THE MODELLING OF COMPETITION AND PARASITISM IN LABORATORY INSECT POPULATIONS

by

Thomas Scott Bellows, Jr. B.S. (Biology)

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Department of Zoology and Applied Entomology,
Imperial College of Science and Technology,
Field Station, Silwood Park,
Ascot, Berkshire

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Abstract

This thesis explored the use of two types of population models in simulating the behaviour of laboratory insect populations. The first type considered were simple analytical difference equation models. By applying such a model to some experimental data on density dependence in the weevils Callosobruchus chinensis (L.) and C. maculatus (F.), single and two-species models were constructed. The single species models predicted stable equilibria; the two species models predicted an unstable two-species equilibrium. Secondly, more detailed models were considered. Simulation models were constructed for the Callosobruchus species which employed a discrete time-step of one day. Provision was made for age specific adult mortality and fecundity and for distributed larval developmental periods. Density dependence was included in the forms of intrastage and interstage competition both within and between species. Results of laboratory experiments were presented which permitted the estimation of the required parameters. Single-species simulations predicted stable equilibria for both species. The two-species model predicted no two-species equilibrium existed and C. chinensis was the successful competitor. Some complex properties of this two-species model are discussed. These simulation models were then extended to include interactions between the hymenopteran parasitoid Lariophagus distinguendus Först. and the Callosobruchus species. Provision was made for age specific adult parasitoid mortality and a distributed larval developmental period. In addition, the effects of host density, the stage attacked, parasitoid density and adult parasitoid age on parasitoid searching efficiency were considered. The required parameters were estimated from laboratory experiments, and the effects of including the parasitoid in the single and two host species simulation models were investigated.

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Chapter I. INTRODUCTION.

Many of the foundations of theoretical population ecology were laid in the early part of this century. Although Verhulst (1838) had originally proposed the familiar logistic equation for single-species population growth, it was not widely appreciated until the work of Pearl & Reed (1920). Lotka (1925) and Volterra(1926) included in this model interspecific competition and Thompson (1924), Lotka (1925), Volterra (1926) and Nicholson (1933) considered models for predator-prey interactions. In spite of the early interest aroused by these models, there was little attempt made to examine the validity of their assumptions and there were only a few experimental studies conducted in which models played an important role in interpreting the observed dynamics of a particular system (e.g. Pearl & Parker 1922; Crombie 1945). More recently, however, there has been a greater appreciation for the need to achieve a harmony between models and observations in population ecology (e.g. Hassell, Lawton & Beddington 1976; Hassell, Lawton & May 1976; Beddington, Free & Lawton 1978; Hassell 1978). This thesis sets out to examine two aspects of the relationship between mathematical models and biological populations with special reference to a particular laboratory system consisting of two stored product beetles, Callosobruchus chinensis (L.) and C. maculatus (F.) and their pteromalid parasitoid Lariophagus distinguendus Först. These insects are easily bred in the laboratory (the beetles breed in dried pulses), have a short generation time and relatively simple biology and are hence particularly suited to such a study.

The first topic investigated here is the use of simple analytical models in describing the dynamics of single and two competing species populations. Attention will be concentrated on models framed in difference equations as these are most appropriate for the modelling of many insect populations (e.g. May & Oster 1976). Such models are typically based on an equation for density dependent mortality. Thus as an initial step, the descriptive properties of a number of such equations are compared in chapter 2. A surprizing number of these equations are found to have a common fault, and only one of them is sufficiently flexible to be considered as having a general form. This equation is then used in chapter 3 as the basis for single-species population models for C. chinensis and C. maculatus, making use of the results of short-term laboratory investigations into the processes affecting population growth. The models predict dynamic behaviour of the two species in accord with the results of long-term studies reported in the literature. As a final step in this first investigation, models for two-species competition are constructed for interactions between the two Callosobruchus species (chapter 5). The models are again based on the general equation of chapter 2 and competition coefficients for the two species are estimated from short-term experiments. The properties and predicted outcomes of these models are discussed.

The second theme of this study involves the use of detailed simulation models for investigating the dynamic behaviour of biological systems. Attention is again concentrated on the Callosobruchus species, and in chapter 4 a simulation model is constructed for both single-species populations. The important components of the model are again investigated using short-term experiments. The dynamic behaviour of these models is similiar to that of the analytical models of chapter 3 but some differences arise and are discussed. These single species

simulation models are then used to form a model for two competing species in chapter 5. Some previously unappreciated properties of such systems emerge and are discussed. Finally, in Chapter 6, a simulation model for interactions between insect parasitoids and their hosts is developed. Some experiments on the biology and searching behaviour of Lariophagus distinguendus provide information on which the details of the model are based. This model is used together with the single and two host species simulation models to investigate the importance of multiple age-class interactions in parasitoid-host systems.

Chapter II. SOME MODELS FOR DENSITY DEPENDENCE

2.1 Introduction

It has been appreciated since the early work of Verhulst (1838) and Pearl & Reed (1920) that many biological populations exhibit negative feedback mechanisms which restrict their growth. These mechanisms, often referred to as density dependent processes, play an important role in determining the dynamics of such populations (May et al. 1974) and consequently are also of importance when considering the construction of population models. There is a constant need for simple but general functions to describe density dependent processes; simple so that their properties may be determined analytically, but sufficiently general so that they are capable of describing the varied forms in which density dependence may occur.

A number of difference equation models for describing density dependence have appeared in the literature, either as descriptive tools for quantifying density dependence (e.g. Ullyett 1950; Varley & Gradwell 1963; Hassell & Huffaker 1969; Hassell, Lawton & May 1976) or as regulatory functions in population models (e.g. Cook 1965; Pennycuik, Compton & Beckingham 1968; Varley & Gradwell 1968; Usher 1972; Maynard Smith & Slatkin 1973; Varley, Gradwell & Hassell 1973; Hassell 1975; May 1975). The characteristic dynamics of these models have been recently reviewed by May & Oster (1976), who have emphasized the range of possible dynamics shown by difference equation models. Although the models considered by May and Oster all show similiar ranges of dynamic behaviour, they differ widely in their ability to describe different types of density dependence. It is the object of

this chapter to examine the different forms of density dependent models in the literature and compare their descriptive abilities.

The comparative review presented here follows two lines : (i) a qualitative consideration of the forms of density dependence described by each model; (ii) a quantitative comparison of the fit of several of the models to a number of sets of data showing density dependent mortality. The qualitative study begins with a consideration of different methods of graphical presentation of density dependence in data. This is followed by the derivation of a general difference equation model for density dependence and a discussion of the relationship between this general model and those existing in the literature. These two sections lead to a qualitative comparison of the forms of density dependence that the various models can describe. The data on which the quantitative comparison is based is presented next, and the results of fitting some of the models to the data are discussed. In this section, the views of Hassell, Lawton & May (1976) concerning the effect of density dependence on single-species population dynamics are reexamined, and their conclusions upheld. In the final section, the descriptive properties of the models are compared and some remarks about their potential uses are made.

2.2 The presentation of density dependence data

Although a variety of methods of graphically presenting density dependence data have appeared in the literature, a primary aim common to them all is to demonstrate whether or not data show evidence of density dependence. A secondary, but also important, objective is to determine whether the data indicate a compensatory (contest competition in the sense of Nicholson (1954)) or an overcompensatory (scramble competition) process. Four common methods of presenting such data will be discussed here, with particular reference to data

dealing with density dependant mortality.

The most immediate method of presenting density dependence data is to plot the number of survivors $\underline{S}$ against the initial density $\underline{N}$. Any deviation from a straight line through the origin indicates density dependence. Data plotted in this way usually show either a monotonic curve (contest competition, figures 2.1a and 2.7a) or a humped curve (scramble competition, figures 2.1b, c, d). Another useful method is to plot proportionate survival S/N against density. Such plots often show a sigmoid relationship between S/N and $\underline{N}$ (figures 2.2b, c, d) but may also indicate a monotonically decreasing curve (figures 2.2a and 2.5a). Deviation from a line with zero slope now indicates density dependence, but there is not a simple interpretation of these plots which reflects the type of competition involved. Two further methods are based on plotting proportionate survival on logarithmic scales (the k-value of Haldane (1949) and Varley & Gradwell (1960)). When k-value ($=-\ln(S/N)$[1]) is plotted against ln density, density dependence is shown by deviation from a line with zero slope. Data plotted in this way often indicate linearly or exponentially (but not logarithmically) increasing curves (figures 2.3 and 2.5b). At high densities the relationship between k-value and log density often appears nearly linear. When the slope of this linear portion of a k-value plot is near unity contest competition is implied, while a slope much greater than unity indicates scramble competition. The final method is that of plotting k-value against density (arithmetic scale). Such plots may show either logarithmically (figures 2.4a and 2.5c) or exponentially (figures 2.4b, c, d) increasing

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[1] Throughout this thesis the conventions that $\ln(x)=\log_e(x)$ and $\log(x)=\log_{10}(x)$ will be followed.

FIGURE 2.1 The relationship between number of survivors (mean $\pm$ s.e.) and density for four stored product beetles (for experimental details see page 35). The fitted curves are from the density dependent mode entry 5 of table 2.1, $S = dN / (1+(aN)^b)$.

(a) Stegobuim paneceum; d=0.711, a=0.110, b=0.950.

(b) Lasioderma serricorne; d=0.806, a=0.0114, b=7.53.

(c) Tribolium confusum; d=0.610, a=0.0116, b=3.12.

(d) Tribolium castaneum; d=0.800, a=0.0149, b=4.21.

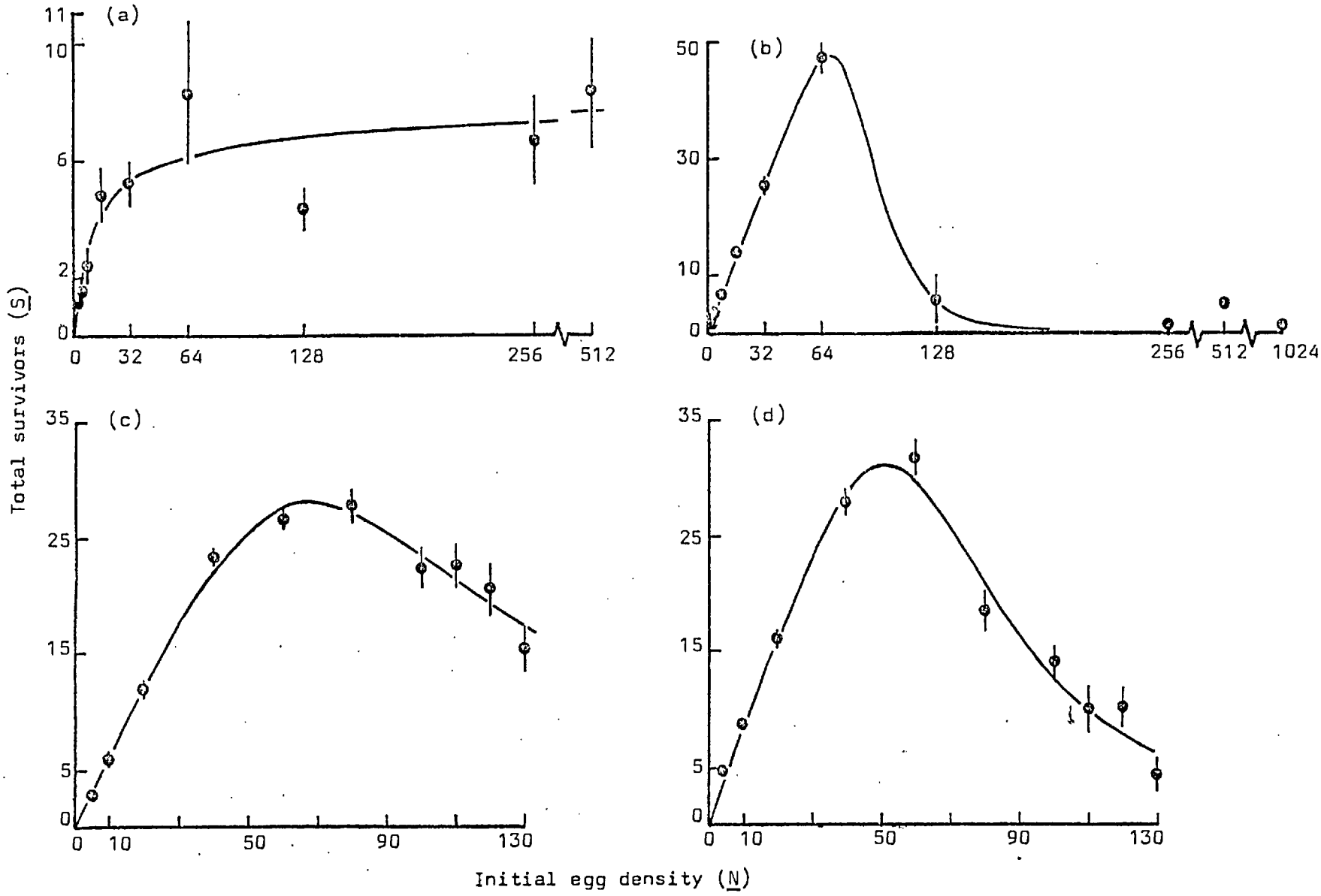

(a)
(b)
(c)
(d)
Total survivors (S)
Initial egg density (N)
0
32
64
128
256
512
1024
10
50
90
130

FIGURE 2.2 The data of figure 2.1 expressed as percentage survival (transformation on the means) against density. Fitted lines were obtained by transforming the predicted number of survivors to percentage survivorship. (a) Stegobium paneceum. (b) Lasioderma serricorne. (c) Tribolium confusum. (d) Tribolium castaneum.

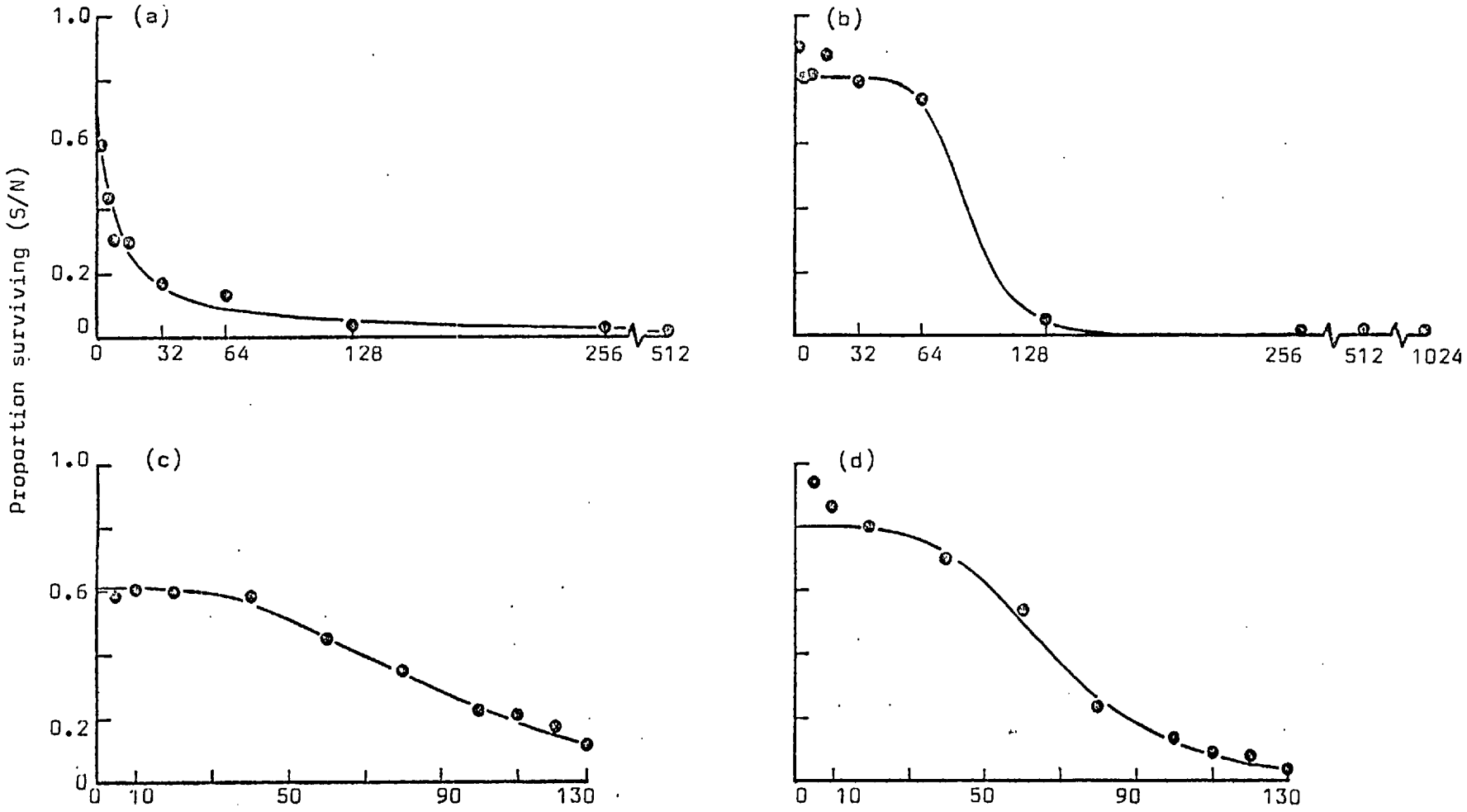

(a)
(b)
(c)
(d)
1.0
0.6
0.2
0
0 32 64 128 256 512
0 32 64 128 256 512 1024
0 10 50 90 130
Proportion surviving (S/N)
Initial egg density (N)

FIGURE 2.3 The data of figure 2.1 expressed as k-value (transformation on the means) against ln density. Fitted lines were obtained by transforming the predicted number of survivors to k-value. (a) Stegobium paneceum. (b) Lasioderma serricorne. (c) Tribolium confusum. (d) Triboluim castaneum. (N.B. The overestimates of k-value at high densities of Lasioderma serricorne in (b) are due to the relatively small contribution of these data points to the fitting of the model to the original data in figure 2.1b.)

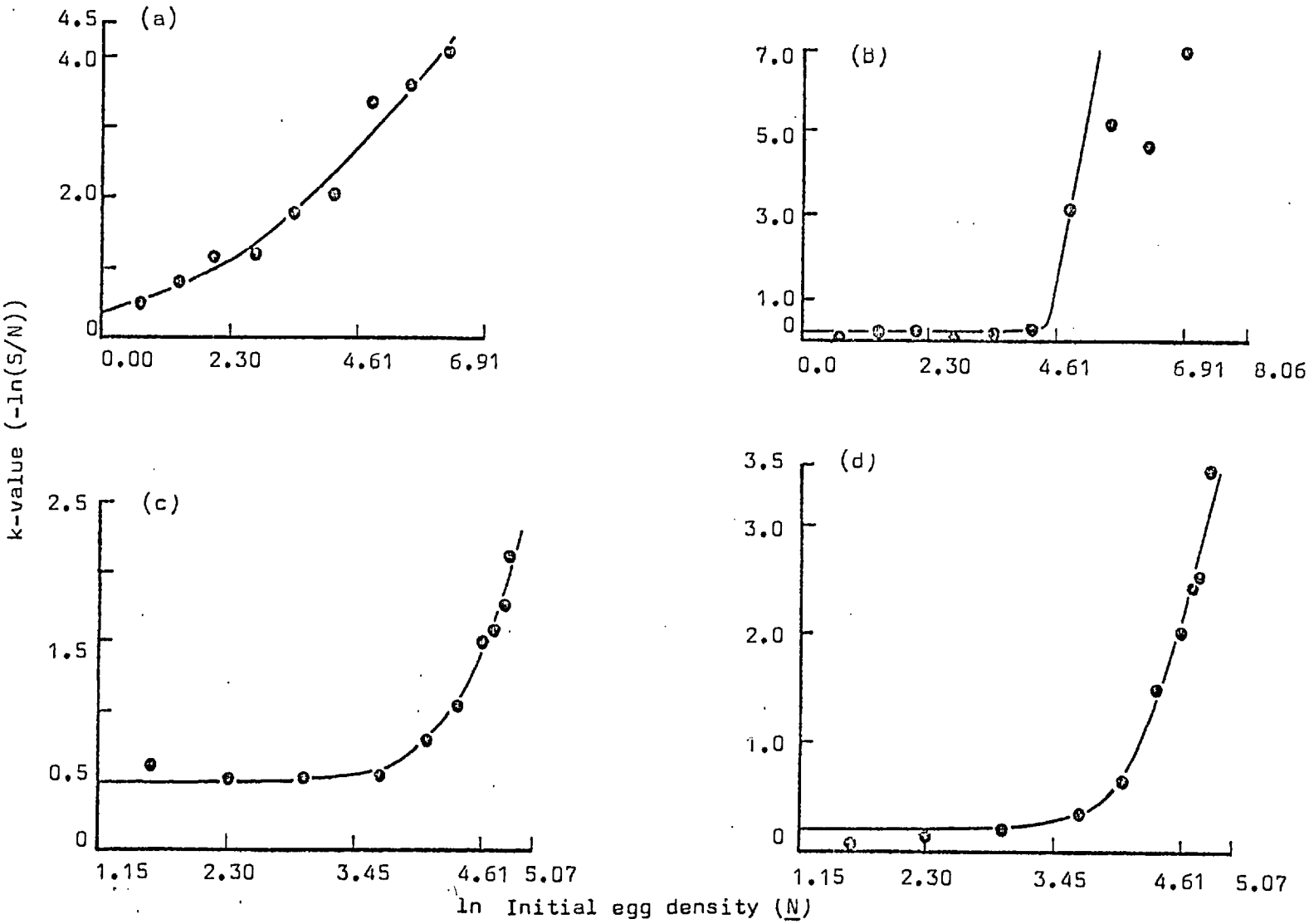

(a)
4.5
4.0
2.0
0
0.00
2.30
4.61
6.91
(B)
7.0
5.0
3.0
1.0
0
0.0
2.30
4.61
6.91
8.06
(c)
2.5
1.5
0.5
0
1.15
2.30
3.45
4.61
5.07
(d)
3.5
3.0
2.0
1.0
0
1.15
2.30
3.45
4.61
5.07
k-value (-ln(S/N))
ln Initial egg density (N)

FIGURE 2.4 The data of figure 2.1 expressed as k-value against density. Fitted lines were obtained by transforming the predicted number of survivors to k-value. (a) Stegobuim paneceum. (b) Lasioderma serricorne. (c) Tribolium confusum. (d) Tribolium castaneum. (N.B. See note in legend of figure 2.3.)

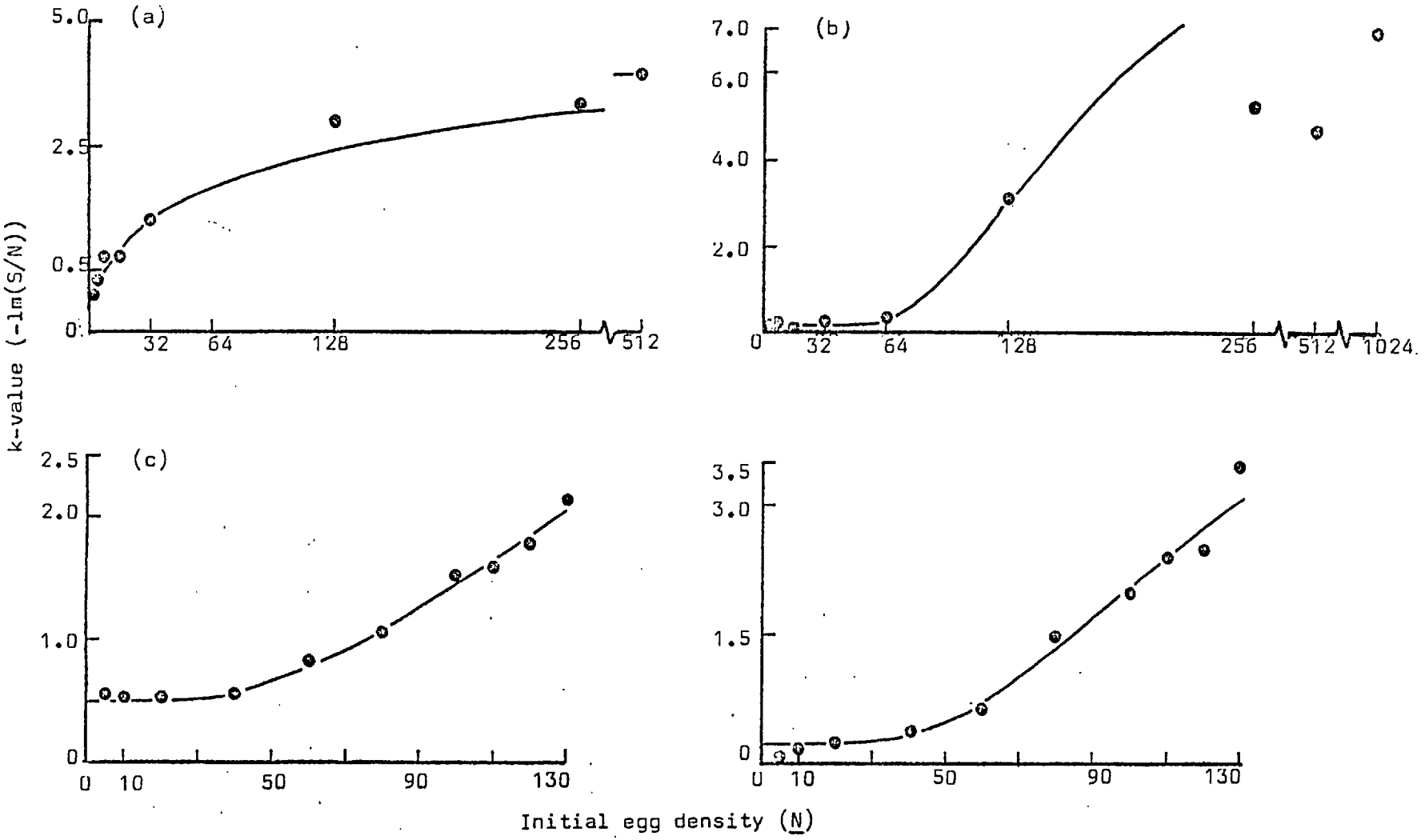
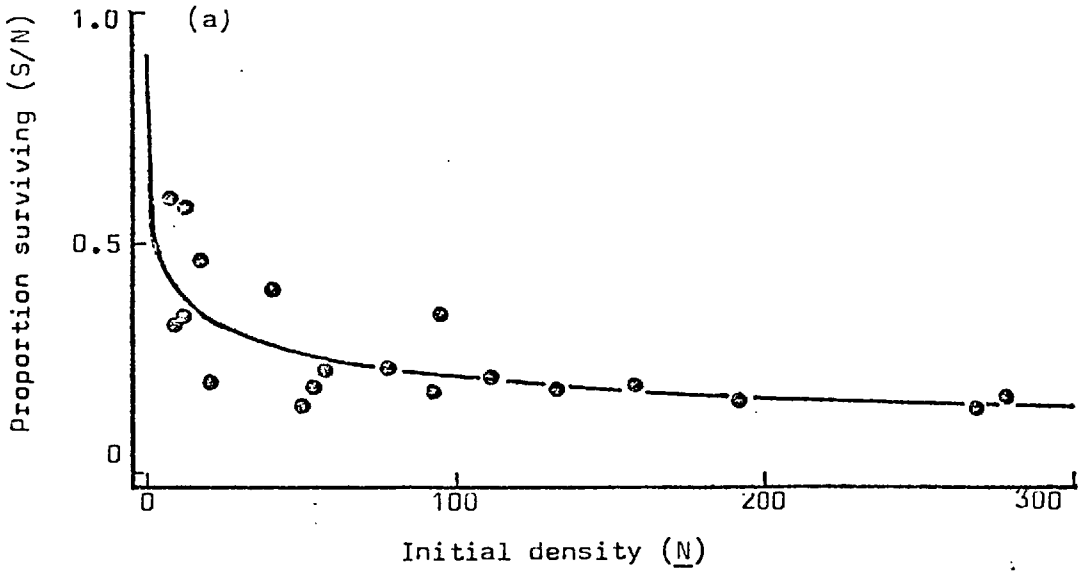
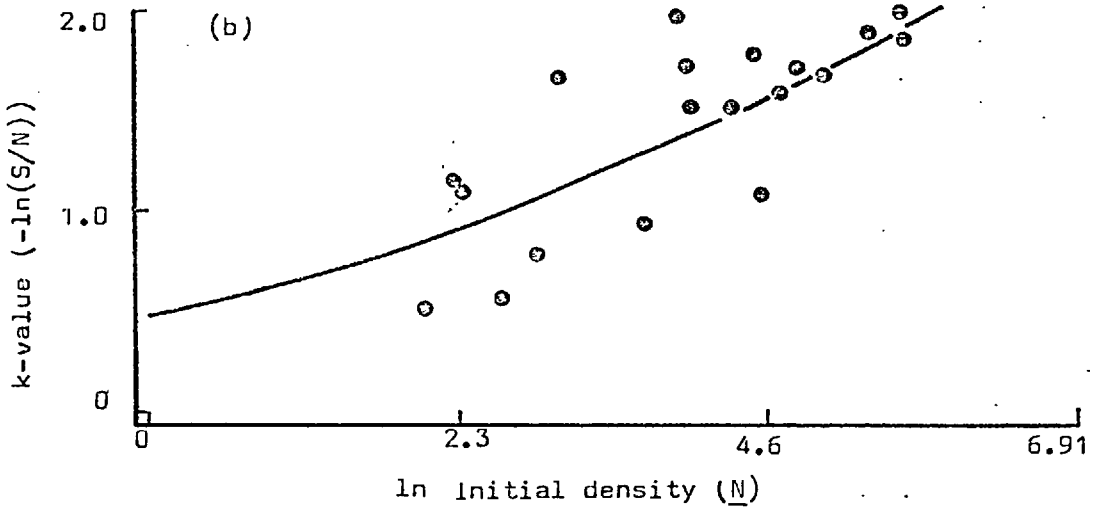
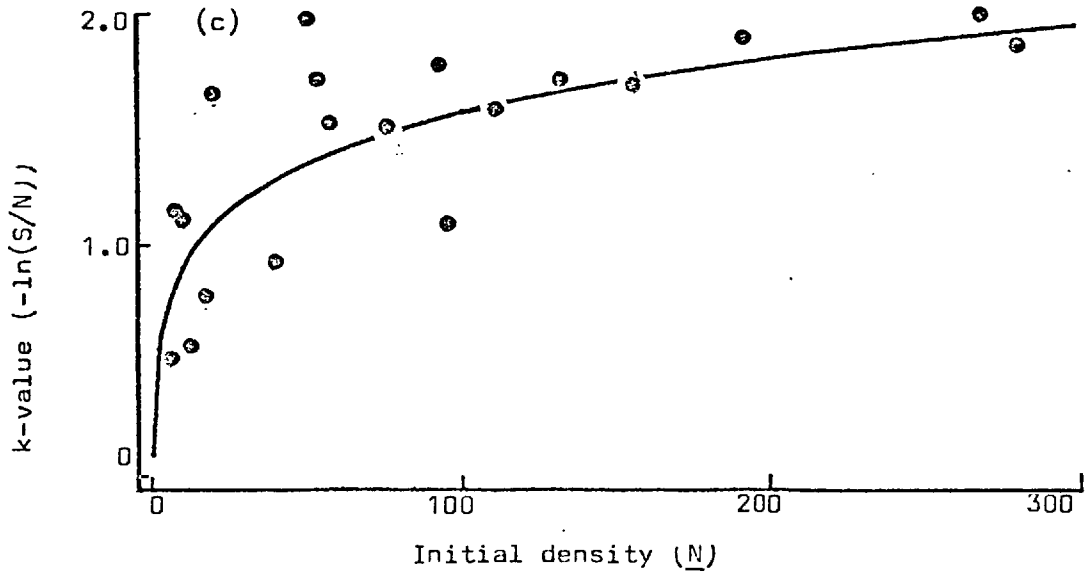

(a)
5.0
2.5
0.5
0
32
64
128
256
512
(b)
7.0
6.0
4.0
2.0
0
32
64
128
256
512
1024
(c)
2.5
2.0
1.0
0
0
10
50
90
130
3.5
3.0
1.5
0
0
10
50
90
130
k-value (-ln(S/N))
Initial egg density (N)

FIGURE 2.5 The plots of (a) proportionate survival against density, (b) k-value against log density and (c) k-value against density for Operophtera brumata (L.) (data from Varley & Gradwell 1968). The fitted curves were obtained by transforming the predicted number of survivors (see figure 2.7a) to these measures of mortality.


(a)
Proportion surviving (S/N)
1.0
0.5
0
0
100
200
300
Initial density (N)


(b)
k-value (-ln(S/N))
2.0
1.0
0
0
2.3
4.6
6.91
ln Initial density (N)


(c)
k-value (-ln(S/N))
2.0
1.0
0
0
100
200
300
Initial density (N)

curves. When these plots appear logarithmic, contest competition is implied, while exponential plots indicate scramble competition. Density dependence is again shown by deviation from a line with zero slope.

2.3 Density dependence in models

Models describing density dependent mortality are often framed in difference equations of the form

$$S = Nf(N), \tag{2.1}$$

where S is the number of survivors, N is the initial number of individuals, and $f(N)$ is a function which relates proportionate survival to density. The function $f(N)$ must take values in the range 0-1 for positive values of N.

An approach to defining a general form for the function $f(N)$ can be made by considering a differential equation of the form

$$\frac{dN}{dt} = -N\,\mu(N) \tag{2.2}$$

where N is the population size and $\mu(N)$ is a function relating mortality rate to density. A homologous discrete time formulation of equation 2.2 can be constructed by integrating at a fixed density, say N_o, to give

$$N_t = N_o \exp(-\mu(N_o)t). \tag{2.3}$$

Here, N_o is the initial population size and N_t is the number of survivors at time t. When t is taken to be unity, equation 2.3 may be written in the form of equation 2.1,

$$S = N \exp(-\mu(N)), \tag{2.4}$$

where $N = N_o$, $S = N_t$ and $f(N) = \exp(-\mu(N))$. Isolating $\mu(N)$ (the mortality rate) from equation 2.3 gives

$$\mu(N) = \frac{1}{t} \ln(N_o/N_t). \tag{2.5}$$

If t is again taken as unity, $\mu(N)$ becomes the familiar k-value for mortality of Haldane (1949) and Varley & Gradwell (1960). A general formula for expressing the relationship between mortality rate and

density may be postulated :

$$\mu(N) = c + aN^b \; ; \; a,b,c \geq 0. \qquad (2.6)$$

Substituting equation 2.6 into equation 2.4 gives a general model for density dependent survivorship,

$$S = N \exp(- c - aN^b)$$

or

$$S = dN \exp(- aN^b), \quad d = \exp(-c). \qquad (2.7)$$

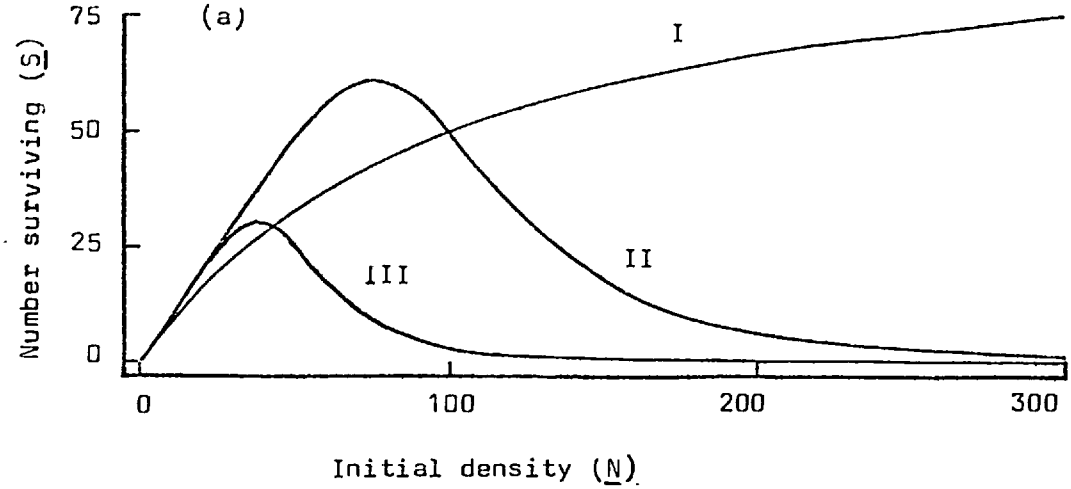
The parameters in equation 2.7 are restricted such that $0 \leq d \leq 1$ and $a,b \geq 0$. The function $f(N)$ is now given by $f(N) = d \exp(-aN^b)$.

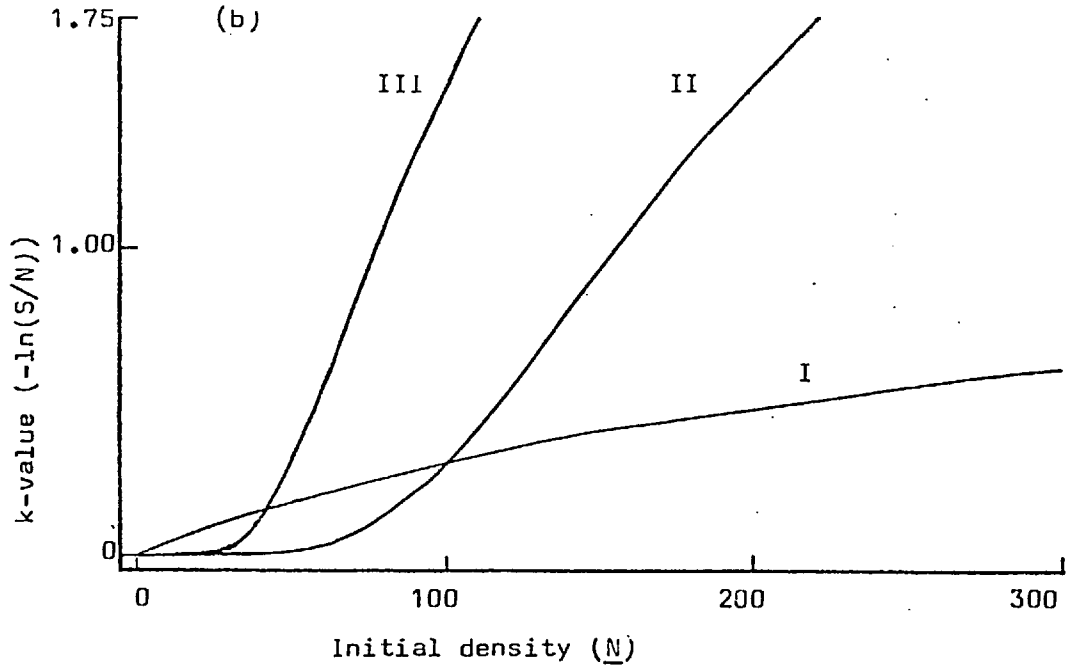
Although the model of equation 2.7 has three parameters, the parameter d only determines the density independent level of mortality. The density dependent form of the curve is determined by the two parameters a and b. The parameter a is a scaling constant which determines, for a given value of b, the density at which proportionate mortality reaches a fixed value. The parameter b determines the severity of the density dependence. Increasing values of b imply movement along the continuum of contest-scramble competition towards more severe scramble. The precise relationship between the parameters a and b and the type of competition implied is more easily discussed for the related model (see below) of entry 5 in table 2.1. In the model of entry 5, the roles of the parameters a and b are the same as in equation 2.7. In addition, a plot of k-value against ln density for this model is linear at high densities and reaches an asymptotic slope of b, providing a readily interpretable relationship between this parameter and the type of competition implied (Varley, Gradwell & Hassell 1973; Hassell 1975, 1976). The slope of a plot of k-value against ln density for equation 2.7 increases without bound as density increases, and consequently the relationship between the parameters a and b and the type of competition is more complex.

TABLE 2.1 Some density dependent functions f(N) (equation 2.1), μ(N) (equation 2.5) and their second derivatives. A more complete list of references concerning each model is given by May & Oster (1976).

Entry	f(N)	μ(N)=k-value	sign of d^2f/dN^2	sign of $d^2\mu/dN^2$	Authors
1.	N^{-b}	$b \ln N$	+	-	Varley & Gradwell (1960)
2.	$\exp(-aN)$	aN	+	0	Cook (1965); MacFadyen (1963)
3.	$(1+aN)^{-1}$	$\ln(1+aN)$	+	-	Pielon (1969); Skellam (1952)
4.	$\exp(-aN^b)$	aN^b	+-	+-	this study
5.	$(1+(aN)^b)^{-1}$	$\ln(1+(aN)^b)$	+-	+-	Maynard Smith & Slatkin (1973)
6.	$(1+aN)^{-b}$	$b \ln(1+aN)$	+	-	Hassell (1975); Hassell, Lawton & May (1976)
7.	$(1 + \exp(bN - a))^{-1}$	$\ln(1 + \exp(bN-a))$	+-	+	Pennycuik, Compton & Beckingham (1968); Ullyett (1950); Usher (1972)

FIGURE 2.6 The effect of the parameters a and b in the density dependent model entry 5 of table 2.1. Curve I (a = 0.01, b = 1) indicates contest competition where the number of survivors increases monotonically with density (a), where k-value increases exponentially with ln density (c) and where k-value increases logarithmically with density (b). Curves II and III (b=5) indicate scramble competition, showing a humped curve of number surviving against density, a steeply increasing curve of k-value against log density and a sigmoid curve of k-value against density which increases exponentially at low densities and logarithmically at high densities. In curve II, a=.01 so that density dependent mortality is 50% at N= 1/a = 100. In curve III, a = .02 and density dependent mortality is 50% at N = 50.


(a)
75
50
25
0
Number surviving (S)
I
II
III
0
100
200
300
Initial density (N)


(b)
1.75
1.00
0
k-value (-ln(S/N))
III
II
I
0
100
200
300
Initial density (N)

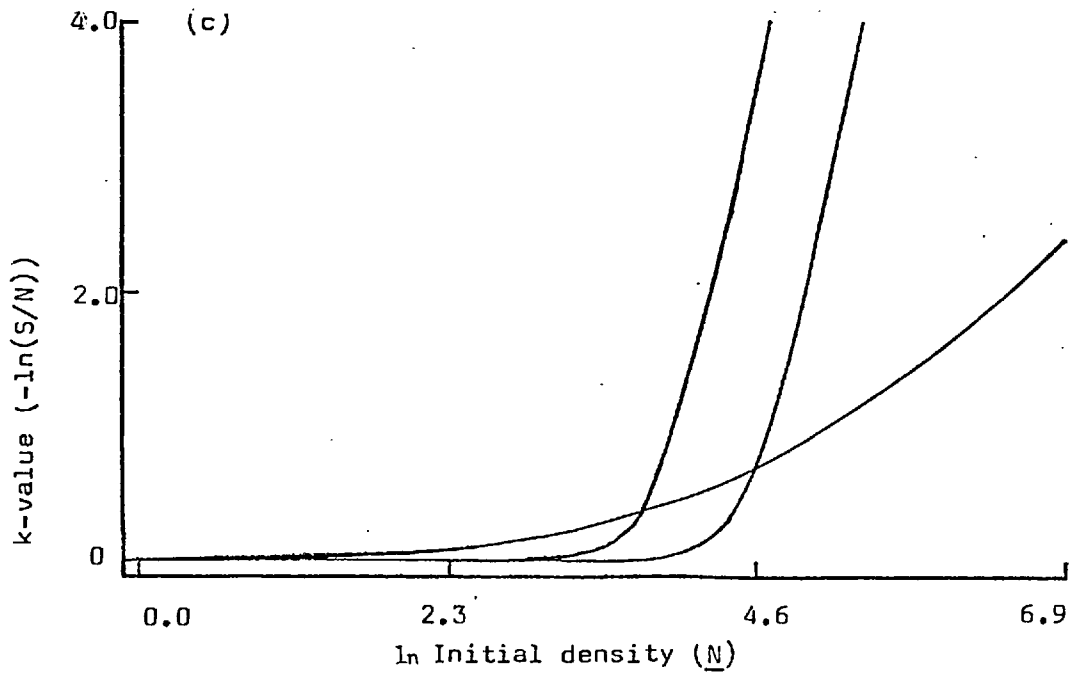

(c)
4.0
2.0
0
k-value (-ln(S/N))
0.0
2.3
4.6
6.9
ln Initial density (N)

Figure 2.6 shows how changes in the parameters a and b in model 5 of table 2.1 effect the shape of the plot of survivors against density and the plots of k-value against density and ln density. When b=1 (curves I), contest competition is implied. Here the number of survivors increases monotonically with density to an asymptotic maximum of 1/a (figure 2.6a), k-value increases logarithmically with density (figure 2.6b), and k-value increases exponentially with ln density reaching an asymptotic slope of b=1. For values of $b > 1$ (curves II and III), mortality overcompensates at high densities, resulting in few survivors (scramble competition). Here the plot of k-value against density shows an initial exponential increase which changes to a logarithmic increase at high densities (figure 2.6b). The plot of k-value against ln density increases exponentially, again reaching an asymptotic slope of b (for curves II and III in figure 2.6, b=5). Varying the parameter a effectively changes the scale of density on which the mortality acts; as the value of a increases (for a fixed b) the number of survivors at any given density decreases. More precisely, density dependence accounts for a fifty per cent mortality when the initial density is 1/a.

For the model of equation 2.7, similiar interpretations can be made concerning the effect of the parameters a and b, specifically that contest competition is indicated by values of $b \cong 1$ and scramble competition by values of $b > 1$. However, the distinction between contest and scramble is not as sharply defined in this model as in the model discussed above. For given values of a and b the type of competition implied depends in part on the range of densities concerned. Even for values of $b < 1$, sufficiently high values of N (density) in equation 2.7 can cause a reduction in the number of survivors.

The general difference equation model for density dependence of equation 2.7 has not appeared in the literature, although a homologous

differential form has been suggested by Goel, Maitra & Montroll (1971). This model can easily be related to some of the existing difference equation models for density dependence in the literature (table 2.1). The general model (entry 4 of table 2.1) can be expanded in Taylor-series and truncated after the first order term to obtain entry 5. When the parameter b of entry 4 is set equal to unity, entry 2 is obtained, or from a truncated Taylor-series expansion entry 3 is obtained. The other models in table 2.1 are less clearly related to the general model of entry 4. Entry 1 is a linear model on a logarithmic scales of density and proportionate survival, and arises from the linear k-value analysis for density dependence of Varley & Gradwell (1963). Entry 6 is a more flexible formulation of a k-value analysis model, which is curvilinear on logarithmic scales (Hassell 1975). Entry 7 describes a symmetric sigmoid curve of precentage survival against density.

Important to the understanding of the general descriptive abilities of these models is a consideration of the different types of density dependent curves that they describe. This is most easily discussed with reference to two specific ways of expressing density dependence.

(1) Consider a plot of proportionate survival (S/N) against density (N). Such a plot may appear as a monotonically decreasing curve (figures 2.2a and 2.5a) or as a nonsymmetric sigmoid curve (figures 2.2b, c, d). A simple mathmatical way to express the difference between these two types of curves is to consider the second derivative of (S/N) with respect to N, $d^2(S/N)/dN^2$. When the curve of proportionate survival is of the monotonically decreasing form, this derivative is positive over the entire range of density. When the curve is of the sigmoid type, however, this derivative changes from negative to positive as density increases. A general

model for density dependence, then, would have a form such that $d^2f(N)/dN^2$ could either be positive for any value of N, or could change from negative to positive as N increased. Table 2.1 gives the potential signs of $d^2f(N)/dN^2$ for the models presented there. All of the one-parameter models (entries 1, 2 and 3) and one of the two-parameter models (entry 6) have forms for which this derivative is always positive, and consequently can only describe monotonically decreasing curves of proportionate survival against denstiy. The remaining two-parameter models (entries 4, 5 and 7) can describe both monotonic and sigmoid curves of proportionate survival. Entry 7 describes these curves as symmetric, which does not appear to be a general feature of density dependence data.

(2) Consider a plot of k-value ($= \mu(N)$) against density. A general model would be required to describe both logarithmically (figures 2.4a and 2.5c) and exponentially (figures 2.4b, c, d) increasing curves. Expressed mathmatically, the second derivative $d^2\mu/dN^2$ may be either negative or positive. Table 2.1 also gives the potential signs of these derivatives. Only the general model entry 4 and its Taylor-series approximation entry 5 have forms which may describe both types of curves for $\mu(N)$. Entries 1, 3 and 6 describe only logarithmic curves of $\mu(N)$ against density, entry 2 depicts these curves as linear, and 7 only describes exponential increases for $\mu(N)$.

2.4 A quantitative comparison of the models

The discussion presented above indicates that only two of the models presented in table 2.1 may be considered as having a general form. Differences in the descriptive ability of the models in table 2.1 may be further clarified by a quantitative comparison provided by fitting the models to various sets of data. For this

purpose, a selection of data showing density dependent mortality has been taken from the entomological literature and supplemented by further experiments in this study. The data may be divided into two primary categories. The first set of data (table 2.2) arises from experiments where varying numbers of individuals, usually in an early developmental stage such as eggs or larvae, were confined with a fixed amount of food. At some later stage or time the survivors were scored. The data for the four beetles Stegobium paneceum L., Lasioderma serricorne (F.), Tribolium castaneum (Herbst.) and Tribolium confusum Duval are typical examples. Eggs of these species were collected by sieving flour from oviposition chambers at 24 hour intervals. Varying numbers of 0-24 hour old eggs were isolated in glass tubes (2.2 cm x 7 cm) with 0.5 g medium (commercial fine white flour with added yeast, 10% by weight). The glass tubes were closed with cotton wool and kept at either 28.5° C, 70% relative humidity (Stegobium and Lasioderma) or 30° C, 70% relative humidity (Tribolium spp.). After the adults eclosed the total number of survivors in each tube were scored.

The second set of data (table 2.3) was compiled from long term censuses of insect populations. Data were taken both from field studies and studies of populations maintained in the laboratory. Table 2.3 is abbreviated from a similiar list given by Hassell, Lawton and May (1976). Data have been omitted here which failed to demonstrate density dependence when analysed by the method discussed below.

The data in tables 2.2 and 2.3 were fitted to the two parameter models of table 2.1 (entries 4, 5, 6 and 7). The models were used in the general form of equation 2.1 with the addition of a parameter quantifying density independent mortality, d, so that

TABLE 2.2 Some experimental studies on the effect of density on survival in insects.

Species	Author(s)
Coleoptera	
1. *Lasioderma sericorne* (F.)	this study
2. *Stegobium paneceum* L.	this study
3. *Rhyzopertha dominica* (F.)	Crombie (1944)
4. *Tribolium castaneum* (Herbst.)	this study
5. *Tribolium confusum* Duval	this study
Lepidoptera	
6. *Ephestia cautella* Walker	Takahashi (1956)
7. *Anagasta kühniella* Zell.	Ullyett & van der Merwe (1947)
8. *Plodia interounctella* Hübn.	Snyman (1949)
9. *Sitotroga cerealella* (Oliv.)	Crombie (1944)
Diptera	
10. *Chrysomyia albiceps* Wied.	Ullyett (1950)
11. *Chrysomyia chloropyga* Wied.	Ullyett (1950)
12. *Drosophila melanogaster* (Meig.)	Miller (1964)
13. *Drosophila simulans* Sturtevant	Miller (1964)
14. *Lucilia cuprina* Wied.	Nicholson (1954)
15. *Lucilia serricata* Mg.	Ullyett (1950)
16. *Musca domestica* L. strain Bell	Sullivan & Sokal (1963)

TABLE 2.3 Sources of data on density dependent mortality from long-term censuses of insect populations. Values for λ are taken from Hassell, Lawton & May (1976). Values for the parameters d and b were obtained by fitting the general density dependent model to the data. Numbers correspond to the numbered points in figure 2.9.

	Species	λ	$d\lambda$	b	Author(s)
Hemiptera					
1.	*Anthocorus confusus* (Reuter)	1.6	1.1	2.7	Evans (1973)
2.	*Leptoterna dolobrata* (L.)	2.2	2.2	1.4	McNeill (1973)
3.	*Neophilaenus lineatus* (L.)	9.2	1.4	0.7	Whittaker (1971)
4.	*Saccarosydne saccharivora* (Wiv.)	13.5	1.0	2.8	Metcalf (1972)
Coleoptera					
5.	*Callosobruchus chinensis* (L.)	22.5	15.5	1.0	Fujii (1968)
6.	*Callosobruchus maculatus* (F.)	32.5	18.4	1.9	Utida (1967)
7.	*Callosobruchus maculatus* (F.) strain a0	37.5	29.5	1.6	Fujii (1967)
8.	*Leptinotarsa decemlineata* (Say)	75.0	75.0	4.8	Harcourt (1971)

TABLE 2.3 (continued)

Species	λ	dλ	b	Author(s)
Lepidoptera				
9. *Acleris variana* Fern.	13.0	3.5	2.7	Morris (1959)
10. *Anagasta kühniella* (Zell.)	8.6	1.2	1.6	Hassell & Huffaker (1969)
11. *Erannis defoliaria* (Clerk)	3.0	1.8	2.0	Ekanayake (1967)
12. *Hyphantria cunea* Drury	1.7	1.7	0.4	Ito, Shibajaki & Iwahashi (1969)
13. *Operophtera brumata* (L.)	5.5	5.0	0.4	Varley & Gradwell (1968)
Diptera				
14. *Erioischia brassicae* (L.)	3.3	2.1	1.7	Mujerji (1971)

$$S = dNf(N). \tag{2.8}$$

As before, d is constrained such that $0 \leq d \leq 1$. The parameter d is an important addition to the models when they are to be fitted to data. If some degree of density independent mortality is present, the omission of this parameter would result in an overestimate of the amount of density dependence shown by the data.

The models were fitted to the data by minimizing the residual sum of squares using the method of Fletcher & Powell (1963) for finding the minimum of a nonlinear function. This method had been programmed by Powell (1963) for finding the minimum of a nonlinear residual sum of squares. The method worked well for all the models except entry 6, where it was subject to rounding errors. Consequently, the method of Powell (1964) for minimizing a general function was used to minimize the residual sum of squares for this model.

The fit of the models to the data is most easily compared by considering the percent of the variance explained by each model for each data set. In linear regression analysis this is usually done by considering the parameter r^2,

$$r^2 = 100\left(1 - \frac{\text{residual sum of squares}}{\text{sum of squares about the mean}}\right). \tag{2.9}$$

In the fraction in equation 2.9, the sum of squares in the denominator is taken about the mean observed value of the dependent variable, $\bar{Y}$, and the null hypothesis is that there is no dependence of Y on the independent variable X.

$$H_o : Y = \bar{Y} \tag{2.10}$$

In the analyses presented here, the null hypothesis is that the observed mortality is due only to density independent factors causing a constant proportionate mortality, say p.

$$H_o : S = pN \tag{2.11}$$

Consequently, an appropriate measure of the percent variance explained by the nonlinear models considered here is

$$r' = 100\left(1 - \frac{\text{residual sum of squares}}{\text{sum of squares about the line } pN}\right). \qquad (2.12)$$

The sum of squares in the denominator of the fraction in equation 2.12 is the residual sum of squares obtained by fitting a straight line through the origin to the data, and the numerator is the residual sum of squares obtained by fitting a nonlinear model to the data. The values for per cent variance explained presented in tables 2.4 and 2.5 have been computed in this way.

The definition of the null hypothesis in equation 2.10 provides the basis for a method of determining whether or not a particular data set demonstrates density dependent mortality (figure 2.7). The model of the null hypothesis, $S=pN$, may be fitted to the data and the residuals plotted against the density at which they occur. If the plot shows no systematic pattern in the residuals (figure 2.7d), there is no evidence that the model of density independent mortality is inadequate (Draper & Smith, 1966). If some pattern does appear, such as a negative trend in the residuals (figure 2.7b), a more complex relationship between number of survivors and density (i.e. density dependence) may be assumed. Some of the data considered by Hassell, Lawton & May (1976), when examined in this way, did not show any evidence of density dependence and consequently were not included in table 2.3.

2.5 Results

A consideration of the values of percent variance explained, given in tables 2.4 and 2.5, shows that all four models usually explained roughly the same amount of variance; for some data sets there was practically no distinction between some of the models. The models of entries 4 and 5 in table 2.1 gave better fits to most of the data than entries 6 and 7. Entry 5 provided the best fit to 18 of the data sets, entry 4 best described seven data sets, and

FIGURE 2.7 A test for density dependence applied to two sets of data.(a) and (b) are for pupal predation of Operophtera brumata (Varley & Gradwell 1968); (c) and (d) are for parasitism of third instar Parlatoria oleae (Colvee) by Aphytus maculicornis (Masi) (Huffaker & Kennett 1966). After fitting the model of density independent mortality S = pN to the data (solid lines in (a) and (c)), residuals are plotted against density. A negative trend in the residuals indicates density dependence (b). If the residual plot does not show any trend (d), then the model S=pN adequately describes the data. The broken line in (a) is the best fit of the density dependent model entry 5 of table 2.1 (d=0.913, a=0.174, b=0.428).

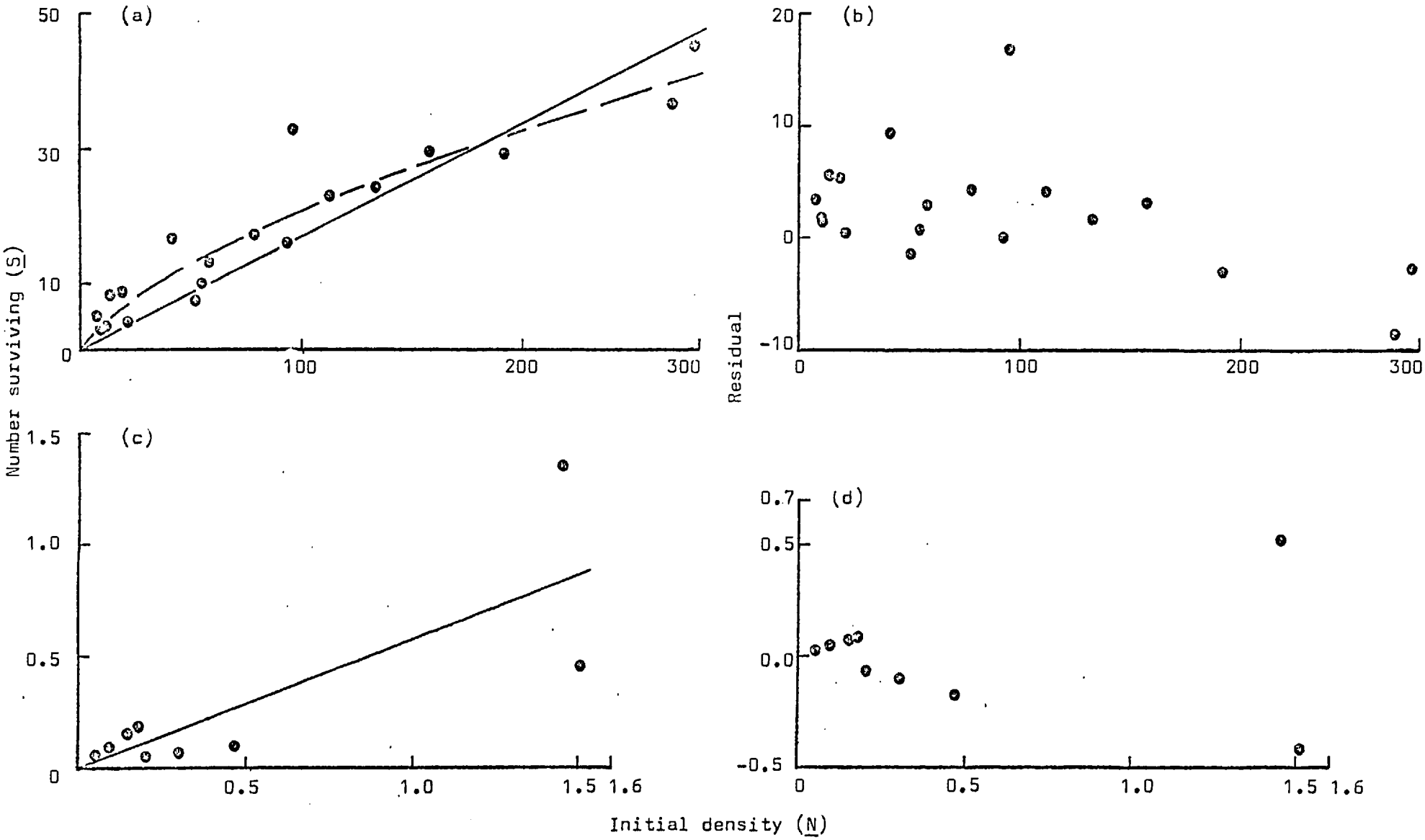

(a)
(b)
(c)
(d)
Number surviving (S)
Residual
Initial density (N)
50
30
10
0
100
200
300
20
-10
1.5
1.0
0.5
1.6
0.7
-0.5

TABLE 2.4 The percent of the variance explained by the four two-parameter density dependent models of table 2.1 applied to the data from the sources given in table 2.2.

(+) best fit occurred when d = 1.

(*) best fit occurred at unreasonable values of a and b.

Species	model (entry in table 2.1) 4	5	6	7
Coleoptera				
1. Lasioderma serricorne	96.35	96.36	72.78+*	96.36
2. Stegobium paneceum	62.36+	66.57	66.62	36.67+
3. Rhyzopertha dominica	93.65+	98.29+	97.25+	80.03+
4. Tribolium castaneum	90.03	90.86	74.43+*	90.32+
5. Tribolium confusum	82.67	82.61	78.48+*	82.60
Lepidoptera				
6. Ephestia cautella	95.28+	96.93	92.43*	95.68+
7. Anagasta kühniella	97.92+	98.49+	97.16+*	93.78+
8. Plodia interpunctella	98.63	99.12	87.08+*	98.93
9. Sitotroga cerealella	95.03+	97.89+	97.45+	83.75+
Diptera				
10. Chrysomyia albiceps	97.92	99.03	95.85+*	99.82
11. Chrysomyia chloropyga	98.72	97.61	89.18+*	98.37
12. Drosophila melanogaster	98.26	99.36	90.30+*	97.78+
13. Drosophila simulans	98.35	99.06	78.68+*	98.83
14. Lucilia cuprina	99.31+	99.60	95.81+*	98.85+
15. Lucilia sericata	96.44	95.93	89.65+*	96.65
16. Musca domestica	99.54	99.29	92.97*	99.60
Number of times each model explains maximum variance	3	9	1	3

TABLE 2.5 The percent of the variance explained by the four two-parameter density dependent models applied to the data listed in table 2.3.

(+) best fit occurred when d = 1.

(*) best fit occurred at unreasonable values of *a* and *b*.

Species	model (entry in table 2.1) 4	5	6	7
Hemiptera				
1. *Anthocorus confusus*	88.60	88.27	79.19+	88.79
2. *Leptoterna dolobrata*	67.01+	71.17+	69.35+	57.82+
3. *Neophilaenus lineatus*	95.58	95.56+	95.54	94.16
4. *Saccarosydne saccharivora*	61.14	61.78	60.21*	61.11
Coleoptera				
5. *Callosobruchus chinensis*	97.21+	98.84	98.84	75.64+
6. *Callosobruchus maculatus*	97.31+	99.24	99.22	80.40+
7. *Callosobruchus maculatus*	86.77+	85.51	86.28+	82.59+
8. *Leptinotarsa decemlineata*	97.70+	99.05+	76.85+*	98.68+
Lepidoptera				
9. *Acleris variana*	68.61	75.43	69.05	68.41+
10. *Anagasta kuhniella*	73.46	73.51	72.83*	73.52
11. *Erannis defoliaria*	47.02	47.22	46.64*	45.98+
12. *Hyphantria cunea*	89.42+	94.89+	94.14+	76.62+
13. *Operophtera brumata*	46.67+	46.67	46.58	43.01+
Diptera				
14. *Erioischia brassicae*	23.22	23.13	23.20*	23.06+
Number of times each model explains maximum variance	4	9	0	2

entries 6 and 7 best described one and five data sets respectively.

In several analyses, the best fit to the data occurred when the parameter d was constrained to unity (higher values of d give better fits to the data), and these are indicated in tables 2.4 and 2.5. Occasionally, this was an artifact of the data, but for the models of entries 6 and 7 it was often caused by the forms of these models being inappropriate for description of the data. The form of model 6 also caused unreasonable estimates of the parameters when the data showed an exponential curve of k-value against density, which this model cannot describe. In these cases, the estimated values of the parameter b were very high (>1000) and the values for a were very small ($< 10^{-6}$), which resulted in an approximately linear relationship between k-value and density (see figure 2.8d). This problem did not arise when the plot of k-value against density appeared logarithmic. Poor fits were also obtained when entry 7 was fitted to data where the plot of k-value against density appeared logarithmic (this model only describes exponential curves of k-value against density), but this form was less prone to uninterpretable estimates of the parameters.

The fit of the four models to the data on Stegobium paneceum and Tribolium castaneum are shown in figure 2.8. The data and model predictions are presented in the original form (number of survivors against density, figures 2.8a and c) and after transforming to k-value (k-value against density, figures 2.8b and d). Models 4 and 5 described both sets of data well, and there was little difference in the predicted curves for these models. Model 6 fitted the Stegobium data well (in figures 2.8a and b models 5 and 6 are coincident), but did not give a good description of the Tribolium data. Model 7 gave a poor fit to the Stegobium data, but fitted the Tribolium data reasonably well.

FIGURE 2.8 The predicted curves of the four two-parameter models of table 2.1 when fitted to the data for Stegobium paneceum (a,b) (contest type competition) and Tribolium castaneum (c,d) (scramble type competition) presented as numbers surviving (a,c) or k-value (b,d) against density. The models were fitted to the data in (a) and (c) and these parameter values were used to provide the curves in (b) and (d). Model 4 (————): (a) d=1.00, a=0.265, b=0.295; (c) d=0.925, a=0.0137, b=2.04. Model 5 (— — —): (a) d=0.711, a=0.110, b=0.950; (c) d=0.800, a=0.0149, b=4.21. Model 6 (————): (a) d=0.691, a=0.113, b=0.936; (c) d=1.00, $a=8.86\times10^{-7}$, $b=6.05\times10^{8}$. Model 7 (– — — —): (a) d=1.00, a=-0.00186, b=0.00409; (c) d=1.00, a=0.0172, b=0.0448.

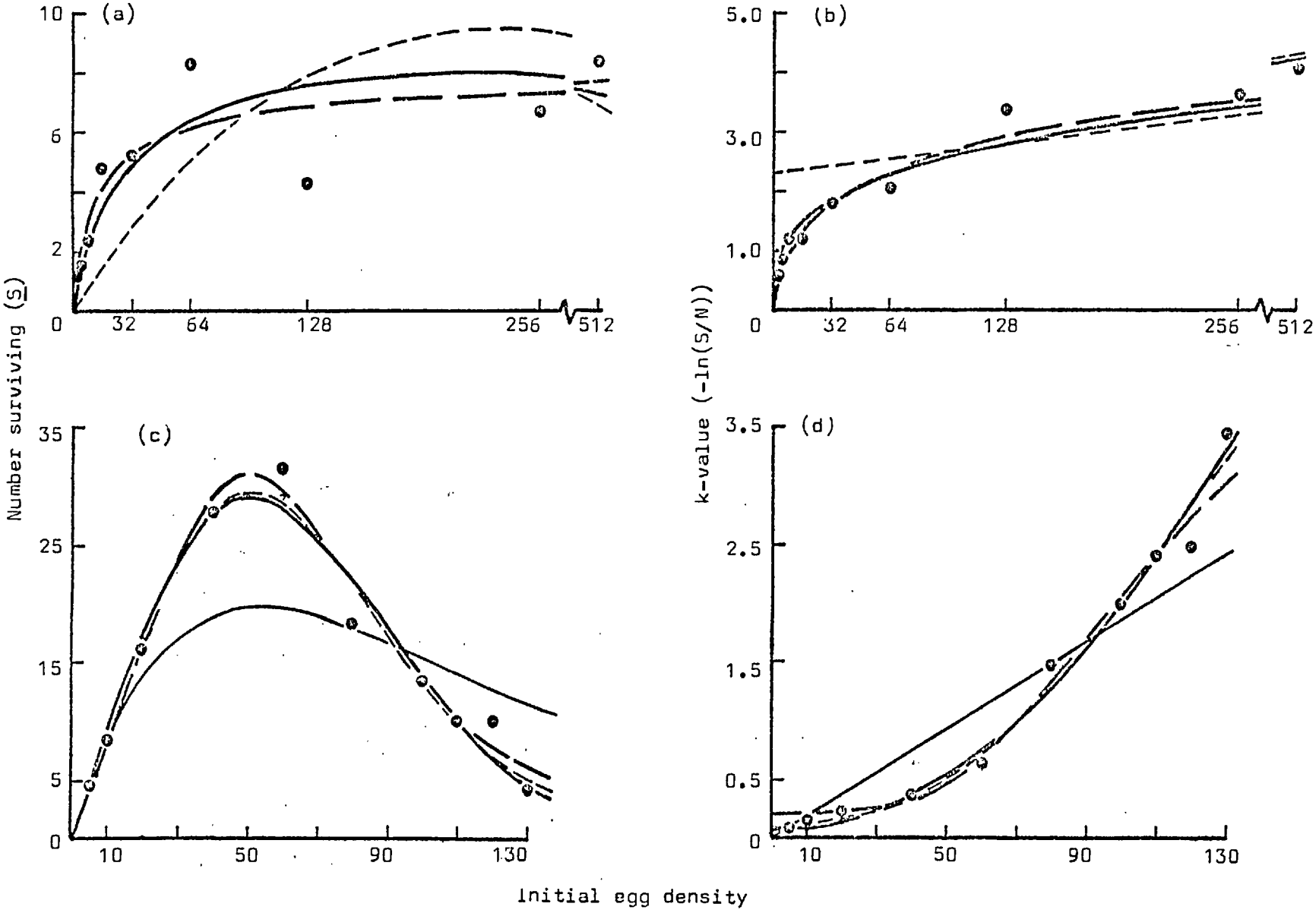
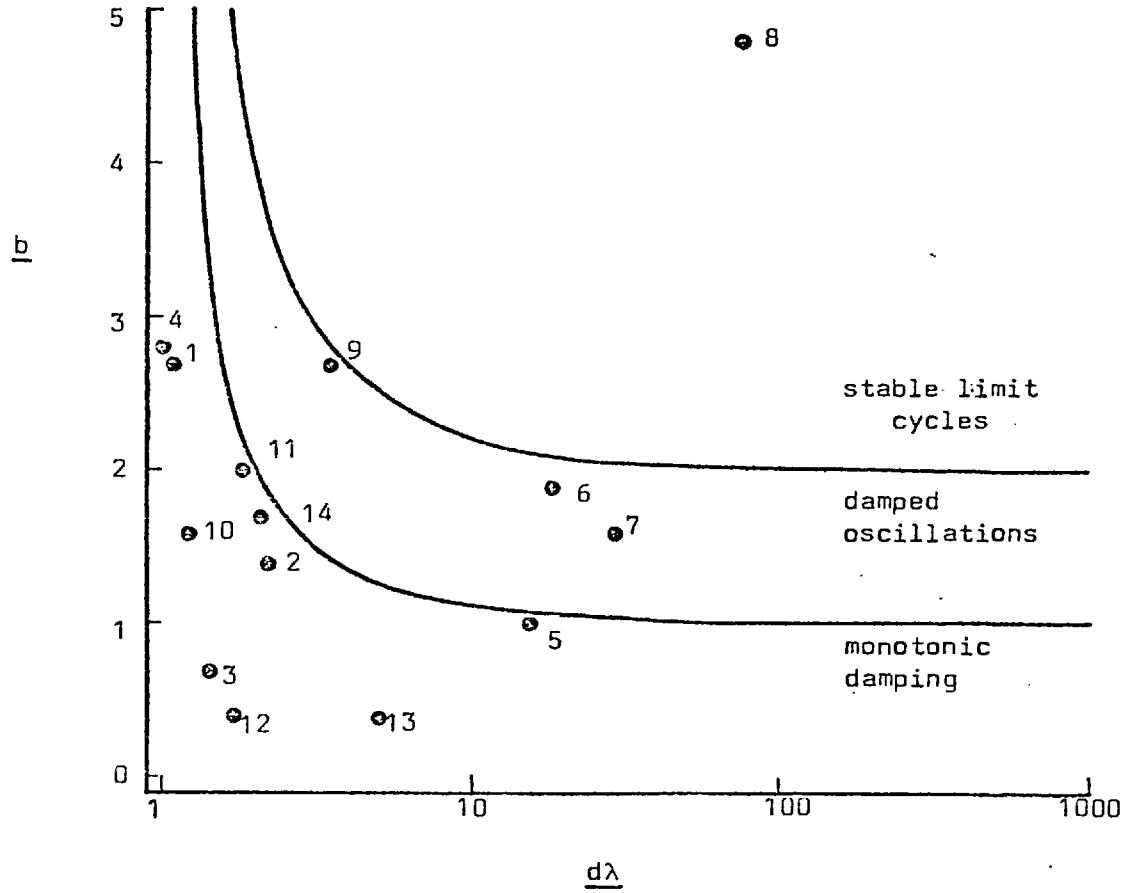

(a)
(b)
(c)
(d)
Number surviving (S)
k-value (-ln(S/N))
Initial egg density
0
2
6
10
32
64
128
256
512
1.0
3.0
5.0
5
15
25
35
50
90
130
0.5
1.5
2.5
3.5

FIGURE 2.9 The boundries separating regions of different dynamic behaviours as functions of the density dependent parameter $\underline{b}$ and the effective rate of increase $\underline{d\lambda}$ for the population model of equation 2.13. The numbered points correspond to the data sets of table 2.3. See text for discussion.


b
5
4
3
2
1
0
1
10
100
1000
dλ
stable limit cycles
damped oscillations
monotonic damping
1
2
3
4
5
6
7
8
9
10
11
12
13
14

Following Hassell, Lawton & May (1976), the fitted parameters from the data in table 2.3 may be used to characterize the nature of the population dynamics shown by these species. Figure 2.9 shows the regions of dynamic behaviour of the population model (based on entry 5 of table 2.1)

$$N_{t+1} = d\lambda N_t(1 + (aN_t)^b)^{-1} \qquad (2.13)$$

The boundaries between the regions were found by a linearized stability analysis of equation 2.13, the details of which are given in appendix A. After weighting the values of λ given by Hassell, Lawton & May by the density independent mortality estimated by fitting entry 5 to the data, the values of the parameters b and $d\lambda$ may be used to position the species listed in table 2.3 in figure 2.9. Ten of the fourteen species were placed in the region of monotonic damping, which supports the conclusion of these authors that most natural single-species populations exhibit monotonic damping to an equilibrium. Three species were placed in the region of damped oscillations, two of which (data sets 6 and 7) are from laboratory populations of the beetle Callosobruchus maculatus (F.) which show evidence of this behaviour. The only species placed in the region of limit cycles was Leptinotarsa decimlineata (Say), and this is consistent with Harcourt's (1971) remarks that populations of this species fluctuate markedly, and tend to overcompensate from generation to generation.

2.6 Conclusions

The one parameter models of table 2.1 all have forms sufficiently restrictive to exclude them as general descriptive models of density dependence. The two parameter models 6 and 7 also have forms which are only capable of describing certain types of density dependence. Although they do not have general forms, these models may be useful

in describing data when their forms are appropriate, such as describing logarithmic curves of k-value against density (models 1, 3 and 6), linear curves of k-value against density (model 2) or symmetric sigmoid curves of proportionate survival against density (model 7).

Two of the models in table 2.1 (entries 4 and 5) have forms which describe both logarithmic and exponential curves of k-value against density, and hence may be considered as having a general form. Of these, model 5 has a more flexible and better descriptive form and seems to be less prone to overestimates of density independant mortality than model 4. In addition curves of k-value against density for model 5 may be sigmoid, where at high densities the exponential increase in k-value becomes logarithmically increasing, and consequently the relationship between k-value and log density is approximately linear at high densities.. This may be important in light of the view of some authors that plots of k-value against log density are linear at high densities (Varley, Gradwell & Hassell 1973; Hassell 1975; Stubbs 1977).

In light of these considerations, model 5 has been used for the analysis of density dependence in populations of Callosobruchus chinensis (L.) and Callosobruchus maculatus presented in the following chapters, and has also been used in the development of population models for these species.

Chapter III. INTRASPECIFIC COMPETITION I

3.1 Introduction

In a number of studies of insect populations, quantification of life-table parameters has led directly to the development of population models (e.g. Utida 1967; Varley & Gradwell 1968; Hassell & Huffaker 1969; Benson 1974; Podoler 1974). In these studies the life tables have been constructed from long-term (many generation) population censuses. An alternate approach is taken here, where the density dependent processes affecting a population are determined from single-generation experiments. Simple difference equations will be used to describe the outcome of these experiments, and will then be used to develop population models for the species.

In order to investigate fully this approach to population modelling, a study was made of the laboratory population biology of two stored product beetles, Callosobruchus chinensis and C. malculatus. The biology of these species is briefly reviewed in the next section. In the subsequent section experiments are described which were designed to determine how changes in density effected the reproductive success of these species, and the results of the experiments will be discussed in the light of similar studies on other laboratory insect populations. The data will then be used to develop a single age-class and a pair of two age-class models for each species. The dynamics of the models will be contrasted and compared with long-term studies from the literature on the population dynamics of these species. In the final section some advantages and possible extensions of this approach to population modelling will be discussed.

3.2 The biology of Callosobruchus chinensis and C. maculatus

The weevils Callosobruchus chinensis and C. maculatus (Coleoptera, Bruchidae) are well known as pests of leguminous crops. Although capable of infesting crops in the field, they also breed in dried pulses and consequently are serious pests of pulses in store. They are capable of breeding on the seeds of a number of legumes, but relatively few may be considered suitable hosts for both species (Howe & Currie 1964). These include the azuki bean (Phaseolus angularis Wight), green gram (P. aureus Roxb.) and cowpea (Vigna unguiculata Walp.).

