

Chapter 5

Structured populations: discrete time

Population structure refers to consistent demographic differences among individuals as a function of some other attribute such as age, size, physiological state, or the history of conditions experienced as they develop. A structured population model tracks the dynamics not only of total population, but also the distribution of the variables that differentiate individuals. Change in the population are then predicted from the collective behavior of the individuals comprising the population, which therefore depends on the current composition of the population (e.g., the fraction of individuals who are old enough and large enough to breed).

Over the last 30 years structured population models have become a central modeling formalism in theoretical ecology, and one of the most widely used. Ecological theory was initially grounded mostly in unstructured models like those we have been studying so far. These models ignore within-species variability, so model predictions result from interactions between species, or between species and their environment. The current approach is to start at the level of individual organisms. Higher-level properties are derived as consequences of what happens to individual organisms. A natural result is a focus on the causes and consequences of differences between individuals.

This chapter covers some classical material on structured population models, rather tersely, so that we can get on to newer stuff. For more details, you can see the chapter on matrix models in Ellner and Guckenheimer (2006) which has considerable overlap with this chapter. For complete details and applications, there is no better source than the authoritative, entertaining and highly readable monograph by Caswell (2001).

5.1 The life table and Leslie matrix models

We consider first a population in which only individual age matters, and without any effects of population density. This is the simplest structured-population analog to $n(t+1) = \lambda n(t)$. The traditional model is female-based. If the species reproduces sexually, we tacitly assume that reproduction is never limited by a shortage of mates. We assume (to begin with) an annual birth-pulse – all births for the year happen “at once”. We census the population immediately after the birth-pulse (this is called a “post-breeding” census), so that the age of newborn individuals is 0.

Definitions for the life table model

- $n_a(t)$ = number of females age a at time t
- m_a = per-capita fecundity (daughters) of age- a females
- p_a = survivorship of age- a females to age $a+1$
- $l_a = p_0 p_1 p_2 \cdots p_{a-1}$ = survival from birth to age a
- $f_a = p_a m_{a+1}$ = average fecundity at age $a+1$ of females now age a = number of newborns “next year” per age- a female “now”.

m_a is daughters “now” – this year’s birth pulse – for a female whose age now is a . It’s about the present, not the future. f_a is daughters next year for a female whose age now is a . So for forecasting the population, the relevant quantity is f_a .

Population dynamics

$$\begin{aligned} n_0(t+1) &= f_0 n_0(t) + f_1 n_1(t) + \cdots = \sum_{a \geq 0} f_a n_a(t) \\ n_a(t+1) &= p_{a-1} n_{a-1}(t) \end{aligned} \tag{5.1}$$

There is another convention in which the population is censused just before the birth pulse, so all individuals are at least 1 year old. This is called a “pre-breeding census”. Pre-breeding census also changes the interpretation of f_a in the equations above - instead of the definition above, we have

$$\text{pre-breeding } f_a = m_a p_0$$

. Births occur “now” (immediately after the current census) – m_a daughters per age- a female now), and then p_0 is the fraction of those kids who survive until the next census (when they are 1 year old and first appear in a population count). So when the model is expressed in terms of m ’s and p ’s rather than f ’s and p ’s, there are two different versions depending on whether a pre-breeding or post-breeding census is assumed. This is very confusing, especially to experts. One often finds the two versions intermingled in a single paper or book, and even cases where the author state one convention, e.g. that newborns are age 0, but uses the other one. Beware and read carefully!

Leslie matrix Suppose that there is a finite age A beyond which no individuals can live, i.e. $l_A > 0, l_{A+1} = 0$. The population dynamics (5.1) then consists of finitely many equations and can be written in matrix form:

$$\begin{bmatrix} n_0(t+1) \\ n_1(t+1) \\ \vdots \\ n_A(t+1) \end{bmatrix} = \begin{bmatrix} f_0 & f_1 & f_2 & \cdots & f_A \\ p_0 & 0 & 0 & \cdots & 0 \\ 0 & p_1 & 0 & \cdots & 0 \\ \vdots & \vdots & \ddots & & \vdots \\ 0 & 0 & & p_{A-1} & 0 \end{bmatrix} \begin{bmatrix} n_0(t) \\ n_1(t) \\ \vdots \\ n_A(t) \end{bmatrix} \quad (5.2)$$

or simply

$$\mathbf{n}(t+1) = \mathbf{L}\mathbf{n}(t) \quad (5.3)$$

\mathbf{L} is called the *Leslie matrix* after P.H. Leslie. Leslie popularized its use in animal population ecology in the mid 20th century, initially as an approximation to models with continuous age structure from human demography.

