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GENERATION CYCLES IN STAGE STRUCTURED POPULATIONS

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Some insect populations exhibit cycles in which successive population peaks may correspond to effectively discrete generations. Motivated by this observation, we investigate the structure of matriarchal generations in five simple, continuous-time, stage structure models in order to determine the proportion of individuals in one population peak who are the offspring of individuals in the pervious peak. We conclude that in certain models (including a model of Nicholson's blowflies) successive population peaks do not correspond to discrete generations, whereas in others (including some models of uniform larval competition) successive peaks may well approximate discrete generations. In all models, however, there is eventually significant overlap of generations.

1. Introduction. It is widely believed that insect populations often show well separated generations, even in the absence of strong external cues. In the literature (e.g. Ebenman, 1988; Godfray and Hassell, 1989 and the references therein) there are examples of both laboratory and natural populations exhibiting generation cycles without any obvious exogenous excitation. There are several possible mechanisms for such cycles: uniform larval competition (Gurney *et al.*, 1983, Gurney and Nisbet, 1985), asymmetric larval competition (Bellows, 1982; Lawton and Hassell, 1981; Bellows and Hassell, 1988), egg cannibalism (Diekmann *et al.*, 1986; Hastings, 1987; Hastings and Constantino, 1987) and several forms of adult competition (Gurney *et al.*, 1980; Nisbet and Bence, 1989).

Some of Nicholson's (1954, 1957) experiments on the Australian sheep blowfly *Lucilia cuprina* (Wied.) provide classic examples of cycles with a period comparable in magnitude to the generation time. The limiting factor in these experiments was the availability of protein food (needed for production of eggs) for the adult flies. The mechanism which causes the cycles is believed to be the delay between the change in fecundity and the subsequent change in the rate of recruitment to the adult population. A number of models have been developed,

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all showing cycling behaviour as a result of this mechanism (Varley *et al.*, 1973; May, 1974; Maynard Smith, 1974; Oster, 1976; Gurney *et al.*, 1980; Readshaw and Cuff, 1980; Gurney *et al.*, 1983). Generation cycles also occur in populations regulated by larval competition (Takahashi, 1973; White and Huffaker, 1969; Gurney *et al.*, 1983). To model the effect of uniform larval competition for food, Gurney and Nisbet (1985) [see also Jones *et al.* (1988) for a more rigorous mathematical treatment of one model] studied several continuous-time, stage-structure models which under certain conditions can exhibit cyclic fluctuations. The period of the cycles may range from one to several times the development time, depending on whether the feedback on larval recruitment or loss rates is immediate or delayed. Immediate expression causes cycles with a period between one and two times the development time, delayed expression results in periods between two and four development times.

In the literature cited above, terms like "generation cycles" or "discrete generations" are used to describe cycling behaviour, but are not always defined precisely. In the present paper, we use the term "generation cycles" as a catch-all phrase covering any cycles or quasi-cycles with a period comparable in magnitude to the generation time. However, the word generation itself has (at least) two different meanings which are not always distinguished: it can either refer to a group of individuals born in the same time interval or may be defined (iteratively) as a group whose parents formed the previous generation. Rubinow and Oppenheim Berger (1979) use the words "temporal" and "matriarchal" generations to express this difference. In this paper, we concentrate on matriarchal generations and ask whether the generation cycles in several of the models cited above reflect the generation structure; for example we explore the extent to which the individuals in one population peak are the offspring of individuals in a previous peak. We also try to relate the generations of continuous models to the predictions of discrete generation models, because of the existence of a wide body of literature on population regulatory mechanisms and population genetics that assume non-overlapping generations.

We answer these questions for the "blowfly" model of Gurney *et al.* (1980) and for four models of larval competition, formulated in Gurney and Nisbet (1985). The use of existing models, enables us to take advantage of known results concerning equilibria and stability. Furthermore these models turn out to offer examples of single generation cycles and also of much more complex generation structures because of the different regulatory mechanisms involved. However, our basic formalism, which generalizes some preliminary work by Nisbet *at al.* (1988), is applicable to a wide class of models.

In all the models we study, the life history of the insects is divided into four developmental stages of which only two occupy a significant time span: the larval and adult stage. The egg and pupal stage are both assumed to be infinitesimally short. This results in the following pair of coupled delay-difference equations describing the dynamics of the adults and larvae:

$$\dot{L}(t) = B(t) - M(t) - \Delta(t)L(t), \tag{1a}$$

$$\dot{A}(t) = \alpha(t)M(t) - \delta A(t), \tag{1b}$$

where:

$$M(t) = B(t-\tau(t))P(t)\{1-\dot{\tau}(t)\}, \tag{1c}$$

$$B(t) = f(t)A(t), \tag{1d}$$

$$P(t) = \exp\left[-\int_{t-\tau(t)}^{t} \Delta(x)\,\mathrm{d}x\right]. \tag{1e}$$

$$W(t) = \int_{t-\tau(t)}^{t} G(x)\,\mathrm{d}x, \tag{1f}$$

with: $A(t)$ the number of adults at time t; $B(t)$ the number of eggs laid per unit time at time t; $G(t)$ the larval growth rate at time t; $L(t)$ the number of larvae at time t; $M(t)$ rate of entry into the pupal stage at time t; $\tau(t)$ development time from egg to adult for an individual maturing at time t; $P(t)$ proportion of larvae hatched at $t-\tau(t)$ who survive to t; $W(t)$ weight of pupating larvae at time t; $\alpha(t)$ proportion of successful pupations at time t; δ adult per capita death rate, assumed constant in all models; $\Delta(t)$ larval per capita death rate at time t; $f(t)$ the number of eggs laid per adult per unit time at time t.

Equations (1a) and (1b) simply state that changes in the number of individuals in a particular stage can only arise through recruitment to the stage, maturation from the stage, or death. The remaining equations give receipes for calculating these quantities.