The simple biology of C. chinensis and C. maculatus render them particularly suitable for laboratory studies. The adults are short-lived and do not feed, although they will drink if offered water or sucrose solution (Howe & Currie 1964), and this may lengthen adult life-span and fecundity by as much as fifty per cent (Umeya & Shimizu 1968). The eggs are laid on, and adhere to, the surface of the host seed or pod. This adhesion is effected in C. chinensis by a fluid secreted by the ovipositor immediately prior to oviposition (Arora & Singh 1970). During hatching of the egg the first instar larva burrows directly into the cotyledon of the seed. The apodous eucephalous larva passes through four instars entirely concealed within a single seed. Pupation occurs in the cell created by larval feeding, and the adult emerges one or two days after eclosion. During the final instar the larval cell is enlarged so that it is adjacent to the seed testa, and the presence of the larva may be detected by the small grey "window" which appears as a result. In order to emerge, the adult must chew a hole through the testa. Occasionally pupation occurs in a cell not adjacent to the testa, and the adult cannot free itself from the seed and dies. Copulation takes place shortly after emergence and may reoccur several times during the

adult's life. Oviposition usually begins on the day of emergence. Virgin females isolated with seeds lay infertile eggs.

The effect of environmental conditions on developmental period, oviposition and mortality in these species has been extensively investigated by Howe & Currie (1964). They determined that the developmental threshold temperature for C. chinensis was approximately 17.5°C and that for C. maculatus it was approximately 20°C. The upper limit for development was just over 35°C for both species. When reared on cowpeas, most rapid development occurred at 25°C for C. chinensis (28 days) and at 30°C for C. maculatus (20 days), the highest temperatures investigated on this food. On garden peas (Pisum sativum L.), developmental period was more variable and was shortest at 32.5°C for both C. chinensis (18 days) and C. maculatus (21 days). Differences in relative humidity did not greatly effect developmental period; the optimum relative humidity was approximately 70% for both species. Mean fecundity was greatest at 22.5°C for C.chinensis (56 eggs per female) and at 35°C for C. maculatus (98 eggs per female), and varied only slightly between 22.5°C and 35°C in both species. At 30°C, fecundity was higher at higher relative humidities. Developmental mortality was generally low, less than twenty per cent at favourable conditions.

These results agree with less extensive investigations by other workers. Raina (1970) found that developmental period depended on parent age at oviposition for both C. chinensis and C. maculatus. Progeny developed slightly (by less than three days) faster from eggs laid early in adult life than those laid later. This phenomenon has also been observed in C. maculatus by Larson & Simmons (1923) and Howe & Currie (1964). Utida (1941a) found that the fecundity of C. chinensis was higher at 30.4°C than at 24.8°C for a fixed relative

humidity, and that fecundity was highest at both temperatures at high (75%) relative humidity. Arora & Singh (1970) reported maximum fecundity for C. chinensis at 30°C and 90% relative humidity. Raina (1970) reported higher developmental mortality in progeny from eggs laid late in adult life, due largely to a reduced proportion of eggs hatching. The findings of these workers have supported the use of 30°C and 70% relative humidity as standard for laboratory culturing and experiments with these species (e.g. Utida 1942; Fujii 1965; Okamoto 1971a) (see below).

A number of investigations have shown differences in adult size, fecundity and population dynamics for different strains of C. chinensis and C. maculatus (Fujii 1968; Nakamura 1969; Utida 1959), although the differences were usually small. Adults of C. maculatus are also known to occur in two "phases" (Utida 1954, Caswell 1959), a "normal" nonflying form with high fecundity and short adult life and an "active" flying form with low fecundity, longer adult life and a preoviposition period of several days. Utida (1972) has reviewed the biology of the two forms and has shown that the active form disappears from populations maintained in the laboratory. No adults of the active form were observed in the populations of C. maculatus used in this study.

The initial stocks of C. chinensis and C. maculatus used in this study were obtained from Dr. B.J. Southgate of the Pest Infestation Control Laboratory, Slough, Berkshire. Cultures of these species were maintained at 30°C and 70% relative humidity with a 16L/8D photoperiod. The host seed used was cowpea (Vigna unguiculata) and was obtained in bulk from California, U.S.A. Details of the culturing procedure are given in appendix B.

3.3 Density dependent processes in Callosobruchus

To determine the effects of density on the processes of oviposition, development and survival in *C. chinensis* and *C. maculatus*, the following experiments were performed. Freshly emerged adults (0-2½ hours old) were collected from stock cultures at 1130 hours. Varying numbers of adult pairs (1, 5, 20, 40, 60, 80, 100 and 120 pairs) were placed in small plastic dishes (3.5 cm high and 4.0 cm in diameter) containing a single layer (3.70 g, 14-16 beans) of cowpeas. The beans had been kept at 30°C , 70% relative humidity for at least four days prior to use to allow their water content to become stable (see appendix B). The dishes were covered with a square of muslin secured in place with a plastic lid in which a large hole had been cut for ventilation. Each density was replicated between four and twelve times.

The dishes were kept at 30°C, 70% relative humidity until the adults had died and sufficient time had passed to ensure the hatching of all viable eggs. The dead adults were removed, the total and hatched eggs were counted and the dishes were returned to the environmental chamber. The day of first adult emergence in each of the dishes was recorded, and after all the survivors had emerged the total number of male and female progeny were scored. During the period of progeny emergence, pairs of 0-2½ hour old adult progeny were selected from individual dishes and isolated with 3.70 g of beans. The total number of eggs laid by each of these pairs was scored.

The models used to describe the effect of density on fecundity and survival were based on the density dependent model of Maynard Smith & Slatkin (1973) discussed in the previous chapter. The general form of the model is

$$S = dN(1+(aN)^b)^{-1} \qquad (3.1)$$

where the number of survivors S depends on the intial density N in

the manner determined by the parameters d (the proportionate density independent survival), a (a scaling constant) and b (the severity of the density dependence). The roles of these parameters and the general form of the model have been thoroughly discussed in chapter 2.

Equation 3.1 may be modified by the inclusion of a reproductive parameter in order to describe a density dependent reproduction curve,

$$N_{t+1} = \lambda S = \lambda N_t(1+(aN_t)^b)^{-1}, \qquad (3.2)$$

where N_{t+1} is the number of progeny from S individuals, and λ is the net rate of increase per individual. This parameter is composed of the maximum fecundity per female λmax, the proportion of the females in the population p and the proportionate density independent survival d, so that

$$\lambda = dp\ \lambda_{max}. \qquad (3.3)$$

Equation 3.2 may also describe a density dependent relationship between initial adult density A and the number of total or hatched eggs laid E,

$$E = \lambda A(1+(aA)^b)^{-1}. \qquad (3.4)$$

The relationship between density of hatched eggs and the number of surviving progeny may described by equation 3.1 by considering the initial density to be the number of hatched eggs.

All of these models were fitted to the appropriate sets of data using the method of Fletcher & Powell (1963) discussed in the previous chapter.

3.4 Results

The results will be presented by considering the relationships between (i) adult density (N_t) and the number of their progeny surviving to adults in the next generation (N_{t+1}), (ii) adult density and fecundity, (iii) the density of hatched eggs and the number of adult progeny, (iv) hatched egg density and the developmental period

of the progeny, (v) hatched egg density and the sex ratio of the progeny and (vi) hatched egg density and the fecundity of the progeny.

(i) The reproduction curves for C. chinensis and C. maculatus are shown in figure 3.1. The number of progeny increased with adult density to a maximum after which it decreased. The maximum mean number of progeny was highest at an initial density of 40 adults (20 pairs) for both species; the mean number of progeny was higher for C. chinensis (117) than for C. maculatus(78). The decrease in the number of progeny above an adult density of 20 pairs was much more severe in C. maculatus than in C. chinensis. The solid lines in figure 3.1 show the fit of equation 3.2 and describes both set of data reasonably well (the broken line is discussed on page 89). There was, however, a regular overestimation of the number of C. maculatus progeny at high densities.

(ii) Increasing adult density decreased the fecundity per female in both species, as demonstrated by the nonlinear increase in total eggs laid with increasing adult density (figures 3.2a, 3.3a). The reduction in number of hatched eggs per female as density increased was more severe than the reduction in total eggs in both species, and showed humped relationships similiar to those in figure 3.1. The maximum mean number of hatched eggs ocurred at a density of 60 adult pairs for C. chinensis (331 hatched eggs) and at a density of 20 pairs for C. maculatus (201 hatched eggs). The reduction in the number of hatched eggs above these densities was more severe in C. maculatus than in C. chinensis. The curves in figures 3.2a and 3.3a were fitted using equation 3.4 and gave a good description of the data for both total eggs laid (solid line) and total eggs hatched (broken line). There was, however, a regular overestimation of the number of hatched eggs at high densities of C. maculatus similar to that noted for total

FIGURE 3.1 The reproduction curves for (a) Callosobruchus chinensis and (b) C. maculatus. Data are given as mean ± s.e. The solid lines are the fitted single age-class models of equation 3.2, the parameter values for which are given in table 3.1. The broken lines indicate the predicted reproduction curves from the two age-class models of equation 3.6 (see text for discussion, page 89).

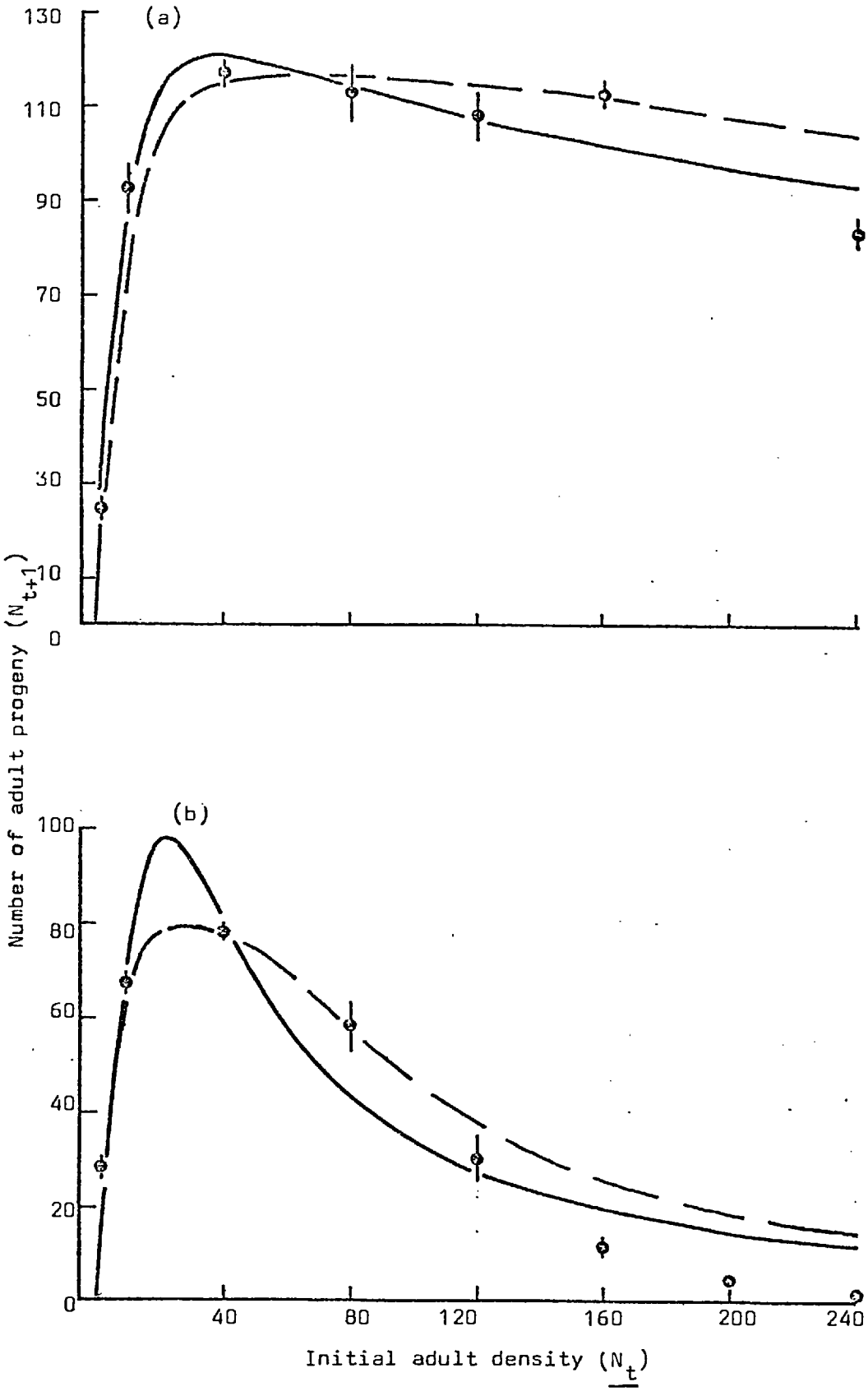
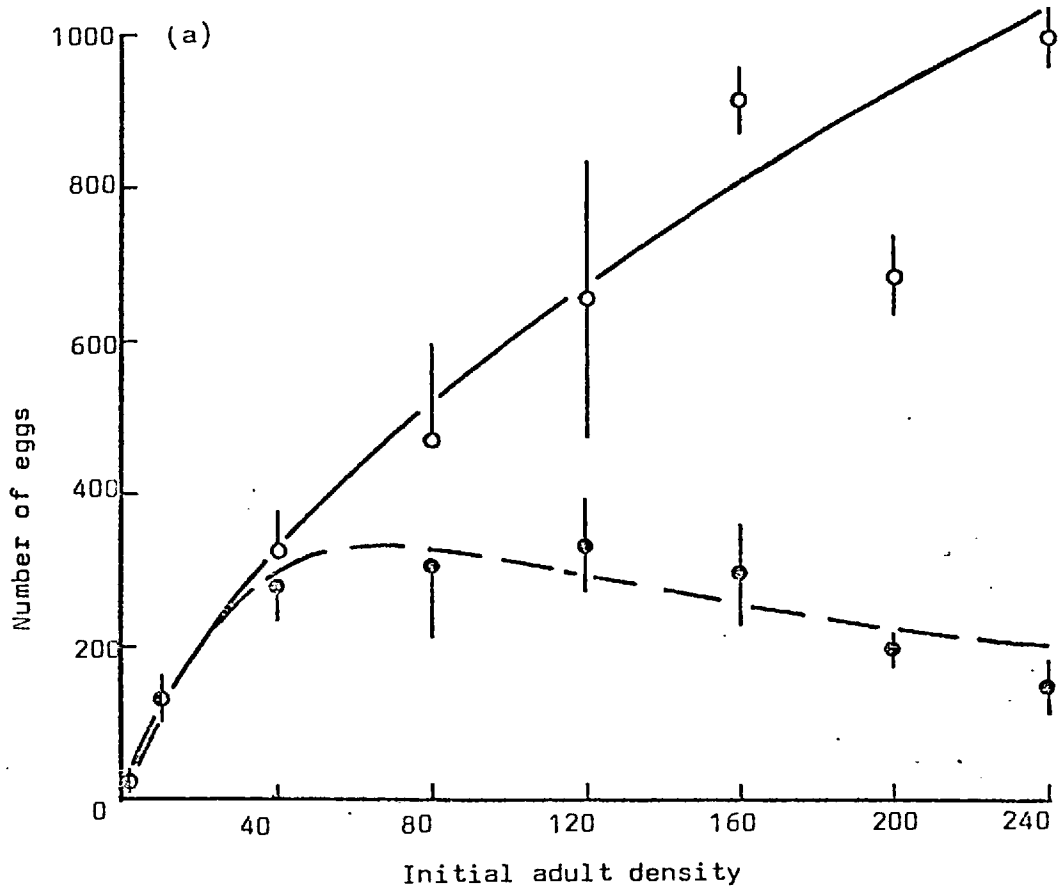

(a)
130
110
90
70
50
30
10
0
(b)
100
80
60
40
20
0
40
80
120
160
200
240
Number of adult progeny (N_{t+1})
Initial adult density (N_t)

FIGURE 3.2 (a) The number of total eggs (open circles) and hatched eggs (closed circles) laid at various densities of C. chinensis adults. Fitted curves are from equation 3.4. Parameters for solid line: λ = 22.928, a = 0.073775, b = 0.50905. Parameters for broken line are given in table 3.2a. Data given as mean ± standard deviation.

(b) The relationship between density of hatched eggs and total number of surviving adults. Fitted curve is from equation 3.1, parameters given in table 3.2b.


(a)
1000
800
600
400
200
0
Number of eggs
40
80
120
160
200
240
Initial adult density

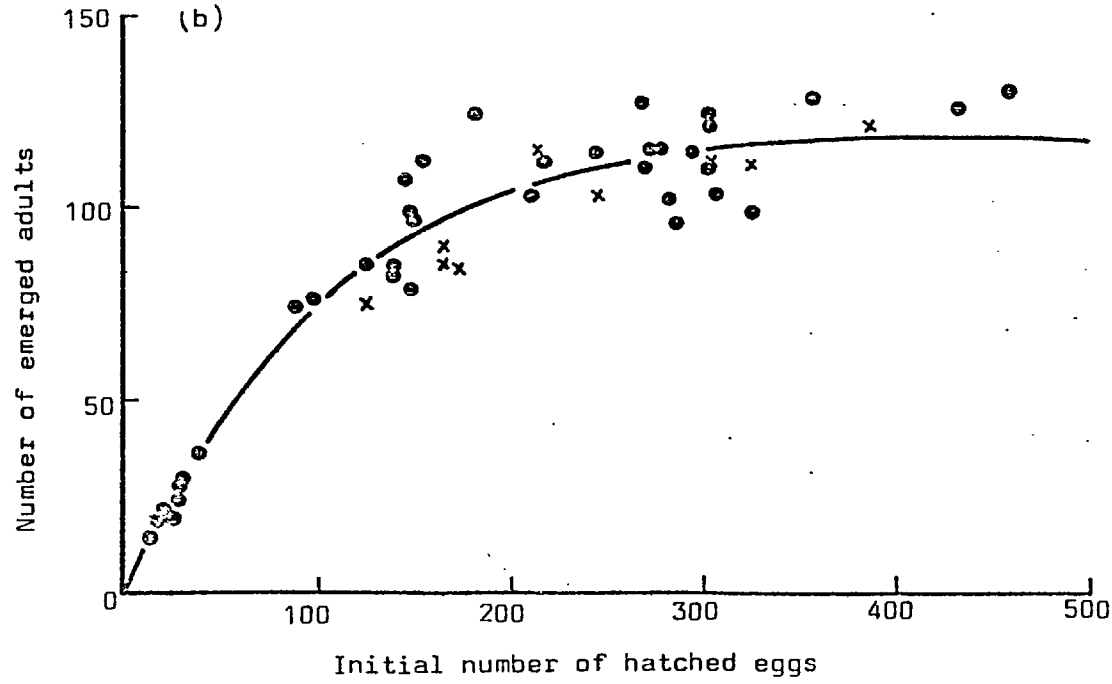
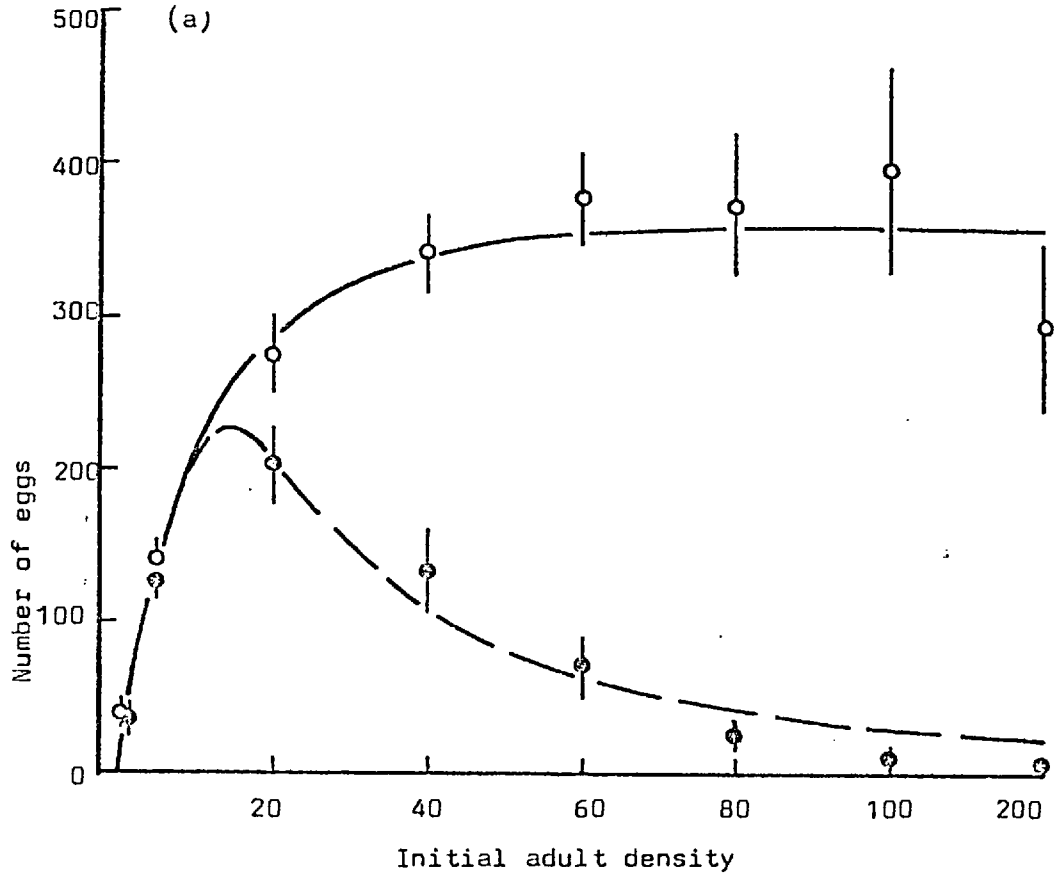
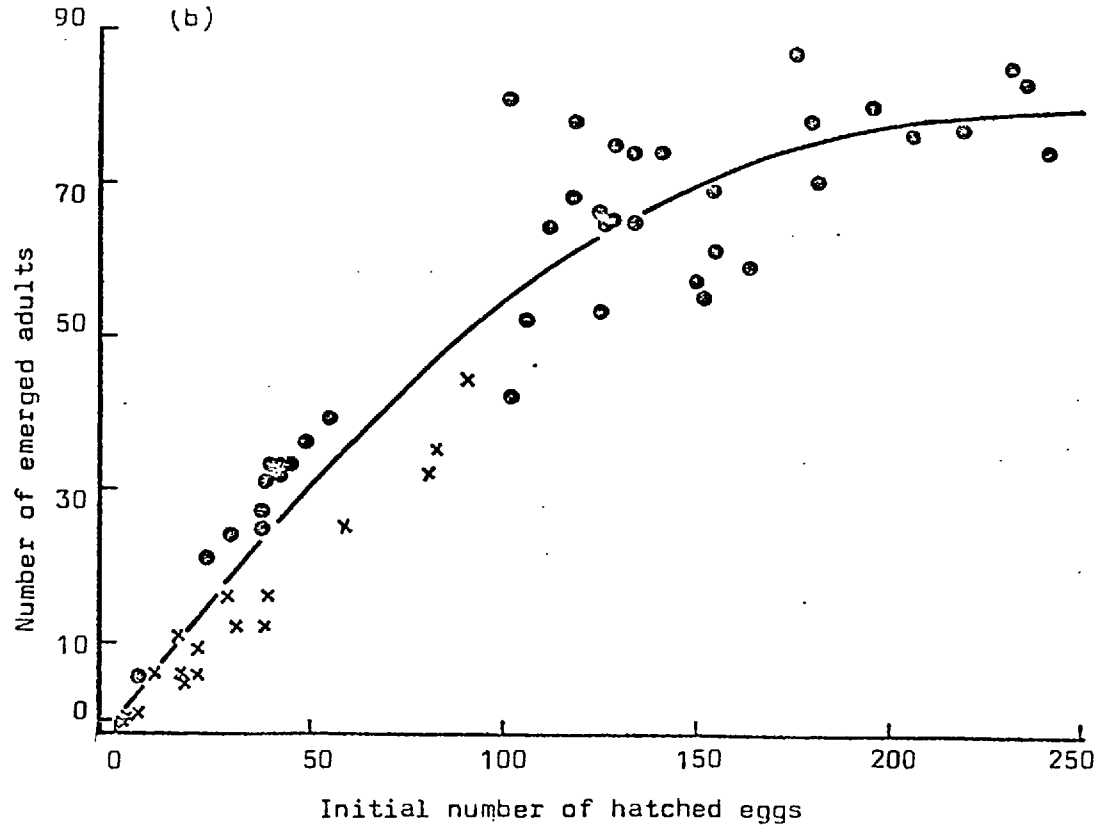

(b)
150
100
50
0
Number of emerged adults
100
200
300
400
500
Initial number of hatched eggs

FIGURE 3.3 (a) The number of total eggs (open circles) and hatched eggs (closed circles) laid at various densities of C. maculatus adults. Fitted curves are from equation 3.4. Parameters for solid line : λ = 17.5702, a = 0.034789, b = 1.1237. Parameters for broken line are given in table 3.2a. Data given as mean ± standard deviation.

(b) The relationship between density of hatched eggs and total number of surviving adults. Fitted curves is from equation 3.1, parameters given in table 3.2b.


(a)
500
400
300
200
100
0
Number of eggs
20
40
60
80
100
200
Initial adult density


(b)
90
70
50
30
10
0
Number of emerged adults
0
50
100
150
200
250
Initial number of hatched eggs

progeny.

The data for total eggs laid at a density of 100 pairs for C. chinensis lie well below the other data for this species at densities of 80 or 120 pairs. Additionally, the fecundity of the progeny of these adults was significantly lower ($p < .01$) than the fecundity of progeny from other densities. The adults used for the replicates at 100 pairs were taken from a stock culture not used at other densities. It appears, for some reason as yet unclear, that these adults were not typical of the population of C. chinensis, and consequently the data from this density have been excluded from the analyses in this thesis.

(iii) The relationships between density of hatched eggs and the total number of surviving adults are shown in figures 3.2b and 3.3b. They provide a clear example of contest competition, the number of survivors reaching a plateau for both species as egg density increased. In addition, the number of survivors from high hatched egg densities was higher in C. chinensis (approximately 120) than in C. maculatus (80). The fitted curves (equation 3.1) describe both sets of data well.

A more detailed examination of the data in figures 3.2b and 3.3b reveals a comples relationship between adult density, hatched egg density and the number of survivors. At hatched egg densities associated with high adult densities (crosses in figures 3.2b and 3.3b) the number of survivors was usually lower than at similiar hatched egg densities arising from low adult densities.. This is particularly evident for the C. maculatus data in figure 3.3b.

(iv) The relationships between day of first progeny emergence and hatched egg density and adult density are shown in figures 3.4 (C. chinensis) and 3.5 (C. maculatus). The C. chinensis data (figure 3.4a) showed a significant linear relationship between hatched egg density and day of first progeny emergence ($.05 > p > .01$). In

FIGURE 3.4 The relationships between day of first emergence and (a) hatched egg density and (b) initial adult density for C. chinensis. Open circles in (a) are for data from one adult pair, closed circles are from 5-60 pairs, and crosses are from 80 and 120 pairs. The regression line is $y = 23.68 - 0.00620\ x$; $.05 > p > .01$. Data in (b) are given as mean $\pm$ s.e.

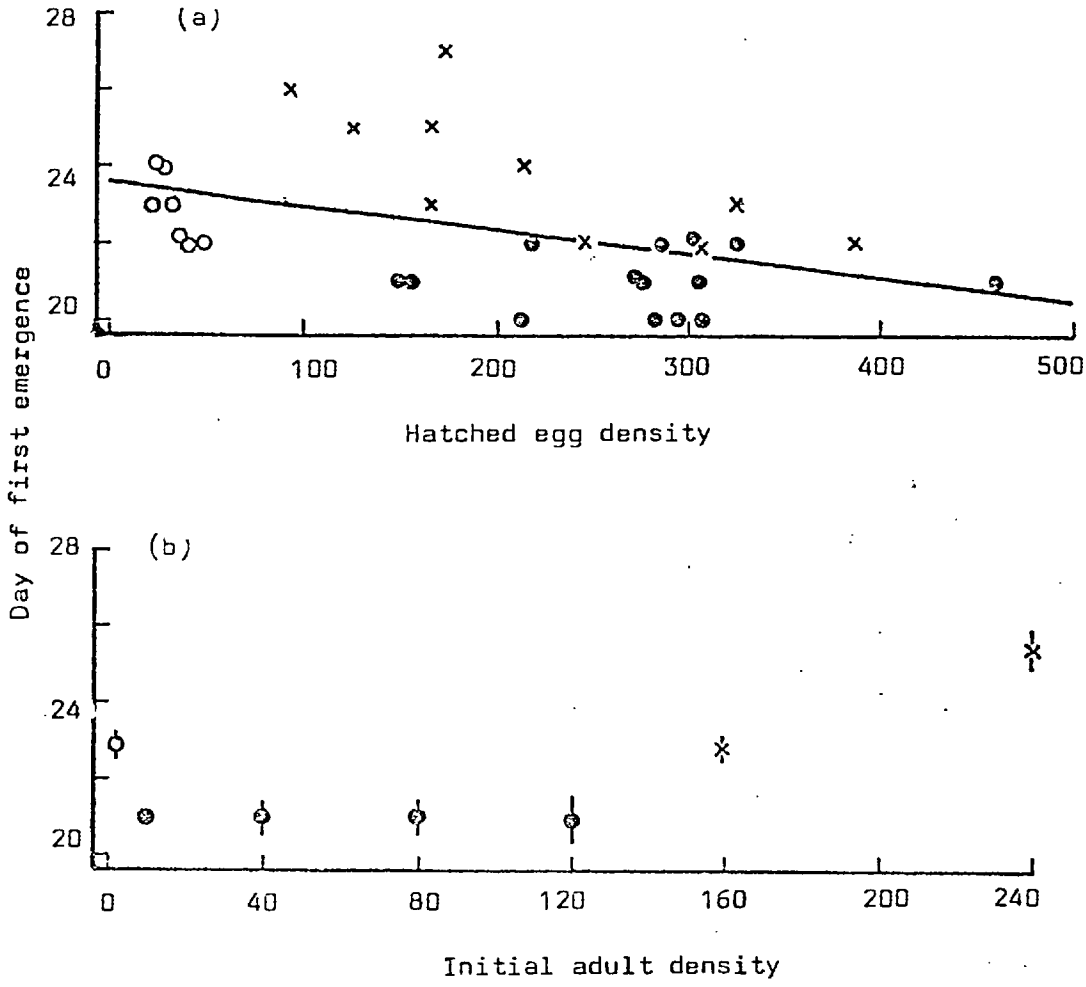
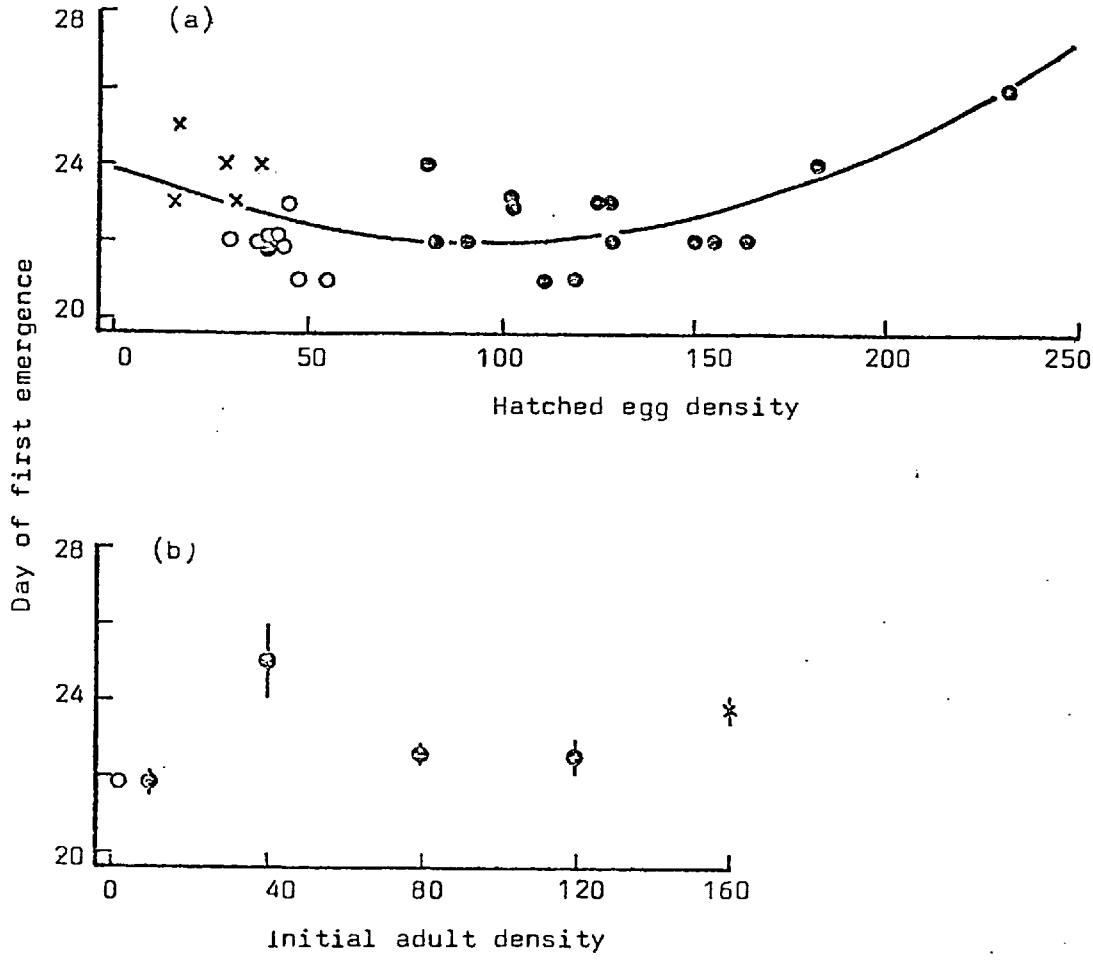

(a)
28
24
20
0
100
200
300
400
500
Hatched egg density
Day of first emergence
(b)
28
24
20
0
40
80
120
160
200
240
Initial adult density

FIGURE 3.5 The relationships between day of first emergence and (a) hatched egg density and (b) initial adult density for C. maculatus. Open circles in (a) are for data from one adult pair, closed circles are from 5-60 pairs and crosses are from 80 and 120 pairs. The curve is $y = 25.96 - 0.0418x + 0.00022x^2$; $.01 > p > .001$. Data in (b) are given as mean $\pm$ s.e.


(a)
28
24
20
0
50
100
150
200
250
Hatched egg density
Day of first emergence
(b)
28
24
20
0
40
80
120
160
Initial adult density

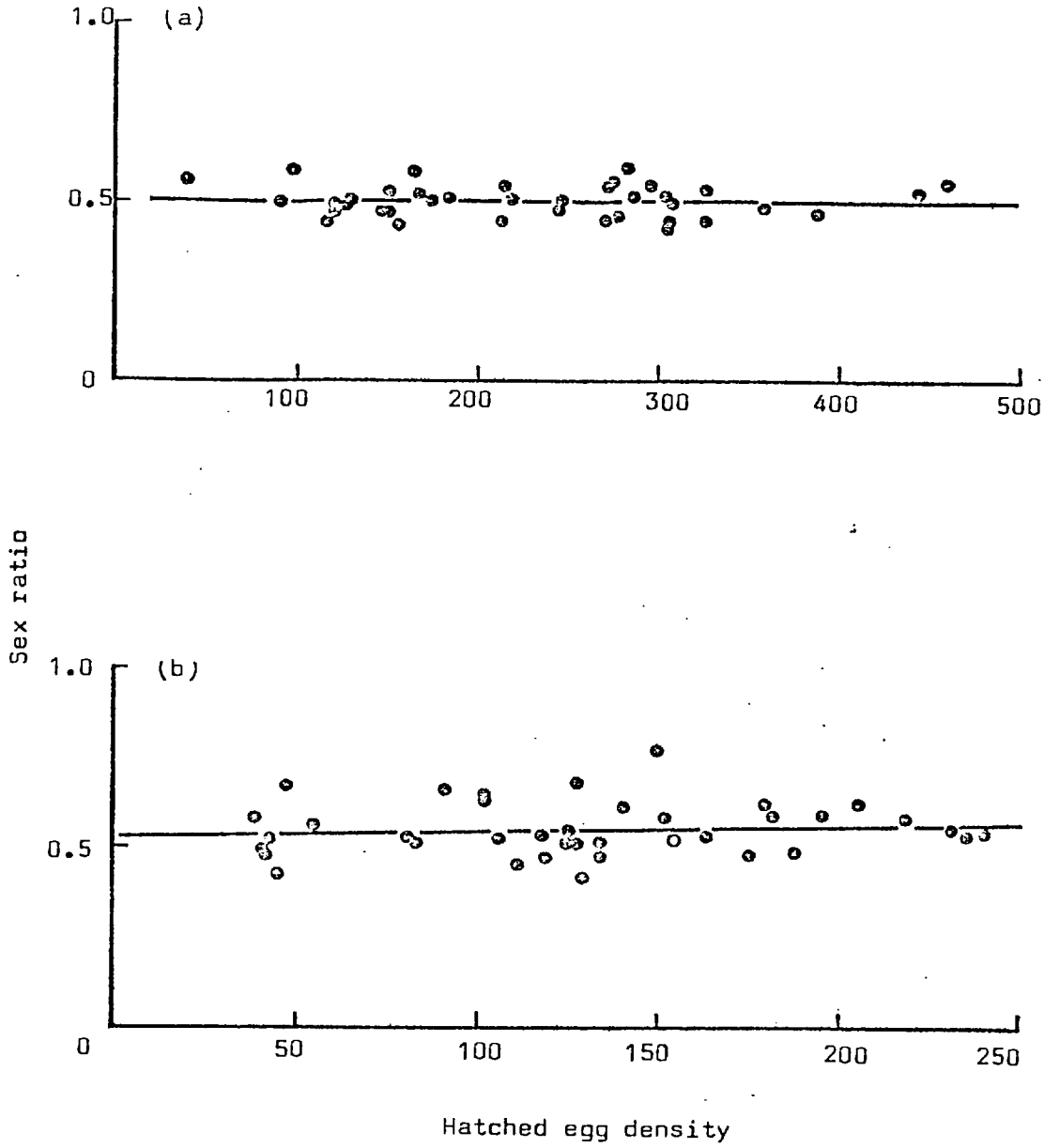
addition, the data in figure 3.4a can be divided into three groups. The hollow circles correspond to the day of first emergence at hatched egg densities arising from a single pair of adults, where the mean was 22.9 days. The solid circles correspond to hatched egg densities arising from intermediate adult densities (5 to 60 pairs, figure 3.4b). Here the mean first day of emergence was slightly earlier (21.0 days). Finally, the crosses in figure 3.4a indicate the hatched egg densities associated with high adult densities (80 and 120 pairs), where the mean first day of emergence was later(23.9 days) than for one pair.

The data for C. maculatus (figure 3.5a) showed a significant quadratic relationship between hatched egg density and day of first progeny emergence ($.01 > p > .001$). These data can also be divided into three groups. The mean first day of emergence at hatched egg densities arising from one adult pair (hollow circles) was 23.9 days.. At hatched egg densities associated with five, 40 and 60 adult pairs (solid circles) the mean first day of emergence was similiar, 24.3 days. At hatched egg densities above 180, there was some indication of later first emergence. This may have been due to increased initial density in the larval stage, but as these two data are the only results from dishes with an initial adult density of 20 pairs, they must be regarded with caution due to lack of replication. Finally, at low hatched egg densities arising from 80 adult pairs (crosses in figure 3.5) there was a longer period to first emergence (25.8 days).

(v) In analyzing the data on progeny sex ratio, only data from dishes where the number of survivors was greater than 30 were used. There was no significant relationship between hatched egg density and the sex ratio of the survivors in either C. chinensis (figure 3.6a) or C. maculatus (figure 3.6b).

The mean proportion of male progeny in C. chinensis was 0.498 ± 0.0452 (s.d.) and C. maculatus was 0.549 ± 0.0742. Of these, only the

FIGURE 3.6 The relationship between hatched egg density and sex ratio (expressed as proportion of males) of the surviving adults. (a) C. chinensis. The regression line is $y = 0.5039 - 0.000024x$; $.80 > p > .20$. (b) C. maculatus. The regression line is $y = 0.5271 + 0.000161x$; $.80 > p > .20$.


(a)
1.0
0.5
0
100
200
300
400
500
Sex ratio
(b)
1.0
0.5
0
50
100
150
200
250
Hatched egg density

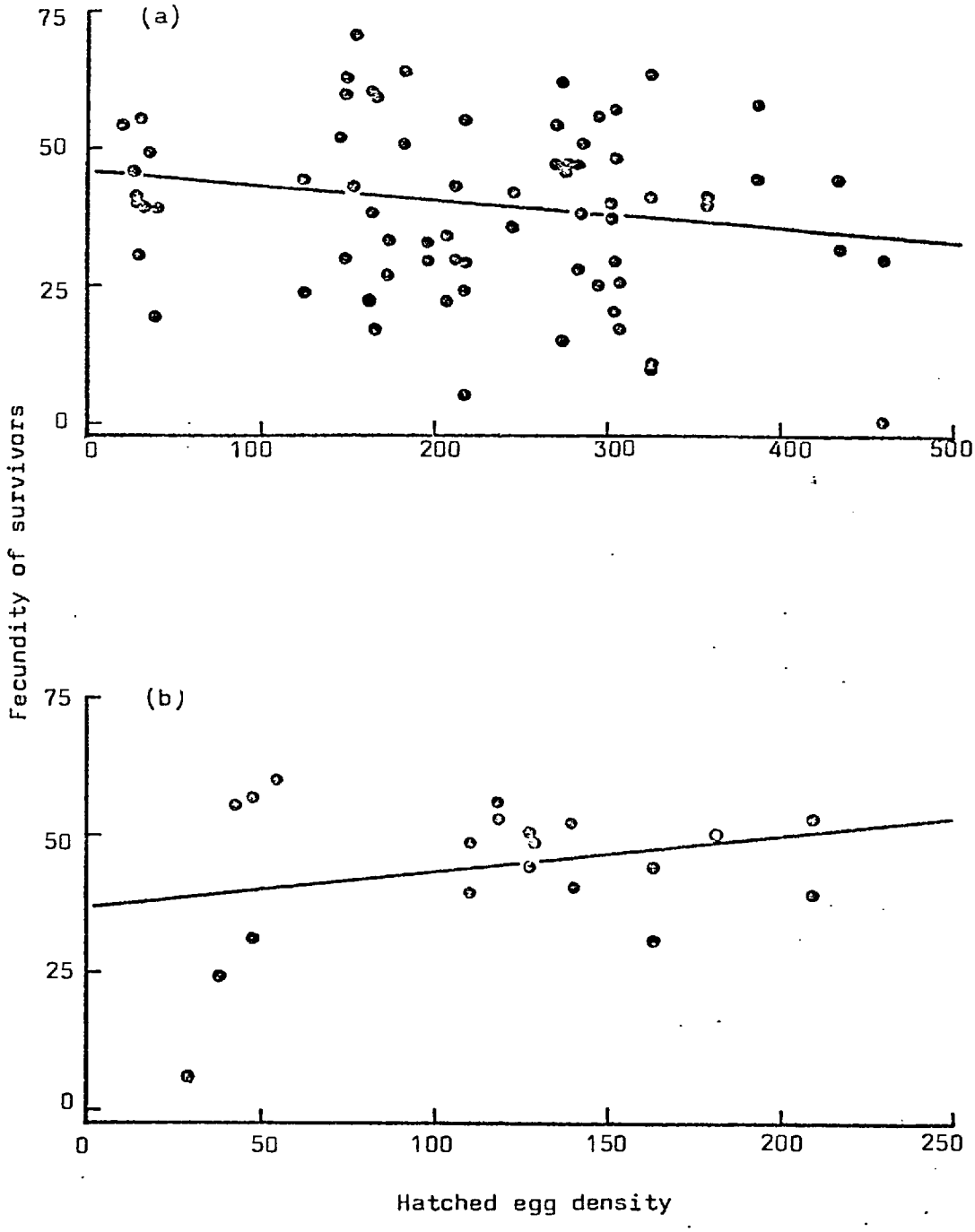
sex ratio of C. maculatus proved to be significantly different from 1:1. To show this, the data must first be examined in such a way that a false acceptance of the null hypothesis is avoided (the null hypothesis here is that the proportion of males is 0.5). This involves a type II error, and a t-test with a confidence level of 0.50 is appropriate. When tested in this way, the mean observed sex ratio of C. chinensis was not significantly different from 1:1. However, the mean observed sex ratio of C. maculatus was significantly different from 1:1, and the null hypothesis was rejected. To ensure that a false rejection has not been made, the data may be retested avoiding a type I error. The data for C. maculatus were retested in this way and the null hypothesis was rejected with $p < .001$ (i.e. the sex ratio of C. maculatus was significantly different from 1:1). These results were also obtained when the data were transformed to angles (where the analyses were performed on the new variable $y=\arcsin((\text{sex ratio})^{\frac{1}{2}})$. This transformation improves the distribution properties of proportions, but is only of particular value when some of the proportions lie outside the range of 0.3-0.7 (Snedecor & Cochron 1972).

(vi) There was no significant relationship between hatched egg density and the fecundity of the progeny in either species (figure 3.7). The mean fecundity of C. chinensis progeny was 40.2 ± 15.6(s.d.) and of C. maculatus progeny was 44.6 ± 12.6 eggs per female.

3.5 Discussion of results

Monotonically increasing or humped reproduction curves such as those found in this study for C. chinensis and C. maculatus (figure 3.1) indicate the presence of regulatory mechanisms acting on a population (density dependence). Comprehensive reviews of populations showing these types of reproduction curves have been given by Tanner (1966) and Hassell, Lawton & May (1976). These types of reproduction

FIGURE 3.7 The relationships between hatched egg density and fecundity of the progeny (total eggs laid by isolated pairs) (a) C. chinensis. The regression line is y = 45.82 - 0.0247x; .20 > p > .10. (b) C. maculatus. The regression line is y = 37.00 + 0.0635x; .80 > p > .20. The hollow circle in (b) indicates a repeated point.


(a)
75
50
25
0
0
100
200
300
400
500
(b)
75
50
25
0
0
50
100
150
200
250
Fecundity of survivors
Hatched egg density

curves are common in insect populations maintained in the laboratory, and have been found in the Coleoptera (e.g. Park 1932; Utida 1941b; Crombie 1945), Diptera (e.g. Pearl & Parker 1922), Lepidoptera (e.g. Crombie 1945; Hassell & Huffaker 1969) and the Hymenoptera (e.g. Utida 1943a; Hassell & Huffaker 1969; Hassell & Varley 1969). In particular, a number of workers have noted reproduction curves for C. chinensis and C. maculatus similiar to those in figure 3.1. Utida (1941b) defined the reproduction curve of C. chinensis by an experimental approach similiar to that taken here. In other studies the shape of these curves have been determined by considering succesive population sizes in long-term cultures (e.g. Utida 1959; Fujii 1968; Nakamura 1969; Okamoto 1971b). The results of all these studies confirm the present findings that the reproduction curve of C. chinensis is nearly monotonic, showing only a slight hump, while that of C. maculatus is more steeply humped, showing a severe reduction in the number of progeny at high densities. From these results, inferences can be drawn concerning the expected population dynamics of these species, specifically that populations of C. chinensis should show quickly damped oscillations following a disturbance from equilibrium, while populations of C. maculatus would show more sustained oscillations or stable cyclic behaviour followinga disturbance from equalibrium. This subject will be treated more fully in the next section.

The reduction in fecundity in response to adult crowding, such as observed here in these species of Callosobruchus, is well known in laboratory insect populations. The work of Crombie (1942, 1943), Ullyett & van der Merwe (1947) and Snyman (1949) on grain insects and Hassell & Huffaker (1969), Hassell & Varley (1969) and Hassell (1971) on parasitic Hymenoptera have demonstrated the generality of this phenomenon. It has also been observed by Utida (1941a) in C. chinensis. Fujii (1968), however, working in larger experimental cages than either those used here or by Utida (1941a), did not find any reduction in

fecundity in either C. chinensis or C. maculatus as adult density increased.

The reduction in percentage of eggs hatching as adult density increases does not appear to have been reported except in populations of C. chinensis (Utida 1941a, c). Utida (1941c) suggested that this was a result of mechanical damage to the eggs by the adults moving over the beans. Although this phenomenon has not been reported for C. maculatus, Utida's suggestion appears to account for the more severe density dependent reduction in the percentage of eggs hatched in this species than in C. chinensis. C. maculatus adults were less capable of climbing the walls of the experimental dishes, and were generally more active than adults of C. chinensis, possibly resulting in more damage to the eggs. It is noteworthy, however, that Oshima, Honda & Yamamoto (1973) have isolated an oviposition marker from C. chinensis that is ovicidal at high concentrations (Honda, Oshima & Yamamoto 1976).

The relationship between hatched egg density and the number of survivors was a monotonically increasing curve for both species, indicating contest competition in the larval stage with little or no overexploitation of resource. This type of competition has also been found in larvae of Rhyzopertha dominica (F.) and Sitotroga cerealella (Oliv.) infesting whole wheat grains (Crombie 1944). More generally in laboratory insect populations there is a humped relationship between initial density and number of survivors (e.g. Park 1938; Snyman 1949; Ullyett 1950; Nicholson 1954; Miller 1964). These humped relations reflect scramble competition where at high initial densities the resource is overexploited, resulting in high mortality. A monotonic relationship between hatched egg density and larval survival has been demonstrated by Utida (1942) for C. chinensis, but both Utida (1967) and Fujii (1968) have reported a humped relationship

for C. maculatus. Fujii (1965) recorded hatched egg densities for C. maculatus as high as 50 per bean on a host whose seed is slightly smaller than that used here. This is more than twice the maximum density of hatched eggs per bean recorded for this species in this study. At such high densities overexploitation may have resulted in considerable mortality and a humped relationship between hatched egg density and the number of survivors.

The larval mortality observed at low hatched egg densities in these species was considerably higher in dishes with high initial adult densities than in those with fewer adults. In dishes with high adult densities, where there was considerable egg mortality (resulting in few hatched eggs), there also appeared to be a higher mortality among hatching larvae than in dishes with fewer adults. This was possibly due to the same cause that effected the high egg mortality. This phenomenon was more pronounced in C. maculatus than in C. chinensis.

The processes responsible for the density dependent reproduction curves in figure 3.1 can be clearly divided into two groups, those which limited the number of recruits to the larval stage and the subsequent process of larval competition. It is clear from a consideration of figures 3.2b and 3.3b that competition in the larval stage was compensatory; the number of survivors reached a plateau as density increased. As oviposition by these species was not overcompensating (figures 3.2a and 3.3a), the hump in the reproduction curves was due to the overcompensatory processes which limited egg hatching. Consideration of the density dependence shown here by the adult stage is crucial to the understanding of the regulatory mechanisms acting on these populations and it will be seen in the next section that competition in the adult stage is responsible for oscillatory behaviour in the models developed for these species.

The first day of emergence was nearly constant over a considerable range of hatched egg densities for both species. This is in agreement with the qualitative observations on the effect of adult density on developmental period made by Utida (1967) and Fujii (1965, 1967). Crombie (1944) also noted a density independent developmental period for Rhyzopertha and Sitotroga. Park (1938), however, found that larval development in Tribolium confusum (where larval competition is of the scramble type) was considerably prolonged at high larval densities. In the populations of C. chinensis and C. maculatus studied here, the first day of emergence was later in dishes with high initial adult densities, and this was probably due to mortality of the eggs laid early in the experiment when adult activity was highest. The slight advance in the day of first emergence at intermediate and high hatched egg densities observed in C. chinensis might have been due either to a lack of a preoviposition period in the crowded adults or to a slightly higher temperature, and hence quicker development, in the more dense larval populations.

The sex ratio in both species was constant over the range of hatched egg densities investigated, implying no competitive advantage to either sex. The 1:1 sex ratio observed here for C. chinensis agrees with the findings of Utida (1941a) and Howe & Currie (1964). Howe and Currie also reported a 1:1 sex ratio in C. maculatus, but in the present study the sex ratio observed in this species was 1.10:1 in favour of males. The reason for this is not clear.

There was no significant relationship between hatched egg density and progeny fecundity in either C. chinensis or C. maculatus. A number of authors, however, have reported a reduction in adult size or weight as larval density increased for a variety of insects (e.g. Park 1938; Snyman 1949; Ullyett 1950; Nicholson 1954; Bakker 1961) and this reduction in size may suggest a reduction in adult fecundity

(Varley, Gradwell & Hassell 1973). In both the Lepidoptera (Plodia interpunctella Hübner, Snyman (1949)) and in the Diptera (Ullyett (1950) working with three species of blowflies) positive relationships between adult weight and fecundity have been demonstrated. Ullyett (1950) has also measured directly a reduction in fecundity with increasing density in the larval stage. All of these studies have dealt with species in which larval competition is of the scramble type. In C. chinensis, and in this study in C. maculatus, larval competition is of the contest type. In such cases the larval population does not overexploit its resource, and adult weight and fecundity may be less affected by density than in cases of scramble competition. Although Utida (1941b) has shown for C. chinensis a slight reduction in adult weight as hatched egg density increased, the results presented here indicate that there is no effect of hatched egg density on progeny fecundity in either species.

3.6 Development of models

The population models developed here for C. chinensis and C. maculatus have been based on the quantified reproduction and survival curves of figures 3.1, 3.2 and 3.3. The interpretation of these curves as simple population models has been suggested by a number of authors (e.g. May & Oster 1976; Varley, Gradwell & Hassell 1973). The single age-class models have been based on the reproduction curves in figure 3.1, and the two age-class models were developed from the density dependent oviposition and survival curves of figures 3.2 and 3.3. In this section the assumptions made in the construction of the models will be briefly examined, the single and two age-class models will be explicitly developed, their stability properties will be discussed, and finally the predictions of the models will be compared with published results on the long-term population dynamics of these species.

3.6.1 The assumptions of the models

Population models framed in difference equations have a number of implicit assumptions, the most important of which is discreteness of generations or stages. In these experimental systems this assumption is well founded, since the adults are short lived and the length of the oviposition period is less than one third of the preimaginal developmental period. More importantly, Fujii (1968) and Utida (1941d, 1967) have noted that generations remain discrete in long-term laboratory cultures of these species. A less critical assumption is that generation time is constant, so that populations in different generations are subject to unit time intervals of competition. Finally, for the formulations used here, it is important that there is no delayed effect of density between succesive generations, such as changes in fecundity or sex ratio. Experimental results have confirmed that these assumptions are not violated in the experimental systems used here. Although significant relationships were found between density and developmental period, the range of developmental period in relation to the mean was small, and is here assumed constant.

3.6.2 Single age-class models

The single age-class population models developed here were based on the reproduction curves shown in figure 3.1. The models have the form

$$N_{t+1} = \lambda p N_t (1+(aN_t)^b)^{-1}. \qquad (3.5)$$

The parameters a and b define the density dependent shape of the curve as in equation 3.1 (see also page 32), λ is the effective net rate of increase per female, and p is the proportion of females in the population. The value of p was taken as 0.500 for C. chinensis and 0.451 for C. maculatus. The values of the other parameters were

taken from the fitted curves in figure 3.1 and are given in table 3.1. The fitted value for λ may be compared with the mean number of progeny from one pair of adults (table 3.1). In neither species were the estimates in close agreement; λ was estimated higher than the mean number of progeny from one pair for C. chinensis and lower for C. maculatus.

The simulations of the single species models for C. chinensis and C. maculatus are shown in figures 3.8a and 3.9a, respectively. Both models demonstrated an oscillatory approach to a stable equilibrium. The model for C. chinensis was more stable than the model for C. maculatus, as discussed more fully below.

3.6.3 Two-age class models

Populations of Callosobruchus may be easily divided into two stages, adults and "larvae", where the "larval" stage includes all the non-ovipositing developmental stages (eggs, larvae, pupae and pre-emergent adults). The two age-class models developed here were based on such a division, and the models for the two phases of adult oviposition and larval development were based on the fitted curves in figures 3.2 and 3.3. Oviposition was considered to be the number of hatched eggs laid (broken lines in figures 3.2a and 3.3a). The models for larval competition were based on the fitted curves in figures 3.2b and 3.3b.

There are two approaches which may be taken for the development of a two age-class population model. The usual approach has been to consider the time required for the completion of one generation to be unity, and that development within both stages occurs in one time step (Varley & Gradwell 1968 ; Hassell & Huffaker 1969; Benson 1974; Hassell 1975). In this approach the model has the form

$$L_{t+1} = A_t f(A_t), \qquad (3.6a)$$

$$A_{t+1} = L_{t+1} g(L_{t+1}). \qquad (3.6b)$$

TABLE 3.1 The parameters used in the single age-class model, obtained by fitting equation 3.2 to the data in figure 3.1. The mean numbers of progeny from isolated pairs are included for comparison with the fitted values of λ.

parameter	C. chinensis	C. maculatus
a	0.078738	0.040590
b	1.2591	2.2178
λ	31.373	15.849
mean number of progeny from one pair	24.6	28.3

FIGURE 3.8 The simulations of the (a) single age-class, (b) two age-class model (I) and (c) two age-class model (II) for C. chinensis. The single age-class model is from equation 3.5, the two age class models arise from equations 3.7, 3.9, 3.10 and 3.11. Fitted parameters are given in tables 3.1 and 3.2.

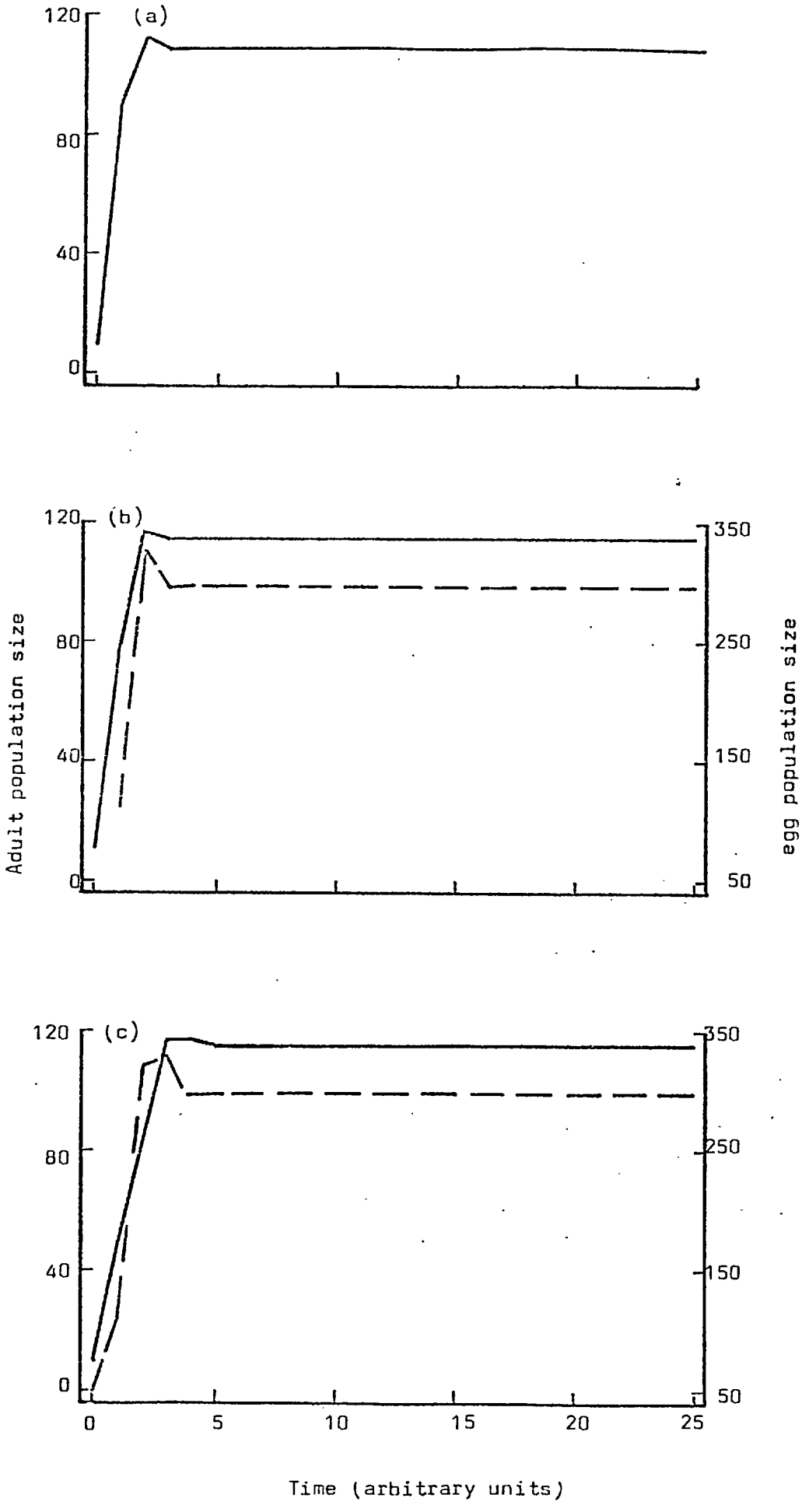
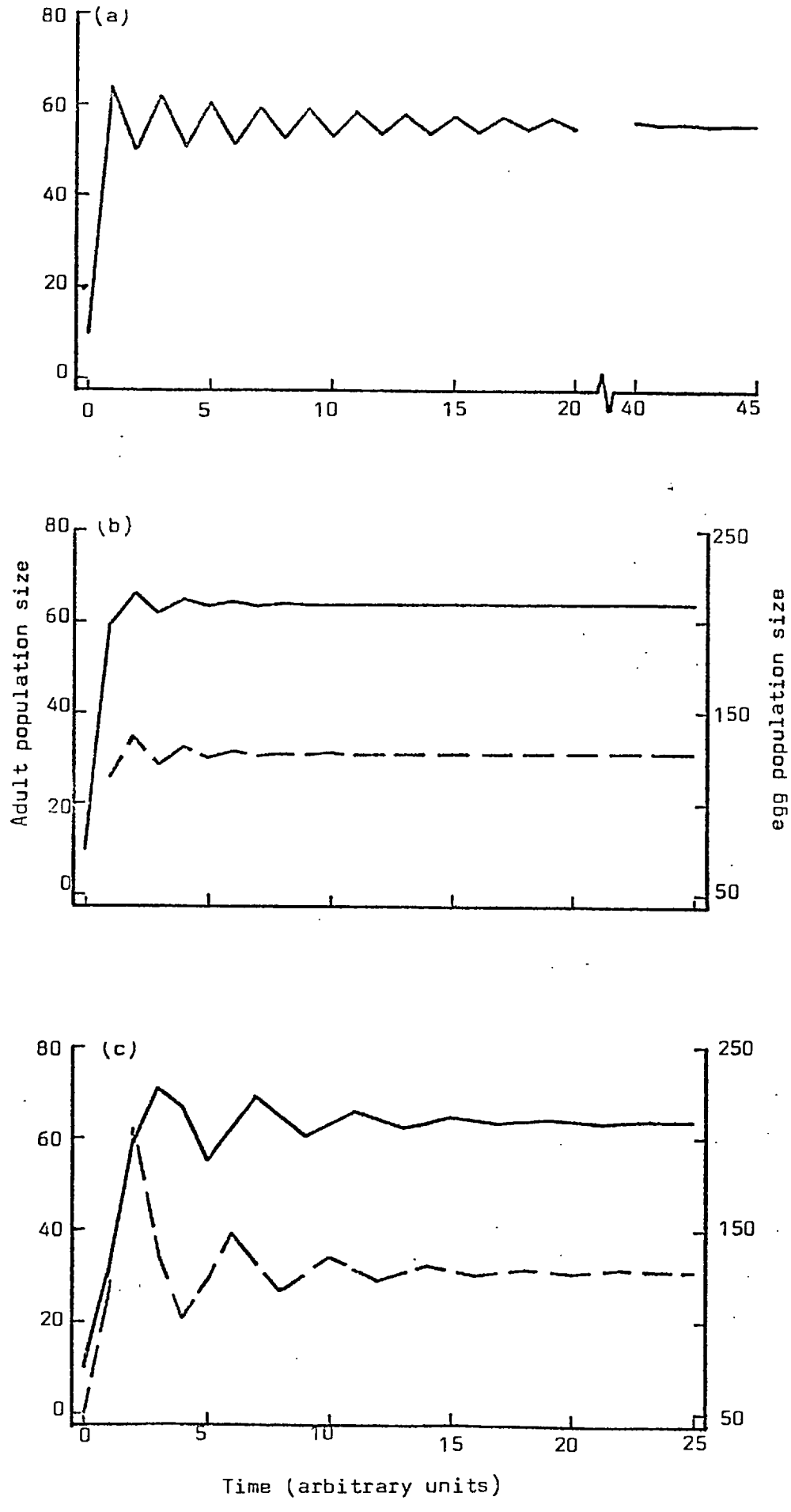

(a)
120
80
40
0
(b)
120
80
40
0
350
250
150
50
Adult population size
egg population size
(c)
120
80
40
0
350
250
150
50
0
5
10
15
20
25
Time (arbitrary units)

FIGURE 3.9 The simulations of the (a) single age-class, (b) two age-class model (I) and (c) the two age-class model (II) for C. maculatus. The single age-class model is from equation 3.5, the two age class models arise from equations 3.7, 3.9, 3.10 and 3.11. Fitted parameters are given in tables 3.1 and 3.2.


(a)
80
60
40
20
0
0
5
10
15
20
40
45
(b)
80
60
40
20
0
250
150
50
Adult population size
egg population size
(c)
80
60
40
20
0
250
150
50
0
5
10
15
20
25
Time (arbitrary units)

The function f(A) defines the net per capita oviposition, and the function g(L) defines the proportionate survival during development from larvae to adults. The equation for larval recriutment (oviposition) of equation 3.6a may be subsituted into equation 3.6b to give

$$A_{t+1} = A_t f(A_t) g(A_t(f(A_t)) \qquad (3.7a)$$

or

$$A_{t+1} = A_t h(A_t) \quad , \; h(A) = f(A)g(Af(A)). \qquad (3.7b)$$

This formulation is analogous to a single age-class model where the function h(A) now defines the net per capita reproduction. Equation 3.7 may be considered as a two age-class reproduction curve, and the predicted forms of these curves are presented as broken lines in figure 3.1 for the fitted equations of f(A) and g(L) discussed below. The population model of equation 3.7 will be referred to as the two age-class model I.

An alternate approach has been discussed by May et al. (1974). In this approach the time step is also unity, but development in each stage requires one unit of time so that two time steps are required for the completion of a generation. Both larvae and adults are present in each time step, and the form of the model is

$$L_{t+1} = A_t f(L_t, A_t), \qquad (3.8a)$$

$$A_{t+1} = L_t g(L_t, A_t). \qquad (3.8b)$$

Note this model includes the potential for interaction between the larval and adult stages, since the functions f and g depend on both larval and adult population sizes. Where oviposition and larval development are independent, as is the case with C. chinensis and C. maculatus, the functions f and g depend only on the number of adults and larvae, respectively. Equation 3.8 now becomes

$$L_{t+1} = A_t f(A_t), \qquad (3.9a)$$

$$A_{t+1} = L_t g(L_t). \qquad (3.9b)$$

In the model of equation 3.9 the population consists of two non-interacting cohorts or subpopulations, one which is in the adult stage at times t, t+2, t+4, etc. and one which is in the adult stage at times t+1, t+3, t+5, etc. (This phenomenon has also been observed in a similiar two-species two age-class model developed by Hassell & Comins (1976).) The model of equations 3.9 will be referred to as the two age-class model II.

In both of these two age-class models the forms of the functions f(A) and g(L) are the same:

$$f(A_t) = p\lambda\ (1+(aA_t)^b)^{-1}, \qquad (3.10)$$

$$g(L_t) = s(1+(cL_t)^d)^{-1}. \qquad (3.11)$$

The parameters p, λ , a and b in equation 3.10 have the same interpretation as in equation 3.5. The parameters c and d in equation 3.11 determine the density dependent form of the function g as described above for the parameters a and b in equation 3.5. The parameter s is the density independent proportionate survival in the larval stage. The values used for the parameter p were 0.500 for C. chinensis and 0.451 for C. maculatus as for the single age-class models. The values of the other parameters were obtained by fitting the models to the data in figures 3.2 and 3.3, and are given in table 3.2. In both species the estimated value for λ was considerably less than the observed number of hatched eggs laid by isolated pairs (table 3.2). The fitted parameters and equations 3.10 and 3.11 may be used with equation 3.7 to provide an estimate of the reproduction curve for these species, and these curves are shown as broken lines in figure 3.1. These two age-class reproduction curves provide a reasonable description of the data, but their fit at high densities was poorer than that of the fitted single age-class model.

The simulations of the two age-class models I and II are shown in figure 3.8 (b,c) for C. chinensis and in figure 3.9 (b,c) for

TABLE 3.2 The parameters used in the two age-class models. The values in (a) were obtained by fitting equation 3.4 to the data on number of hatched eggs in figures 3.2a and 3.3b. The mean number of hatched eggs laid by one pair are included for comparison with the fitted values of λ. The values in (b) were obtained by fitting equation 3.1 to the data on larval survival in figures 3.2b and 3.3b.

parameter	C. chinensis	C. maculatus
a	0.017429	0.030014
b	1.7737	2.4806
λ	22.929	26.588
mean number of hatched eggs from one pair	30.0	37.4

(a)

parameter	C. chinensis	C. maculatus
c	0.0047084	0.0039716
d	1.3738	1.9503
s	1.0000	0.63335

(b)

C. maculatus. All of the models showed oscillatory damping to an equilibrium, which is in accord with their local stablity properties discussed below. Since one generation requires two time steps in model II, the time taken to reach equilibrium is longer than for model I. However, if the subpopulations in model II were given values equal to the initial population size in model I, the number of generations required to reach equilibrium would be the same in both models. In the single age-class model and in the two age-class models I the oscillations have a period of two time steps (twice the generation time). In the two age-class models II (with a generation time of t = 2) the oscillations have a period of approximately four time steps. May et al. (1974) have pointed out that models of this type (II) may have oscillations of any period.

3.6.4 The local stability of the models

Although the stability properties of all these models may be roughly characterized by inspection of the simulations in figures 3.8 and 3.9, a more quantative comparison is possible by considering their local stability properties. Such a comparison may be based on the dominant eigenvalue of the interaction function (for single age-class or two age-class models I).or of the interaction matrix (for two age-class models II). These ideas are set out more formally in appendix A, and it is sufficient here to note that the models are locally stable only when the magnitude of their dominant eigenvalue is less than unity (May 1974), that is $|\chi|<1$. In the region $0<|\chi|<1$, models are more stable as $|\chi|$ approaches zero and less stable as $|\chi|$ approached unity. For single age-class and type I two age-class models, approach to equilibrium is monotonic for values of $0<\chi<1$ and oscillatory for $-1<\chi<0$. For type II two age - class models, eigenvalues may in general be complex numbers, and damping is monotonic if all the eigenvalues have zero imaginary parts.

The eigenvalues and their magnitudes for the six models developed above are given in table 3.3.

All of the eigenvalues were either negative or had nonzero imaginary parts, implying an oscillatory approach to equilibrium. The models developed for C. chinensis were all more stable (had smaller values for $|X|$) than those for C. maculatus. For C. chinensis the two age-class model I was more stable than the single age-class model, and for C. maculatus both two age-class models were more stable than the single age-class model. Furthermore, both of the type I two age-class models were more stable than the corresponding type II models. This is a general feature of any two models of type I and II of any number of age-classes which are defined by the same density dependent functions. A type I model of n age-classes which completes a generation in one time step will be more stable than the corresponding type II model which completes a generation in n time steps (see appendix A).

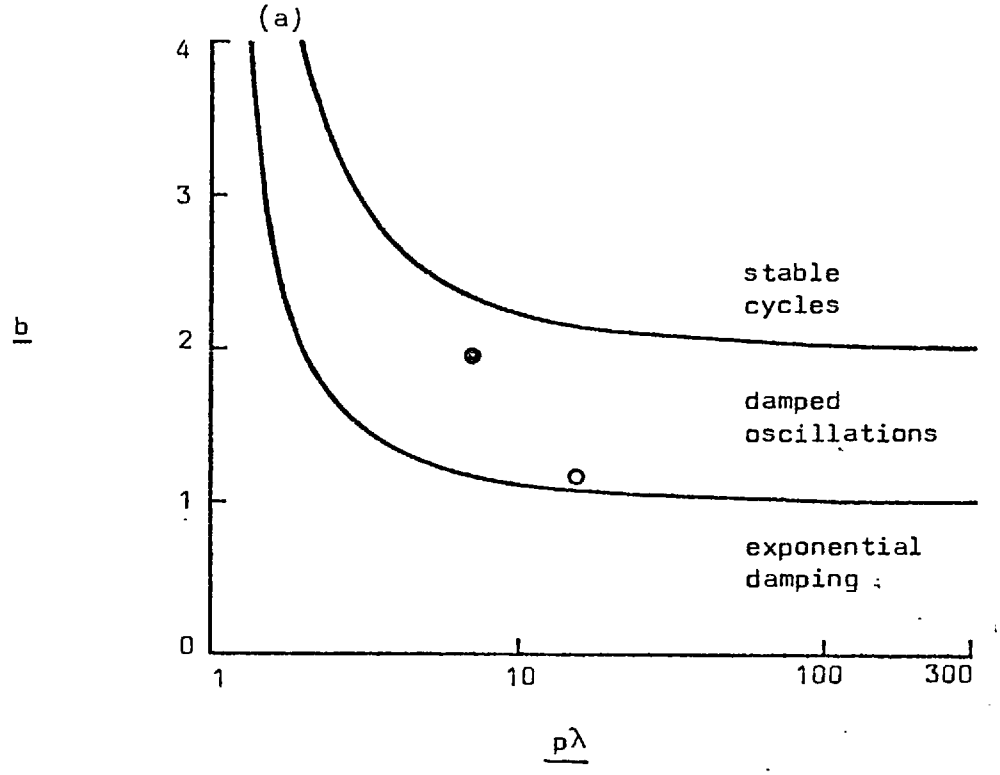
The stability of the single age-class models may also be determined by considering their position in the stability diagram of figure 3.10a. Here the regions of different dynamic behaviour are defined by the values of the parameters p, λ and b of equation 3.5. The boundaries between these regions have been determined by a linearized stability analysis, the details of which are given in appendix A. Both models were placed in the region of oscillatory damping, and the model for C. chinensis was positioned nearer the more stable region of monotonic damping than the model for C. maculatus.

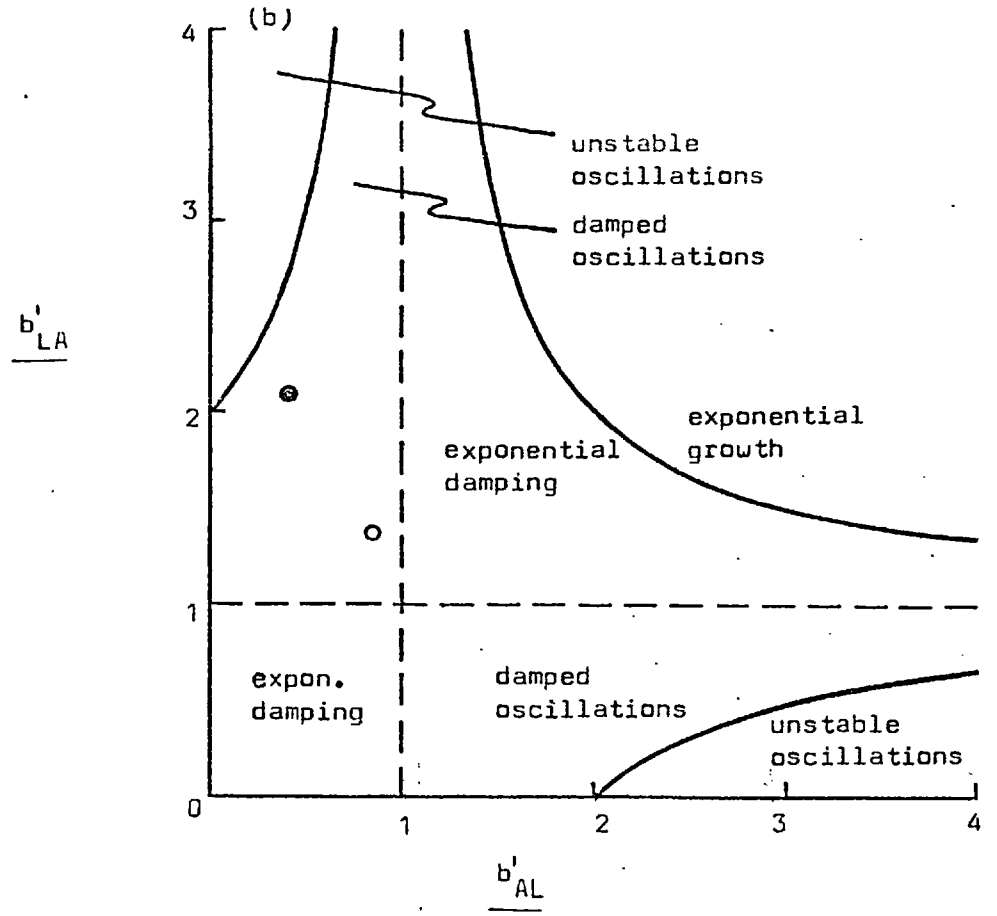
May et al. (1974) have outlined a procedure which determines the relative contributions of density dependence in the adult and larval stages to the stability of type II two age-class models. In mathematical terms, the density dependence in the adult (oviposition) stage is characterized by the value of the derivative of the logarithm

TABLE 3.3 The eigenvalues and their magnitude for the six population models developed for *C. chinensis* (figure 3.11) and *C. maculatus* (figure 3.12).

Model	*C. chinensis*		*C. maculatus*	
single age-class	-0.170	0.170	-0.908	0.908
two age-class (I)	-0.059	0.059	-0.632	0.632
two age-class (II)	0.059i	0.242	0.632i	0.795

FIGURE 3.10 The stability boundaries for (a) the single age-class model of equation 3.5 and (b) the two age-class model (II) of equations 3.9. ((b) after May *et al.* 1974). Open circles indicate the models for *C. chinensis*. Closed circles indicate the models for *C. maculatus*.


