Resonant Population Cycles in Temporally Fluctuating Habitats

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Experiments with the flour beetle *Tribolium* have revealed that animal numbers were larger in cultures grown in a periodically fluctuating volume of medium than in cultures grown in a constant volume of the same average size. In this paper we derive and analyze a discrete stage-structured mathematical model that explains this phenomenon as a kind of resonance effect. Habitat volume is incorporated into the model by the assumption that all rates of cannibalism (larvae on eggs, adults on eggs and pupae) are inversely proportional to the volume of the culture medium. We tested this modeling assumption by conducting and statistically analyzing laboratory experiments. For parameter estimates derived from experimental data, our model indeed predicts, under certain circumstances, a larger

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(cycle-average) total population abundance when the habitat volume periodically fluctuates than when the habitat volume is held constant at the average volume. The model also correctly predicts certain phase relationships and transient dynamics observed in data. The analyses involve a thorough integration of mathematics, statistical methods, biological details and experimental data.

1. INTRODUCTION

Natural populations live in changing environments; indeed, animal numbers may be intricately linked to environmental periodicities (Morris, 1963; Wellington, 1964; MacArther, 1968; Barbosa and Shultz, 1987; Tuljapurkar, 1990; Caswell and Trevisan, 1991; McFadden, 1991). Although it is widely recognized that environments are often not constant in time, the vast majority of mathematical models in population dynamics and ecology are autonomous and assume a constant environment. One of the main reasons for this is mathematical tractability. There is, however, a (relatively small) body of literature dealing with nonautonomous population models and, in particular, with models that assume periodic environmental fluctuations (e.g. see Fretwell, 1973; May, 1973; Koch, 1974; May, 1976; Cushing, 1977; Smith, 1981; Cushing, 1982; deMottoni and Schiaffino, 1982; Nisbet and Gurney, 1982; Bardi, 1983; Cushing, 1984; Namba, 1984; Cushing, 1986; Cushing, 1987; Smith and Waltmand, 1995). One theoretical tenet that resulted from early investigations of periodically forced models was that a periodically fluctuating environment has a deleterious effect on the population (in the sense that average population numbers are less than they would be in a constant environment held at the averaged environment level). It was shown, on the other hand, that this tenet is model dependent and depends on the nature of nonlinearities as well as the nature of the periodic flucuations (Rosenblat, 1980; Cushing, 1987). This literature is, however, virtually all theoretical; little attempt is made to connect theory with data. Indeed there is little population data, either field or laboratory, that addresses the effect of periodically fluctuating environments on population density.

One notable exception comes from the controlled, replicated laboratory experiments utilizing flour beetles (*Tribolium*) reported by Jillson (1980) in which the habitat size (i.e. flour volume) was periodically altered and the resulting life cycle stages of the beetle were counted. The most striking result of Jillson's experiment was that the beetle populations can have significantly *larger* total numbers in a periodically fluctuating habitat than in a constant habitat of the same average size. Specifically, this was the case when the flour volume was fluctuated with a period of four weeks. (Jillson also carried out experiments with longer periods in which increased numbers were not observed.)

Our aim in this paper is to show that an existing model for flour beetle population dynamics that has been thoroughly parameterized and validated (Costantino

et al., 1995; Costantino *et al.*, 1997; Dennis *et al.*, 1995) predicts, when appropriately modified to account for a periodically fluctuating volume of flour, the increased population numbers observed by Jillson in a periodic environment. We will also show that the model accurately describes a number of other dynamical features of Jillson's experimental data.

There have been two other modeling exercises that relate to the Jillson experiment, neither of which addresses the increased population numbers that was the main point of Jillson (1980). Nisbet and Gurney (1982) and Renshaw (1989) treated the Jillson experimental set-up as a square-wave variation in carrying capacity and argued that this results in population fluctuations. They only treated longer periods in Jillson's experiments (eight weeks and 12 weeks respectively) in which the increased population numbers are not observed. They do not construct detailed models nor do they fit the data in any statistical way, but simply observe that the experimental mean population data was seen to be similar to the predictions of their periodically forced models. By contrast, we will consider here the Jillson experiment in which the flour volume was fluctuated with a period of four weeks and address the unusual result that population numbers were greatly enhanced. Furthermore, our model assumes a fundamentally different nonlinear mechanism that is responsible for the dynamics of flour beetles. Contrary to the assumption in Nisbet and Gurney (1982) and Renshaw (1989) that the beetle dynamics are driven by resource-limited density dependence, we assume that the driving nonlinear mechanism is interstage cannibalism (Costantino *et al.*, 1995; Dennis *et al.*, 1995; Costantino *et al.*, 1997) and that this interaction is inversely related to flour volume. We have conducted laboratory experiments to validate this latter assumption (see section 3.3).

In section 2 we review the experimental protocol and the results of the empirical study using laboratory cultures of flour beetles (*Tribolium*) conducted by Jillson (1980). In section 3 we describe a discrete, nonlinear stage-structured model for flour beetle cultures in a constant habitat that has been extensively parameterized and validated by means of both existent historical data and our own laboratory experiments (Costantino *et al.*, 1995; Dennis *et al.*, 1995; Costantino *et al.*, 1997). This 'LPA' model (see (3.2) below) is then modified to account for periodic fluctuations of flour volume. Laboratory experiments that support the modeling assumption underlying this modification are described. Some of the mathematical properties of the resulting nonautonomous, periodically forced LPA model (see (3.3) below) are discussed in section 4, in particular with respect to its relationship to the constant habitat LPA model and the possible increase or decrease in population numbers. The ability of the periodically forced LPA model to describe and explain the empirical observations of Jillson are discussed in section 5. Finally, in section 6 some unusual predictions of the periodically forced model are pointed out that suggest new laboratory experiments (which are currently in progress).

2. THE JILLSON EXPERIMENT

In the experiment conducted by Jillson (1980), cultures of the flour beetle *Tribolium castaneum* (Herbst) were initiated with 30 adults and 75 small larvae. All cultures were grown on 20 g of standard medium (95% flour, 5% dried brewer's yeast) for the first 18 weeks of the study. Following the census at week 18, six populations were assigned to the constant 20 g habitat and six were placed in a habitat that alternated between 32 g and 8 g every two weeks. Note that the average flour volume[†] in the alternating 32–8 g habitat is the volume of the constant habitat cultures. All cultures were censused (larvae, pupae, adults) at two week intervals. Four of the constant habitat cultures and four of the alternating habitat cultures were maintained and censused in this way for 70 weeks, and it is on these eight remarkably long time series that we focus our analysis.

The total number of animals for individual beetle cultures grown in the four constant 20 g habitats and in the four alternating 32–8 g habitats are listed in Tables 1 and 2 respectively. In the 32–8 g cultures the data reveal a marked increase in insect numbers beginning at week 28, an increase which is sustained throughout the remaining weeks of the study. At some time in each of the cultures grown in the oscillating volumes of flour, there were more than 1000 individuals. In only one replicate of the constant habitat cultures (#20) did total animal numbers ever exceed 600, and in that replicate this occurs at only two census times. The data clearly support Jillson's conclusion that there was an increase in beetle numbers in the alternating 32–8 g habitat as compared with the constant 20 g habitat.