To specify one particular solution for this system, an initial history for the number of adults and larvae between time $-\tau(0)$ and 0 needs to be given. Beyond positivity, there is no restriction on the form of this initial history, and we shall restrict our attention to specific models where, as far as we can tell from numerical studies, the long term fate of the population (equilibrium, stable limit cycle or possibly chaos) does not depend on the selection of initial history. For convenience we therefore always assume no animals to be present before time zero and start the calculation with an initial number of adults at time zero. This mimics the inoculation of a laboratory experiment or the immigration of a group of adults into an unoccupied territory.

Our models make different assumptions concerning functional relations between $\alpha(t)$, $\Delta(t)$, $\theta(t)$ or $f(t)$ and the stage populations, with each model including only a single regulatory factor. The five models are as follows.

The NB (*Nicholson blowfly*) model, in which the adult fecundity $f(t)$ depends on the number of adults.

The LD model, in which the *larval death* rate $\Delta(t)$ depends on the number of larvae.

The MT model, in which the *maturation time* $\tau(t)$ depends on the history of the growth of the larvae.

The PS model, in which *pupation success* $\alpha(t)$ depends on the weight of the larvae.

The AF model, in which the *adult fecundity* $f(t)$ depends on the weight of the larvae at pupation. [Note that equation (1d) requires modification for this model.]

The functional forms used in each model are listed in Table 1.

Table 1. The five "stage structure" models used in this paper. A full account of the NB model is in Chapter 8 of Nisbet and Gurney (1982). Details of the other four models are in Gurney and Nisbet (1985). All models follow equations (1a–f); the table gives the (only) density dependent function for each model

Model	Density dependence	Functional form
NB	$f(t)$	$f(t)=q\exp[-N(t)/N_0]$
LD	$\Delta(t)$	$\Delta(t)=X[1/(1+L(t)/L_0)-Y]^{-1}\quad(L<L_0(1-Y)/Y)$
MT	$G(t)$	$G(t)=[g_m/(1+L(t)/L_0)-\Gamma)_+$, Maturation at $W=W_p$
PS	$G(t)$, $\alpha(t)$	$G(t)$ as in MT
		$\alpha(t)=[(W(t)-W_m)/(W_H+W(t)-W_m)]_+$
AF	$G(t), f(t)$	$G(t)$ as in MT
		$\dot{B}(t)=qM(t)W(t)-\delta B$ (instead of 1d)

The equations (1a–c) which characterize all the models are special cases of a general linear form for the adult dynamics, namely:

$$\dot{A}(t)=r(t)A(t-\tau(t))-\delta A(t), \tag{2}$$

with:

$$r(t)=\alpha(t)f(t-\tau(t))P(t)[1-\dot{\tau}(t)\}. \tag{3}$$

Consequently, we can generalize our methods of analysis to any stage structure models reduceable to this form. We shall show that if $r(t)$ and $\tau(t)$ are known, the generation structure of a model population can be calculated without having to compute the actual number of adults and larvae.

2. Modelling the Generation Structure

2.1. General formalism. We now write down equations, valid for all our models except AF and easily adapted for that model, describing the matriarchal generations, which are defined recursively as groups of individuals whose mothers belonged to the previous generation. Because of the recursive nature of this definition an initial generation needs to be given and we arbitrarily assign I adults out of those present at $t=0$ to the initial gneration. From this we find the equations describing the k^{th} adult generation, $A_k(t)$ to be:

$$\dot{A}_k(t)=\alpha(t)M_k(t)-\delta A_k(t), \tag{4a}$$

$$M_k(t)=B_k(t-\tau(t))P(t)\{1-\dot{\tau}(t)\}, \tag{4b}$$

$$B_k(t)=f(t)A_{k-1}(t), \tag{4c}$$

or, in terms of the regulatory function:

$$\dot{A}_k(t)=r(t)A_{k-1}(t-\tau(t))-\delta A_k(t). \tag{5}$$

The initial generation is given by:

$$A_0(t)=I\,e^{-\delta t}, \quad t\geqslant 0, \tag{6a}$$

and the system of equations is solved with the assumed initial histories:

$$A_k(t)=0 \text{ (for all } k \text{ and all } t<0). \tag{6b}$$

Equations (4)–(6) do not involve $L(t)$ or $A(t)$ explicitly, and with these equations we can calculate any number of generations for a given $r(t)$ and $\tau(t)$. In models where the delay is constant, the total number of adults in the generations at any given time (i.e. any survivors from the initial I individuals and their descendents) is given by the generation sum:

$$A(t)=\sum_{k=0}^{\infty} A_k(t). \tag{7}$$

For any finite value of t, there are of course only a finite number of non-zero terms in the sum. When the delay τ is fixed, the upper summation limit is $[t/\tau]$ (where $[x]$ denotes largest integer less than or equal to x). In models (such as MT) with variable delay, the sum must run to $[t/\tau_{\min}]$ where $\tau_{\min}$ is the minimum development time permitted by the assumed functional form for the development rate $G(t)$ in the model under study.

Because of the assumption of a constant *per capita* death rate for adults, the present models cannot produce truly discrete generations. Even if over some time interval maturation into the adult stage stops totally, the number of adults will decrease exponentially but never become zero. When the next generation starts, some adults of the former generation must therefore still be alive; consequently the generations will always overlap. However, it is of interest to know whether there exist conditions under which there is only a small amount of overlap. We investigate this later in the paper.

2.2. The generation structure of a population in equilibrium. All of our models can have a steady-state, and it is thus instructive to study the generation structure of the models at equilibrium, where, at all times t:

$$r(t)=\delta, \quad \tau(t)=\text{constant}. \tag{8}$$

The equilibrium matriarchal generations are calculated from equations (5) and (6), with $r(t)$ set equal to δ:

$$\dot{A}_k(t)=\delta A_{k-1}(t-\tau)-\delta A_k(t), \tag{9a}$$

$$A_0(t)=I\exp(-\delta t) \qquad t\geqslant 0, \tag{9b}$$

which are to be solved with the initial conditions:

$$A_k(t)=0 \quad t<k\tau. \tag{9c}$$

This set of equations can be solved analytically, the successive generations being given by:

$$A_k(t)=I\exp\{-\delta(t-k\tau)\}\delta^k(t-k\tau)^k/k! \quad t\geqslant k\tau, \tag{10a}$$

$$A_k(t)=0 \qquad t<k\tau, \tag{10b}$$

sample plots of which are shown in Fig. 1. This figure also has plots of the generation sum which represents the sum of the adults assigned to the initial generation and their offspring, and is given by:

$$A_g(t)=\sum_{k=0}^{[t/\tau]}\exp\{-\delta(t-k\tau)\}\delta^k(t-k\tau)^k/k! \tag{11}$$

Note that $A_g(t)$ will always be smaller than or at most equal to A^*, the equilibrium population, because there will normally exist a group of individuals (the offspring of individuals who were in the larval stage at $t=0$) not assigned to the generations.