(a)
b
4
3
2
1
0
1
10
100
300
pλ
stable
cycles
damped
oscillations
exponential
damping


(b)
b'LA
4
3
2
1
0
1
2
3
4
b'AL
unstable
oscillations
damped
oscillations
exponential
damping
exponential
growth
expon.
damping
damped
oscillations
unstable
oscillations

of the function f(A) (equation 3.10) with respect to the logarithm of adult density, evaluated at equilibrium,

$$b'_{LA} = - \left(\frac{d \ln f}{d \ln A}\right)^{*}. \qquad (3.12)$$

Similarly, density dependence in the larval stage is defined by

$$b'_{AL} = - \left(\frac{d \ln g}{d \ln L}\right)^{*}. \qquad (3.14)$$

Stability boundaries for the two age-class models (II) based on the parameters b'_{LA} and b'_{AL} have been given by May et al. (1974) and are shown in figure 3.10b. The position of the models in this stability plane indicate the higher relative stability (nearness to the region of monotonic damping) of the C. chinensis model. In addition, it may be seen that density dependence (at the equilibrium) is greater in both models in the adult stage than in the larval stage ($b'_{LA} > b'_{AL}$). It is this greater overcompensating density dependence in the adult stage which positions the models in the region of damped oscillations in figure 3.10b and gives rise to the oscillatory behaviour of the models. Finally, in the model for C. maculatus density dependence (at equilibrium) in the adult stage was greater than in the model for C. chinensis, and in the larval stage density dependence was greater in the model for C. chinensis than in the model for C. maculatus.

3.6.5 Comparison of model predictions with literature studies

One objective in the construction of these models was to provide a mathematical description of the population dynamics of these species. The success in achieving this objective may be partially measured by comparing the simulations in figures 3.8 and 3.9 with the results of long term studies of populations of the two species. A number of such studies have appeared in the literature, and the findings of a selection of these are presented in figures 3.11 for C. chinensis and figure 3.12 for C. maculatus. The general implications of these results may be discussed without involving them in detailed analyses.

FIGURE 3.11 Some representative studies on the dynamic behaviour of populations of C. chinensis. Data in (a)-(d) from Fujii (1968) and in (e) from Utida (1967). Note the general monotonic or slight oscillatory approach to equilibrium.

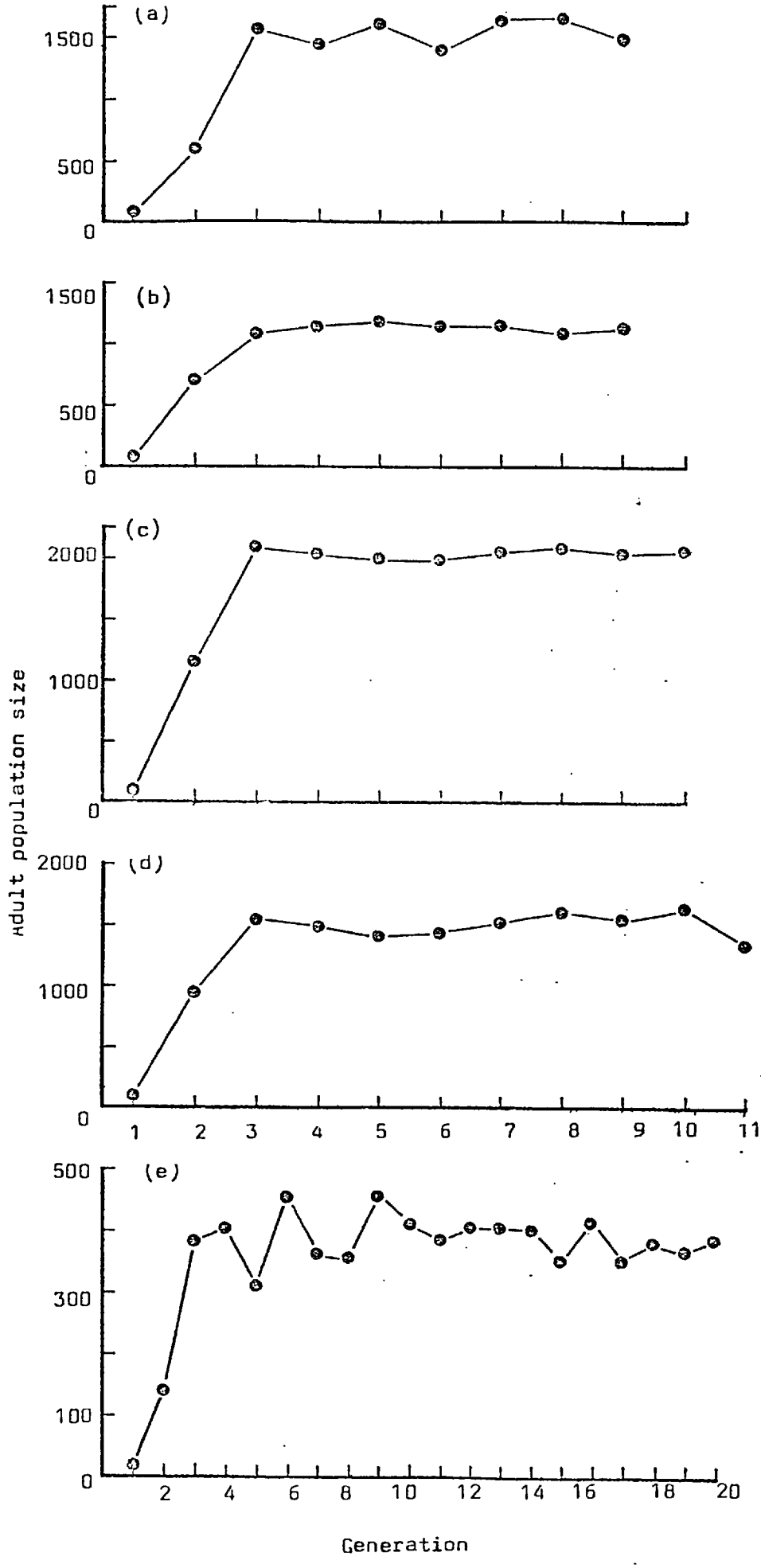
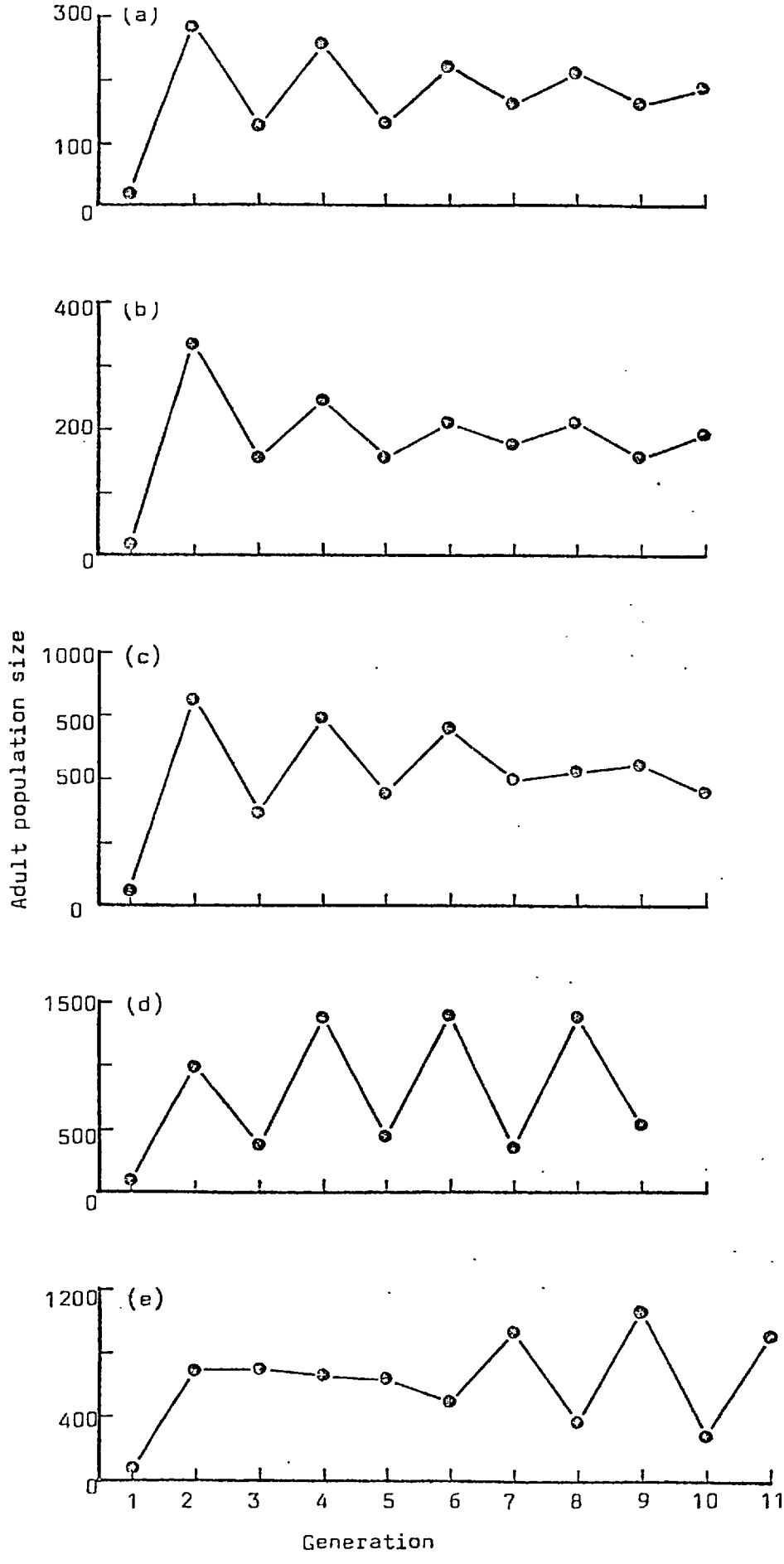

(a)
1500
500
0
(b)
1500
500
0
(c)
2000
1000
0
(d)
2000
1000
0
1 2 3 4 5 6 7 8 9 10 11
(e)
500
300
100
0
2 4 6 8 10 12 14 16 18 20
Adult population size
Generation

FIGURE 3.12 Some representative studies on the dynamic behaviour of populations of C. maculatus. Data in (a) and (b) from Utida (1967) and in (c)-(d) from Fujii (1968). Note the general occurrence of oscillatory behaviour.


(a)
300
100
0
(b)
400
200
0
Adult population size
(c)
1000
500
500
0
(d)
1500
500
0
(e)
1200
400
0
1 2 3 4 5 6 7 8 9 10 11
Generation

The results in figure 3.11 indicate that populations of C. chinensis generally show monotonic or slightly oscillatory approaches to equilibrium, and those in figure 3.12 indicate that C. maculatus populations show either more prolonged oscillatory damping to an equilbrium or stable cycles. These findings are in qualitative agreement with the dynamics of the models developed here, specifically that the models for C. chinensis show rapidly damped oscillations to equilibrium and those for C. maculatus show a longer period of oscillatory behaviour before equilibrium is reached.

The single age-class models and the two age-class models I showed oscillations with a period of two generations. This is in accord with most of the populations showing oscillatory behaviour in figures 3.11 and 3.12. The type II models developed here showed oscillations with a period of $t \cong 4$, but as the generation time for these models was two time units, the oscillations in these models also had a period of approximately two generations. All of the studies presented in figures 3.11 and 3.12 were started with a single initial cohort of adults and, since the generations remained discrete, they may be considered as validation studies for the single age-class and type I two age-class models. In order to validate the type II models, long term experiments would have to commence with two cohorts of adults, one at $t = 0$ and another after these adults had finished ovipositing but prior to the emergence of their progeny, say at $t = \frac{1}{2}$. It would also be necessary to provide the second cohort of adults with fresh host beans for oviposition to ensure that the assumption of non-interaction between the cohorts was not inolated. Although such a study has not appeared in the literature, the success of the other models in predicting the dynamics of these species suggests that the type II models presented here would provide reasonable descriptions of the dynamics of such systems.

3.7 Conclusions

Insect population models have often been based on quantified reproduction and survival curves arising from data taken from long-term population studies. An alternate and complimentary approach has been taken here where the form of these curves are determined by single-generation experiments. Such an approach has a number of advantages related primarily to the ease of manipulation of an experimental system. Factors of interest can be thoroughly investigated in regions where long term population fluctuations rarely occur, such as extremely high or low densities. Complex phenomena, such as interactions between cohorts of different ages, may be more easily studied than in natural populations. Finally, observations may be repeated or experiments designed with particular analyses in view providing easier analysis of results.

Models developed from experimentally determined reproduction curves may be validated by comparison of model predictions with results of long-term studies. Where quantitative predictions are of interest, validation studies would neccesarily involve a system immediately related to that from which the models were developed (i.e. identical strains of species and host food, same environmental conditions, etc.). Where qualitative comparisons are adequate, as was the case in this study, published studies on related systems may provide sufficient information for validation. Although the development of models by the method proposed here is probably limited to the study of laboratory populations, the finding of such studies may provide general insight into the problems involved in insect population modelling and consequently generate a sound basis for more conventional model development from, or life-table analysis of, data from field populations.

Chapter IV. INTRASPECIFIC COMPETITION II.

4.1 Introduction

In the previous chapter, models were developed which provided simple mathematical descriptions of the single-species population dynamics of the two weeviles Callosobruchus chinensis and C. maculatus. It is the object of this chapter to develop a more detailed model of these populations. The model will be framed in difference equations using a time step of one day, and the purpose of the model will be to predict changes in population size and composition from one day to the next. The model will be primarily concerned with the processes of oviposition, instar development and mortality, and each stage of the life history of the weevil (i.e. eggs, four larval instars, pupae and adults) will be individually considered.

This chapter is roughly divisible into three parts. The first section (following this introduction) sets out the explicit development of the model, initially by constructing a submodel for oviposition and adult mortality and subsequently constructing a submodel which describes development and mortality of the pre-imagined stages. In the second section, data are presented which permit the quantification of the model's parameters. In the last section, the model is used to simulate the behaviour of populations of C. chinensis and C. maculatus and the results of these simulations are discussed.

4.2 Development of the model

4.2.1 The oviposition submodel

The object of this submodel is to provide a prediction of the total number of eggs laid on any day t by a population of adults with

a specified age structure. The model will be developed here in three stages. First, the life-span of the adults will be described by an age specific survivorship function. Secondly, the daily oviposition record of the adults will be included. Finally, provision will be made for a density dependent reduction in fecundity due to either egg or adult crowding.

The model for adult life span is based on the simple premise that the adults have age specific density independent probabilities of daily survival. (Utida (1941c) has shown a decrease in mean adult life span at high densities in C. chinensis, but these decreases were small and this phenomena will not be considered here.) Suppose the probability of an adult surviving to age j is $p(j)$ so that the probability of an adult dying before age j is $1 - p(j)$. The probability $p(j)$ may be viewed as the proportion of a cohort surviving to age j and the number of adults surving to time t ($A(t)$) of an initial cohort of $A(0)$ adults will thus be given by

$$A(t) = p(t)\ A(0). \tag{4.1}$$

Equation 4.1 assumes that the age specific survival probabilities are the same for both sexes. This is unlikely to be the case but an extension to different $p(j)$'s for the two sexes is straightforward. For the sake of simplicity the continued development of the model will incorporate only one set of $p(j)$'s for the adults irrespective of sex. If there are several cohorts present which have at time t ages $0,1,2,\ldots,t$ then the total number of live adults at time t is given by

$$A(t) = \sum_{j=0}^{t} p(j)\ A(t-j) \tag{4.2}$$

where $A(t-j)$ is the initial size of the cohort of adults having age j at time t. Equation 4.2 forms the basis for the oviposition sub-model.

In order for equation 4.2 to be used in a population model it is

necessary to quantify the elements p(j). These elements could be set equal to the observed proportion of a cohort of adults survivng to age j, or a parametric distribution which defines the p(j)'s might be specified, and the parameters of the distribution estimated from data on adult life-span (Birley 1977). The parametric approach was taken here, and the function used was a discrete form of the normal distribution where p(j) is given by

$$p(j) = 1 - (k\sigma\sqrt{2\pi})^{-1} \int_{-\infty}^{j} \exp(-\tfrac{1}{2}((t-\mu)/\sigma)^2)\, dt. \qquad (4.3)$$

The elements p(j) are here specified by the two parameters μ and σ^2 which approximate the mean and the variance of adult life span. This is only an approximation since the age index j is not permitted to be negative and hence the distribution p(j) is truncated at zero; this approximation is more precise when $\mu >> \sigma^2$. Since the elements p(j) represent a probability density function it is necessary that their sum is equal to unity, but the truncation of p(j) at zero will cause their sum to be too small. Thus a normalizing constant k is required to ensure that the sum of p(j) over the range of j required is unity.

Equation 4.2 may be modified by including age specific fecundities l(j) to give the number of eggs laid during the interval t to t+1,

$$e(t) = \sum_{j=0}^{t} q\, l(j)\, p(j)\, A(t-j). \qquad (4.4)$$

Here e(t) is the number of eggs appearing, l(j) is the number of eggs laid by a female of age j, q is the proportion of females in the population and p(j) and A(t-j) are defined as for equation 4.2. The values of l(j) will be defined here as the experimentally determined fecundity of females of different ages; it is unlikely that a parametric distribution would be found suitable for describing daily fecundity.

It remains to include density dependence in the oviposition model of equation 4.4. As was discussed on page 58, the number of eggs laid by females of C. chinensis and C. maculatus decreases as adult density

increases. This reduction in fecundity might have been due simply to adult crowding or possibly to a reduction in oviposition in enviroments which contain large numbers of eggs. If these two responses are independent of adult age they may be included in the submodel by adding to equation 4.4 two density dependent functions $h_a(A)$ and $h'_a(E)$:

$$e(t) = \sum_{j=0}^{t} h_a(A)\, h'_a(E)\, q\, l(j)\, p(j)\, A(t-j). \qquad (4.5)$$

The number of eggs appearing between times t and $t+1$ depends, as before, on the number and age of the adults present and also on the total egg density E. The terms $h_a(A)$ and $h'_a(E)$ (the subscript a indicates that these functions act on the adult stage) are density dependent functions which represent the proportionate reduction in daily fecundity due to adult or egg density and must take values in the range 0-1. A suitable formula for these functions is the density dependent model of Maynard Smith & Slatkin (1973),

$$h_a(A) = (1 + (aA)^b)^{-1}, \qquad (4.6)$$

$$h'_a(E) = (1 + (cE)^d)^{-1}. \qquad (4.7)$$

The parameters a and c are scaling constants which determine the densities at which adult or egg crowding causes a given proportionate reduction in fecundity. The parameters b and d determine the severity of the density dependence (see page 32), with the severity increasing as b (or d) increases from zero (no density dependence).

4.2.2 The larval population submodel

It is the object of this section to develop a model which predicts the changes due to development and mortality which occur in a cohort of individuals as it proceeds from entry into a given stage until it leaves that stage (a cohort is here taken to be a group of individuals entering a stage at the same time). The approach taken here is to construct a new model of a cohort life-table. The model is structured in such a way that it may be used for analysis as well as prediction,

and consequently parameters of the model may be directly estimated from data. The model will be developed in three steps. First, a cohort life-table model will be developed which predicts the changes which occur in a cohort due to development and density independent mortality. The model will then be extended to include density dependent mortality in the form of intrastage competition. Finally, provision will be made for interstage competition. The model is intended to apply to all the non-ovipositing stages of the two Callosobruchus species which includes the eggs, four larval instars, pupae and the pre-emergent adults. The model will be constructed using a time step of one day and will finally consist of a recursive relation which describes the size, stage-composition and age-structure of a population at time t as a function of those at time t-1.

The development of this submodel begins with the premise that the developmental period of an instar is not constant, but different individuals develop at different rates so that there is a distribution through time of individuals from a single cohort completing development of an instar. This distribution of the developmental period may be described by a probability distribution function f_i whose elements $f_i(j)$ specify the probability of an individual in stage i moulting to stage i+1 at age j (age is here measured from entry to instar i). These probabilities $f_i(j)$ may be interpreted as the proportion of individuals of an initial cohort $x_i(0)$ which moult to the next stage upon reaching age j so that the number of individuals moulting to stage i+1 between times t and t+1 (assuming for the moment that no mortality occurs) is described by

$$x_{i+1}(t) = x_i(0)\, f_i(t). \qquad (4.8)$$

The total number of individuals of the initial cohort $x_i(0)$ which have moulted to stage i+1 by time t, $X_{i+1}(t)$, is given by

$$X_{i+1}(t) = x_i(0) \sum_{j=0}^{t} f_i(j), \qquad (4.9)$$

and the total number of individuals remaining in stage i, $X_i(t)$, is

$$X_i(t) = x_i(0) \sum_{j=0}^{t} f_i(j) + x_i(0)$$

$$= x_i(0) \left(1 - \sum_{j=0}^{t} f_i(j)\right). \qquad (4.10)$$

The summation of the probability distribution f_i from zero to t in equations 4.9 and 4.10 is the value of the cumulative probability distribution $F_i(t)$,

$$F_i(t) = \sum_{j=0}^{t} f_i(j). \qquad (4.11)$$

The value $F_i(t)$ is the probability of an individual having moulted from stage i to stage i+1 before time t+1 (time is again measured from entry to stage i) and may be viewed as specifying the proportion of a cohort which has moulted to stage i+1 up to and including time t. Similarly, the value $1-F_i(t)$ gives the proportion of the cohort still present in stage i at time t. The total number of individuals present in stage i may be now represented as (substituting equation 4.11 into 4.10)

$$X_i(t) = x_i(0) \left(1 - F_i(t)\right). \qquad (4.12)$$

The distribution f_i gives the proportion of the initial number of individuals in a cohort which moult to the next stage at different ages. It is well appreciated, however, that the number of individuals in stage i of any cohort may be reduced not only through losses due to moulting but also through mortality. In order that this model of a cohort life-table may allow for mortality it is useful at this point to specify one further distribution G_i whiches gives the proportion of individuals in a cohort moulting to stage i+1 as a function of the number of the individuals of the cohort present in stage i, rather than as a function of the initial number of individuals in

the cohort. The elements $G_i(j)$ of this distribution specify the conditional probabilities of an individual moulting to stage i+1 at age j given that the individual was still in stage i at age $j-1$. The distribution G_i may be derived from the distributions f_i and F_i as follows. It is necessary to define the proportion of those individuals of a cohort still in stage i at time t-1 which moult to stage i+1 at time t. Recalling from equation 4.12 that the number of individuals present in stage i at time t-1 is

$$X_i(t-1) = x_i(0)\ (1 - F_i(t-1)) \qquad (4.13)$$

and that the number of individuals changing stages at time t is (from equation 4.8)

$$x_{i+1}(t) = x_i(0)\ f_i(t), \qquad (4.14)$$

then the required proportion of individuals changing stages is given by dividing equation 4.14 by 4.13,

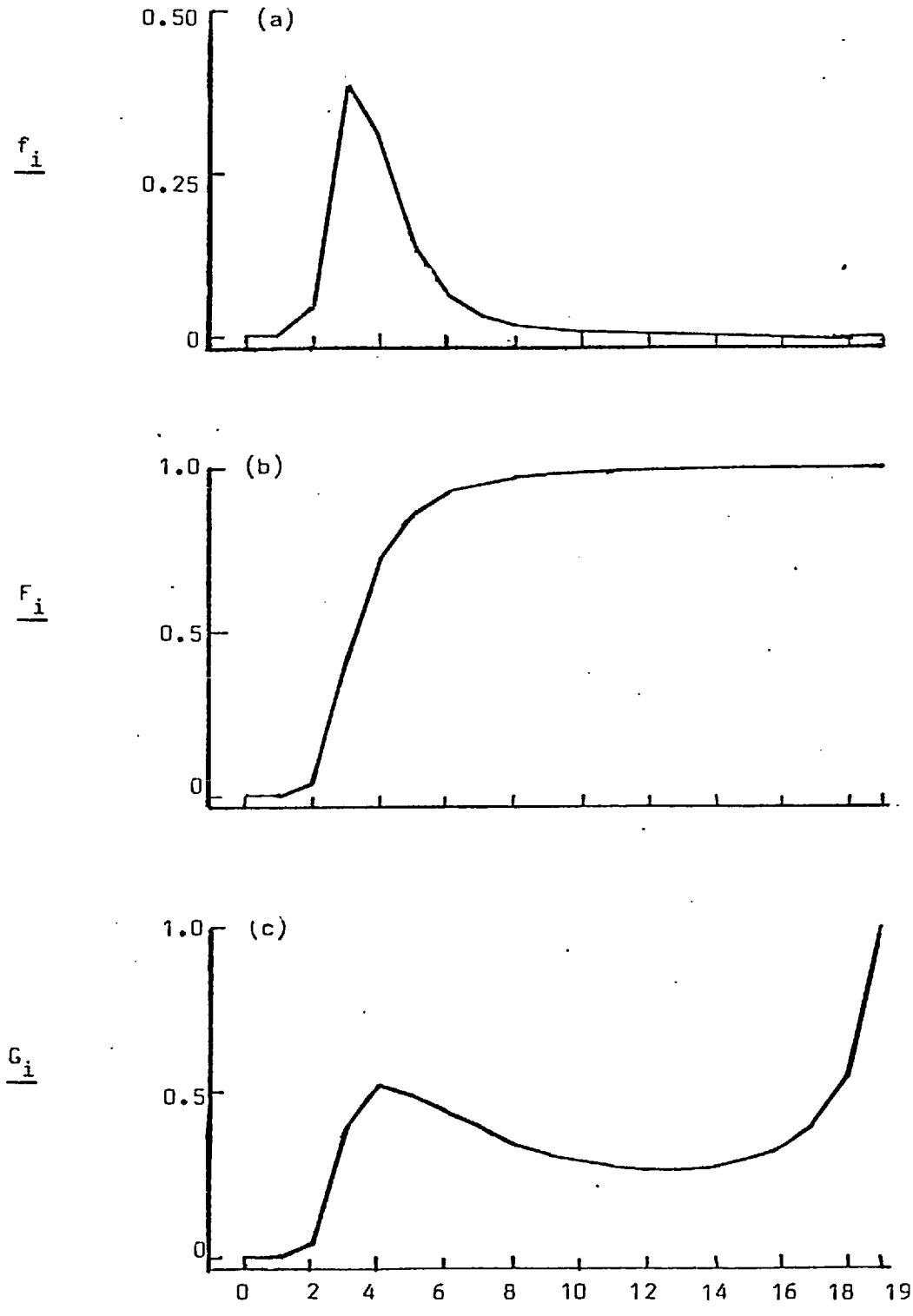
$$\frac{x_{i+1}(t)}{X_i(t-1)} = \frac{x_i(0)\ f_i(t)}{x_i(0)\ (1 - F_i(t-1))}. \qquad (4.15)$$

The ratio of equation 4.15 defines the value of $G_i(t)$,

$$G_i(t) = \frac{f_i(t)}{1 - F_i(t-1)}, \qquad (4.16)$$

and to complete the definition of the distribution it is only necessary to define $F_i(-1) = 0$ (the distribution F_i is normally truncated at zero) so that $G_i(0) = f_i(0)$. The relationships between the distributions f_i, F_i and G_i are shown for a hypothetical case in figure 4.1. The unimodal (singly peaked) developmental period distribution f_i in figure 4.1a gives rise to the sigmoid cumulative distribution F_i in figure 4.1b. These two distributions were compounded using equation 4.16 to give the conditional distribution of development G_i in figure 4.1c. In this example G_i has a complex shape, but when the

FIGURE 4.1 A positively skewed developmental period distribution $f_i(a)$ and the resulting distribution of cumulative development $F_i(b)$ and conditional distribution of development $G_i(c)$. The distributions shown arise form equation 4.22 where $\mu = 0.3$ and $\sigma = 0.1$. See text for discussion.


0.50
(a)
f_i
0.25
0
1.0
(b)
F_i
0.5
0
1.0
(c)
G_i
0.5
0
0 2 4 6 8 10 12 14 16 18 19

distribution f_i is narrower or symmetric the form of G_i is a sigmoid relationship similiar to that described by F_i.

The use of the distribution G_i permits development of a life-table analysis where the fate of any cohort may be described by two recursive relationships. Considering first the effects of development, the changes in a cohort are specified by the two equations

$$x_{i+1}(t) = G_i(t) \quad X_i(t-1), \tag{4.17}$$

$$X_i(t) = (1 - G_i(t)) \quad X_i(t-1). \tag{4.18}$$

Equation 4.17 gives the number of individuals of the cohort moulting to stage i+1 at time t, and equation 4.18 accounts for these losses in the current size of the cohort (since $G_i(t)$ is the proportion of individuals changing stages at time t, $1-G_i(t)$ is the proportion remaining in stage i). It is possible in this framework to consider additionally the effects of mortality on a cohort. The mortality will be assumed age-independent within a stage although it may differ between stages. This assumption is necessary if parameters are to be estimated from data since the age-dependent developmental period would obscure any age-dependent mortality; in other words the disappearance of individuals from a cohort may be due either to development or mortality, but only one of these processes may be assigned age-dependency during parameter estimation. A constant stage-specific daily survival s_i may be included in the model by modifying equation 4.18 to

$$X_i(t) = s_i(1 - G_i(t)) \quad X_i(t-1). \tag{4.19}$$

Equation 4.19 implies that those individuals remaining in stage i suffer a proportionate mortality of $1-s_i$ during the interval t to t+1. The individuals which have moulted to stage i+1 form a new cohort of individuals in that stage and now have age zero; they would be subject to a mortality of $1-s_{i+1}$ during the interval t to t+1.

Equations 4.17 and 4.19 complete the initial specification of the cohort life-table model which now accounts for the processes of development and density independent mortality. These equations may be used either in analysis or prediction by applying them to all the cohorts present in each stage at every time step. The model as now developed will be used later in the analysis of cohort life-tables for C. chinensis and C. maculatus.

The introduction of density dependent mortality into the life-table model follows the same lines as for density independent mortality. It is necessary, however, to make some assumptions about the relationship between density and developmental rate. The developmental rate may be independent of density, density dependent or inversely density dependent. We will see below that development in these species is nearly independent of density and the model will be based on that assumption. To include density dependent mortality in the model requires the simple addition of a stage specific function h_i which specifies the relation between density and proportionate daily survival. Equation 4.19 now becomes

$$X_i(t) = h_i(D_i(t))\ s_i(1 - G_i(t))\ X_i(t-1) \qquad (4.20)$$

where $D_i(t)$ is the density of competitors present during the interval t to $t+1$. In the case of intrastage density dependence, $D_i(t)$ is the density of individuals in stage i at time t after development for the time step has been completed, that is $D_i(t) = X_i(t-1)\ (1-G_i(t))$. Where there is interstage competition the value of $D_i(t)$ reflects the effective total density of competitors in all stages and may be represented by

$$D_i(t) = X_i(t-1)\ (1-G_i(t)) + \sum_{j \neq i} (\alpha_{ij}\ X_j(t-1)\ (1-G_j(t))) \qquad (4.21)$$

where the sum is over all stages and α_{ij} is a constant which specifies the density of stage j that causes a reduction in the proportionate

survival of stage i equivalent to that caused when the density of stage i is increased by one individual. The parameters α_{ij} are analagous to the interspecific competition coefficient of some two-species competition models (e.g. Lotka 1925; Volterra 1926; May 1974; Hassell & Comins 1976).

Although the inclusion of density dependence (equation 4.20) completes the development of the cohort life-table model it is necessary to specify formulae for the developmental distributions f_i and the density dependent functions h_i. A number of distributions have been used to describe the developmental period of insects. Although the normal (symetric) distribution has been used by Manly (1974) in the analysis of life-table data, a large amount of evidence indicates that developmental period in insects is positively skewed (see the review by Howe (1966) and also Stinner *et al.* (1975), Barfield, Sharpe & Bottrell (1977) and Sharpe *et al.* (1977)). Consequently, developmental periods have often been described by skewed probability distributions such as the gamma or log-normal distributions (Howe 1966), special Erlangian distributions (Ashford, Read & Vickers 1970) or the beta distribution (Stinner et al. 1975). In contrast to these empirical approaches, Sharpe *et al.* (1977) have described positively skewed developmental distributions by a model which arises from a relatively simple assumption. They assume that the developmental rate of individuals in a population is symetrically distributed about a mean value. Transforming a symetric distribution of developmental *rate* to developmental *time* or period results in a positively skewed distribution. The approach of Sharpe *et al.* is adopted here primarily because the distributions which arise may be defined by parameters with simple biological interpretations (in contrast to the other probability distributions mentioned above) and also because such

distributions have already been successfully used to describe insect development (Barfield, Sharpe & Bottrell 1977; Sharpe et al. 1977). The formulation used here is based on the assumption that the distribution of developmental rates of individuals in a population follows a normal distribution. This gives rise to a positively skewed distribution of developmental period whose elements are defined by

$$f_i(j) = (k\sigma\sqrt{2\pi})^{-1} \int_j^{j+1} \exp(-\tfrac{1}{2}((\tfrac{1}{t} - \mu_i) / \sigma_i)^2)\, dt. \quad (4.22)$$

The distribution is specified by the two parameters μ_i, the mean developmental rate of stage i, and σ_i^2, the variance of the developmental rate. The parameter k is a normalizing constant which ensures that the sum of $f_i(j)$ over the range of j required is unity. This formulation depicts a positively skewed distribution of developmental period such as that shown in figure 4.1a.

As before, an appropriate formula for the density dependent function h_i is the model of Maynard Smith & Slatkin (1973),

$$h_i(D_i) = (1 + (a_i D_i)^{b_i})^{-1}. \quad (4.23)$$

The parameter a_i is a scaling constant and b_i determines the severity of the density dependence as discussed on page 32 . However, during the analysis of data there was usually insufficient mortality in any stage to permit satisfactory estimation of both parameters. Consequently the parameter b_i was set equal to unity for all stages, and the simplified model

$$h_i(D_i) = (1 + a_i D_i)^{-1} \quad (4.24)$$

was used. As the parameter a_i in equation 4.24 increases from zero (no density dependence) the mortality at a given density increases. Since the parameter b_i has been set equal to unity, the simplified model only describes contest competition, but this restriction is of little importance for Callosobruchus species whose larval competition is clearly of this type (see chapter 3). Finally, where there is no

intrastage density dependence (a_i=0), difficulties will arise in the analysis of interstage competition since, irrespective of the total density of competitors defined by equation 4.21, a zero value of a_i in equation 4.24 will result in zero predicted mortality. To overcome this, equation 4.24 was modified for the analysis of interstage competition to

$$h_i(D_i) = (1 + D_i)^{-1}, \qquad (4.25a)$$

$$D_i = a_i \; X_i(t-1) \; (1 - G_i(t)) + \sum_{j \neq i} (\alpha_{ij} \; X_j(t-1) \; (1 - G_j(t))) \qquad (4.25b)$$

Equation 4.25 is precisely the same as equation 4.24 when D_i is defined by equation 4.21 with the exception that the density of competitors is not subject to the scale effects of a_i. Consequently the parameters α_{ij} no longer represent the relationship between stage j and stage i per individual of stage i but rather reflect the effective per capita density of stage j on an absolute scale. The values for the α_{ij}'s arising from equation 4.25 will be smaller by a factor of $1/a_i$ than those expected from equation 4.21. This formulation (equation 4.25) of interstage competition is more nearly analagous to the usual matrix models of multispecies competition than that of equation 4.21.

There is one final process, that of egg mortality, which requires consideration before a complete representation of the life histories of the Callosobruchus species being studied is possible. Natural egg infertility is easily included in the model by multiplying every new cohort of eggs by a constant which reflects the proportion of eggs laid which are fertile. There is, however, an additional mortality in these species which is clearly related to adult density (see page 77) and appears to be a result of mechanical damage to the eggs by the adults. If there is a daily rate of fatal encounters m between adults and eggs which is independent of adult age and sex,

the total number of encounters between A adults and E eggs in the interval t to t+1 is mAE. It was found that the rate m appeared dependent on adult density and a simple power model was used to describe this relationship, $m \equiv mA^{Z-1}$. The total number of encounters per egg is now mA^{Z}, and these encounters may be distributed randomly among the eggs present so that the proportionate daily mortality of eggs is

$$1 - \exp(-mA^{Z}). \qquad (4.26)$$

The total number of eggs surviving the interval t to t+1 is given by

$$E(t)\ \exp(-m(A(t))^{Z}) \qquad (4.27)$$

where E(t) and A(t) are the number of live eggs and adults at time t.

4.3 Quantifying the parameters in the model

This section presents the experimental results and analyses that permit quantification of the parameters required by the oviposition and larval submodels. It begins with two discussions on the experimental procedures and the numerical techniques used for parameter estimation. The results of the experiments and analyses are then presented and discussed.

In each of these subsections material relevant to the oviposition submodel will be presented before material on larval development and mortality.

4.3.1 Experimental materials and methods

The stocks of C. chinensis, C. maculatus and cowpea used here were the same as those used previously. All experiments were performed at 30°C and 70% relative humidity.

Three oviposition experiments were performed. The adult life-

span and daily oviposition were firstly determined by isolating 0-2½ hour old pairs of adults with 3.7g of cowpea in plastic dishes 3.5 cm high and 4.0cm in diameter. The dishes were covered with muslin held in place by a plastic lid in which a large hole was cut for ventilation. The cowpeas were replaced daily and the number of eggs deposited by each pair and the number of living adults of each sex were scored. The experiment was continued until all the adults had died. Approximately 30 pairs of adults were used for each species and any pair which did not oviposit was excluded from any analysis. In a second experiment the effect of egg density on fecundity was determined. Varying numbers of adults were placed with about 500 beans in each of five large plastic boxes (9cm high, 15.5cm wide and 27.5cm long); this provided stocks of beans which contained varying numbers of eggs. After 24 hours (48 hours in the C. maculatus chamber with the most adults) the adults were removed and 20 sets of 3.7g of beans were taken from each chamber and placed in small plastic dishes. The total number of eggs on the beans in each dish were recorded and a 0-2½ hour old pair of adults was placed with each set of beans. An additional 20 pairs of adults were each isolated with 3.7g of beans on which no eggs had been laid. After the adults had died the total number of eggs on each set of beans was again scored and the fecundities of the adults were recorded as the difference between this count and the original one. Finally, the effect of adult density on fecundity was determined by isolating varying numbers (1,5,20,40,60,80,100 or 120) of pairs of 0-2½ hour old adults with 3.7g of beans and, after the adults had died, scoring the number of total and hatched eggs. The results of this experiment have also been discussed in chapter 3.

Two experiments concerning larval development and mortality were performed. The first dealt with the effects of density on

development and mortality due to interstage competition. Varying numbers of adults were isolated with cowpeas in large plastic boxes for 24 hours. Four of these chambers were set up with C. chinensis and three with C. maculatus. A number of beans were taken daily from each chamber, the number of hatched eggs on each bean was recorded and each bean was then dissected in order to score the number and stage of the living individuals present. On each day at least ten beans were sampled from each chamber and from low density chambers sufficient beans were dissected so that a minimum of 50 living individuals were recorded per chamber. Sampling was continued until all the observed survivors were in the emerged adult stage - 26 days for C. chinensis and 31 days for C. maculatus. These data provided a record of the number of individuals in each stage each day over a range of hatched egg densities and were used to construct life-tables for these species. The second experiment was designed to determine what effects interstage competition had on stage-specific mortalities. For this experiment a single 24-hour oviposition chamber was set up with a large number of beans. At suitable later times approximately 20 beans were taken from this stock, the number of hatched eggs on each bean was recorded and the beans were again subjected to 24 hours of oviposition. There were thus two cohorts of individuals started at different times in the beans, and by later dissecting the beans the number of survivors in the two cohorts were scored (the initial number of individuals in the second cohort was determined by counting the total hatched eggs on each bean at the time of dissection and subtracting the initial count of hatched eggs). Fifteen combinations of cohorts were set up corresponding to all the possible interstage combinations of first, second, third and fourth instar larvae, pupae and pre-emergent adults. The details of the timing of the second oviposition and scoring for this experiment are

given later.

4.3.2 The estimation of parameters

It is easily appreciated that the formulations used in the development of the simulation model do not lend themselves to straightforward statistical analysis, and the methods used here for parameter estimation require at least a brief discussion. Some further details about the computer programmes used here may be found in appendix C.

The general problem of estimating parameters of models has been treated in a variety of textbooks (see, for example, Kendall & Stuart 1967). Two approaches are generally available, that of maximum likelyhood estimation or a family of empirical approaches. The most widespread of these empirical approaches is to treat the parameters of a model as variables and find the values which minimize the sum of squared deviations between model predictions and observed results (the residuals). This technique, known as "least-squares" estimation, has the property of providing maximum likelyhood parameter estimates when the model is linear in the parameters. When the model is not linear in the parameters, the exact relation between least-squares parameter estimates and maximum likelyhood parameter estimates cannot usually be specified. However, in nonlinear models for which maximum likelyhood estimation is not available the least squares technique is often employed. For the models used here methods for maximum likelyhood estimation have not been developed and all the parameter estimates have been found by least-squares techniques. The algorithm used for fitting the multi-parameter models was that of Powell (1968), and worked well in all the applications required. When a single-parameter model was fitted to data a quadratic approximation algorithm was used to find the minimum residual sum of squares (Powell 1964, Murray 1972).

It is useful when fitting models to data to be able to describe the relative contribution a parameter makes towards description of the data; that is, to determine the significance of a parameter with respect to a particular data set. As discussed by Draper & Smith(1966), there are a variety of ways of accomplishing this in least-squares analysis, but only one method was found suitable for the models developed here. This method is based on an application of the "extra sum of squares" principle discussed by Draper & Smith (1966), and involves examining the reduction in the residual sum of squares achieved by adding parameters to a model. Consider, for example, an initial model of p parameters fitted to a sample of n data points which results in a residual sum of squares S_0. The addition to this simple model of q more parameters will result in a smaller residual sum of squares S_1. The hypothesis that the additional q parameters have not made a significant reduction in the residual sum of squares may be tested by comparing the ratio

$$\frac{(S_0 - S_1) / q}{S_1 / (n-p-q)} \qquad (4.28)$$

to the value of the F distribution with q and $n-p-q$ degrees of freedom. This test, which considers the significance of all q parameters together, is exact in analyses with linear models where errors are normally distributed and independent. In the case of nonlinear models, the ratio of equation 4.28 may be useful as a guide to significance. In addition to this test the importance of a parameter may be judged by examining the plots of residuals before and after the addition of the parameter (Draper & Smith 1966). Although exact tests are again not available in the nonlinear case, examination of such plots may be useful in indicating whether the addition of a parameter has corrected any deviations between the model and the data.

The oviposition submodel of equation 4.5 posed few problems when fitted to the data presented below. The parameters were estimated by a stepwise consideration of the functions in the submodel. Initially the mean and the variance of the adult life-span were estimated for both males and females from data from the first oviposition experiment. Since only one life-span distribution is required in the model the female life span was used during further parameter estimation (it will be seen, however, that the life spans of the two sexes were similar). The age specific fecundities of the adults were then specified as the mean observed number of eggs laid per day. This provided a model which predicts the total number of eggs laid by a cohort of individuals in a renewed, uncrowded environment. The parameters of the density dependent function $\underline{h'_a(E)}$ (egg crowding) were then estimated by fitting the model to the data from the second experiment. Finally, the response to adult crowding was quantified by adding the function $\underline{h_a(A)}$ to the model and fitting it to the data on total eggs laid at different adult densities obtained from the third experiment. In fitting the two functions $\underline{h_a}$ and $\underline{h'_a}$, the signifigances of the parameters were examined by the methods discussed above.

Quantifying parameters for the larval submodel (equations 4.17 and 4.20) required slightly more complex procedures. The completed life-table model (excluding for the moment interstage interactions) has provision for five parameters (a mean developmental rate and its variance, daily survival and two density dependent parameters) for each of seven instars. It was possible, then, to estimate 35 life-table parameters simultaneously from the more than 1000 data points available, but such an approach proved to be impractical. To overcome this problem the life-table parameters were estimated in two stages:

an initial analysis of density independent cohort life-table data provided estimates for the developmental and density independent mortality parameters, and a second analysis was performed to estimate the density dependent mortality parameters. In the initial analysis it was necessary to average data from the daily samples of survivors from beans with few hatched eggs in order to provide a density independent life-table. Parameters were estimated from this life-table by first estimating the mean rate and variance in equation 4.22 for development of eggs to first instar larvae (egg mortality will be considered later). This provided a prediction of the number of daily recruits (cohorts) to the first instar stage and this predicted recruitment was used together with the observed daily record of the numbers of first instar larvae present in order to estimate the mean and variance of the developmental rate and daily survival of first instar larvae. The resulting fitted model provided a prediction of the cohorts recruited to the second instar stage and the analysis was repeated for the second instar and subsequently in this stepwise manner for all the other stages. This method worked well and provided reasonable predictions of the parameters. However, occasionally the estimate of daily survival for a particular instar would exceed unity indicating perhaps an overestimate of the mortality in the previous stage. These errors, presumably due to the nature of the sampling regime, were overcome by a simple refinement. Whenever the problem arose, the parameters for development and survival for the instar were estimated again simultaneously with the parameters for the previous instar (i.e. six parameters were estimated for the two instars together). This usually provided acceptable parameter estimates, but if the daily survival estimate was again too large it was fixed arbitrarily at unity and the developmental parameters only were

reestimated for that instar together with the development and mortality parameters for the previous instar. The test for significance outlined above could not be applied to the estimates of the mean and variance of the developmental rate as there was no residual sum of squares from an *a priori* model to use in the test. Due to the nature of the data the test was also insensitive to the addition to the model of the parameter for daily survival. A consideration of the data, however, clearly shows some mortality between the first instar larval and adult stages, so whenever the survival parameter was estimated at less than unity its value was accepted as indicating mortality in the stage and was included in the model.

The analysis of stage specific density dependent mortality was accomplished by considering data collected from all the oviposition chambers in the first larval experiment. This provided information on survival over a range of hatched egg densities per bean. Data were considered from six sampling days which corresponded to the periods of maximum presence of the six immature stages (the details are given later). The analysis was accomplished in a stepwise manner where parameters for the first instar were estimated first, followed by those for the second instar and so on. At each step in the analysis the function h_i (equation 4.23) was included in the life-table model (equation 4.20) and the value of the parameter a_i was found (with b_i fixed at unity) which best predicted the total number of survivors on the appropriate day. The significance of the estimate of a_i was tested as described above (equation 4.28), where the initial sum of squares S_0 was found when the model did not include density dependence and the sum of squares S_1 was that associated with the estimate of a_i. If the estimate of a_i was judged significant, then the two parameter model (where both a_i and b_i

were allowed to vary) was fitted to the data. The significance of the estimate of b_i was tested in the same way by considering the new residual sum of squares and the sum of squares obtained when b_i was fixed at unity. If the estimate of b_i was not significant then the original estimate of a_i was used in the one-parameter model of equation 4.24 for that particular instar. This procedure was repeated for all the stages. It should be noted that if parameter estimates for any stage were significant they were included in the life-table model during the analysis of all subsequent stages. In this way the parameters estimated for h_i only reflect density dependence occurring between the sampling days for stages i-1 and i.

To complete the analysis required by the larval population sub-model it only remained to estimate the interstage competition coefficients α_{ij}. A stepwise procedure was again adopted where the data for the interaction between first and second instar larvae were considered first, providing estimates of α_{12} and α_{21}. The data for third and first instar interactions were then considered, followed by third and second instar data, fourth and first instar data and so on. The parameters associated with each interaction were estimated by comparing the number of survivors of both initial cohorts predicted by the model on the sampling day with the observed number of survivors. During the analysis of each data set the two relevant parameters α_{ij} and α_{ji} were first estimated independently and their significance was examined by comparing the residual sums of squares when the model either included or excluded the parameter. If both parameters were significant they were reestimated simultaneously. The significant estimates of the parameters of the early instars were included in the model when estimating the competition coefficients of later instars; for example, when the effect of pupae on second instar larvae was

being considered, the model included the previously estimated effects of fourth instar larvae on firsts. Since the effects of fourths on firsts is to reduce considerably the survival of the second cohort, only a few individuals survive to second instar. This results in very little interaction between the cohorts during the pupal and second instar stages, and consequently the estimated competition coefficients between these two stages were small and not statistically significant. These estimates may not accurately represent the quantitative competitive relationships between the stages, but this is unlikely to be important in describing the outcome of competition in Callosobruchus since their life histories do not permit the association of (for example) seconds and pupae without prior competition between firsts and fourths.

4.3.3 Results

In this section, the results concerned with the oviposition submodel are considered first and then those with the larval population submodel.

The results of fitting the truncated normal distribution (equation 4.3) to the data on adult life-span are shown in figure 4.2, and the fitted parameter values for the life-span means and variances are given in table 4.1. The model described each of the data sets well. Adults of C. chinensis were slightly longer lived than adults of C. maculatus, and in both species the males were slightly longer lived than the females. The life-span of C. chinensis was more variable than that of C. maculatus. The estimated variances for males and females were similiar in C. chinensis, but higher for males in C. maculatus.

The oviposition record of C. chinensis (figure 4.3a) showed maximum oviposition on the third day after emergence which is in

FIGURE 4.2 The observed and predicted (from equation 4.3) distribution of adult life-span in (a) C. chinensis and (b) C. maculatus. Closed circles are for males; open circles are for females.

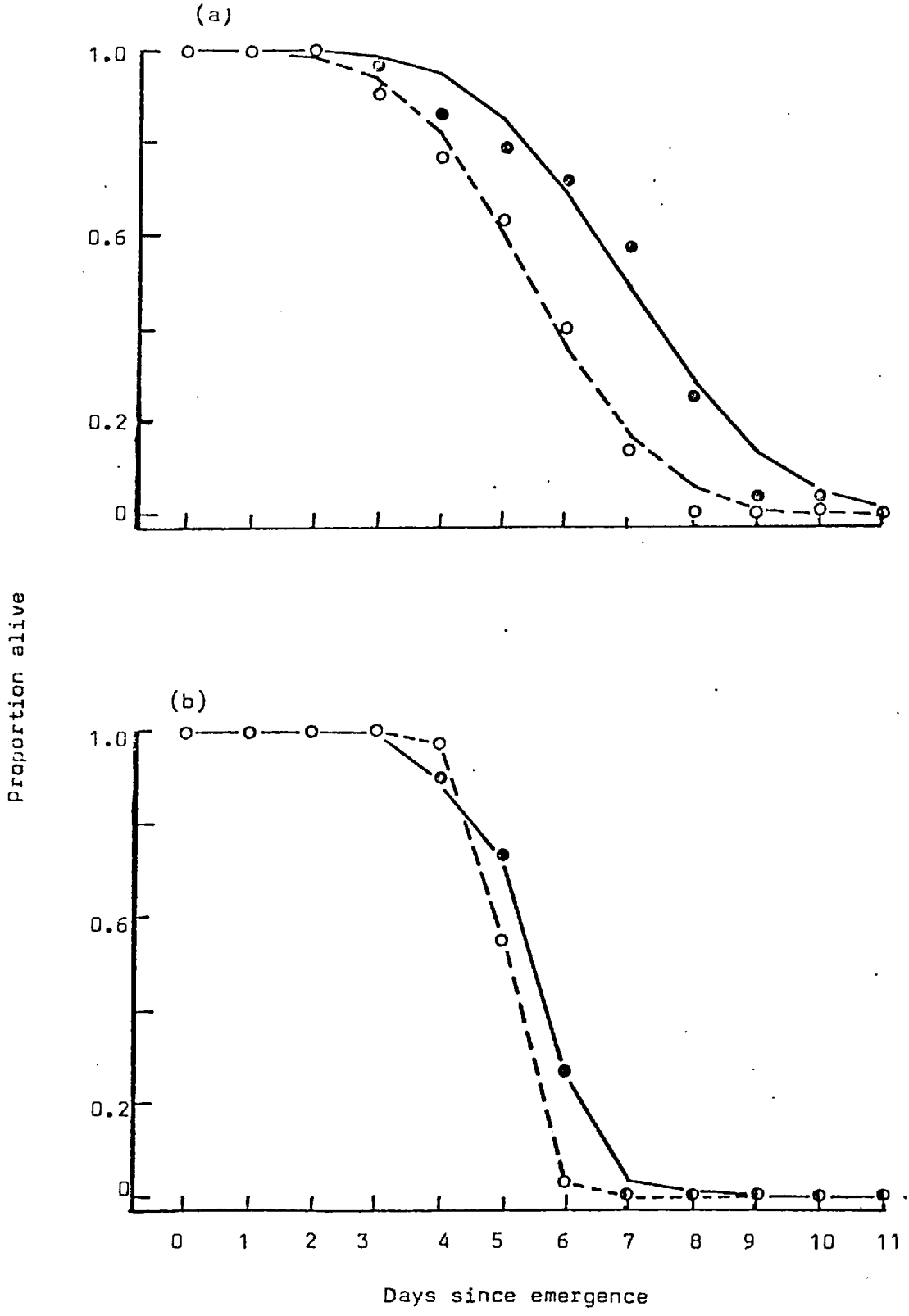

(a)
1.0
0.6
0.2
0
(b)
1.0
0.6
0.2
0
Proportion alive
0 1 2 3 4 5 6 7 8 9 10 11
Days since emergence

TABLE 4.1 The estimates of the parameters for the oviposition submodel for (a) C. chinensis and (b) C. maculatus.

(a) C. chinensis

adult life-span	mean, μ	$\sqrt{\text{variance}}$, σ
males	6.9684	1.8457
females	5.4617	1.6115

density dependence	a or c	b or d	n	F-value
$h'(E)$	0.033080	0.34480	119	250.34, $p<.001$
$h(A)$	0.0028188	1.6681	50	166.29, $p<.001$

egg mortality	m	Z	n	F-value
	3.2278×10^{-4}	1.3585	61	2464.9, $p<.001$

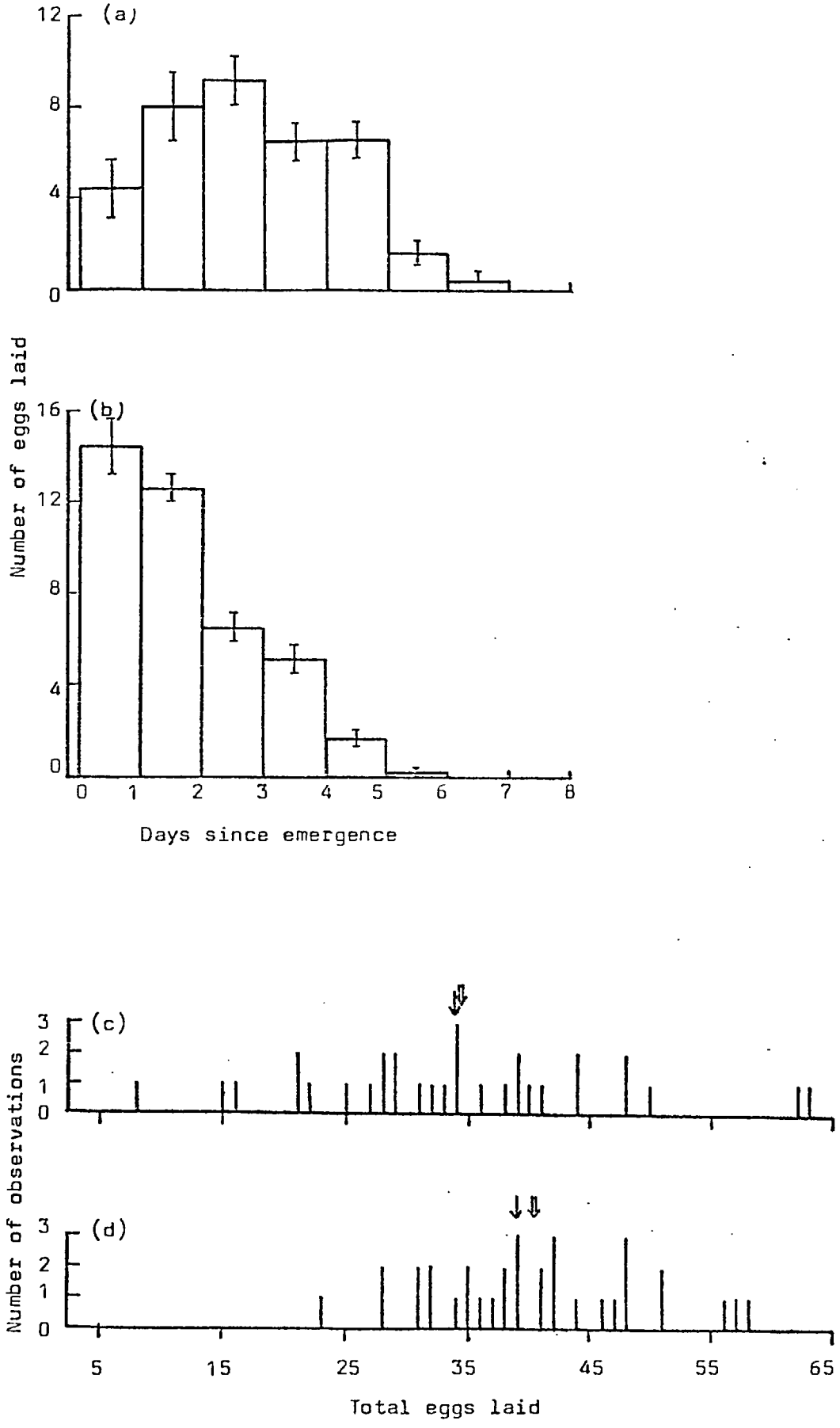
(b) C. maculatus

adult life-span	mean, μ	$\sqrt{\text{variance}}$, σ
males	5.5225	0.84674
females	5.1083	0.52279

density dependence	a or c	b or d	n	F-value
$h'(E)$	0.0051901	1.4969	111	107.10, $p<.001$
$h(A)$	0.022760	1.1639	61	1565.6, $p<.001$

egg mortality	m	Z	n	F-value
	3.7081×10^{-4}	1.3622	50	7190.4, $p<.001$

FIGURE 4.3 The daily oviposition records of (a) C. chinensis and (b) C. maculatus and the observed distribution of total fecundities of (c) C. chinensis and (d) C. maculatus. In (a) and (b) the vertical lines at the centre of each bar bar give the standard error of the mean for that day. In (c) and (d) the single arrow indicates the mode of the distribution and the double arrow indicates the mean.

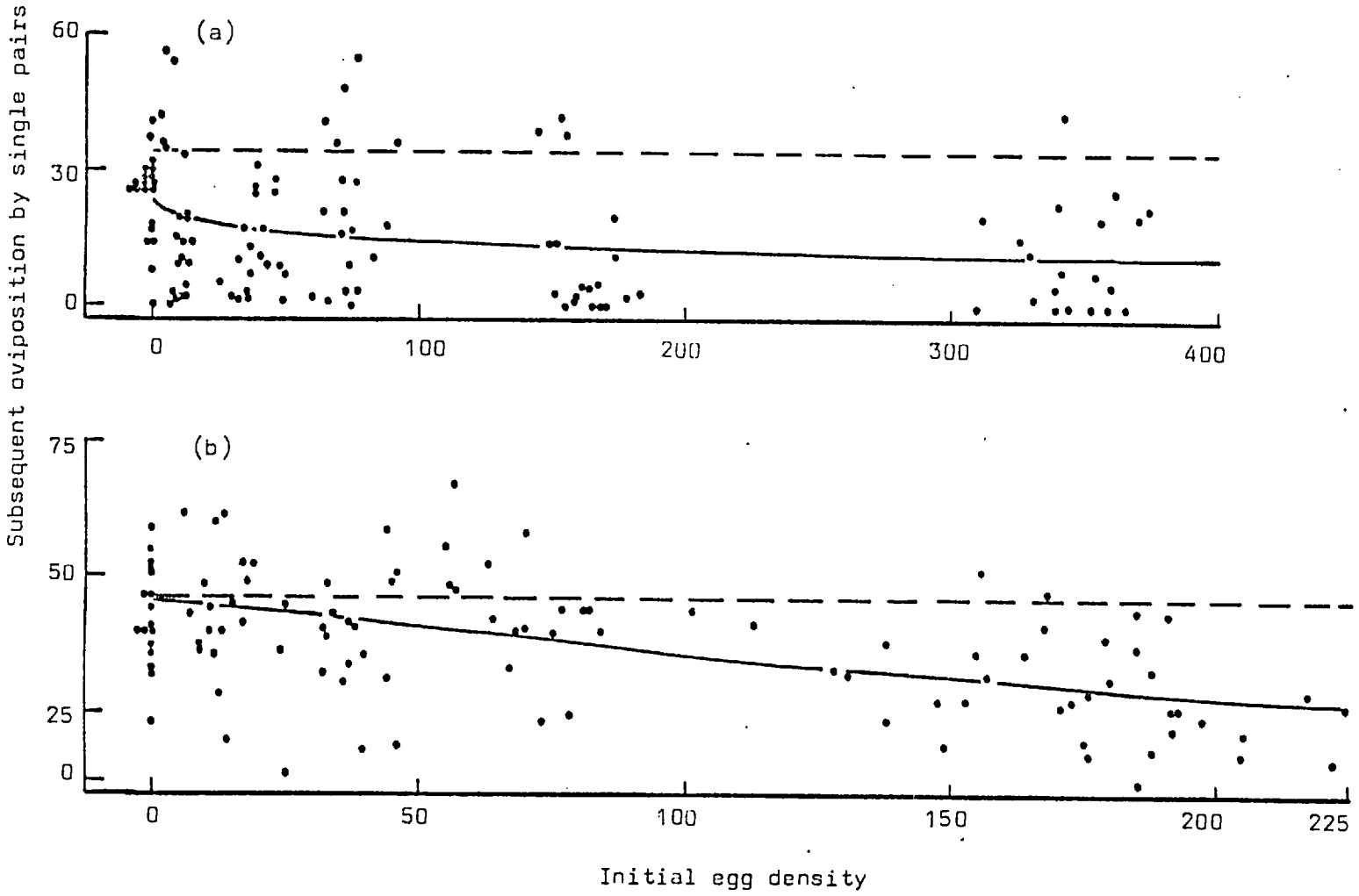

(a)
12
8
4
0
(b)
16
12
8
4
0
0 1 2 3 4 5 6 7 8
Number of eggs laid
Days since emergence
(c)
3
2
1
0
(d)
3
2
1
0
5 15 25 35 45 55 65
Number of observations
Total eggs laid

contrast to the findings of Howe & Currie (1964) who reported greatest oviposition on the first day. A number of the C. chinensis pairs did not lay any eggs for one or two days. This preoviposition period has not been reported as a usual occurrence in this species, so a further oviposition experiment of 30 replicates was performed where one female and two males were used (instead of a single pair of adults) to determine whether the preoviposition period was possibly due to unsuccessful mating. In this experiment, however, all of the females had a preoviposition period of at least one day and it was concluded that this occasional tardiness in oviposition was simply a feature of the strain of C. chinensis being studied. The oviposition record of C. maculatus (figure 4.3b) showed greatest oviposition on the first day after emergence which agrees with the finding of Howe & Currie (1964). The distributions of observed total fecundities for C. chinensis and C. maculatus are shown in figures 4.3c and 4.3d, respectively. The mean observed fecundity of C. maculatus (40.52 $\pm$ 8.16 (s.d.) eggs) was higher than that of C. chinensis (34.23 $\pm$ 12.54 eggs). The variance and range of observed fecundities for C. chinensis was larger than that for C. maculatus.

The results of the experiments on reduction of fecundity in response to egg density are shown in figure 4.4a for C. chinensis and 4.4b for C. maculatus. Although the data show considerable variation it is clear that the fitted models (from equation 4.7, solid lines in figure 4.4) provided a better description of the results than the models without density dependence (broken lines). The estimated values of the parameters for both species were significant ($p < .001$) and are given in table 4.1.

The relationships between adult density and total fecundity for C. chinensis and C. maculatus are shown as hollow circles in figure

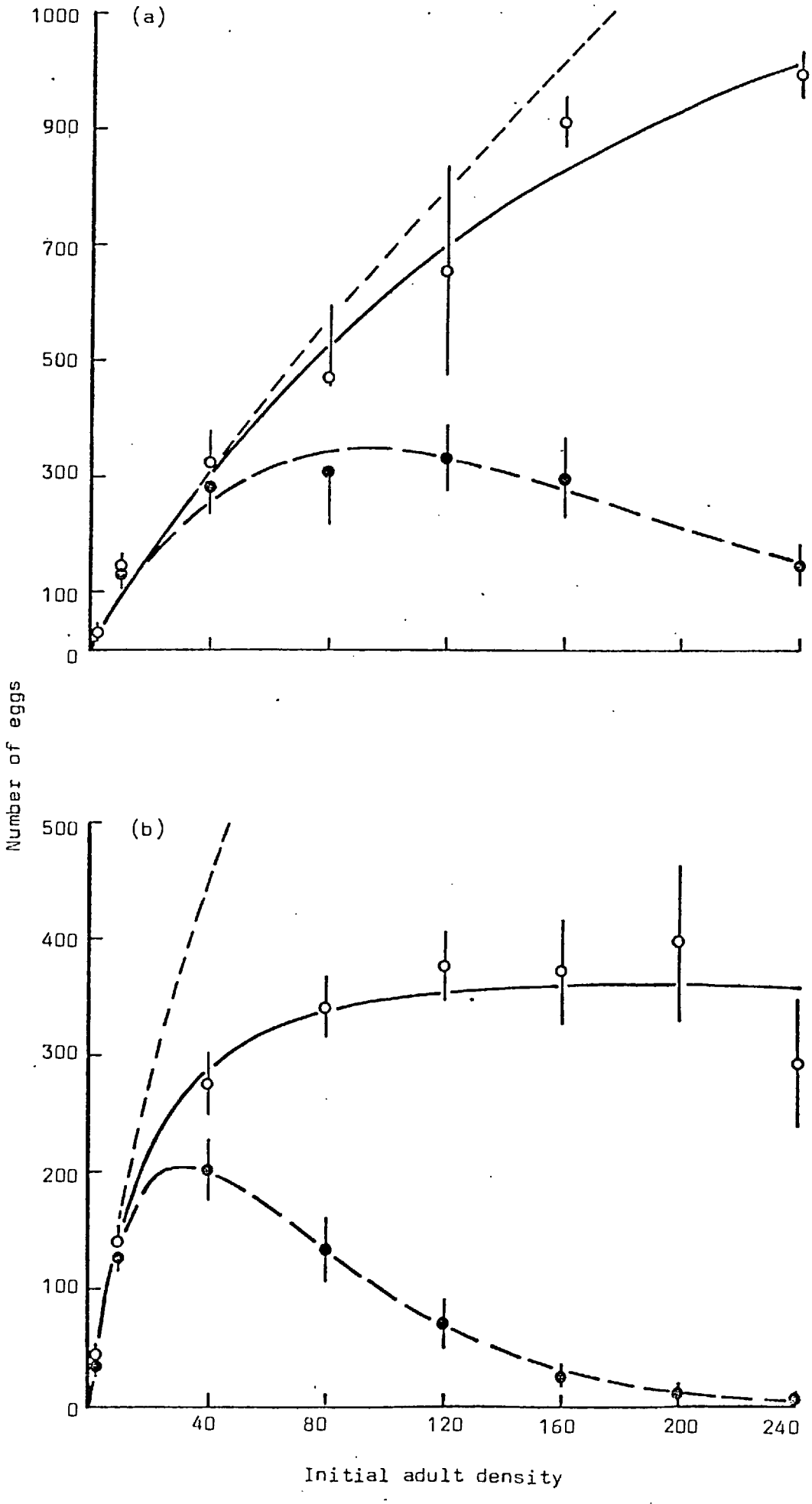
FIGURE 4.4 The fecundity of single pairs of adults when isolated with beans already containing eggs. (a) *C. chinensis*. (b) *C. maculatus*. The broken line indicates the predictions of the model when no dependence on egg density is considered; the solid line shows the fitted model including density dependence (equation 4.5). The fitted parameters are given in table 4.1.


Subsequent oviposition by single pairs
(a)
60
30
0
0
100
200
300
400
(b)
75
50
25
0
0
50
100
150
200
225
Initial egg density

4.5a and 4.5b. The light broken lines in figure 4.5 give the predicted total fecundity of the oviposition submodel when only a response to egg density is included; the nonlinear increase in total fecundity depicted by these lines is caused by the response of the adults to the accumulating density of eggs. These predictions of total eggs laid are clearly improved by the addition of a response to adult density (equation 4.6) as is shown by the solid lines in figure 4.4. These fitted models described the data well; the estimated values of the parameters were significant for both species ($p < .001$) and are given in table 4.1.

Although considering density dependence in the oviposition submodel complates the parameter estimation, it is convenient before proceding to the larval submodel to consider the processes effecting egg mortality. The proportionate egg fertility in the species was estimated as the average observed proportionate fertility of eggs laid by isolated pairs of adults. The data were averaged after first transforming proportionate fertility to angles for each pair, and this resulted in an estimated mean fertility of 98.9% for C. chinensis (data from 12 pairs) and 95.5% for C. maculatus (data from 11 pairs, one pair laying only 15 eggs of which six hatched was excluded). These estimated egg fertilities were significantly different from 100% at the 0.01 and 0.005 per cent level, respectively and were included in the model. The additional egg mortality associated in these species with increasing adult density was modelled by the egg mortality function of equation 4.27, and the fitted models provided a good description of the data on the number of hatched eggs occurring at various adult densities (heavy broken lines and solid circles in figure 4.5). The estimated parameter values for both species were significant ($p < .001$) and are given in table 4.1. During parameter

FIGURE 4.5 The number of total (hollow circles) and hatched (solid circles) eggs at different densities of (a) *C. chinensis* and (b) *C. maculatus*. The light broken line is the prediction of total fecundity when no dependence on adult density is included in the model; the solid line is the fitted model of equation 4.5 including adult density dependence. The heavy broken line gives the predicted number of hatched eggs arising from the fitted egg mortality function. The estimated parameters are given for all four fitted models in table 4.5. Data given as mean ± standard deviation


(a)
1000
900
700
500
300
100
0
(b)
500
400
300
200
100
0
40
80
120
160
200
240
Number of eggs
Initial adult density

estimation the parameter Z was initially set equal to unity and only the parameter m was allowed to vary; this provided a residual sum of squares against which the addition of the parameter Z as a variable could be tested. In both species the addition of this parameter Z caused a significant reduction in the residual sum of squares with $p < .01$ for C. chinensis and $p < .001$ for C. maculatus.

The first step in quantifying the parameters of the larval population submodel was to construct a density independent cohort life-table for both species. In order to ensure that the life-table data would not be influenced by density, all of the data collected during the daily samples of the first larval experiment were grouped according to the number of hatched eggs per bean. The total number of observed hatched eggs and the total number of survivors were pooled for all the sampling days for each hatched egg density and the overall proportionate survival at each density was recorded. This information is given for both species in table 4.2 for beans with six or fewer hatched eggs. It was concluded, after considering the per cent survival and cumulative per cent survival at successive densities, that data from beans with five and fewer hatched eggs for C. chinensis and four and fewer hatched eggs for C. maculatus would provide information suitable for preparing density-independent cohort life-tables. This provided a sample of over 1600 hatched eggs from 21 sampling days for C. chinensis, or approximately 70 eggs per day, and a sample of over 900 hatched eggs or 35 eggs per day from 26 sampling days for C. maculatus.

The life-tables for C. chinensis (table 4.3) and C. maculatus (table 4.4) were constructed by pooling the data from all the low density beans on a given day. The observed number of survivors present in each stage is given as a percentage of the number of hatched eggs observed on each day. The data for days one to five (before all the

TABLE 4.2 The observed mortalities in beans with various numbers of hatched eggs (pooled from all sampling days) for (a) C. chinensis and (b) C. maculatus. The data selected for construction of density independent cohort life-tables were based on beans with five or fewer hatched eggs for C. chinensis and four or fewer eggs for C. maculatus.

no. of hatched eggs per bean	1	2	3	4	5	6
			(a) C. chinensis			
Total observed hatched eggs	102	314	453	400	360	270
Total observed survivors	100	302	433	379	338	242
Per cent survival	98.0	96.2	95.6	94.8	93.9	89.6
Cumulative per cent survival	98.0	96.6	96.1	95.7	95.3	94.5
			(b) C. maculatus			
Total observed hatched eggs	153	258	264	228	155	216
Total observed survivors	151	231	240	198	128	177
Per cent survival	98.7	89.5	90.9	86.8	82.6	81.9
Cumulative per cent survival	98.7	92.9	92.1	90.8	89.6	88.3

TABLE 4.3 *C. chinensis* life-table data (per 100 hatched eggs).

Day	Eggs	1°	2°	3°	4°	Pupae	Adults in Pea	Emerged Adults	Total
1	100.00								100.00
2	100.00								100.00
3	100.00								100.00
4	59.00	41.00							100.00
5		96.77							96.77
6		91.78							91.78
7		23.08	71.79						94.87
8		4.84	74.19	17.74					96.77
9		1.05	57.89	40.00					98.94
10		1.85	3.70	89.81	.93				96.29
11			4.76	41.67	48.81				95.24
12			.00	3.53	90.59				94.12
13			1.23	.00	96.30				97.53
14				.00	100.00				100.00
15				1,16	82.56	15.12			98.84
16					37.68	57.97			95.65
17					10.61	74.24			84.85
18					10.47	81.40		1.16	93.03
19					2.08	70.83	18.75	.00	91.66
20						22.62	72.62	1.19	96.43
21						8.22	75.34	16.44	100.00
22						4.82	38.55	53.01	96.38
23							12.68	85.92	98.50
24							8.51	91.49	100.00
25							1.96	88.24	90.20
26								88.41	88.41

TABLE 4.4 *C. maculatus* life-table data(per 100 hatched eggs).

Day	Eggs	1°	2°	3°	4°	Pupae	Adults in pea	Emerged Adults	Total
1	100.00								100.00
2	100.00								100.00
3	100.00								100.00
4	100.00								100.00
5		100.00							100.00
6		94.12							94.12
7		88.00							88.00
8		54.76	42.86						97.62
9		2.63	94.74						97.37
10		6.12	83.67	10.20					99.99
11		.00	23.53	73.53					97.06
12		3.13	3.13	90.63					96.89
13				57.14	28.57				85.71
14				8.16	79.59				87.75
15				3.45	86.21				89.66
16					89.66				89.66
17					88.46	3.85			92.31
18					36.00	52.00			88.00
19					22.22	55.56			77.78
20					7.41	88.89			96.30
21					2.70	72.97	2.70		78.37
22					.00	48.28	37.93		86.21
23					.00	20.45	56.82	6.89	84.16
24					2.78	8.33	52.78	19.44	83.33
25					.00	2.94	35.29	52.94	91.17
26					3.23	3.23	9.68	77.42	93.36
27						.00	9.38	81.25	90.63
28						.00	2.38	85.71	88.09
29						.00	4.17	83.33	87.50
30						.00	4.00	88.00	92.00
31						4.00		84.00	88.00

eggs had hatched) represent a cohort of 100 live eggs and no egg mortality considered here. The total numbers of individuals observed each day are also given in tables 4.3 and 4.4, from which we see that the number of individuals present on successive days does not always remain constant or decrease (as would be the case if individuals from a single cohort were observed throughout their life), but occasionally increases. This is an artifact of the sampling programme where the fate of a single cohort is being approximated by the average fate of many cohorts undergoing sequentially destructive sampling. However, this did not cause any problems when estimating the life-table parameters so no smoothing of the data was necessary, in contrast to Sokal & Bryant's (1967) life-table analysis for the house fly.

The life-table model of equations 4.17 and 4.19 was fitted to the data of tables 4.3 and 4.4 by the method discussed on page 123 and the results of these analyses are presented in table 4.5. In both species the estimated mean developmental rates of the egg, fourth instar larval and pupal stages were lower than those of the other stages. The developmental rates of the first instar larval and pupal stages were slightly lower in C. maculatus than in C. chinensis although the developmental rates of the other stages were similar in the two species. The estimated variances of the development rates were small for all stages of both species. This is partly a reflection of the rapid development of these species in the experimental conditions used and also indicates that a sampling interval of less than one day might have been useful in determining the parameter values more accurately. In two cases, the third instar larval stage of C. chinensis and the egg stage of C. maculatus, the estimated variance is sufficiently small that the predicted distribution of development occurs entirely

TABLE 4.5 The estimates of life-table parameters from the analysis of the data in tables 4.3 and 4.4.

Instar	Developmental rate, μ_i (days^{-1})	Developmental $\sqrt{\text{variance}}$, σ (days^{-1})	Proportionate daily survival	Number entering stage	% stage mortality
		(a) *C. chinensis*			
Eggs	0.31684	0.013903	----	100.00	0.00
1st larvae	0.46924	0.022266	1.00	100.00	0.00
2nd larvae	0.48279	0.028208	0.99430	100.00	1.32
3rd larvae	0.48655	0.0024353	1.00	98.68	0.00
4th larvae	0.22580	0.017163	1.00	98.68	0.00
Pupae	0.31564	0.011727	0.98662	98.68	4.79
Adults in pea	0.47338	0.026537	1.00	93.95	0.00
Emerged Adults	----	----	----	93.95	----
		(b) *C. maculatus*			
Eggs	0.29967	0.0035979	----	100.00	0.00
1st larvae	0.31525	0.028145	0.98342	100.00	5.79
2nd larvae	0.46964	0.0068272	1.00	94.21	0.00
3rd larvae	0.46926	0.016057	1.00	94.21	0.00
4th larvae	0.22562	0.035348	0.99501	94.21	2.43
Pupae	0.25078	0.0098714	0.97983	91.92	8.20
Adults in pea	0.46778	0.024154	1.00	84.38	0.00
Emerged Adults	----	----	----	84.38	----

FIGURE 4.6 The life-table 4.3 for C. chinensis (solid circles) and the predicted presence of the instars(heavy line) given by the fitted model of equations 4.17 and 4.19. The fitted parameters may be found in table 4.5. The light line indicates the predicted recruitment to each stage. (a) Eggs; (b) First instar larvae; (c) second instar larvae; (d) third instar larvae; (e) fourth instar larvae; (f) pupae; (g) pre-emergent adults; (h) emerged adults.