3. THE MODEL

3.1. The LPA model. To begin our analysis of the Jillson data (Jillson, 1980), we focus on the numbers of larvae, pupae, and adults (rather than the total number of individuals) and introduce a recently developed demographic model based on the biology of the flour beetle (Costantino *et al.*, 1995; Cushing *et al.*, 1996; Dennis *et al.*, 1995). This stochastic model assumes a constant habitat size. Three difference equations describe the dynamics of larvae, pupae and adults in *Tribolium* cultures:

$$(a) \quad L_{t+1} = bA_t \exp(-c_{ea}A_t - c_{el}L_t + E_{1t})$$

$$(b) \quad P_{t+1} = (1 - \mu_l)L_t \exp(E_{2t}) \tag{3.1}$$

$$(c) \quad A_{t+1} = [P_t \exp(-c_{pa}A_t) + (1 - \mu_a)A_t] \exp(E_{3t}).$$

[†]We take the unit of volume to be the volume occupied by 1 g of flour.

Table 1. Total animal numbers for cultures grown in a constant habitat. Replicate culture numbers correspond to the numbers used in the original Jillson data set.

Week	Flour (grams)	Total Numbers Replicate Cultures			
		#13	#18	#20	#23
0	20	105	105	105	105
2	20	109	117	103	92
4	20	93	88	87	80
6	20	256	243	233	243
8	20	207	185	194	211
10	20	334	224	361	286
12	20	330	233	266	232
14	20	347	234	184	229
16	20	221	156	140	167
18	20	240	228	129	265
20	20	203	173	133	198
22	20	365	398	132	353
24	20	263	265	98	248
26	20	281	330	129	315
28	20	215	235	133	274
30	20	262	316	124	315
32	20	207	215	153	286
34	20	263	354	120	365
36	20	209	366	136	282
38	20	302	345	187	321
40	20	281	362	121	279
42	20	247	294	191	298
44	20	237	230	154	275
46	20	293	257	411	406
48	20	259	231	344	280
50	20	440	225	573	538
52	20	233	201	288	288
54	20	470	313	552	498
56	20	383	266	380	337
58	20	387	318	535	407
60	20	284	208	272	258
62	20	486	472	640	428
64	20	281	277	352	296
66	20	449	447	604	524
68	20	218	214	312	324
70	20	466	417	515	390

Table 2. Total animal numbers for cultures grown in a periodic habitat. Replicate culture numbers correspond to the numbers used in the original Jillson data set. The grams of flour represent the habitat volume into which the animals were returned after the census.

Week	Flour (grams)	Total Numbers Replicate Cultures			
		#5	#11	#24	#25
0	20	105	105	105	105
2	20	124	134	146	105
4	20	95	101	103	103
6	20	94	334	283	150
8	20	72	247	211	104
10	20	209	425	293	212
12	20	185	256	199	170
14	20	175	228	179	223
16	20	176	195	155	185
18	32	170	237	207	293
20	8	266	212	247	278
22	32	189	94	111	137
24	8	191	211	381	178
26	32	148	160	230	148
28	8	588	225	449	467
30	32	425	158	375	369
32	8	748	637	399	710
34	32	569	610	306	635
36	8	423	544	443	648
38	32	342	567	396	609
40	8	470	449	797	560
42	32	483	384	872	668
44	8	565	823	947	1045
46	32	598	778	928	987
48	8	929	889	645	846
50	32	870	815	580	846
52	8	1046	994	897	1001
54	32	796	977	756	781
56	8	480	470	521	423
58	32	382	407	435	302
60	8	736	572	587	802
62	32	716	460	498	704
64	8	568	696	1041	742
66	32	474	578	834	695
68	8	508	1040	807	725
70	32	415	973	622	592

L_t is the number of small feeding larvae (called the L-stage), P_t is the number large larvae, nonfeeding larvae, pupae and callow adults (called the P-stage), and A_t denotes the number of reproductive adults (referred to as the A-stage). The unit of time (two weeks) is taken to be the feeding larval maturation interval so that after one unit of time a larvae either dies or survives and pupates. This unit of time is also the cumulative time spent in the P-stage. The quantity $b > 0$ is the number

of larval recruits produced per adult per time unit in the absence of cannibalism. The fractions μ_l and μ_a are the L-stage and A-stage probabilities, respectively, of dying from causes other than cannibalism. The exponential nonlinearities account for the cannibalism of eggs by both adults, $\exp(-c_{ea}A_t)$, and larvae, $\exp(-c_{el}L_t)$, and the cannibalism of pupae by adults, $\exp(-c_{pa}A_t)$. It is assumed that the only significant source of pupal mortality is cannibalism by adults. In equations (3.1), $E_t = [E_{1t}, E_{2t}, E_{3t}]$ is a random vector that is assumed to have a trivariate normal distribution with a mean vector of $[0, 0, 0]$ and a variance–covariance matrix of $\sum$. Covariances among E_{1t}, E_{2t}, and E_{3t} at any given time t are assumed (and represented by off-diagonal elements of $\sum$), but we expect the covariances between times to be small in comparison. Thus, $E_0, E_1, E_2, \ldots$ are assumed uncorrelated. Models with noise additive on a logarithmic scale correspond to environmental-type fluctuations (Dennis *et al.*, 1991). At the large population numbers typical of *Tribolium* cultures, we expect the variability component due to environmental fluctuations to outweigh the component due to demographic fluctuations (Dennis and Costantino, 1988).

The 'deterministic skeleton' of the stochastic model (3.1) given by the system of difference equations

$$(a) \quad L_{t+1} = bA_t \exp(-c_{ea}A_t - c_{el}L_t)$$

$$(b) \quad P_{t+1} = (1 - \mu_l)L_t \tag{3.2}$$

$$(c) \quad A_{t+1} = P_t \exp(-c_{pa}A_t) + (1 - \mu_a)A_t$$

will be referred to in this paper as the 'LPA' model. This system has been used to design and predict the asymptotic outcome of several long-term laboratory experiments (Costantino *et al.*, 1995; Costantino *et al.*, 1997; Dennis *et al.*, 1997). We will use a periodically forced version of this system to address Jillson's experimental results.

3.2. The periodic LPA model. How is the alternating size of the habitat from 32 to 8 g to be accommodated in the LPA model (3.2)? Very early in the long history of modeling the dynamics of flour beetle populations, cannibalism is described as a random collision between the mobile (adults and larvae) and immobile (eggs and pupae) life stages (Stanley, 1932). The random encounter interpretation of cannibalism appears throughout the *Tribolium* literature (Crombie, 1943; Landahl, 1955; Lloyd, 1968; Mertz and Davies, 1968; Neyman *et al.*, 1956; Park *et al.*, 1974).

