailey *et al.* (1962) and negative-binomial models, except that parasitoid density is expressed as a time average. Just as in those discrete-time models,

variation in the relative risk of parasitism apparently induces pseudo-interference in our model, with the degree of interference increasing as k decreases.

Given the above assumptions, we can now fully formulate and analyse the dynamics of the model. In the model, relative risk (θ) has a continuous distribution across host patches, as is also assumed by its discrete-time analogue. In discrete-time models this poses no problem of analysis, because these models have an implicit (and complete) mixing of the host and parasitoid populations once each generation (Chesson & Murdoch 1986), a feature that considerably simplifies their mathematics. This route is not available for our continuous-time model, however, and instead we approximate a continuous range of variation by dividing the distribution of θ into a number of discrete categories. In particular, we divide the distribution of θ into 10 categories using the quantiles of the gamma distribution, setting $\theta_1 = q_{.05}$, $\theta_2 = q_{.15}, \ldots, \theta_{10} = q_{.95}$, where q_x is the xth quantile of the gamma distribution. We then model the dynamics of eggs in each category of risk using a separate equation. This procedure allows us to approximate a continuous range of variation in relative risk, using only a finite number of equations.

Consider the dynamics of eggs in host patches in the ith category of risk. Eggs will be generated in this category through oviposition by adult hoppers, and leave it by maturing into nymphs, and through parasitism and other sources of mortality. We have

$$\frac{dE_i}{dt} = \lambda A(t) - \lambda A(t - T_E)S_i(t)e^{-\delta_E T_E}$$
$$- aP(t)\theta_i E_i(t) - \delta_E E_i(t), \qquad \text{eqn 3}$$

where $E_i(t)$ is the density of eggs at time t, and $A(t)$ and $P(t)$ are the densities of adult hoppers and parasitoids across all patch categories (these are identical across all categories because of rapid adult movement). Here, λ is the daily fecundity of the hopper, a the attack rate of the parasitoid, δ_E the mortality rate from sources other than parasitism and T_E the development time of the egg. The second term in the equation describes the rate at which eggs mature and become hopper nymphs. It is the product of the rate at which eggs were laid at time $t - T_E$, and the probability of surviving parasitism (and other sources of mortality) during the egg stage. The probability of surviving parasitism is defined by the equation

$$S_i(t) = \exp\left(-\int_{t-T_E}^{t} aP(x)\theta_i dx\right). \qquad \text{eqn 4}$$

The expected value of S for our discrete approximation is $\Sigma S_i(t)/n$, where n is the number of categories ($n = 10$). This average should approximate equation 2 for sufficiently large n.

Two other equations are needed to complete the

model. For the adult hopper, we have

$$\frac{dA}{dt} = \lambda A(t - T_E - T_N)\frac{\Sigma S_i(t - T_N)}{n}e^{-\delta_E T_E}e^{-\delta_N T_N}$$

$$-\delta_A A(t), \qquad\qquad \text{eqn 5}$$

where $A(t)$ is the density of adults at time t, δ_N and δ_A are the mortality rates of the nymphal and adult stages, and T_N is the development time of the nymphs. The first term in this equation describes the rate at which nymphs mature into adult hoppers, the second the rate at which adult hoppers die off. For the adult parasitoid, we have

$$\frac{dP}{dt} = \frac{\Sigma aP(t - T_J)\theta_i E_i(t - T_J)}{n}e^{-\delta_J T_J} - \delta_P P(t) \qquad \text{eqn 6}$$

where δ_J and δ_P are the mortality rates of juvenile and adult parasitoids, respectively, and T_J is the development time of the parasitoid. The first term here is the expected rate at which host eggs are parasitized and turned into immature parasitoids, the second the rate at which adult parasitoids die.