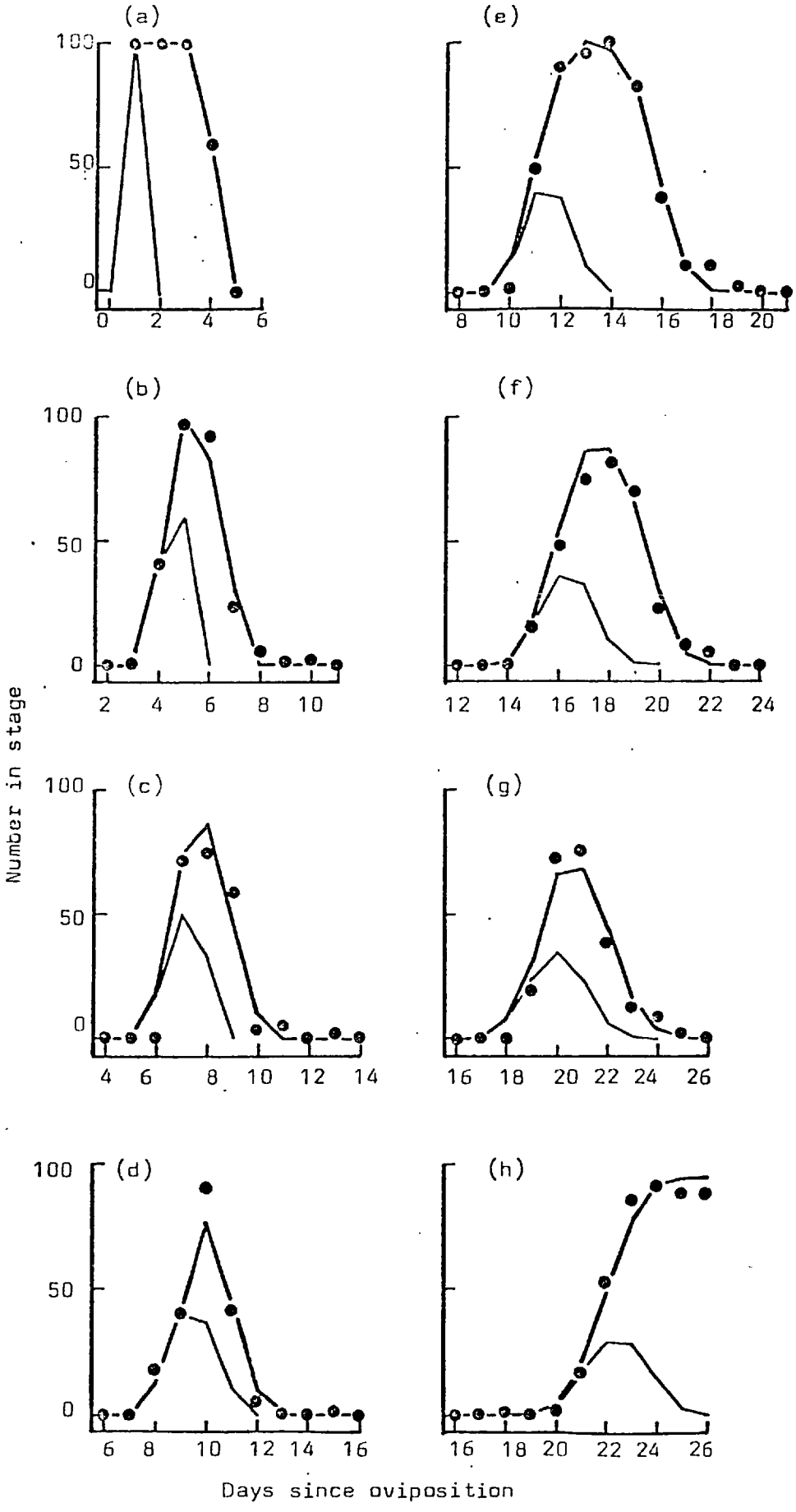
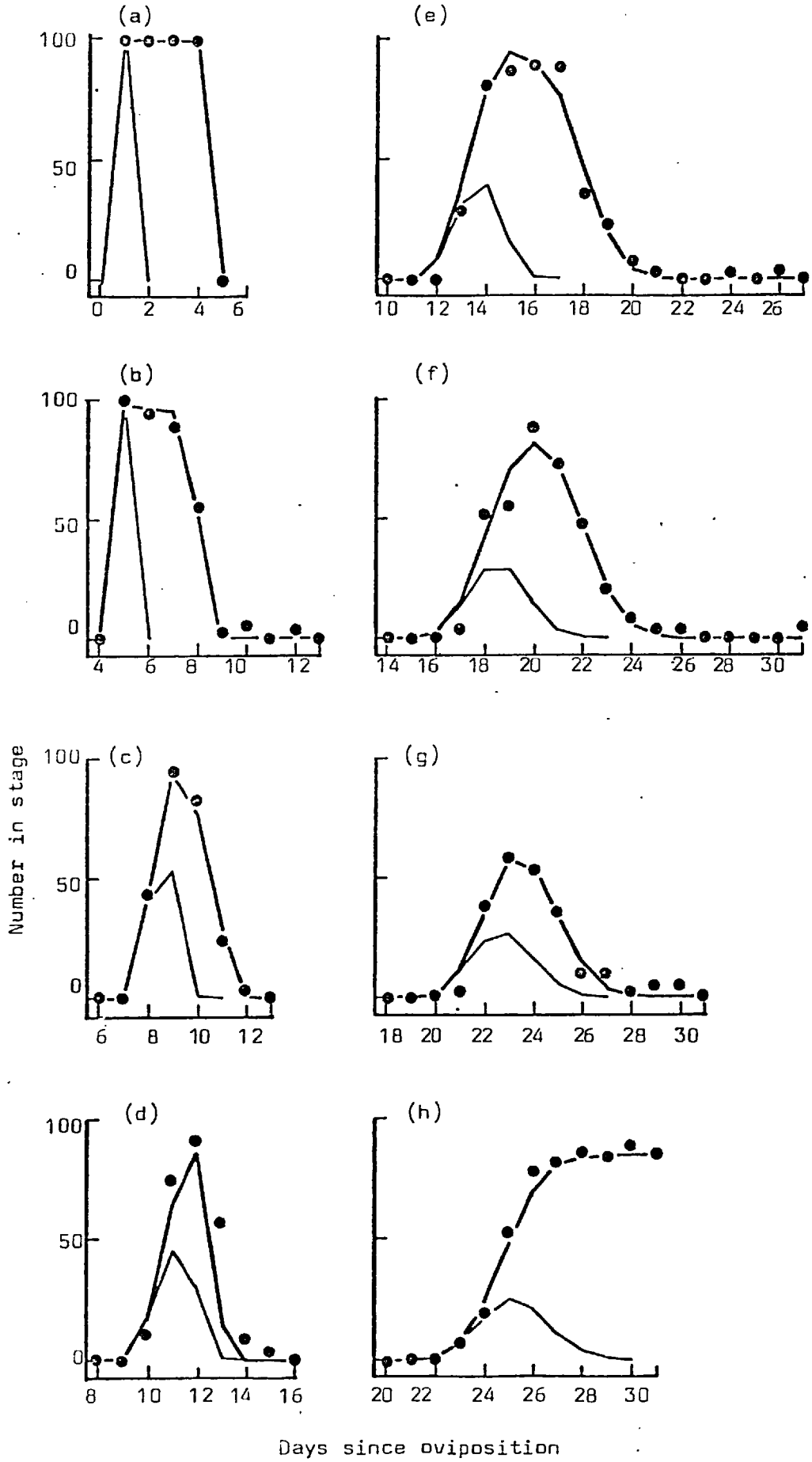

(a)
(b)
(c)
(d)
(e)
(f)
(g)
(h)
100
50
0
Number in stage
Days since oviposition

FIGURE 4.7 The life-table 4.4 for *L. maculatus* (solid circles) and the predicted presence of the instars (heavy line) given by the fitted model of equations 4.17 and 4.19. The fitted parameters may be found in table 4.5. The light line indicates the predicted recruitment to each stage. (a) Eggs; (b) First instar larvae: (c) second instar larvae; (d) third instar larvae; (e) fourth instar larvae; (f) pupae; (g) pre-emergent adults; (h) emerged adults.


(a)
(b)
(c)
(d)
(e)
(f)
(g)
(h)
100
50
0
Number in stage
Days since oviposition

within a period of one day and for these stages the estimated value of the variance parameter is viewed only as an upper limit on their actual value since smaller variances would produce the same results. The estimates of daily survival rates for all the stages of both species were high resulting in a high predicted overall survival: 94% in C. chinensis and 84% in C. maculatus. The estimated mortalities in the early stages (second instar larvae in C. chinensis and first instar larvae in C. maculatus) probably represent mortality due to failure to become established in the bean, although the estimated value for second instar C. chinensis is sufficiently close to unity that it may be due only to sampling errors. Similarly the small estimated mortality in fourth instar C. maculatus larvae may be due to sampling errors or possibly some unavoidable competition between individuals. In both species the lowest estimated survival rate was for the pupal stage and this accounted for the largest portion of the overall mortality. This mortality was probably due to the death of individuals which failed to accumulate sufficient resource to permit completion of pupation.

The fitted life-table model provides a prediction of the number of individuals present in each stage through the course of a cohort's development and these predictions are presented graphically, together with the observed numbers, in figures 4.6 (C. chinensis) and 4.7 (C. maculatus). The model describes well the presence of the various instars in both species, and these predictions will be used in the continued quantifying of larval submodel parameters and later in the simulation models developed for these species. The predicted number present in each instar have been drawn on continous time scales for each species in figure 4.8.

The distribution of the developmental periods predicted by the model for these species are shown in figure 4.9. An initial impression

FIGURE 4.8 The development of a single cohort of 100 eggs as predicted by the density independent life-table model. (a) C. chinensis; (b) C. maculatus. The symbols next to the curves in (a) represent the various stages as follows: E, eggs; I-IV, the four larval instars; P, pupae; A_1, pre-emergent adults; A_2, emerged adults.

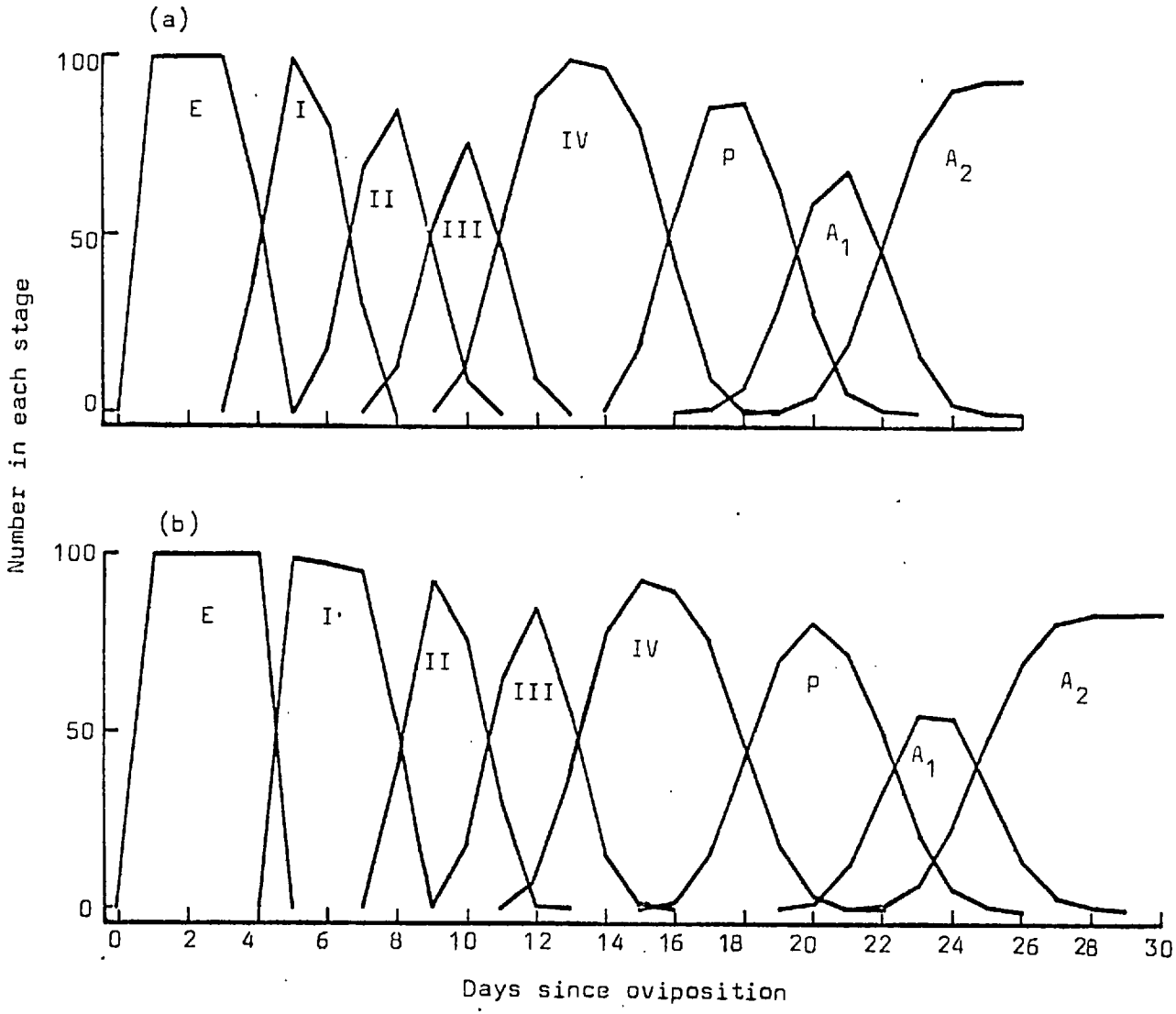
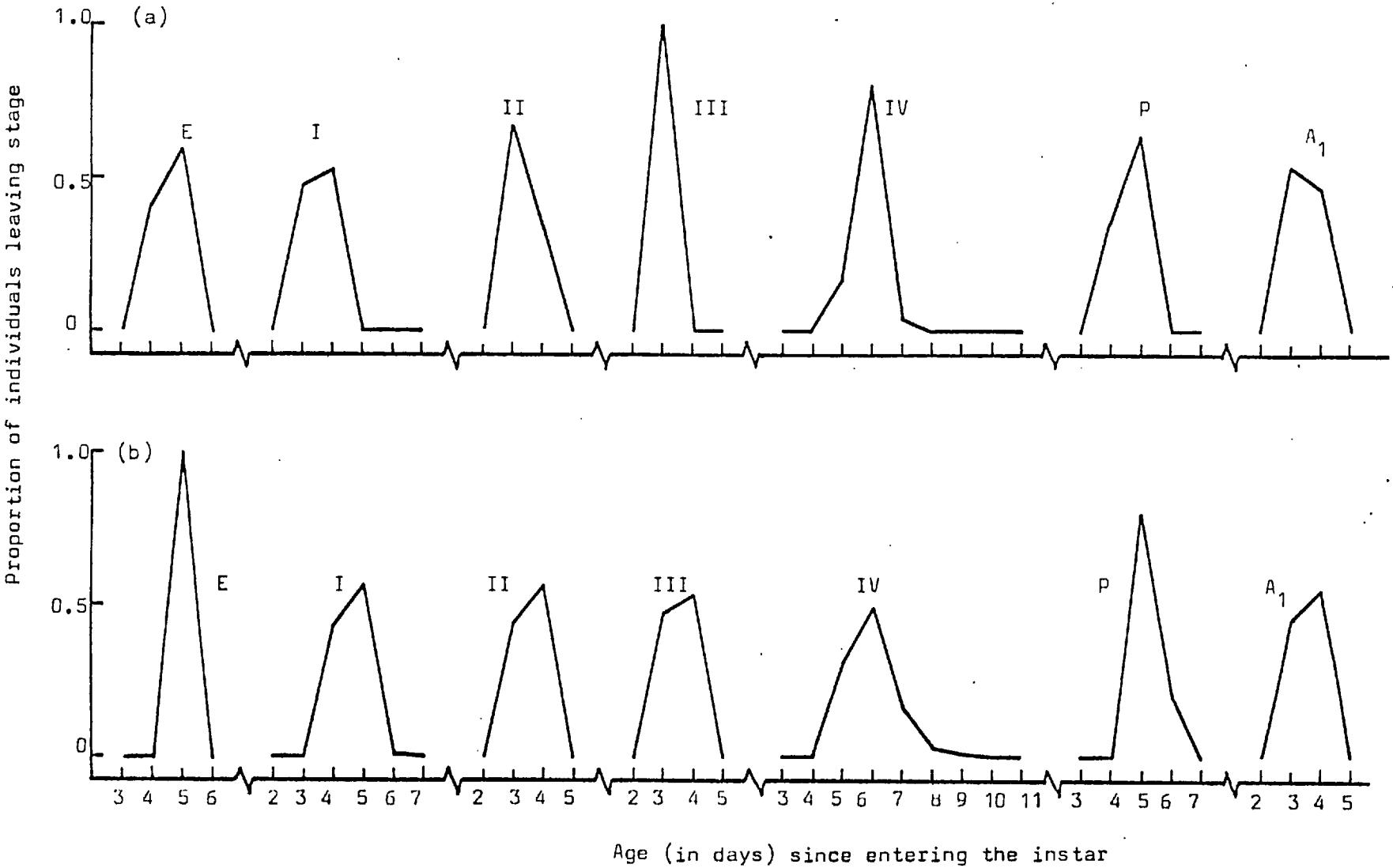

(a)
100
50
0
E
I
II
III
IV
P
A1
A2
(b)
100
50
0
E
I
II
III
IV
P
A1
A2
0 2 4 6 8 10 12 14 16 18 20 22 24 26 28 30
Number in each stage
Days since oviposition

FIGURE 4.9 The predicted developmental periods of the immature stages of (a) C. chinensis and (b) C. maculatus. See text for discussion.


1.0
(a)
0.5
0
E
I
II
III
IV
P
A1
1.0
(b)
0.5
0
E
I
II
III
IV
P
A1
3 4 5 6
2 3 4 5 6 7
2 3 4 5
2 3 4 5
3 4 5 6 7 8 9 10 11
3 4 5 6 7
2 3 4 5
Proportion of individuals leaving stage
Age (in days) since entering the instar

of these distributions is that they are all somewhat kurtotic (narrow); indeed two of them are contained entirely within one sampling period. This emphasizes the effect of the small estimated variances of the developmental rates in table 4.5. The developmental period distributions are roughly similar between the two species; the third instar larvae of C. maculatus had a less narrow distribution than those of C. chinensis and development of fourth instar larvae in C. maculatus was slightly more protracted than in C. chinensis. There is a notable similarity in the predicted developmental period distributions of the first three larval instars of C. maculatus but the narrowness of these distributions makes them unsuitable for inferring any definite similarities in the development of these stages. This concludes the consideration of the density independent life-tables analyses and attention will now be given to density dependent mortality due to intrastage and interstage competition.

Before undertaking the analysis of density dependent mortality in these species it was necessary to determine whether or not larval density had any effect on development. To do this the censuses taken from each oviposition chamber in the first larval experiment were considered seperately by plotting the number present in each stage on each day as a proportion of the total number of individuals observed on the day (figures 4.10 and 4.11). It is evident by considering the mean number of hatched eggs per bean in each of the oviposition chambers (also given in figures 4.10 and 4.11) that the data span a wide range of initial larval densities. There does not, however, appear to have been any acceleration or deceleration in development as density increased. The first day of appearance of each of the stages never varied by more than one day in the C. chinensis populations and was constant in the C. maculatus populations. The period

FIGURE 4.10 The proportion of total individuals observed in each stage in beans sampled from the four oviposition chambers in the first larval experiment for C. chinensis. The numbers at the right of each figure give the estimated mean and standard deviation of the number of hatched eggs per bean in each chamber. The successive stages are represented by : eggs, ● ; first instar, X ; second instar, O; third instar, +; fourth instar, ◉ ; pupae, X ; pre-emergent adults, O ; emerged adults, +.

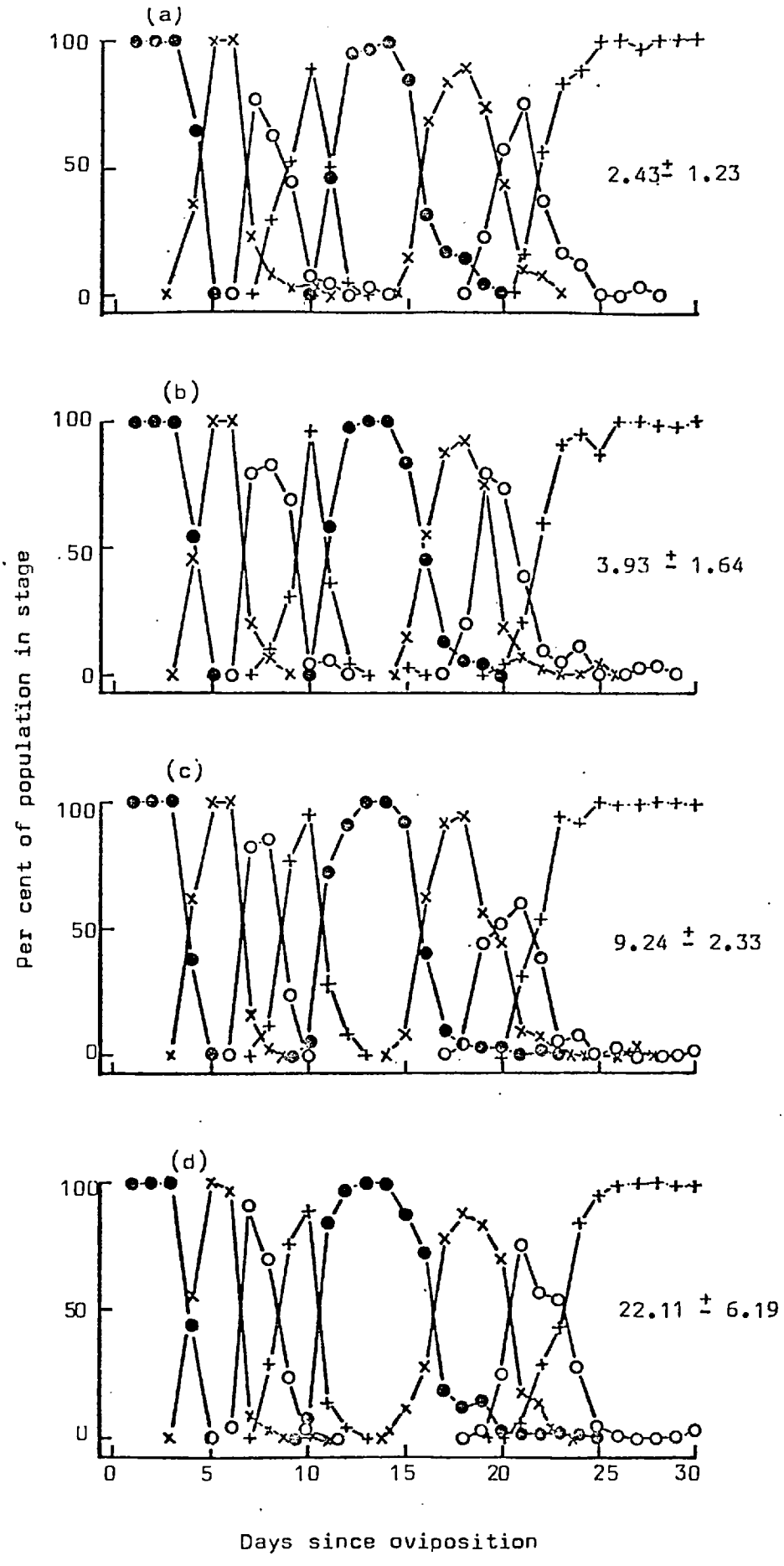
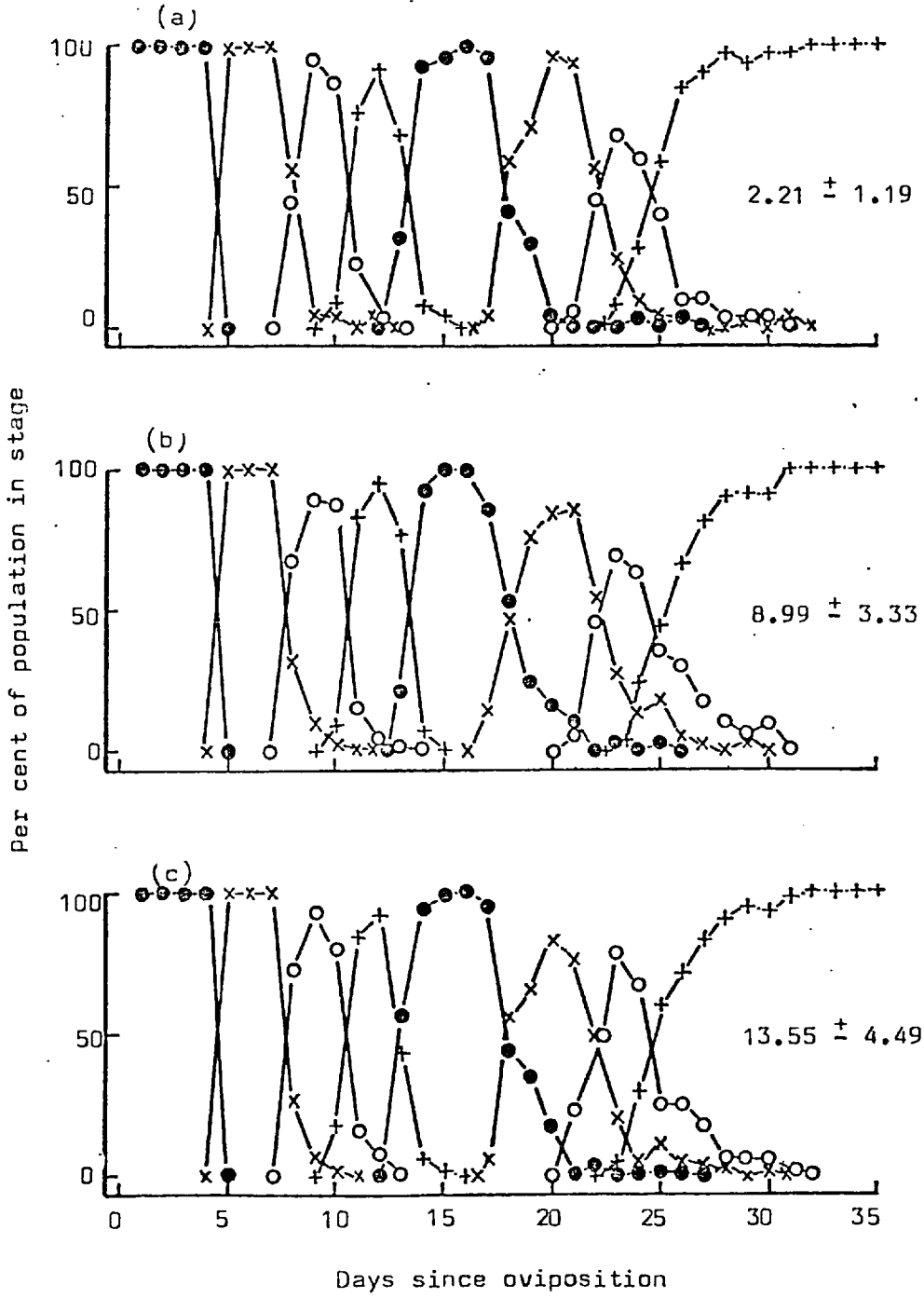

(a)
100
50
0
2.43 ± 1.23
(b)
100
50
0
3.93 ± 1.64
(c)
100
50
0
9.24 ± 2.33
(d)
100
50
0
22.11 ± 6.19
0
5
10
15
20
25
30
Per cent of population in stage
Days since oviposition

FIGURE 4.11 The proportion of total individuals observed in each stage in beans sampled from three oviposition chambers in the first larval experiment for C. maculatus. The numbers at the right of each figure give the estimated mean and standard deviation of the number of hatched eggs per bean in each chamber. The successive stages are represented by: eggs, ⊘; first instar, X; second instar, O; third instar, +; fourth instar, ⊙; pupae, X; pre-emergent adults, O; emerged adults, +.


(a)
100
50
0
2.21 ± 1.19
(b)
100
50
0
8.99 ± 3.33
(c)
100
50
0
13.55 ± 4.49
0
5
10
15
20
25
30
35
Per cent of population in stage
Days since oviposition

of maximum presence of each instar agreed well between populations in both species. The mean day of adult emergence did not vary in the C. chinensis populations and was only later by one day in the middle density C. maculatus populations. Similarly, the spread of development appears nearly constant in all the populations for both species, although the fourth instar larval stage of C. chinensis may have been present for slightly longer in the highest density populations than in others. It was thus thought unnecessary to include any dependence on density in the developmental parameters of the model.

The analysis for density dependent mortality outlined above (see page 124) considers the total number of survivors on a given day in beans with differing numbers of hatched eggs. The days selected for analysis of the six stages of first instar larvae through pre-emergent adults for C. chinensis were days six, eight, 10, 12, 14, 19 and 22 and for C. maculatus were days seven, 10, 12, 16, 21 and 24. These days were selected as being representative of the maximum presence of the various instars and were chosen by examining the data shown in figures 4.10 and 4.11. The data from these sampling days are shown in figures 4.12 for C. chinensis and 4.13 for C. maculatus; the solid lines in the figures represent the fitted models obtained by substiting equation 4.23 into equation 4.20. The parameters a_i and b_i were estimated for each set of data by the method described above and the results of these analyses are summarized in table 4.6. There was significant density dependence in three stages of C. chinensis and in two stages in C. maculatus and the estimated values of the parameters a_i are given in the table. The value of the parameter b_i was not significantly different from unity in any analysis and was set equal to unity for all stages in both species. In C. chinensis the density dependent parameter a_1 (corresponding to first instar

FIGURE 4.12 The total number of survivors in single beans with various numbers of hatched eggs on different sampling days in C. chinensis. The sampling days for (a) through (g) were selected as representing the maximum presence of the stages -- first instar larvae to emerged adults. Hollow circles indicate repeated points The solid lines are given by the fitted model of equation 4.20 and the parameters values in table 4.6.

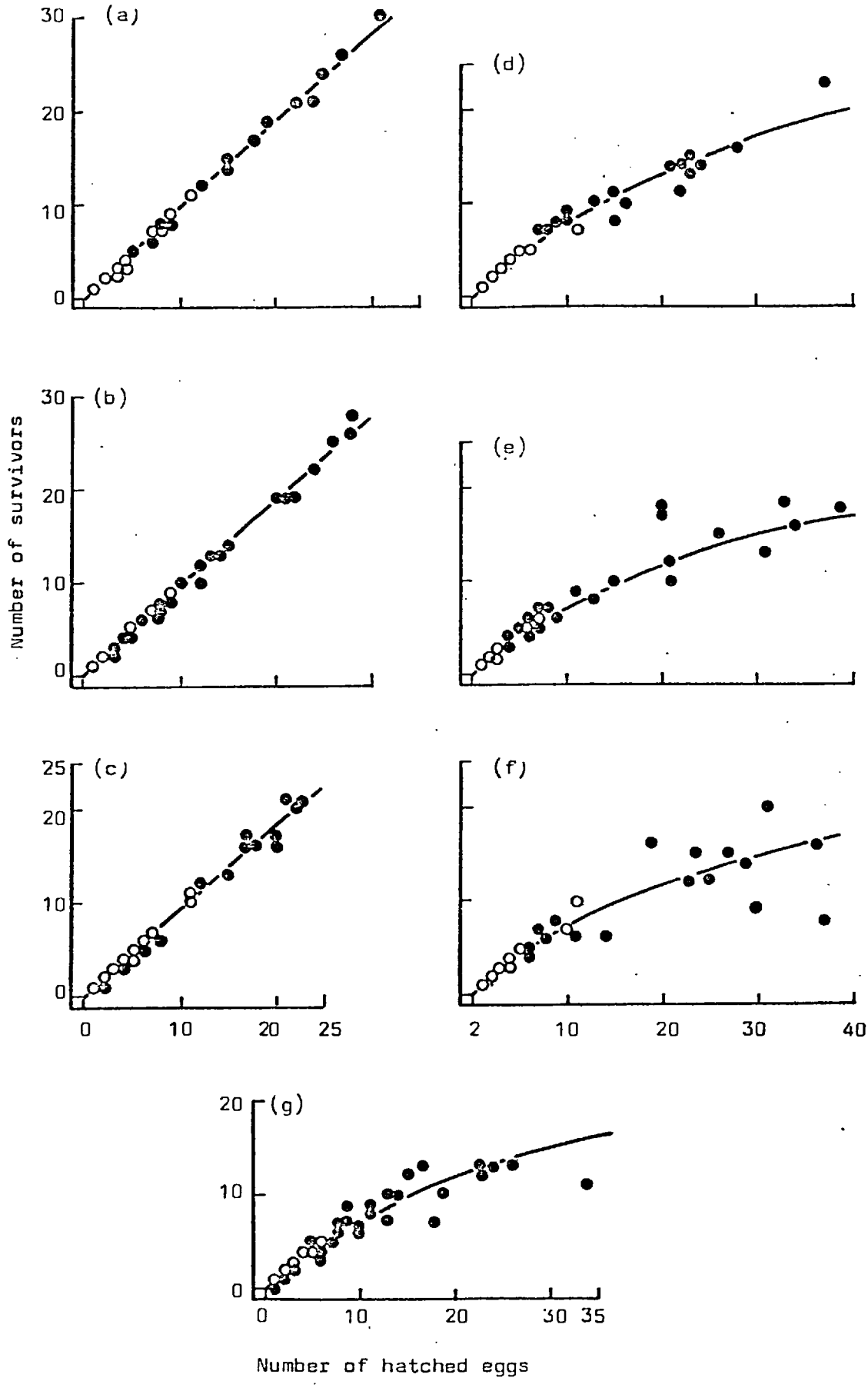

(a)
(b)
(c)
(d)
(e)
(f)
(g)
Number of survivors
Number of hatched eggs

FIGURE 4.13 The total number of survivors in single beans with various numbers of hatched eggs on different sampling days in C. maculatus. The sampling days for (a) through (g) were selected as representing the maximum presence of the stages -- first instar larvae to emerged adults. Hollow circles indicate repeated points. The solid lines are given by the fitted model of equation 4.20 and the parameters values in table 4.6.

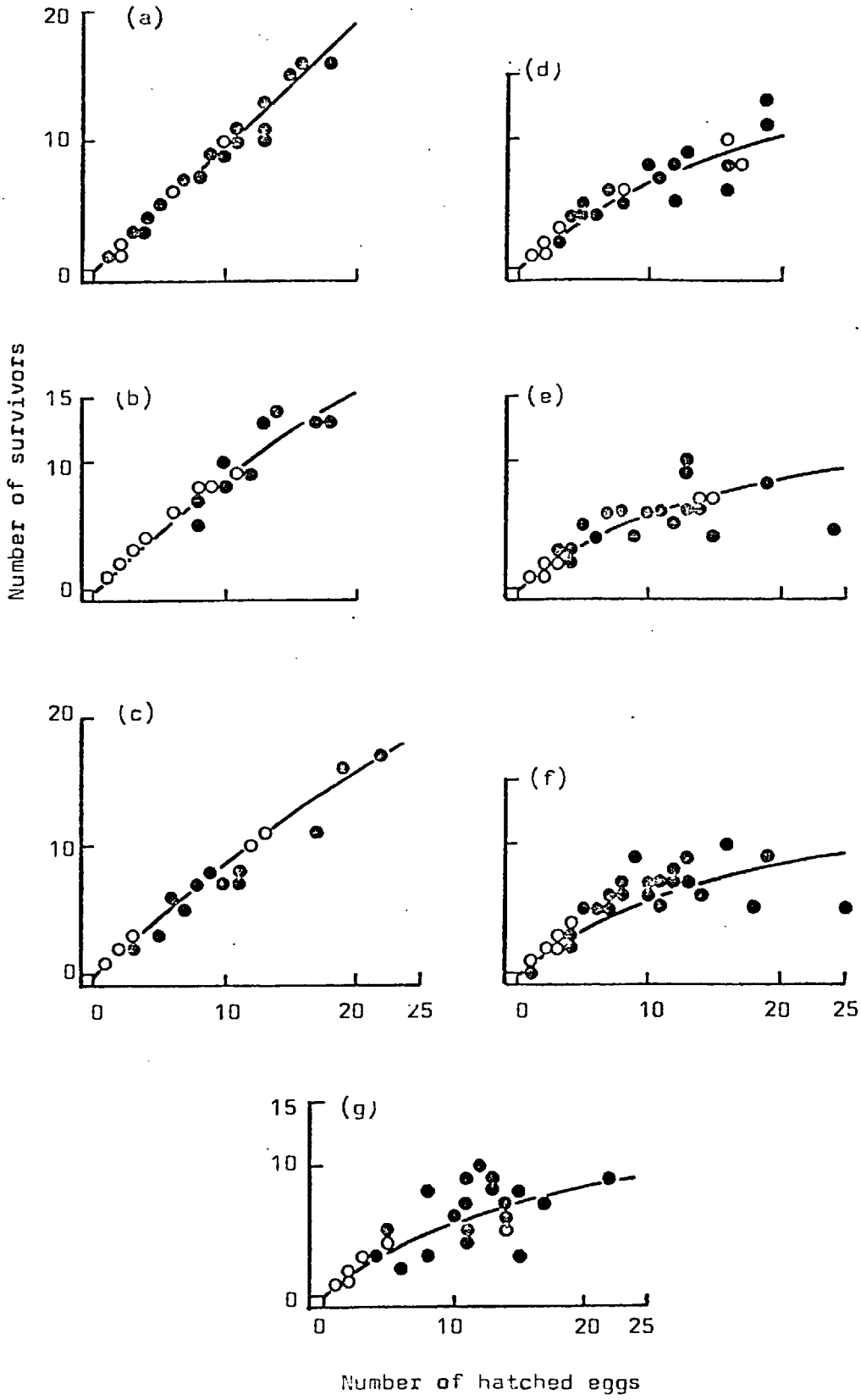

(a)
(b)
(c)
(d)
(e)
(f)
(g)
Number of survivors
Number of hatched eggs
0
10
15
20
25

TABLE 4.6 The estimates of the density dependent parameter a_i in three larval stages of C. chinensis (a) and two larval stages of C. maculatus (b). The parameter a_i for all other stages was not significantly different from zero.

Stage	estimated value of a_i	n	F-value
	(a) C. chinensis		
First instar larvae	0.0010994	50	3.233, $p < .001$
Third instar larvae	0.0025422	56	13.50, $p < .001$
Fourth instar larvae	0.0066029	42	367.17, $p < .001$
	(b) C. maculatus		
Second instar larvae	0.0055076	39	36.19, $p < .001$
Fourth instar larvae	0.011684	35	137.69, $p < .001$

larvae) was very small and represents losses during hatching when eggs were oviposited on top of one another at high densities. There was no significant density dependence in second instar larvae. The density dependence found in the third and fourth instars represents competition for space within the bean. The value of a_4 for the fourth instar is larger than that for the third instar, reflecting the larger size of the fourth instar or conversely the smaller per bean carrying capacity for fourth instar larvae than for thirds. There was no significant competition in the nonfeeding pupal and pre-emergent adult stages. The fitted models described the C. chinensis data well and also gave a reasonable prediction of survival to the emerged adult stage (figure 4.12g). In C. maculatus there was no significant density dependence in the first instar larval stage, possibly due to the limited range of hatched egg densities observed. The second and fourth instar stages did show significant density dependence and, as expected, the estimated value of a_4 was larger than the value of a_2. There was no significant competition in the third instar larval, pupal or pre-emergent adult stages. The fitted models described the data well and gave a reasonable prediction of survival to the adult stage (figure 4.13g).

The design of the interstage competition experiment required the initiation of two cohorts of individuals at different times in a single set of beans for each interaction of interest, and the details of the different times employed are given in table 4.7. The initial cohort of eggs for all the interactions was provided by adults placed with the beans on day zero and removed on day one. The second cohort of eggs was provided by a second group of adults placed with the beans on the day given in the table and removed one day later. The timing of this second oviposition was determined by considering the differences in the sampling day given above for the two instars

TABLE 4.7 The details of the timing of the second oviposition and sampling in the second (interstage) larval competition experiments.

Stages involved	Day of second oviposition		Sampling day	
	C. chinensis	*C. maculatus*	*C. chinensis*	*C. maculatus*
Second vs first	2	3	8(19)	10(18)
Third vs first	4	5	10(21)	12(19)
Third vs second	2	2	10(20)	12(22)
Fourth vs first	8	9	14(20)	16(17)
Fourth vs second	6	6	14(20)	16(20)
Fourth vs third	4	4	14(21)	16(23)
Pupae vs first	13	14	19(19)	21(22)
Pupae vs second	11	11	19(16)	21(21)
Pupae vs third	9	9	19(20)	21(16)
Pupae vs fourth	5	5	19(20)	21(20)
Adult vs first	16	17	22(17)	24(19)
Adult vs second	14	14	22(18)	24(26)
Adult vs third	12	12	22(16)	24(21)
Adult vs fourth	8	8	22(19)	24(16)
Adult vs pupae	3	3	22(19)	24(18)

concerned. For example, in C. chinensis the sampling day for second instar larvae was day eight and that for first instar larvae was day six and the difference between these two sampling days (i.e. two days) fixed the timing of the second oviposition. In this way, when beans were sampled on the day appropriate for the required stage from the first cohort, the second cohort would have the age appropriate for censusing the second stage. The days on which each set of beans was sampled and the number of beans in each sample are given in table 4.7.

The results of the analysis of the interstage competition data are summarized in tables 4.8 (C. chinensis) and 4.9 (C. maculatus). The data were analyzed twice. In the first analysis all the estimated competition coefficients which were judged significant at the 0.05 level were included in the model and the results of these analyses are given in tables 4.8a and 4.9a. Some unexpected results were obtained in this way, notably the significant effects of first or second instar larvae on larger instars, although the estimates for these α's were in general smaller than those for other interactions. An examination of residuals from the analyses leading to these initial competition matrices indicated that the marginally significant parameters (those with $.05 > p > .01$) did not contribute substantially to an improved description of the data. Further it appeared that the ratio of equation 4.28 tested in these cases was inflated due to the low integer values of the data considered. Consequently the data were reanalysed and only estimates of α_{ij} which had significances of $p < .01$ were included in the model. In addition, estimates of competition coefficients were only considered which reflected interaction between a stage and all smaller stages, and the effects of smaller instars on larger ones were arbitrarily set equal to zero. The only two parameters included in the model which did not strictly

TABLE 4.8 The original (a) and revised (b) estimates of interstage competition coefficients for C. chinensis. The values across each row give the effect on that stage by the stages identified at the top of each column. Values marked with (+) have significances of $.05 > p > .01$, those marked with (*) have significances of $.01 > p > .001$ and those marked with (**) have significances of $p < .001$. See text for discussion.

	Stage	First	Second	Third	Fourth	Pupae	pre-emergent Adults
(a)	First	----	0.00	0.0125*	0.0709**	0.0926**	0.392**
	Second	0.00	----	0.00	0.00	0.00	0.00
	Third	0.00467*	0.00586+	----	0.101**	0.0657*	0.00
	Fourth	0.0109*	0.00	0.00	----	0.0225+	0.00
	Pupae	0.00	0.00	0.00	0.00	----	0.00
	pre-emergent Adults	0.00	0.00	0.00	0.00	0.00	----
(b)	First	----	0.00	0.0123*	0.0675**	0.0918**	0.0918**
	Second	0.00	-----	0.00	0.00	0.00	0.00
	Third	0.00	0.00	----	0.0827**	0.0408*	0.00
	Fourth	0.00	0.00	0.00	----	0.00	0.00
	Pupae	0.00	0.00	0.00	0.00	----	0.00
	pre-emergent Adults	0.00	0.00	0.00	0.00	0.00	----

TABLE 4.9 The orginal and revised estimates of interstage competition coefficients for C. maculatus. The values across each row give the effect on that stage by the stages identified at the top of each column. Values marked with (+) have significances of .05 > p > .01, those marked with (*) have significances of .01 > p > .001 and those marked with (**) have significance of p < .001. See text for discussion.

Stage	First	Second	Third	Fourth	Pupae	pre-emergent Adults
(a)						
First	---	0.0259+	0.00	0.0246**	0.0360**	0.0336+
Second	0.00	---	0.00	0.0719**	0.00	0.00
Third	0.0230*	0.00	---	0.00	0.00	0.00
Fourth	0.00	0.00	0.00	---	0.00	0.00
Pupae	0.0190**	0.00	0.00	0.00	---	0.122+
pre-emergent Adults	0.00	0.00	0.00	0.00	0.00	---
(b)						
First	---	0.00	0.00	0.0242**	0.0340**	0.0315+
Second	0.00	---	0.00	0.0550**	0.00	0.00
Third	0.00	0.00	---	0.0539**	0.00	0.00
Fourth	0.00	0.00	0.00	---	0.00	0.00
Pupae	0.00	0.00	0.00	0.00	---	0.00
pre-emergent Adults	0.00	0.00	0.00	0.00	0.00	---

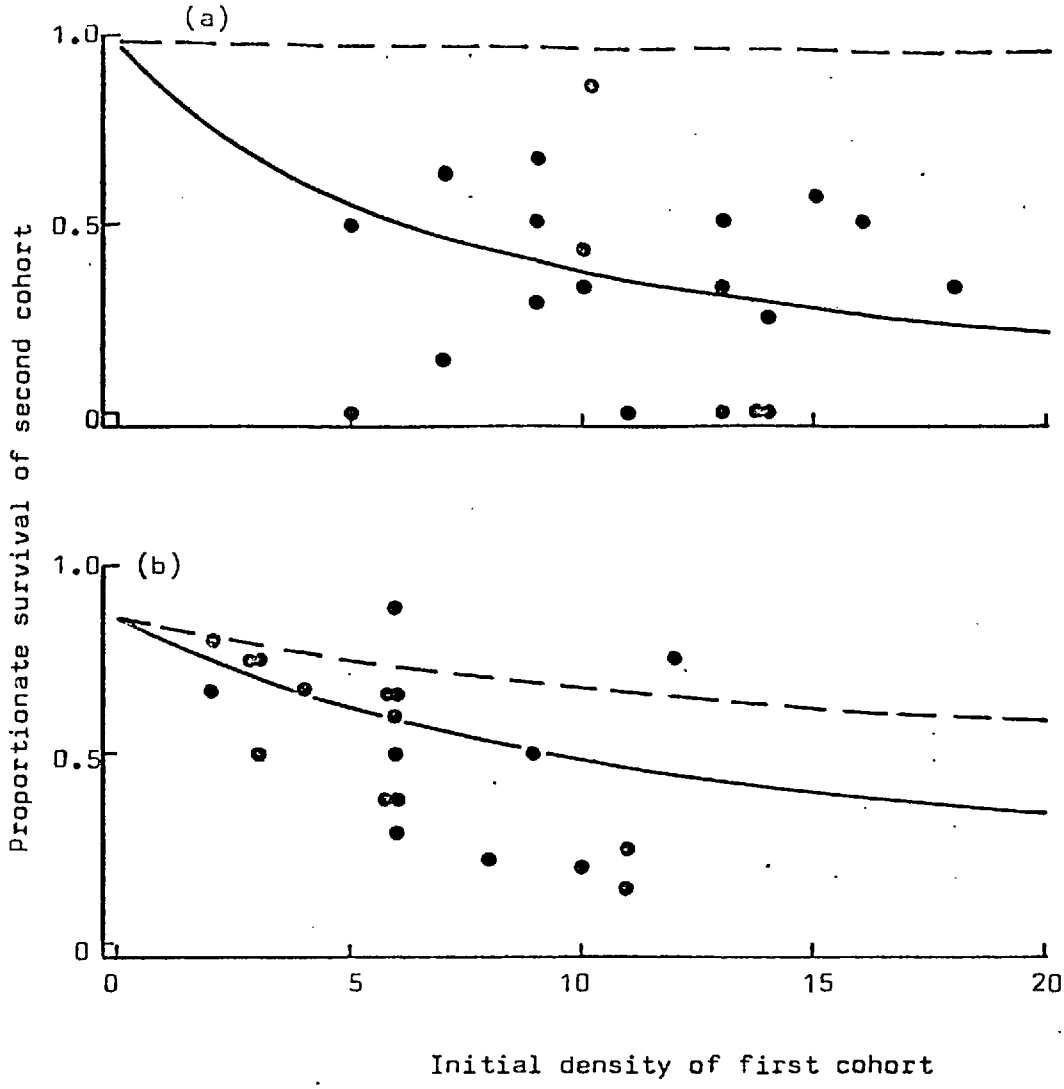
fulfill these requirements relate the interaction between adults and first instar larvae of both species. In C. chinensis the initial cohort (of adults) caused the death of practically all of the second cohort of individuals and because of the large number of zeros recorded the minimum sum of squares for these data occurred at a very high value of α_{1A} (.392, table 4.8a). It is unlikely, in view of the nature of the competition (for space within the bean) in these species that adults should have any larger effect than pupae on the first instar larvae, so the value of α_{1A} in the revised matrix was set equal to the value for α_{1p}, the estimated competition coefficient between pupae and firsts. This assumption of equal effects of pupae and adults on first instar larvae is supported by the estimated values for these stages in C. maculatus where the two parameter estimates were very similar. The value for α_{1A} in C. maculatus only had significance of $p < .05$ but because of the certainty of the biological importance of the interaction it was included in the revised matrix of competition coefficients. All of the parameters included in this second analysis were also judged by the examination of residuals as having provided an important improvement in description of the data. These initial and revised competition coeffeicient matrices will be used later in the validation of the larval submodel. It should be noted that when the initial C. maculatus matrix was used, the value of the competition coefficient α_{pA} (competition between adults and pupae) was set equal to zero. The estimate of this parameter is almost certainly due to sampling errors caused by the inability to distinguish between survivors from the two cohorts due to the considerable spread in the time of development of these two stages.

A few conclusions on the nature of interstage competition in these species may be drawn from the revised matrices of competition

coefficients in tables 4.8b and 4.9b. Considering the effects of the various stages on the first instar larvae, the estimated competition coefficient increases as the size of the stages increase and this reflects an increasing probability of a fatal encounter (for the first instar larvae) between the stages. The effects of the fourth instar larvae on the other stages increases as the size of the other stage increases which similarly reflects the higher probablity of an inter-stage encounter occurring as the size of the stages increase. In general the outcome of competition between cohorts is determined largely by the timing of recruitment and individuals established first have a competitive advantage over later cohorts. This is similar to the consequences of interspecific interstage larval competition between Rhyzopertha dominica and Sitotroga cereallela in whole wheat grains reported by Crombie (1944) where the first established individuals were more successful than those which entered the grain later.

The results of these experiments consist of a pair of independent variables represented by the initial recruits (the number of hatched eggs) to both cohorts and a pair of dependent variables represented by the number of survivors in both cohorts for each of the 15 interactions listed in table 4.7. The presentation of these data may be achieved by plotting the two independent variables and one of the dependent variables in three dimensions but the resulting figure is not very helpful in interpreting the data. An alternate method is to plot proportionate survival of one cohort against the initial recruits to the other and this method has been used here to present the data for one interaction for both species in figure 4.14. The two curves shown in figures 4.14a and 4.14b indicate how the predictions of mortality were improved by the addition of the parameters α_{ij}. In both cases the estimated value of α_{ij} clearly provides a

FIGURE 4.14 An example of the inclusion of interstage density dependence improving the prediction of mortality of (a) first instar larvae competing with fourth instar larvae in C. chinensis and (b) second instar larvae competing with fourth instar larvae in C. maculatus. The broken line gives the prediction of the model when no interaction between the stages is included. These predictions decrease with increased initial density of the first cohort due to interactions between late developing third instar larvae in the initial cohort and first instar larvae in the second cohort in (a) and between late developing first instar larvae in the second cohort and fourth instar larvae in the first cohort in (b). The description of these data was improved by the addition of interstage competition coefficient to the model as is shown by the solid lines in (a) and (b).


(a)
1.0
0.5
0
(b)
1.0
0.5
0
0
5
10
15
20
Proportionate survival of second cohort
Initial density of first cohort

better description of the data (solid lines in figure 4.14) than the predictions when α_{ij} was set at zero (broken lines). The predicted curves in the figure were obtained from the revised competition coefficient matrices.

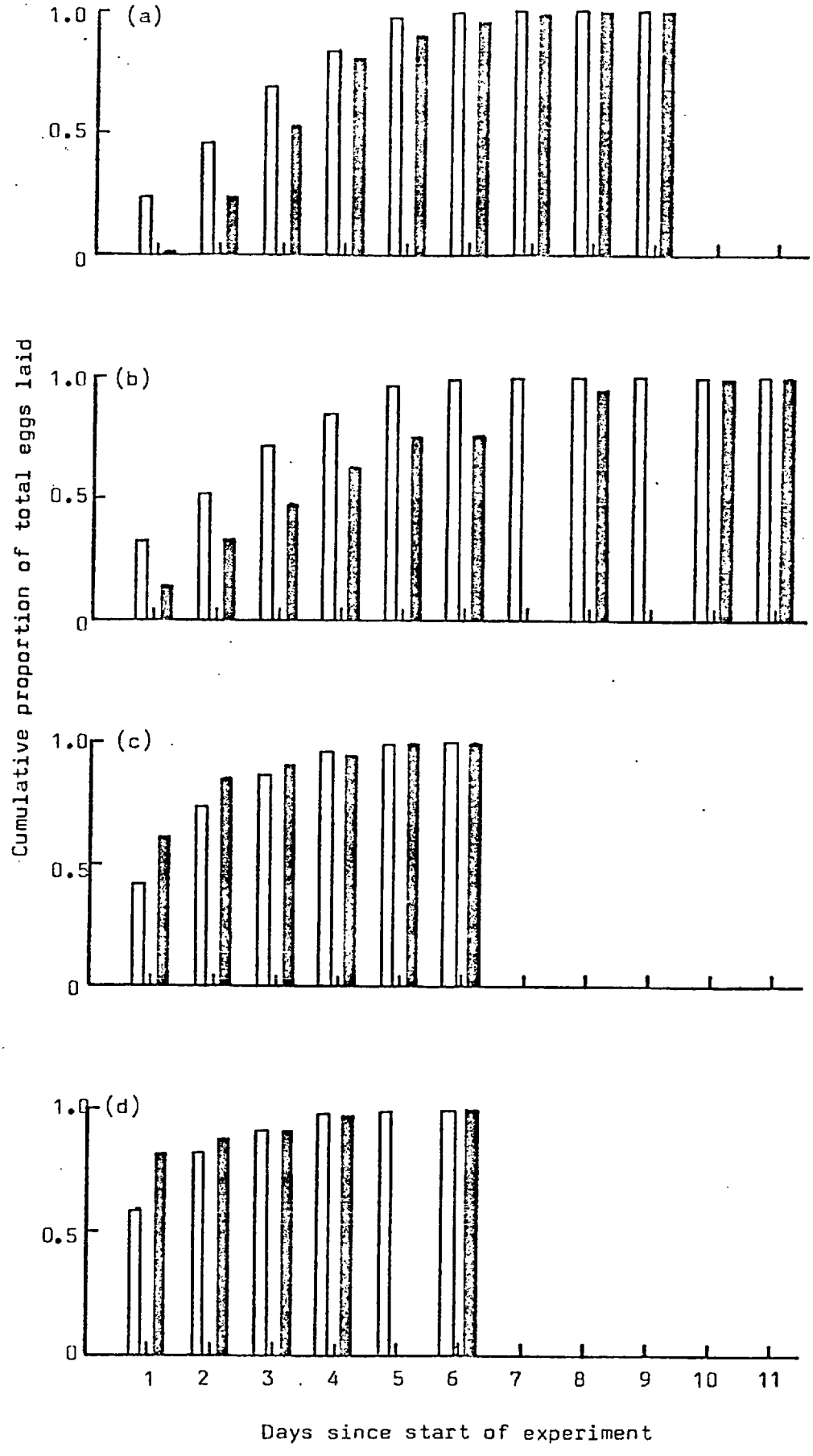
4.4 Validation of the model and simulations

Having developed a complex model based on description of the underlying processes, it is useful to compare the model's predictions with some independent experimental results. This is the best test of the models adequacy. This section reports on some investigations which permit to a greater or lesser degree such validation of the oviposition and larval population submodels. Finally the two submodels will be considered together as a simulation model for the growth of a Callosobruchus population and the results of these simulations discussed.

4.4.1 Some further oviposition experiments

The oviposition submodels developed above clearly provide reasonable descriptions of the number of total and hatched eggs laid by adults of these species at different densities as seen in figure 4.5. It is important, however, to consider the number of eggs appearing each day since this will determine the timing of recruitment to the larval stage which, as discussed above, is of considerable importance in determining the outcome of larval competition. Two simple experiments were therefore performed for each species where five and 60 pairs of 0-2½ hour old adults were placed in small plastic dishes with 3.70g of beans. The dishes were kept at 30°C, 70% relative humidity until the adults had died (except in the case of the single dish of 60 pairs of C. maculatus adults which was not kept after day six) and the total number of eggs present on the beans were recorded each day. These data are presented in figure 4.15 (solid bars) as

FIGURE 4.15 The observed (solid bars) and predicted (open bars) cumulative proportion of eggs laid by adults of C. chinensis (a,b) and C. maculatus (c,d) at densities of five pairs (a,c) and sixty pairs (b,d). The experiment in (d) was terminated after six days; all other experiments ended after the death of all the adults. See text for discussion.


(a)
(b)
(c)
(d)
1.0
0.5
0
Cumulative proportion of total eggs laid
1 2 3 4 5 6 7 8 9 10 11
Days since start of experiment

the cumulative proportion of the final total number of eggs laid. The oviposition submodel has also been used to provide the expected cumulative proportion of eggs laid and these expected results are also given (hollow bars) in figure 4.15.

The predicted oviposition records of C. chinensis at five and 60 pairs did not agree with the observed records (figure 4.15a, b); the predicted proportions of eggs present was considerably higher than the observed proportions during the early period of oviposition. There may be several reasons for this, such as the density dependent functions $h_a(A)$ or $h'_a(E)$ not being constant with adult age. The most probable cause for the disagreement, however, was that the oviposition record of the crowded adults used in the experiments was different from that used in the model. It may be seen that the predicted proportions of eggs present are in close agreement with the observed proportions present one day later, possibly indicating that many of the adults used in the experiments delayed the start of their oviposition by one day. It may be recalled that in the repeated oviposition record experiment for C. chinensis (page 132) all 30 replicates showed a preoviposition period of at least one day in contrast to the results of the first experiment which provided the oviposition record for the model. This emphasizes the variable nature of oviposition behaviour in the strains of C. chinensis used here. In addition, the data presented here arise from only a few replicates (five and one replicate at densities of five pairs and 60 pairs, respectively) and this may have contributed to the discrepancies between the observed and predicted results.

The oviposition records of C. maculatus at densities of 5 pairs (two replicates) and 60 pairs (one replicate which was not recorded after day six) are presented in figures 4.15c and d. The expected

oviposition record of five pairs was in close agreement with the observed record. At a density of 60 pairs the predicted proportion of eggs appearing on the first day was notably less than was observed although the predictions for the other days were in better agreement with the data. This discrepancy may be due to the premature termination of the experiment since more eggs might have been laid after day six; however the total number of eggs observed in this experiment was 372 which is in close agreement with the mean total fecundity of 60 pairs of adults (figure 4.5a).

These experimental results thus generally support the distribution of oviposition predicted by the submodel, but some improvement is likely from further investigations into the effects of density on adult life-span and oviposition.

4.4.2 Validation of the larval submodel

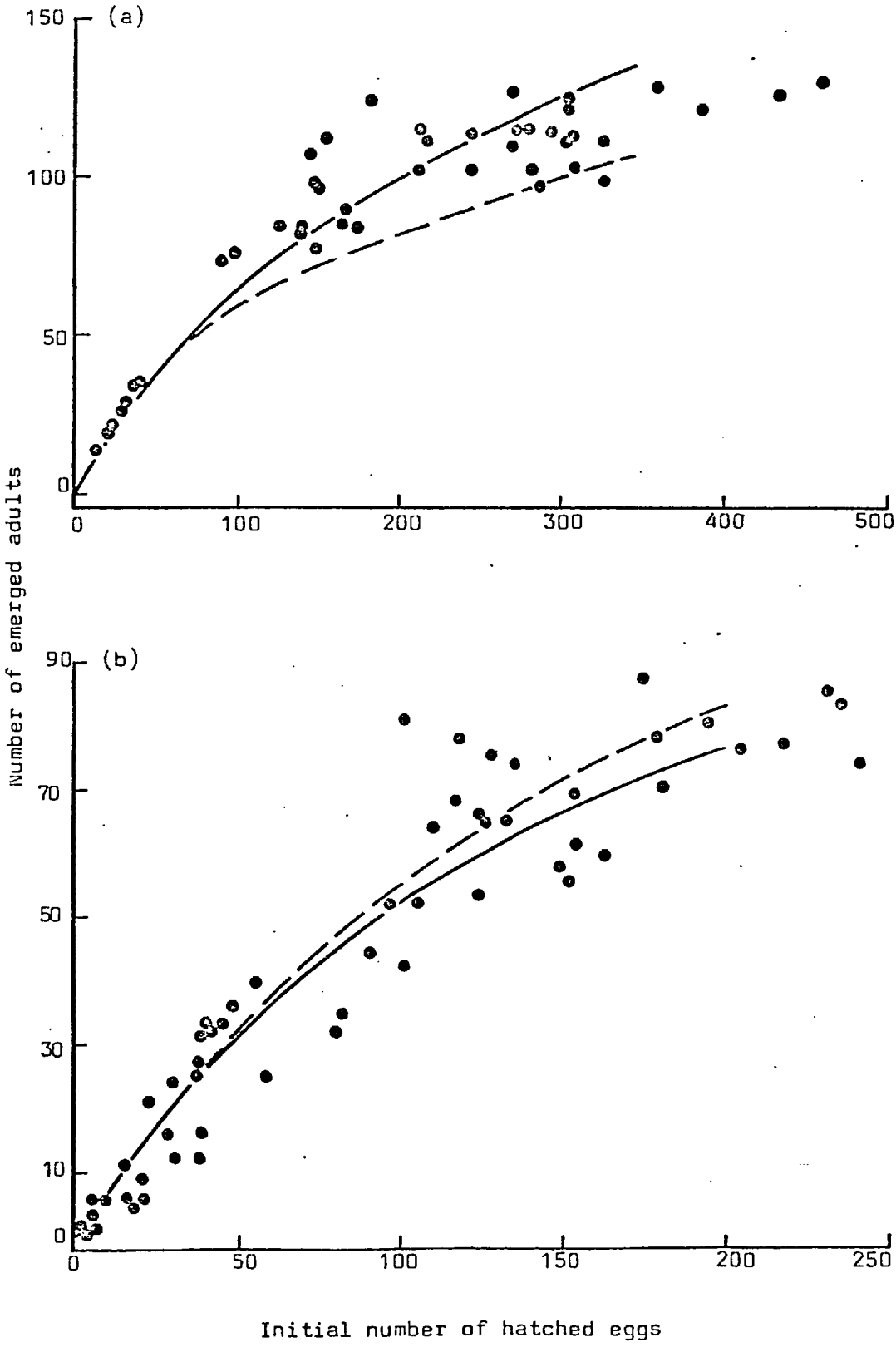
In order to compare model predictions with some observed, independent results, it is useful to return to the experimentally determined reproduction and larval survival curves discussed in the previous chapter. In these experiments the total number of hatched eggs and adult progeny arising from adults at different densities were scored and the results used to define the single generation reproduction curves discussed on page 58 . Comparable, predicted reproduction curves may also be obtained by linking together the oviposition and larval submodels. The details of how this was achieved are given in the next section. In principle, the number of recruits to the larval stage at different adult densities was determined from the predicted number of hatched eggs, and the subsequent predicted larval development and competition (from the larval submodel) then determined the number of surviving adult progeny. Since oviposition

occurred over several days, the recruitment to the larval stage was also distributed through time. The larval survival was determined by both intrastage and interstage competition and it is the predicted outcome of this competition which is being considered here.

The observed and predicted survival from the egg to adult stages is shown over a range of hatched ednsities in figure 4.16a for C. chinensis and figure 4.16b for C. maculatus. Two predicted curves are given in each figure; the broken lines give the predictions when the initially estimated competition matrices were used and the solid lines give the predictions when the revised matrices were used. The predicted curves do not span the entire range of observed egg densities since the number of hatched eggs predicted by the model does not exceed 344 for C. chinensis or 201 for C. maculatus. However, as larval competition is largely of the contest type it is reasonable to assume that an extension of the predicted curves to cover the remaining portion of the data would not misrepresent the expected outcome at these slightly higher densities.

The predictions for C. chinensis were in reasonable agreement with the data although the models seemed to predict a slightly more undercompensatory density dependent process than was indicated by the data. The prediction from the revised matrix gave a better description of the data than that from the initially estimated matrix which generally underestimated larval survival. The model for C. maculatus provided a good description of the observed results and here the predictions given by the two matrices were similar. The general agreement in both species is particularly encouraging since these data have not been used in quantifying any of the parameters in the model and hence provide independent information for comparison with model predictions.

FIGURE 4.16 The number of adult survivors at different densities of hatched eggs arising from single generation experiments for C. chinensis (a) and C. maculatus (b). The simulation model was used to provide a predicted curve from both the initially estimated (broken line) and revised (solid line) competition coefficient matrices.

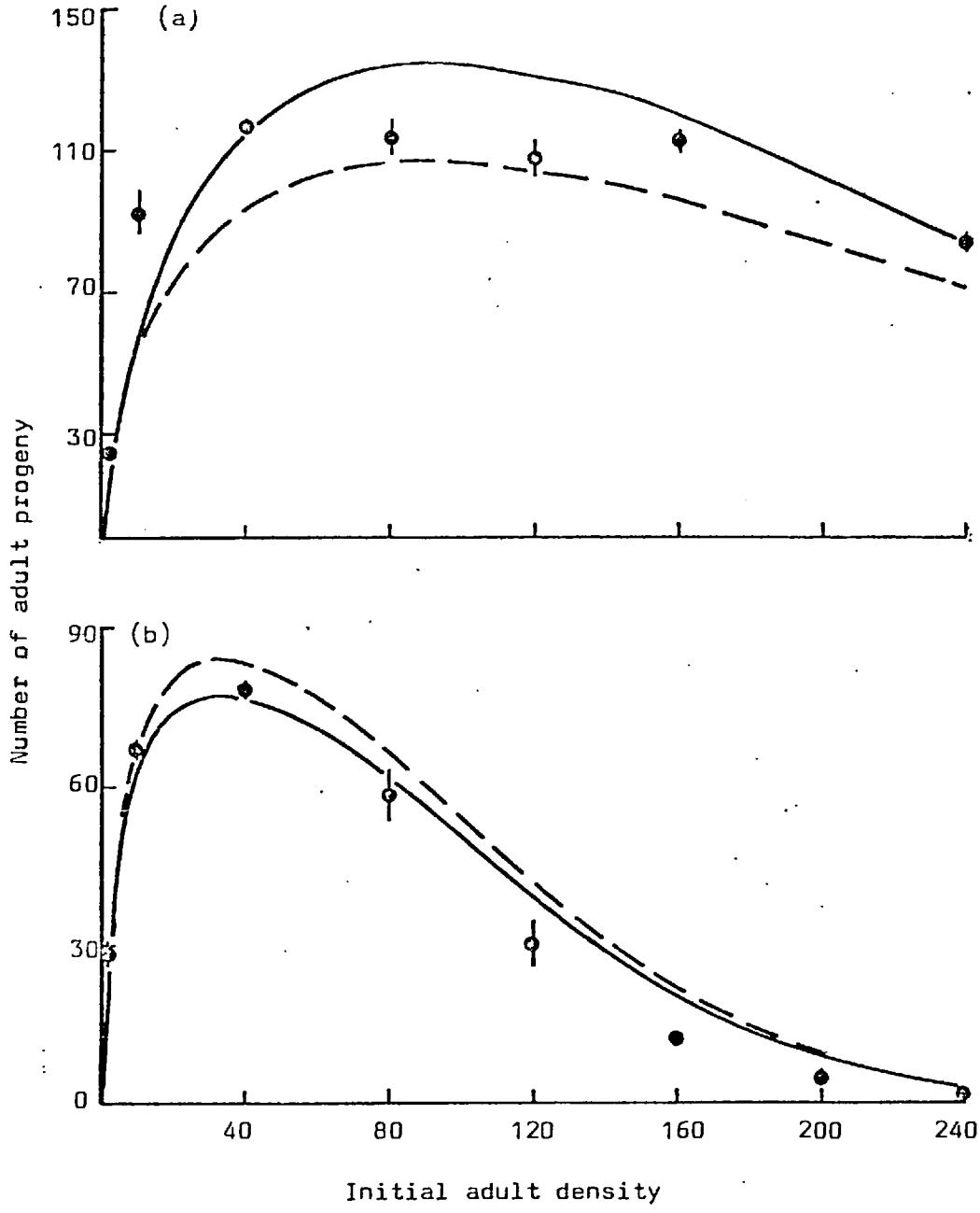

(a)
150
100
50
0
0
100
200
300
400
500
(b)
90
70
50
30
10
0
0
50
100
150
200
250
Number of emerged adults
Initial number of hatched eggs

The predicted and observed number of adult progeny at different adult densities are shown for both species in figure 4.17. It should be recalled that adult density dependence and egg mortality are of considerable importance in determining the shape of these curves, and consequently they must be viewed with caution when considered as validation of the larval submodel. The predictions for both species, however, were in reasonable agreement with the observed data and the predictions given by the revised competition matrix (solid lines in figures 4.17a, b) provided a better description than was provided by the initially estimated matrices. A few points require discussion. The C. chinensis predicted reproduction curve (given by the revised matrix) grossly underestimates the number of progeny from 10 pairs of adults due largely to an underestimate of the number of eggs laid at this density. The overestimation of the number of progeny at moderate densities in this species is due to the underestimation of larval mortality. Finally, at high densities of C. maculatus there were fewer observed progeny than were predicted by the model. As discussed on page 78 this was due to a higher mortality in hatching larvae at these densities than at lower adult densities and the model as here developed does not consider this problem.

4.4.3 Long-term simulations of Callosobruchus populations

The final portion of this investigation into the detailed modelling of these Callosobruchus species is to consider the consequences of using the oviposition and larval submodels to predict their long term population dynamics. Since the model as developed predicts the development of a population in a finite resource it was necessary before simulating the dynamics of the populations of these species to specify a schedule by which the population's resources, in this case the cowpeas, would be renewed. The details of the food renewal

FIGURE 4.17 The observed and predicted single-generation reproduction curves for C. chinensis (a) and C. maculatus (b). The broken lines give the predictions from the simulation model with the initial competition matrix and the solid lines give the predictions from the revised competition matrix. See text for discussion. Data given as mean ± s.e.


(a)
150
110
70
30
(b)
90
60
30
0
Number of adult progeny
40
80
120
160
200
240
Initial adult density

regime adopted were designed to mimic a procedure for studying the long-term dynamics of laboratory Callosobruchus populations developed by Dr. M. P. Hassell of the Department of Zoology, Imperial College, London. Populations are initialized by placing adults with a fixed weight of fresh beans and are left with those beans for 21 days. At this time any remaining live adults are provided with fresh beans and the old beans are kept for a further 21 days to permit immature individuals in these beans to complete their development. During this period adults emerging from the old beans are transferred each day to the dish containing the new beans. After this second 21 day period the old beans are discarded, and any live adults are transferred to a new container with fresh beans. The beans on which they were ovipositing are again kept for 21 days and any adults emerging are transferred daily to the new beans. This procedure is continued as long as required. After the initial 21 days the population is characterized by two sets of beans, one in which larvae are developing and no oviposition takes place (the "breeding" container) and one in which both oviposition and larval development take place (the "oviposition" container). This culturing practice is similiar to those used by other workers for the study of long-term populations of Callosobruchus species (e.g. Utida 1967; Fujii 1968).

In reporting the results of the simulations it is useful to consider the growth of a population in terms of generations. A useful definition of what constituted a single "generation" in these long term simulations, where generations may in principle overlap, was to consider all the individuals developing from eggs laid on one set of beans as a single generation. This definition worked well for C. maculatus where the first adults appeared on day 21 and there was little overlap between the eggs of two generations.

In C. chinensis, where adults first appeared 18 days after oviposition, there was some overlap between two successive generations since eggs laid by adults emerging in the oviposition chamber would be considered as part of the previous generation. However, these few late recruits to the egg stage represented only a small proportion of the total eggs laid on one set of beans. Furthermore, few of the larvae developing from these eggs survived beyond the second instar due to interstage competition. Consequently, there was no appreciable overlap between adults of successive generations and this definition was also used in considering the simulation results for this species.

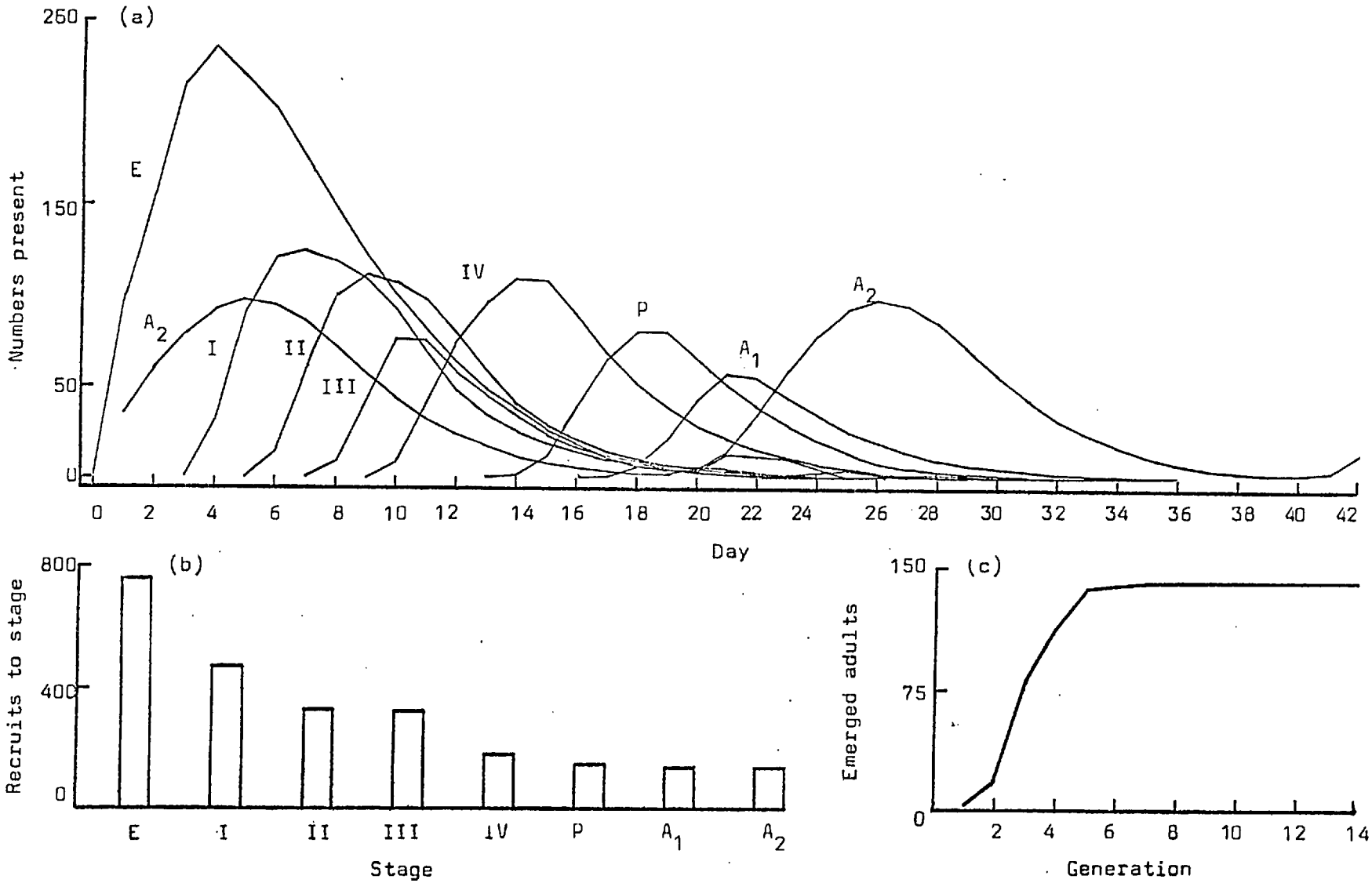
There were only two serious problems to overcome in the linking of the oviposition submodel to the larval submodel. Firstly, the parameters of the oviposition submodel were estimated from experiments with a fixed weight (3.70g) of resource which represented about 15 beans. The parameters of the larval submodel, however, were estimated from experiments where larval density was considered at the "per bean" level. Consequently it is necessary to make some assumption about the distribution of eggs oviposited on the beans by this species. This problem has been considered by Utida (1943b) and Iwao (1968) for C. chinensis and by Mitchell (1975) for C. maculatus. In both species adults tend to oviposit uniformly on beans at low adult densities and C. chinensis oviposits at random at high adult densities. However, in the simulations reported here the density of eggs per bean was considered uniform at all densities resulting in equal numbers of larvae in all of the beans present throughout larval development. This simplifying assumption is unlikely to have had any serious effect on the predictions of the models. The contest competition during the larval stage would in any case cause the distribution of individuals among beans to become more regular as develop-

ment progressed (Utida 1943b). The only important consequence of the assumption of uniform distribution of eggs might be to predict slightly higher equilibrium densities than if a random distribution was considered.

The second problem to be faced was the modelling of larval mortality in beans from which individuals had emerged as adults. As individuals emerge from a bean, the density of competitors in the bean decreases. However, the amount of resource available to individuals remaining in the bean does not increase accordingly since it is consumed during larval development. In order to account for this, the number of competitiors in beans in the breeding container was considered to consist of those present in the beans (as usual) plus the number of individuals which had entered the fourth instar stage at any time during the development of larvae in those beans. In this way the exploitation of the beans could be easily accounted for; the fourth instar was used instead of emerged adults because of the previously discussed problem of estimating competition coefficients between the pre-emergent adults and any stage other than the first instar.

The complete model was now used to simulate the growth of the Callosobruchus populations subject to the particular food renewal schedule discussed above. These simulations are shown in figures 4.18 and 4.19. Populations of C. chinensis started with a single pair of adults showed an initially sigmoid but subsequently monotonic approach to a stable equilibrium (figure 4.18c). This is in accord with much of the data in the literature on the long term dynamics of this species (see page 101 and figure 3.11). After the population reached equilibrium the numbers of individuals entering each stage and the numbers of individuals present daily in each stage were constant in successive generations. This equilibrium age structure was reached

FIGURE 4.18 The results of the model simulations for C. chinensis using the revised competition coefficient matrix. (a) the partial population curves for a single generation at equilibrium. (b) the number of individuals entering each stage in a generation at equilibrium. (c) the predicted growth of a population started from a single pair of adults. The symbols next to the curves in (a) represent the various stages as follows: E, eggs; I-IV, the four larval instars; P, pupae; A_1, pre-emergent adults; A_2, emerged adults. See text for discussion.