We assume that each cannibalism coefficient in the deterministic model (3.2) is inversely proportional to flour volume V:

$$c_{el} = \frac{k_{el}}{V}, \qquad c_{ea} = \frac{k_{ea}}{V}, \qquad c_{pa} = \frac{k_{pa}}{V}.$$

This parameterization arises from the following random encounter mechanism. Suppose the average effective volume of flour searched per adult for, say, pupae, is k_{pa} in a unit of time. Then the probability that a pupa is not included in the search volumes of A_t adults is

$$\left[1 - \frac{k_{pa}}{V}\right]^{A_t},$$

with limiting approximation

$$\exp\left(-k_{pa}\frac{A_t}{V}\right).$$

We next consider the case when the flour volume oscillates with period of 2 around an average V_{ave} with a relative amplitude of α. Thus we write

$$V = V_{\text{ave}}\left(1 + \alpha(-1)^t\right)$$

and the cannibalism coefficients in the LPA model become, respectively,

$$\frac{k_{el}}{V_{\text{ave}}(1 + \alpha(-1)^t)}, \qquad \frac{k_{ea}}{V_{\text{ave}}(1 + \alpha(-1)^t)}, \qquad \frac{k_{pa}}{V_{\text{ave}}(1 + \alpha(-1)^t)}.$$

Letting $c_{el}, c_{ea},$ and c_{pa} now denote the cannibalism coefficients in the average volume of flour, i.e.

$$c_{el} = \frac{k_{el}}{V_{\text{ave}}}, \qquad c_{ea} = \frac{k_{el}}{V_{\text{ave}}}, \qquad c_{pa} = \frac{k_{pa}}{V_{\text{ave}}}$$

we obtain the 'periodic LPA' model given by the equations

$$(a) \quad L_{t+1} = bA_t \exp\left(\frac{-c_{ea}A_t - c_{el}L_t}{1 + \alpha(-1)^t}\right)$$

$$(b) \quad P_{t+1} = (1 - \mu_l)L_t \tag{3.3}$$

$$(c) \quad A_{t+1} = P_t \exp\left(\frac{-c_{pa}A_t}{1 + \alpha(-1)^t}\right) + (1 - \mu_a)A_t$$

for relative amplitude $0 < \alpha < 1$. Note that the autonomous LPA model (3.2) is obtained by setting $\alpha = 0$ in this periodic LPA model and interpreting the cannibalism coefficients as those associated with a constant habitat with the flour volume fixed at the average amount V_{ave}.

3.3. Test of the cannibalism survival model. An experiment was carried out to test the assumed relationship between flour volume and cannibalism survival rate for pupae. In the experiment, 50 pupae were placed in each of 30 glass vials. Each vial was assigned a different treatment combination of the amount of flour and the number of adults in a factorial design. The treatments for various amounts of flour were: 8 g, 16 g, 20 g, 24 g, 28 g, and 32 g. The numbers of adults were: 0, 50, 100, 150, and 200. There was one vial for each treatment combination. The vials were placed in a dark incubator at 34 °C for 48 h, and the numbers of surviving pupae in the vials were counted. The results appear in Table 3.

Table 3. Observed number of survivors out of 50 initial pupae placed in vials with different numbers of adults and different amounts of flour.

Flour	Number of adults				
Amt (g)	0	50	100	150	200
8	50	43	39	42	31
16	50	44	44	43	33
20	49	44	45	45	42
24	49	45	45	46	40
28	49	47	46	46	45
32	50	47	48	47	46

According to the model, the dependence of pupal survival probability on adult numbers and flour amount should be of the form

$$s = \exp\left(-\frac{c}{v}a\right)$$

where a is the number of adults, v is the weight of flour (in grams corresponding to V units of volume), and s is the 48 h survival probability. In this experiment, a small amount of noncannibalistic mortality was observed in the $a = 0$ treatments, and consequently an extra parameter was included in the data analysis to represent the background survival rate. Thus, the survival probability s_{ij} for a pupa in the presence of a_i adults and in v_j grams of flour was taken to be

$$s_{ij} = \exp\left(-c_0 - \frac{c}{v_j}a_i\right)$$

where c_0 and c are unknown parameters.

If survival of each pupa is an independent event with probability given by s_{ij}, then the number of survivors y_{ij} observed out of 50 pupae at adult treatment a_i and flour treatment v_j is the outcome of a binomial random variable:

$$P(Y_{ij} = y_{ij}) = \binom{50}{y_{ij}} s_{ij}^{y_{ij}}(1 - s_{ij})^{50-y_{ij}}.$$

The likelihood function $L(c_0, c)$ for the unknown parameters c_0 and c is the joint probability of the independent binomial outcomes of the 30 treatment combinations:

$$L(c_0, c) = \prod_{i=1}^{5} \prod_{j=1}^{6} \binom{50}{y_{ij}} s_{ij}^{y_{ij}} (1 - s_{ij})^{50 - y_{ij}}.$$

Maximum likelihood (ML) estimates $\hat{c}_0$ and $\hat{c}$ were calculated by numerically maximizing $\log L(c_0, c)$. The results were $\hat{c}_0 = 0.01577$ and $\hat{c} = 0.0008784$.

Two hypotheses were tested statistically against the proposed survival model. The first is that a simpler model is adequate to describe the data. The simpler hypothesis is of the form

$$H_0 : c = 0.$$

That is to say, the null hypothesis is that survival is constant and does not depend on adult treatment or flour treatment. The hypothesis H_0 was tested against the alternative hypothesis

$$H_1 : c \neq 0$$

(i.e. the survival model) using the likelihood ratio statistic

$$G^2 = -2 \log \left(\frac{\hat{L}_0}{\hat{L}_1} \right).$$

Here $\hat{L}_0$ is the likelihood function $L(c_0, c)$ maximized under the null hypothesis constraint $c = 0$ and $\hat{L}_1$ is the unconstrained maximum. The sampling distribution of G^2 under the null hypothesis is well approximated by a chi-square distribution with degrees of freedom (DOF) equal to the number of free parameters estimated in H_1 minus the number of free parameters estimated in H_0 (Serfling, 1980). The test *rejects* the simpler model in favor of the proposed survival model ($G^2 = 90.6$, DOF $= 1$, $P < 0.0001$).

The second hypothesis is that a more complex model is necessary to describe the data. The hypothesis, denoted H_2, is that every treatment combination has a separate survival probability. The hypothesis can be parameterized as

$$H_2 : s_{ij} = \exp(-c_0 - c_{ij}), \qquad \sum_{i,j} c_{ij} = 0,$$

$$i = 1, 2, \ldots 5, \qquad j = 1, 2, \ldots 6.$$

This model has 30 free parameters. The likelihood ratio statistic

$$G^2 = \log \left(\frac{\hat{L}_1}{\hat{L}_2} \right)$$

for testing the null hypothesis H_1 (the proposed survival model) against the complex alternative H_2 is a standard goodness-of-fit statistic (Read and Cressie, 1988). As the simpler model, the proposed survival model H_1 plays the role of the null hypothesis. The test *fails* to reject the null hypothesis, indicating that the proposed survival model fits acceptably well ($G^2 = 27.3$, DOF $= 30 - 2 = 28$, $P = 0.50$).

In the dynamical LPA model (3.2) we dispense with the term for noncannibalistic mortality of pupae. Parameter estimates of P-stage mortality obtained from time series data are negligibly small. Thus, the functional form used for A-stage recruitment (3.2c) has P_t as the potential recruits (in the absence of cannibalism) and not $(1 - \mu_p)P_t$.

3.4.   *Parameter estimation.* We used the four constant habitat cultures to estimate model parameters (see Table 1). The model was fitted to combined data from all four cultures, resulting in a single set of parameter estimates. The four alternating habitat cultures (Table 2) were withheld from the estimation process and used to evaluate the model's alternating habitat predictions. In this way, the model can be 'validated' in the sense that its ability to *predict* can be analyzed by means of data that were not used in the parameter estimation procedure (as opposed to its ability to describe data to which it has been 'fit'). See Dennis *et al.* (1995) for details of the statistical methodology. The predictive capability of the LPA model is unusually accurate relative to other models in population dynamics; for more applications of the LPA model see Costantino *et al.* (1995); Costantino *et al.* (1997); Dennis *et al.* (1995); Dennis *et al.* (1997); Cushing *et al.* (1998).