The model proved too complex for stability analysis and so we examined its behaviour numerically using the software package SOLVER (Blythe *et al.* 1990), across a range of values of k. Table 1 summarizes the parameter values used in our numerical solutions of the system. Estimates were available for most of the parameters in the model, except the nymphal and adult hopper mortality rates. Both rates would be difficult to measure in the field, but are probably high. For adult hoppers, we assume that they live for 5 days on average ($\delta_A = 0.2$ day^{-1}), long enough to lay approximately half of their total egg complement. This short reproductive life span is in accord with our own observations that pulses of adult hoppers persist only a short time in the field and that adult mortality is thought to be high (Denno, Olmstead & McCloud 1989). To simplify the model, we shifted the short (2–3-day) preoviposition period of the adult hopper to the nymphal stage, slightly lengthening its duration. Because the nymphal mortality rate (δ_N) is unknown,

we examined the model's behaviour across a broad range of values of this parameter. Finally, we used a single value of the parasitoid attack rate (a), because this parameter only scales the densities of host and parasitoid in the model.

Figure 3a summarizes the different outcomes we obtained in numerical solutions of the model, across a grid of k and $\delta_N T_N$ values (the product $\delta_N T_N$ is equivalent to the k-value for nymphal mortality), and using the parameter estimates in Table 1. The model was initially perturbed from equilibrium by a brief doubling of the nymphal mortality rate. Several different types of dynamic behaviour occurred after this perturbation. At the points in parameter space marked **S**, the model was stable, with overlapping generations and a stable age structure for both organisms. Cycles in the host and parasitoid age structure with a period of one generation (i.e. generation cycles) occurred at the points marked **GC**. At points marked **U**, long-term oscillations in host and parasitoid density occurred; sometimes these were diverging oscillations, while at other points long-term limit cycles occurred. Generation cycles were often superimposed on these long-term oscillations. Given that the median value of k obtained from our field study was 0·479 (Reeve *et al.* 1994), the model suggests that *Anagrus* has the potential to induce generation cycles in the system, except at very high nymphal mortality rates. Large values of $\delta_N T_N$ reduce the overall growth rate of the hopper population, and as in most predator–prey models this has a stabilizing effect on the system (Hassell 1978).

What is the source of the stability in the model? Is it due to variation in the relative risk of parasitism, or does it arise from the invulnerable (but brief) adult hopper stage? To answer this question, we reduced the influence of the invulnerable stage by increasing the adult mortality rate (δ_A), while simultaneously increasing the host fecundity (λ), so that the number of eggs laid during the average adult life span (λ/δ_A) remained constant. This reduces the length of adult stage without affecting the rate of increase of the hopper population. The effect of this manipulation is nearly to eliminate the region of stability in favour of generation cycles (Fig. 3b). Thus, stability in the model is dependent on the existence of an invulnerable stage in the hopper. In its absence *Anagrus* would have a net destabilizing effect on the hopper age structure, no matter the value of k, because of the pronounced asynchrony between host and parasitoid development.

Also shown in Fig. 3 are the local stability boundaries for a model which incorporates heterogeneity in risk in a phenomenological way, patterned after one developed by Godfray & Hassell (1989), and analysed using the methods described in Murdoch *et al.* (1987) and Gordon *et al.* (1991). The model is composed of three equations, describing the dynamics of the hopper eggs and adults, and adult parasitoids:

Table 1. Parameter estimates used in Models A and B

Parameter	Estimate	Source
λ	3·0 eggs day^{-1}	Denno & McCloud (1985)
a	1·0 day^{-1}	Scaling parameter
k	varies	
δ_E	0·0 day^{-1}	R.F. Denno, unpublished data
δ_N	varies	
δ_A	0·2 day^{-1}	See text
δ_J	0·0098 day^{-1}	Cronin & Strong (1990a)
δ_P	0·5 day^{-1}	Cronin & Strong (1990a)
T_E	14 days	Roderick (1987)
T_N	28 days	Roderick (1987)
T_J	28 days	Cronin & Strong (1990a)

$$\frac{dE}{dt} = \lambda A(t) - \lambda A(t - T_E)S(t)e^{-\delta_E T_E}$$

$$- \frac{k}{T_E} \ln\left(1 + \frac{aT_E P(t)}{k}\right)E(t) - \delta_E E(t), \qquad \text{eqn 7}$$