(a)
260
150
50
0
Numbers present
E
A2
I
II
III
IV
P
A1
A2
0 2 4 6 8 10 12 14 16 18 20 22 24 26 28 30 32 34 36 38 40 42
Day
(b)
800
400
0
Recruits to stage
E I II III IV P A1 A2
Stage
(c)
150
75
0
Emerged adults
2 4 6 8 10 12 14
Generation

regardless of the initial density or composition of the population. The numbers of individuals entering each stage (figure 4.18b) indicate the relative importance of mortality in the different stages. There was a large mortality of eggs (38%) due to adult trampling. Larval density dependent mortality accounted for losses in the first (30%) and third (45%) instars. There was little mortality in the second instar in accord with the lack of competition in this stage. There was only moderate mortality in the fourth instar stage (17%) since prior interstage competition had reduced the size of the larval populations to a level near the carrying capacity of the beans. There was also little mortality in the pupal stage and none in the pre-emergent adult stage. Figure 4.18a shows the predicted partial population curves for the inidividuals present in a set of beans from the first day in the oviposition chamber to day 42 when they were discarded. The second generation of adults appearing after day 21 was actually present in the oviposition chamber but is included in the figure for convenience. It is noteworthy that the adults of the two generations overlap very little. The skewed nature of the partial population curves was due partly to the skewed distribution of development but also to the skewed initial recruitment to the egg stage due to decreased oviposition after the density of eggs has increased. A distinction must be made here between the partial population curve for the egg stage shown in figure 4.18a which depicts the number of live eggs present, and the total number of live eggs, dead eggs and egg shells which were present on the beans. This latter cumulative total number of eggs was used to determine the reduction in fecundity due to egg density as it seems unlikely that adults of these species are capable of distinguishing hatched eggs from live or dead eggs. The minor increase in the number of eggs present which occurred on day 21 arose from oviposition by the few adults which emerged before

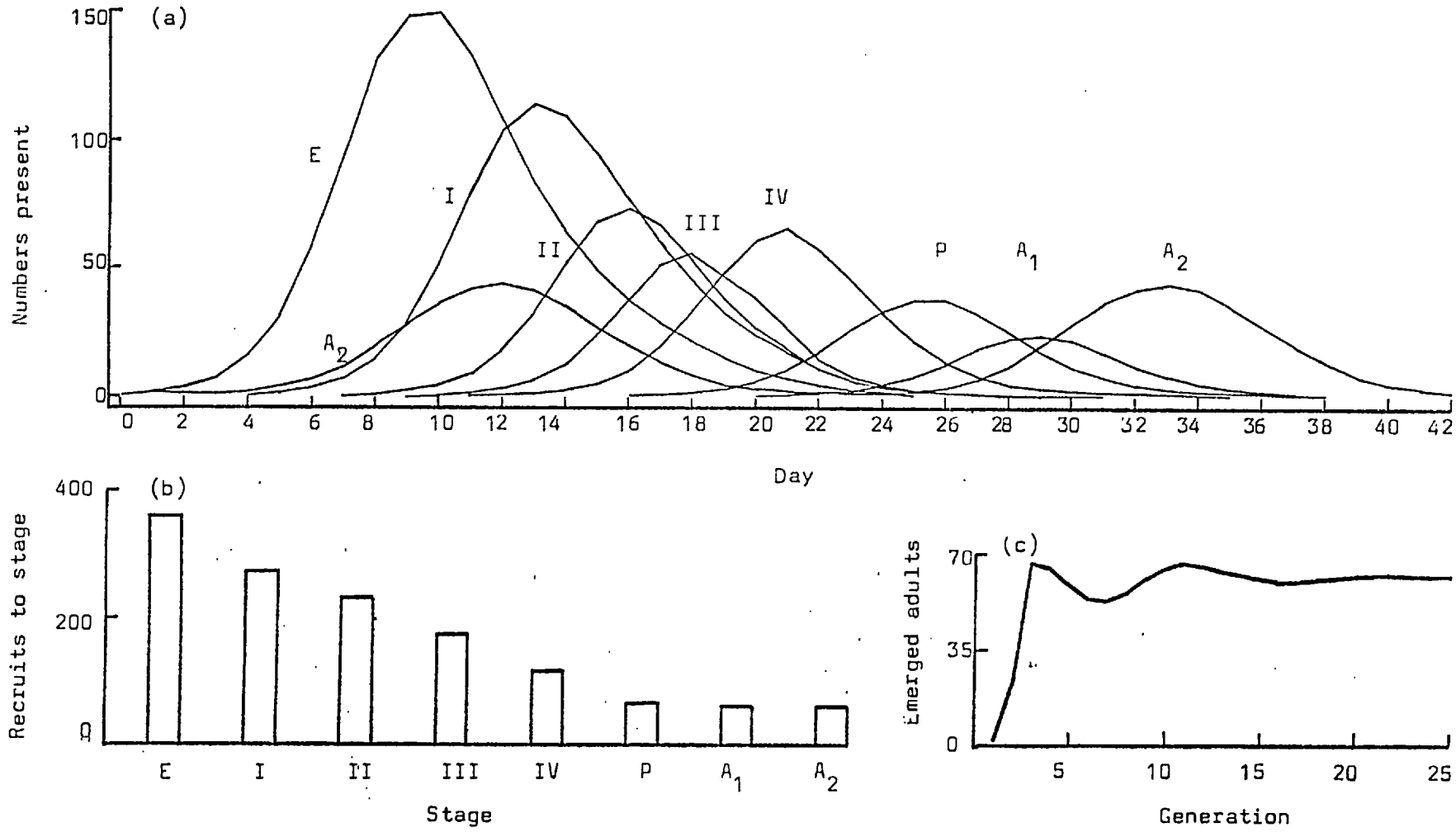
the beans were transferred to the breeding container. Finally it may be noted that the predicted equilibrium adult population (141 individuals) was higher than that given by the models developed in the previous chapter (approximately 110 individuals).

The most useful validation of these simulations results is to compare them with results of long term studies on the particular strain of C. chinensis used here. Such studies have been undertaken by Dr. M. P. Hassell (personal communication). In his studies 24.5 g of cowpea were used. The equilibrium was approached monotonically and the equilibrium density attained was approximately 800 adults, or 120 adults per 3.7 g of beans.

The predicted equilibrium (141 adults) was in general agreement with this value and it was concluded that the simulation model provides a reasonable representation of population growth and dynamics in this species.

The results of the C. maculatus simulations are shown in figure 4.19. The most notable difference between the two simulations was the oscillatory approach to equilibrium shown in figure 4.19c. This was not due to overcompensatory density dependence but rather to asynchrony between the developing population and the schedule of food renewal (the mean period for development from egg to adult in this species was approximately 25 days). This asynchrony caused an oscillation with a period of approximately 10 generations. The decreasing phase of each oscillation occurred when the adult population was emerging late in the sampling period and consequently some immature individuals were discarded with the beans on day 42. The increasing phase corresponded to generations where the adults emerged earlier in the sampling period and had fewer progeny lost when the beans were discarded. These oscillations are in contrast with those reported in the

FIGURE 4.19 The results of the model simulations for C. maculatus using the revised competition coefficient matrix. (a) the partial population curves for a single generation at equilibrium. (b) the number of individuals entering each stage in a generation at equilibrium. (c) the predicted growth of a population started from a single pair of adults. The symbols next to the curves in (a) represent the various stages as follows: E, eggs; I-IV, the four larval instars; P, pupae; A_1, pre-emergent adults; A_2, emerged adults. See text for discussion.


(a)
Numbers present
150
100
50
0
E
I
II
III
IV
P
A1
A2
A2
0 2 4 6 8 10 12 14 16 18 20 22 24 26 28 30 32 34 36 38 40 42
Day
(b)
Recruits to stage
400
200
0
E I II III IV P A1 A2
Stage
(c)
Emerged adults
70
35
0
5 10 15 20 25
Generation

literature showing a period of two generations. As previously discussed (see page 78), however, these two-generation oscillations were due to overcompensatory larval competition. In the system studied here larval competition was compensatory and consequently the differences between these simulation results and the results of long term studies in the literature do not reflect any serious deficiencies in the model. In spite of the differences between the food renewal schedule and the developmental period of this species, the population eventually reached a stable equilibrium with constant partial population curves and numbers entering each stage in successive generations. As before, this stable age-structure was independent of the size or composition of the initial population. At equilibrium, the predicted mortalities in the larval stages (figure 4.19b) were more constant and the partial population curves (figure 4.19a) were more symmetric than for C. chinensis. The equilibrium density predicted by the simulation model (61 adults per generation) agreed favourably with that predicted by the models of the previous chapter (approximately 60 adults).

The predicted equilibrium was in reasonable agreement with that observed in long term studies on this strain of C. maculatus (M. P. Hassell, personal communication). The observed equilibrium was 520 per 24.5 g of beans or approximately 79 per 3.7 g. There was also some indication in these studies of an oscillatory approach to equilibrium with a period of several generation, as was predicted by the model.

4.5 Conclusions

The most important contribution made in this chapter to the modelling of insect populations was the development of the cohort life-table model of section 4.2.2. This model has two features of distinct value. (i) It may be used to analyse cohort life-table data and provides readily interpretable parameters of biological importance.

(ii) Its simple predictive structure permits the easy incorporation of the estimated parameters into a population submodel. Furthermore, the two recursive relationships (equation 4.17 and 4.20) which define the model provide a framework in which a number of important processes may be included. In this chapter the process of density dependent mortality was added to the life-table model in order to simulate a well known regulated laboratory system, but the model may also be extended to include other processes such as predation or parasitism, as will be seen in chapter 6.

Chapter V. INTERSPECIFIC COMPETITION.

5.1 Introduction

The previous two chapters have outlined two distinct approaches for constructing models of single-species populations: (i) where density dependent processes have been described by simple functions which are then treated directly as population models (chapter 3) and (ii) where the processes of population growth and development have been described using complex formulations (chapter 4). In this chapter both approaches will be used to develop models for two competing populations using the results of some laboratory investigations on the interactions between Callosobruchus chinensis and C. maculatus. This will enable interspecific competition to be quantified and will lead to the development of a single age-class two-species model, a two age-class two-species model and a two-species simulation model.

This chapter is divided into two sections. Firstly, there is a brief outline of the development of simple two-species models and data are presented which permit the parameters required for the single and two age-class models to be quantified. In the second section the simulation model developed in the previous chapter is modified to include interactions between the two species. The necessary parameters are quantified and the dynamics of the two-species simulation model are presented.

5.2. Constructing simple two-species models

5.2.1 The models

Models for the growth of two competing species were initially introduced by Lotka (1925) and Volterra (1926), who independently proposed the familiar two-species logistic growth model:

$$\frac{dX}{dt} = rX(1 - a(X + \alpha Y)), \qquad (5.1a)$$

$$\frac{dY}{dt} = r'Y(1 - a'(Y + \alpha' X)). \qquad (5.1b)$$

In this model the growth rate of species X (dX/dt) is determined by the species' intrinsic rate of increase r, the carrying capacity for species X (1/a) and the density of individuals of both species X and Y (similarly for species Y). The parameters α and α' in equation 5.1 reflect the per capita equivalence in density between the two species and are commonly termed competition coefficients. The outcome of the interspecific interaction in this model is determined by the relative carrying capacities for the two species and the intensity of interspecific competition. There is a two species equilibrium only when the zero-growth isoclines for the two species intersect and the product $\alpha\alpha' < 1$. More appropriate for the study of many insect populations is the general discrete-time formulation of a two-species model (Hassell & Comins 1976):

$$X_{t+1} = X_t f(X_t + \alpha Y_t), \qquad (5.2a)$$

$$Y_{t+1} = Y_t f'(Y_t + \alpha' X_t), \qquad (5.2a)$$

where the per capita reproduction of species X is a function of the density of both species (and similarly for species Y). The functions f and f' determine how density affects reproduction, and the effects of interspecific competition are defined as in equation 5.1 by the competition coefficients α and α'.

Equation 5.2 was used here as a basis for the single age-class models for competition between C. chinensis and C. maculatus. The development of this model follows that of the single species models in chapter 3, where the density dependent function

$$f(X) = \lambda (1 + (aX)^b)^{-1} \qquad (5.3)$$

was used to describe the single-species reproduction curves. In this equation, λ is the finite net rate of increase and the form

of density dependence is determined by the parameters a and b. The parameter a is a scaling constant and the parameter b determines the severity of the density dependence. As b increases from zero (no density dependence) the severity of competition increases. The roles of the parameters a and b have been fully discussed in chapter 2. Substitution of the equation 5.3 into the general model of equation 5.2 yeilds the single age-class model used here:

$$X_{t+1} = \lambda X_t(1 + a(X_t + \alpha Y_t)^b)^{-1}, \qquad (5.4a)$$

$$Y_{t+1} = \lambda' Y_t(1 + a'(Y_t + \alpha' X_t)^{b'})^{-1}. \qquad (5.4b)$$

The construction of the two age-class two-species model similarly followed the developments in chapter 3. The single-species two age-class models were based on the premise that the adults and immature stages of these species do not interact, and took the form

$$x_{t+1} = X_t f(X_t), \qquad (5.5a)$$

$$X_{t+1} = x_{t+1} g(x_{t+1}). \qquad (5.5b)$$

Here the populations consist of adults X and "larvae" x (which includes all the nonovipositing stages). Oviposition by the adults is governed by the density dependent function f and larval survival is determined by the function g. This model may be easily modified to include interspecific competition:

$$x_{t+1} = X_t f(X_t + \alpha Y_t), \qquad (5.6a)$$

$$y_{t+1} = Y_t f'(Y_t + \alpha' X_t); \qquad (5.6b)$$

$$X_{t+1} = x_t g(x_t + \beta y_t), \qquad (5.6c)$$

$$Y_{t+1} = y_t g'(y_t + \beta' x_t), \qquad (5.6d)$$

where y and Y are the larval and adults of the second species and the parameters α and β are the competition coefficients for the larval and adult stages, respectively. This model is similar to that developed by Hassell & Comins (1976), although these authors did not consider interspecific adult competition. As for the single

age-class model, the form of the density dependent functions f and f' used was equation 5.3. The similar density dependent model

$$g(X) = d(1 + (cX)^e)^{-1} \qquad (5.7)$$

was used for the functions g and g'. This model differs from equation 5.3 only in the interpretation of the parameter d which specifies the density independent proportionate larval survival; the parameter d is constrained such that $1 \geq d \geq 0$.

When equations 5.4 and 5.6 were fitted to the data discussed below, the values of the parameters λ, a, b, c, d and e used for each species were those estimated in chapter 3 from single species experiments. Consequently the only parameters which required estimating were the competition coefficients α and β. The values of these parameters were found which minimized the sum of squared differences between model predictions and observed results.

5.2.2 Interspecific competition in Callosobruchus species

In chapter 3, the effects of intraspecific competition on reproduction in *C. chinensis* and *C. maculatus* were determined by experiments in which various numbers of adults were confined with a fixed weight of cowpeas and the numbers of eggs laid by these adults and the number of progeny surviving to the adult stage were scored. This experimental design has also been used to investigate interspecific competition in the following way. Various combinations of densities of 0-2½ hour old pairs of adults of the two species were placed in small plastic dishes (3.5 cm in diameter and 4.0 cm high) with 3.70 g of cowpea. These experimental dishes were kept at 30°C, 70% relative humidity until the adults had died and sufficient time had passed to allow all the viable eggs to hatch. The number of total and hatched eggs of both species in each dish were counted and, after the adult

progeny had emerged, the total number of progeny of both species was scored. Six initial adult densities of both species were used and replicated as in table 5.1.

Figure 5.1 shows the number of progeny of C. chinensis and C. maculatus at varying combinations of densities of both species. The solid lines are given by equation 5.4 with the values of the parameters shown in table 5.2a. The estimates of the competition coefficients were examined by comparing the mean square ratio discussed on page 121 with the appropriate value of the F distribution and in both cases the parameter was judged significant with $p < .001$. The predicted curves for C. chinensis agree well with the observed results at C. maculatus densities of two and 10 individuals, but generally underestimate the number of survivors at higher C. maculatus densities. The data for C. maculatus are less well described by the fitted model although this may be partly a result of the imprecision of the model when describing only the intraspecific data as discussed on page 58 . The estimated values for the competition coefficients given in table 5.2a clearly indicate a competitive superiority of C. maculatus: the value of the coefficient relating the density of C. maculatus to C. chinensis was more than eight times greater than that relating C. chinensis to C. maculatus. This high value raises a question about the use of previously estimated values of the species-specific parameters in the analysis of interspecific competition. If the parameter α is very large, then the effective density of competitiors $X + \alpha Y$ in equation 5.4 may exceed the range of observed intraspecific densities available for quantifying the species-specific parameters. Since the value of α for C. chinensis was much greater than unity the predicted curves at high C. maculatus densities in figure 5.1a arise from effective densities

TABLE 5.1 The number of replicates at various combinations of initial adult densities of *C. chinensis* and *C. maculatus* in the single-generation experiment.

C. chinensis	*C. maculatus* 2	10	40	80	120	160
2	5	5	3	2	2	2
10	3	5	4	2	2	2
40	4	4	5	1	1	1
80	2	3	1	2	1	0
120	0	3	0	1	1	1
160	1	2	1	0	1	1

FIGURE 5.1 The effect of interspecific competition on the reproduction curves of (a) C. chinensis and (b) C. maculatus. The single-species reproduction data of chapter 3 are identified by the symbol (+). The other symbols indicate the density of the competing species as follows: O-2; ◐-10; ●-40; ◑-80; △-120; ▼-160. Solid lines give the predictions of the fitted model of equation 5.4 with the parameter values of table 5.2a.

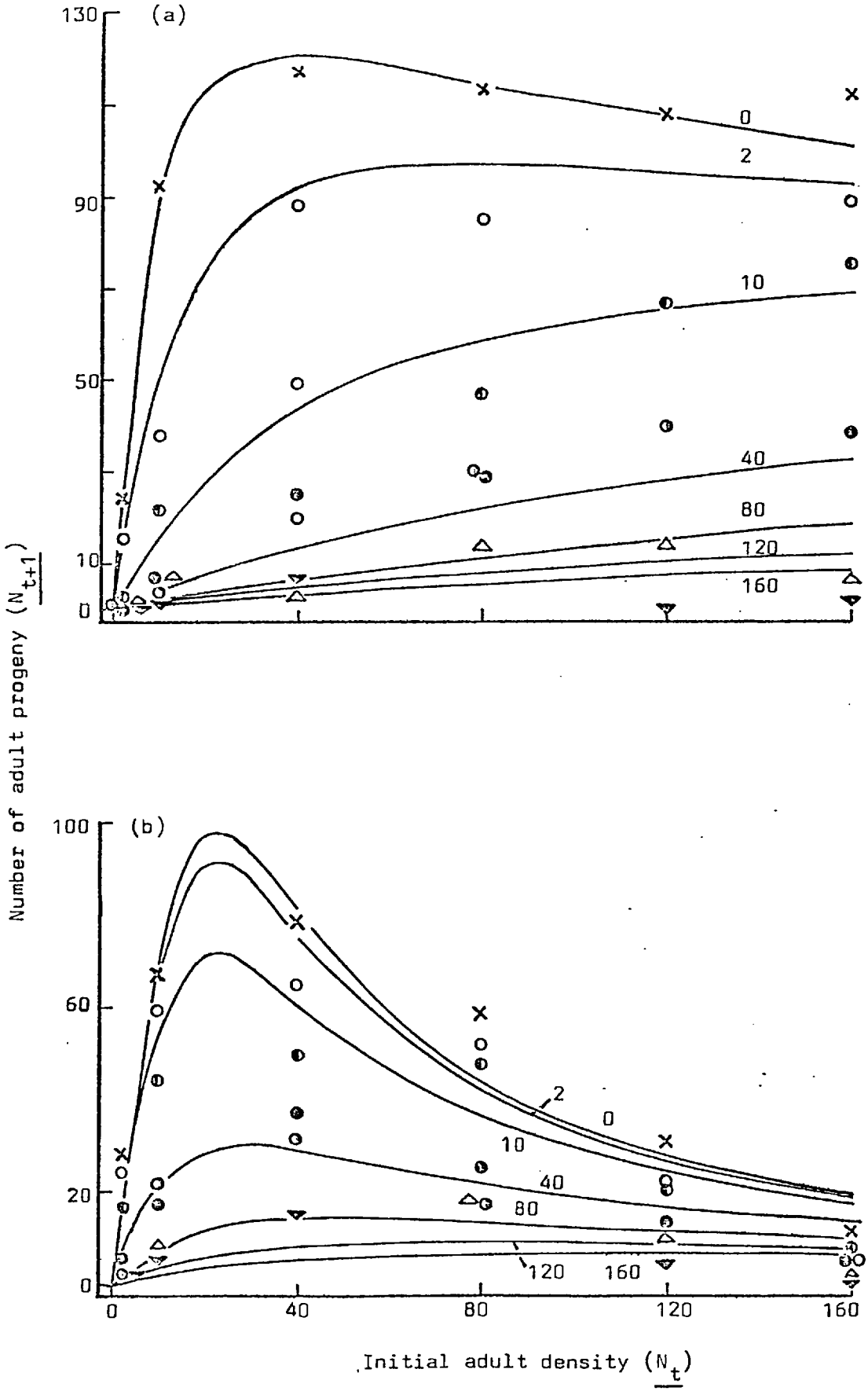

(a)
130
90
50
10
0
0
2
10
40
80
120
160
(b)
100
60
20
0
0
2
10
40
80
120
160
40
80
120
160
Number of adult progeny (N_{t+1})
Initial adult density (N_t)

TABLE 5.2 The estimated values for the parameters of the single and two age-class two-species models. The values for λ, a, b and d are taken from the analyses in chapter 3. The values for α were experimentally determined as discussed in the text.

Parameter	C. chinensis	C. maculatus
	(a) reproduction curves, figure 5.1	
λ	15.687	7.9254
a	0.078738	0.040590
b	1.2501	2.2178
α	6.0016	0.727149
	(b) total fecundity, figure 5.2	
λ	22.928	17.5702
a	0.073775	0.034789
b	0.50905	1.1237
α	50.0316	0.231029
	(c) hatched eggs, figure 5.3	
λ	11.465	13.294
a	0.017429	0.030014
b	1.7737	2.4806
α	5.61171	0.365241
	(d) larval survival, figure 5.4	
d	1.0000	0.63335
a	0.0047084	0.0039716
b	1.3738	1.9503
α	2.66083	1.92314

well outside the range used in the intraspecific experiments. Consequently, it is unsafe to draw any conclusions concerning possible nonlinearity in the competitive relationship, and more complex functions than the assumed species equivalence relation (i.e. constant α) were not considered here.

The data on total fecundity of C. chinensis and C. maculatus are shown in figure 5.2 together with the predictions from the parameter values in table 5.2b. As before, both estimated interspecific competition coefficients were significantly different from zero with $p < .001$. The fitted models provide a reasonable description of the data and it is clear that the C. chinensis adults were more severely affected than C. maculatus by the presence of the other species. The estimated value of α for C. chinensis is so large that its magnitude has little meaning; the predicted effective density of competitors at high C. maculatus densities exceeds the range of densities used in the intraspecific experiments by more than 3000 percent. This high value, however, does support the qualitative observation that the C. maculatus adults were having a large effect on the C. chinensis adults; similarly the small estimated value of the competition coefficient for the effect of C. chinensis on C. maculatus reflects the small observed reduction in fecundity of C. maculatus in the mixed species experiment.

The two-species, two age-class model of equation 5.6 requires a value of the number entering the larval stage as a function of the density of the adults of both species. In order to provide this, the data on the number of hatched eggs which occurred at different combinations of adult densities were considered (figure 5.3). The estimated values of the competition coefficients in table 5.2c were both significant ($p < .001$), and the resulting predictions provide a

FIGURE 5.2 The effect of interspecific competition on total fecundity of (a) C. chinensis and (b) C. maculatus. The single-species data from chapter 3 are identified by the symbol (+). The other symbols indicate the density of the competing species as follows: ○ -2; ◐ -10; ⊗ -40; ◑ -80; △ -120; ▼ -160. Solid lines give the predictions of equations 5.6a and 5.6b with the parameter values given in table 5.2b.

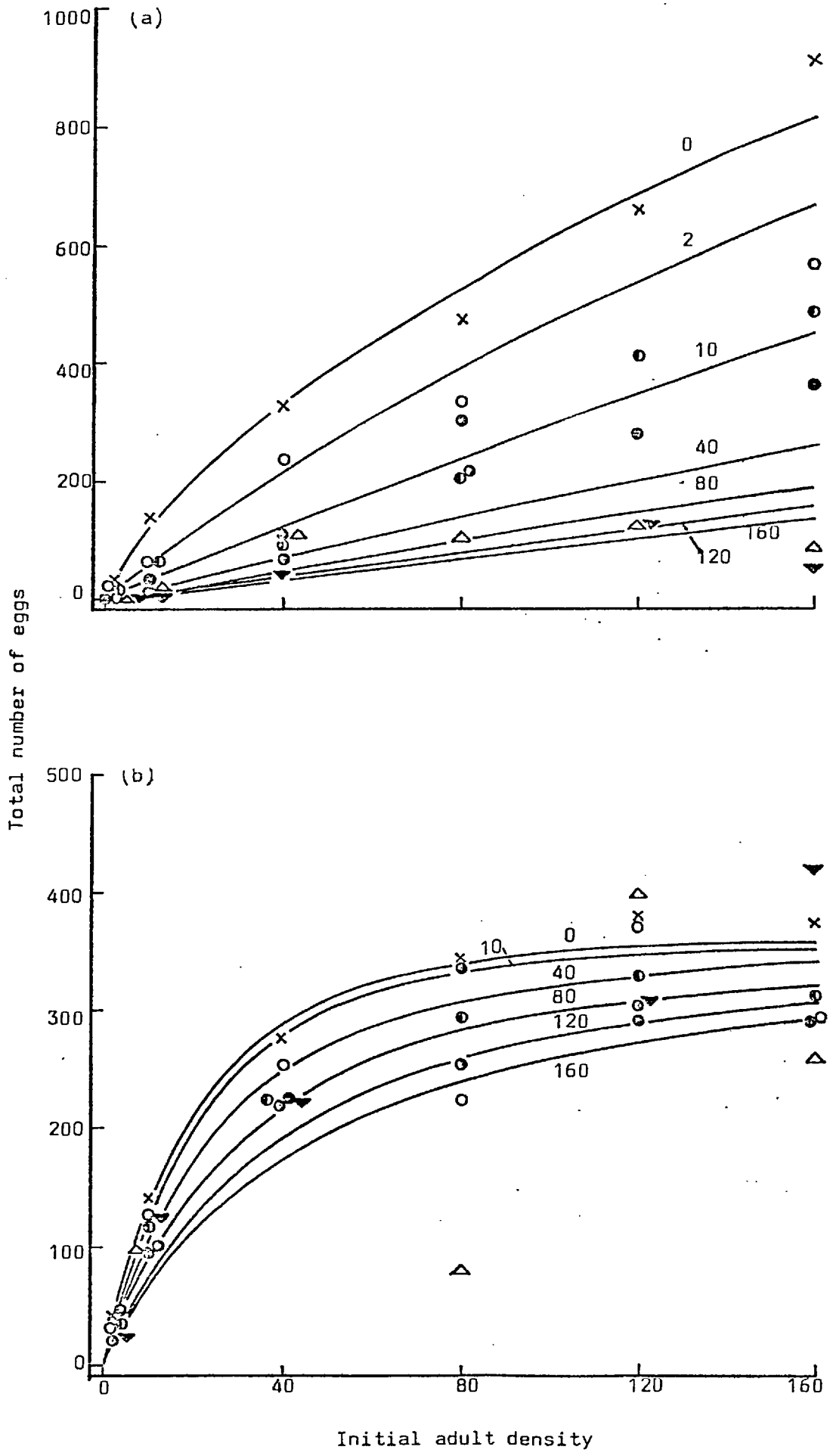

(a)
1000
800
600
400
200
0
0
2
10
40
80
120
160
(b)
500
400
300
200
100
0
0
10
40
80
120
160
0
40
80
120
160
Total number of eggs
Initial adult density

FIGURE 5.3 The effect of interspecific competition on the number of hatched eggs of (a) C. chinensis and (b) C. maculatus. The symbols indicate the density of the competing species as follows: ○ -2; ◐ -10; ◉ -40; ● -80; △ -120; ▼ -160. Solid lines give the predictions of equations 5.6a and 5.6b with the parameters in table 5.2c.

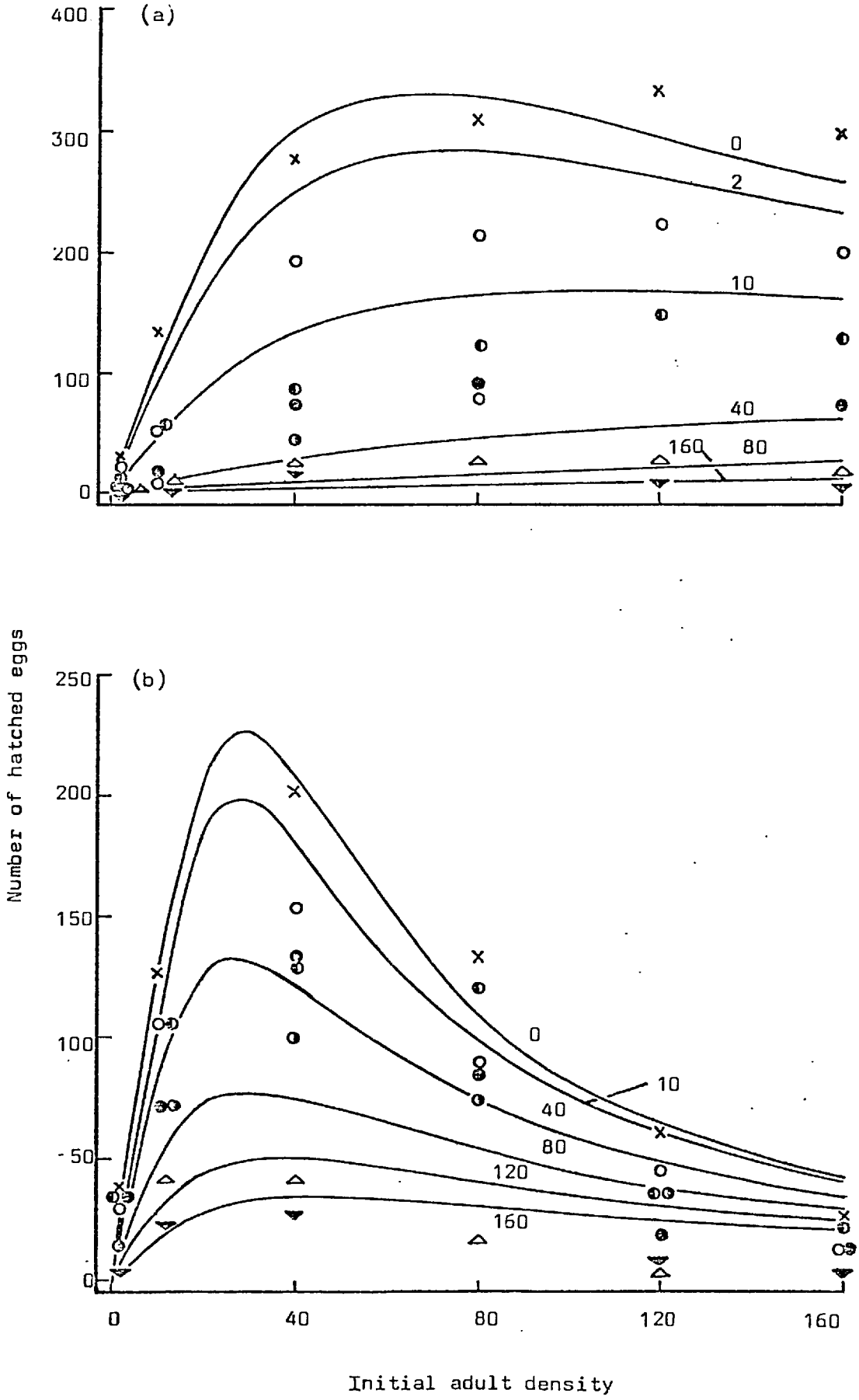
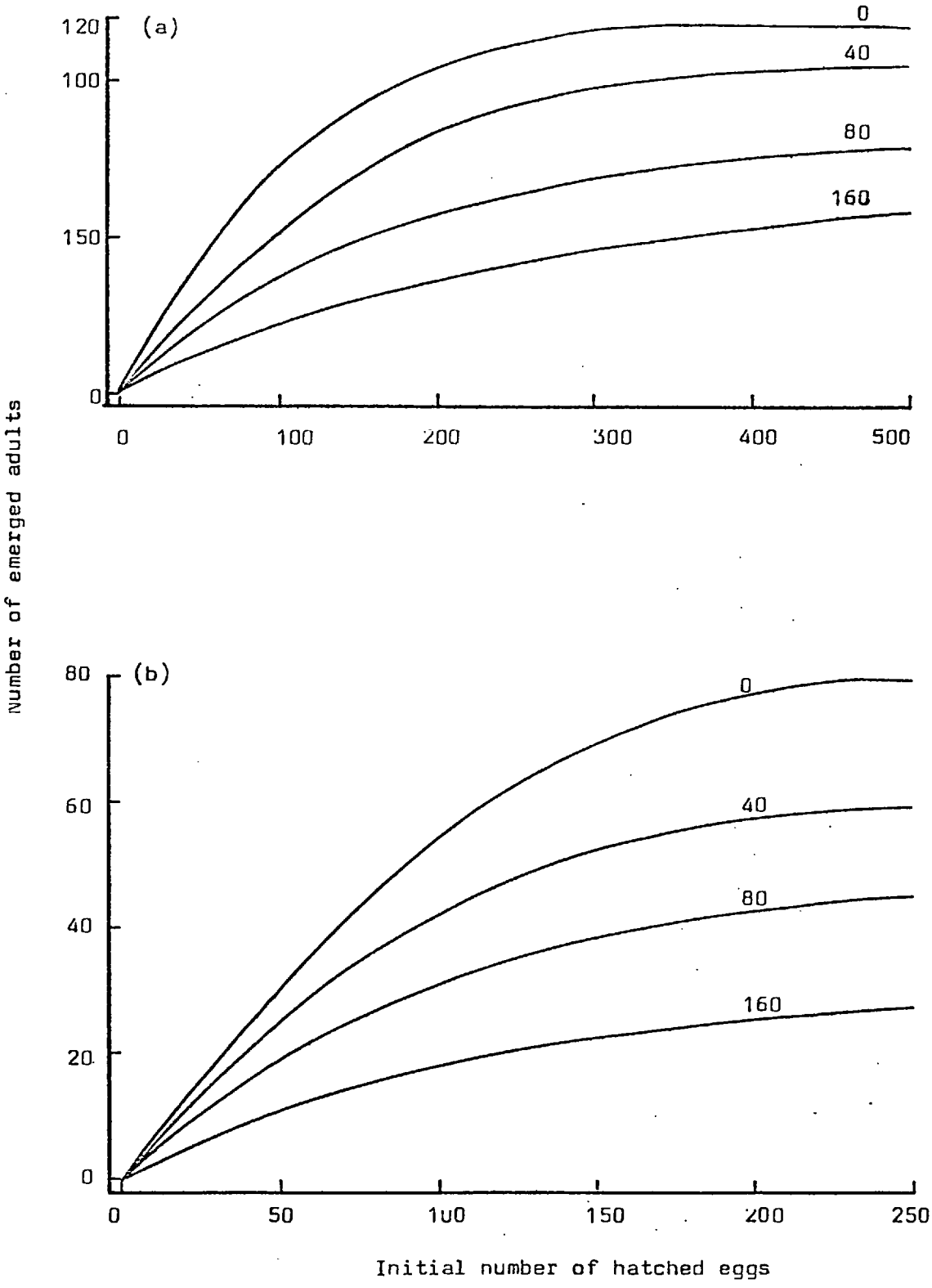

(a)
400
300
200
100
0
0
2
10
40
80
160
(b)
250
200
150
100
50
0
0
10
40
80
120
160
0
40
80
120
160
Number of hatched eggs
Initial adult density

FIGURE 5.4 The predicted effect of interspecific competition on larval survival. The predicted curves are from equations 5.6c and 5.6d with the parameter values given in table 5.2d. The initial density of competitors of the other species is indicated next to each curve.


(a)
120
100
150
0
0
100
200
300
400
500
0
40
80
160
(b)
80
60
40
20
0
0
50
100
150
200
250
0
40
80
160
Number of emerged adults
Initial number of hatched eggs

reasonable description of the data for both species. However, for C. chinensis the predictions overestimate the observed number of hatched eggs at low C. maculatus densities and underestimate the observations at high densities. The predicted number of C. maculatus eggs hatching at high densities of either species generally overestimates the observed numbers due to the original overestimation in the single-species model. The larger competition coefficient for C. chinensis indicates the competitive superiority of C. maculatus adults. However, as these data depend on the total number of eggs laid by both species, this finding merely emphasizes the previous conclusions on interspecific adult competition.

The data on the number of progeny surviving to adults at different hatched egg densities were obtained as discussed above, from which the interspecific larval competition in the two-age class model was quantified. The estimated values of both competition coefficients were significant ($p < .001$, table 5.2d) and examples of the predicted effects of interspecific density on larval survival are shown in figure 5.4. The similarity in size of the estimated competition coefficients indicate that the competitive effects between the larval stages of these two species are much more similar than in the adult stage. The slightly higher value for the effect of C. maculatus on C. chinensis probably reflects a slight advantage due to the larger size of C. maculatus larvae.

5.2.3 The predicted outcome of interspecies competition

The parameters values in table 5.2 now provide the necessary information to investigate the dynamics of competing populations of these two species. The values used for the single age-class model of equation 5.4 are given in table 5.2a and those for the two age-class

model in table 5.2c and 5.2d. It was also necessary to specify a sex-ratio for the two species (during parameter estimation the sex ratio had been assumed to be 0.50 for both species in accord with the experimental design), and the values determined experimentally in chapter 3 of 0.500 for C. chinensis and 0.451 for C. maculatus were used. It should be noted that the values given in table 5.2 for the parameters λ are per capita (not per female) net rates of increase. The dynamic properties of the two models are most easily discussed with reference to the predicted zero-growth isoclines for the two species shown in figure 5.5. The linear isoclines for the single age-class model shown in figure 5.5a (solid lines) were found by rearrangement of equation 5.4 after setting both $X_{t+1} = X_t$ and $Y_{t+1} = Y_t$. The value of X which provides no change in population size between successive generations is now given as a linear function of Y,

$$X = \left(\frac{1}{a}(\lambda - 1)\right)^{1/b} - aY, \qquad (5.8)$$

where the intercept on the abcissa is the single species equilibrium density X*. The two species equilibrium at the intersection of the two isoclines is unstable since the product of the competition coefficients exceeds unity. Any disturbance of the two populations from the equilibrium results in extinction of one or other of the species. The broken line in figure 5.5 divides the phase space into two regions which determine which species survives from any non-equilibrium population densities: densities which lie above the line result in the survival of only C. maculatus while those below the line result in the survival of C. chinensis. Examples of the predicted dynamics of population started at points A and B in figure 5.5a are shown in figure 5.6a and b. Finally it may be noted that the competitive superiority of C. maculatus predicted by its larger competition coefficient is reflected by the larger

FIGURE 5.5 The zero-growth iscolines predicted by the simple two species models. (a) The isoclines for the single age-class model. (b) The isoclines for the adult populations of the two age-class model. (c) The isoclines for the larval populations of the two age-class model. The equilibrium indicated by the intersection of the two isoclines in each case is unstable. The points A, B, C, and D correspond to the initial adult population densities in the examples of the two possible outcomes of competition in figure 5.6. See text for further discussion.

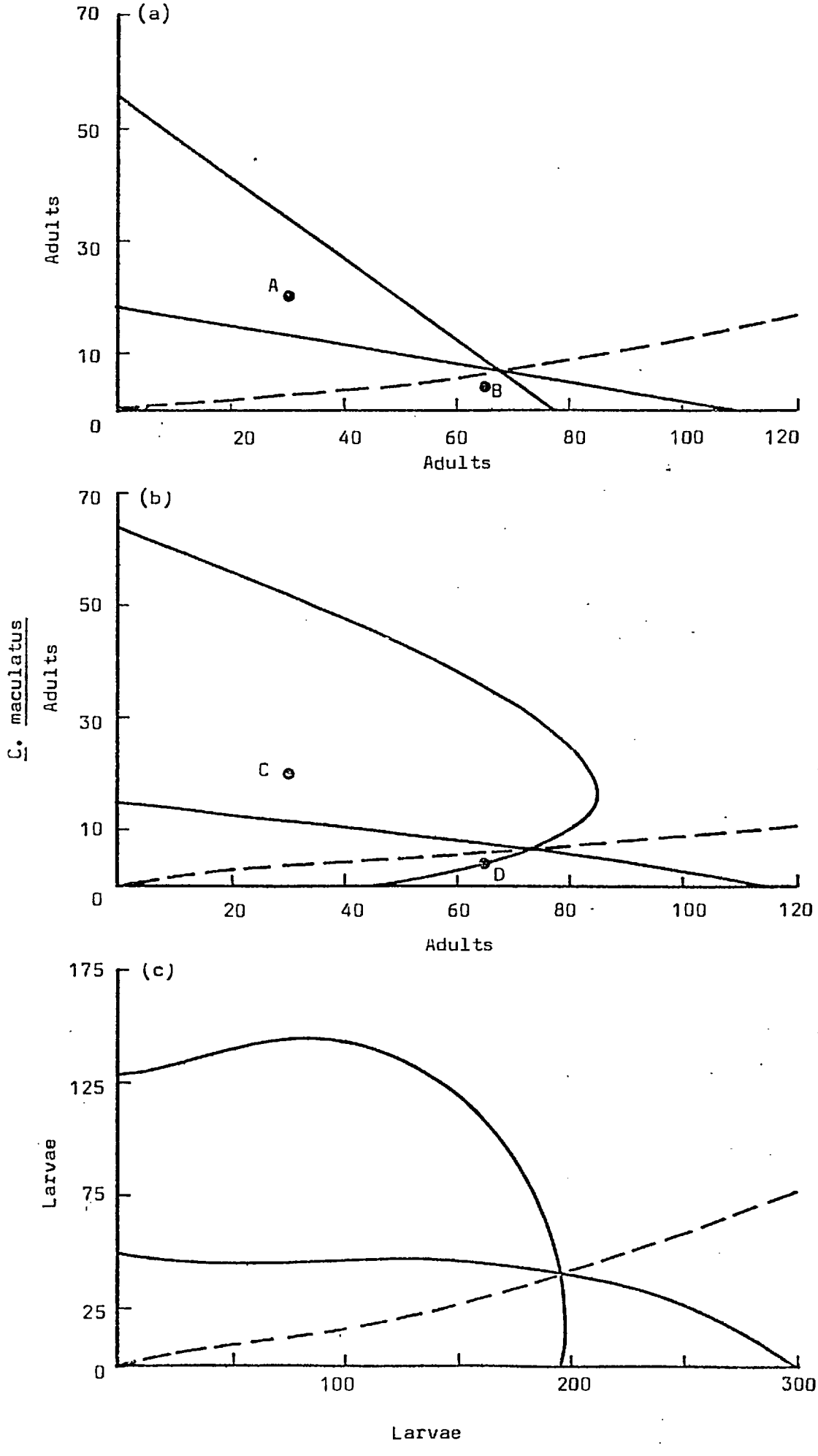
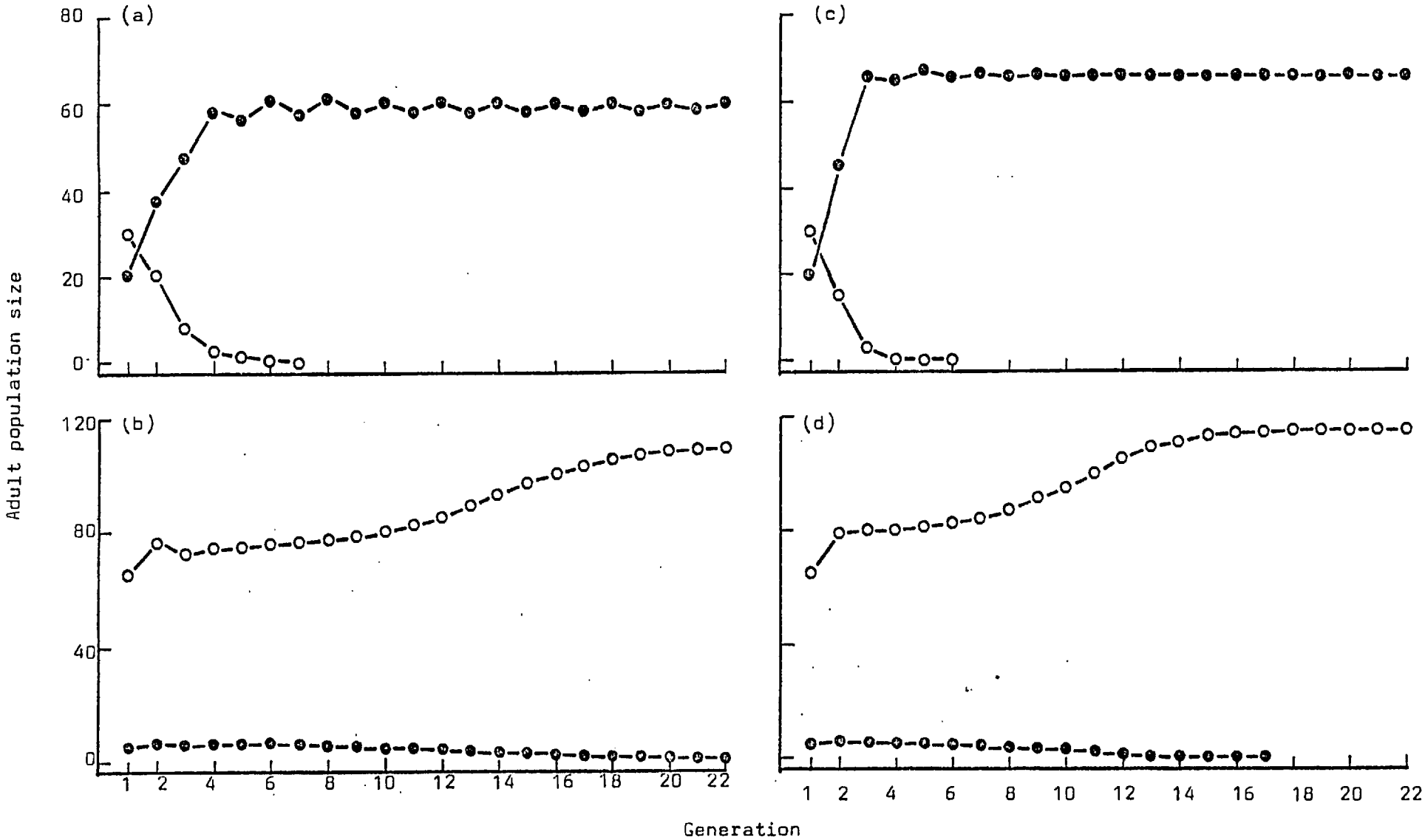

(a)
70
50
30
10
0
Adults
A
B
20
40
60
80
100
120
Adults
(b)
70
50
30
10
0
C. maculatus
Adults
C
D
20
40
60
80
100
120
Adults
(c)
175
125
75
25
0
Larvae
100
200
300
Larvae
C. chinensis

FIGURE 5.6 The outcome of interspecific competition as predicted by the single and two age-class models. Solid circles indicate C. maculatus. Hollow circles indicate C. chinensis. The points A, B, C and D in figure 5.5 correspond to the simulations in figures 5.6a, 5.6b, 5.6c and 5.6d. Note that there is not a stable equilibrium and that the outcome of competition depends on the initial densities.


(a)
(b)
(c)
(d)
Adult population size
Generation
80
60
40
20
0
120
80
40
0
1 2 4 6 8 10 12 14 16 18 20 22

region in the phase space which results in extinction of C. chinensis.

The zero growth isoclines for the adult and larval stages predicted by the two age-class model are shown in figures 5.5b and 5.5c. The isoclines cannot be determined analytically due to the large number of parameters so their positions were found numerically. The most notable feature of these isoclines is their complex shape which arises solely from the multiple age class structure of the model (Hassell & Comins 1976). The predicted adult and larval equilibria are, as in the single age-class model, unstable and once again the competitive superiority, particularly in the adult stage, of C. maculatus is emphasized by the relatively large portion of the phase space which results in the extinction of C. chinensis. The predicted dynamics of populations initiated by adult densities C and D are shown in figures 5.6c and 5.6d.

Both of these simple models predict an unstable equilibrium and indicate that C. maculatus would be the more likely survivor in the long-term mixed cultures of the species. Considerable evidence is available in the literature on the outcome of such long-term experiments and in no study was a stable equilibrium established. The successful species, however, has not been found invariably to be C. maculatus and the outcome of the interaction is dependant on the strains employed. Fujii (1969) investigated competition between four strains of each species (resulting in 16 combinations) and found in six cases C. maculatus to be the successful competitor and in the remaining 10 cases C. chinensis outcompeted C. maculatus. Experimental validation of the model developed here would clearly require long-term experiments to be undertaken with these strains of both species, but in the absence of this information the general impression from the literature of instability of the interaction is encouraging.

Furthermore, Fujii (1970) has also studied the role of adult behaviour in determining the outcome of competition in these species. Of the two cases studies, where C. maculatus was the successful competition there was apparently little interaction between adults of the two species. Where C. chinensis was successful, however, competition between adults was important and C. chinensis adults were found to be more common at the oviposition site than C. maculatus adults. Although the details of the interaction between these strains may differ from those studied here the results obtained by Fujii support the general impression that competition in the adult stage may play a major role in interspecific competition.

5.3 Extending the simulation model to two species

5.3.1 The necessary modifications

In the same manner that the single-species models of chapter 3 have been extended to two-species interactions, the simulation model of chapter 4 is easily modified to include interspecific competition. Since the developmental processes (adult life-span and larval development) in Callosobruchus were found to be independent of intraspecific density, they were also assumed to be independent of interspecific density. Consequently, the only modifications required to the simulation model were in the density dependent processes of fecundity and egg and larval mortality. The modelling of interspecific effects for each of these processes will be considered in this section, and subsequently some experimental data from which the necessary parameters were quantified will be presented and discussed. These estimated parameters will then be used in simulating the outcome of competition between C. chinensis and C. maculatus.

In chapter 4 it was found that intraspecific competition in

adult C. chinensis and C. maculatus includes two density dependent responses which reduce daily fecundity: a response to egg density and a response to adult density. These two responses were characterised by the functions $h'_a(E)$ and $h_a(A)$, respectively (see equation 4.5 & 4.6), which can now be extended to include interspecific competition by introducing a competition coefficient:

$$h'_a(E_x + \gamma_y E_y) = (1 + (a(E_x + \gamma_y E_y))^b)^{-1}, \qquad (5.9)$$

$$h_a(A_x + \beta_y A_y) = (1 + (c(A_x + \beta_y A_y))^d)^{-1}, \qquad (5.10)$$

and similarly for species y. Here E_x and E_y are the densities of eggs and A_x and A_y are the densities of adults of species x and y, respectively. The parameters a, b, c and d are the species-specific constants which determine the density dependent response to intraspecific egg or adult density as discussed on page 106 . The coefficients of interspecific density γ_y and β_y quantify the per capita effect of interspecific egg or adult density, respectively. The four intraspecific parameters have already been experimentaly determined in chapter 4 (see table 4.1) so experimental results were only required here to quantify the interspecific parameters γ and β for both species.

Considering how the presence of adults of the two species affected egg mortality was somewhat more complicated. In the simulation model of chapter 4 egg mortality was considered a function of adult activity and the number of fatal encounters I between eggs and adults was described as a simple function of adult density,

$$I = mA^Z E, \qquad (5.11)$$

where A was the adult density, E was the egg density and m and Z were experimentally determined constants. If two species are present, and assuming there are no interspecific interactions between adults and that the eggs of both species are equally susceptible to damage

from adults of either species, then the number of fatal encounters between adults and eggs of species x (for example) is given by

$$T_x = (m_x A_x^{Z_x} + m_y A_y^{Z_y}) E_x \qquad (5.12)$$

where the subscripts represent the two species. As in chapter 4, the proportionate daily survival S of the eggs of species x is found by distributing the number fatal encounters per individual at random among the eggs;

$$S = \exp(-\frac{1}{E_x} T_x) \qquad (5.13a)$$

or

$$S = \exp(- m_x A_x^{Z_x} - m_y A_y^{Z_y}), \qquad (5.13b)$$

and similarly for species y. Equation 5.12 forms a null hypothesis for a two-species egg mortality function. A number of alternate models may be constructed but only two of them have been considered here. First, the assumption of no interaction between adults of the two species was relaxed to allow interspecific density to affect adult activity. If adult activity is hindered by the presence of adults of the other species, then the activity rate m will be a function of interspecific density,

$$m_x = m_x(1 - \alpha_y A_y), \qquad (5.14)$$

and the total number of fatal encounters between adults and eggs of species x will be given by

$$T_x = E_x\, m_x(1 - \alpha_y A_y)\, A_x^{Z_x} + m_y(1 - \alpha_x A_x)\, A_y^{Z_y} . \qquad (5.15)$$

The proportionate daily survival rates are again obtained by distributing the encounters per egg at random among the eggs by equation 5.13a. When this model was fitted to data, the species-specific parameters m and Z were fixed at the values previously determined by the single-species experiments and it was only necessary to estimate values for the parameters α_y and α_x.

The other modification to the null hypothesis of equation 5.12

was that the eggs of either species might differ in their susceptibility to intra and interspecific adult activity. In other words, the interspecific rate of fatal encounters between eggs and adults was proportional (rather than equal) to the rate of intraspecific encounters. The inclusion of two proportionality constants (one for each species) extended equation 5.12 to include this property:

$$T_x = (m_x A_x^{Zx} + \rho_y m_y A_y^{Zy})\, E_x, \qquad (5.16a)$$

$$T_y = (\rho_x m_x A_x^{Zx} + m_y A_y^{Zy})\, E_y. \qquad (5.16b)$$

The proportionate constants ρ_y and ρ_x relate the intraspecific rate of fatal encounters to an interspecific rate. Proportionate daily survival of eggs of the two species was again found by substituting T_x or T_y into equation 5.13a with the appropriate egg densities E_x or E_y. As before, when fitting this model to data it was only necessary to estimate values for the parameters ρ_x and ρ_y. Neither of these modifications provided a better prediction than equation 5.12 of the data on egg mortality from mixed species experiments and consequently the null hypothesis model was used in the two-species simulation model.

The larval submodel may also be extended to allow for interspecific competition. In chapter 4 (equation 4.25) the daily proportionate survival of the larval stages in Callosobruchus was defined by the stage specific density dependent functions $h_i(D_i)$

$$h_i(D_i) = (1 + D_i)^{-1} \qquad (5.17)$$

where D_i was the effective total density of competitors acting on stage i and represented the total density of all larval stages weighted by their intraspecific interstage competition coefficients:

$$D_i = a_i x_i + \sum_{j \neq i} \alpha_{ij} x_j. \qquad (5.17)$$

Here x_i represents the number of competitiors present in stage i and x_j the number of competitors in the other stages. The parameters a_i

α_{ij} are the density dependent coefficients for intra and interstage competition respectively, as discussed on page 115 .

The affect of interspecific density on the total number of competitors is considered in the same way by letting D_i consist of a weighted sum of individuals in all stages of both species:

$$D_i = a_i x_i + \sum_{j \neq i} \alpha_{ij} x_j + \sum_{\text{all } j} \beta_{ij} y_j . \qquad (5.19)$$

The density of competitors is now composed of the effective densities of the larval stages of species x and y. The parameters β_{ij} are the interspecific interstage competition coefficients relating the density of stage j of species y to the density of stage i of species x. These parameters are on an absolute scale of density as for the intraspecific parameters α_{ij} discussed on page 116 .

These modifications complete the changes to the single-species simulation model necessary for the inclusion of interspecific competition and we now turn to the parameter estimations. All the parameters are estimated, as before, by finding the values which minimize the sum of squared differences between model predictions and observed results. The significance of the estimated parameters is also judged as before by considering the ratio of mean squares discussed on page 121 .

5.3.2 Experimental results

In order to investigate the effect of interspecific egg density on fecundity, five large plastic boxes containing a single layer of cowpeas and various numbers of adults were set up for both species (a total of 10 oviposition chambers). After 24 hours the adults were removed, 20 sets of 3.7g of beans were taken from each chamber and the total number of eggs in each set were counted. Pairs of 0-2½ hour old adults of either *C. chinensis* or *C. maculatus* were then placed in small plastic dishes containing one of the sets of beans bearing

eggs of the other species. The dishes were kept at 30°C, 70% relative humidity until the adults had died and any subsequent oviposition by the adult pairs was scored. The results of this experiment are shown in figure 5.7. It is clear that the fitted models of equation 5.9 (solid lines) provide better descriptions of the data in both species than the models with no interspecific response (broken line). The estimated values of the competition coefficients γ are given for both species in table 5.3; both of these estimates had significance of $p < .001$ and were included in the two species oviposition submodel.

The affects of interspecific adult density on fecundity were investigated using the experimental results on total fecundity at various mixed adult densities (see page 204), which were reanalysed using the simulation oviposition submodel. The data of figure 5.2 are presented again in figure 5.8 together with the predictions of this model (equation 5.9) for both species. The earlier impression that C. chinensis was more affected by interspecific densities than C. maculatus is reinforced by the predictions given here; however, the description of the C. chinensis data was again characterized by overestimates of fecundity at low C. maculatus densities and underestimates of fecundity at high densities. The estimates of the competition coefficients β are also given in table 5.3 and the larger value for C. chinensis emphasizes the higher sensitivity of this species to interspecific competition. When fitting the model to the data the parameters were considered in a stepwise manner. The initial inclusion of the coefficient quantifying the effect of C. maculatus or C. chinensis (β_y) significantly reduced the residual sum of squares with $p < .001$ and the subsequent inclusion of β_x further reduced the residual sum of squares with $p < .01$. The estimated values for both parameters were included in the model.

FIGURE 5.7 The effect of interspecific egg density on fecundity in (a) C. chinensis and (b) C. maculatus. The broken lines indicate the predictions of the oviposition submodel when no interspecific effects are considered. The solid lines give the predictions of the fitted model of equation 5.9 with the parameter values of table 5.3.

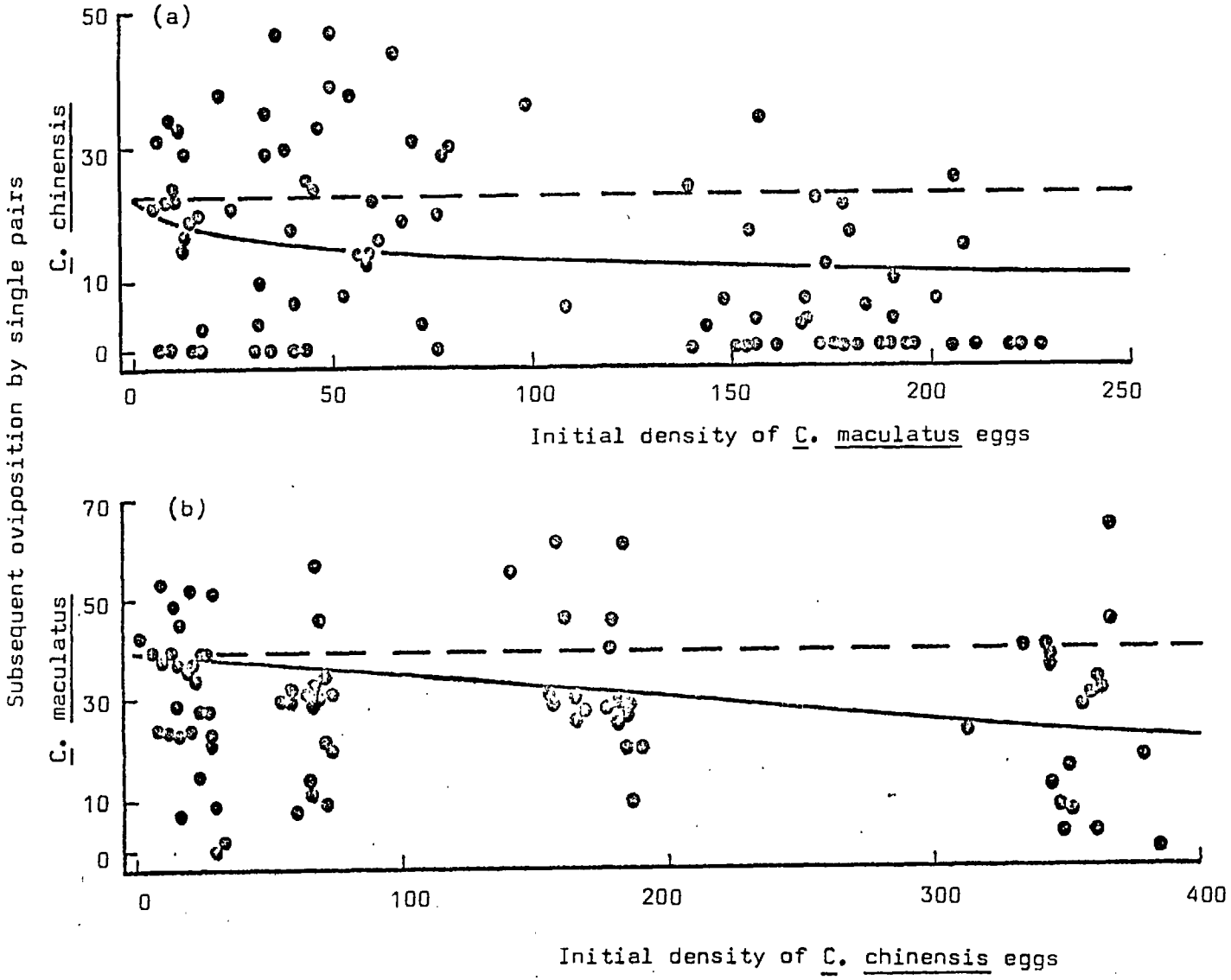
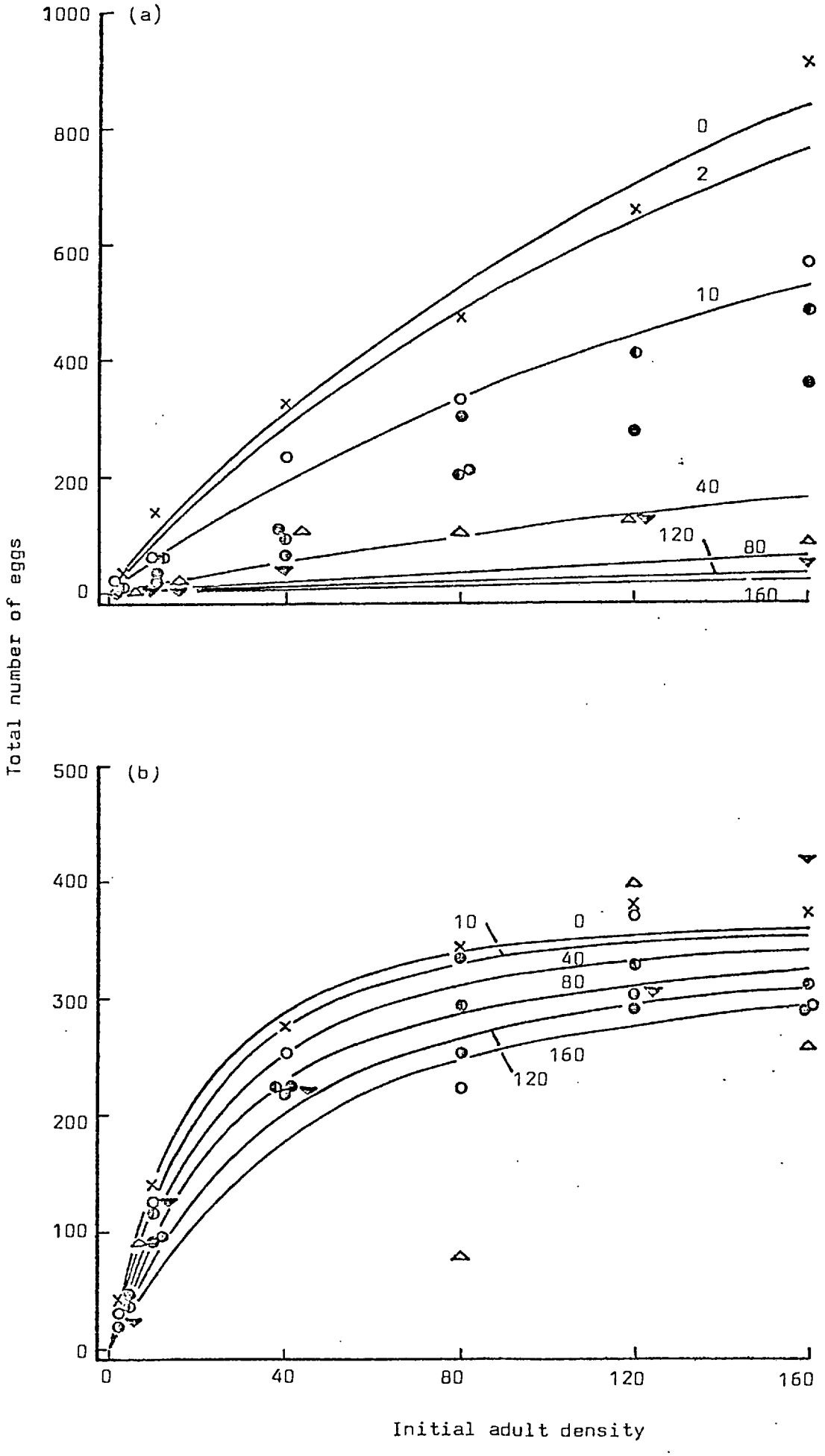

(a)
50
30
10
0
C. chinensis
0
50
100
150
200
250
Initial density of C. maculatus eggs
(b)
70
50
30
10
0
C. maculatus
0
100
200
300
400
Initial density of C. chinensis eggs
Subsequent oviposition by single pairs

TABLE 5.3 The interspecific competition coefficients of egg and adult density estimated from the oviposition submodel of equations 5.9 and 5.10.

	C. chinensis	*C. maculatus*
egg density, γ	1.46542	0.412759
adult density, β	21.8015	0.338288

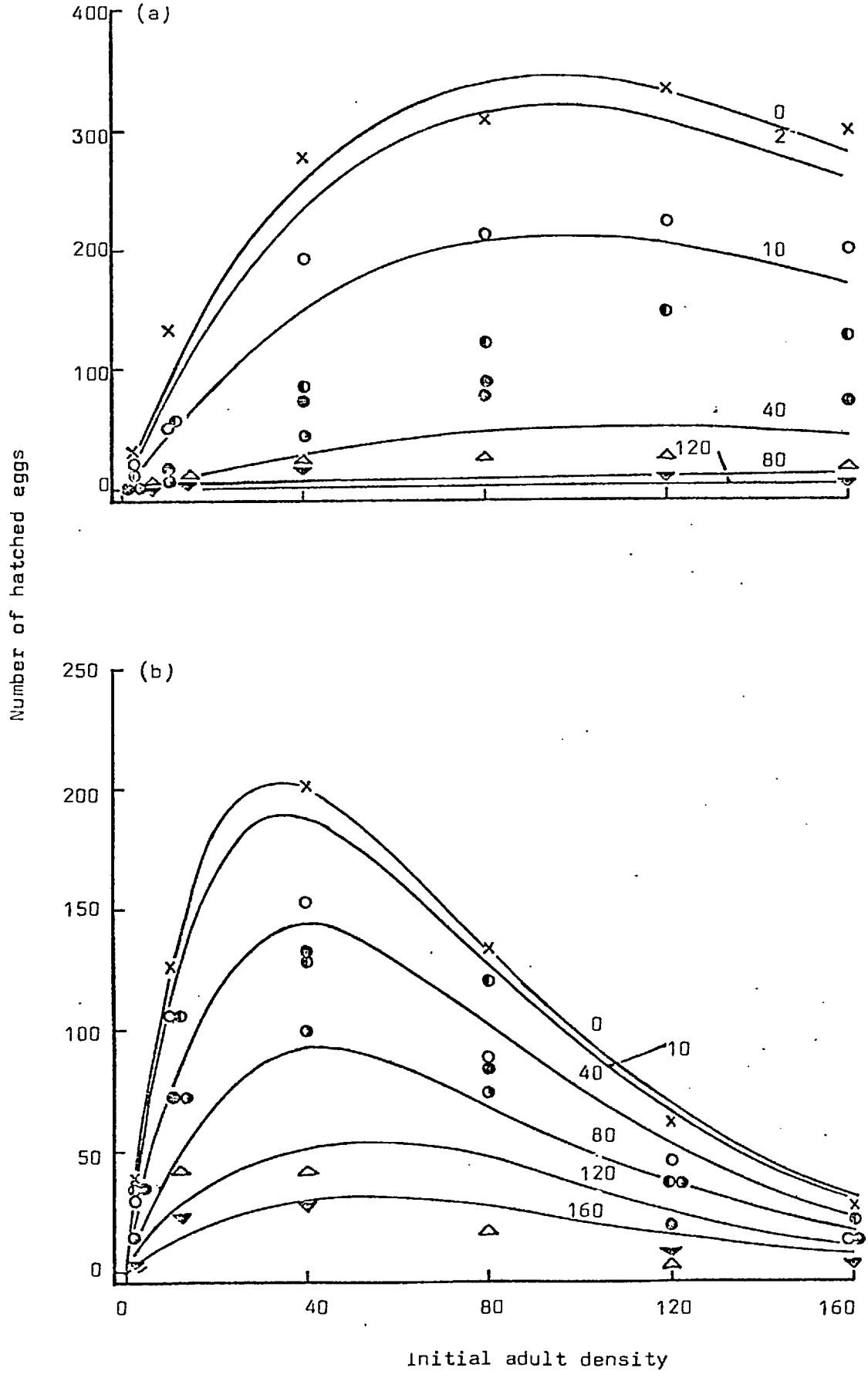
FIGURE 5.8 The oviposition by adults of the two species at different combinations of density as predicted by the oviposition submodel. (a) C. chinensis. (b) C. maculatus. The solid lines were obtained by fitting the oviposition submodel with equation 5.10 to the data. The fitted values of the parameters β are given in table 5.3. The symbols identify the observed results as in the legend of figure 5.2.


(a)
1000
800
600
400
200
0
0
2
10
40
120
80
160
(b)
500
400
300
200
100
0
10
0
40
80
160
120
0
40
80
120
160
Total number of eggs
Initial adult density

The data on the total number of hatched eggs recorded in the single-generation mixed species experiment were used to investigate the effects of interspecific adult activity on egg mortality. As was previously noted, however, no significant improvement in the residual sum of squares provided by the null hypothesis model of equation 5.12 was obtained by fitting either of the alternate models to the data. Consequently, equation 5.12 was used in the oviposition submodel. The observed and predicted numbers of hatched eggs at various combinations of adult densities are given for both species in figure 5.9. Once again there is systematic error in the predicted densities of hatched eggs of C. chinensis which resulted from the previously discussed imprecision of the total fecundity predictions; at low C. maculatus densities the number of hatched eggs was overestimated while at high densities the number of hatched eggs was underestimated. The predictions for the number of C. maculatus eggs hatching at various densities, however, agreed well with the observed results.

The design of the experiment for investigating interspecific interstage larval competition was the same as that used for studying intraspecific competition discussed on page 119 . Two cohorts of individuals were initiated in a single set of beans for every combination of stages studied by permitting adults to oviposit on the beans at different times. For some interactions the first cohort was of C. maculatus; for others it was of C. chinensis. The oviposition initiating the first cohort occurred on day zero and the timing of the second oviposition was determined by the difference in the sampling day of the two stages of interest, as before. The number of hatched eggs of each cohort was recorded for every bean and on the appropriate day the beans were dissected and the number of survivors from each cohort were scored. The details of the timings of the second

FIGURE 5.9 The number of hatched eggs arising from different combinations of adult density as predicted by the oviposition submodel. The symbols identify the observed results as given in the legend of figure 5.3. See text for discussion.


(a)
400
300
200
100
0
0
2
10
40
80
120
(b)
250
200
150
100
50
0
0
10
40
80
120
160
0
40
80
120
160
Number of hatched eggs
Initial adult density

ovipositions and sampling are given in table 5.4.

The analysis of these data was accomplished in the same manner as for the intraspecific studies (see page 125). The interactions between the stages were considered in steps, as before, and the order in which the interactions were analysed is also given in table 5.4. The significance of each estimated competition coefficient was determined from the mean square ratio of equation 4.28 and by examining the residuals. Estimated parameter values were only included in the submodel if they were judged significant with $p < .01$ and they contributed to an improved distribution of residuals.

The results of these analyses are presented in table 5.5. Two matrices of competition coefficients were estimated, one which quantified the effect of the immature stages of C. maculatus on those of C. chinensis and one which quantified the reciprocal effects. Considering first the effects on C. chinensis (table 5.5a) it is clear that interspecific competition was having a significant impact on their survival, particularly in the case of C. maculatus fourth instar larvae, where large interactions were found with every C. chinensis stage except second instar larvae and pre-emergent adults. The reciprocal effects were in general smaller, and it is noteworthy that only one significant interaction (fourth instars effecting pupae) was found between individuals of C. maculatus and C. chinensis individuals of equal or later stages. In at least the first instar of both species, the increasing effects of the successively larger stages is evident. The two particularly large estimates of competition coefficients between C. chinensis pupae and C. maculatus first instar larvae and between C. maculatus adults and C. chinensis first instar larvae were probably inflated by the extremely low survival of the first instar larvae in both cases. Nonetheless, their estimated values were unchanged when the matrices were used in the simulation studies presented

TABLE 5.4 The days of the second oviposition and sampling of the interspecific larval competition experiment. The entry step into the analysis and the number of beans sampled (in parentheses) are also given.

Stages involved	First oviposition by *C. maculatus*			First oviposition by *C. chinensis*		
	Day of second oviposition	Day of sampling	Entry step into analysis	Day of second oviposition	Day of sampling	Entry step into analysis
First *vs* First	1	7	1(20)			
Second *vs* First	4	10	2(13)	1	8	3(19)
Second *vs* Second	2	10	4(19)			
Third *vs* First	6	12	5(17)	3	10	6(18)
Third *vs* Second	4	12	7(15)	0	10	8(18)
Third *vs* Third	2	12	9(16)			
Fourth *vs* First	10	16	10(18)	7	14	11(19)
Fourth *vs* Second	8	16	12(14)	4	14	13(17)
Fourth *vs* Third	6	16	14(20)	2	14	15(18)
Fourth *vs* Fourth	2	16	16(19)			
Pupae *vs* First	15	21	17(19)	12	19	18(18)
Pupae *vs* Second	13	21	19(20)	9	19	20(19)
Pupae *vs* Third	11	21	21(19)	7	19	22(20)
Pupae *vs* Fourth	7	21	23(20)	3	19	24(19)
Pupae *vs* Pupae	2	21	25(17)			
Adult *vs* First	18	24	26(18)	15	22	27(20)
Adult *vs* Second	16	24	28(19)	12	22	29(19)
Adult *vs* Third	14	24	30(17)	10	22	31(17)
Adult *vs* Fourth	10	24	32(19)	6	22	33(20)
Adult *vs* Pupae	5	24	34(18)	1	22	35(19)
Adult *vs* Adult	2	24	36(14)			

TABLE 5.5 The summary of analysis of the results of the larval competition experiment. Values marked with (*) had significance of $p < .01$; those marked with (**) had significance of $p < .001$. See text for discussion.

(a) *C. chinensis*

Stage of *C. chinensis*	Stage of *C. maculatus*					
	First	Second	Third	Fourth	Pupae	Adults in pea
First	0.00	0.01687**	0.02799**	0.05812**	0.07810**	0.4566**
Second	0.01396**	0.00	0.00	0.00	0.00	0.00
Third	0.00	0.00	0.03085*	0.1273*	0.06996*	0.00
Fourth	0.00	0.00	0.00	0.05499**	0.00	0.00
Pupae	0.00	0.00	0.00	0.09623**	0.00	0.00
Adults in pea	0.00	0.00	0.00	0.00	0.00	0.00

(b) *C. maculatus*

Stage of *C. maculatus*	Stage of *C. chinensis*					
	First	Second	Third	Fourth	Pupae	Adults in pea
First	0.00	0.005729**	0.00	0.08171**	0.3315**	0.08203**
Second	0.00	0.00	0.00	0.00	0.00	0.00
Third	0.00	0.00	0.00	0.07771**	0.00	0.00
Fourth	0.00	0.00	0.00	0.00	0.00	0.00
Pupae	0.00	0.00	0.00	0.02241*	0.00	0.00
Adults in pea	0.00	0.00	0.00	0.00	0.00	0.00

in the next section.

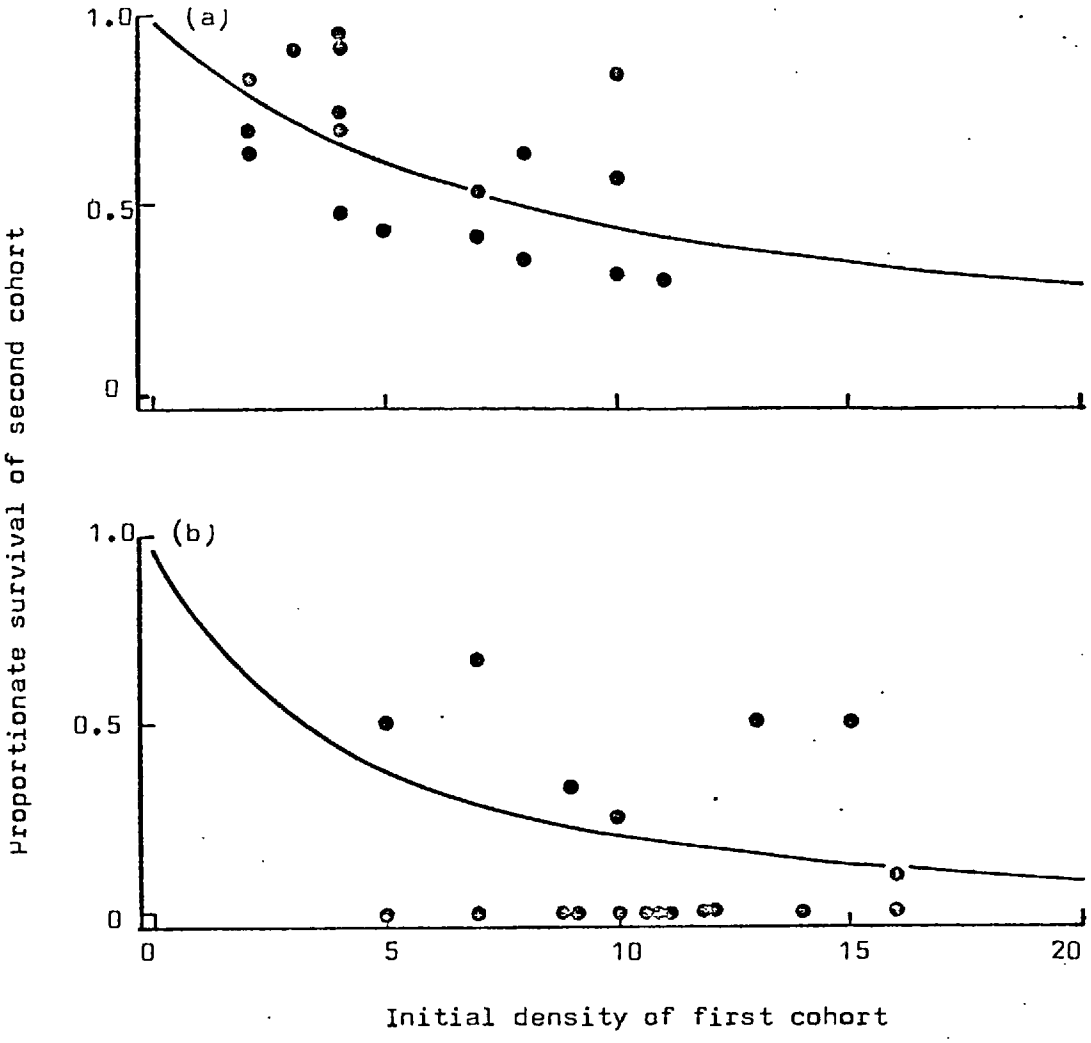
Two examples of how the proportionate survival of the second cohort of individuals was affected by interspecific interstage competition are shown in figure 5.10. The examples shown are for the interactions between fourth and first instar larvae. The proportionate survival of first instar is plotted against the initial number of hatched eggs of the cohort which represents the fourth instar larvae. The steeper relationship in figure 5.9b reflects the combined effect of the larger competition coefficient (table 5.5b) and the higher per bean density of C. chinensis than of C. maculatus fourth instar larvae.