The parameter μ_a was estimated directly from counts of live adults at time t and dead adults at time $t + 1$ (binomial distribution) in the four constant habitat cultures. This estimate is $\mu_a = 0.1542$. The remaining parameters were estimated from the time series observations of the three state variables. Namely, the parameters $b, c_{el}, c_{ea}, c_{pa}$, and μ_l were estimated by means of conditional least squares (CLS) estimation (Klimko and Nelson, 1978). This amounts to minimizing the sum of squared one-time-step prediction errors for each state variable. CLS estimates are known to have desirable statistical properties and be robust to many types of probability structures for describing the residual errors.

Suppose l_{it}, p_{it}, and a_{it} represent the observed values of the state variables in the ith culture at time $t (i = 1, 2, 3, 4; t = 0, 1, \ldots, q)$. The conditional sums of squares for the state variables are as follows

$$s_1(b, c_{el}, c_{ea}) = \sum_{i=1}^{4} \sum_{t=0}^{q-1} \left[l_{i(t+1)} - b a_{it} \exp(-c_{el} l_{it} - c_{ea} a_{it}) \right]^2$$

$$s_2(\mu_l) = \sum_{i=1}^{4} \sum_{t=0}^{q-1} \left[p_{i(t+1)} - (1 - \mu_l) l_{it} \right]^2$$

$$s_3(c_{pa}) = \sum_{i=1}^{4} \sum_{t=0}^{q-1} \left[a_{i(t+1)} - (p_{it} \exp(-c_{pa}a_{it}) + (1 - \mu_a)a_{it}) \right]^2.$$

In these equations, $\mu_a = 0.1524$ is the estimate of the adult death rate obtained directly from the mortality counts. The functions $s_1, s_2,$ and s_3 were minimized for the remaining parameter estimates using the Nelder–Mead simplex algorithm (Press *et al.*, 1992). The parameter estimates

$$
\begin{aligned}
c_{ea} &= 5.785 \times 10^{-3}, & c_{el} &= 5.841 \times 10^{-2}, & c_{pa} &= 1.053 \times 10^{-2} \\
b &= 4.445, & \mu_l &= 4.794 \times 10^{-1}, & \mu_a &= 1.524 \times 10^{-1}
\end{aligned}
$$

(3.4)

were obtained.

3.5. *One-step forecasts.*

The observed time series for one of the constant habitat populations (rep #23 in Table 1) together with the one-step predictions of the LPA model with the parameter estimates obtained above are plotted in Fig. 1. In these graphs solid circles represent census data. Open circles represent the numbers predicted by the LPA model equations (3.2) from the census data at the previous time (i.e. the one-step forecast), using the CLS parameter estimates above. The accuracy of a prediction at a particular time t can be judged by noting the differences between the solid and open circles at that time (i.e. the 'residual'). Overall, from Fig. 1 one sees that there is a close association between the one-step forecasts and the census data.

The observed time series for one of the *periodic* habitat cultures (rep #25 in Table 2) together with the one-step predictions of the periodic LPA model are presented in Fig. 2. Keep in mind the fact that the one-step forecasts are based on a single set of CLS estimates obtained from the *constant* habitat cultures so this comparison can be viewed as a model 'validation'. As can be seen in Fig. 2 the one-step forecasts are, overall, reasonably accurate.

The one-step forecasts as plotted in Figs. 1 and 2 give a visual impression of how successful the LPA and the periodic LPA models are at describing the census data and the dynamics of the beetle populations. Sophisticated statistical analyses have also been performed on the residuals for several other data sets and show the accuracy of the LPA model (Dennis *et al.*, 1995).

4. SOME MATHEMATICAL PROPERTIES OF THE PERIODIC LPA MODEL

For a specified triple of nonnegative initial conditions $L_0 \geq 0$, $P_0 \geq 0$ and $A_0 \geq 0$ the recursive equations (3.3) define a unique sequence of nonnegative triples $L_t \geq 0$, $P_t \geq 0$ and $A_t \geq 0$ for all $t = 1, 2, 3, \ldots$. That is to say, the positive octant is forward invariant for the (semi) dynamical system defined by (3.3). We are interested in the asymptotic behavior of this sequence as $t \to +\infty$.
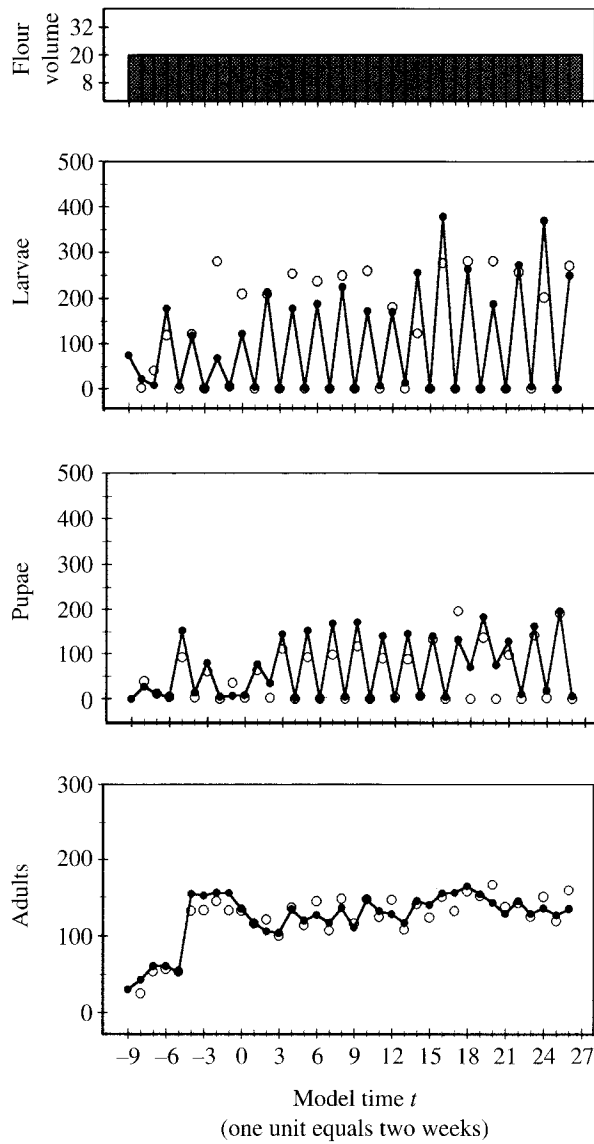
Figure 1. Time series data (solid circles) and the one-step forecasts (open circles) of the LPA model (3.2) with parameter estimates (3.4) for a culture of beetles (replicate #23, Table 1) grown in the constant 20 g habitat.
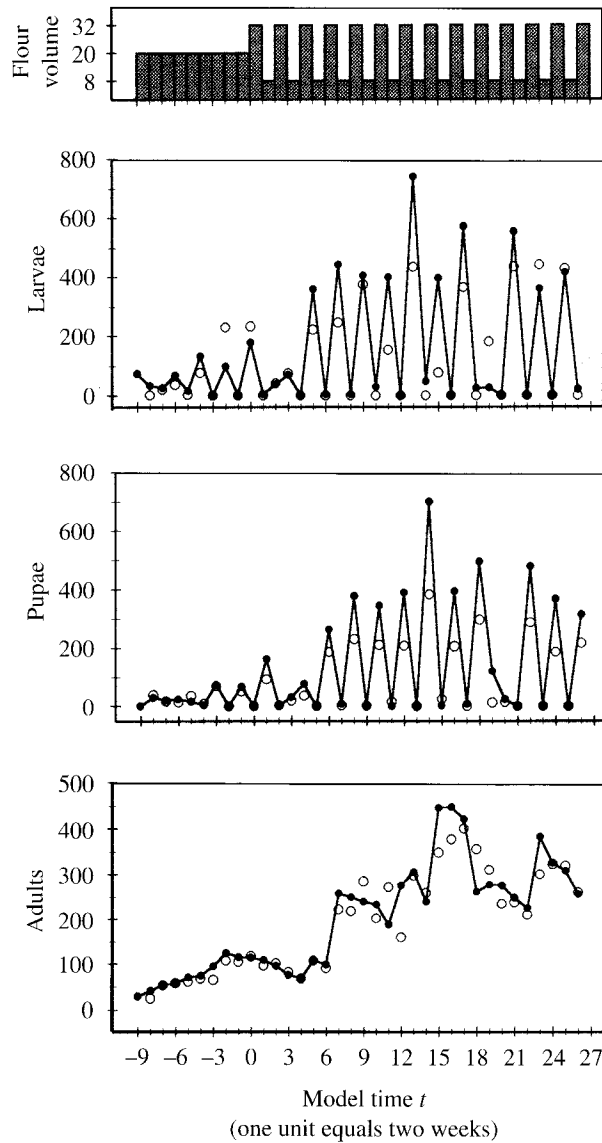
Figure 2. Time series data (solid circles) and one-step forecasts (open circles) for a culture of beetles (replicate #25, Table 2) grown in an alternating, 2-periodic habitat sequence of 32–8 g of flour starting at $t = 0$ (week 18). The one-step forecasts are made by the LPA model (3.2) with parameter estimates (3.4) for $t = -8$ to $t = 0$ and by the periodic LPA model (3.3) with the same parameter estimates and relative amplitude $\alpha = 0.6$ for $t = 1$ to $t = 26$. At $t = 0$ (week 18), the culture with population numbers $L = 178$, $P = 1$, and $A = 114$ was placed in the 32 g habitat. One unit of time equals two weeks.