$$\frac{dA}{dt} = \lambda A(t - T_E - T_N)S(t - t_N)e^{-\delta_E T_E}e^{-\delta_N T_N} - \delta_A A(t),$$

$$\text{eqn 8}$$

and

$$\frac{dP}{dt} = \frac{k}{T_E} \ln\left(1 + \frac{aT_E P(t - T_J)}{k}\right)E(t - T_J)e^{-\delta_J T_J} - \delta_P P(t),$$

$$\text{eqn 9}$$

where

$$S(t) = \exp\left(-\int_{t-T_E}^{t} \frac{k}{T_E} \ln\left(1 + \frac{aT_E P(x)}{k}\right)dx\right).$$

$$\text{eqn 10}$$

In this model the instantaneous rate of parasitism is described by the term

$$\frac{k}{T_E} \ln\left(1 + \frac{aT_E P(t)}{k}\right), \qquad \text{eqn 11}$$

and is a non-linear function of parasitoid density. This term is derived from the discrete-time negative-binomial model (Godfray & Hassell 1989) and assumes that the pseudo-interference found in this model will transfer to a continuous-time framework, leading to density dependence in the parasitoid population. This is not necessarily the case, since heterogeneity in risk generates no pseudo-interference in the continuous-time framework of Murdoch & Stewart-Oaten (1989). It is clear from Fig. 3 that this simple phenomenological model does approximate the behaviour of our more complex one, however, that we derived by making explicit assumptions about host and parasitoid movement. This result provides some justification for the use of the phenomenological model in systems that satisfy these assumptions, namely a sessile vulnerable stage during which relative risk is constant, and mobile adult hosts and parasitoids.

MODEL B

In this model we incorporate the second mechanism that could generate density dependence in the parasitoid population, direct interference among searching *Anagrus*. We develop a separate model for this mechanism, rather than add it to Model A, because we want to determine whether direct interference alone provides sufficient density dependence for generation cycles to occur. In addition, we have no direct evidence that the spatial heterogeneity in parasitism we have observed actually generates density dependence in the parasitoid population, in the field. Although the
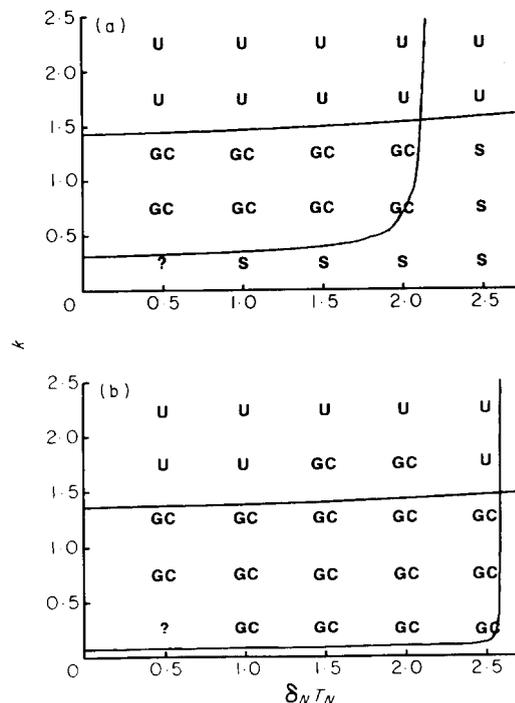

Fig. 3. The behaviour of numerical solutions of Model A, as a function of k and $\delta_N T_N$, for (a) the default parameter values, and (b) $\delta_A = 0.5$, $\lambda = 7.5$. The symbol **S** denotes a stable solution at that point in parameter space, **GC** the occurrence of generation cycles, and **U** long-term oscillations in host and parasitoid density. The symbol **?** denotes a parameter value where numerical difficulties prevented further analysis of model behaviour. Also shown are the stability boundaries for the phenemonological model of Godfray & Hassell (1989).

Prokelisia–Anagrus system seems to satisfy the assumptions necessary for this to occur, we take a cautious approach and separately examine each mechanism for its ability to produce generation cycles.