5.3.3 Simulation results

The simulation model, in contrast to the simpler models discussed above, predicts the inevitable extinction of C. maculatus. This is due to differences in the preimaginal developmental period of the two species. Since C. chinensis individuals developed approximately three days faster than C. maculatus individuals, their progeny gained a three day temporal advantage each generation over C. maculatus progeny. This resulted in the older larvae of C. chinensis outcompeting the younger larvae of C. maculatus and eventually resulted in exclusion of C. maculatus. This result was obtained irrespective of the initial density or composition of the two populations and even a C. maculatus population at equilibrium was eventually excluded by a small initial invasion of C. chinensis.

The dynamic properties of the two-species simulation model may be more fully understood by considering the behaviour of the zero-growth isoclines for the two species. For the simple models of the previous section a single pair of isoclines completely determined

FIGURE 5.10 The effect of interspecific larval competition on survival of the later cohort. The data are for (a) C. chinensis first instar larvae competing with C. maculatus fourths and (b) C. maculatus first instar larvae competing with C. chinensis fourths. The solid line indicates the survival predicted by the larval submodel when interstage competition is included.. See text for discussion.

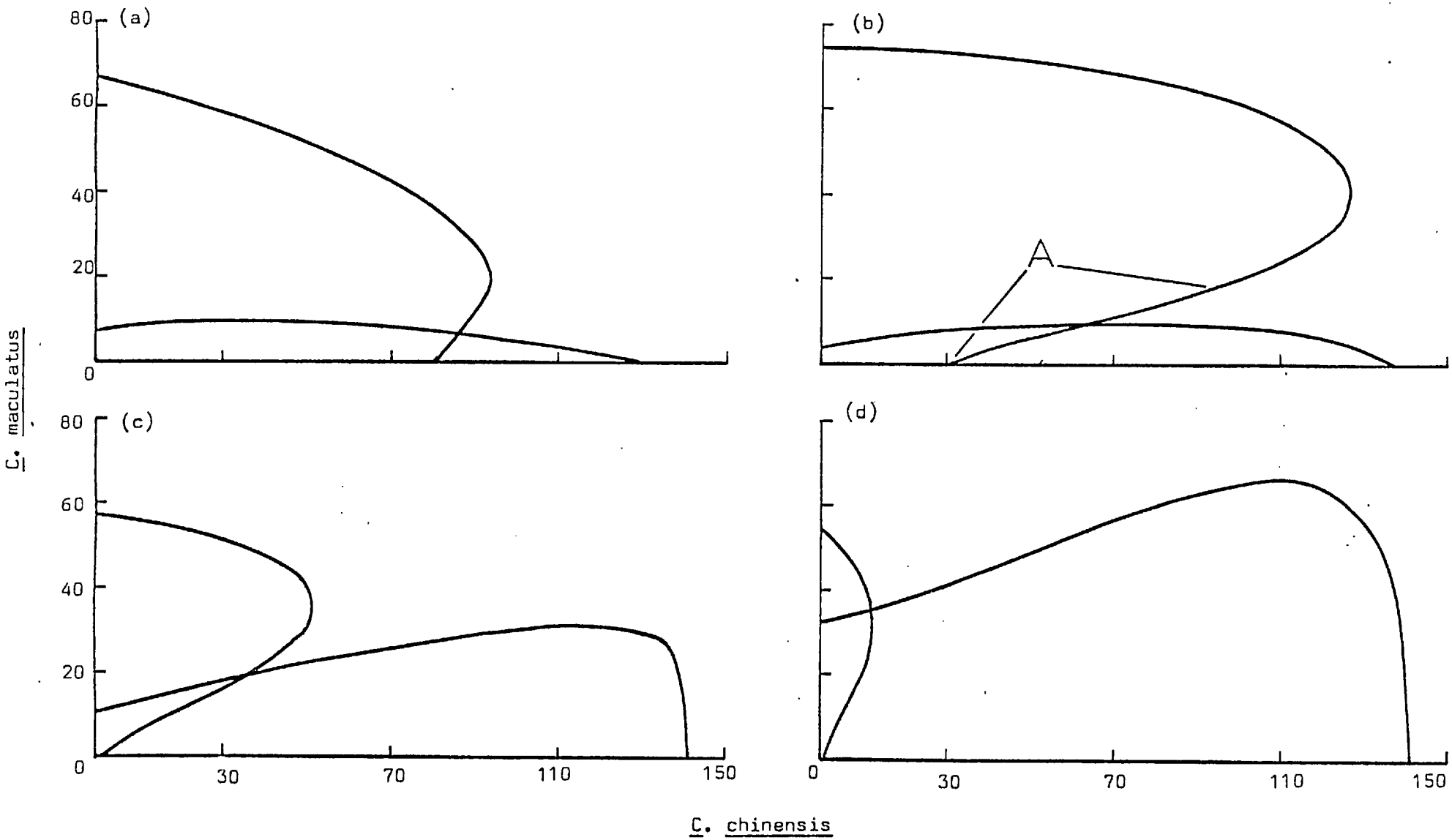

(a)
1.0
0.5
0
(b)
1.0
0.5
0
0
5
10
15
20
Proportionate survival of second cohort
Initial density of first cohort

their properties. However, because of the constantly changing temporal advantage given to C. chinensis, the zero-growth isoclines for the simulation model were not constant but varied in shape as the populations developed. The forms for these isoclines depend somewhat on how the populations are initialized. In all of the examples presented here adults of both species were introduced together on the first day of the simulation.

Four sets of zero-growth isoclines for adult populations are shown in figure 5.11. These isoclines define positions where populations initiated at the first generation will have returned to by either the second (figure 5.11a), third (figure 5.11a), sixth (figure 5.11c) or eighth (figure 5.11d) generation. The shapes of the one-generation isoclines in figure 5.11a are similiar to that defined by the simple two age-class model (see figure 5.5b) and indicate the competitive superiority of C. maculatus. The two-generation isoclines in figure 5.11b are slightly more expanded, particularly for C. maculatus. This indicates the presence of some overcompensation in the density dependent processes determining population growth since populations started at higher densities than in figure 5.11a will decrease in the first generation and susequently increase to their original value. However, at low initial C. maculatus densities the temporal advantage of the second C. chinensis generation has reduced the success of the C. maculatus population, and zero-growth for C. maculatus now only occurs at much lower initial C. chinensis densities. This displacement of the C. maculatus isocline is identified by the region A in figure 5.11b.

As population growth continues the temporal advantage of C. chinensis has an increasing impact on C. maculatus. By the sixth generation the region where an initial C. maculatus population would

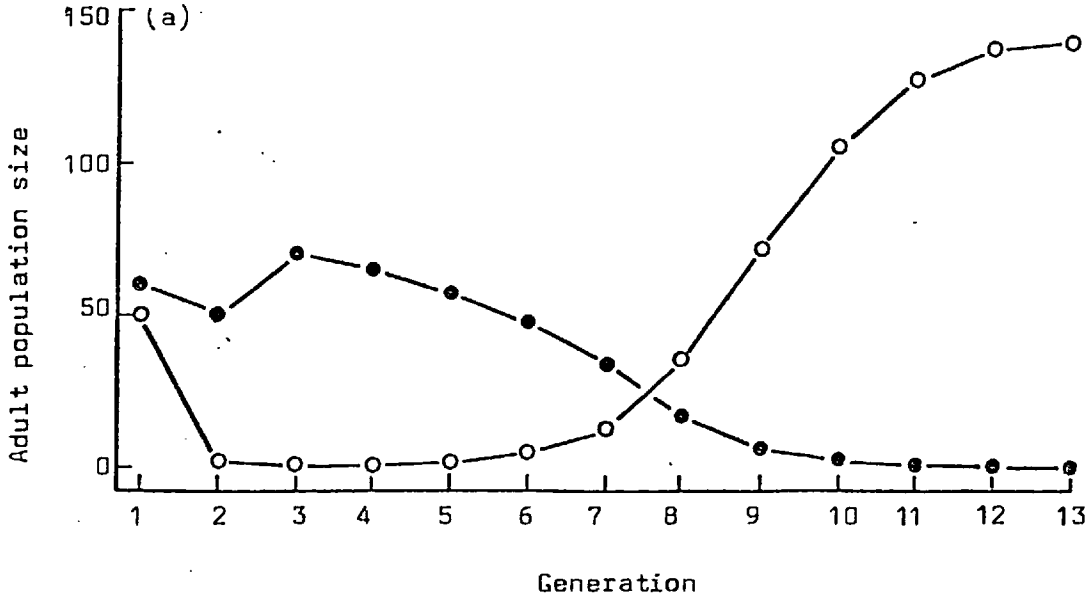
FIGURE 5.11 The changes in the zero-growth isoclines of the simulation model as time progresses from the initial simultaneous initiation of the populations. The changes are due to the differences in developmental period of the two species. In (a) the isoclines indicate positions of zero growth between the first and second generations and clearly indicate the competitive advantage of C. maculatus. In (b) the lines indicate positions of no change between population densities in the first and third generations. The region A indicates densities where the second generation of C. chinensis, due to its temporal advantage, is causing substantial losses to the larval population of C. maculatus. (c) The isoclines for no population change between generations one and six. The region of positive growth for C. maculatus has been considerably reduced while that for C. chinensis has increased. (d) The isoclines for no population change between generations one and eight. The region of positive growth for C. maculatus has been further reduced and the region for positive growth of C. chinensis continues to increase. For further discussion see text.

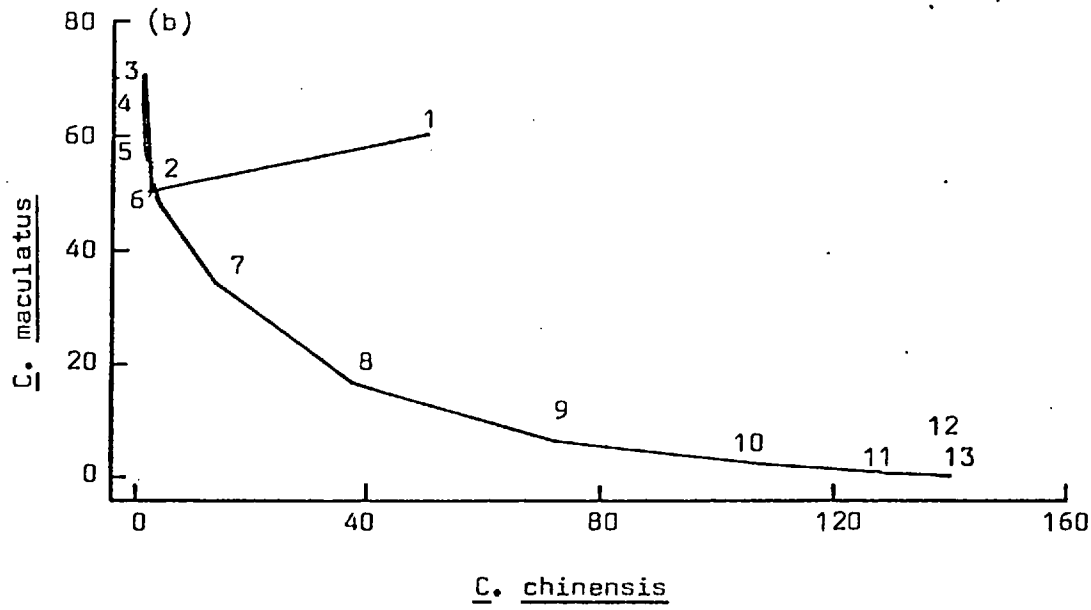

(a)
(b)
(c)
(d)
A
80
60
40
20
0
30
70
110
150
C. maculatus
C. chinensis

have increased is much reduced. Initial C. chinensis densities of more than about 50 adults would have caused the decrease of any initial C. maculatus population. By the eighth generation the inevitable outcome of competition is clear --- the region where initial population densities would permit growth of C. maculatus is decreasing and the region where growth of C. chinensis is possible is increasing. Eventually the phase space will contain only a single vertical isocline (positioned at the C. chinensis equilibrium) dividing the space into regions where an initial population of C. chinensis would either increase or decrease; there will be no region where populations of C. maculatus might increase. Thus it is clear that the single-species equilibrium of C. maculatus is an unstable point and any introduction of C. chinensis into the system results in the extinction of C. maculatus.

These considerations of how zero-growth isoclines alter during the course of population growth have defined more clearly the cause of the predicted extinction of C. maculatus, that is the temporal advantage gained by C. chinensis due to quicker development. However, these predictions consider the populations of these species to be infinitely divisible, and during the initial phase of population growth the competitive superiority of C. maculatus adults may reduce the population of C. chinensis to a very low level. This is more easily appreciated with reference to the particular example in figure 5.12. The competitive superiority of C. maculatus supressed the growth of C. chinensis for several generations and for two generations the predicted density of C. chinensis adults is less than 0.06 per bean. At these extremely low levels chance events might easily cause the extinction of C. chinensis. Consequently it is unclear how the results of long-term validation experiments might be interpreted since the model's predictions might be viewed as indicating the

FIGURE 5.12 The population trajectories of C. chinensis (○) and C. maculatus (●) predicted by the simulation model (a) The population trajectories through time. Note the low population densities of C. chinensis in generations two through five. (b) The population trajectories in the phase space of species density. The numbers correspond to generations. See text for discussion.


(a)
150
100
50
0
Adult population size
1
2
3
4
5
6
7
8
9
10
11
12
13
Generation


(b)
80
60
40
20
0
C. maculatus
1
2
3
4
5
6
7
8
9
10
11
12
13
0
40
80
120
160
C. chinensis

possible extinction of either species. One possible approach would be to initiate cultures with different combinations of densities of the two species and hence investigate the growth of populations in different regions of the phase space. Such work is in progress (Dr. M. P. Hassell, personal communication) and will be reported elsewhere.

5.4 Conclusions

The two approaches taken to constructing two-species population models yeilded apparently contradictory predictions of the outcome of interspecific competition in the two species studied. The simple models predicted an unstable two-species equilibrium and indicated the competitive superiority of C. maculatus, primarily due to competition in the adult stage. The simulation model, however, predicted that no two-species equilibrium existed and, in addition, that any competitive interaction would result in the extinction of C. maculatus. This difference arose because of the different developmental periods for the two-species in the simulation model, whereas the simple models have the implicit assumption of equal generation times.

Finally, in the simulation model the competitive superiority of C. maculatus in the adult stage was capable of causing severe reduction in the growth of C. chinensis populations for several generations. At these very low levels chance events might cause the extinction of C. chinensis, and in a stochastic environment there may be in practice two stable points corresponding to the two single-species equilibria.

Chapter VI. PARASITISM.

6.1 Introduction

One of the most fundamental relationships between coexisting insect populations is that between a host and its parasitoids. Such interactions are common in natural communities, as is evidenced by the enormous number of parasitoid species, and are of further importance in agricultural systems where they have played a major role in controlling pest infestations. The widespread importance of these interactions has led to them recieving considerable attention in the modelling literature (see Hassell (1978) for a review). However, examples where models have been constructed for a particular system, such as those for the winter moth by Varley & Gradwell (1968) and Hassell (1977) or for laboratory systems (e.g. Hassell & Huffaker 1969; Benson 1974; Podoler 1974), are relatively few. In these models the interactions between the parasitoid and the host populations have been considered on a relatively simple basis, usually described by a single equation with few parameters. Even in more complex simulation models such interactions have usually been given little attention. Stinner, Rabb & Bradley (1974) considered parasitism as a seasonal average mortality in their model for Heliothis species. Sasaba, Kiritani & Urabe (1973) included only a simple functional response for spider predation of the green rice leafhopper. Auslander, Uster & Huffaker (1974), however, have considered parasitism in more detail by including age-class interactions between the host and the parasitoid populations.

TABLE 6.1 Host records for *Lariophagus distinguendus*.

Host species	Authors
Coleoptera	
Anobiidae:	
Lasioderma serricorne	Lever (1941)
Stegobium paneceum	Rushka (1921), Pechuman (1937), Kaschef (1955), van den Assem (1970)
Nicobium schneideri Reitt.	Parfent'ev (1952)
Bostrichidae:	
Rhyzopertha dominica	Goodrich (1921), Herdman(1921), Potter (1935), Kaschef (1959a), Frilli (1965)
Bruchidae:	
Bruchus brachialis Fahraeus	Pinckney (1937)
Callosobruchus chinensis	this study
Callosobruchus maculatus	this study
Curculionidae:	
Sitophilus granarius (L.)	Hase (1920), Schulz (1920), Goodrich (1921), Herdman (1921), Ruschka (1921), Romanova & Il'inskaya (1938), Kaschef (1959a)
Sitophilus oryzae (L.)	Cotton (1920), Goodrich(1921) Herdman (1921), Ruschka (1921), Romanova & Il'inskaya (1938), Kaschef (1959a), Gonen & Kugler (1970)
Ptinidae:	
Gibbium psylloides Czemp.	Kaschef (1961)
Ptinus fur (L.)	Husing (1935)
Ptinus tectus Boield.	Kaschef (1959a)
Hymenoptera	
Ichneumonidae:	
Nemeritus canescens Grav.	Voinovskaya-Kriger (1927)
Braconidae:	
Habrabracon juglandis Ashm.	Hase (1924)

TABLE 6.2 Location records for *Lariophagus distinguendus*.

Country	Authors
Egypt	Kaschef (1961)
Fiji	Lever (1941)
France	Kaschef (1955)
Germany	Hase (1920), Schulz (1920) Ruschka(1921)
Great Britain	Goodrich (1921), Herdman (1921)
Israel	Gonen & Kugler (1970)
Italy	Frilli (1965)
Netherlands	van den Assem (1970)
U.S.A.	Pechuman (1937), Pinckney (1937)
U.S.S.R.	Voinovskaya-Kriger (1927), Romanova & Il'inskaya (1938)

In this chapter, a detailed simulation model for Lariophagus distinguendus Först, a hymenopterous parasitoid of Callosobruchus, will be developed. Special attention will be given to the effects of the host stage parasitized on larval development period and adult fecundity and longevity, and some factors affecting the oviposition rate of the adults will also be considered. Finally, the consequences of including the parasitoid model in the previously developed simulation models will be investigated.

6.2 The biology of Lariophagus distinguendus

The strain of L. distinguendus used in this study was obtained from Dr. J. van den Assem of the Zoologisch Laboratorium, Ryksuniversiteit te Leiden, Leiden, the Netherlands and was reared on larvae of C. maculatus As Callosobruchus had not been previously recorded as a host of L. distinguendus it was necessary to investigate the details of their relationship before a model could be developed. In this section a brief review of the literature on L. distinguendus will be presented. This is followed by some experimental results which outline the effects of host age on parasitoid preimaginal development, adult longevity and fecundity. Experiments dealing with its searching behaviour are presented in the next section.

Lariophagus distinguendus is a pteromalid parasitoid which attacks a wide range of hosts (table 6.1) and is cosmopolitan in distribution (table 6.2). There has apparently been little confusion over its taxonomic position; some of the early synonomy is given by Ruschka (1921). Although the adult males live only a few days, the females are long lived (about 15 days at 25^{o}C, Kaschef 1955; Gonen & Kugler 1970) and continually mature eggs throughout their life. The females are arhennotokous and capable of controlling the sex of their progeny

(van den Assem 1971). They are attracted to foodstuffs in which hosts are developing and locate the host larvae by odour (Kaschef 1959b). After a suitable host has been found it is paralysed and the females then feed on the host haemolymph. Although this has not been reported in the literature it has been observed repeatedly in this study. It is not known whether a feeding tube is constructed as observed by Fulton (1933) for the pteromalid Habrocytus cerealella Ashm. When Callosobruchus fourth instar larvae are fed upon (no observations were made on other stages), the host haemolymph exudes through the hole in the seed testa made by the parasitoid's ovipositor. The females then feed on this fluid; males have not been observed to feed. After a host has been paralysed an egg may be laid on it, although some hosts are attacked (and probably fed upon) without being parasitized. The fecundity of this species varies between 50 and 150 eggs per female (Kaschef 1959a; Gonen & Kugler 1970). Usually only one egg is laid on a host (Kaschef 1959a; van den Assem 1970), although two progeny may develop from a single larvae of some host species (van den Assem 1970). Preimaginal development requires approximately 19 days at 25°C (Kaschef 1955; Gonen & Kugler 1970). Kaschef (1955) has given a thorough account of the development and morphology of the preimaginal and adult stages. The mating behaviour has also been discussed by Kaschef (1955) and by van den Assem (1970).

In order to investigate the effects of host stage on parasitoid development, it was necessary to obtain host cultures of known ages. To do this, adults of C. chinensis and C. maculatus were allowed to oviposit on cowpeas for 24 hours. The cowpeas bearing the eggs were kept at 30°C, 70% relative humidity. This procedure was maintained daily and thus provided a regular series of host cultures of known age. The ages of the cultures which corresponded to the maximum presence

of the different stages was determined in chapter 4 (see page 158) and are given in table 6.3. Table 6.3 also gives the mean fresh weights of third and fourth instar larvae and pupae of the specified ages. These were obtained by weighing 10 individuals of each stage separately on a milligram balance except in the case of the third instar larvae where 10 individuals were weighed together. Ten pupae of each sex were weighed. Cultures of L. distinguendus were also maintained by providing adult parasitoids with cowpeas containing 16 day old (fourth instar) C. maculatus for 24 hours. Parasitoids reared in this way were used for most of the experimental work reported here and will be referred to as standard parasitoids.

In an experiment designed to elicidate host stage effects on parasitoid development, host cultures of the various ages in table 6.3 (and one C. chinensis of 18 days) were exposed for 24 hours to parasitoids taken from general stock cultures. These parasitized cultures were then kept at 30°C, 70% relative humidity for 21 days and any parasitoids emerging were removed daily. Additional cultures of first and second instar larvae of both species were exposed to 24 hours of oviposition, and after three days beans from these cultures were dissected to determine the extent of the parasitoid attack. During the period of parasitoid adult emergence, 0-24 hour old adults were collected from each of these cultures and sets of one female and two males were placed in small plastic dishes 3.5cm in diameter and 4.0 cm high. These adults were provided daily with several beans from a 16 day old C. maculatus culture until they died. The beans on which they had oviposited were then dissected and the number of eggs laid each day were scored. After the adults had died the length of one of their hind tibia and the maximum frontal width of the head was measured under a dissecting microscope. These measurements were also taken for other individuals emerging from the parasitized cultures and some 0-24

TABLE 6.3 The age (in days) of host cultures which corresponds to the maximum presence of the immature stages of (a) *C. chinensis* and (b) *C. maculatus*. Cultures were started with a 24 hour pulse of eggs. The means and standard deviations of the fresh weights of the later stages are also given.

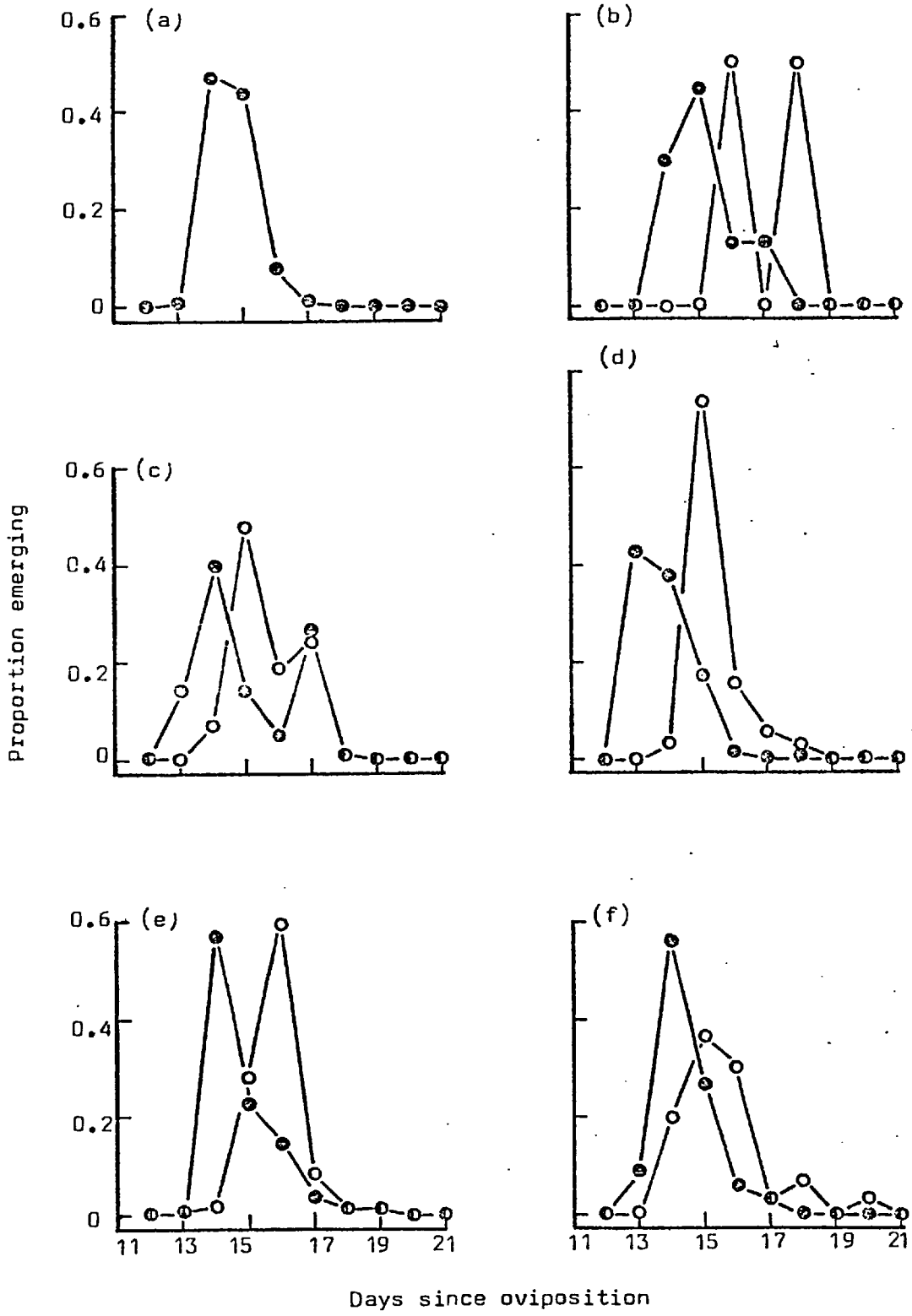
Stage	Age (days)	Fresh weight (mg)
(a) *C. chinensis*		
First instar	5	----
Second instar	7	----
Third instar	9	0.51
Fourth instar	13	7.00 ± 1.15
Pupae (males)	17	5.71 ± 0.74
	19	5.18 ± 0.75
Pupae (females)	17	5.51 ± 0.82
	19	5.34 ± 0.78
Pupae (pooled)	17	5.61 ± 0.77
	19	5.26 ± 0.75
(b) *C. maculatus*		
First instar	6	----
Second instar	9	----
Third instar	11	0.71
Fourth instar	16	9.34 ± 1.90
Pupae (males)	19	5.38 ± 0.55
	21	4.83 ± 0.56
Pupae (females)	19	7.24 ± 1.19
	21	7.16 ± 0.95
Pupae (pooled)	19	6.31 ± 1.31
	21	6.00 ± 1.41

hour old females were dissected to determine the number of ovarian eggs present at emergence. In a final experiment a large number of 0-24 old standard parasitoids were placed in three plastic dishes 10 cm in diameter and 4.0 cm high and were provided daily with either 16 day old C. maculatus (fourth instar), 11 day old C. maculatus (third instar) or no hosts. The numbers of living females in each dish was recorded daily. Two addition dishes containing standard parasitoids and either 16 day old C. maculatus or no hosts were set up and approximately 10 females from each dish were dissected daily to determine the number of ovarian eggs.

The first larval instar of neither host species was attacked. Although the second instar of both species was readily attacked, oviposition on this stage was relatively uncommon and only 9% of the attacked hosts were parasitized. In addition, no progeny ever emerged from beans containing second instar hosts. The third instar was readily parasitized but the progeny reared from this stage were predominantly male (only two of the 240 progeny were female). Van den Assem (1971) has observed that predominantly male progeny are reared from small Sitophilus granarius larvae and has concluded that this indicates regulation of the sex of the progeny by the adult females. Presumably, unfertilized eggs are laid on smaller hosts because of the smaller larval food supply required to produce successful male progeny. Male and female parasitoids were reared from fourth instar larvae and pupae of both hosts.

The developmental period of male and female parasitoids reared on the various host stages are presented in figure 6.1. The developmental period of the sexes was similar on all the host stages; males appeared one day before the females and their peak emergence was one day earlier than that of the females. This is in contrast to the findings of van den Assem (1971), who found development on the smaller

FIGURE 6.1 The proportion of the total L. distinguendus emerging at different times from cultures started with a 24 hour period of oviposition. Solid circles indicate males; hollow circles indicate females. The host stages used were (a) C. chinensis third instar (9 day old) larvae (a total of 191 males and no females emerged), (b) C. maculatus third instar (11 day old) larvae (47 males, 2 females), (c) C. chinensis fourth instar (13 day old) larvae (256 males, 111 females), (d) C. maculatus fourth instar (16 day old) larvae (58 males, 87 females), (e) C. chinensis (18 day old) pupae (123 males, 121 females) and (f) C. maculatus (21 day old) pupae (34 males, 30 females).


(a)
(b)
(c)
(d)
(e)
(f)
0.6
0.4
0.2
0
Proportion emerging
11
13
15
17
19
21
Days since oviposition

of S. granarius
stages to be slightly faster. The developmental period appeared in general to be well defined and unimodal, although the data from C. chinensis fourth instar larvae (figure 6.1c) possibly indicate a more complex situation. Finally it should be noted that, since the age and density of the adults initiating these cultures was variable, no conclusion may be drawn about progeny sex ratio from these data.

Before continuing to discuss the effect of host stage on parasitoid development it is convenient here to note that head capsule width and hind tibia length were highly correlated over the entire range of observations available (figure 6.2). Consequently future consideration of adult size will be made with reference only to head capsule width.

Figure 6.3 shows the relationship between the mean fresh weight of the stage parasitized and the size of the parasitoid progeny. Although there was considerable difference in the size of parasitoids reared on third instar larvae and those reared on fourths, there was very little difference between those reared on fourths and pupae. The effects of this host-mediated variation in size is to produce females which vary considerably in their reproductive potential (see also van den Assem 1971). Larger females lived longer (figure 6.4), had higher total fecundity (figure 6.5a) and laid more eggs per day in the early part of their life (figure 6.5b) than smaller females. In addition it appears that smaller females may have had fewer ovarian eggs at emergence (figure 6.6) although more data are required to establish this clearly. Van den Assem (1971) has reported similar results and also noted that small males were as capable of copulating with large females as large males.

Host feeding played an important role in determining female longevity. Standard females provided with fourth instar C. maculatus

FIGURE 6.2 The relationship between head width and hind tibia length in L. distinguendus for (a) males and (b) females. Hollow circles indicate repeated points.

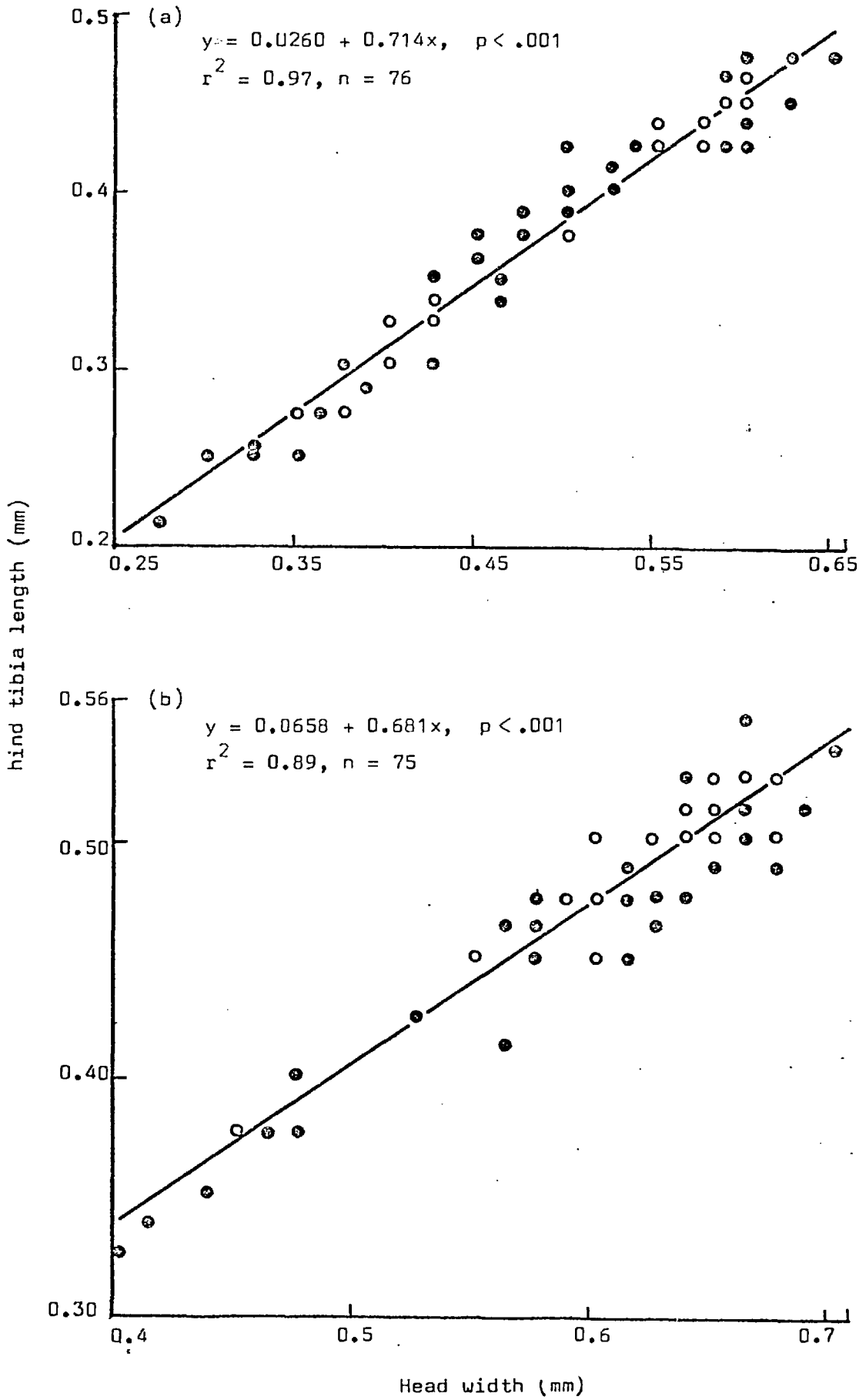

(a)
y = 0.0260 + 0.714x, p < .001
r² = 0.97, n = 76
0.5
0.4
0.3
0.2
0.25
0.35
0.45
0.55
0.65
(b)
y = 0.0658 + 0.681x, p < .001
r² = 0.89, n = 75
0.56
0.50
0.40
0.30
0.4
0.5
0.6
0.7
hind tibia length (mm)
Head width (mm)

FIGURE 6.3 The effect of the host stage parasitized on parasitoid size. The marked positions on the abcissa correspond to the mean fresh weights given in table 6.3 for C. chinensis third instar larvae (c3), fourth instar larvae (c4) and pupae (cP) and similarly for C. maculatus (m3, m4, mP). Hollow circles are females; solid circles are males. Data given as mean ± standard deviation.

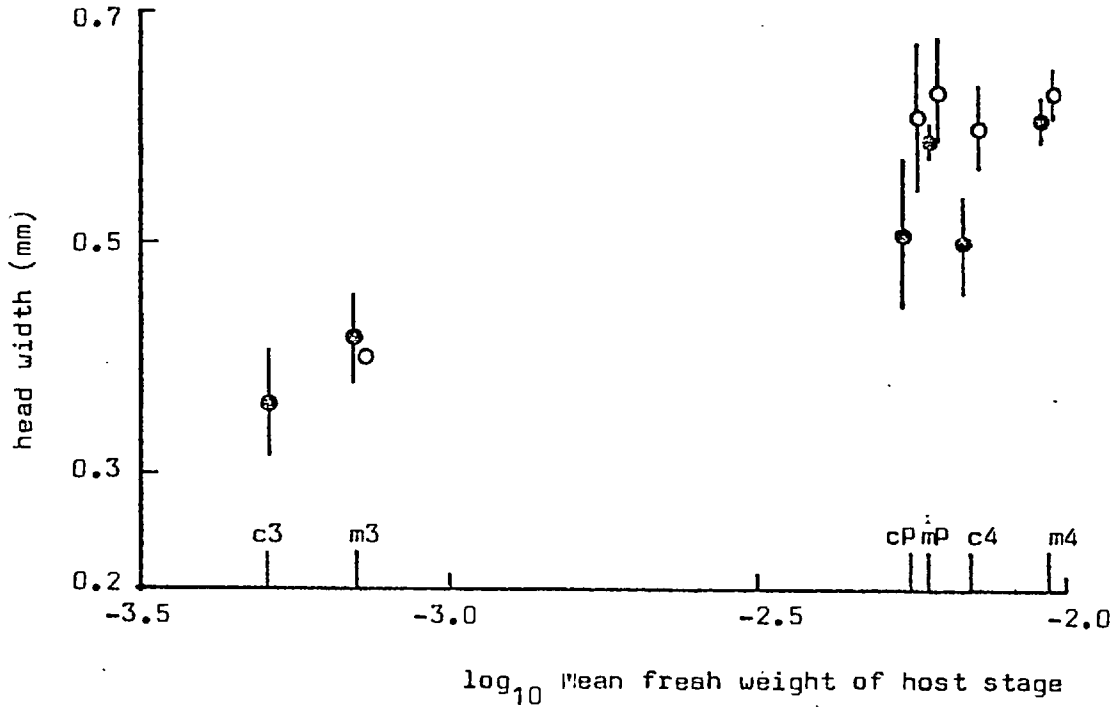

0.7
0.5
0.3
0.2
head width (mm)
c3
m3
cP
mP
c4
m4
-3.5
-3.0
-2.5
-2.0
log10 Mean fresh weight of host stage

FIGURE 6.4 The relationship between adult female parasitoid size and life-span. Hollow circles indicate repeated points.

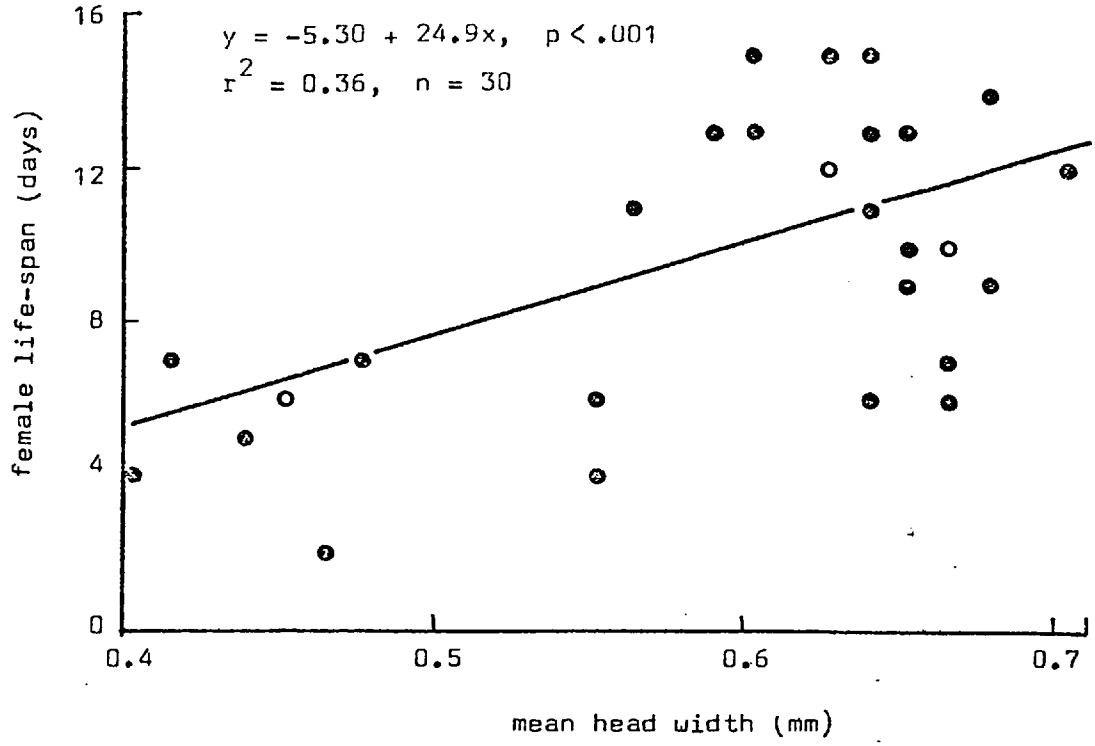
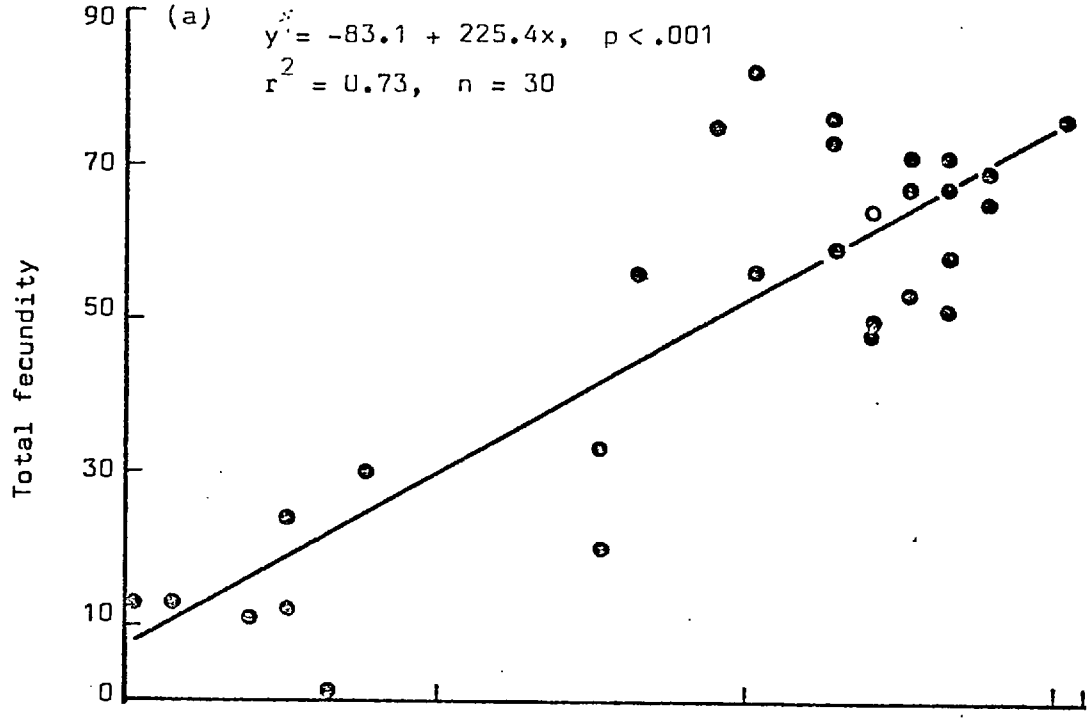

y = -5.30 + 24.9x, p < .001
r² = 0.36, n = 30
female life-span (days)
16
12
8
4
0
0.4
0.5
0.6
0.7
mean head width (mm)

FIGURE 6.5 The relationships between female parasitoid size and two measures of fecundity, (a) total number of eggs laid throughout life and (b) the mean number of eggs laid per day for females aged 1-3 days (before any of the females had died). The hollow circle in (a) indicates a repeated point.


(a)
y = -83.1 + 225.4x, p < .001
r² = 0.73, n = 30
Total fecundity
90
70
50
30
10
0

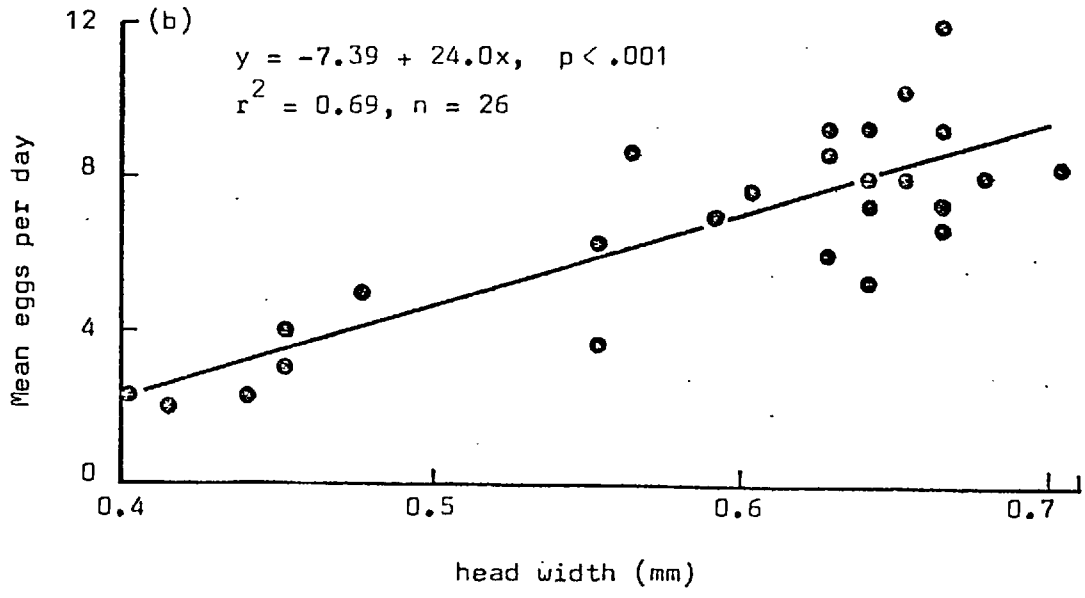
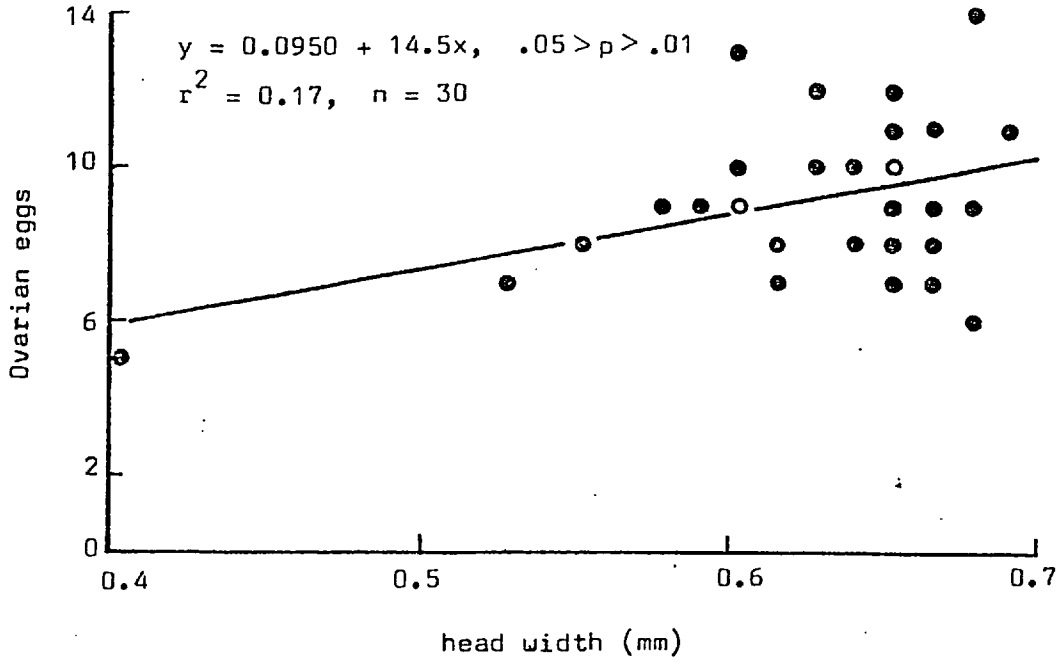

(b)
y = -7.39 + 24.0x, p < .001
r² = 0.69, n = 26
Mean eggs per day
12
8
4
0
0.4
0.5
0.6
0.7
head width (mm)

FIGURE 6.6 The relationship between parasitoid size and the number of ovarian eggs present on the day of emergence. Hollow circles indicate repeated points.


y = 0.0950 + 14.5x, .05 > p > .01
r2 = 0.17, n = 30
Ovarian eggs
14
10
6
2
0
0.4
0.5
0.6
0.7
head width (mm)

had a longer life-span than those confined with third instars (figure 6.7a). This was probably due to the inability to feed effectively on smaller larvae which were not as near the surface of the bean as the larger ones. Females confined with no hosts had initially higher survival rates than those provided with hosts, but after day five they were subject to higher mortalities. Females which had been provided with fourth instar C. maculatus maintained a more or less constant number of ovarian eggs following the first day after emergence (figure 6.7b); starved females began oosorption after day two and apparently continued to resorb eggs until they died.

The oviposition record of standard females provided with excess fourth instar C. maculatus is shown in figure 6.8 (mean of five females). These females maintained a reasonably constant oviposition rate of approximately $7\frac{1}{2}$ eggs per day for the first six days of life, after which fewer eggs were laid. Based on the information in figure 6.7b and figure 6.8 it was decided to use standard females collected over a 24 hour period which had been provided excess fourth instar C. maculatus for 48 hours (i.e. three day old females) in the experiments on searching behaviour reported in the next section.

6.3 A simulation model for parasitism

The general framework for the parasitoid simulation model will be the same as that used previously for the single-species simulation models of chapter 4. The model will employ a discrete time step of one day and will consist of a set of recursive relationships which will define the size and composition of the population at time t as a function of that at time t-1. As before, two submodels will be developed, one for the adult and one for the immature stages. The immature stages will be characterized by a single "larval" stage and

FIGURE 6.7 The effect of host availability on (a) female parasitoid longevity and (b) the number of ovarian eggs present each day. Hollow circles are for females kept with no hosts, half-open circles are for females provided with third instar C. maculatus larvae and solid circles are for females provided with fourth instar C. maculatus larvae. In (a) the numbers of females kept with no hosts, third and fourth instar larvae were 55, 53 and 62, respectively. The data in (b) for starved females six days old were taken from females which died between the fifth and sixth days. Data in (b) given as mean ± standard deviation.

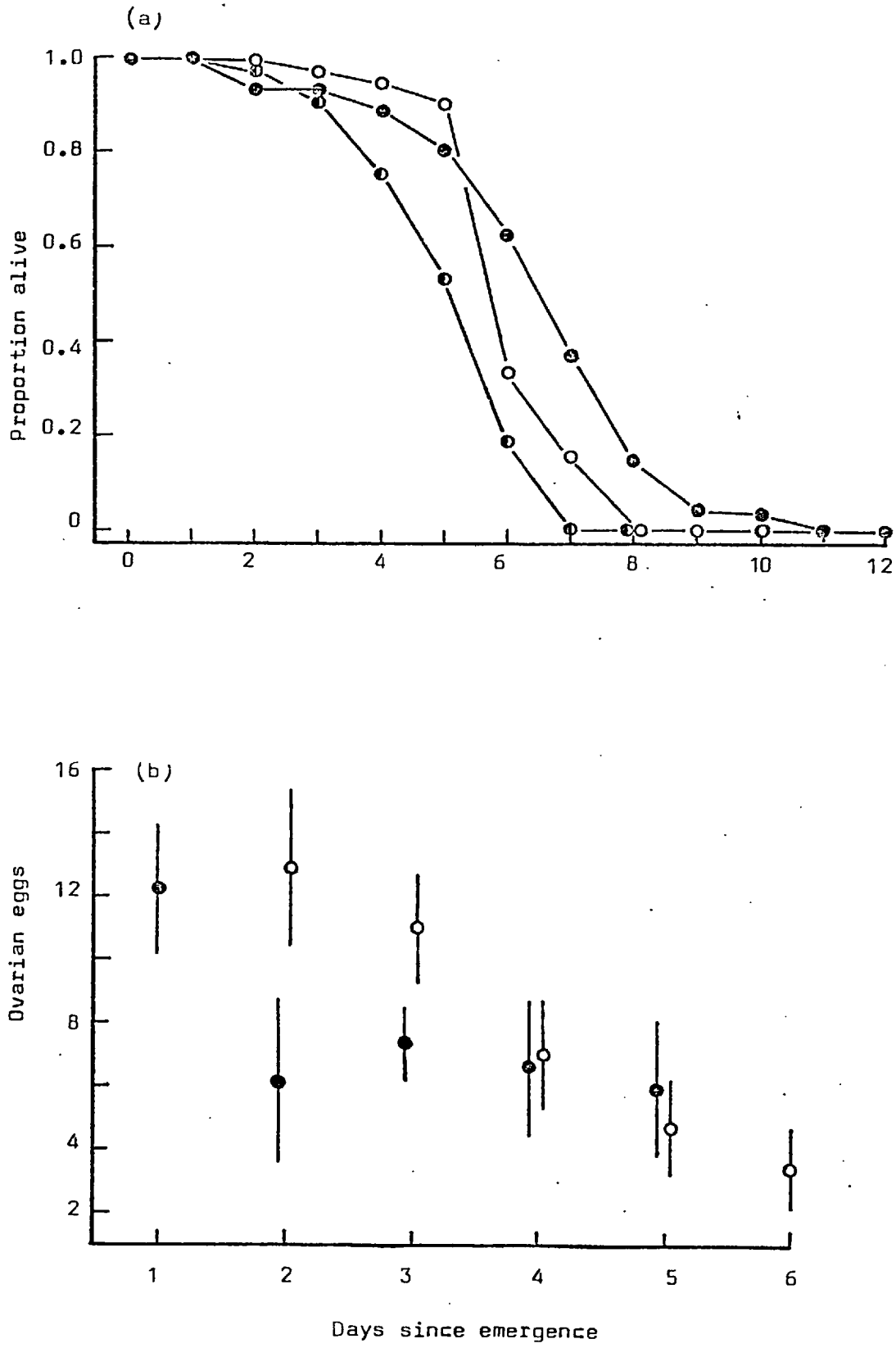
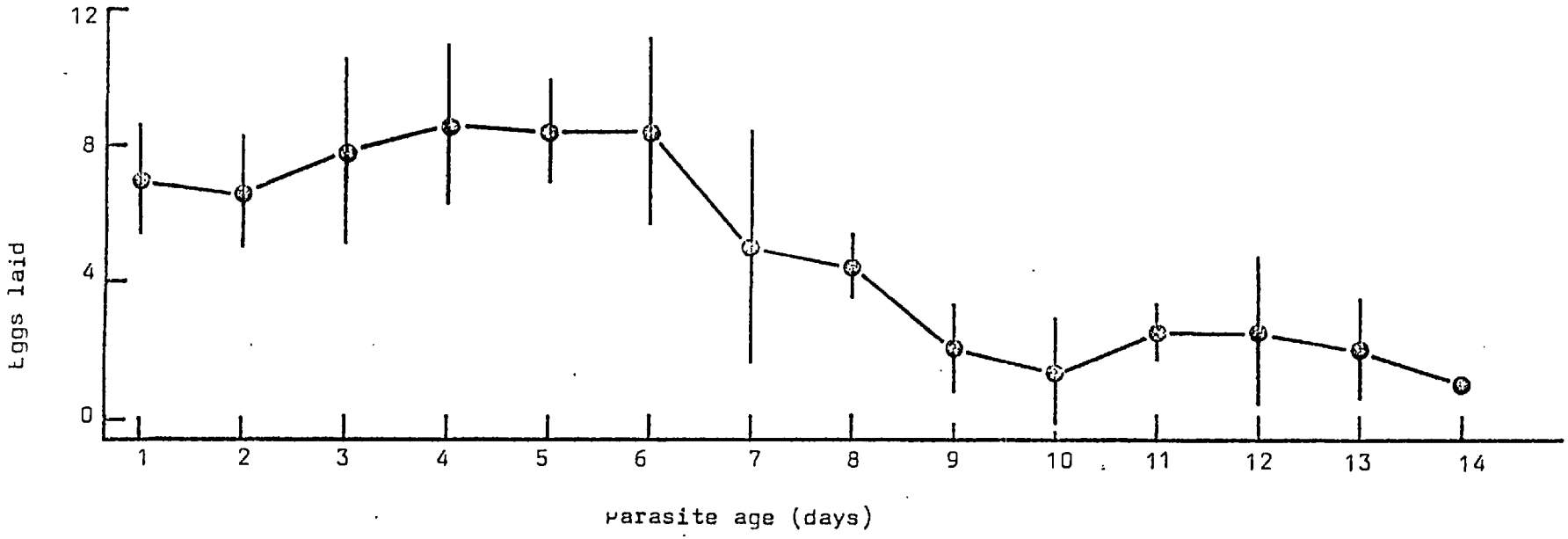

(a)
Proportion alive
1.0
0.8
0.6
0.4
0.2
0
0
2
4
6
8
10
12
(b)
Ovarian eggs
16
12
8
4
2
1
2
3
4
5
6
Days since emergence

FIGURE 6.8 The oviposition record of five standard *L. distinguendus* females provided with excess hosts. The data are given as the mean $\pm$ standard deviation of the oviposition of living females. Females died on days nine (one replicate was also lost on day nine), 10, 13 and 14.


12
8
4
0
Eggs laid
1
2
3
4
5
6
7
8
9
10
11
12
13
14
Parasite age (days)

the larval submodel will predict the number of larvae emerging as adults during each time step. The adult submodel will determine adult parasitoid mortality, recruitment to the larval stage (oviposition) and parasitoid-caused host mortality. The next two sections develop in detail the formulae used and, where appropriate, present data from which values for the necessary parameters were estimated. The larval submodel will be treated first.

6.3.1 The larval population submodel

During preimaginal development, *L. distinguendus* passes through an egg stage, larval feeding stages and a pupal stage. Furthermore, the adults spend a short time within the bean before emerging. It is possible to develop a model which accounts for each of these stages. However, there was no need to consider interactions between the immature stages and consequently development from egg to adult was considered as a single event. The object of this submodel is to predict adult emergence, and the approach taken in chapter 4 for modelling larval development is appropriate. This involves two recursive equations which define the fate of a cohort of larvae during the time interval t:

$$P(t) = G(t)\ X(t-1), \tag{6.1a}$$

$$X(t) = sX(t-1)\ (1 - G(t)). \tag{6.1b}$$

Here $X(t-1)$ is the number of larvae in the cohort at the beginning of the interval, $G(t)$ is the value of the conditional probability distribution for development for a cohort aged t, s is the proportionate daily larval survival and $P(t)$ is the number of adults emerging at time t. Equation 6.1a determines adult recruitment, while equation 6.1b accounts for losses due to mortality and development in the larval cohort. To predict the number of adults emerging at any time t it is

only necessary to apply equation 6.1 to all the larval cohorts of various ages present.

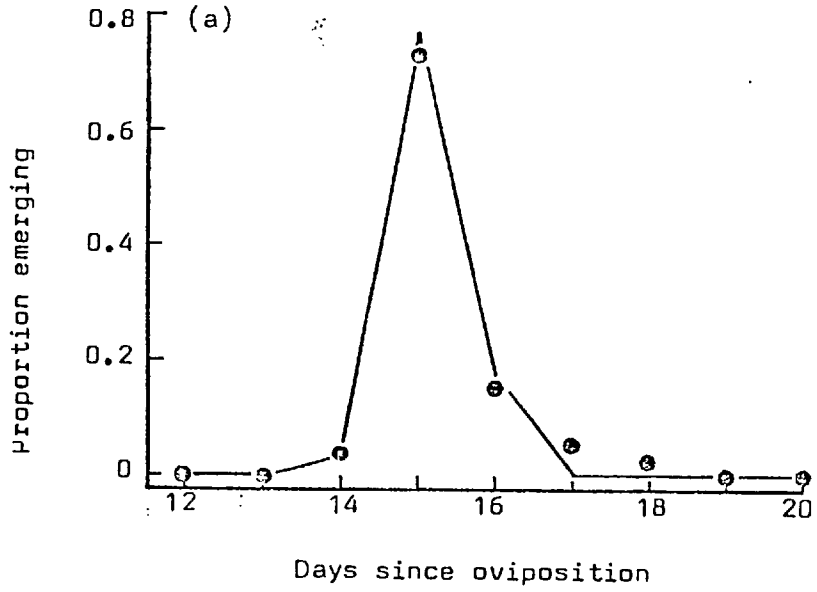
The use of equation 6.1 requires values for the distribution G and the survival parameter s. It may be recalled that the distribution G is determined by the developmental period distribution f (see page 109):

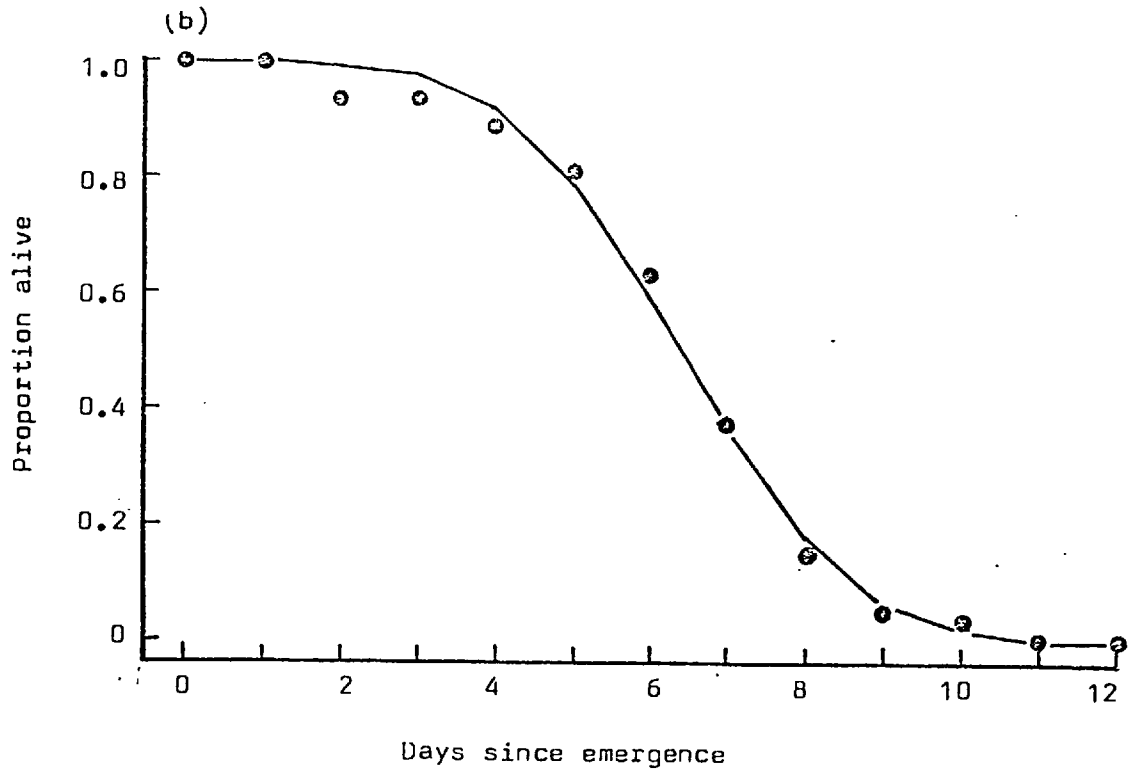
$$G(t) = f(t) \,/\, (1 - \sum_{k=0}^{t-1} f(k)). \qquad (6.2)$$

As discussed in the previous section, the developmental period of L. distinguendus is nearly independent of the host stage parasitized. Furthermore, although males developed slightly faster than females, it was only necessary to use one developmental distribution since adult emergence is only of interest for those individuals which contribute to parasitoid reproduction (i.e. females). Consequently only one distribution was used in the model. The data selected for analysis were for emergence of females from fourth instar C. maculatus. The formula used for the developmental distribution f was the previously discussed model of Sharpe et al. (1977) of equation 4.22. The data were fitted to the model by minimizing the sum of squared differences between observed and expected results as before (see page 120). The fitted model described the data very well (figure 6.9a). The estimated values for the mean and variance of the developmental rate are given in the figure legend.

Estimating the value for the larval survival rate s was more difficult. Since development occurs within the bean, direct observations on individual survival was not possible. A sequential sampling programme such as that used in chapter 4 for the construction of life-tables for the Callosobruchus species was possible but was not undertaken. The reason for this was that of more than 3900 parasitized and attacked hosts examined during this study no unhatched egg or a dead larva or pupa of the parasitoid was observed. It is unclear

FIGURE 6.9 The parasitoid model requires a larval developmental period (a) and a distribution of adult life-span (b). The data selected for analysis in (a) are for emergence of females reared on fourth instar C. maculatus. Fitting the developmental period distribution model (equation 4.22) to these data yeilded a mean developmental rate (μ) of 0.073488 $days^{-1}$ and a variance (σ^2) of $4.9543 \times 10^{-6} days^{-2}$. The data in (b) are for standard females provided excess fourth instar C. maculatus. Equation 4.3 was fitted to the data yeilding an estimated mean life-span of 6.4062 days with a variance of 2.8998 $days^2$.


(a)
0.8
0.6
0.4
0.2
0
Proportion emerging
12
14
16
18
20
Days since oviposition


(b)
1.0
0.8
0.6
0.4
0.2
0
Proportion alive
0
2
4
6
8
10
12
Days since emergence

whether this was due to a naturally high survival of the immature stages or to the inability to locate or recognize them when they were dead. The former seems the more likely case and the value of the s used in the model was unity.

6.3.2 The adult population submodel

The first requirement of this submodel is to predict the number of adults alive at time t from the initial number of adults in each cohort present. If $p(t)$ is the probability of an adult surviving to age t then the number of adults of an initial cohort $P(0)$ still living at time t ($P(t)$) is given by

$$P(t) = p(t)\ P(0), \tag{6.3}$$

and if several cohorts are present the total number of adults alive at time t is given by

$$P(t) = \sum_{j=0}^{t} p(j)\ P(t-j). \tag{6.4}$$

The model requires only one lifespan distribution for all individuals regardless of sex or the stage from which they were reared. The data on the life-span of standard females with excess hosts was used for estimating the distribution p and the formula used was the discrete form of the normal distribution of equation 4.3. The model described the data well (figure 6.9b); the estimated values for the mean and variance of adult life-span are given in the figure legend.

The other requirements of this submodel are the prediction of larval recruitment(oviposition) and parasitoid-caused host mortality. These two events were treated seperately since it is known that female parasitoids may attack a host without ovipositing on it. The host simulation model provided a daily prediction of the number of host larvae present, so it was only necessary to introduce the functions v_i and w_i which specified the proportion of hosts in stage i which

were parasitized and attacked, respectively. From equation 4.20, the number of hosts present (after mortality) in stage i at time t ($X_i(t)$) is

$$X_i(t) = s_i h_i(D_i) \; (1 - G_i(t)) \; X_i(t-1) \qquad (6.5)$$

where s_i is the density independent daily survival of stage i, h_i is a function relating density (D_i) to proportionate survival, G_i is the conditional distribution of development and $X_i(t-1)$ is the number of individuals in the stage at the beginning of the time interval. The number of parasitoid eggs laid on stage i is $v_i X_i(t)$ and the number of hosts killed is $w_i X_i(t)$. The size of the parasite larval cohort appearing at time t is, therefore, the sum of $v_i X_i(t)$ for all the stages parasitized. This concludes the development of the adult sub-model.

The functions v_i and w_i may in principle depend on a number of factors, such as host density (the parasitoid functional response), host distribution (the aggregative response), stage preferences of the parasitoids, adult parasitoid density (interference) and parasitoid age. Only three of these factors, the functional response, interference and the effects of parasitoid age were considered here. Functional response experiments were carried out for both host species on four stages: second, third and fourth instar larvae and pupae. Experiments on interference and the effect of parasitoid age on search efficiency were done only with fourth instar C. maculatus. In all the experiments except that dealing with parasitoid age, standard parasitoids which had been collected over a 24 hour period and then kept with excess fourth instar C. maculatus for 48 hours were used. Male-female pairs were kept seperately in small plastic dishes during the 48 hour period. In the experiment on the effects of parasitoid age standard parasitoids collected over a $2\frac{1}{2}$ hour period were used.

All experiments were carried out in large clear plastic boxes (9.0 cm high, 27.5 cm long and 15.5 cm wide) at 30°C, 70% relative humidity with a 16L/8D 24 hour photoperiod which started at 0600 hours.

For the experiments on the functional responses, a single layer of cowpeas (138 g, about 570 beans) was placed in the plastic boxes. Of these beans either one, two, four, eight, or 12 were replaced with infected beans from host cultures of known ages. The ages of the host cultures used are given in Table 6.3. (Cultures 18 and 20 days old were used for the pupal stage of C. chinensis and C. maculatus, respectively). Male-female pairs of standard parasitoids were placed in the boxes for 24 hours; all experiments were started between 0900 and 1300 hours. After the parasitoids had been removed the infected beans were kept at the experimental conditions for a few days and then dissected. The total number of healthy and parasitized hosts and the total number of hosts attacked (including those parasitized) were recorded. The results of these functional response experiments are shown in figures 6.10 to 6.13.

In order to quantify these results it was necessary to specify a formula for the proportion of hosts parasitized or attacked. Since the form of the results all indicated a type II functional response an appropriate formula might be either the random parasitoid or the random predator equation of Rogers (1972). The random predator equation was adopted for the following reason. During the dissection of more than 3900 parasitized or attacked hosts, only 19 bore two parasitoids; all the rest had only one. As previously discussed, no dead eggs or larvae of the parasitoid were ever observed, and all of the cases of superparasitism were observed in the late larval or pupal stage (of the parasitoid) indicating that both individuals would survive to the adult stage. It appeared, then, that the adult parasitoids could readily distinguish

FIGURE 6.10 The functional response (scored as the number of parasitoid eggs laid) of *L. distinguendus* to *C. chinensis* third instar larvae (a), fourth instar larvae (b) and pupae (c). The random predator model of Rogers (1972) was fitted to the data (equation 6.7) and provided the estimates of *a'* and T_h given in table 6.4. (Hollow circles indicate repeated points in figures 6.10 to 6.15.)

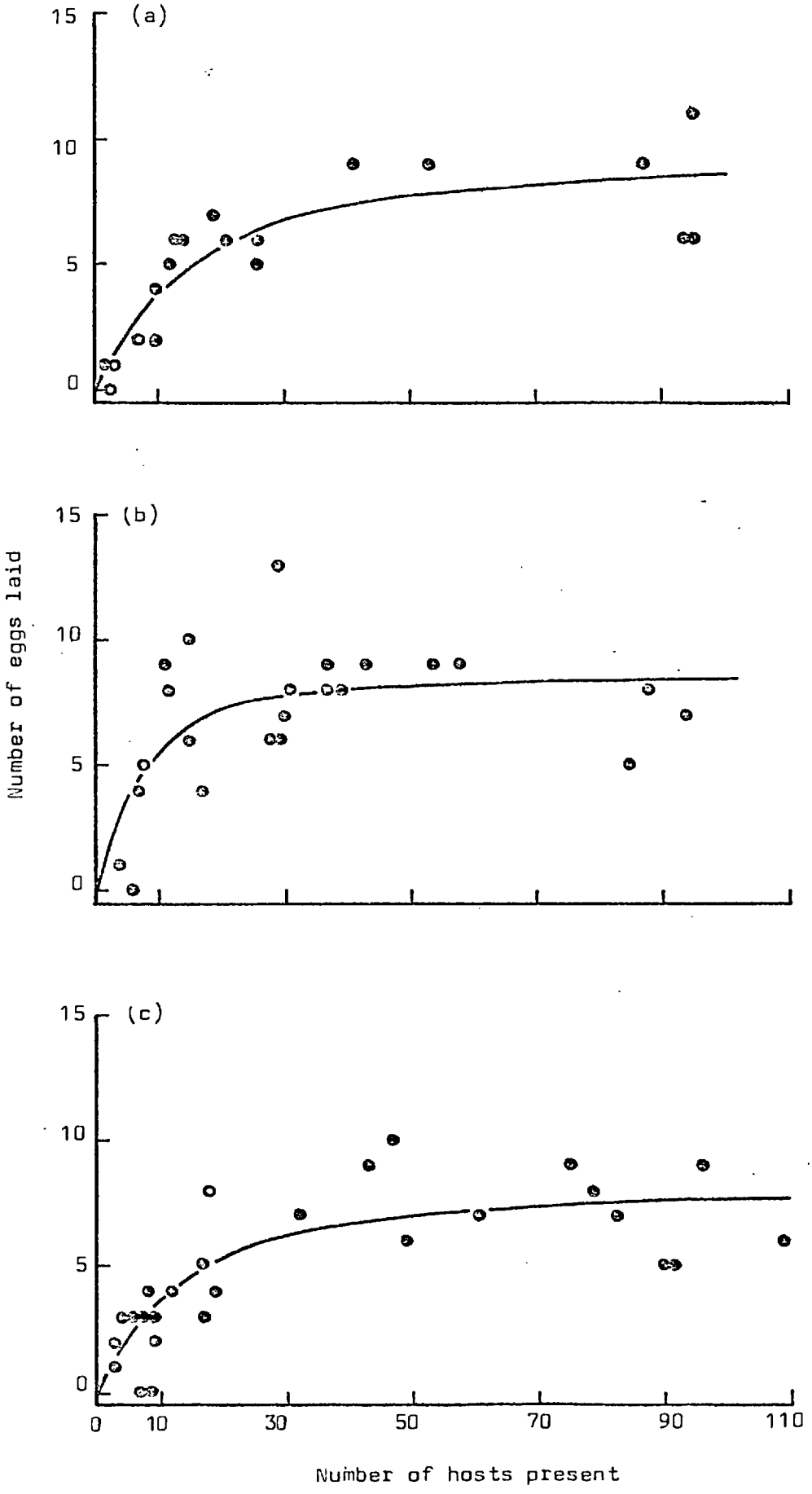
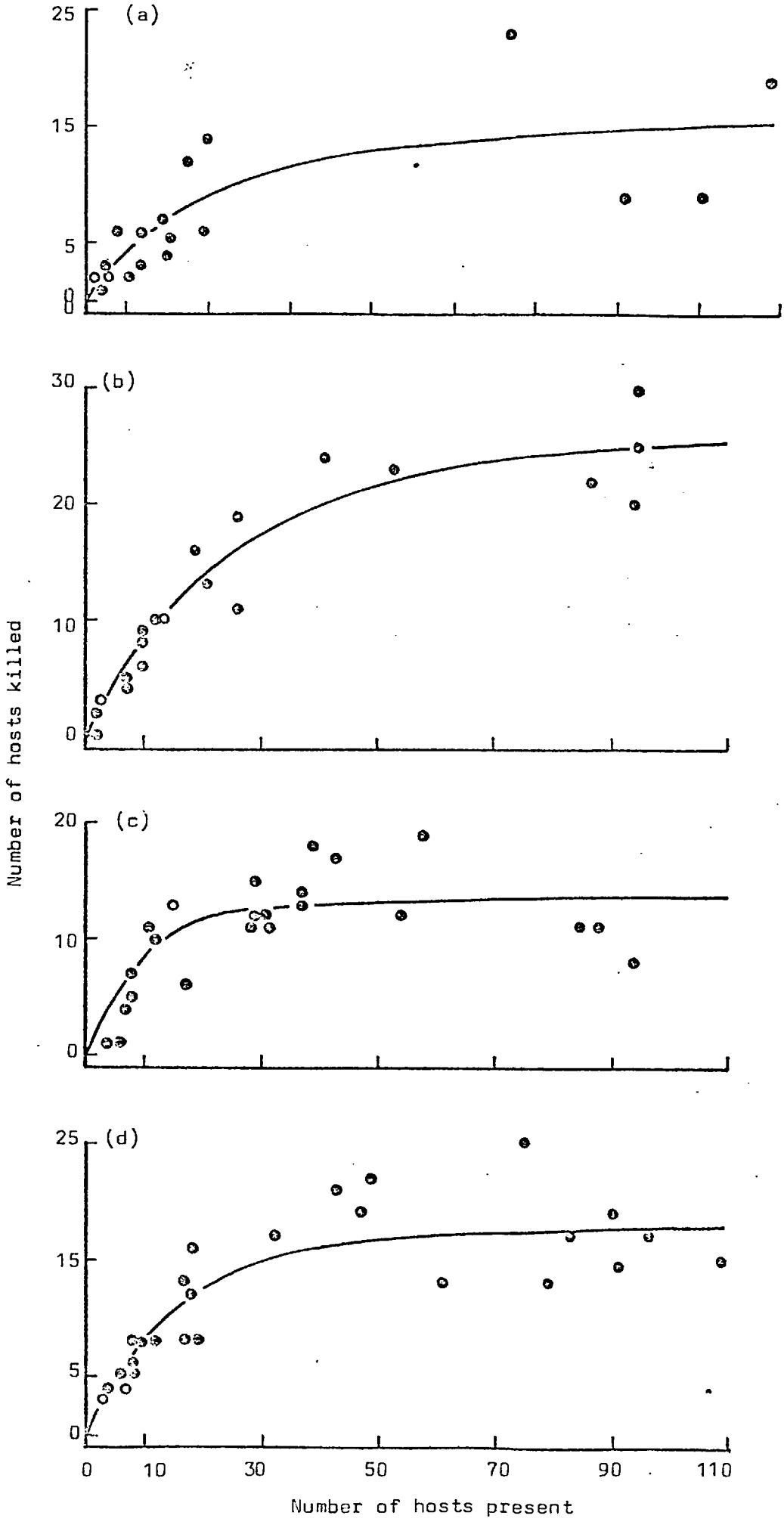

(a)
(b)
(c)
15
10
5
0
Number of eggs laid
0
10
30
50
70
90
110
Number of hosts present

FIGURE 6.11 The functional response (scored as the number of hosts attacked) of L. distinguendus to C. chinensis second instar larvae (a), third instar larvae (b), fourth instar larvae (c) and pupae (d). Equation 6.7 was fitted to the data and provided the estimates of a' and T_h given in table 6.4.