Clearly $L_0 = P_0 = A_0 = 0$ implies $L_t = P_t = A_t = 0$ for all $t = 1, 2, 3, \ldots$; i.e. the origin is a 'trivial' equilibrium point of (3.3) for any fixed amplitude $0 \le \alpha < 1$.

For $\alpha = 0$ the system (3.3) is autonomous (i.e. not periodically forced) and there can exist other 'nontrivial' equilibrium points. Specifically, if

$$b > b_{cr} = \frac{\mu_a}{1 - \mu_l}$$

there exists a unique positive equilibrium $L_t = L_e > 0$, $P_t = P_e > 0$, $A_t = A_e > 0$. These positive equilibria bifurcate from the origin as b is increased through the critical value b_{cr} (that is to say, as a function of the parameter b, the positive equilibria form a continuous branch that coalesces with the trivial equilibrium at $b = b_{cr}$). These positive equilibria may or may not be stable, however. They are known to be (locally asymptotically) stable for b sufficiently close to b_{cr}, but stability is in general lost for larger b. Nonetheless, it is true for $b > b_{cr}$ that all solutions are bounded for $t > 0$ and that the system is uniformly persistent (with respect to the trivial equilibrium, i.e. with respect to the extinction state). On the other hand, for $b < b_{cr}$ there is no nontrivial, nonnegative equilibrium and it can be shown that all solutions of (3.3) starting with nonnegative initial conditions, tend to the origins as $t \rightarrow +\infty$. Thus, under these circumstances the model predicts extinction. All of these facts about the autonomous LPA model (3.2) can be found in Cushing (1995); Henson and Cushing (1997).

For $\alpha > 0$ the periodic LPA model (3.3) is periodically forced and hence nonautonomous. It does not possess any equilibrium points other than the trivial equilibrium. However, as in the autonomous case $\alpha = 0$, it has been shown that all solutions tend to the origin if $b < b_{cr}$, and that for $b > b_{cr}$, all solutions are bounded and the system is uniformly persistent with respect to the origin, i.e. with respect to the extinction state (Henson and Cushing, 1997). Furthermore, when $\alpha > 0$, 2-cycle solutions play the role analogous to equilibria in the $\alpha = 0$ case. Specifically, for any fixed α, $0 < \alpha < 1$, there exists a branch of positive 2-cycle solutions that bifurcates from the origin as b is increased through b_{cr} (Henson and Cushing, 1997) and this branch exists for all $b > b_{cr}$ (Cushing, 1998). It is not known, however, whether there exists a unique positive 2-cycle for each $b > b_{cr}$. For small larval recruitment rates $b > b_{cr}$ the bifurcating 2-cycle solutions can be approximated by Liapunov–Schmidt expansion methods (Henson, 1996). This procedure not only establishes the stability of these 2-cycles for small $b > b_{cr}$, but also allows a study of their oscillatory properties (mean, amplitude, etc) as they depend on the environmental amplitude $\alpha > 0$ (Henson and Cushing, 1997).

For a fixed larval rate $b > b_{cr}$ the properties of the 2-cycle can also be studied by regular perturbation techniques using α as a small parameter. Thus, if the equilibrium when $\alpha = 0$ is hyperbolic (the linearization at the equilibrium has no eigenvalues of magnitude equal to 1), the 2-cycles for small $\alpha > 0$ have the same stability properties as the equilibrium and their oscillatory properties can be approximated to lowest order in α (Henson and Cushing, 1997).

Using the techniques described above, the effect of introducing environmental periodicity can, in principle, be analytically studied by means of the periodic LPA model (3.3). The details are not necessarily tractable, however. In Henson and Cushing (1997) it was shown, by using Liapunov–Schmidt methods, that the periodic LPA model predicts a 'negative effect' of periodicity for small larval recruitment rates $b > b_{cr}$. In fact, for small $b > b_{cr}$ and arbitrary environmental amplitude $\alpha, 0 < \alpha < 1$, the cycle averages of each of the components of the 2-cycle solution of the periodic LPA model (3.3)

$$\langle L_t \rangle = \tfrac{1}{2}(L_0 + L_1)$$

$$\langle P_t \rangle = \tfrac{1}{2}(P_0 + P_1)$$

$$\langle A_t \rangle = \tfrac{1}{2}(A_0 + A_1)$$

are less than the values of the corresponding components of the equilibrium of the autonomous LPA model (3.2), i.e.

$$\langle L_t \rangle < L_e$$

$$\langle P_t \rangle < P_e$$

$$\langle A_t \rangle < A_e.$$

That is, the average number of animals in each life stage is *decreased* by the advent of environmental forcing. This, of course, implies that the cycle-average of the total population size in the periodic habitat is less than the total population at equilibrium

$$\langle L_t + P_t + A_t \rangle < L_e + P_e + A_e. \tag{4.1}$$

This is the opposite effect of that observed in Jillson's experiment.