Our model for direct interference makes use of the model described by equations 7–10. To add direct interference to this model, we replace the instantaneous risk of parasitism with the function:

$$\frac{1}{T_E}\left[aT_E P(t)\right]^{1-m}, \qquad \text{eqn 12}$$

where m is the interference coefficient. This function was derived by Godfray & Hassell (1989) from the discrete-time Hassell & Varley (1969) interference model, and provides an appropriate continuous-time analogue. The local stability boundaries for this model are shown in Fig. 4, as a function of m, and the nymphal mortality rate $\delta_N T_N$, with the other parameters as in Table 1. Given the degree of interference in the real system ($1 - m = 0.413$), Model B suggests that the parasitoid could induce generation cycles in our system, although if nymphal mortality rates are high enough stability occurs (Fig. 4a). However, like Model A the stability in Model B is contingent on the existence of an invulnerable adult host stage. If we
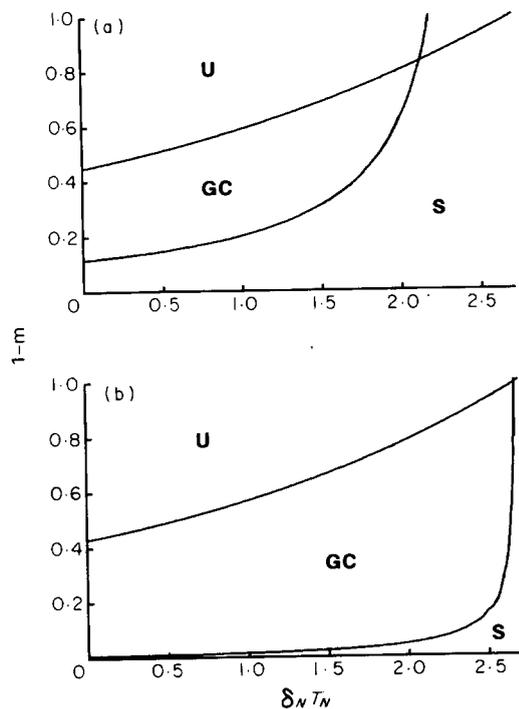
Fig. 4. Stability boundaries for Model B, for (a) the default parameter values, and (b) $\delta_A = 1\cdot0$, $\lambda = 15\cdot0$. Stable age structures occur in the region labelled **S**, generation cycles in the region **GC**, and long-term diverging oscillations in the region **U**.

Fig. 5. Temporal patterns of abundance and parasitism for *Prokelisia* and *Anagrus* on an archipelago of four small *Spartina* islands in Oyster Bay, Florida. (a) Host density (eggs per leaf) and parasitoid density (female *Anagrus* wasps per sticky-trap) across 29 sampling dates. (b) Host density (eggs per leaf) and the fraction of hosts parasitized by *Anagrus*. The x-axis is the day on which the samples were taken, with day zero being the first sampling date.

reduce the influence of this stage as in Model A, the area of stability disappears (Fig. 4b).