The equilibrium generation structure has two further properties that merit attention. Firstly, *each generation has a maximum that is lower than that of the former generation*, provided the time between the maxima of the generations is unequal to τ. This can be proved as follows: let t_k be the moment at which generation k has its absolute maximum. At this moment:

$$\dot{A}_k(t)=0, \tag{12}$$

and thus from equation (9a):

$$A_{k-1}(t_k-\tau)=A_k(t_k). \tag{13}$$

If the time between the maxima is unequal to τ, the maximum value of each

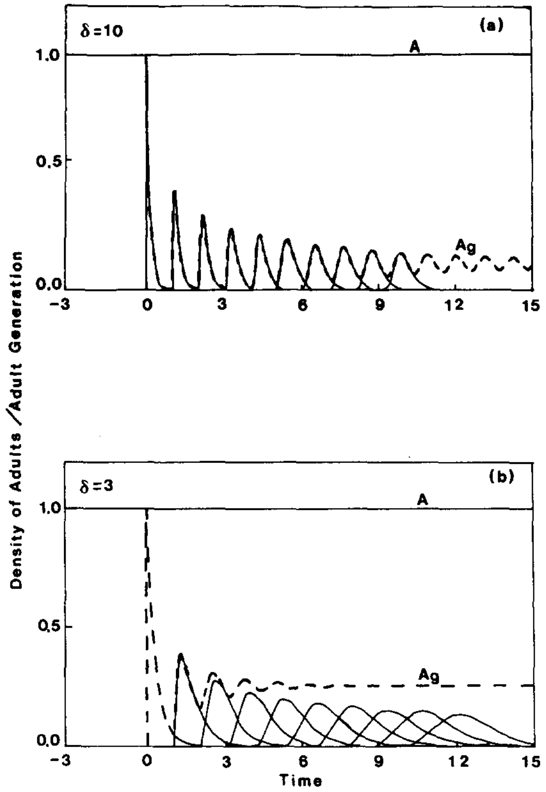

Figure 1. The generation structure during equilibrium. Thick dashed line stands for A_g, thin drawn lines show subsequent generations. The total density of adults A remains contant: (a) $\delta = 10$; (b) $\delta = 3$.

generation will thus be smaller than that of its predecessor. A corollary of this result is that no longlasting, non-zero solutions can exist.

Secondly, *the generations remain constant in size, but tend to spread out as time increases*. To prove this, first note that all generations subsequent to the zero'th start to grow at successive times which equal integer values of τ. Each generation has only one maximum, at time $k(\tau + 1/\delta)$. The value of each maximum is $I\exp(-k)k^k/k!$. As $k \to \infty$ the maximum of a generation thus approaches zero. However, although the maxima of the generations becomes smaller, the total size of the successive generations will remain equal (easily proved by integrating equation 10a). Furthermore, as time goes to infinity the total number of adults summed over all the generations will become a constant number, i.e. the limit:

$$\lim_{t \to \infty} A_g(t) = A_g^*, \tag{14}$$

will converge. In fact the limit can be shown to have the value:

$$A^*_g = I/(1+\delta\tau). \tag{15}$$

We have thus shown that in a population at equilibrium, a generation structure exists in which the generations remain constant in size, but tend to spread out as time increases. In proving these properties we made considerable use of the assumption of a constant *per capita* adult death rate; however the results appear to be quite robust against relaxation of this assumption. For example, if we assume a *fixed lifetime* for each adult and assume no mortality other than through reaching that fixed age, then a broadly similar pattern of generations results (see Appendix A).

2.3. The generation structure of a cycling population. In the special case of a population at equilibrium an analytical solution could be found. The general solutions of the equations with a fixed delay (all models except MT) are integrals of the following form:

$$A_k(t) = e^{-\delta(t-k\tau)} \times \int_{k\tau}^{t} \int_{k\tau}^{x_k} \int_{k\tau}^{x_{k-1}} \cdots$$

$$\int_{k\tau}^{x_1} r(x_k) r(x_{k-1}-\tau) r(x_{k-2}-2\tau) \ldots r(x_1-(k-1)\tau)\, dx_1 \ldots dx_k. \tag{16}$$

and for models with a variable development time a similar, but even more complicated integral can be derived. Unfortunately, this integral is of little practical utility and is numerically less tractable than the original system of delay-differential equations. We therefore use the delay differential equations (1a–c) in studying the generation structure of a cycling population.

Suppose then that the total number of adults is executing a stable limit cycle. It follows from the argument in Section 2.1, that successive population peaks cannot correspond to truly discrete generation. Indeed, we expect some properties qualitatively similar to those already studied in equilibrium: the generations will spread out and their maxima will decrease. However, the cycling regulatory function may cause humps on both sides of the maximum. If, as is normally the case (Jones *et al.*, 1988), the period of the cycles in number of adults (and hence the period of the regulatory function) exceeds the development time, the time between the start of a generation and its principal maximum will increase with increasing generation number. The generation size may thus eventually be influenced by the periodicity in the regulatory function during the "rise" phase and new local maxima may appear. Similarly, new local maxima may appear in the tail depending on the magnitude of the parameter group $\delta\tau$. The bigger δ, the faster a generation will go to zero. For small δ and τ the decay will be so slow that one cycle after the largest peak, the generation size is still considerable. Beyond these general observations, we expect the pattern to be model specific, and hence now turn our attention to numerical results for our five models.