On the other hand, for large larval recruitment rates $b > b_{cr}$, it is known (Henson and Cushing, 1997) that the periodic LPA model can predict a 'positive effect' of periodicity, at least for small environmental amplitudes $\alpha > 0$. Depending on the values of model parameters, either a positive effect

$$\langle L_t + P_t + A_t \rangle > L_e + P_e + A_e \tag{4.2}$$

or a negative effect (4.1) is predicted by the periodic LPA model. This assertion is proved in Henson and Cushing (1997) by regular perturbation methods and is valid for those nontrivial 2-cycles that are 'near' the equilibrium associated with the constant environment $\alpha = 0$. These 2-cycles are small amplitude oscillations that mathematically approach the nontrivial equilibrium as α decreases to 0 in the limit. The results for small amplitude 2-cycles hold regardless of the stability properties of the nontrivial equilibrium, which can be stable or unstable. If the

equilibrium is unstable (which is generally true if b is sufficiently large) then these mathematical results concerning the cycle averages of the resulting unstable 2-cycle are probably of limited interest. However, numerical simulations, using the model parameter estimates (3.4) obtained from Jillson's data, demonstrate that positive effects do indeed occur for small α near *stable* equilibria (i.e. for values of the larval recruitment rate $b > b_{cr}$ that are not so large that the equilibrium of the constant environment is destabilized) (Henson and Cushing, 1997) (see Fig. 3).

The mathematical results described above prove that the periodic LPA model (3.3) is theoretically able to predict an *increase* in average total population size due to environmental periodicities, at least for certain parameter values. These analytical results do not, however, apply directly to Jillson's experiment for two reasons. First, at the estimated value of the larval recruitment rate $b = 4.4450$ for Jillson's data the nontrivial equilibrium of the LPA model (3.2) is unstable (see Fig. 3). The model attractor for the LPA model (3.2) in this case is, in fact, a stable 2-cycle. Second, the relative amplitude $\alpha = 0.6$ in Jillson's experiment is not 'small'.

The predictions of the periodic LPA model (3.3) with the parameter estimates (3.4) can, however, be investigated numerically and compared with Jillson's experimental results. This is done in the next section.

5. THE PERIODIC LPA MODEL AND JILLSON'S EXPERIMENT

For the parameter estimates (3.4) it can be shown mathematically, by standard regular perturbation arguments, that for small relative amplitudes $\alpha > 0$ there exist *two* stable nontrivial 2-cycles solutions of (3.3) near the stable, constant environment ($\alpha = 0$) 2-cycle. This is because a 2-cycle in the autonomous LPA model (3.2) is really 'two' 2-cycles; a 2-cycle and its shift by one time step. These 2-cycles can be viewed as two different cycles from each of which a 2-cycle arises when periodicity is added. Unlike in the autonomous case, however, the two perturbed 2-cycles of the periodically forced system (3.3) are not time shifts of each other and represent two different cycles. By continuity (of the eigenvalues of the linearization as functions of α) both 2-cycles are stable.

Numerical simulations show, for small $\alpha > 0$ that one of the two stable 2-cycles exhibits a negative effect due to periodic forcing (in the sense that the cycle average is decreased) and that the other exhibits a positive effect (in the sense that the cycle average is increased) (see Fig. 4). These facts have not been proved rigorously. As α is increased, the former 2-cycle abruptly disappears as a critical value α_{cr} of the amplitude α is surpassed. This disappearance is apparently due to a saddle-node bifurcation as the stable 2-cycle coalesces with the unstable 2-cycle that bifurcates from the unstable equilibrium of the $\alpha = 0$ autonomous model. On the other hand, the 2-cycle exhibiting a positive effect persists for all amplitudes $0 < \alpha < 1$.
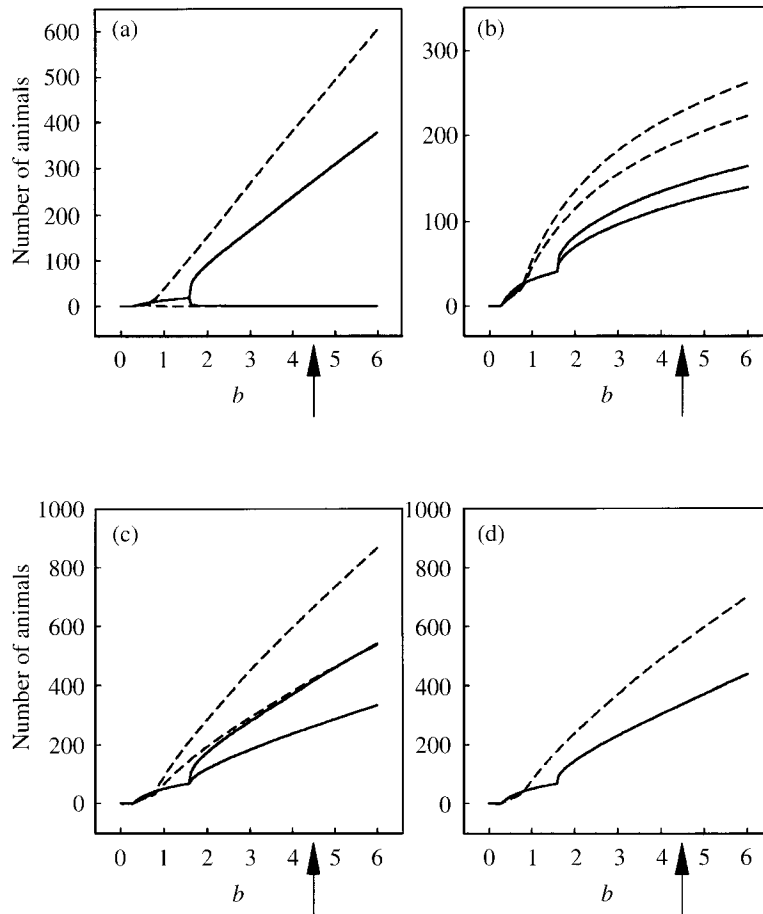
Figure 3. Orbit diagrams for (a) larval, (b) adult, (c) total numbers, and (d) cycle-average total numbers for the constant habitat ($\alpha = 0$) LPA model (solid lines) and the periodically forced ($\alpha = 0.6$) LPA model (broken lines) using the parameter estimates (3.4) obtained from the Jillson data. The asymptotic states (shown in numbers of animals) are shown plotted against the larval recruitment rate b. The arrows locate the estimated value of $b = 4.4450$ where Jillson's experiment took place. At this value of b both the constant habitat and the periodically forced LPA model predict a 2-cycle attractor, with the average total population number being smaller in the constant habitat than in the periodic habitat.
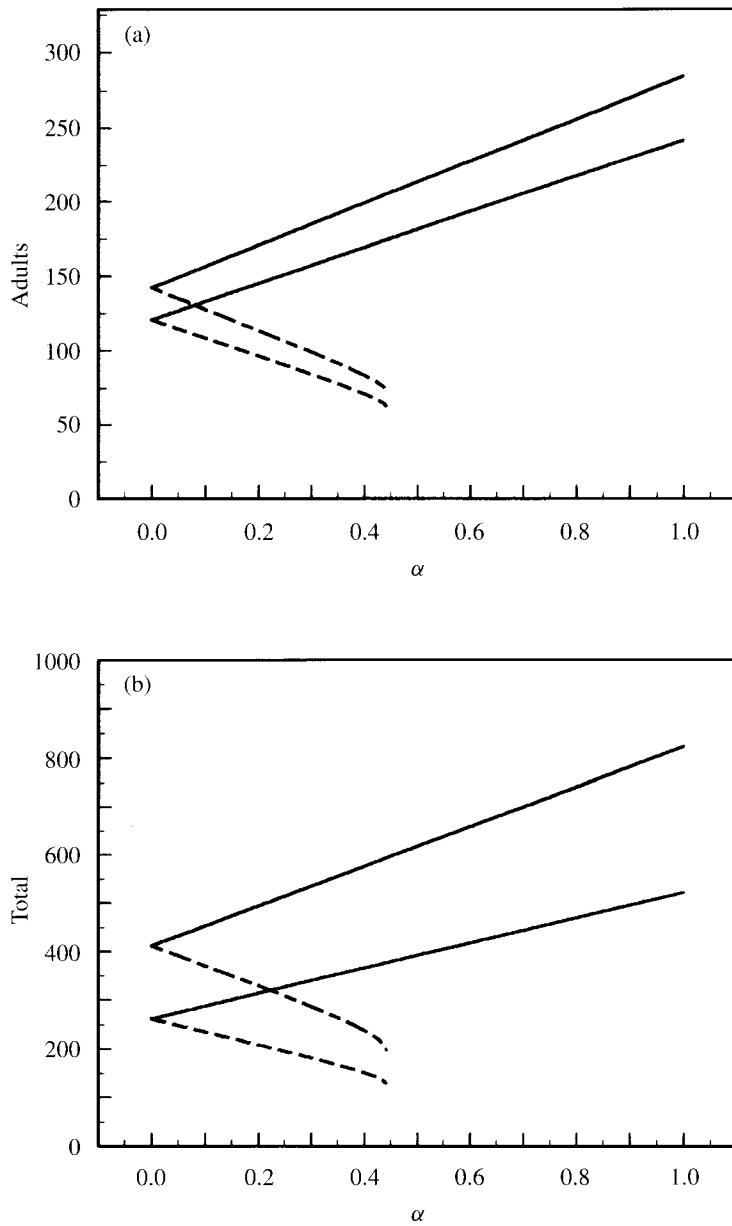
Figure 4. The asymptotic attractor for (a) adults and (b) total numbers of animals obtained from the periodically forced LPA model (3.3) is plotted against the relative amplitude α of the flour volume oscillation. Solid lines indicate the 'resonant' 2-cycle that has higher numbers than those in the constant habitat. Broken lines reveal another lower cycle that has fewer animals than the constant habitat.