(a)
(b)
(c)
(d)
Number of hosts killed
Number of hosts present
0
5
10
15
20
25
30
0
10
30
50
70
90
110

parasitized from healthy hosts and did not oviposit on them. The handling time of a healthy host was determined by observation to be of the order of one hour, but much of this time was spent in host feeding which probably would not have taken place on a parasitized host. If the time spent in determining whether or not a host was healthy was much smaller than the total handling time of a healthy host then the random predator model would be more applicable for describing the search behaviour of this species than the random parasitoid model. Consequently, the form of the function v (and similarly for w) used here was (after Rogers 1972)

$$v = 1 - \exp(-a'(PT_t - T_h X_p)) \qquad (6.6)$$

where a' is the rate of encounters between the female parasitoids P and the hosts present (the "search efficiency"), T_t is the total time available for parasitoid search (in this case, one day), T_h is the time spent handling a host and X_p is the number of hosts parasitized. Equation 6.6 may be used for predicting the number of initially healthy individuals X which are parasitized during an experiment:

$$X_p = vX = X(1 - \exp(-a'(PT_t - T_h X_p)). \qquad (6.7)$$

Equation 6.7 was fitted to the data in figures 6.10 to 6.13 by minimizing the sum of squared differences between observed and predicted results. The estimated values of the parameters a' and T_h for each of the sets of data are given in table 6.4. In every case the model described the data well.

The functional responses to different stages of *C. chinensis* are shown in figures 6.10 (number of eggs laid) and figure 6.11 (number of hosts killed). No functional response for oviposition on seconds is shown as too few hosts were parasitized to permit any meaningful conclusions. The estimated values of the handling time for oviposition on the different stages were quite similar (table 6.4) and this probably

TABLE 6.4 The estimated values of the searching efficiency (a') and handling time (T_h) for *L. distinguendus* attacking various stages of *C. chinensis* (a) and *C. maculatus* (b). Two values of each parameter for each stage are given and these apply to the number of parasitoid eggs laid (figures 6.10 and 6.12) and the number of hosts attacked (figures 6.11 and 6.13). The parameters estimates were obtained by fitting equation 6.7 to the data.

Stage	Eggs laid		Hosts attacked	
	a'	T_h	a'	T_h
		(a) *C. chinensis*		
Second instar	---	---	0.73896	0.056408
Third instar	0.81436	0.10306	2.2719	0.034747
Fourth instar	2.3897	0.11337	4.5927	0.071655
Pupae	0.81373	0.11746	2.9439	0.051963
		(b) *C. maculatus*		
Second instar	---	---	0.46366	0.023079
Third instar	0.55836	0.093326	1.7234	0.056104
Fourth instar	3.7243	0.089125	7.2349	0.070338
Pupae	0.91780	0.087848	2.4012	0.050203

indicates that the parasites were limited by the number of eggs maturing during the experiment. The searching efficiency for the fourth instar was considerably larger than for either thirds on pupae. The smaller value for *a'* for the third instar clearly reflects their smaller size. There was little difference in size between the fourth instar larvae and pupae (table 6.3), however, so the smaller value for pupae must reflect some other difference between the stages. Possibly pupae were not found as suitable for oviposition as fourth instar larvae. The results for the number of host killed show more variation between instars (figure 6.11). Considerably more third instar larvae and pupae were killed than oviposited on as reflected by the lower estimate of T_h for the number of hosts killed in these stages. The estimate of T_h for the number of fourth instar larvae killed was somewhat higher than for the other stages and possibly indicates that more time was spent host feeding on this stage. The estimated searching efficiencies for number of hosts killed was higher than that for the number of eggs laid for all stages. The value for the fourth instar was again higher than for the other stages. The value for second instar larvae was particularly low and reflects their considerably smaller size. Similiar results were obtained for *C. maculatus* (figure 6.12 and 6.13; table 6.4). Searching efficiencies were higher and handling times were lower for number of hosts killed than for number of eggs laid. Searching efficiency for the fourth instar was higher than for other stages. The most striking differences between the parameters for the two host species are the higher search efficiency for fourth instar larvae of *C. maculatus* and the generally lower handling times for oviposition on all stages of *C. maculatus*. The higher search efficiency was probably due to the larger size of the *C. maculatus* fourth instar but, if this was the case, it is unclear why searching efficiencies were

FIGURE 6.12 The functional response (scored as the number of parasitoid eggs laid) of L. distinguendus to C. maculatus third instar larvae (a), fourth instar larvae (b) and pupae (c). Equation 6.7 was fitted to the data and provided the estimates of a' and T_h given in table 6.4.

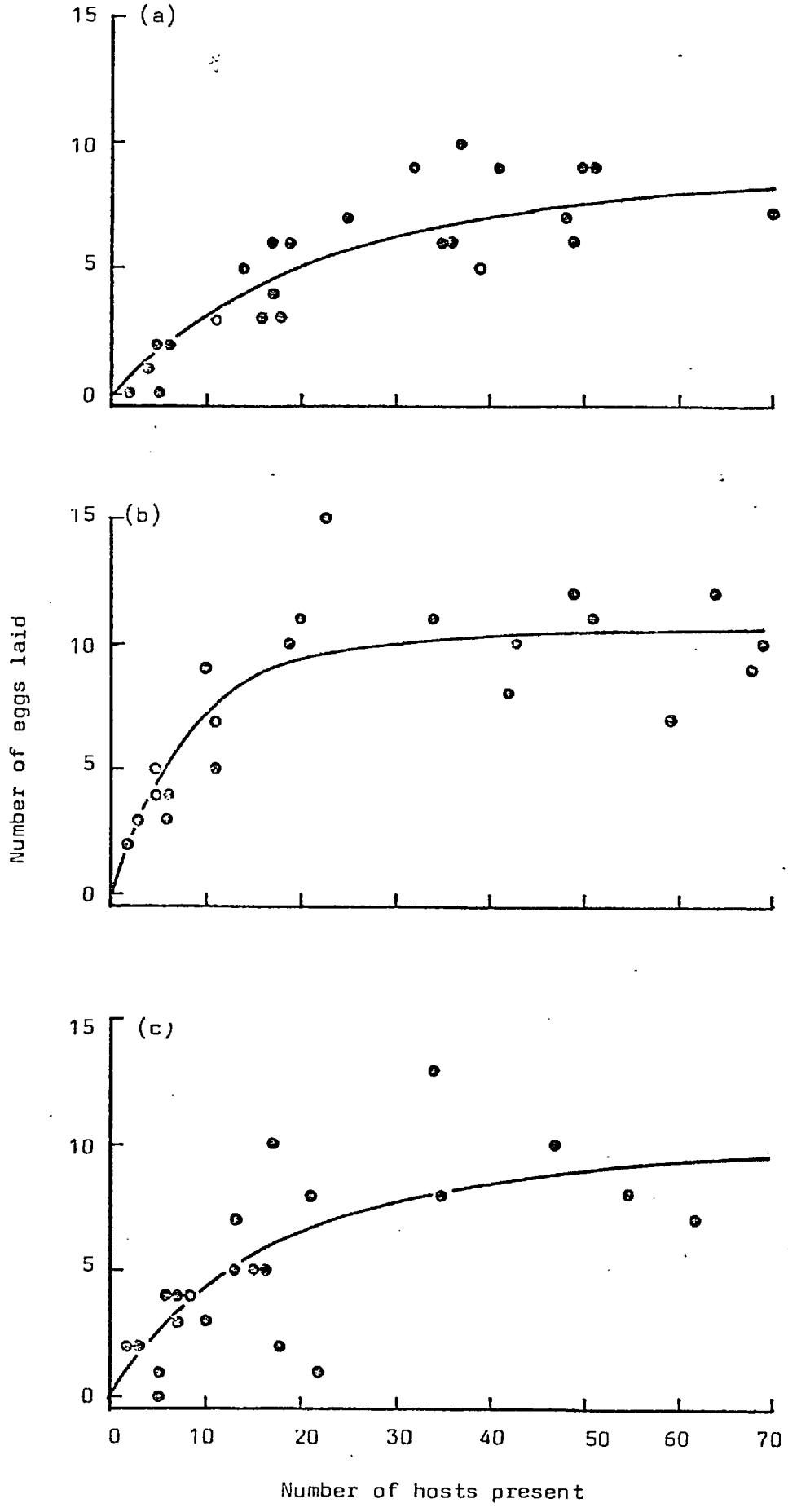
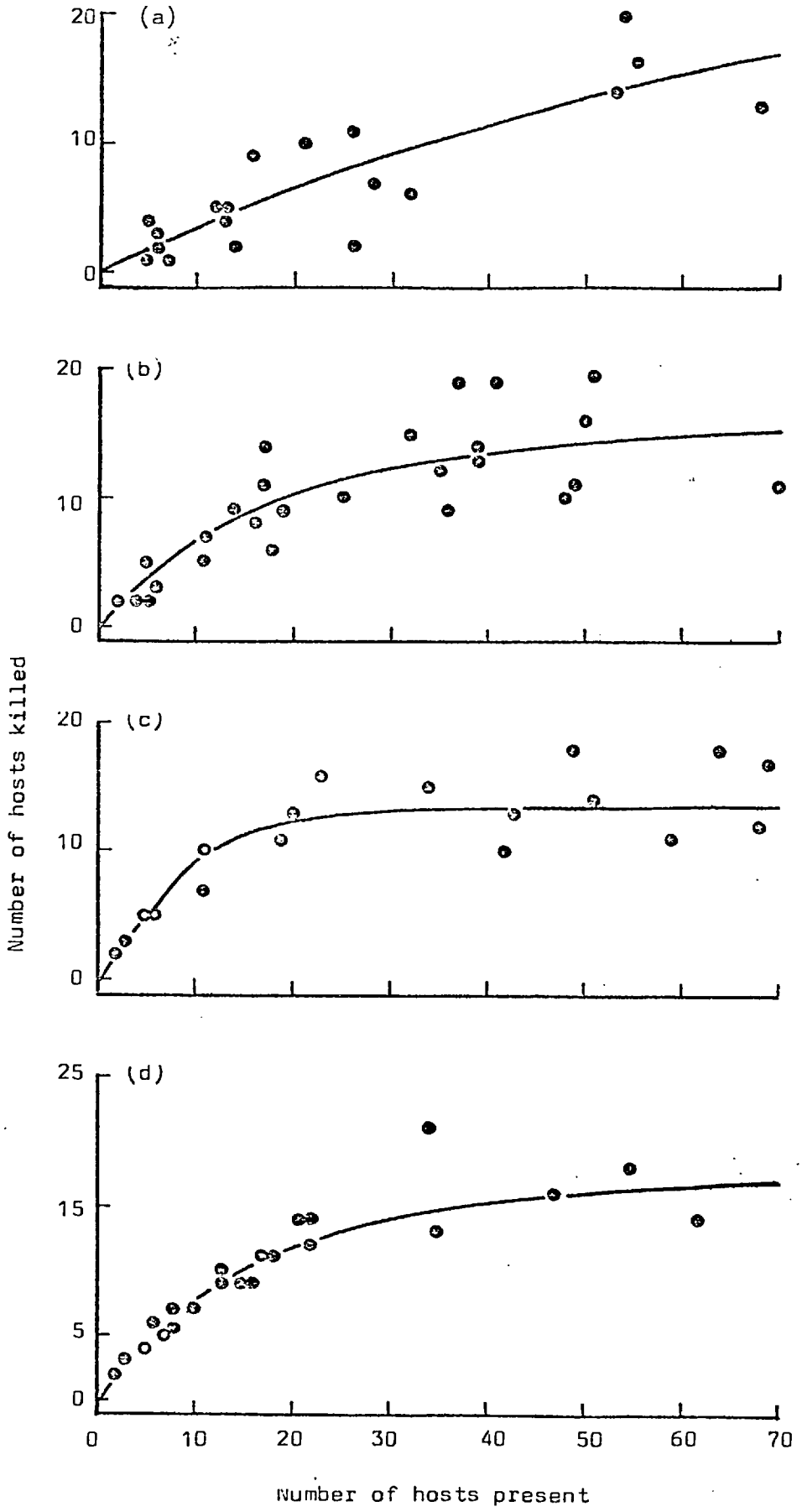

(a)
(b)
(c)
15
10
5
0
0
10
20
30
40
50
60
70
Number of eggs laid
Number of hosts present

FIGURE 6.13 The functional response (scored as the number of hosts attacked) of *L. distinguendus* to *C. maculatus* second instar larvae(a), third instar larvae (b), fourth instar larvae (c) and pupae (d). Equation 6.7 was fitted to the data and provided the estimates of a' and T_h given in table 6.4.

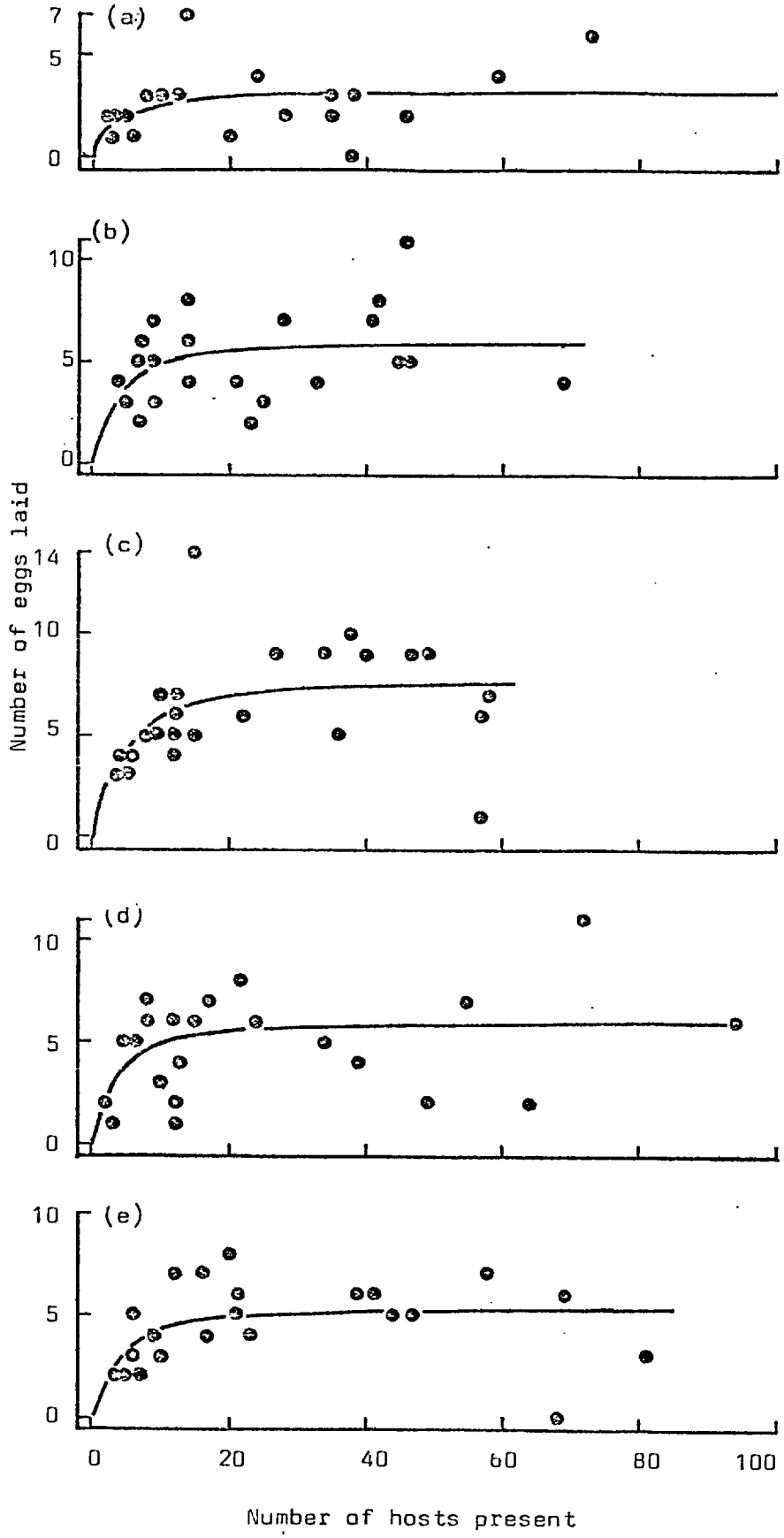

(a)
(b)
(c)
(d)
Number of hosts killed
Number of hosts present
0
10
20
30
40
50
60
70
5
15
25

not higher for the other stages. The lower handling times possibly reflect more rapid host feeding and consequently quicker maturation of eggs on the relatively larger C. maculatus stages, thus permitting greater oviposition during the experiment.

The experiment on the effect of adult density on searching efficiency was also performed with a single layer of beans in the plastic boxes. For this experiment eight beans from each box were replaced with beans containing fourth instar C. maculatus. Standard parasitoids which had emerged over a 24 hour period were collected and either four, eight, 16 or 24 females and half as many males were placed in each box. These parasitoids were provided with eight new infected beans each day for three days and, after a further few days, these beans were dissected and the total number of healthy and attacked individuals were scored. In all the results examined practically all the hosts had been attacked and it was clear that a greater number of infected beans would have been required in order to quantify any reduction in searching efficiency with increased parasitoid density. The experiment was not repeated, however. General observations on crowded adults searching in few beans failed to indicate any behavioural interference and as many as 11 females were observed searching on a single bean. Consequently, no dependence of searching efficiency on adult density was included in the model.

The experiment on the effect of age on parasitoid search was generally designed to provide functional response data for females of different ages, thus providing information on how the values of the parameters a' and T_h changed with age. Pairs of newly emerged male and female parasitoids (0-2½ hours old) were collected from standard cultures and were placed in large plastic boxes containing a single layer of cowpeas. In these boxes either one, two, four,

FIGURE 6.14 The functional responses (scored as the number of parasitoid eggs laid) of L. distinguendus females of different ages. The data in (a) through (i) are for females aged zero days to eight days, respectively. The data for females aged nine to 13 days are pooled in (j). Equation 6.7 was fitted to each set of data and provided the estimates of a' and T_h given in table 6.5.


(a)
(b)
(c)
(d)
(e)
Number of eggs laid
Number of hosts present
0
20
40
60
80
100

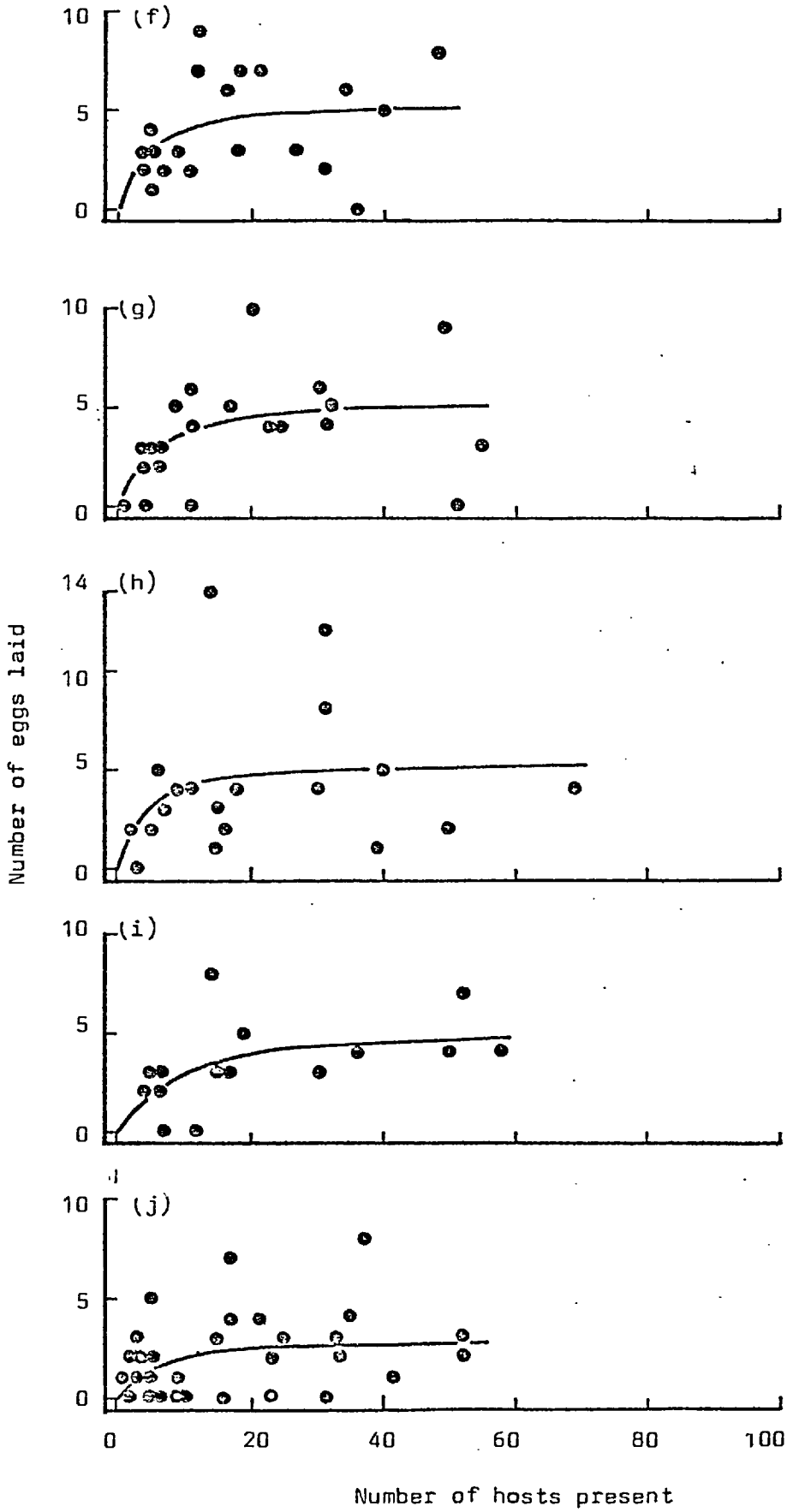
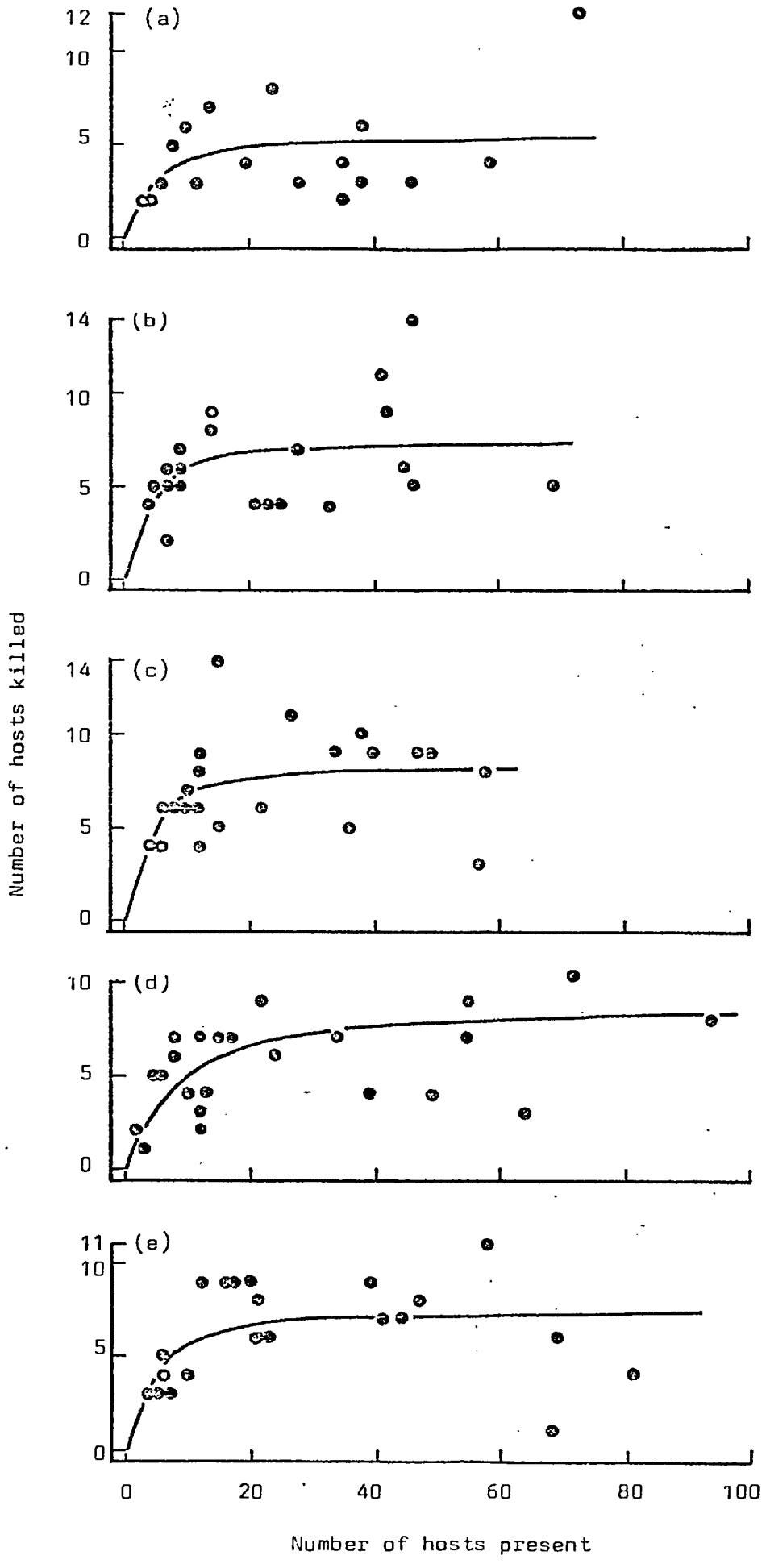
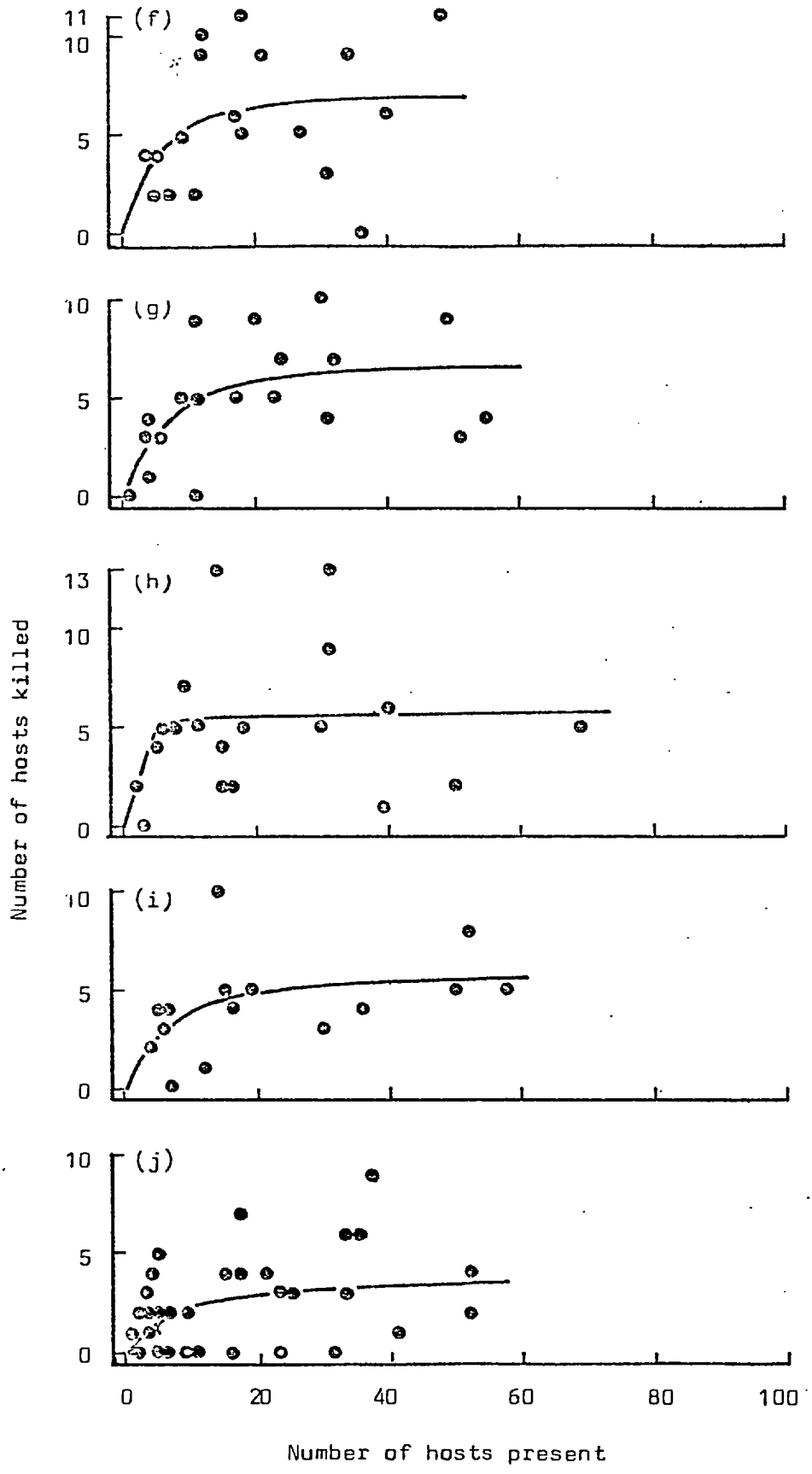

(f)
(g)
(h)
(i)
(j)
Number of eggs laid
Number of hosts present
0
5
10
14
20
40
60
80
100

FIGURE 6.15 The functional responses (scored as the number of hosts attacked) of L. distinguendus females of of different ages. The data in (a) through (i) are for females aged zero days to eight days, respectively. The data for females aged nine to 13 days are pooled in (j). Equation 6.7 was fitted to each set of data and provided the estimates of a' and T_h given in table 6.5.


(a)
(b)
(c)
(d)
(e)
Number of hosts killed
Number of hosts present
0
20
40
60
80
100


(f)
(g)
(h)
(i)
(j)
Number of hosts killed
Number of hosts present
0
20
40
60
80
100

eight or 12 beans had been replaced with beans containing fourth instar C. maculatus. The infected beans were replaced each day until the parasitoids died; each female parasitoid was provided with the same number of beans throughout her life. The infected beans were later dissected and the number of healthy, parasitized and attacked hosts were scored. The results of this experiment are presented in figures 6.14 (number of eggs laid) and 6.15 (number of hosts killed). Note that the data for parasitoids aged 9-13 days were pooled in figures 6.14j and 6.15j. Equation 6.7 was fitted to each set of data in the manner described above and estimated parameters are given in table 6.5. Firstly, it should be noted that the values for a' for oviposition and for the number of hosts attacked after the parasitoids had spent two days with the hosts agreed favourably with those for C. maculatus fourth instar larvae given in table 6.4. Secondly, the values for T_h were higher than those in table 6.4 indicating that female parasitoids searching for hosts in the large boxes matured fewer eggs per day than those offered excess hosts in smaller containers. With the exception of the data for day seven, the values for a' were highest on about the third day of adult life and showed a general decline afterwards (figure 6.16). The values for T_h were smallest around the third day, remained more or less constant for parasitoids aged four to six days and were higher near the end of adult life. The estimated values for a' for day seven were inflated due to the nature of the data for that day and do not reflect an increased searching efficiency. The estimated values for T_h for day $\overset{\text{seven}}{h}$ were apparently less affected. The estimated searching efficiency for attacked hosts for parasitoids aged three days also appears rather low, but the cause of this is not clear. In conclusion, the parameters a' and T_h were found to vary with age in what may be considered a biologically reasonable way and

TABLE 6.5 The results of fitting equation 6.7 to the functional responses of *L. distinguendus* females of different ages. Both the number of parasitoid progeny and the total number of hosts attacked were scored giving rise to two estimates for a' and for T_h.

Parasite age (days)	Oviposition		Host mortality	
	a'	T_h	a'	T_h
0	1.65	.307	1.99	.179
1	3.69	.167	4.70	.134
2	3.51	.126	6.03	.119
3	3.39	.165	1.58	.113
4	2.51	.184	3.91	.134
5	2.20	.186	3.31	.139
6	1.50	.183	1.93	.142
7	2.47	.186	18.4	.176
8	.737	.183	1.35	.168
9-13 pooled	.710	.344	.652	.255

FIGURE 6.16 The estimated values of $\underline{a'}$ and $\underline{T_h}$ for the number of parasitoid progeny (a) and the number of hosts attacked (b) plotted against female age (see table 6.5). The values for females aged seven days in (b) are excluded. See text for discussion.

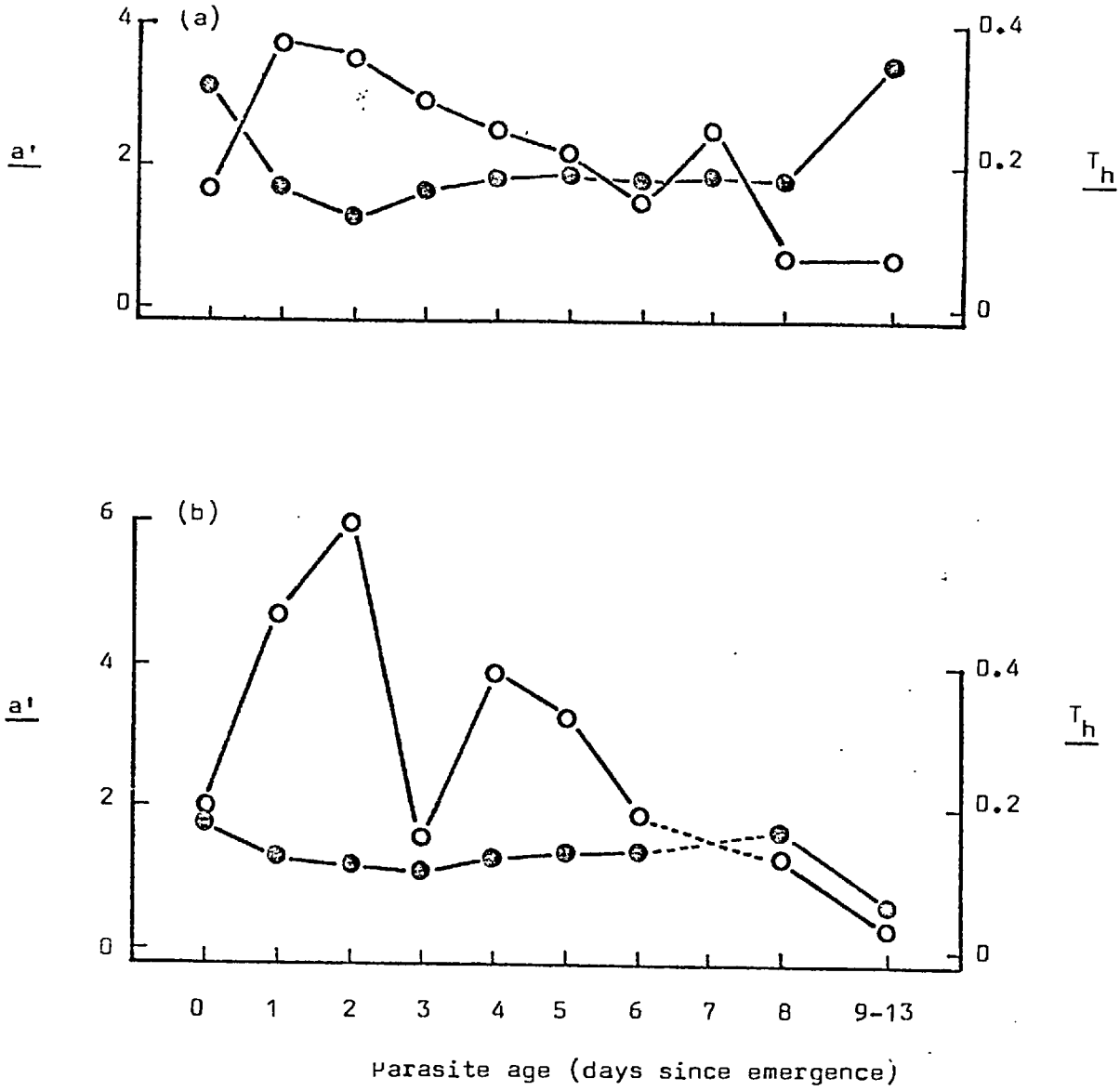

(a)
a'
4
2
0
0.4
0.2
0
T_h
(b)
a'
6
4
2
0
0.4
0.2
0
T_h
0 1 2 3 4 5 6 7 8 9-13
Parasite age (days since emergence)

FIGURE 6.17 When two or more host stages are present different values of *a'* and T_h for the various stages will cause them to be attacked disproportionately to their presence in the population. This figure demonstrates this affect for various combinations of two stages of *C. chinensis*. (a) third and second instar larvae. (b) fourth and second instar larvae. (c) fourth and third instar larvae. (d) pupae and second instar larvae. (e) pupae and third instar larvae. (f) pupae and fourth instar larvae. The curves are given for a total host density of 100 individuals and were obtained using the values of *a'* and T_h in table 6.4 with equation 6.8 Note the general heavier attack of the larger instar.

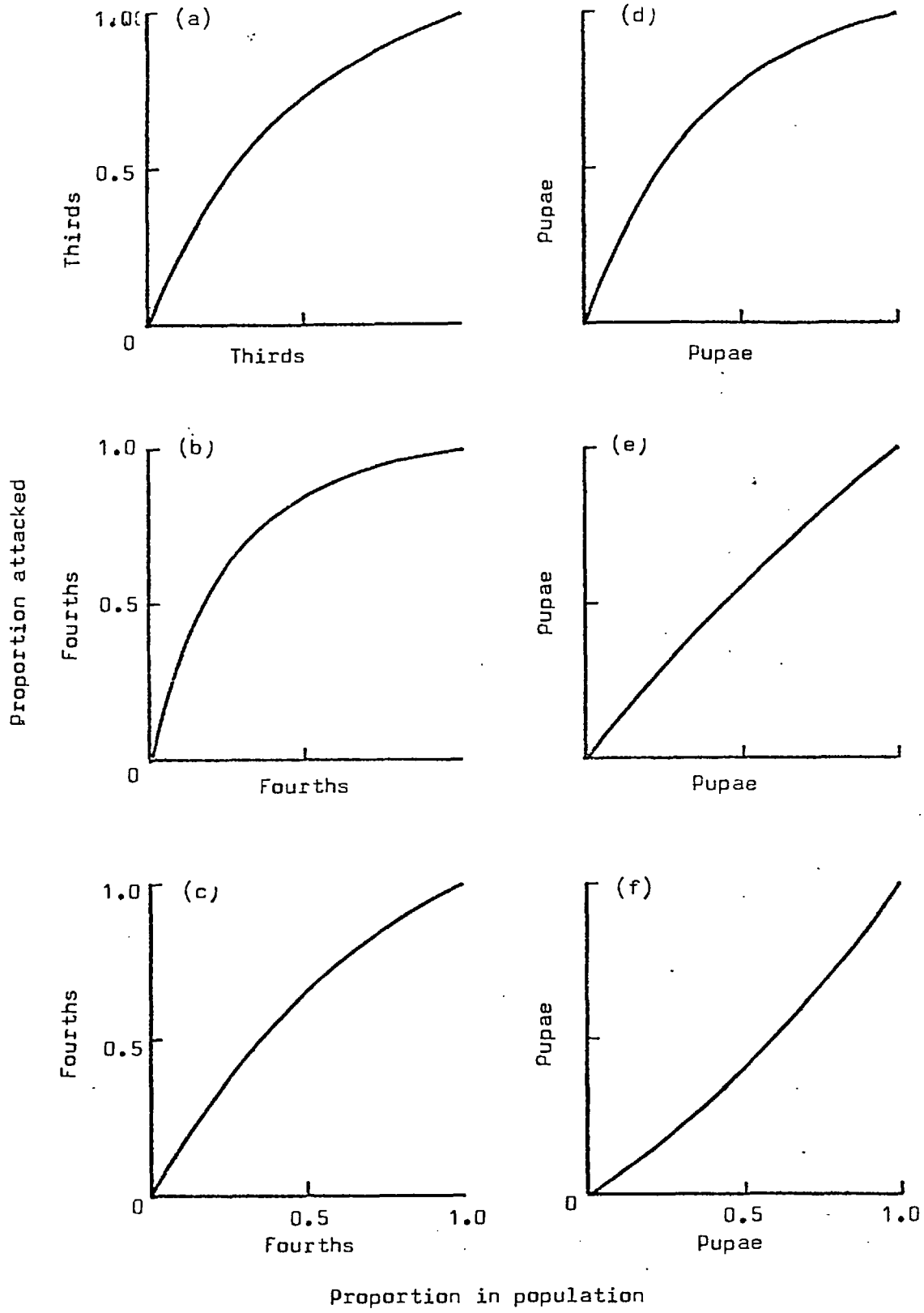
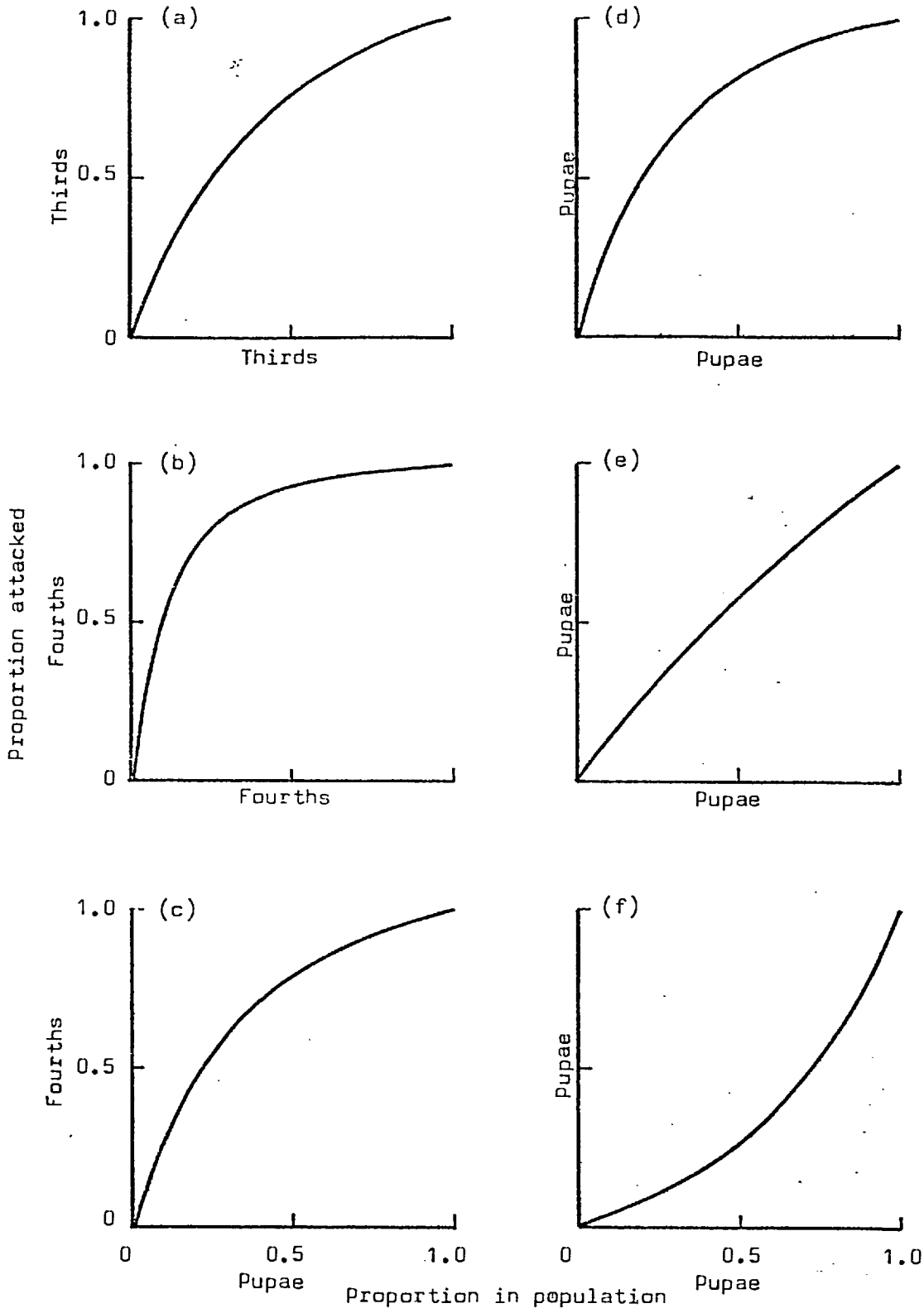

(a)
1.0
0.5
0
Thirds
Thirds
(d)
Pupae
Pupae
(b)
1.0
0.5
0
Fourths
Fourths
(e)
Pupae
Pupae
Proportion attacked
(c)
1.0
0.5
0
Fourths
0.5
1.0
Fourths
(f)
Pupae
0
0.5
1.0
Pupae
Proportion in population

FIGURE 6.18 When two or more host stages are present different values of *a'* and T_h for the various stages will cause them to be attacked disproportionately to their presence in the population. This figure demonstrates this affect for various combinations of two stages of *C. maculatus*. (a) third and second instar larvae. (b) fourth and second instar larvae. (c) fourth and third instar larvae. (d) pupae and second instar larvae. (e) pupae and third instar larvae. (f) pupae and fourth instar larvae. The curves are given for a total host density of 100 individuals and were obtained using the values of *a'* and T_h in table 6.4 with equation 6.8. Note the general heavier attack of the larger instar.


(a)
1.0
0.5
0
Thirds
Thirds
(d)
Pupae
Pupae
(b)
Proportion attacked
Fourths
Fourths
(e)
Pupae
Pupae
(c)
Fourths
0.5
0
0
0.5
1.0
Pupae
(f)
Pupae
0
0.5
1.0
Pupae
Proportion in population

the details of the parasitism model discussed next will include this phenomenon.

6.3.3 Details of the simulation model

In order to complete the development of the parasitoid simulation model it is necessary to consider three problems. The first of these deals with how parasitoid attacks (and ovipositions) will be distributed among hosts when more than one host stage is present. Equation 6.7, which was used to quantify the functional responses, can be extended to include more than one stage, but the resulting formula can be solved for the number attacked in each stage only by complex numerical analyses. Consequently, the similar random parasitoid equation of Rogers (1972) was adopted for use in the simulation model. The number of hosts oviposited on (or attacked) in stage i during time t (X_{ip}) is now given by

$$X_{ip} = X_i(1 - \exp(-a'_i PT_t / (1 + \sum_{all\ k} a'_k T_{hk} X_k))), \qquad (6.8)$$

where the symbols are defined as in equation 6.7 and subscripts indicate the stage specificity of the parameters a' and T_h. The summation in the exponent of equation 6.8 accounts for the time spent handling the hosts parasitized in each stage present. Whenever the values of a' and T_h are different for the various stages present, then the stages will not be attacked in proportion to their presence in the population. This is emphasized in figures 6.17 (*C. chinensis*) and 6.18 (*C. maculatus*), where the values of the parameters in table 6.4 have been used with equation 6.8 to predict the proportion of each stage attacked for various combinations of two stages. For both species these predictions indicate that the larger of two instars would be attacked more often.

The second problem to be faced was how to model the effects of

parasitoid age on the parameters a' and T_h. Equation 6.8 may be modified to allow these parameters to be age-dependent. If adults of several ages are present, then the number of hosts in stage i parasitized during time t is

$$X_{ip} = X_i\left(1 - \exp\left\{-\sum_{j=0}^{t}\left[\frac{a'_i(j)\, P(t-j)\, T_t}{\left(1 + \sum_{\text{all } k}\left(a'_k(j)T_{hk}(j)X_k\right)\right)}\right]\right\}\right). \qquad (6.9)$$

The parameters a' and T_h are now indexed to indicate their age-dependency and $P(t-j)$ is the number of females present which have age j. In order to determine how a' and T_h changed with age, the values in table 6.5 were expressed as proportions of the values for parasites two days old (table 6.6). These proportions were similar for both attacks and ovipositions. Consequently, only one set of proportions was included in the model (table 6.6) and these were used to weight the values of a' and T_h given in table 6.4 for parasitoids of different ages. Equation 6.9 is the full specification of parasitoid searching behaviour used in the model. It was applied twice during each time interval; once with parameter values for oviposition to determine the number of parasitoid eggs laid and once with values for hosts attacked to determine parasitoid-caused host mortality.

Finally, it was necessary to define the sex ratio of the parasitoid progeny. No information was available for the system used here, and values in literature vary from 40% (Kaschef 1961) to 67% females (Romanova & Il'inskaya 1938). In the simulations reported here the sex ratio used was 3:2 in favour of females since only the results of Romanova and Il'inskaya were at hand at the time. However, since very few females were reared from third instar larvae of either host, it was assumed that no eggs were laid on this stage. This was accomplished by setting the value of a'_3 for oviposition to zero; the value for host mortality was unchanged.

TABLE 6.6 The values of the search parameters of table 6.5 expressed as a proportion of the value for two day old parasitoids. The values of a' for hosts attacked for parasitoids aged three and seven days were not considered when selecting the proportions used in the model. See text for further discussion.

Parasite age (days)	a'			T_h		
	eggs laid	hosts attacked	model	eggs laid	hosts attacked	model
0	0.470	0.330	0.40	2.437	1.504	2.00
1	1.051	0.779	0.90	1.325	1.126	1.25
2	1.000	1.000	1.00	1.000	1.000	1.00
3	0.966	(0.262)	0.95	1.300	0.950	1.10
4	0.715	0.648	0.70	1.460	1.126	1.35
5	0.627	0.549	0.60	1.476	1.168	1.30
6	0.425	0.320	0.40	1.452	1.193	1.30
7	0.704	(3.051)	0.30	1.476	1.412	1.30
8	0.210	0.224	0.20	1.452	1.479	1.45
9-13	0.202	0.108	0.15	2.730	2.143	2.45
>13	---	---	0.00	---	---	0.00

It should be noted that the values of the search parameters used in the model (tables 6.4 and 6.5) were determined in a much larger experimental system than was used in developing the host model in chapter 4. This was necessary in order to obtain meaningful results, but the resulting parameter values may not be appropriate for parasitoids searching in smaller containers. Consequently, the affects of changes in their magnitude will be briefly investigated in the next section.

6.4 Simulation results

6.4.1 Single host species simulations

The parasitism model was added to the single-species simulation models developed in chapter 4 and the predicted dynamics of the systems are shown in figure 6.19 for C. chinensis and 6.20 for C. maculatus. The most remarkable feature of these simulations was the sustained aperiodic oscillations. Considering first the C. chinensis simulation (figure 6.19) it may be noted that after generation 20, peaks of the parasitoid population occurred approximately every three or four generations. This was partly due to the asynchrony between the development of the immature stages of the hosts and parasitoids. The reproduction of the parasitoids was greater in generations where the appearance of the fourth instar larvae coincided more with the presence of the parasitoid adults than in following generations, when the parasitoids emerged before many of the hosts had reached the fourth instar. The parasitoid population in the eleventh generation was added on day 15 and the subsequent low parasitoid population levels were caused by poor reproduction of their progeny which emerged when most of the hosts were in second and third instar. Heavy attack of these younger hosts in generation 12 caused the host population

FIGURE 6.19 The predicted dynamics of interacting populations of C. chinensis and L. distinguendus. The aperiodic fluctuations in population density are a consequence of the multiple age-class structure of the model. The simulation was started with 20 C. chinensis on day one and three parasites (two females and one male) were added on day 15 of the eleventh generation. See text for discussion. O - C. chinensis. X - L. distinguendus.

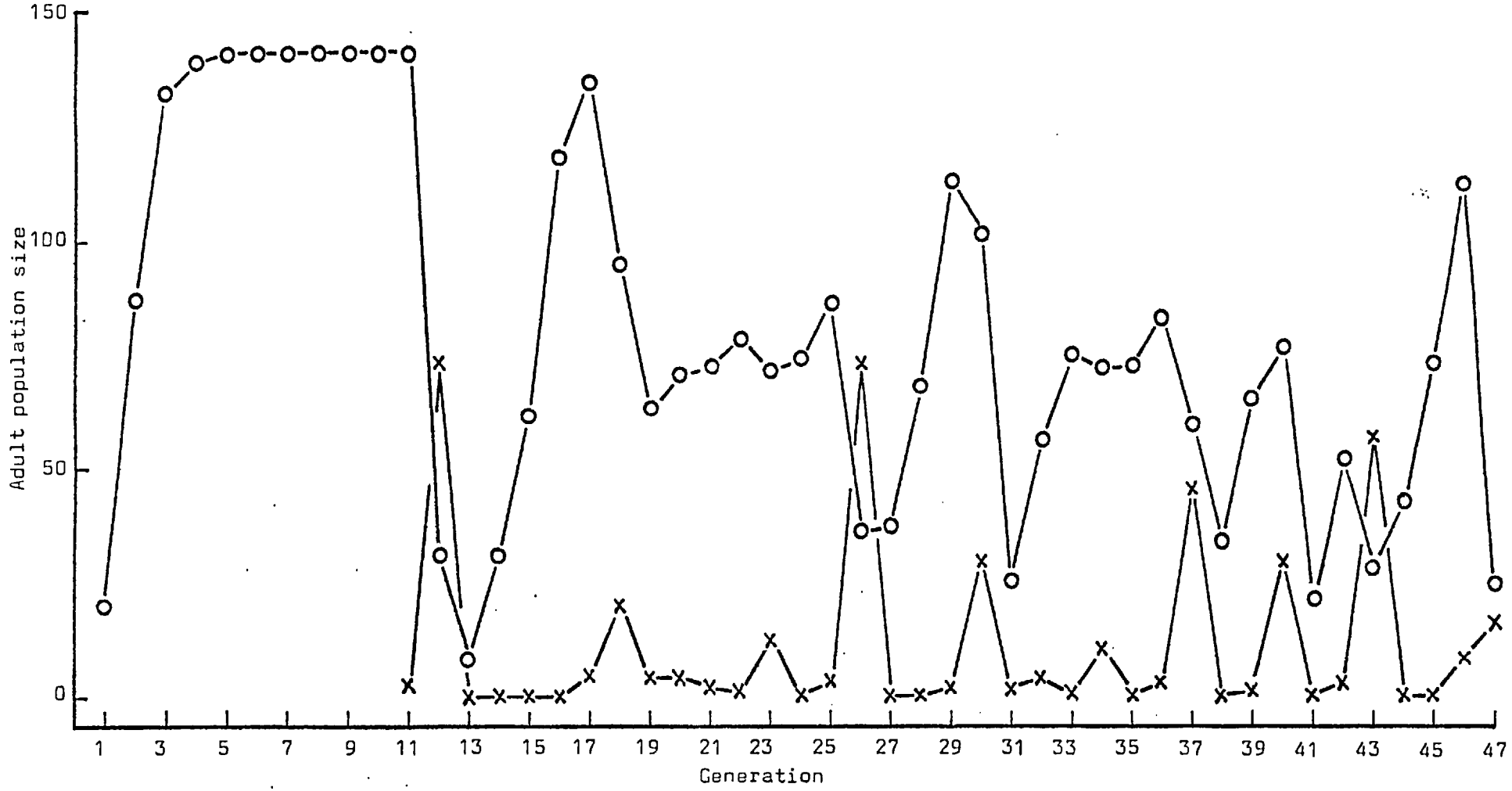

150
100
50
0
Adult population size
1 3 5 7 9 11 13 15 17 19 21 23 25 27 29 31 33 35 37 39 41 43 45 47
Generation

FIGURE 6.20 The predicted dynamics of interacting populations of C. maculatus and L. distinguendus. The aperiodic fluctuations in population density are a consequence of the multiple age-class structure of the model. The simulation was started with 20 C. maculatus on day one and three parasites (two females and one male) were added on day 15 of the eleventh generation. See text for discussion. ● — C. maculatus. × — L. distinguendus.


Adult population size
80
60
40
20
0
1
3
5
7
9
11
13
15
17
19
21
23
25
27
29
31
33
35
37
39
41
43
45
47
Generation

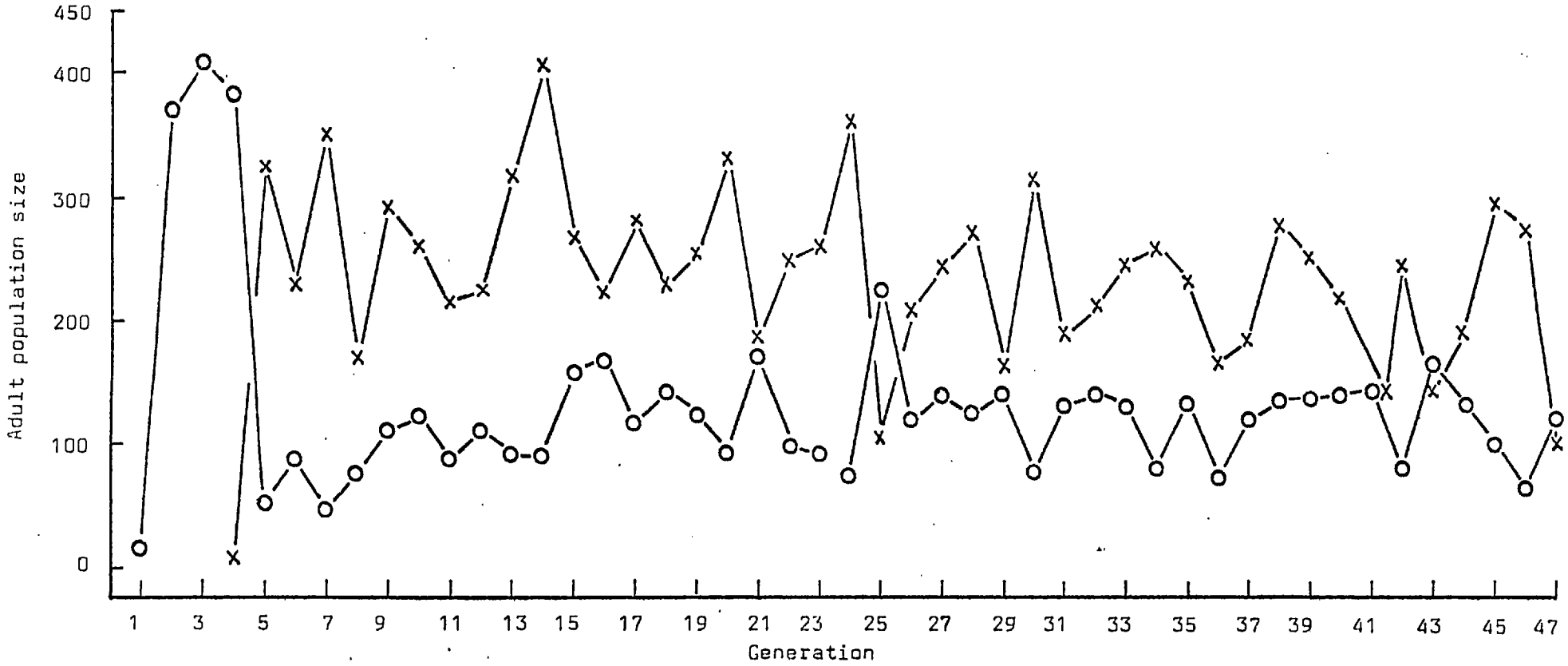
to decrease without contributing to the next parasitoid generation since no eggs were considered to be laid on these stages. The host and parasitoid populations both persisted after this initial decrease in the parasitoid population; the lowest parasitoid population levels reached, however, were less than 10^{-2} individuals and their probable extinction was indicated. This is even more pronounced in the simulations for C. maculatus. The parasitoid adults were again added on day 15 of the eleventh generation and the progeny of these adults emerged prior to the development of any hosts suitable for oviposition. The parasitoid population was reduced in the third generation to less than 10^{-5} individuals which clearly indicates extinction. However, later recovery of the population established an apparently persistent interaction indicating that other initial densities or timings of introduction would have caused a less serious initial fluctuation. The two oscillations of the host population between generations two and 11 (prior to the introduction of the parasitoids) and between generations 16 and 24 (when the population of the parasitoids was very small) were due to the asynchrony between the host population and the food renewal regime as discussed in chapter 4. Following generation 24 the recovery of the parasitoid population induced aperiodic fluctuations as observed in the C. chinensis simulation. The fluctuations were smaller in magnitude than those observed for C. chinensis. Parasitoid population levels during this period fell below 10^{-2} only after generation 45.

As discussed in the previous section, the magnitude of the search parameters of table 6.4 may be inappropriate for the simulation model developed in chapter 4, so a brief investigation was made into the effects of the values of the parameters a_i' on the dynamics of these systems. Two C. chinensis simulations were run where a_4' for the fourth

instar (for both oviposition and host mortality) was set at 0.01 and 0.0001 (the potential effects of higher values were not investigated). The values for a' for the other stages were set at zero. In the first of these simulations (a'_4 = 0.01) the population oscillated in a manner similar to that shown in figure 6.18. In the second simulation (a'_4 = 0.0001) parasitoid reproduction was sufficiently suppressed so that no persistent interaction was possible and the parasitoid population was lost. A further investigation into the effect of developmental asynchrony between the host and the parasitoid was conducted, again using the C. chinensis model. The adult mean life-span of the parasitoids was increased to 10 days and the adults were given a five day preoviposition period. Since the mode of parasitoid larval emergence was 15 days, this preoviposition period increased the time between reproduction of successive parasitoid generations to approximately 20 days. However, numerous simulations including this feature but with different values for the search parameters a' failed to alter the dynamics of the model. In all cases where there was a persistent interaction the populations showed aperiodic oscillations.

The predictions of these simulations may be usefully compared with the results of long-term studies of these species and such work is in progress (Dr. M. P. Hassell, personal communication). The long-term dynamics of a similar system have been studied by Utida (1950), who used C. chinensis and the pteromalid Anisopteromalus calandrae How. (figure 6.21). The principle difference between Utida's results and the simulations presented here is that in the observed system there was generally a higher number of parasitoid adults than host adults. This may reflect the higher fecundity of A. calandrae (approximately 170 eggs per female; Cotton 1923) than of L. distinguendus (about 60 eggs, see figure 6.5a). There were, however,

FIGURE 6.21 The observed dynamics of interacting populations of C. chinensis and Anisopteromalus calandrae (from Utida 1950). Note the aperiodic fluctuations similar in character to those predicted by the model (cf. figures 6.19 and 6.20). O - C. chinensis. X - A. calandrae.


Adult population size
450
400
300
200
100
0
1
3
5
7
9
11
13
15
17
19
21
23
25
27
29
31
33
35
37
39
41
43
45
47
Generation

aperiodic fluctuations similiar to those in figure 6.18, thus providing qualitative validation of the model.

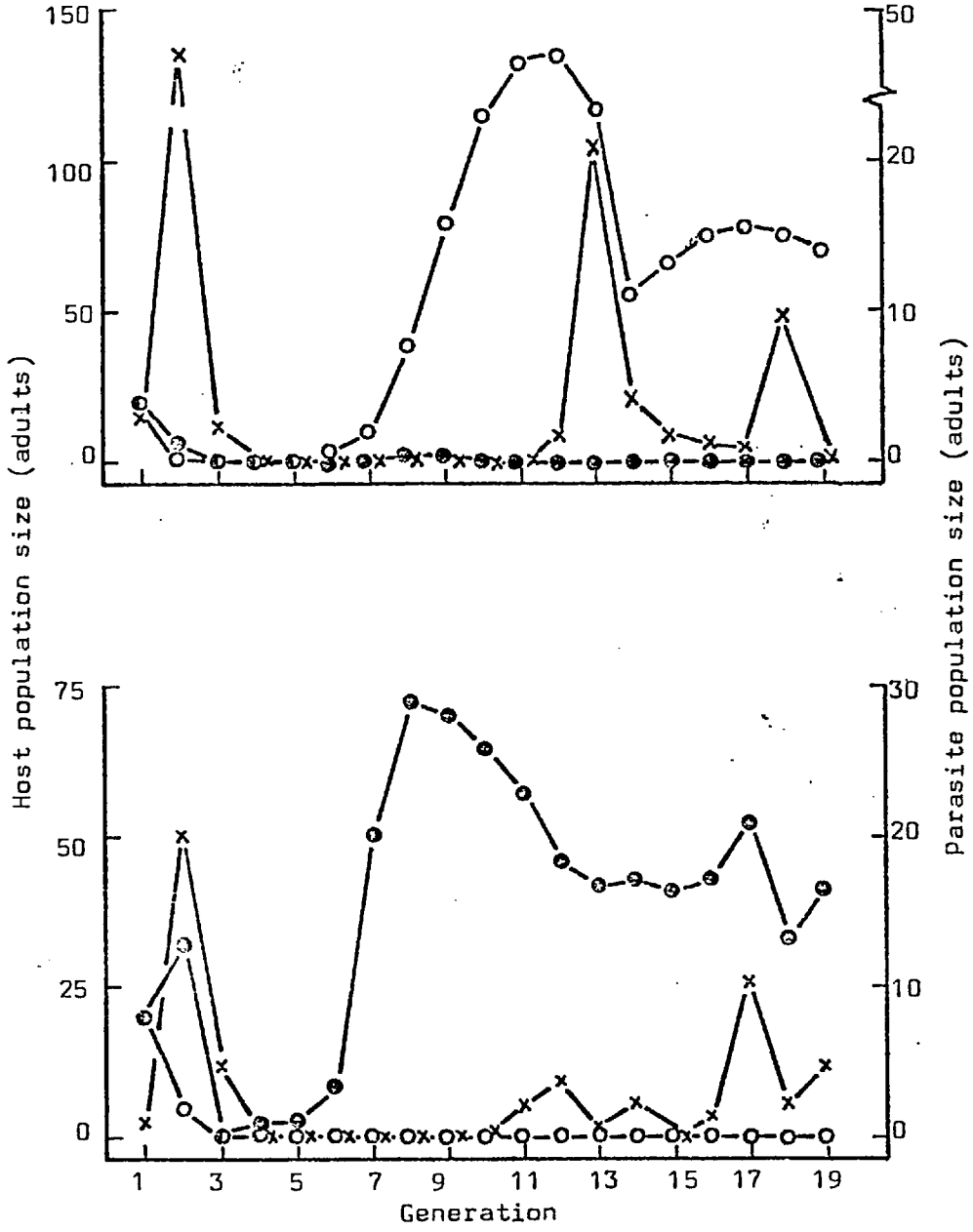
6.4.2 Two host species simulations

Two examples of the predictions of the two host species simulation model with the addition of the parasitoid model are given in figure 6.22. The model shows two stable domains (in contrast to the model without the parasitoid) corresponding to the persistence of the parasitoid with either of the hosts. A third stable domain where all three species persisted was not found although Utida (1953) reported such an interaction between C. chinensis, C. maculatus and A. calandrae. The appearance of the stable domain in the model corresponding to the coexistence of C. maculatus and L. distinguendus (figure 6.22b) arose from the faster developing C. chinensis larvae suffering a heavier mortality due to parasitism. The earlier appearance of fourth instar larvae (the most heavily attacked stage) of C. chinensis resulted in heavy attack and the later appearing C. maculatus larvae (which were less in phase with the parasitoids) were exposed to less parasitism and interspecific competition. The higher larval survival of C. maculatus resulted in its persistence where previously (without the parasitoid) the temporal advantage of C. chinensis larvae had eventually caused extinction.

6.5 Conclusions

The primary object of this chapter was to extend the simulation models of chapters 4 and 5 to include interactions between the Callosobruchus species and the parasitoid Lariophagus distinguendus. The structure of the host models permitted the simple inclusion of a function specifying the proportion of hosts parasitized each day. The development of immature parasitoids and the longevity of the adults

FIGURE 6.22 The addition of the parasitoid to the two-species simulation models permits the extinction of either host. Both simulations were initialized by 20 adults of both host species; adult parasitoids were added on day 18. In (a) the addition of three parasitoids led to the eventual extinction of *C. maculatus*. However, when only one parasitoid was added *C. maculatus* survived and *C. chinensis* was excluded. See text for further discussion. ○ - *C. chinensis*. ● - *C. maculatus*. × - *L. distinguendus*.


150
100
50
0
50
20
10
0
75
50
25
0
30
20
10
0
1
3
5
7
9
11
13
15
17
19
Generation
Host population size (adults)
Parasite population size (adults)

was treated in the same way as for the hosts.

A detailed investiation of the properties of the models constructed here and, more importantly, validation of their predictions must await further study. However, the predictions of the single host species models were in qualitative agreement with the results of long-term studies on a similar system reported in the literature. The addition of the parasitoid to the two host species model resulted in the appearance of two stable domains. This is hardly surprising considering the complexity of the model. Multiple domains of dynamic behaviour have also been observed by Auslander, Oster & Huffaker (1974) in a multiple age-class parasitoid-host model and by Gilpin & Case (1976) in multispecies competition models. In addition, Comins & Hassell (1976) have noted that the addition of a top predator to a system of two competing species can have marked affects on the system's stability properties.

The aperiodic fluctuations in population density predicted by the models were a consequence of their multiple age-class structure and do not seem to indicate a hierarchy of dynamic behaviour (i.e. stable points, stable cycles and aperiodic cycles) such as observed in difference equation models for parasitoid-host systems by Beddington, Free & Lawton (1975).

Chapter VII. SUMMARY AND DISCUSSION.

This chapter summarizes and briefly discusses some of the more important findings of this work.

Chapter 2 was concerned with the descriptive abilities of a variety of simple density dependent models. Special reference is made to data on density dependent mortality. Initially, the flexibilities of the different models are compared on a qualitative basis in relation to the forms shown by such data when plotted in four ways: (i) plotting the number of survivors against the initial density of competitors, (ii) plotting proportionate survival against initial density, (iii) plotting proportionate survival on logarithmic scales (k-values for mortality) against log initial density and (iv) plotting k-values against initial density. It is shown that most of the models are incapable of describing a sigmoid plot of proportionate survival against density, a feature typical of much laboratory data on density dependent mortality. Secondly, four of the more flexible models are compared on a quantitative basis. This is done by fitting them to a variety of data on density dependent mortality from both field and laboratory insect populations. It is concluded that, of the models considered, that of Maynard Smith & Slatkin (1973) has the most flexible form. This model is then used to describe some density dependent life-table data taken from the literature for a number of insect species, and the fitted parameters are used to characterize their population dynamics. The results of this investigation agree with the findings of Hassell, Lawton, & May (1976) in indicating that most natural insect populations which exhibit

evidence of density dependence do so in an undercompensating way.

The difference equation models considered in chapter 2 may be used in the construction of simple analytical models for insect populations (e.g. Varley & Gradwell 1968; Hassell & Huffaker 1969; Hassell 1977). An example of how this may be accomplished is given in chapter 3 where the outcome of density dependent processes in laboratory populations of Callosobruchus chinensis and C. maculatus are described by the equation of Maynard Smith & Slatkin (1973). This has led to the development of single and two age-class population models for each species. These models predict an oscillatory approach to a stable equilibrium and those for C. chinensis generally show quicker damping of the oscillations than those for C. maculatus. These prediction are in accord with much of the available literature on the long-term dynamics of laboratory populations of these species (e.g. Utida 1967; Fujii 1968). A further two age-class model is constructed for each species in a framework discussed by May et al. (1974). These authors have outlined the stability properties of this type of model in such a way that the relative contribution to the models' stability of density dependence in the two age classes may be compared. Applying these ideas to the Callosobruchus models indicates that the oscillatory behaviour is due to density dependence in the adult stage causing an overcompensatory egg mortality.

A different approach to modelling single-species populations was taken in chapter 4. A discrete-time simulation model employing a time step of one day was constructed for each of the Callosobruchus species. This model considers in detail the processes affecting population growth. The description of adult reproduction includes age specific fecundity and mortality and also density dependent responses which reduce the adult's fecundity. The process of larval development is

described by a life-table model which, based on some assumptions about distributed larval development, predicts the number of individuals from a cohort which complete development of a particular stage each day. Larval mortality is included from both density independent and density dependent causes. Although the dynamic properties of these models cannot be determined analytically, simulation studies indicate that both of the models have a globally stable equilibrium which is approached monotonically in the case of C. chinensis and by damped oscillations in the case of C. maculatus. In contrast to the models of chapter 3, the oscillations of the simulation model were not due to overcompensatory density dependence but rather to asynchrony between the food renewal schedule and the larval developmental period (the faster developing C. chinensis avoided this asynchrony). These simulations agree in general with the preliminary results of related long-term laboratory studies (M. P. Hassell, personal communication). In addition to predicting the sizes of consecutive generations, the models specify in detail the age structure of each generation. It is found that mortality at the equilibrium occurs primarily in the egg stage (from adult trampling) and in the early larval stages (from intrastage and interstage competition). In addition, interstage competition is largely responsible for maintaining discrete generations even after a considerable period of continuous growth.

In chapter 5, the single-species models of chapters 3 and 4 are extended to include interspecific competition, and competition coefficients for adult and larval interactions between the two Callosobruchus species are estimated. This leads to the construction of a single and a two age-class model and a simulation model for two-species competition. The properties of the single and two age-class models, because of their implicit assumption of equal generation

times for the two species, could be readily determined from their zero-growth isoclines. These models predict the presence of an unstable two species equilibrium and indicate that C. maculatus, largely because of its superiority in the adult stage, is the favoured competitor. In contrast, the two-species simulation model predicts that no stable equilibrium exists and, because of its quicker development, C. chinensis would inevitably exclude C. maculatus. The superiority of C. maculatus adults, however, could cause very low reproduction of C. chinensis during initial growth of the populations and this may indicate the potential extinction of C. chinensis in a stochastic environment. This difference between the models' predictions may be relatively unimportant in natural situations. Insect populations rarely undergo continuous growth for more than a few generations, and events such as emergence from winter diapause may regularly synchronize initial growth or development. In such cases the speed of development of the various instars and interspecific interstage competition may determine the outcome of competition, but a cumulative temporal advantage (such as observed here) would be of little importance. Experiments using C. chinensis and C. maculatus which are designed to investigate the trajectories of populations started at different positions in the phase space are in progress (M. P. Hassell, personal communication), and the results of these experiments may well clarify the relative importance of developmental period and competitive superiority in determining the outcome of interspecific competition.

A simulation model for insect parasitoid-host systems is developed in chapter 6. Its structure is based on that of the simulation model of chapter 4, and is designed to predict the two events of reproduction and larval development. The model is developed with special reference to Lariophagus distinguendus, a larval parasitoid

of Callosobruchus. Attention is given to the effects of host age on parasitoid development and also to some factors affecting the parasitoid's rate of reproduction. The model was added to the single-species simulation models and this resulted in dynamic behaviour characterized by aperiodic oscillations. This agrees qualitatively with the results of a long-term study on a similiar system reported by Utida (1950). These oscillations were due only to the detailed age structure of the model and were not a function of the parasitoid's searching efficiency. Thus it appears that apparently chaotic dynamics may occur in complex models independently of the parameters determining the systems quantitative behaviour (cf. Beddington, Free & Lawton 1975), and this emphasizes the need for a clear understanding of the details of any biological interaction before conclusions can be drawn on the factors contributing to its observed dynamics. When the parasitoid model was included in the two-species simulation model an additional stable domain appeared and, although coexistence of all three species was not established, this further emphasises the potential dynamic complexity of insect parasitoid-host systems.

In developing a model for a particular laboratory system there are four important tools available to the population ecologist. (1) Short term experiments may be employed to define the important influences on the populations and to determine the details of the processes involved. (2) Simple analytical models may be constructed to investigate the system's dynamic behaviour. (3) Detailed simulation models may be developed to ensure that the processes affecting the populations are clearly understood. (4) Finally, long-term experiments can provide a knowledge of the system's observed dynamics against which the accuracy of the models' predictions may be examined. The combination of these four working together is a powerful approach in further-

ing our understanding of the role of such crucial biological processes as competition and predation in determining the dynamic behaviour of insect populations.

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Appendix A. THE STABILITY OF DIFFERENCE EQUATION SYSTEMS.

This appendix outlines only the details relevant to determining the local (linearized) stability of the difference equation population models of chapters 2 and 3. For a more thorough discussion of the topic the reader is referred to May(1974) and May *et al.*(1974).

In chapters 2 and 3, single age-class difference equation models of the form

$$N_{t+1} = N_t f(N_t) \tag{A.1}$$

were considered. Models of this form have an equilibrium density which is defined when $N_{t+1}=N_t=N^*$, so that at equilibrium,

$$f(N^*) = 1. \tag{A.2}$$

The local stability of this equilibrium is determined by the slope of the curve of $\log N_{t+1}/N_t$ plotted against $\log N_t$ evaluated at the equilibrium,

$$b' = -\left[\frac{d \log N_{t+1}/N_t}{d \log N_t}\right]^* = -\left[\frac{d \log f(N_t)}{d \log N_t}\right]^* . \tag{A.3}$$

By virtue of equation A.2, this derivative may be rewritten as

$$b' = -N^*\left(\frac{d\, f(N_t)}{d\, N}\right)^* . \tag{A.4}$$

The local stability of the equilibrium of equation A.1 is determined by the value b'. When $0<b'<1$, the equilibrium is stable and approached monotonically following a small disturbance of the population away from it. For $1 \leq b' < 2$, the approach to the equilibrium is oscillatory. When $b' > 2$, the equilibrium is unstable and any disturbance of the population away from it results in limit cycle behaviour. The boundaries separating these three types of dynamic behaviour occur at $b'= 1$ and $b'= 2$.