We have seen (5.3) before, in the context of local stability analysis, so we know what to expect: exponential solutions constructed from the eigenvalues λ_j and corresponding eigenvectors w_j of the Leslie matrix,

$$n(t) = c_1 \lambda_1^t w_1 + c_2 \lambda_2^t w_2 + \cdots + c_A \lambda_A^t w_A$$

and for large t the solution is dominated by the term from the dominant eigenvalue (the one with the largest absolute value):

$$n(t) \sim c_1 \lambda_1^t w_1.$$

The existence of a dominant eigenvalue is guaranteed so long as the matrix \mathbf{L} is power-positive: some power L^m has all entries > 0 , where the exponentiation here is in the sense of matrix multiplication, not entry-by-entry. For example, the matrix $\mathbf{L} = \begin{bmatrix} 0.5 & 3 \\ 0.8 & 0 \end{bmatrix}$ is power positive with $m = 2$

```
> L=matrix(c(0.5,0.8,3,0),2,2); L%*%L;
      [,1] [,2]
[1,] 2.65  1.5
[2,] 0.40  2.4
```

If a non-negative matrix \mathbf{L} is power-positive, the Perron-Frobenius Theorem implies that \mathbf{L} has a unique dominant eigenvalue λ_1 which is positive, real, and strictly larger in magnitude than any other eigenvalue of \mathbf{L} . Moreover, there is a strictly positive eigenvector w_1 corresponding to λ_1 . As $t \rightarrow \infty$ the population vector $\mathbf{n}(t)$ converges a stable age distribution proportional to w_1 in the sense that

$$\frac{\mathbf{n}(t)}{\lambda_1^t} \rightarrow c w_1 \quad (5.4)$$

for some constant c that depends only on $\mathbf{n}(0)$, unless $\mathbf{n}(0) = 0$. Since $\log(\lambda_1^t) = t \log(\lambda_1)$,

Note that “stable” is used here in a distinctive sense. The population itself is growing, but the *relative numbers* in different age classes are becoming stable. In order for power-positivity to hold, we have to restrict the model to reproductive age-classes, i.e. $f_A > 0$ must be true (proof: Otherwise a population started with only post-reproductive individuals would die out, implying that for any m and any sufficiently large k we would have $\mathbf{L}^{km}n(0) = 0$. But if all entries of \mathbf{L}^m are positive so are all entries of \mathbf{L}^{km} , hence \mathbf{L} cannot be power positive). If $f_A > 0$, and any two consecutive f 's are positive, then \mathbf{L} will be power-positive. Note that it is safe to treat post-reproductives as if they were dead (for purposes of calculating λ) because they make no contribution to future population growth.

To illustrate these properties, consider the simplest possible age-structured case, a 2×2 matrix with $A = 1$. For example, consider

$$\mathbf{L} = \begin{bmatrix} .2 & 1.5 \\ .8 & 0 \end{bmatrix} \quad (5.5)$$

Using **R** we find that the eigenvalues are $\lambda_1 = 1.2, \lambda_2 = -1$, and the eigenvector associated with λ_1 is $w_1 = (0.832, 0.555)$. To get the proportions of the population in the different ages, we normalize w_1 so that its entries sum to 1:

```
w1=eigen(L)$vectors[,1]; w1=w1/sum(w1); w1
[1] 0.6 0.4
```

In the long run, we should see 60% of the population being age 0, and 40% being age 1, regardless of what the population state is initially, and the total population size should grow by 20% per year. Figure 5.1 shows that these occur within about the first 20 generations, even from extreme initial states (all age 0, or all age 1).