3. Generation Structure Related to the Mechanism of Population Regulation.

The general theory in the preceding section establishes that the generation structure at equilibrium is independent of any specific regulatory mechanism. However we know from the work of Gurney and Nisbet (1985) that the period of population cycles *is* affected by the mechanism of intraspecific competition, so it is natural to investigate how the generation structure of populations executing large amplitude cycles reflects the mechanisms that produce the cycles. We therefore now present sample numerical calculations of the generation structure for each of our five models, using where possible the same parameters as in previous published work on these models (Gurney and Nisbet, 1985; Gurney *et al.*, 1980; Nisbet *et al.*, 1989).

3.1. The NB model.

It is well known from previous work on this model that limit cycles, if they occur, have a period greater than twice the developmental delay. Figure 2 contains an example of such cycles obtained with parameters appropriate to Nicholson's blowflies. Also illustrated on that figure are two additional curves which help tease out the demography of the cycles: total egg production rate $B(t)$ and the average age of the adult population (computed by a method outlined in Appendix B). Starting at a peak in the adult population, the cycle has a decline phase during which the population drops (through mortality) to a level at which significant egg production is possible, a period of egg production which continues until sufficient young become adults and suppress further reproduction, and finally an interval (roughly equal to the development time) in which remaining juveniles mature to become adults. Thus the cycles cannot even approximate discrete generations since the essential feature of the demography is that the adults in any one population peak are a mixture of those with very old and very young mothers. The "average adult age" plot confirms this: although the cycle period is over 38 days, the maximum value of the average age is around 33 days and occurs during a burst of egg production.

Figure 3 illustrates how the generations rapidly spread over the successive peaks of the population cycles. We arbitrarily defined as generation zero all adults present at $t = 50$ days (during a decline and before the onset of significant egg production). Unsurprisingly virtually all the members of generation one appear in the next population peak, but that peak also contains a significant contribution from members of generation two, in agreement with our understanding of the demography. Successive generations spread over an increasing number of population peaks.

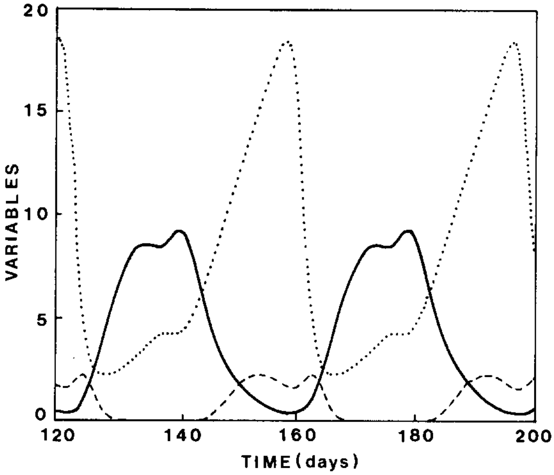

Figure 2. Demography of cycles in the "Nicholson blowfly" (NB) model. The continuous curve is the adult population, the broken curve the egg production rate, and the dotted curve the average adult age (i.e. time since recruitment to the adult stage; add 15 days to get time since egg hatch). Parameters: $q=6$ day^{-1}; $N_0=1$, $m=0.2$ day^{-1}; $T=15$ days.

3.2 The LD and MT models. Figures 4a and b show the total number of adults and the regulatory function for the selected parameter sets. As expected, the cycles for both models have a period between τ and 2τ, and the same period is recognizable in the regulatory function.

Figures 5a and b show the first six generations of these models, with the same parameters as in Fig. 4. The MT model clearly shows spreading generations and gives multiple humped generations. The LD model (with our choice of parameters) seems to have single humped generations; to graphical accuracy, each peak seems to be merely one generation and the figure does not give the impression that the generations are rapidly spreading. However, in the previous section we demonstrated that no stable single generation cycle can exist and that ultimately significant overlap will occur. Figure 6 confirms this, though significant spreading only occurs after fifty generations. It turns out that the rate of spreading is largely determined by the dimensionless parameter group $\delta\tau$; plots of the MT model with $\delta=10$ are very similar to Fig. 5.

With our choice of parameters, humps appear faster in the MT than in the LD model, but in both models, the overlap of generations is much slower than with NB. To understand why, we have to consider the time between the start and the maximum of a generation. Each generation starts at $t=k\tau$. The generations during steady-state have their maxima at $t=k(\tau+1/\delta)$, and this is a good approximation to the period of population cycles for the models LD and MT (Gurney and Nisbet, 1985; Jones *et al.*, 1988). The difference between the start and maximum depends on the generation number and approaches k/δ for

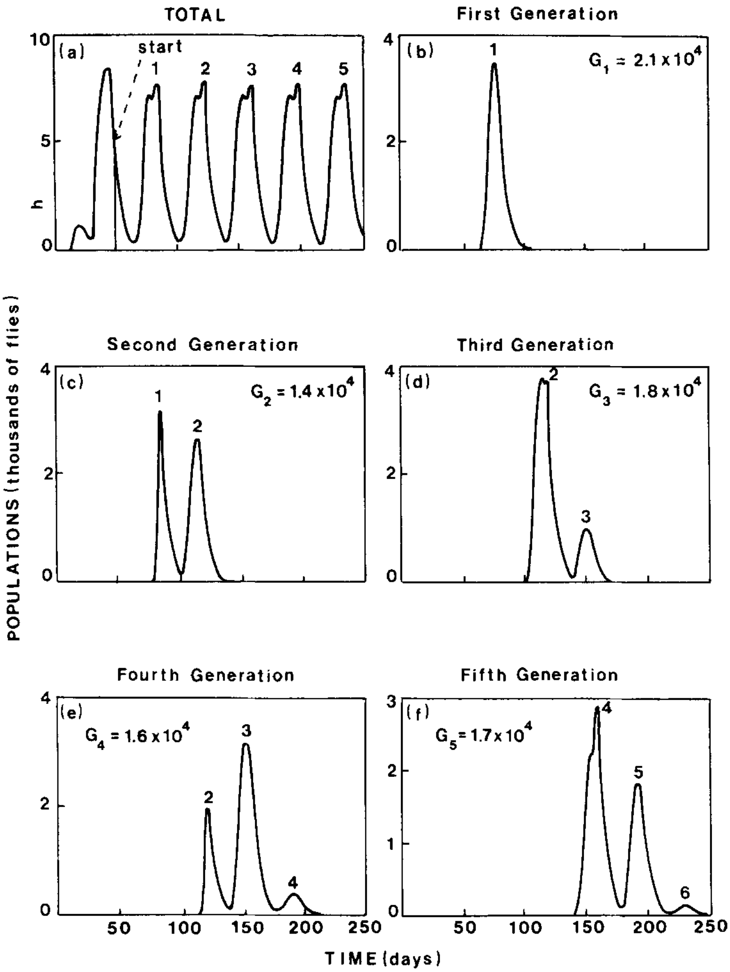

Figure 3. Generation structure corresponding to the cycles in Fig. 2 (from Nisbet *et al.*, 1988). (a) Adult population; (b)–(f) generations 1–5.