Temporal patterns of abundance and parasitism

If *Anagrus* were contributing to the formation of generation cycles in *Prokelisia*, we would expect to see a characteristic cyclic pattern of adult parasitoid abundance (see Godfray & Hassell 1989), with peaks of adult *Anagrus* occurring several weeks after peaks of egg density, midway through the host life cycle. Parasitism rates should also cycle in this way, with the highest rates occurring at low egg density, and vice versa. There is evidence for both temporal patterns (Fig. 5). In the same study that yielded the data in Fig. 1, *Prokelisia* and *Anagrus* densities were censused approximately weekly on an archipelago of four small islands, for 29 consecutive dates. On each date, a sample of 92 *Spartina* leaves was taken and dissected to estimate host density and parasitism rates, while adult parasitoid densities were censused with a grid of 48 yellow sticky traps (for further details see Strong 1989). Adult parasitoid density clearly shows two distinct, delayed, peaks in response to two large pulses in host density (Fig. 5a). Moreover, parasitism rates reached their highest levels immediately following the two peaks in hopper density, when egg densities were lowest (Fig. 5b). This cyclic (and inversely density-dependent) pattern of parasitism has been encountered in other field studies (Stiling & Strong 1982b;
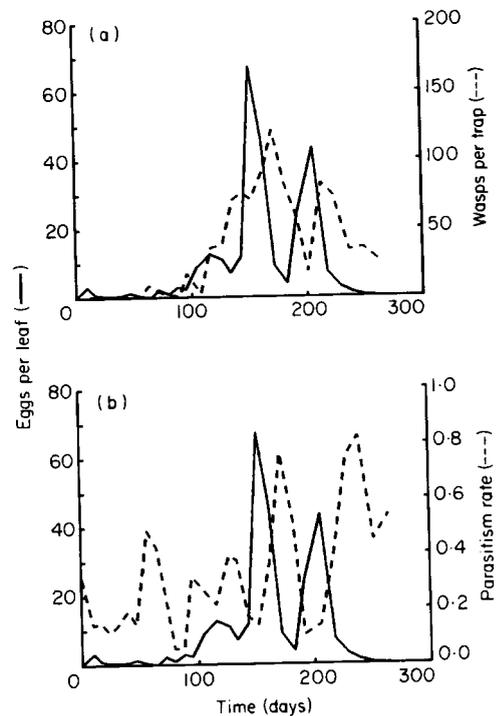
Stiling *et al.* 1991) and is a characteristic feature of this system.

Discussion

The *Prokelisia–Anagrus* system appears to have all the theoretical prerequisites for generation cycles to occur. The life cycle of *Anagrus* is considerably shorter than that of the hopper, and just as critical, the adult hopper probably only lives and reproduces for a few days. There is also evidence for two separate mechanisms that could generate the necessary density dependence in the parasitoid population; pseudo-interference arising from heterogeneity in the risk of parasitism, and direct interference. Our modelling results confirm that *Anagrus* has the potential to induce generation cycles in the hopper, except at very high nymphal mortality rates, where stability occurs because the rate of increase of the hopper population is low. Even if high mortality rates are common, however, we would still expect *Anagrus* to contribute to generation cycles, although it would not be the sole agent. Figure 5 provides empirical evidence that *Anagrus* can contribute to generation cycles in this system. Parasitism rates were low during peaks of egg density and high during troughs, a pattern of mortality that would reinforce cycles in the age structure of the host.

Model A further illustrates how the details of a

specific continuous-time model can affect its stability. In this model, pseudo-interference can arise through differences in the vulnerability of hosts to parasitism, or from parasitoid aggregation, just as in its discrete-time counterparts (Bailey *et al.* 1962; May 1978). For small k ($k < 1.5$) there is apparently sufficient pseudo-interference to prevent long-term oscillations in host and parasitoid density, and in this way the model is similar to its discrete-time analogue. However, pseudo-interference alone is insufficient to fully stabilize the system. In Model A, stability depends not only on the value of k, but on nymphal mortality rates, and especially the presence of an invulnerable adult host. Without this stage *Anagrus* would destabilize the system, whatever the value of k (or the degree of direct interference, see Model B), because of the asynchrony between host and parasitoid development.

The models examined in this paper, and the temporal pattern of parasitism and parasitoid abundance, suggest that *Anagrus* at least contributes to the formation of generation cycles in this system. There are two other factors, however, that could potentially combine with *Anagrus* to produce generation cycles. One is another natural enemy, the strepsipteran *Elenchus koebelei*, that sometimes infects a substantial fraction of *Prokelisia* nymphs and adults (Stiling *et al.* 1991). Strepsipterans are believed to cause generation cycles in another delphacid planthopper, the West Indian cane-fly *Saccharosydne saccharivora* (Metcalfe 1971), and might act in concert with *Anagrus* in our system. There may also be occasional environmental fluctuations that perturb the age structure of the hopper and so produce transient generation cycles. Although both *Prokelisia* and *Anagrus* can reproduce throughout the year in Florida, extreme temperatures and tides do occur, and these might inflict differential mortality on the more vulnerable life-history stages. Additional studies will be necessary to measure the effects of *Elenchus*, and the environment, on *Prokelisia* dynamics, and so define the unique contribution of *Anagrus*.

Acknowledgements

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