Some other properties of the stable age distribution and long-term growth rate λ_1 are developed in the following exercises.

Exercise 5.1 Explain in words why

$$n_0(t+1) = \sum_{a=0}^A f_a l_a n_0(t-a) \quad (5.6)$$

Exercise 5.2 Once the population is growing at rate λ_1 (i.e. once it converges to the stable age distribution) then in particular $n_0(t) = C\lambda_1^t$ for some constant $C > 0$. Use this observation and (5.6) to deduce the Euler-Lotka equation

$$\sum_{a=0}^A \lambda^{-(a+1)} l_a f_a = 1. \quad (5.7)$$

Exercise 5.3 Show that the Euler-Lotka equation can be written in the form (which is the most often-used version)

$$\sum_{x=1}^A \lambda^{-x} l_x m_x = 1. \quad (5.8)$$

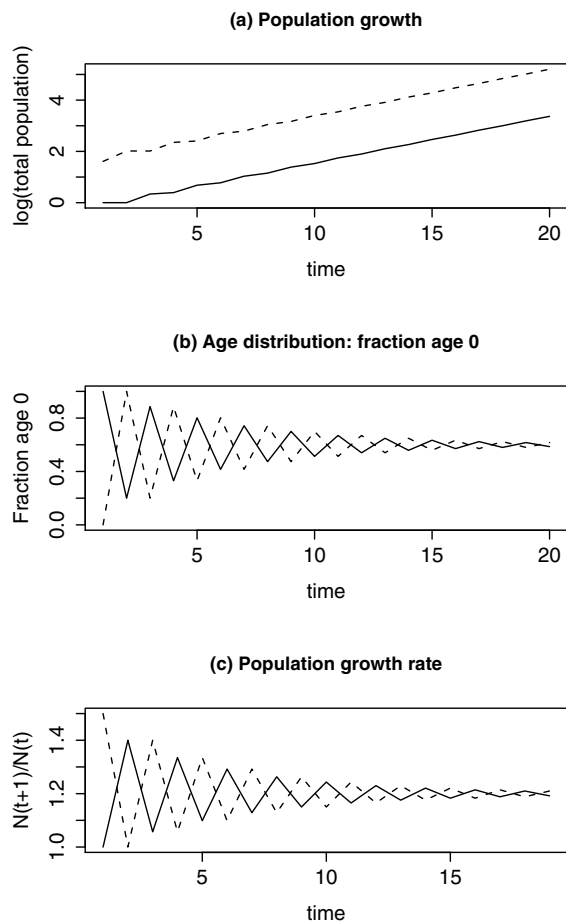


Figure 5.1: Convergence to stable age distribution for the Leslie matrix model (5.5), with two different initial populations: 1 newborn and no adults (solid lines), 5 adults and no newborns (dashed lines). (a) Growth of total population size, on log scale. (b) Convergence of the age distribution; values plotted are the number of newborns (age 0) divided by the total population (age 0 + age 1) (c) Annual population growth rate, $N(t+1)/N(t)$, where $N(t) = n_0(t) + n_1(t)$. A high fraction of newborns in a given year implies a low growth rate that year, and vice versa.

Exercise 5.4 Assuming again that the population has converged to its stable age distribution, explain why the population's age distribution is proportional to

$$(1, l_1/\lambda_1, l_2/\lambda_1^2, \dots, l_A/\lambda_1^A). \quad (5.9)$$

[HINT: to be 19 years old now, you must have been born (WHEN?) and then (WHAT?)]

The left-hand side of the Euler-Lotka equation is a decreasing function of λ_1 for $0 < \lambda_1 < \infty$. Conse-

quently we have that

$$\lambda > 1 \text{ if and only if } R_0 > 1 \text{ where } R_0 = \sum_{a=0}^A l_a f_a.$$

R_0 is the expected number of offspring to a newborn female over her lifetime; so we find (not surprisingly) that the population grows in the long run if and only if each newborn female can expect to have more than 1 daughter, on average.