LD and MT. For higher generation numbers this will exceed τ and the generations will be exposed to at least one other cycle of the regulatory function and this will cause a small hump in front of the maximum. For later generations this interval will get larger and they will have more humps. Something similar happens at the tails where the rate of decrease (relative to the cycle period) depends on $\delta\tau$. A small $\delta\tau$ will cause a slow decay, so that one period after the start of the decline phase, a considerable population will still be influenced by the cycling regulatory function.

3.3. The PS and AF models. The total number of adults and the regulatory function for these two models (with one set of parameters) are shown in Figs 4c

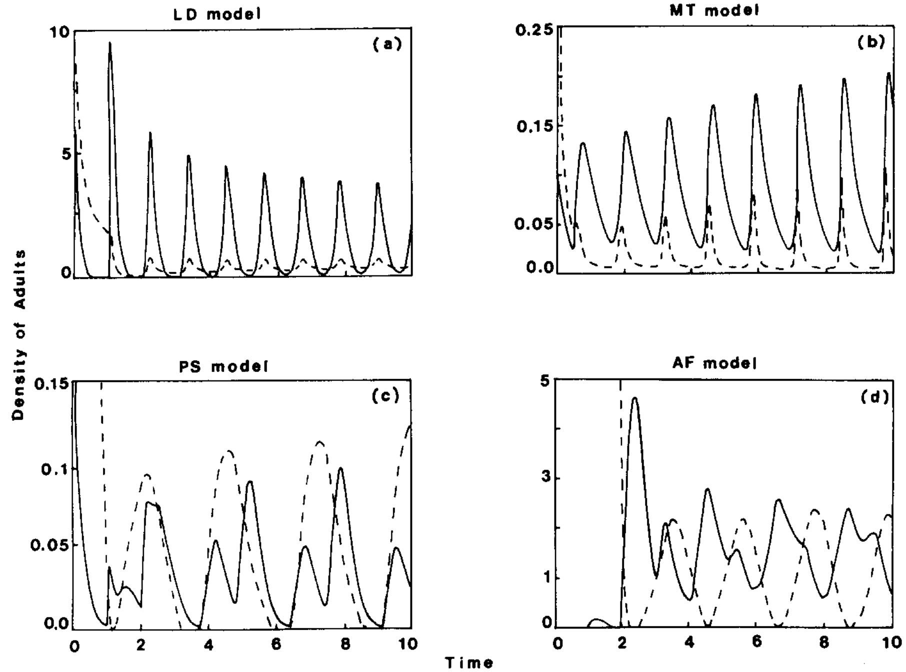

Figure 4. Population trajectories for the four different larval competition models with the selected parameter sets. The density of adults is shown by the continuous line while the dashed line shows the regulatory function: (a) the LD model with $f=200, \tau=1, \delta=10, X=0.01, L_0=1, Y=0.01$; (b) the MT model with $f=180, \delta=3, g_m=1, L_0=1, \Gamma=0.1, W_p=0.15$ (weight at population), $\Delta=4.09$; (c) the PS model with $f=200, \tau=1, \delta=5, g_m=1, L_0=1, \Gamma=0.05, W_m=0.05, W_h=1$; (d) the AF model with $q=300, \tau=1, \delta=5, g_m=1, L_0=1, \Gamma=0.1$.

and d. Again we see that the population oscillates with the same period as the regulatory function. However with these models, the period to delay ratio is always greater than 2 (Gurney and Nisbet, 1985) and *prima facie* we might expect behaviour similar to NB. The first six generations are shown in Figs 5c and d from which we see that each of the humps of the double humped cycles is largely formed by a generation. Thus the double humped structure is much more tightly related to the generation structure than in the NB model.

The first generation of the PS model in Fig. 3c is double humped. We can find an explanation for this in the regulatory mechanism of the PS model, which involves two thresholds: one where growth stops, the other where pupation success drops to zero. Whether these thresholds are crossed depends on the initial numbers of the zeroth generation. A large zeroth generation will produce so many offspring that the number of larvae rapidly grows so large that maturation stops altogether. If this happens before τ, i.e. before the first larvae of the first generation pupate, there will be no maturation at τ and it will only start when the number of larvae has gone down sufficiently to allow