The critical value of the relative amplitude, for the parameter values (3.4), is approximately $\alpha_{cr} = 0.45$ (see Fig. 4). In Jillson's experiment the relative amplitude $\alpha = 0.6$ exceeds this critical value. Consequently, the periodic LPA model (3.3) predicts an increased cycle average for total population numbers, exactly as Jillson observed in Jillson (1980).

More specifically, the attractor of the periodic LPA model (3.3) is a 2-cycle that oscillates between the life cycle stage distributions given by (rounded to the nearest whole integer)

$$
\begin{pmatrix} L \\ P \\ A \end{pmatrix} = \begin{cases} \begin{pmatrix} 0 \\ 221 \\ 189 \end{pmatrix} & \text{in 32 g of flour} \\ \begin{pmatrix} 424 \\ 0 \\ 224 \end{pmatrix} & \text{in 8 g of flour.} \end{cases} \tag{5.1}
$$

The resulting total population number $T = L + P + A$ oscillates between

$$
T = \begin{cases} 410 & \text{in 32 g of flour} \\ 647 & \text{in 8 g of flour} \end{cases} \tag{5.2}
$$

with an average of $T_{\text{ave}} = 529$. This 2-cycle attractor of the periodic LPA model (3.3) is to be contrasted with the 2-cycle attractor the LPA model (3.2) (using again the parameter estimates (3.4)). The 2-cycle attractor of (3.2) oscillates between the distributions

$$
\begin{pmatrix} L \\ P \\ A \end{pmatrix} = \begin{pmatrix} 0 \\ 138 \\ 118 \end{pmatrix} \quad \text{and} \quad \begin{pmatrix} 265 \\ 0 \\ 140 \end{pmatrix} \tag{5.3}
$$

and the resulting 2-cycle oscillation of total population number alternates between

$$
T = 256 \quad \text{and} \quad 405 \tag{5.4}
$$

with an average total population size of $T_{\text{ave}} = 331$. Thus, there is nearly a 60% model predicted increase in the average total population numbers in the periodic environment, above that in the constant environment. These numbers are quantitatively commensurate with the Jillson data in Tables 1 and 2, although the data often reach levels even higher than those predicted by the model.

The periodic LPA model (3.3) not only accounts for the increased population numbers observed by Jillson in the periodic habitat, but also for other features of the data as well. One prediction of the model is that there exists a certain phase relationship between each life cycle stage in the 2-cycle attractor and the oscillations of the flour volume (see (5.1)). For example, the L-stage oscillation

between a low of 0 and a high of 424 is out-of-phase with the flour volume oscillation from a low of 8 g to a high of 32 g (i.e. the L-stage low coincides with the flour volume high of 32 g and the L-stage high coincides with the flour volume low of 8 g). The A-stage is also similarly out-of-phase with the flour volume oscillation, while the P-stage is in-phase. These relative phase relationships predicted by the periodic LPA model are strikingly evident in the L- and P-stage experimental data plotted in Fig. 2. (The A-stage data does not exhibit a 2-cycle oscillation. One explanation for this is that the amplitude of the predicted A-stage 2-cycle is relatively small, unlike those of the L- and A-stages, and hence the A-stage 2-cycle is obscured by stochastic fluctuations in the data.)

There is a biological explanation for the observed (and model predicted) phase relationship between the oscillations in life cycle stage numbers and flour volume. Notice that there are no L-stage animals when the population is placed into the 32 g habitat and that their numbers swell during that interval to 424 when, following census, they are placed into the 8 g habitat. In the 32 g habitat, larval recruitment is enhanced by the absence of larval cannibalism on eggs and by the reduced egg eating by adults. In the 8 g habitat, L-stage animals undergo metamorphosis to pupae and then emerge as F adults. The latter is a series of biological changes that can occur quite satisfactorily in 8 g of flour.

Another interesting accurate correspondence between the periodic LPA model (3.3) and the experimental data of Jillson concerns transient phenomena. When the volume oscillation began in the Jillson experiment (at $t = 0$, i.e. at week 20) the data stage distributions were not near the model predicted 2-cycle distributions (5.1). For example, the stage structure of replicate #25 in the Jillson experiment (Fig. 2), when the animals were initially placed into the 32 g habitat, was

$$\begin{pmatrix} L \\ P \\ A \end{pmatrix} = \begin{pmatrix} 178 \\ 1 \\ 114 \end{pmatrix}.$$

Clearly, this stage distribution vector does not correspond well to the model predicted distribution in 32 g given in (5.1). As a result the periodic LPA model (3.3) predicts that transients will occur as the time series moves to the 2-cycle attractor. The features of these predicted transients can be seen in Fig. 5. Notice that larval and pupal numbers are initially relatively low (i.e. at $t = 0$ when the onset of volume oscillations occurs) and that they show a decreasing trend before increasing to the 2-cycle attractor. Even more striking is the adult transient behavior. Adult numbers show a monotonic decrease for six time units before beginning an increase towards the stable 2-cycle attractor. Also during the transient phase, larval and pupal numbers exhibit a 'stutter step' (from $t = 4$–5 and $t = 5$–6 respectively) that brings them into the proper phase relationship that the attractor has with the oscillating flour volume.