The survival and fecundity parameters can also be used to derive a number of summaries of the life history, such as the mean age at reproduction, generation time, life expectancy, and so on (see e.g. Chapter 4 of Bulmer). For our purposes here these are not important.

One common extension of the Leslie matrix is to let age A represent “old” individuals – age A or older – and assume that survival and fecundity are the same for all “old” individuals. The only change in the Leslie matrix is that the bottom-right entry is then p_A rather than 0, where p_A is the probability that an “old” individual survives an additional year. Formally this allows individuals to live forever, but since there is no actual distinction by age in the “old” category this is not a problem for the model. And, since by definition few individuals reach extreme old age, an approximate treatment of the very oldest segment of the population will not be a major cause of error in population forecasts.

5.2 Stage structured matrix models

In place of \mathbf{L} we can consider populations classified by any discrete variable and governed by a population projection matrix \mathbf{M} ,

$$\mathbf{n}(t+1) = \mathbf{M}\mathbf{n}(t) \tag{5.10}$$

Perron-Frobenius still applies so long as \mathbf{M} is power-positive:

$$n(t) \sim c\lambda_1^t w_1$$

That is, we have a long-term growth rate given by the dominant eigenvalue λ_1 of the matrix \mathbf{M} , and convergence to a stable stage distribution (proportions of individuals in the different stages) given by the corresponding eigenvector w_1 .

The terms “stage” or “stage-class” are often used for the different groups of individuals recognized in the model. Sometimes they really are distinct life stages, but more often they are categories imposed by the modeler on a continuously varying trait such as size (or age). Caswell (2000) presents size-based models for sea turtles, desert tortoise, killer whales, geese, striped bass, bryozoan corals, and spotted owls.

The matrix \mathbf{M} then describes all the ways that an individual in one stage class “now” can contribute to another stage class “next year” (or whatever the time step is in the model). To see how this works in detail it is (for once) convenient to use the algebraic definition of matrix multiplication. The vector

form of the model (5.10) decodes into the entry-by-entry formulas

$$n_i(t+1) = \sum_j M_{ij} n_j(t) \quad (5.11)$$

Thus M_{ij} quantifies how many stage- i individuals are produced “next time” by each stage- j individual now. This provides a recipe for “reading” a projection matrix. Each stage-1 individual “now” produces

$$\begin{array}{l} M_{11} \text{ type 1 individuals} \\ M_{21} \text{ type 2 individuals} \\ M_{31} \text{ type 2 individuals} \\ \vdots \\ M_{k1} \text{ type } k \text{ individuals} \end{array}$$

at the next time step. The M values listed above comprise the first column of the projection matrix \mathbf{M} . Similarly, what you get from a stage-2 individual will be given by the entries in the second column.

Matrix models are extremely popular because they are simple, easy to construct and give a lot of information. Elasticity analysis of these matrix models has become a major tool in conservation biology (elasticities describe how the value of λ_1 changes in response to changes in different matrix entries; entries with large elasticities are identified as good “targets” management intervention, because relatively small changes have relatively large effects). Because all this is covered extensively in the Conservation Biology course (NTRES 405) here we only give a few examples.

5.2.1 Teasel, Werner and Caswell (1977)

Matrix for Field A teasel population (corrected version, Caswell 2001 p. 60).

$$\mathbf{M} = \begin{pmatrix} 0 & 0 & 0 & 0 & 0 & 322.38 \\ .966 & 0 & 0 & 0 & 0 & 0 \\ .013 & 0.01 & .125 & 0 & 0 & 3.448 \\ .007 & 0 & .125 & .238 & 0 & 30.170 \\ .008 & 0 & 0 & .245 & .167 & 0.862 \\ 0 & 0 & 0 & .023 & .750 & 0 \end{pmatrix}$$

1=Dormant seeds, year 1; 2=Dormant seeds, year 2

3,4,5 =Small,Medium,Large rosettes

6=Flowering plants

Exercise 5.5 . Using the recipe given above for “reading” a transition matrix, decode and state in words what the first column of the matrix for teasel says about dormant seeds, and what the last column says about flowering plants.