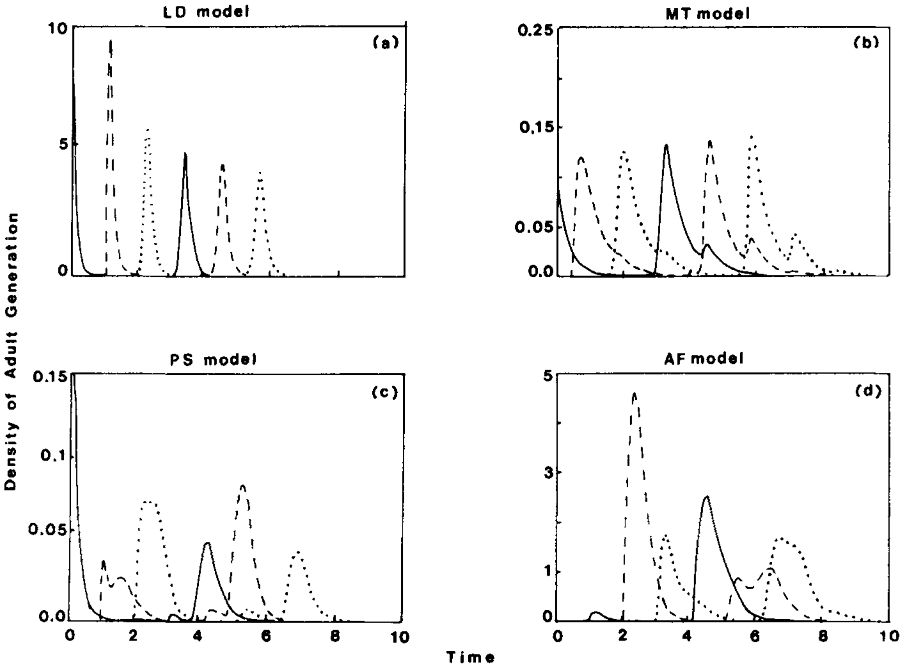

Figure 5. The first six generations for the four larval competition models. Parameters the same as in Fig. 4. Different line types show different generations: (a) the LD model; (b) the MT model; (c) the PS model; (d) the AF model.

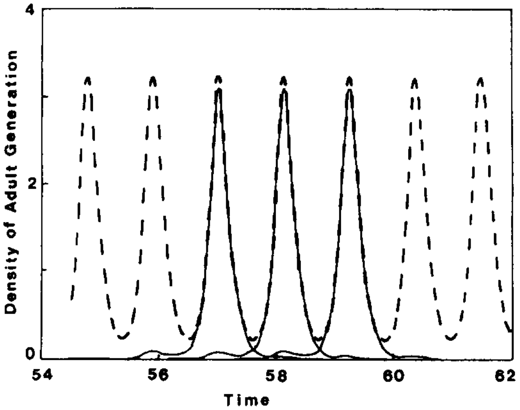

Figure 6. Generations 51, 52 and 53 for the LD model. Parameters the same as in Fig. 4a.

growth or pupation again. This delays the start of the first generation. A condition for the lowest initial number of adults which will cause no maturation at τ can be derived. If the initial number of adults is somewhat lower, some maturation will happen at time τ and for some short time interval thereafter; these adults will then produce offspring causing the number of larvae to rise beyond the threshold at which growth (and hence maturation) will stop. From then on both the number of adults and larvae will decrease till pupation becomes successful again, thus causing double humped generations. For low initial numbers the thresholds are never reached and the first generation is single humped. These double humped first generations do not propagate successfully into the next generations. An analogous argument can be developed for the AF model.

4. From Continuous to Discrete Models. Discrete generation models of a single species take the general form:

$$G_{k+1}=h(G_k), \tag{17}$$

with G_k the size of generation number k and $h(G_k)$ describing some function over G_k. The size of a generation is assumed to depend only on the size of its predecessor and on nothing else. In the continuous models, such a relationship between the magnitude of successive generations is impossible since it woud require an effect to precede its cause (in view of the exponential tail to all generations); however where overlap between generations is small, it might still be valid to approximate a continuous model with a discrete model. In this section we therefore consider discrete models in which population regulation involves similar mechanisms to those already studied, and assess the robustness of the new models as approximations to their continuous counterparts.

If we define the generation size as the total number of adults that once belonged to that generation, then there are two (equivalent) ways to compute the generation size: either you count the emerging pupae or you count the dead adults. This gives:

$$G_k=\lim_{t\to\infty}\int_0^t \alpha(x)M_k(x)\,\mathrm{d}x=\lim_{t\to\infty}\int_0^t \delta A_k(x)\,\mathrm{d}x. \tag{18}$$

For three of our models (LD, MT and PS), we studied the relationship between successive generations by computing the above integrals. In the Figs 7a–c the generation size is plotted against the size of the previous generation. The continuous line connects the points which map the initial value (which equals the size of the zeroth generation) to the size of the first generation (G_1 vs G_0). The other points result from calculations up to the fifth generation. In all models the relationship is not strictly functional; the points exhibit some scatter and there is no perfect fitting discrete model.

It is nevertheless possible, with additional assumptions, to derive approximate discrete models; to illustrate this we now formulate a discrete model

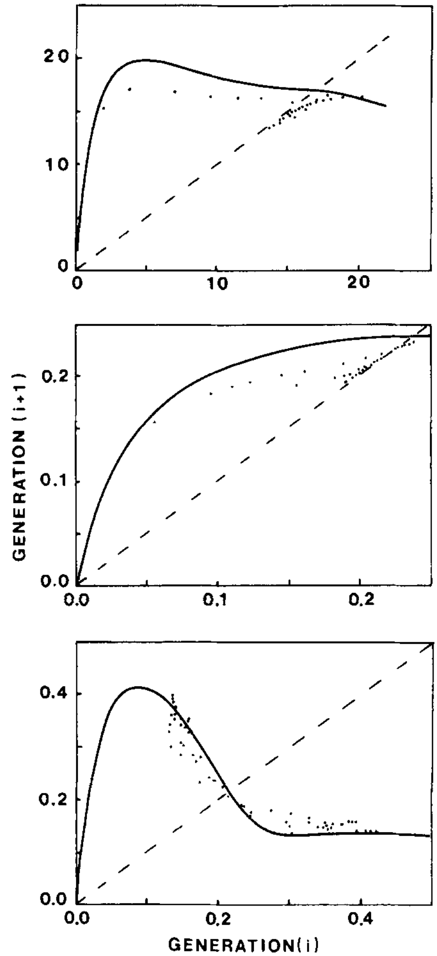

Figure 7. Size of generation against size of the previous generation. Drawn line connects points resulting of zeroth against first generation, dots result from generation sizes up to the fifth generation: (a) the LD model, parameters as in Fig. 4a; (b) the MT model, $f=180$, $\delta=10$, $g_m=1$, $L_0=1$, $\Gamma=0.25$, $W_p=0.25$, $\Delta=3$; (c) the PS model, parameters as in Fig. 4c.

comparable to MT. We choose the MT model because the empirical relationship (Fig. 7b) was not too discouraging, it being much more complicated to derive a discrete model for the PS model because of the form of the graph in Fig. 7c which can be regarded as the superposition of two other curves: the size of the generations in the first hump and the size of the generation in the second hump which can develop for different initial values as we explained in the previous section. The LD and AF models are algebraically not very tractable.