Although the (stochastic) data tends towards the 2-cycle attractor sooner then the model time series predicts, all of these features of the transient dynamics of
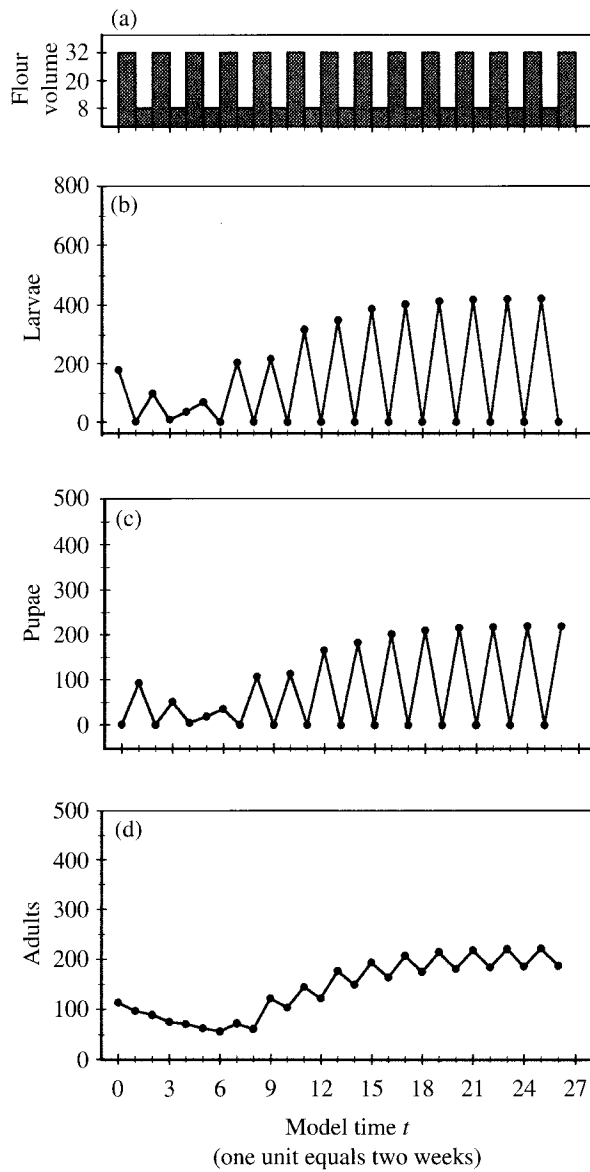
Figure 5. Transient behavior for (a) larval, (b) pupal and (c) adult numbers for time series obtained from the periodic LPA model (3.3) with parameter estimates (3.4) and a relative amplitude of $\alpha = 0.6$. The initial conditions are $L_0 = 178$, $P_0 = 1$, $A_0 = 114$, which are the numbers in replicate #25 of Table 2.

the periodic LPA model (3.3) described above can be seen in the experimental data of Jillson. From the data time series plots in Fig. 2 the adult numbers are seen to monotonically decrease from (model time) $t = 0$–4 before beginning a marked increase. The 'stutter steps' occur in the larval and pupal data at time $t = 2$–3 and $t = 3$–4 respectively and after this phase adjustment both larvae and pupae numbers quickly move to the 2-cycle attractor (i.e. begin large increasing amplitude oscillations of period 2).

6. CONCLUDING REMARKS

The periodically forced LPA model (3.3) is based on the premise that all rates of cannibalism (larvae on eggs, adults on eggs and pupae) are inversely proportional to flour volume. In a 32 g habitat, cannibalism rates are expected to be lower than in an 8 g habitat. Our experiments and analysis described in section 3.3 provide strong evidence of the validity of this premise. As we have seen, this model provides an explanation for the experimentally observed increase in total animal numbers or biomass in the periodic 32–8 g habitat as compared to the constant 20 g habitat.

The basic features common to a resonance phenomenon are present in the Jillson experiment. First, there is an inherent 2-cycle oscillation that occurs in the constant habitat. Second, there is an external periodic forcing, namely the 32–8 g oscillation of the flour volume, which is of the same period as the inherent biological oscillation. Third, the population's response to the periodic habitat forcing is an increase in animal numbers or biomass. In this sense, the population 2-cycle resonates with the habitat 2-cycle. The inherent biological 2-cycle can be interpreted as an interval with high rates of larval recruitment followed by an interval with low rates of larval recruitment. The oscillating flour habitat can be viewed as alternating intervals with low rates of egg cannibalism (thus high larval recruitment) with intervals of high rates of egg cannibalism (thus low larval recruitment). So the inherent high larval recruitment cycle is enhanced in the 32 g habitat, which in turn lowers the rates of egg cannibalism, and the inherent low larval recruitment cycle is intensified in the 8 g habitat, which in turn increases the rates of egg cannibalism.

Our main conclusion is that the Jillson experiments and our mathematical analysis suggest periodic habitat oscillations can result in a resonance-induced increase in population biomass. Conservation biologists, wildlife managers, and others may view this assertion as one possible way of increasing population numbers without altering the total available resources. This resonance occurs only under suitable circumstances, however. For example, in the case of flour beetles as studied here a sufficiently large larval recruitment rate and the presence of an inherent (constant habitat) oscillation are required. Under these circumstances, the total population biomass monotonically increases with an increase in large amplitudes α of the habitat oscillation. (However, as noted above, the model

also predicts a biomass increase in the absence of inherent oscillations, but this theoretical prediction has not been observed in data.)

It is interesting to note that the periodic LPA model (3.3) makes an unusual prediction when the circumstances for resonance are present and the relative amplitude α of the habitat oscillations are increased, but is *small*. As discussed in section 5 there exists two stable, model-predicted 2-cycle oscillations, one exhibiting an increased population biomass and the other exhibiting a decreased biomass (Fig. 4). For example, with relative amplitude $\alpha = 0.25$ (i.e. flour volumes that fluctuate between 25 and 15 g with an average still equal to 20 g) the initial distribution vector

$$\begin{pmatrix} L_0 \\ P_0 \\ A_0 \end{pmatrix} = \begin{pmatrix} 10 \\ 0 \\ 100 \end{pmatrix}$$

in the periodic LPA model (3.3) leads asymptotically to the 2-cycle

$$\begin{pmatrix} L \\ P \\ A \end{pmatrix} = \begin{cases} \begin{pmatrix} 0 \\ 172 \\ 148 \end{pmatrix} & \text{in 25 g of flour} \\[2em] \begin{pmatrix} 331 \\ 0 \\ 174 \end{pmatrix} & \text{in 15 g of flour} \end{cases}$$

while the initial distribution vector

$$\begin{pmatrix} L_0 \\ P_0 \\ A_0 \end{pmatrix} = \begin{pmatrix} 100 \\ 0 \\ 100 \end{pmatrix}$$

leads asymptotically to the 2-cycle

$$\begin{pmatrix} L \\ P \\ A \end{pmatrix} = \begin{cases} \begin{pmatrix} 198 \\ 0 \\ 105 \end{pmatrix} & \text{in 25 g of flour} \\[2em] \begin{pmatrix} 0 \\ 103 \\ 89 \end{pmatrix} & \text{in 15 g of flour.} \end{cases}$$

Note that the high and low cycles in L, P, and A numbers implied by the latter (nonresonant) 2-cycle bear a quite different phase relationship to the flour volume oscillation than the former (resonant) 2-cycle does. The existence of this nonresonant stable 2-cycle in the periodic habitat is somewhat counter-intuitive biologically and laboratory experiments to document its existence are currently underway.

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