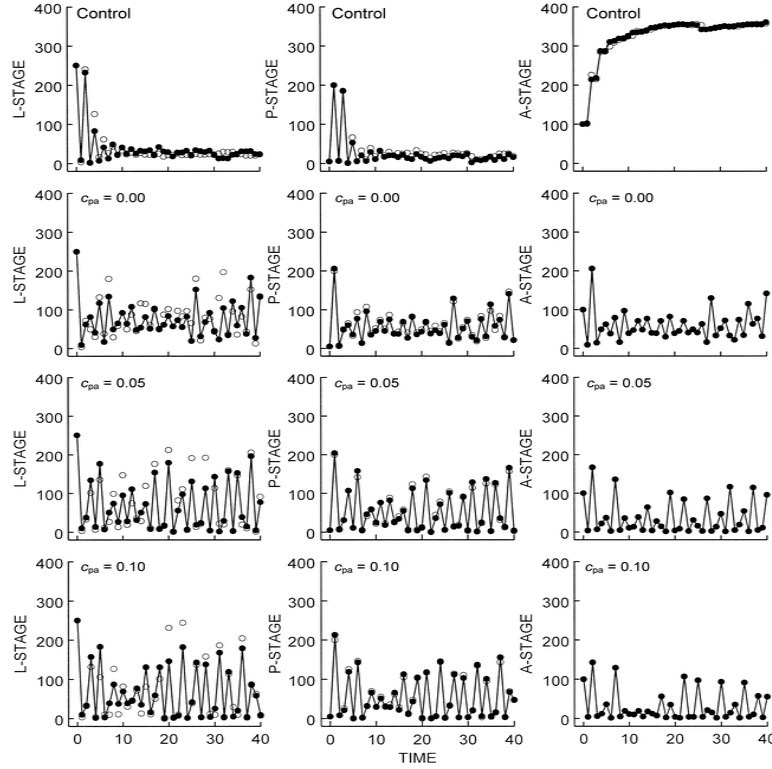


Figure 5.2: Time-series data (open circles) and one-step predictions from the LPA model (closed circles) for representative cultures from four experimental treatments: control, and c_{pa} (adultpupa cannibalism coefficient) = 0.00, 0.05, and 0.10. The unit of time is two weeks. This figure is from Dennis et al. (2001).

5.2.2 Flour beetles *Tribolium*

Costantino et al. (1995), Dennis et al. (2001) describe experiments on laboratory populations of flour beetles. The time step is 2 weeks, roughly equal to the durations of the egg+larval and pupal stages.

$$\mathbf{M} = \begin{pmatrix} 0 & 0 & F_3(n) \\ P_1 & 0 & 0 \\ 0 & P_2(n) & P_3 \end{pmatrix}$$

1=Larvae, 2=Pupae, 3=Adults

$$F_3(n) = b \exp(-c_{ea}n_3 - c_{el}n_1) \quad P_2(n) = \exp(-c_{pa}n_3)$$

The density-dependence is due to cannibalism of immobile stages (eggs, pupae) by mobile stages (larvae, adults) with rates based on random encounter (as in Nicholson-Bailey, survival is the zero term of a Poisson distribution for the number of mobile individuals encountering the spot where the immobile one is sitting). In more familiar terms, it's as if butterflies were to eat any cocoons they encounter (including

their own offspring), and caterpillars ate any butterfly eggs they happened to find; it's no wonder that flour beetles are generally regarded as a “pest”, except by scientists. Based on the stage names, this is called the LPA model. Figures 5.2 and 5.3 show the kinds of dynamics it can produce, and how well the LPA model (either deterministic as above, or with random perturbations to represent finite population effects) succeeds in predicting the outcome of experiments (these being genuine predictions: the model was not fitted to these data, rather its parameters were estimated from independent data and then one parameter (c_{pa}) was varied in the model and in experimental cultures).