The discrete "MT" model is derived by assuming that all larvae of one generation are born at the same time. Because all larvae are then of the same age, they all have the same maturation time. Let G_{k-1} be the number of adults in the previous generation. The number of larvae in generation k is then given by:

$$L_k(t) = G_{k-1} f \delta^{-1} \exp(-\Delta t). \tag{19}$$

Since in the MT model all pupating larvae are assumed to survice, the number of adults in the next generation is given by:

$$G_k = L_k(\tau) = G_{k-1} f \delta^{-1} \exp(-\Delta \tau). \tag{20}$$

The problem is to find the maturation time τ for this cohort, i.e. the time in which the larvae reach their weight at pupation. This is given by the integral relationship:

$$W(\tau) = \int_0^\tau \left[\frac{g_m}{(1 + L(x)/L_0)} - \Gamma \right]_+ \mathrm{d}x = W_p, \tag{21}$$

which, on substituting from (19) gives:

$$\int_0^\tau \left[\frac{g_m}{1 + G_{k-1} f/(\delta L_0) \exp(-\Delta x)} - \Gamma \right]_+ \mathrm{d}x = W_p, \tag{22}$$

and after evaluating the integral:

$$\frac{g_m}{\Delta} \ln \left[\frac{G_{k-1} f/(\delta z l_0) + \exp(\Delta \tau)}{G_{k-1} f/(\delta L_0) + 1} \right] - \Gamma \tau - W_p = 0. \tag{23}$$

Now τ is simply the positive root of equation (23) which can easily be computed numerically using Newton's method. Once this is done, the relationship between G_k and G_{k-1} follows from equation (20). Figure 8 contains the result of one such calculation ($\delta = 10$). The dots in the figure come from the generation sizes in the continuous model. The correspondence is not total but qualitative prediction of the form of the relationship is good.

5. Discussion. The analysis in this paper has significance beyond the five special models; indeed because of the linear form of equation (5), our methods are applicable to any stage structure models with an unrestricted adult life time and constant adult death rate. Recognizing that the regulatory function and the maturation time contain all information needed for computation of the generation structure can be a powerful tool in analysis of these models.

The results for the generation structure during equilibrium apply to an even

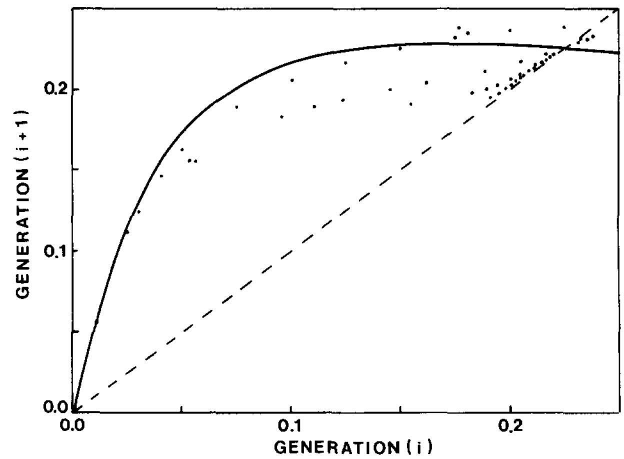

Figure 8. Generation size against previous generation size. Drawn line represents results for equation (20) and (23), dots result from continuous MT model. parameters as in Fig. 7b.

wider class of models, the steady-states of all models in which the recruitment is of the form $r(t)A(t-\tau)$ and the adult death rate is age—but not necessarily density-independent. The analytical form of these solutions make them a useful point of reference for interpreting complex generation patterns in cycling populations, a property we exploited in our numerical studies of the LD and MT models.

It would be interesting to know if there are any circumstances in which sustained, separate generations are possible in stage structure models. In models of the sort studied in the present paper, formally separate generations are not possible, regardless of the form of $r(t)$. One of the reasons for this is the fixed, age independent, *per capita* death rate, which allows infinite lifetimes and causes the long trails of the generations. One might conjecture that models with a finite maximum adult lifetime allow separate generations; however as we showed in Appendix B the time between the start and maximum of a generation will normally increase, potentially causing spreading in the same way as in the present models. It is certainly true that a discrete adult lifetime commonly sharpens single generation cycles in both single-species and host–parasitoid models (Gurney *et al.*, 1983; Godfray and Hassell, 1989), but it seems most implausible that perfect synchrony of reproduction which would be necessary for formally discrete generations ever occurs.

The main conclusion we can draw from this work is thus the limited validity of discrete time models. Under our assumptions truly discrete generations cannot persist; it follows that discrete generation models lack a fundamental basis when made under the same assumptions. Furthermore, except when the average adult life time is *much* shorter than the juvenile development time, the generations start overlapping very quickly. We know [for example from MacDonald's (1976) study of discrete models with "extended diapause"] that the dynamic subtleties of discrete generation models are not robust against the introduction of even a small amount of overlap. Thus considerable caution is required before assuming non-overlapping generations except in situations (such as truly univoltine populations) where the assumption is obviously valid.

The fragility of discrete time models is particularly relevant to insect population dynamics where experiments on fecundity and on larval survival of *cohurts* are frequently used to derive relationships analogous to the continuous curves in Figs 7a–c (e.g. Bellows, 1981; Prout and McChesney, 1985). One example of such data (reproduced in Fig. 9) illustrates the possibility of both the monotonic or near-monotonic relationships that we found with the MT and LD models, and the humped relationship obtained for PS. However, the

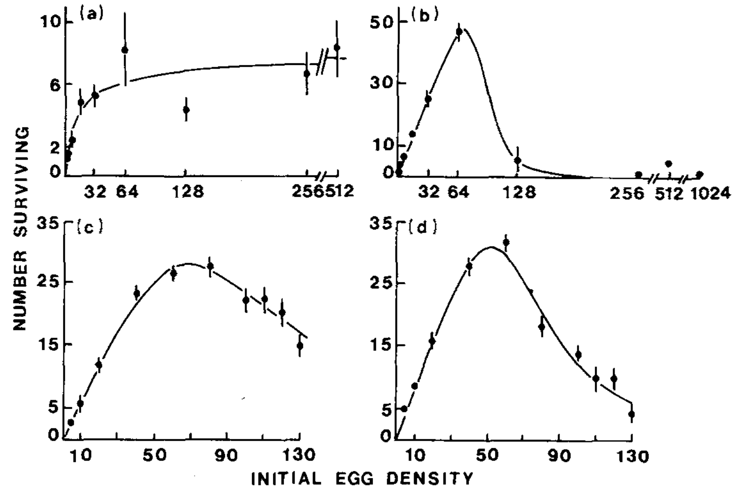

Figure 9. Experimental data producing inter-generation relationships of the type considered in this paper: the relationship between number of larvae surviving to adulthood and initial egg density for four stored product beetles (from Fig. 1 of Bellows, 1981).

significant deviation of the continuous curves in Fig. 7 from the points derived from generations other than the first, and in particular the variations in form near the 45° line (intersection with which determines stability in discrete time models) demonstrate the need for caution in making inferences on population dynamics from the results of such experiments. As a piece of mathematics, this result is obvious—we are merely confirming that cohort experiments give too little information for us to unambiguously construct a structured population model. However almost all practical population models *are* based on inadequate information on interactions between individuals; the biological importance of the present results is that except in certain very special circumstances, the discrete generation models may be rather bad (and potentially misleading) approximations.

Thus we conclude that while discrete generation models constitute a powerful modelling tool for the description of short-term population dynamics, they may give misleading predictions over longer (and in particular evolutionary) time scales. For such models to be useful approximations over a large number of generations, there must normally be some exogenous factor that synchronizes the generations. Simulations by Crowley *et al.* (1987), using a complex model with both "LD" and "MT" regulatory mechanisms as well as a variety of environmental "cues", suggest that the dynamics of generation separation via exogenous forcing may be quite subtle. Two of us (WSCG and RMN) are currently studying this phenomenon in a family of simple models which will be the subject of a future publication.

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APPENDIX A

Generation Structure for a Population with Fixed Adult Lifetime. The models considered in the text assume a constant, age- and density-independent *per capita* death rate δ. This extreme idealization is known in some contexts to influence population dynamics (e.g. Gurney *et al.*, 1983); consequently we now check the robustness of the observations in Section 2.2 against relaxation of the assumption.

The most obvious alternative assumption is that all adults have a fixed lifetime S, with no cause of death other than senescence. Equation (2), which describes the adult population dynamics is then replaced by:

$$\dot{A}(t)=r(t)A(t-\tau(t))-r(t-S)A(t-S-\tau(t-S)), \tag{A1}$$

while equation (5) which describes the generation structure is replaced by:

$$\dot{A}_k(t)=r(t)A_{k-1}(t-\tau(t))-r(t-S)A_{k-1}(t-S-\tau(t-S)). \tag{A2}$$

With the juvenile developmental delay, τ, constant, the equilibrium generations have the following properties (illustrated in Fig. 10 for the case $\tau=1$, $S=1$):

(1) Generation k starts at time $k\tau$ and ends at time $k(\tau+S)$.

(2) The population in any one generation has its maximum at $k(\tau+S/2)$, i.e. mid-way between start and finish.

(3) The magnitude of the population maximum for generation k is lower than for $k-1$.

Thus the generation structure "smears" in much the same way as with the model in the text.

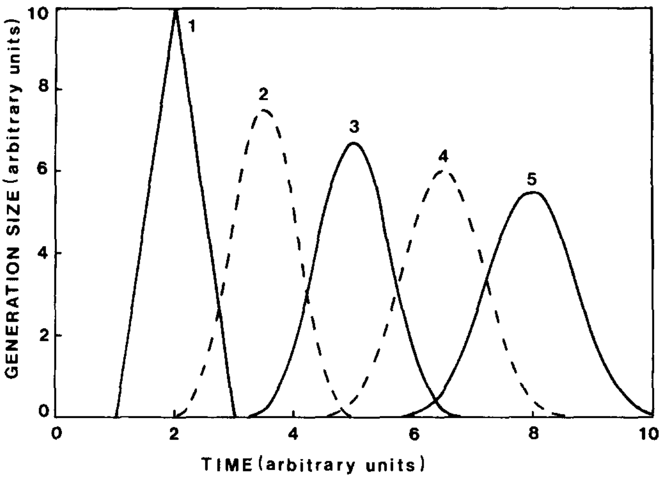

Figure 10. Generation structure for the "discrete adult life time" model of Appendix A.

Moreover, although the generations formally persist to time $k(\tau+S)$, for all but the first few generations the populations tail off to very low values well in advance of this nominal limit.

APPENDIX B

Calculation of Average Adult Age in a Cycling Population. We denote by a the age of an adult with the convention that $a=0$ on entry to the adult stage. Retaining the notation used in the text where $M(t)$ is the instantaneous recruitment rate to the adult stage, and introducing an age distribution $f(a, t)$ defined by:

$$f(a, t)\, \mathrm{d}a = \text{Number of adults aged } a \to a + \mathrm{d}a \text{ at time } t, \tag{B1}$$

then (*cf.* Ch. 3, Nisbet and Gurney, 1982):

$$f(a, t) = \begin{cases} f_0(a-t)\mathrm{e}^{-\delta t} & \text{for } t<a, \\ M(t-a)\mathrm{e}^{-\delta a} & \text{for } t>a, \end{cases} \tag{B2}$$

where $f_0(a)$ is the initial age distribution. The total adult population $A(t)$ and the average age $\langle a \rangle$ are then given by:

$$A(t) = \int_0^\infty f(a, t)\, \mathrm{d}a, \quad \langle a \rangle = [A(t)]^{-1} \int_0^\infty af(a, t)\, \mathrm{d}a. \tag{B3}$$

It can then be shown by substituting from equation (B2) for $f(a, t)$ in the formula for $\langle a \rangle$, and then differentiating with respect to time that:

$$\langle \dot{a} \rangle = 1 - M(t)[A(t)]^{-1} \langle a \rangle. \tag{B4}$$

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