5.2.3 Vegetation dynamics in England

Usher (1972): The “individuals” are plots of land, and the stages are 1=Bog, 2=Heath, 3=Woodland, 4=Grazed.

$$\mathbf{M} = \begin{pmatrix} .65 & .30 & 0 & 0 \\ .29 & .33 & .28 & .4 \\ .06 & .30 & .69 & .2 \\ 0 & .07 & .03 & .4 \end{pmatrix}$$

Each column sums to 1, indicating that the total amount of area neither grows nor shrinks.

Exercise 5.6 . What is the dominant eigenvalue λ_1 for the vegetation dynamics matrix, and why?

5.2.4 Sea turtles: Crouse, Crowder, Heppell et al.

Stage	Description	Duration(yr) T_i	Survival σ_i	Fecundity F_i
1	Eggs	1	0.6747	0
2	Small juveniles	~ 7	0.75	0
3	Large juveniles	~ 8	0.6758	0
4	Subadults	~ 6	0.7425	0
5	Adults	> 32	0.8091	76.5

Because stages are really age-classes in this model, individuals can grow or stay the same “size”, but not shrink. This leads to a simple form for the transition matrix.

Transition Matrix

$$A = \begin{bmatrix} P_1 & 0 & 0 & 0 & F_5 \\ G_1 & P_2 & 0 & 0 & 0 \\ 0 & G_2 & P_3 & 0 & 0 \\ 0 & 0 & G_3 & P_4 & 0 \\ 0 & 0 & 0 & G_4 & P_5 \end{bmatrix} \quad \begin{array}{l} P_i = \sigma_i(1 - \gamma_i) \text{ survive and remain in stage} \\ G_i = \sigma_i\gamma_i \text{ survive and grow to next stage} \end{array}$$

Growth probabilities γ_i were computed by assuming fixed stage durations, and stable age distribution

within each stage, so γ_i is the fraction of individuals in the last year of the stage:

$$\gamma_i = (z^{T_i} - z^{T_i-1}) / (z^{T_i} - 1), \quad \text{where} \quad z = \sigma_i / \lambda_1$$

A general size-based model is more complicated to parameterize, because there is the possibility of individuals shrinking as well as growing.

The model (in various versions) was used to compare the effectiveness of headstarting (save turtles on the beach) versus TEDs (turtle excluder devices on shrimping boats, that can catch and kill juveniles at sea; see the papers by Heppell, Crouse, Crowder et al. given below). This story is an often-repeated “poster child” for matrix models in conservation biology, because a model-based change in conservation strategy has apparently halted and even reversed a longstanding decline of Atlantic sea turtle populations.

5.3 Limitations and alternatives

The main intrinsic limitations of the matrix model come from the fact that individual state is discrete – a finite list of options. All individuals within a given stage therefore are assumed to be identical, in terms of their possible fates and the odds for each possible fate. Sometimes this is reasonable, and sometimes it is less reasonable. For example in the sea turtle models, it is not really the case that all small juveniles have the same chance of maturing into the large juvenile class – one who hatched last year has no chance, one who hatched 6 years ago has a very good chance. Similar issues are present if individuals are classified based on some physiological variable – such as size – that really varies continuously: an individual that just grew into a size category will probably stay there for a while, but an individual who is close to the upper size limit for the category has a good chance of growing out of it soon.

Dealing with these problems requires models having a continuous individual-level state variable. If we modify the basic matrix model in this way alone, the result is an integral model (Easterling et al. 2000). The state of the population is described by a distribution function $n(x, t)$ that can be thought of (loosely) as the number of state- x individuals at time t . More precisely, $n(x, t)$ is the state density function such that

$$\int_{x_1}^{x_2} n(x, t) dx$$

is the number of individuals between sizes x_1 and x_2 at time t . The matrix iteration (5.11) is then replaced by

$$n(x, t+1) = \int_{\Omega} K(y, x) n(y, t) dy$$

where the *kernel function* $K(y, x)$ gives (loosely) the number of state- y individuals “next year”, per state- x individual “now”, and Ω is the set of possible sizes. The papers by Rees and Rose (2002) and Childs et al. (2003, 2004) describe some applications of integral models to plant populations structured by size and age, with size as a continuous variable. The change to a continuous structuring variable turns out

to have very little impact on the behavior of the model. For example, if the kernel function is continuous and power-positive then there is a dominant eigenvalue and corresponding dominant eigenvector that give the long-term growth rate and structure of the population, and formulas similar to those in the matrix model are available to compute the sensitivity of the dominant eigenvalue to changes in the kernel (Ellner and Rees 2005).

Integral models are a relatively recent innovation, so it remains to be seen whether they will catch on. Like matrix models, they make it easy to represent situations where growth is not deterministic – i.e. size “next year” is not perfectly predicted by size “now”. If growth is modeled as deterministic, it is more convenient to use models with continuous time as well as continuous state. Those are the subject of the following chapter.

5.4 References

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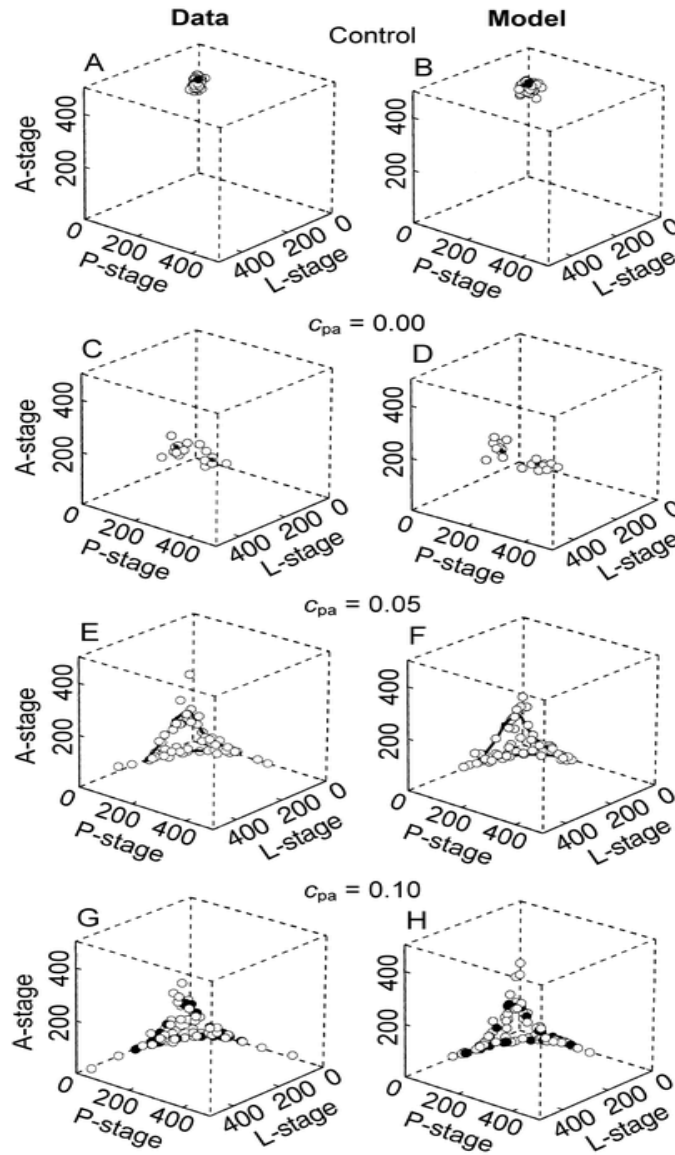


Figure 5.3: Plots in (L, P, A) space of the data (A, C, E, G) and stochastic model (B, D, F, H) for weeks 4080 (open circles) together with the deterministic model attractor (solid circles or lines) for four experimental treatments: control, and $c_{pa} = 0.00, 0.05$, and 0.10 . Model simulations used the same initial conditions, number of replicates, and experiment duration as the real experiments data. Data from the start of each experiment (weeks 0–38 for control, $c_{pa}=0.05$ and 0.10 , weeks 0–66 for $c_{pa}=0.00$) were discarded as representing transient behavior, in order to focus attention on comparing the long-run behavior of the experiments and model. This figure is from Dennis et al. (2001).