The population model of equations 2.13 and 3.5 may be written in the form of equation A.1,

$$N_{t+1} = N_t \frac{d\lambda}{(1+(aN_t)^b)} \tag{A.5}$$

and the function $f(N_t)$ is

$$f(N_t) = \frac{d\lambda}{(1+(aN_t)^b)} \tag{A.6}$$

The equilibrium density N* is found by setting $f(N_t)=1$,

$$N^* = \frac{1}{a}\left(d\lambda - 1\right)^{1/b} . \tag{A.7}$$

The derivative b' is given by

$$b' = \frac{b(d\lambda - 1)}{d} . \tag{A.8}$$

Equation A.8 gives the relation between the parameters b, d and λ which determines the boundaries between the different regions of dynamic behaviour shown in figures 2.9 and 3.10a.

In chapter 3, two types of multiple age-class models were considered. In the first of these (the type I models), individuals pass through all of the age classes in one time step and the generation time is unity. This type of model for n age-classes may be written

$$x_1(t) = f_1(x_n(t)) \tag{A.9a}$$

$$x_2(t) = f_2(x_1(t)) \tag{A.9b}$$

$$\vdots$$

$$x_n(t+1) = f_n(x_{n-1}(t)) \tag{A.9c}$$

so that

$$x_n(t+1) = f_n(f_{n-1}(\cdots f_1(x_n(t)))). \tag{A.10}$$

The equilibrium occurs when $x_n(t+1)=x_n(t)$ and its local stability is determined by the derivative df_n/dx_n evaluated at the equilibrium.

By applying the chain rule to equation A.10, this derivative becomes

$$\frac{df_n}{dx_n} = \frac{df_n}{df_{n-1}} \frac{df_{n-1}}{df_{n-2}} \cdots \frac{df_1}{dx_n} . \qquad (A.11)$$

where f_i indicates the compound function $f_i(f_{i-1}(\cdots f_1(x_n)))$. In short, the local stability is determined by the absolute value of the eigenvalue χ_I ,

$$\chi_I = \frac{df_n}{dx_n}^{*} = (f'_n\ f'_{n-1} \cdots f'_1)^* = \prod_{i=1}^{n} f'_i \qquad (A.12)$$

where f'_i indicates df_i/df_{i-1} and $f'_1=df_1/dx_n$. when $-1<\chi_I<1$, or alternatively when $|\chi_I|<1$, the equilibrium is stable. It will be approached monotonically when $0>\chi_I>1$ and by damped oscillations when $-1<\chi_I<0$. The equilibrium is unstable if $|\chi_I|>1$.

In the second type of multiple age-class model (the type II models), the development of each age class requires one time step and completion of a single generation requires $\underline{n}$ time steps. This type of model may be written

$$x_1(t+1) = f_1(x_n(t)) \qquad (A.13a)$$

$$x_2(t+1) = f_2(x_1(t)) \qquad (A.13b)$$

$$\vdots$$

$$x_n(t+1) = f_n(x_{n-1}(t)) \qquad (A.13c)$$

or in matrix form

$$\begin{bmatrix} x_1(t+1) \\ x_2(t+1) \\ x_3(t+1) \\ \vdots \\ x_n(t+1) \end{bmatrix} = \begin{bmatrix} 0 & 0 & \cdots & 0 & f_1 \\ f_2 & 0 & \cdots & 0 & 0 \\ 0 & f_3 & \cdots & 0 & 0 \\ \vdots & \vdots & & \vdots & \vdots \\ 0 & 0 & \cdots & f_n & 0 \end{bmatrix} \begin{bmatrix} x_1(t) \\ x_2(t) \\ x_3(t) \\ \vdots \\ x_n(t) \end{bmatrix} . \qquad (A.14)$$

Equilibrium again occurs at $x_n(t+1)=x_n(t)$. In this case, however, the stability of the equilibrium is determined by the dominant eigen-

value of the matrix $\underline{A}$,

$$A = \begin{bmatrix} 0 & 0 & \cdots & 0 & f_1' \\ f_2' & 0 & \cdots & 0 & 0 \\ 0 & f_3' & \cdots & 0 & 0 \\ \vdots & \vdots & & \vdots & \vdots \\ 0 & 0 & \cdots & f_n' & 0 \end{bmatrix} \tag{A.15}$$

where the derivatives f_i' are defined as before. The eigenvalues of $\underline{A}$ are given by (see proof below)

$$(\chi_{II})^n = \prod_{i=1}^{n} f_i' \,. \tag{A.16}$$

If $\underline{n}$ is even, there are two non-zero eigenvalues which consist of either a pair of real numbers equal in magnitude but opposite in sign or a conjugate pair of imaginary numbers with zero real parts. If $\underline{n}$ is odd, then n-1 of the eigenvalues are zero and one is a real number. In either case, the magnitude of the eigenvalues is given by

$$\left|\chi_{II}\right| = \left| \left(\prod_{i=1}^{n} f_i' \right)^{1/n} \right| . \tag{A.17}$$

The equilibrium is again stable only if $\left|\chi_{II}\right| < 1$. It is clear from a comparison of equations A.12 and A.17 that any type I and type II systems defined by the same functions $\underline{f_i}$ will have the same qualitative stability, since for any number $y<1$, then $y^{1/n}<1$. Furthermore, a stable type I system will be more stable (have eigenvalues with smaller magnitude) than the related type II system since for any $y<1$, then $y<y^{1/n}$.

Proof of equation A.16. The eigenvalues of the matrix $\underline{A}$ of equation A.15 are given by the solutions to the equation

$$\left| A - \chi I \right| = 0. \tag{A.18}$$

The determinant in this equation may be written

$$\left| A - \chi I \right| = \begin{vmatrix} -\chi & 0 & \cdots & 0 & f_1' \\ f_2' & -\chi & \cdots & 0 & 0 \\ 0 & f_3' & \cdots & 0 & 0 \\ \vdots & \vdots & & \vdots & \vdots \\ 0 & 0 & & f_n' & -\chi \end{vmatrix} . \tag{A.19}$$

Expanding about the last row gives

$$|A - \chi I| = (-1)^{2n-1} f'_n \begin{vmatrix} -\chi & 0 & \cdots & 0 & f'_1 \\ f'_2 & -\chi & \cdots & 0 & 0 \\ \vdots & \vdots & & \vdots & \vdots \\ 0 & 0 & \cdots & f'_{n-1} & 0 \end{vmatrix}$$

$$+(-1)^{2n}(-\chi) \begin{vmatrix} -\chi & 0 & \cdots & 0 & f'_1 \\ f'_2 & -\chi & \cdots & 0 & 0 \\ \vdots & \vdots & & \vdots & \vdots \\ 0 & 0 & \cdots & f'_{n-1} & -\chi \end{vmatrix} \qquad \text{(A.20a)}$$

or

$$|A - \chi I| = -f'_n |D_{n-1}| + (-\chi)|E_{n-1}| \qquad \text{(A.20b)}$$

where the definitions of the determinants $|D_{n-1}|$ and $|E_{n-1}|$ are clear.

The value of the determinant $|D_{n-1}|$ may be found by induction as follows. For a determinant of arbitrary order $\underline{k}$,

$$|D_k| = \begin{vmatrix} -\chi & 0 & \cdots & 0 & f'_1 \\ f'_2 & -\chi & \cdots & 0 & 0 \\ \vdots & \vdots & & \vdots & \vdots \\ 0 & 0 & \cdots & f'_k & 0 \end{vmatrix} . \qquad \text{(A.21)}$$

Expanding this determinant about the last row gives

$$|D_k| = (-1)^{2k-1} f'_k \begin{vmatrix} -\chi & 0 & \cdots & 0 & f'_1 \\ f'_2 & -\chi & \cdots & 0 & 0 \\ \vdots & \vdots & & \vdots & \vdots \\ 0 & 0 & \cdots & f'_{k-1} & 0 \end{vmatrix}$$

$$= (-1)^{2k-1} f'_k |D_{k-1}| . \qquad \text{(A.22)}$$

If $|D_{k-1}| = (-1)^{k-2} \prod_{i=1}^{n} f'_i$, then from equation A.22

$$|D_k| = (-1)^{3k-3} \prod_{i=1}^{n} f'_i$$

$$= (-1)^{k-1} \prod_{i=1}^{n} f'_i . \qquad \text{(A.23)}$$

Noting that when k=1, $|D_1| = f_1' = (-1)^{k-1} f_1'$ completes an inductive proof of equation A.23 for any k.

The value of $|E_{n-1}|$ may similarly be found by induction. If this determinant has order k=1, then

$$|E_1| = -\chi = (-\chi)^k \quad . \tag{A.24}$$

A determinant of any order k>1 may be expanded about the last column:

$$|E_k| = \begin{vmatrix} -\chi & 0 & \cdots & 0 & 0 \\ f_2' & -\chi & \cdots & 0 & 0 \\ \vdots & \vdots & & \vdots & \vdots \\ 0 & 0 & \cdots & f_k' & -\chi \end{vmatrix}$$

$$= (-1)^{2k}(-\chi)\begin{vmatrix} -\chi & 0 & \cdots & 0 & 0 \\ f_2' & -\chi & \cdots & 0 & 0 \\ \vdots & \vdots & & \vdots & \vdots \\ 0 & 0 & & f_{k-1}' & -\chi \end{vmatrix}$$

$$= (-\chi)\, E_{k-1} \quad . \tag{A.25}$$

If $|E_{k-1}| = (-\chi)^{k-1}$, then from equation A.25

$$|E_k| = (-\chi)^k \quad . \tag{A.26}$$

Equation A.24 completes an inductive proof of equation A.26 for any k.

Substituting equations A.23 and A.26 into equation A.20b gives

$$|A - \chi I| = (-1)\left[(-1)^{n-2} \prod_{i=1}^{n} f_i'\right] + (-\chi)^n$$

$$= (-1)^{n-1} \prod_{i=1}^{n} f_i' + (-\chi)^n \quad , \tag{A.27}$$

which, after being set equal to zero and rearranged, reduces to

$$(-\chi)^n = (-1)^n \prod_{i=1}^{n} f_i' \quad , \tag{A.28}$$

or

$$(\chi)^n = \prod_{i=1}^{n} f_i' \tag{A.29}$$

which is equation A.16.

Appendix B. THE LABORATORY CULTURE OF CALLOSOBRUCHUS SPECIES.

The cowpeas used as the food source for the Callosobruchus species were stored at 5^{o} C. After being placed at the experimental conditions of 30^{o} C, 70% relative humidity these beans lost weight for approximately four days (figure B.1) before reaching a constant water content of about 9 % by weight. Consequently, beans were kept at the experimental conditions for at least four days before use in experiments.

The Callosobruchus species were cultured by placing about 500 g of cowpeas in a large plastic box (9 cm high, 15.5 cm wide and 27.5 cm long) which was covered with a plastic lid. In the lid several large holes were cut to permit ventilation; these holes were covered by muslin. Large numbers of newly emerged adults (0-2 days old) were collected and placed with the beans for two days, after which they were removed. Three cultures of each species were set up each week; th s provided a continuous source of material for experimental work.

The handling of the adults was often facilitated by lightly aenesthetizing them with carbon dioxide. Aenesthetized adults could be easily collected from cultures by passing the beans over a mesh of a size (approximately 0.5 cm) which permitted the adults to pass through but retained the beans.

During the period of adult emergence in a culture, the frass created during larval feeding collected in the bottom of the culture boxes. This frass could be removed by seiving with a fine mesh. The frass was found irritating to the nose and throat and a dust-proof respiration mask was used to avoid any unecessary exposure. Finally, the beans were subject to attack by mites after the adults emerged. Consequently, cultures were not kept longer than a single generation (about four weeks).

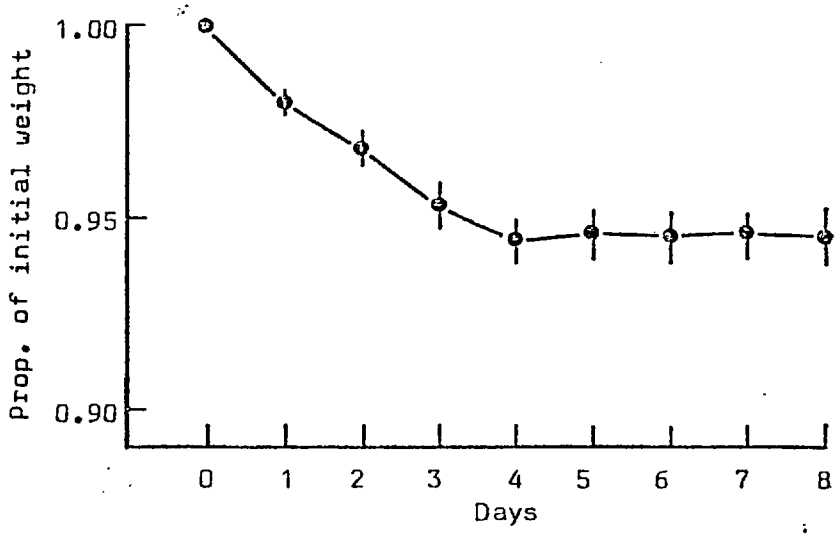


FIGURE 8.1 The percentage weight loss of cowpeas taken from cold storage and placed at 30°C, 70% relative humidity. Mean (± 95% confidence limits) of ten replicates.

Appendix C. SOME COMPUTER PROGRAMMES.

C.1 Notes on the programmes.

This appendix includes the listings of five of the FORTRAN programmes developed in this study. These programmes make use of a non-standard interactive feature (the READLIST statement) available on the Imperial College time sharing system. No attempt has been made to rewrite these programmes in standard FORTRAN, and consequently their descriptions here are limited to a list of the more important READLIST variables and execution options. It is anticipated that standard batch versions of these programmes will be developed shortly.

The five programmes included here are the two simulation models (SIMUL1 and SIMUL2) of chapters 4 and 5 (which include the parasitism submodel) and three data fitting routines. The programme DENDEP estimates parameters for the two-parameter density dependent models considered in chapter 2. LTANA estimates parameters for the density independent life-table model of chapter 3. Finally, FRESAN estimates parameters for some models for predator and parasitoid functional responses. These fitting routines utilized published algorithms for parameter estimation and, where possible, the source code for these routines is included in section C.7. Listings for the subroutines E04CAF and E04FBF are not included as this material is the copyright of NAG(1976).

C.2 Execution files MARLS and MARLS2

These programmes were used in executing the other programmes included in this appendix. All of the files accessed by these two execution programmes are standard facilities at the Imperial College Computer Centre except the file LIBM. This file is a binary library containing the subroutines included in section C.7. The use of these execution files is as follows:

Call, MARLS (S = programme)

and Call, MARLS2 (S = programme, DATA = data file)

where "programme" is the name of the desired programme to be executed and "data file" is the name of an optional data file. The use of MARLS2 is restricted to the programmes DENDEP and FRESAN when the data for analysis are stored as a permanent file. MARLS may be used with all of the programmes.

MARLS

```
RETURN,BATCH.
RETURN,PLTFIL.
RETURN,BATCH1.
IF(FL.LT.45000B)SETFL,45000
IF(NUM(S))GOTO,2A.
GET,S.
REWIND,S.
RETURN,TSFCMP,TSFBIN.
GET,LISTPP/UN=UMBZS27.
LISTPP,S,,TSFCMP,LISTRS.
TSF,I=TSFCMP,B=TSFBIN,E=3.
2A,GET,LIBT/UN=UMBZS27.
PROC,N=NAG5F
GET,LIBM.
LDSET(LIB=LIBM/LIBT/NAG5F)
TSFBIN.
IF(FILE(BATCH,LB))QUEUE(BATCH=PS/D=SILW80D)
IF(FILE(PLTFIL,LB))GOTO,3A
GOTO,4A
3A,GET,PLOTFR.
TSF(I=PLOTFR,B=BIN,E=3)
LDSET(LIB=LIBM)
BIN.
QUEUE(BATCH1=PS/D=SILW80D)
4A,RETURN,SCRATCH.
```

MARLS2

```
RETURN,BATCH.
RETURN,PLTFIL.
RETURN,BATCH1.
IF(FL.LT.45000B)SETFL,45000
IF(NUM(DATA))GOTO,5A
GET,DATA.
RETURN,DATA1.
REWIND,DATA
COPY(DATA,DATA1)
REWIND,DATA1.
5A,IF(NUM(S))GOTO,2A
GET,S.
REWIND,S.
RETURN,TSFCMP,TSFBIN.
GET,LISTPP/UN=UMBZS27.
LISTPP,S,,TSFCMP,LISTRS.
TSF,I=TSFCMP,B=TSFBIN,E=3.
2A,GET,LIBT/UN=UMBZS27.
PROC,N=NAG5F
GET,LIBM.
LDSET(LIB=LIBM/LIBT/NAG5F)
TSFBIN.
IF(FILE(BATCH,LB))QUEUE(BATCH=PS/D=SILW80D)
IF(FILE(PLTFIL,LB))GOTO,3A
GOTO,4A
3A,GET,PLOTFR.
TSF(I=PLOTFR,B=BIN,E=3)
LDSET(LIB=LIBM)
BIN.
QUEUE(BATCH1=PS/D=SILW80D)
4A,RETURN,SCRATCH.
```

C.3 SIMUL1 and SIMUL2

Object: to simulate the dynamics of single or two host species populations either with or without a parasitoid. The variables and control options are the same for both programmes, with the exception of some additional variables in SIMUL2. Only a brief outline of the more important parameters is given here.

Readlist variables:

ISTART: the next day of the simulation.
IEND: last day of the simulation.
IPARAS: specifies the presence (=1) or absence (=0) of the parasitoid.
HDISMU, HDISSG, DDS, ALPHA: host larval development and mortality parameters.
LAMBDA, DDA, DDB, EGFERT, TRAMPL, POWER: adult life-table and oviposition parameters.
PDISMU, PDISSG, PEGFRT: parasitoid life-table parameters.
APATT, THATT, APOVIP, THOVIP, APAGE, THAGE: parasitoid search parameters.
ADULTS: initial number of host adults.

Readlist execution options:

GETDIS: initialize developmental distributions.
BEGIN: required step prior to a simulation.
GO: execute simulation.
PARMS: output of life-table parameters.
OUTPUT: output of simulation results.

SIMUL1

```
      NOTRACE
      PROGRAM SIMUL1(INPUT,OUTPUT,TAPE1,TAPE2,BATCH,TAPE6=OUTPUT,
     +           TAPE7=BATCH)
C  SINGLE SPECIES SIMULATION MODEL.  T.S. BELLOWS,JR. DEC 1978
C
      DIMENSION HGENER(50),PGENER(50),TOTRCO(8),TOTRC1(8),TOTPRO(2),TOTP
     +R1(2),  COHTHO(21,8),TOTLHO(21,7),COHTPO(21,2),COHTH1(21,8),TOTLH1
     +(21,8),          COHTP1(21,2),TOTLP1(21,2),GDUM(20,8),IDUM(8),HDISM
     +U(9),HDISSG(8),          PDISMU(2),PDISSG(2),TOTLPO(21,1)
      REAL LAMBDA(15)
      COMMON IGDAYS(8),GDIS(20,8),ALPHA(6,6),DDB(8),DDS(7),LAMBDA,DDA(2)
     +,        EGFERT,TRAMPL,IPDAYS(2),PGDIS(20,2),THAGE(20),APAGE(20),TH
     +ATT(6),          APATT(6),THOVIP(6),APOVIP(6),PEGFRT,HSEXRT,PSEXRT,
     +XNOONS,POWER
      DATA COHTHO,TOTLHO,COHTPO,TOTLPO,COHTH1,TOTLH1,COHTP1,TOTLP1/798*0
     +./
      DATA IOUT/6/,NAME/1/,ISHORT/1/
C
C
   20 READLIST IOUT,ISTART,IEND,IDAY,HGENER,PGENER,TOTRCO,TOTRC1,TOTPRO,
     +    TOTPR1,IPARAS,HDISMU,HDISSG,PDISMU,PDISSG,ALPHA,DDB,DDS,LAMBDA
     +,DDA,        EGFERT,TRAMPL,THAGE,APAGE,THATT,APATT,THOVIP,APOVIP,PE
     +GFRT,                COHTHO,TOTLHO,COHTPO,TOTLPO,COHTH1,TOTLH1,COHT
     +P1,TOTLP1,                    GETDIS=21,GO=22,PARMS=23,OUTPUT=24,END
     +=99                                    ,XNOONS,ORGNHL,ORGNHA,ORGNPL,O
     +RGNPA,HSEXRT,PSEXRT                                  ,POWER,GDIS,IGDAYS,PGD
     +IS,IPDAYS,IGEN,ISHORT,                                       BEGIN=25,ADULT
     +S,NAME
C
   25 DO 251 I=1,21
      TOTLPO(I,1)=0.
      TOTLP1(I,1)=0.
      TOTLP1(I,2)=0.
      COHTPO(I,1)=0.
      COHTPO(I,2)=0.
      COHTP1(I,1)=0.
      COHTP1(I,2)=0.
      COHTHO(I,8)=0.
      COHTH1(I,8)=0.
      TOTLH1(I,8)=0.
      DO 251 K=1,7
      COHTHO(I,K)=0.
      COHTH1(I,K)=0.
      TOTLHO(I,K)=0.
  251 TOTLH1(I,K)=0.
      ISTART=1
      COHTH1(1,8)=ADULTS
      GOTO20
C  CREATE DEVELOPMENTAL DISTRIBUTIONS G.
C  HOST.
   21 CALL GETDIS3(HDISMU,HDISSG,0,GDUM,IDUM,ORGNHL,ORGNHA)
      DO 211 K=1,8
      IGDAYS(K)=IDUM(K)
      DO 211 I=1,20
  211 GDIS(I,K)=GDUM(I,K)
C  PARASITE
      IF(IPARAS.EQ.0)GOTO20
      CALL GETDIS3(PDISMU,PDISSG,2,GDUM,IDUM,ORGNPL,ORGNPA)
      DO 212 K=1,2
      IPDAYS(K)=IDUM(K)
      DO 212 I=1,20
  212 PGDIS(I,K)=GDUM(I,K)
      GOTO20
C
C  SIMULATION SECTION
   22 IF(ISTART.GT.1)GOTO3
C  INITIALIZE SOME STORAGE VECTORS BEFORE DAY 1.
      DO 4 K=1,8
      TOTRCO(K)=0.
    4 TOTRC1(K)=0.
      DO 5 K=1,2
      TOTPRO(K)=0.
    5 TOTPR1(K)=0.
      IGEN=1
C SUM INITIAL ADULTS.
      S=0.
      SP=0.
      DO 6 I=1,21
      S=S+COHTH1(I,8)
    6 SP=SP+COHTP1(I,2)
      HGENER(1)=S
      PGENER(1)=SP
    3 CONTINUE
C
C SIMULATION LOOP.
      DO 1 I=ISTART,IEND
C
      IDAY=MOD(I,21)
      IF(IDAY.EQ.0)IDAY=21
      IF(I.LT.21)GOTO31
      IF(IDAY.NE.1)GOTO31
      IF(I.EQ.22)GOTO7
C  STORE GENERATION COUNTS.
      IGEN=IGEN+1
      HGENER(IGEN)=TOTRCO(8)
      PGENER(IGEN)=TOTPRO(2)
C  IF IDAY=1, SWITCH OLD BEANS FOR NEW, STORE RECRUITS AND START AGAIN.
    7 DO 8 J=1,21
      DO 81 K=1,7
      COHTHO(J,K)=COHTH1(J,K)
      COHTH1(J,K)=0.
      TOTLHO(J,K)=TOTLH1(J,K)
   81 TOTLH1(J,K)=0.
      COHTPO(J,1)=COHTP1(J,1)
      COHTP1(J,1)=0.
      TOTLPO(J,1)=TOTLP1(J,1)
    8 TOTLP1(J,1)=0.
      DO 83 K=1,8
      TOTRCO(K)=TOTRC1(K)
   83 TOTRC1(K)=0.
      TOTPRO(1)=TOTPR1(1)
      TOTPRO(2)=TOTPR1(2)
      TOTPR1(1)=0.
      TOTPR1(2)=0.
C
   31 ADNEW=0.
      PADNEW=0.
C  SKIP OLD BEANS IF TIME .LT. 21.
      IF (I.LE.21)GOTO2
C  DEVELOPMENT AND MORTALITY IN OLD BEANS.
      CALL MODEL1(0,IDAY,COHTHO,TOTLHO,7,TOTRCO,ADNEW,IPARAS,COHTPO,TOTL
     +PO,      1,TOTPRO,PADNEW)
C  DEVELOPMENT, MORTALITY AND OVIPOSITION IN NEW BEANS.
    2 CALL MODEL1(1,IDAY,COHTH1,TOTLH1,0,TOTRC1,ADNEW,IPARAS,COHTP1,TOTL
     +P1,    2,TOTPR1,PADNEW)
C
    1 CONTINUE
      ISTART=IEND+1
```

```
C  END OF SIMULATION LOOP AND SECTION
      GOTO20
C
C  OUTPUT OF PARAMETERS.
   23 GDUM(1,1)=0.
      IF(IPARAS.EQ.2)GOTO2331
      GDUM(1,2)=0.
      DO 231 I=1,6
      GDUM(I+1,1)=ALPHA(I,I)
      GDUM(I+1,2)=DDB(I)
  231 ALPHA(I,I)=0.
      WRITE(IOUT,1000)NAME
      WRITE(IOUT,100)HDISMU(8),HDISSG(8),ORGNHA,HSEXRT,DDA(1),DDB(7),DDA
     +(2),    DDB(8),
     +                (I,I=1,8),(LAMBDA(I),I=1,8),(I,I=9,15),(LAMBDA(I),
     +I=9,15),EGFERT,TRAMPL   ,POWER
      WRITE(IOUT,101)ORGNHL,(I,HDISMU(I),HDISSG(I),DDS(I),GDUM(I,1),GDUM
     +(I,2),   I=1,7)
      WRITE(IOUT,102)(I,I=1,6),(I,(ALPHA(I,J),J=1,6),I=1,6)
      DO 232 I=1,6
  232 ALPHA(I,I)=GDUM(I+1,1)
      IF(IPARAS.EQ.0)GOTO20
 2331 CONTINUE
      WRITE(IOUT,103)PDISMU(1),PDISSG(1),ORGNPL,PDISMU(2),PDISSG(2),ORGN
     +PA,     PSEXRT,PEGFRT
      WRITE(IOUT,104)(I,APATT(I),TWATT(I),APOVIP(I),TWOVIP(I),I=1,6)
      WRITE(IOUT,105)(I,I=1,5),(APAGE(I),I=1,5),(TWAGE(I),I=1,5),(I,I=6,
     +10),    (APAGE(I),I=6,10),(TWAGE(I),I=6,10),(I,I=11,15),(APAGE(I),
     +I=11,15),       (TWAGE(I),I=11,15),(I,I=16,20),(APAGE(I),I=16,20),
     +(TWAGE(I),I=16,20)
      GOTO20
C
C OUTPUT OF RESULTS
   24 WRITE(IOUT,1000)NAME
      WRITE(IOUT,106)IEND,IDAY,IGEN,(I,HGENER(I),PGENER(I),I=1,IGEN)
      IF(ISHORT.EQ.1)GOTO20
      WRITE(IOUT,107)TOTRC0,TOTRC1,(I,(TOTLH0(I,J),J=1,7),I=1,21),
     +          (I,(TOTLH1(I,J),J=1,8),I=1,21)
      IF(IPARAS.EQ.0)GOTO20
      WRITE(IOUT,108)TOTPR0,TOTPR1,(I,TOTLP0(I,1),TOTLP1(I,1),TOTLP1(I,2
     +),      I=1,21)
      GOTO20
C
  100 FORMAT(1H ,//,1H ,"PARAMETERS FOR SIMULATION",/,1H ,25(1H-),//,
     +    1H ,5X,"A. HOST PARAMETERS.",/,1H ,10X,"(1) ADULTS LIFE-TABLE
     +PARAM",     "ETERS.",/,1H ,14X,"ADULT LIFE SPAN   MEAN",3X,F15.10,
     +/,1H ,22X,"SQRT",   "VARIANCE",3X,F15.10,/,1H ,30X,"ORIGIN",5X,F8.
     +5,/,1H ,21X,"SEX RATIO ",   "(FEMD ",5X,F8.5,//,1H ,14X,"ADULT ",
     +                          "DENSITY DEPENDENCE PARAMETERS
     + FOR OVIPOSITION",/,T22,"EGG CROWDING",     3X,"A= ",F15.10,3X,"B=
     + ",F15.10,/,1H ,T20,"ADULT CROWDING   A= ",F15.10,  3X,"B= ",F15.1
     +0,//,1H ,14X,"DAILY OVIPOSITIN RECORD",/,1H ,19X,"DAY",     1X,8(3
     +X,I2,2X)/,1H ,18X,"EGGS",1X,8F7.3,//,1H ,10X,"DAY",1X,7(3X,I2,2X)
     +, /,1H ,18X,"EGGS",1X,7F7.3,//,1H ,14X,"PROP. OF EGGS FERTILE",3X,
     +F8.5,     /,1H ,14X,"EGG MORTALITY PARAMETERS (FROM ADULT TRAMPLIN
     +G)",/,1H ,T19,    "M (=TRAMPL) = ",F15.10,3X,"Z (=POWER) = ",F15.1
     +0)
C
  101 FORMAT(1H ,//,1H ,10X,"(2) LARVAL LIFE-TABLE PARAMETERS.",5X,
     +    "NOTE EGGS = INSTAR 1.",//,1H ,14X,"ORIGIN",3X,F8.5,//,1H ,"IN
     +STAR",4X,   "MU",12X,"SIG",7X,"PROP. DAILY SURV",6X,"A",15X,"B",/,
     +1H ,78(1H-),       7(/,1H ,I3,5F15.10))
C
  102 FORMAT(1H ,//,1H ,10X,"(3) LARVAL INTERSTAGE COMPETITION COEFFI",
     +    "CIENT MATRIX.",/,15X,"NOTE EGGS = INSTAR 0.",/,1H ,"STAGE 2",
     +1X,          6(3X,I1,6X),/,1H ,
     +                    "STG 1 ",I1,1X,6F10.7,5(/,1H ,I7,1X,6F10.7))
C
  103 FORMAT(1H ,//,1H ,5X,"B. PARASITE PARAMETERS.",/,1H ,10X,"(1) LIFE
     +-", "TABLE PARAMETERS.",5X,"MEAN",6X,"SQRT(VARIANCE)     ORIGIN",/
     +,1H ,16X,   "LARVAL DEV. RATE",2X,2F15.10,3X,F8.5,/,1H ,17X,"ADULT
     + LIFE SPAN",2X,     2F15.10,3X,F8.5,//,1H ,14X,"ADULT SEX RATIO (F
     +EMD ",2X,F8.5,/,1H ,          14X,"PROP. EGGS FERTILE   ",2X,F8.5)
C
  104 FORMAT(1H ,/,11X,"(2) SEARCH PARAMETERS.",/,15X,"PRIMARY VALUES FO
     +R"   ,7X,"ATTACK",13X,"OVIPOSITION",/,20X,"STAGE (EGGS=1)",2X,2("A"
     +,10X,"TH",   9X),/,1H ,24X,11,7X,4F11.7))
C
  105 FORMAT(1H ,/,15X,"DAILY CHANGES IN SEARCH PARAMS (PROP. OF PRIMARY
     + ", "VALUE)",4(//,20X,"ADULT AGE",3X,I2,4I9,/,24X,"A",4X,5F10.7,/,
     +23X,"TH",   4X,5F10.7))
C
  106 FORMAT(1H ,//,1H ,"RESULTS OF SIMULATION",/,1H ,21(1H-),/,6X,
     +    "THIS SIMULATION RAN FOR ",I5," DAYS.",/,6X,"THE LAST DAY OF T
     +HE ",       "CURRENT SAMPLING PERIOD WAS DAY ",I2,".",/,6X,"THERE
     + WERE ",I2,          " COMPLETE GENERATIONS.",//,4X,"A. ADULT POPUL
     +ATION SIZES.",/,          9X,"GENERATION",5X,"HOST",8X,"PARASITE
     +",50(/,13X,I2,4X,2F14.5))
C
  107 FORMAT(1H ,/,4X,"B. INFORMATION ON THE CURRENT (INCOMPLETE)",
     +    " GENERATION.",/,9X,"(1) HOST POPULATION.",/,14X,"THE TOTAL RE
     +CRUITS ",   "INTO EACH STAGE FROM THE OLD AND THE NEW BEANS",//,1H
     + ,5X,"EGGS",7X,     "1",8X,"2",8X,"3",8X,"4",6X,"PUPAE",2X,"AD IN
     +PEA",2X,"EM AD",/,1H ,       "OLD",8F9.4,/,1H ,"NEW",8F9.4,//,14X,"
     +THE TOTAL NUMBERS PRESENT IN EACH ","INSTAR ON EACH DAY WERE",/,1H
     + ,"OLD BEANS",/,1H ,"DAY",2X,"EGGS",6X,"1",  8X,"2",8X,"3",8X,"4",6
     +X,"PUPAE",2X,"AD IN PEA",21(/,1H ,I2,7F9.4),//,     1H ,"NEW BEANS
     +",/,1H ,"DAY",2X,"EGGS",6X,"1",8X,"2",8X,"3",8X,"4",6X,     "PUPAE
     +",2X,"AD IN PEA",2X,"EM AD",21(/,1H ,I2,8F9.4))
C
  108 FORMAT(1H ,//,9X,"(2) PARASITE POPULATION.",/,14X,"THE TOTAL RECRU
     +ITS"," TO THE LARVAL ( = EGGS + LARVAE + PUPAE +",/,14X,"PRE-EMERG
     +ENT ",      "ADULTS ) AND ADULT STAGES.",//,20X,"LARVAE",6X,"ADULT
     +S",/,14X,"OLD",     2F12.4,/,14X,"NEW",2F12.4,//,14X,"THE TOTAL NU
     +MBERS PRESENT ON EACH ",    "DAY WERE",//,14X,"DAY",3X,"LARVAE (OL
     +D BNS)   LARVAE (NEW BNS)",8X,      "ADULTS",21(/,15X,I2,3F19.4))
C
 1000 FORMAT(1H ,///,1H ,"NAME= ",I4)
C
C  END OF MAIN ROUTINE SIMUL1.
   99 STOP
      END
C
C
      SUBROUTINE MODEL1(IFLG,IDAY,COHORT,TOTALS,N,TOTREC,ADLNEW,IPARAS,
     +     PCOHT,TOTLP,NP,TOTPRC,PADNEW)
C SUBROUTINE FOR SINGLE SPECIES SIMUL. MODEL WITH PARASITE.
C T.S. BELLOWS,JR. DEC 1978
C
C INPUT AND COMMON VARIABLES DIMENSIONED
      DIMENSION COHORT(21,8),TOTALS(21,N),TOTREC(8),PCOHT(21,2),TOTLP(21
     +,NP),    TOTPRC(2)
      REAL LAMBDA(15)
      COMMON IGDAYS(8),GDIS(20,8),ALPHA(6,6),DDB(8),DDS(7),LAMBDA,DDA(2)
     +,       EGFERT,TRAMPL,IPDAYS(2),PGDIS(20,2),THAGE(20),APAGE(20),TH
     +ATT(6),          APATT(6),THOVIP(6),APOVIP(6),PEGFRT,HSEXRT,PSEXRT,
     +XNBBNS,POWER
C LOCAL VARIABLES
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      DIMENSION JEND(7),HDENS(6),PSURV(6),PDVIP(6)
C
C  SOME INITIAL DEFINITIONS.
      IFLAG=IFLG
      IDD=IDAY
      ID=IDD-1
      IF(ID.EQ.0) ID=21
      IF(IFLAG.EQ.1.AND.IDD.EQ.1) COHORT(1,8)=COHORT(1,8)+ADLNEW
      IF(IFLAG.EQ.1.AND.IDD.EQ.1) GOTO10
      IF(IFLAG.EQ.0) COHORT(IDD,1)=0.
C
C  HOST DEVELOPMENT - EGGS THROUGH ADULTS.
      DO 1 K=1,7
      RNEW=0.
      SUM=0.
      JEND(K)=IGDAYS(K)
      IF(IFLAG.EQ.1.AND.JEND(K).GT.IDD) JEND(K)=IDD
C  BREED COHORTS FROM IDD BACK TO TIME IDY
      DO 11 I=1,JEND(K)
      IDY=IDD-I+1
      IF(IDY.LE.0) IDY=IDY+21
      RNEW=RNEW+COHORT(IDY,K)*GDIS(I,K)
      COHORT(IDY,K)=COHORT(IDY,K)*(1.-GDIS(I,K))
   11 SUM=SUM+COHORT(IDY,K)
      TOTALS(IDD,K)=SUM
C  NEW COHORT=RNEW. ADD THOSES IN COHORT (USUALLY ZERO) TO PERMIT
C  USER TO ADD RECRUITS.
      IF(IFLAG.EQ.1) RNEW=RNEW+COHORT(IDD,K+1)
      COHORT(IDD,K+1)=RNEW
    1 TOTREC(K+1)=TOTREC(K+1)+RNEW
C  ADD ADULT RECRUITS FROM BREEDING CONTAINER (IF NECESSARY).
      COHORT(IDD,8)=COHORT(IDD,8)+ADLNEW
      ADLNEW=COHORT(IDD,8)
C
C  LARVAL MORTALITY.
      DO 2 K=2,7
      KI=K-1
      HDENS(KI)=1.
      IF(TOTALS(IDD,K).LE.0.) GOTO2
      TCMPS=0.
C SUM TOTAL EFFECTIVE COMPETITORS.
      DO 21 KK=2,7
   21 TCMPS=TCMPS+ALPHA(KI,KK-1)*TOTALS(IDD,KK)
C  ALLOW FOR PAST BEAN EXPLOITATION IN BREEDING CONTAINER.
      IF(IFLAG.EQ.0) TCMPS=TCMPS+TOTREC(5)*ALPHA(KI,4)
C  FIND PROPORTIONATE DENSITY DEPENDENT SURVIVAL.
C  (BY CONSIDERING THE PER BEAN DENSITY)
      DENOM=1.
      IF(TCMPS.GT.0.) DENOM=1.+(TCMPS/XNOBNS)**DDB(KI)
      HDENS(KI)=DDS(K)/DENOM
C  UPDATE LARVAL COHORTS BY PROPORTIONATE MORTALITY.
      DO 22 I=1,JEND(K)
      IDY=IDD-I+1
      IF(IDY.LE.0) IDY=IDY+21
   22 COHORT(IDY,K)=COHORT(IDY,K)*HDENS(KI)
    2 CONTINUE
C  ACCOUNT FOR MORTALITY IN TOTALS.
      DO 23 K=2,7
   23 TOTALS(IDD,K)=TOTALS(IDD,K)*HDENS(K-1)
C
C  OVIPOSITION, ADULT MORTALITY AND EGG MORTALITY (SKIP IF IFLAG=0
C  IMPLYING BREEDING CONTAINER).
      IF(IFLAG.EQ.0) GOTO50
   10 TADS=TOTALS(ID,8)+COHORT(IDD,8)
      IF(TADS.LE.0.) GOTO50
      SUM=0.
      RNEW=0.
      TOTEGG=TOTREC(1)
C  OVIPOSITION AND ADULT MORTALITY.
      DENOM=1.
      IF(TOTEGG.GT.0..AND.DDA(1).GT.0.) DENOM=1.+(DDA(1)*TOTEGG)**DDB(7)
      IF(DDA(2).GT.0.) DENOM=DENOM*(1.+(DDA(2)*TADS)**DDB(8))
      DO 3 I=1,IGDAYS(8)
      IDY=IDD-I+1
      IF(IDY.LE.0) IDY=IDY+21
      RNEW=RNEW+COHORT(IDY,8)*LAMBDA(I)/DENOM
      COHORT(IDY,8)=COHORT(IDY,8)*(1.-GDIS(I,8))
    3 SUM=SUM+COHORT(IDY,8)
      TOTALS(IDD,8)=SUM
C  REDUCE OVIPOSITION BE SEX RATIO AND EGG INFERTILITY
      RNEW=HSEXRT*RNEW+COHORT(IDD,1)
      COHORT(IDD,1)=RNEW*EGFERT
      TOTREC(1)=TOTREC(1)+RNEW
C  EGG MORTALITY.
      DENOM=EXP(-(TRAMPL*TADS)**POWER)
      DO 4 I=1,JEND(1)
    4 COHORT(IDD-I+1,1)=COHORT(IDD-I+1,1)*DENOM
      TOTALS(IDD,1)=TOTALS(IDD,1)*DENOM+COHORT(IDD,1)
C
C  END OF HOST SIMULATION, BEGINNING OF PARASITE SIMULATION.
C  RETURN IF IPARAS=0 IMPLYING NO PARASITES.
   50 IF(IPARAS.EQ.0) RETURN
      IF(IFLAG.EQ.1.AND.IDD.EQ.1) PCOHT(1,2)=PCOHT(1,2)+PADNEW
      IF(IFLAG.EQ.1.AND.IDD.EQ.1) GOTO100
      IF(IFLAG.EQ.0) PCOHT(IDD,1)=0.
C
C  PARASITE DEVELOPMENT FROM EGGS TO ADULTS AS ONE STAGE.
      TOTLP(IDD,1)=0.
      RNEW=0.
      SUM=0.
      J=IPDAYS(1)
      IF(IFLAG.EQ.1.AND.J.GT.IDD) J=IDD
      DO 5 I=1,J
      IDY=IDD-I+1
      IF(IDY.LE.0) IDY=IDY+21
      RNEW=RNEW+PCOHT(IDY,1)*PGDIS(I,1)
      PCOHT(IDY,1)=PCOHT(IDY,1)*(1.-PGDIS(I,1))
    5 SUM=SUM+PCOHT(IDY,1)
      TOTLP(IDD,1)=SUM
      IF(IFLAG.EQ.1) RNEW=RNEW+PCOHT(IDD,2)
      PCOHT(IDD,2)=RNEW
      TOTPRC(2)=TOTPRC(2)+RNEW
      PCOHT(IDD,2)=PCOHT(IDD,2)+RNEW
      PADNEW=PCOHT(IDD,2)
C
C  ATTACKS AND OVIPOSITIONS. NOTE 2 EQUATIONS FOR PARASITE SEARCH, ONE
C  FOR ATTACKS AND ONE FOR OVIPOSITIONS. USES RANDOM PARASITE EQUATION.
C  SKIP IF IFLAG=0 IMPLYING BREEDING CONTAINER.
      IF(IFLAG.EQ.0) RETURN
  100 TPADS=TOTLP(ID,2)+PCOHT(IDD,2)
      IF(TPADS.LE.0.) RETURN
      J=IPDAYS(2)
      DO 6 K=1,6
      PSURV(K)=0.
    6 PDVIP(K)=0.
      SUM=0.
C  LOOP 7 FINDS THE TOTAL ATTACKS AND OVIPOSITIONS ON EACH HOST STAGE
C  BY EACH PARASITE ADULT COHORT (AGE GROUP).
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      DO 7 I=1,J
      IDY=IDD-I+1
      IF(IDY.LE.0.) IDY=IDY+21
      DENATT=0.
      DENOVP=0.
      TH=THAGE(I)
      AP=APAGE(I)
C  FIND DENOMINATOR IN EXPONENT OF ATTACK EQUATION FOR ATTS AND OVIPS.
      DO 71 K=1,6
      DENATT=DENATT+APATT(K)*AP*THATT(K)*TH*TOTALS(IDD,K)
   71 DENOVP=DENOVP+APOVIP(K)*AP*THOVIP(K)*TH*TOTALS(IDD,K)
      DENATT=1.+DENATT
      DENOVP=1.+DENOVP
C  SUM ATTACKS AND OVIPS BY PARASITE AGE GROUP FOR EACH HOST STAGE.
C  (FIRST ALLOW FOR SEX RATIO)
      PARA=AP*PSEXRT*PCOHT(IDY,2)
      DO 72 K=1,6
      PSURV(K)=PSURV(K)+APATT(K)*PARA/DENATT
   72 POVIP(K)=POVIP(K)+APOVIP(K)*PARA/DENOVP
C  ADULT MORTALITIES.
      PCOHT(IDY,2)=PCOHT(IDY,2)*(1.-PGDIS(I,2))
    7 SUM=SUM+PCOHT(IDY,2)
      TOTLP(IDD,2)=SUM
C  DISTRIBUTE ATTACKS AND OVIPS AT RANDOM WITHIN A STAGE.
      RNEW=0.
      DO 8 K=1,6
      PSUR=EXP(-PSURV(K))
      POVP=1.-EXP(-POVIP(K))
      RNEW=RNEW+POVP*TOTALS(IDD,K)
      IF(PSUR.GE.1.) GOTO8
      DO 81 I=1,JEND(K)
   81 COHORT(IDD-I+1,K)=PSUR*COHORT(IDD-I+1,K)
      TOTALS(IDD,K)=TOTALS(IDD,K)*PSUR
    8 CONTINUE
      PCOHT(IDD,1)=RNEW*PEGFRT
      TOTPRC(1)=TOTPRC(1)+RNEW
      TOTLP(IDD,1)=TOTLP(IDD,1)+PCOHT(IDD,1)
C
C END OF PARASITE SIMULATION.  END OF MODEL1 SUBROUTINE.
      RETURN
      END
C
C
      SUBROUTINE GETDIS3(DM,DSIG,N,GDIS,IGDAYS,ORIGNL,ORIGNA)
C  SUBROUTINE FOR DEFINING THE DEVELOPMENTAL DISTRIBUTION G FOR SIMULATI
C  MODELS.  USES SKEWED DISTRIBUTION FOR FIRST N-1 INSTARS (LARVAE) AND
C  NORMAL DISTRIBUTION FOR LAST INSTAR (ADULT). T.S. BELLOWS,JR  DEC 197
C
      DIMENSION DM(N),DSIG(N),GDIS(20,N),IGDAYS(N),FDIS(20),CUMDIS(20)
C
      ORIGIN=ORIGNL
      DO 10 K=1,N
      DO 1 I=1,20
    1 GDIS(I,K)=0.
      NAD=N
C
C GET FDIS
      IF(K.EQ.NAD) ORIGIN=ORIGNA
      XU=DM(K)
      XS=DSIG(K)
      S=0.
      FDIS(1)=0.
      DO 2 I=1,20
      IF(K.EQ.N) ORIGIN=ORIGNA
      XC=FLOAT(I)-1.+ORIGIN
      IF(K.EQ.NAD) GOTO20
C  SKEWED MODEL.
      IF(XC.EQ.0..OR.XC.EQ.1.) GOTO2
      Y=(1./XC-XU)/XS
      YP=(1./(XC-1.)-XU)/XS
      S1=1.
      IF(XC.GE.1.) S1=S15ABF(YP,IFAIL)
      FDIS(I)=S1-S15ABF(Y,IFAIL)
      IF(FDIS(I).LT.1.0E-08) FDIS(I)=0.
      GOTO2
C  NORMAL MODEL.
   20 Y=(XC-XU)/XS
      YP=-XU/XS
      IF(XC.GT.1.) YP=(XC-XU-1.)/XS
      FDIS(I)=S15ABF(Y,IFAIL)-S15ABF(YP,IFAIL)
      IF(FDIS(I).LT.1.0E-08) FDIS(I)=0.
    2 S=S+FDIS(I)
C
C  FIX CUMDIS,GDIS
      FDIS(1)=FDIS(1)/S
      CUMDIS(1)=FDIS(1)
      GDIS(1,K)=FDIS(1)
      DO 10 I=2,20
      FDIS(I)=FDIS(I)/S
      CUMDIS(I)=CUMDIS(I-1)+FDIS(I)
      DUM=1.-CUMDIS(I-1)
      IF(DUM.LE.0.) GOTO3
      GDIS(I,K)=FDIS(I)/DUM
      IF(GDIS(I,K).GT.1.) GDIS(I,K)=1.
      GOTO10
    3 GDIS(I,K)=1.
   10 IF(GDIS(I,K).LT.1.) IGDAYS(K)=I
C
C  CORRECT IGDAYS
      DO 11 K=1,N
      IGDAYS(K)=IGDAYS(K)+1
   11 IF(IGDAYS(K).GT.20) IGDAYS(K)=20
C
C  END OF GETDIS3.
      RETURN
      END
C
C  END OF SIMUL1 PACKAGE.
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      NOTRACE
      PROGRAM SIMUL2(INPUT,OUTPUT,TAPE1,TAPE2,BATCH,TAPE6=OUTPUT,TAPE7=
     +          BATCH)
C  TWO-SPECIES SIMULATION MODEL.  T.S. BELLOWS,JR.  JAN 1979.
C
      REAL LAMBDA(15,2)
      DIMENSION HGEN1(100),HGEN2(100),PGEN(100),COHTHO(21,8,2),COHTH1(21
     +,8,2),  TOTLHO(21,7,2),TOTLH1(21,8,2),TOTRCO(8,2),TOTRC1(8,2),COHT
     +PO(21,2),          COHTP1(21,2),TOTLPO(21,1),TOTLP1(21,2),TOTPRO(2),T
     +OTPR1(2),GDUM(20,8),     IDUM(8),HDISMJ(8,2),HDISSG(8,2),PDISMJ(2),
     +PDISSG(2),ADULTS(2),HMJDUM(8),  HSGDUM(8),ADNEW(2)
      COMMON IGDAYS(8,2),GDIS(20,8,2),ALPHA(6,6,2),DDB(8,2),DDS(7,2),LAM
     +BDA,     DDA(2,2),EGFERT(2),BETA(6,6,2),EGMORT(5,2),IPDAYS(2),PGDIS
     +(20,2),          THAGE(20),APAGE(20),THATT(6,2),APATT(6,2),THOVIP(6
     +,2),APOVIP(6,2),          PEGFRT,HSEXRT(2),PSEXRT,XNOBNS,ADALPH(2,2)
      DIMENSION TITLE(2),ISPOUT(2),SPOUT(2)
      DATA IOUT/6/,NAME/1/,ISPOUT/3,4/,TITLE/2HA.,2HB./,SPOUT/4HNTRA,4HN
     +TER/     ,ISHORT/1/
C
C
   20 READLIST IOUT,ISTART,IEND,IDAY,HGEN1,HGEN2,PGEN,TOTRCO,TOTRC1,TOTP
     +RO,  TOTPR1,IPARAS,HDISMJ,HDISSG,PDISMJ,PDISSG,ALPHA,BETA,DDB,DDS,
     +LAMBDA,DDA,  EGFERT,EGMORT,ADALPH,THAGE,APAGE,THATT,APATT,THOVIP,A
     +POVIP,PEGFRT,          COHTH1,TOTLH1,COHTP1,TOTLP1,
     +                                ORGNHA,ORGNHL,ORGNPA,ORGNPL,HSEXRT,PS
     +EXRT,ADULTS,NAME,                          BEGIN=21,GETDIS=22,GO=23,PARM
     +S=24,OUTPUT=25,END=99                                ,XNOBNS,GDIS,PGDIS,IG
     +DAYS,IPDAYS,IGEN,ISHORT
C
C  INITIALIZE BEFORE START.
   21 DO 211 I=1,21
      TOTLPO(I,1)=0.
      DO 212 J=1,2
      TOTLP1(I,J)=0.
      COHTPO(I,J)=0.
  212 COHTP1(I,J)=0.
      DO 211 K=1,2
      COHTHO(I,8,K)=0.
      COHTH1(I,8,K)=0.
      TOTLH1(I,8,K)=0.
      DO 211 J=1,7
      COHTHO(I,J,K)=0.
      COHTH1(I,J,K)=0.
      TOTLHO(I,J,K)=0.
      TOTLH1(I,J,K)=0.
  211 CONTINUE
      ISTART=1
      COHTH1(1,8,1)=ADULTS(1)
      COHTH1(1,8,2)=ADULTS(2)
      GOTO20
C
C  CREATE DEVELOPMENTAL DISTRIBUTIONS G.
C  HOSTS.
   22 DO 221 K=1,2
      DO 222 I=1,8
      HMJDUM(I)=HDISMJ(I,K)
  222 HSGDUM(I)=HDISSG(I,K)
      CALL GETDIS3(HMJDUM,HSGDUM,8,GDUM,IDUM,ORGNHL,ORGNHA)
      DO 221 J=1,8
      IGDAYS(J,K)=IDUM(J)
      DO 221 I=1,20
  221 GDIS(I,J,K)=GDUM(I,J)
C  PARASITE.
      IF(IPARAS.EQ.0)GOTO20
      CALL GETDIS3(PDISMJ,PDISSG,2,GDUM,IDUM,ORGNPL,ORGNPA)
      DO 223 J=1,2
      IPDAYS(J)=IDUM(J)
      DO 223 I=1,20
  223 PGDIS(I,J)=GDUM(I,J)
      GOTO20
C
C  SIMULATION SECTION.
   23 IF(ISTART.GT.1)GOTO3
C  INITIALIZE SOM STORAGE VECTORS BEFORE DAY 1.
      DO 4 K=1,2
      TOTPRO(K)=0.
      TOTPR1(K)=0.
      DO 4 J=1,8
      TOTRCO(J,K)=0.
    4 TOTRC1(J,K)=0.
      IGEN=1
C  SUM INITIAL ADULTS.
      S1=0.
      S2=0.
      SP=0.
      DO 6 I=1,21
      S1=S1+COHTH1(I,8,1)
      S2=S2+COHTH1(I,8,2)
    6 SP=SP+COHTP1(I,2)
      HGEN1(1)=S1
      HGEN2(1)=S2
      PGEN(1)=SP
C
    3 CONTINUE
C  SIMULATION LOOP.
      DO 1 I=ISTART,IEND
C
      IDAY=MOD(I,21)
      IF(IDAY.EQ.0)IDAY=21
      IF(I.LT.21)GOTO31
      IF(IDAY.NE.1)GOTO31
      IF(I.EQ.22)GOTO7
C  STORE GENERATION COUNTS.
      IGEN=IGEN+1
      HGEN1(IGEN)=TOTRCO(8,1)
      HGEN2(IGEN)=TOTRCO(8,2)
      PGEN(IGEN)=TOTPRO(2)
C  IF IDAY=1, SWITCH OLD BEANS FOR NEW, STORE RECRUITS AND START AGAIN.
    7 DO 8 J=1,21
      COHTPO(J,1)=COHTP1(J,1)
      COHTP1(J,1)=0.
      TOTLPO(J,1)=TOTLP1(J,1)
      TOTLP1(J,1)=0.
      DO 8 K=1,2
      DO 8 L=1,7
      COHTHO(J,L,K)=COHTH1(J,L,K)
      COHTH1(J,L,K)=0.
      TOTLHO(J,L,K)=TOTLH1(J,L,K)
    8 TOTLH1(J,L,K)=0.
      DO 81 K=1,2
      DO 81 J=1,8
      TOTRCO(J,K)=TOTRC1(J,K)
   81 TOTRC1(J,K)=0.
      TOTPRO(1)=TOTPR1(1)
      TOTPRO(2)=TOTPR1(2)
      TOTPR1(1)=0.
      TOTPR1(2)=0.
C
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   31 ADNEW(1)=0.
      ADNEW(2)=0.
      PADNEW=0.
C  SKIP OLD BEANS IF TIME .LT. 21.
      IF(I.LE.21)GOTO2
C  DEVELOPMENT AND MORTALITY IN OLD BEANS.
      CALL MODEL2(0,IDAY,COHTHO,TOTLHO,7,TOTRCO,ADNEW,IPARAS,COHTPO,TOTL
     +PO,     1,TOTPRO,PADNEW)
C  DEVELOPMENT, MORTALITY AND OVIPOSITION IN NEW BEANS.
    2 CALL MODEL2(1,IDAY,COHTH1,TOTLH1,0,TOTRC1,ADNEW,IPARAS,COHTP1,TOTL
     +P1,   2,TOTPR1,PADNEW)
C
    1 CONTINUE
      ISTART=IEND+1
C  END OF SIMULATION LOOP AND SECTION.
      GOTO20
C
C  OUTPUT OF PARAMETERS.
   24 CONTINUE
      WRITE(IOUT,1000)NAME
      WRITE(IOUT,100)
      IF(IPARAS.EQ.2)GOTO2331
C  HOSTS.
      DO 241 K=1,2
      GDUM(1,K)=0.
      GDUM(1,K+2)=0.
      DO 241 I=1,6
      GDUM(I+1,K)=ALPHA(I,I,K)
      GDUM(I+1,K+2)=DDB(I,K)
  241 ALPHA(I,I,K)=0.
      DO 242 K=1,2
      WRITE(IOUT,110)TITLE(K),K,HDISMU(8,K),HDISSG(8,K),ORGNHA,HSEXRT(K)
     +,     DDA(1,K),DDB(7,K),DDA(2,K),DDB(8,K),ADALPH(K,1),ADALPH(K,2
     +),          (I,I=1,8),(LAMBDA(I,K),I=1,8),
     +                    (I,I=9,15),(LAMBDA(I,K),I=9,15),EGFERT(K),
     +(EGMORT(I,K),I=1,5)
      WRITE(IOUT,101)ORGNHL,(I,HDISMU(I,K),HDISSG(I,K),DDS(I,K),GDUM(I,K
     +),     GDUM(I,K+2),I=1,7)
      WRITE(IOUT,102)ISPOUT(1),SPOUT(1),(I,I=1,6),(I,(ALPHA(I,J,K),
     +     J=1,6),I=1,6)
      WRITE(IOUT,102)ISPOUT(2),SPOUT(2),(I,I=1,6),(I,(BETA(I,J,K),
     +     J=1,6),I=1,6)
      DO 242 I=1,6
  242 ALPHA(I,I,K)=GDUM(I+1,K)
C  PARASITE.
      IF(IPARAS.EQ.0)GOTO20
 2331 CONTINUE
      WRITE(IOUT,103)PDISMU(1),PDISSG(1),ORIGNPL,PDISMU(2),PDISSG(2),ORG
     +NPA,     PSEXRT,PEGFRT
      WRITE(IOUT,104)
      DO 243 K=1,2
  243 WRITE(IOUT,114)K,(I,APATT(I,K),THATT(I,K),APOVIP(I,K),THOVIP(I,K),
     +     I=1,6)
      WRITE(IOUT,105)(I,I=1,5),(APAGE(I),I=1,5),(THAGE(I),I=1,5),(I,I=6,
     +10),     (APAGE(I),I=6,10),(THAGE(I),I=6,10),(I,I=11,15),(APAGE(I),
     +I=11,15),     (THAGE(I),I=11,15),(I,I=16,20),(APAGE(I),I=16,20),
     +(THAGE(I),I=16,20)
      GOTO20
C
C  OUTPUT OF RESULTS.
   25 CONTINUE
      WRITE(IOUT,1000)NAME
      WRITE(IOUT,106)IEND,IDAY,IGEN,(I,HGEN1(I),HGEN2(I),PGEN(I),I=1,IGE
     +N)
      IF(ISHORT.EQ.1)GOTO20
      WRITE(IOUT,107)
      DO 251 K=1,2
  251 WRITE(IOUT,117)K,K,(TOTRCO(I,K),I=1,8),(TOTRC1(I,K),I=1,8),
     +     (I,(TOTLHO(I,J,K),J=1,7),I=1,21),(I,(TOTLH1(I,J,K),J=1,8),I=1,
     +21)
      IF(IPARAS.EQ.0)GOTO20
      WRITE(IOUT,108)TOTPRO,TOTPR1,(I,TOTLPO(I,1),TOTLP1(I,1),TOTLP1(I,2
     +),     I=1,21)
      GOTO20
C
  100 FORMAT(1H ,//,1H ,"PARAMETERS FOR SIMULATION",/,1H ,25(1H-))
  110 FORMAT(1H ,//,1H ,5X,A2," HOST PARAMETERS, SPECIES",I2,".",
     +     /,1H ,10X,"(1) ADULT LIFE-TABLE PARAM",
     +          "ETERS.",/,1H ,14X,"ADULT LIFE SPAN   MEAN",3X,F15.10,
     +/,1H ,22X,"SQRT",    "(VARIANCE)",3X,F15.10,/,1H ,3DX,"ORIGIN",5X,F
     +0.5,/,1H ,21X,"SEX RATIO ", "(FEM",5X,F8.5,//,1H ,14X,"ADULT DENS
     +ITY DEPENDENT PARAMETERS FOR ",     "OVIPOSITION",/,T17,"INTRASPEC
     +IFIC",/,T22,"EGG CROWDING",                    3X,"A= ",F15.10,3X,"B=
     + ",F15.10,/,1H ,T20,"ADULT CROWDING   A= ",F15.10,  3X,"B= ",F15.1
     +0,/,T17,"INTERSPECIFIC",/,T22,"EGG CROWDING   ALPHA= ",     F15.10
     +,/,T20,"ADULT CROWDING   ALPHA= ",F15.10,//,1H ,14X,
     +  "DAILY OVIPOSITION RECORD",/,1H ,19X,"DAY",
     +          1X,8(3X,I2,2X),/,1H ,18X,"EGGS",1X,8F7.3,//,1H ,19X,"DAY
     +",1X,7(3X,I2,2X),  /,1H ,18X,"EGGS",1X,7F7.3,//,1H ,14X,"PROP. OF E
     +GGS FERTILE",3X,F8.5,     /,1H ,14X,"EGG MORTALITY PARAMETERS (FRO
     +M ADULT TRAMPLING)",/,1H ,T19,    "M=",F15.10,3X,"Z=",F15.10,/,1H
     +,T19,"ALPHA=",F13.9,2X,"RHO=",F13.9,2X,   "THETA=",F13.9)
C
  101 FORMAT(1H ,//,1H ,10X,"(2) LARVAL LIFE-TABLE PARAMETERS.",5X,
     +     "NOTE EGGS = INSTAR 1.",//,1H ,14X,"ORIGIN",3X,F8.5,//,1H ,"IN
     +STAR",4X,   "MU",12X,"SIG",7X,"PROP. DAILY SURV",6X,"A",15X,"B",/,
     +1H ,78(1H-),          7(/,1H ,I3,5F15.10))
C
  102 FORMAT(1H ,//,1H ,10X,"(",I1,") I",A4,"SPECIFIC LARVAL INTERSTAGE
     +",  "COMPETITION COEFFI",
     +          "CIENT MATRIX.",/,15X,"NOTE EGGS = INSTAR 0.",/,1H ,"S
     +TAGE 2",1X,          6(3X,I1,6X),/,1H ,
     +                         "STG 1 ",I1,1X,6F10.7,5(/,1H ,I7,1X,6F
     +10.7))
C
  103 FORMAT(1H ,//,1H ,5X,"C. PARASITE PARAMETERS.",/,1H ,10X,"(1) LIFE
     +-", "TABLE PARAMETERS.",5X,"MEAN",6X,"SQRT(VARIANCE)     ORIGIN",/
     +,1H ,16X,   "LARVAL DEV. RATE",2X,2F15.10,3X,F8.5,/,1H ,17X,"ADULT
     + LIFE SPAN",2X,     2F15.10,3X,F8.5,//,1H ,14X,"ADULT SEX RATIO (F
     +EM",2X,F8.5,/,1H ,          14X,"PROP. EGGS FERTILE   ",2X,F8.5)
C
  104 FORMAT(1H ,/,11X,"(2) PRIMARY VALUES OF SEARCH PARAMETERS.")
  114 FORMAT(1H ,/,15X,"HOST SPECIES",I2,12X,"ATTACK",13X,"OVIPOSITION",
     +/,  20X,"STAGE (EGGS=1)",2X,2("A",10X,"TH",9X),6(/,1H ,24X,I1,7X,4
     +F11.7))
C
  105 FORMAT(1H ,/,15X,"DAILY CHANGES IN SEARCH PARAMS (PROP. OF PRIMARY
     + ", "VALUE)",4(//,20X,"ADULT AGE",3X,I2,4I9,/,24X,"A",4X,5F10.7,/,
     +23X,"TH",   4X,5F10.7))
C
  106 FORMAT(1H ,//,1H ,"RESULTS OF SIMULATION",/,1H ,21(1H-),/,6X,
     +     "THIS SIMULATION RAN FOR ",I5," DAYS.",/,6X,"THE LAST DAY OF T
     +HE ",       "CURRENT SAMPLING PERIOD WAS DAY ",I2,".",/,6X,"THERE
     +WERE ",I2,          " COMPLETE GENERATIONS.",//,4X,"A. ADULT POPUL
     +ATION SIZES.",/,          ,0X,"GENERATION",5X,"HOST 1",7X,"HOST
     +2",6X,"PARASITE",50(/,12X,I3,4X,    3F14.5))
C
  107 FORMAT(1H ,/,4X,"B. INFORMATION ON THE CURRENT (INCOMPLETE)",
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     +    " GENERATION.")
  117 FORMAT(1H ,/,9X,"(",I1,") HOST POPULATION, SPECIES",I2,".",/,14X,
     +    "THE TOTAL RECRUITS ",
     +         "INTO EACH STAGE FROM THE OLD AND THE NEW BEANS",//,1H
     + ,5X,"EGGS",7X,      "1",8X,"2",8X,"3",8X,"4",6X,"PUPAE",2X,"AD IN
     +PEA",2X,"EM AD",/,1H ,       "OLD",8F9.4,/,1H ,"NEW",8F9.4,//,14X,"
     +THE TOTAL NUMBERS PRESENT IN EACH ","INSTAR ON EACH DAY WERE",/,1H
     + ,"OLD BEANS",/,1H ,"DAY",2X,"EGGS",6X,"1",  8X,"2",8X,"3",8X,"4",6
     +X,"PUPAE",2X,"AD IN PEA",21(/,1H ,I2,7F9.4),//,      1H ,"NEW BEANS
     +",/,1H ,"DAY",2X,"EGGS",6X,"1",8X,"2",8X,"3",8X,"4",6X,      "PUPAE
     +",2X,"AD IN PEA",2X,"EM AD",21(/,1H ,I2,8F9.4))
C
  108 FORMAT(1H ,//,9X,"(2) PARASITE POPULATION.",/,14X,"THE TOTAL RECRU
     +ITS"," TO THE LARVAL ( = EGGS + LARVAE + PUPAE +",/,14X,"PRE-EMERG
     +ENT ",      "ADULTS ) AND ADULT STAGES.",//,20X,"LARVAE",6X,"ADULT
     +S",/,14X,"OLD",      2F12.4,/,14X,"NEW",2F12.4,//,14X,"THE TOTAL NU
     +MBERS PRESENT ON EACH ",      "DAY WERE",//,14X,"DAY",3X,"LARVAE (OL
     +D BNS)   LARVAE (NEW BNS)",8X,      "ADULTS",21(/,15X,I2,3F19.4))
C
 1000 FORMAT(1H ,//,1H ,"OUTPUT FROM THE 2-SPECIES SIMULATION PROGRAM",/
     +,  1H ,"PROBLEM NAME ",I4)
C
C  END OF MAIN ROUTINE SIMUL2.
   99 STOP
      END
C
C
      SUBROUTINE MODEL2(IFLG,IDAY,COHORT,TOTALS,N,TOTREC,ADLNEW,IPARAS,
     +         PCOHT,TOTLP,NP,TOTPRC,PADNEW)
C  SUBROUTINE FOR 2-SPP SIMULATION MODEL WITH PARASITE.
C  T.S. BELLOWS,JR. JAN 1979
C
C  INPUT AND COMMON VARIABLES.
      DIMENSION COHORT(21,8,2),TOTALS(21,N,2),TOTREC(8,2),PCOHT(21,2),
     +         TOTLP(21,NP),TOTPRC(2),ADLNEW(2)
      REAL LAMBDA(15,2)
      COMMON IGDAYS(8,2),GDIS(20,8,2),ALPHA(6,6,2),DDB(8,2),DDS(7,2),LAM
     +BDA,     DDA(2,2),EGFERT(2),BETA(6,6,2),EGMORT(5,2),IPDAYS(2),PGDIS
     +(20,2),          THAGE(20),APAGE(20),THATT(6,2),APATT(6,2),THOVIP(6
     +,2),APOVIP(6,2),          PEGFRT,HSEXRT(2),PSEXRT,XNOBNS,ADALPH(2,2)
C  LOCAL VARIABLES.
      DIMENSION JEND(7,2),HDENS(6,2),PSURV(6,2),POVIP(6,2),CEGGS(2),CADS
     +(2),     TADS(2)
C
C  SOME INITIAL DEFINITIONS.
      IFLAG=IFLG
      IDD=IDAY
      ID=IDD-I
      IF(ID.EQ.0) ID=21
      JEND(1,1)=IDD
      JEND(1,2)=IDD
      IF(IFLAG.NE.1.OR.IDD.NE.1)GOTO9
      COHORT(1,8,1)=COHORT(1,8,1)+ADLNEW(1)
      COHORT(1,8,2)=COHORT(1,8,2)+ADLNEW(2)
      GOTO10
    9 IF(IFLAG.NE.0)GOTO91
      COHORT(IDD,1,1)=0.
      COHORT(IDD,1,2)=0.
   91 CONTINUE
C
C  HOST DEVELOPMENT - EGGS THROUGH ADULTS (BOTH SPECIES).
      DO 100 ISP=1,2
      DO 1 K=1,7
      RNEW=0.
      SUM=0.
      JEND(K,ISP)=IGDAYS(K,ISP)
      IF(IFLAG.EQ.1.AND.JEND(K,ISP).GT.IDD)JEND(K,ISP)=IDD
C  BREED COHORTS FROM IDD BACK TO TIME IDY
      DO 11 I=1,JEND(K,ISP)
      IDY=IDD-I+1
      IF(IDY.LE.0) IDY=IDY+21
      RNEW=RNEW+COHORT(IDY,K,ISP)*GDIS(I,K,ISP)
      COHORT(IDY,K,ISP)=COHORT(IDY,K,ISP)*(1.-GDIS(I,K,ISP))
   11 SUM=SUM+COHORT(IDY,K,ISP)
      TOTALS(IDD,K,ISP)=SUM
C  NEW COHORT=RNEW. ADD THOSES IN COHORT (USUALLY ZERO) TO PERMIT
C  USER TO ADD RECRUITS.
      IF(IFLAG.EQ.1)RNEW=RNEW+COHORT(IDD,K+1,ISP)
      COHORT(IDD,K+1,ISP)=RNEW
    1 TOTREC(K+1,ISP)=TOTREC(K+1,ISP)+RNEW
C  ADD ADULT RECRUITS FROM BREEDING CONTAINER (IF NECESSARY).
      COHORT(IDD,8,ISP)=COHORT(IDD,8,ISP)+ADLNEW(ISP)
      ADLNEW(ISP)=COHORT(IDD,8,ISP)
  100 CONTINUE
C
C  LARVAL MORTALITY.
      DO 200 ISP=1,2
      ISP2=2
      IF(ISP.EQ.2)ISP2=1
      DO 2 K=2,7
      KI=K-1
      HDENS(KI,ISP)=1.
      IF(TOTALS(IDD,K,ISP).LE.0.)GOTO2
      TEMPS=0.
C SUM TOTAL EFFECTIVE COMPETITORS.
      DO 21 KK=2,7
   21 TEMPS=TEMPS+ALPHA(KI,KK-1,ISP)*TOTALS(IDD,KK,ISP)+BETA(KI,KK-1,ISP
     +)*   TOTALS(IDD,KK,ISP2)
C  ALLOW FOR PAST BEAN EXPLOITATION IN BREEDING CONTAINER.
      IF(IFLAG.EQ.0)TEMPS=TEMPS+TOTREC(5,ISP)*ALPHA(KI,4,ISP)+TOTREC(5,I
     +SP2)*   BETA(KI,4,ISP)
C  FIND PROPORTIONATE DENSITY DEPENDENT SURVIVAL.
C  (BY CONSIDERING THE PER BEAN DENSITY)
      DENOM=1.
      IF(TEMPS.GT.0.)DENOM=1.+(TEMPS/XNOBNS)**DDB(KI,ISP)
      HDENS(KI,ISP)=DDS(K,ISP)/DENOM
C  UPDATE LARVAL COHORTS BY PROPORTIONATE MORTALITY.
      DO 22 I=1,JEND(K,ISP)
      IDY=IDD-I+1
      IF(IDY.LE.0)IDY=IDY+21
   22 COHORT(IDY,K,ISP)=COHORT(IDY,K,ISP)*HDENS(KI,ISP)
    2 CONTINUE
  200 CONTINUE
C  ACCOUNT FOR MORTALITY IN TOTALS.
      DO 230 ISP=1,2
      DO 23 K=2,7
   23 TOTALS(IDD,K,ISP)=TOTALS(IDD,K,ISP)*HDENS(K-1,ISP)
  230 CONTINUE
C
C  OVIPOSITION, ADULT MORTALITY AND EGG MORTALITY (SKIP IF IFLAG=0
C  IMPLYING BREEDING CONTAINER).
      IF(IFLAG.EQ.0)GOTO50
   10 CONTINUE
      TADS(1)=TOTALS(ID,8,1)+COHORT(IDD,8,1)
      TADS(2)=TOTALS(ID,8,2)+COHORT(IDD,8,2)
      CADS(1)=TADS(1)+ADALPH(1,2)*TADS(2)
      CADS(2)=TADS(2)+ADALPH(2,2)*TADS(1)
      CEGGS(1)=TOTREC(1,1)+TOTREC(1,2)*ADALPH(1,1)
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      CEGGS(2)=TOTREC(1,2)+TOTREC(1,1)*ADALPH(2,1)
      DO 400 ISP=1,2
      IF(TADS(ISP).LE.0.)GOTO400
      SUM=0.
      RNEW=0.
C  OVIPOSITION AND ADULT MORTALITY.
      DENOM=1.
      IF(CEGGS(ISP).GT.0..AND.DDA(1,ISP).GT.0.)DENOM=1.+(DDA(1,ISP)*CEGG
     +S(ISP))  **DDB(7,ISP)
      IF(DDA(2,ISP).GT.0.)DENOM=DENOM*(1.+(DDA(2,ISP)*CADS(ISP))**DDB(8,
     +ISP))
      DO 3 I=1,IGDAYS(8,ISP)
      IDY=IDD-I+1
      IF(IDY.LE.0)IDY=IDY+21
      RNEW=RNEW+COHORT(IDY,8,ISP)*LAMBDA(I,ISP)/DENOM
      COHORT(IDY,8,ISP)=COHORT(IDY,8,ISP)*(1.-GDIS(I,8,ISP))
    3 SUM=SUM+COHORT(IDY,8,ISP)
      TOTALS(IDD,8,ISP)=SUM
C  REDUCE OVIPOSITION BY SEX RATIO AND EGG INFERTILITY.
      RNEW=HSEXRT(ISP)*RNEW+COHORT(IDD,1,ISP)
      COHORT(IDD,1,ISP)=RNEW*EGFERT(ISP)
      TOTREC(1,ISP)=TOTREC(1,ISP)+RNEW
  400 CONTINUE
C  EGG MORTALITY. STORE PROP. SURV. IN CEGGS.
      STO1=EGMORT(1,1)*(1.-EGMORT(3,1)*TADS(2)**EGMORT(5,1))*
     +          TADS(1)**EGMORT(2,1)
      STO2=EGMORT(1,2)*(1.-EGMORT(3,2)*TADS(1)**EGMORT(5,2))*
     +          TADS(2)**EGMORT(2,2)
      CEGGS(1)=EXP(-STO1-EGMORT(4,1)*STO2)
      CEGGS(2)=EXP(-EGMORT(4,2)*STO1-STO2)
      DO 300 ISP=1,2
      DO 4 I=1,JEND(1,ISP)
    4 COHORT(IDD-I+1,1,ISP)=COHORT(IDD-I+1,1,ISP)*CEGGS(ISP)
      TOTALS(IDD,1,ISP)=TOTALS(IDD,1,ISP)*CEGGS(ISP)+COHORT(IDD,1,ISP)
  300 CONTINUE
C
C  END OF HOST SIMULATION. BEGINNING OF PARASITE SIMULATION.
C  RETURN IF IPARAS=0 IMPLYING NO PARASITES.
   50 IF(IPARAS.EQ.0)RETURN
      IF(IFLAG.EQ.1.AND.IDD.EQ.1)PCOHT(1,2)=PCOHT(1,2)+PADNEW
      IF(IFLAG.EQ.1.AND.IDD.EQ.1)GOTO1000
      IF(IFLAG.EQ.0)PCOHT(IDD,1)=0.
C
C  PARASITE DEVELOPMENT FROM EGGS TO ADULTS AS ONE STAGE.
      TOTLP(IDD,1)=0.
      RNEW=0.
      SUM=0.
      J=IPDAYS(1)
      IF(IFLAG.EQ.1.AND.J.GT.IDD)J=IDD
      DO 5 I=1,J
      IDY=IDD-I+1
      IF(IDY.LE.0)IDY=IDY+21
      RNEW=RNEW+PCOHT(IDY,1)*PGDIS(I,1)
      PCOHT(IDY,1)=PCOHT(IDY,1)*(1.-PGDIS(I,1))
    5 SUM=SUM+PCOHT(IDY,1)
      TOTLP(IDD,1)=SUM
      IF(IFLAG.EQ.1)RNEW=RNEW+PCOHT(IDD,2)
      PCOHT(IDD,2)=RNEW
      TOTPRC(2)=TOTPRC(2)+RNEW
      PCOHT(IDD,2)=PCOHT(IDD,2)+PADNEW
      PADNEW=PCOHT(IDD,2)
C
C  ATTACKS AND OVIPOSITIONS. NOTE 2 EQUATIONS FOR PARASITE SEARCH, ONE
C  FOR ATTACKS AND ONE FOR OVIPOSITIONS. USES RANDOM PARASITE EQUATION.
C  SKIP IF IFLAG=0 IMPLYING BREEDING CONTAINER.
      IF(IFLAG.EQ.0)RETURN
 1000 TPADS=TOTLP(IDD,2)+PCOHT(IDD,2)
      IF(TPADS.LE.0.)RETURN
      J=IPDAYS(2)
      DO 6 K=1,6
      PSURV(K,1)=0.
      PSURV(K,2)=0.
      POVIP(K,1)=0.
    6 POVIP(K,2)=0.
      SUM=0.
C  LOOP 7 FINDS THE TOTAL ATTACKS AND OVIPOSITIONS ON EACH HOST STAGE
C  BY EACH PARASITE ADULT COHORT (AGE GROUP).
      DO 7 I=1,J
      IDY=IDD-I+1
      IF(IDY.LE.0.)IDY=IDY+21
      DENATT=0.
      DENOVP=0.
      TH=THAGE(I)
      AP=APAGE(I)
C  FIND DENOMINATOR IN EXPONENT OF ATTACK EQUATION FOR ATTS AND OVIPS.
      DO 71 K=1,6
      DENATT=DENATT+APATT(K,1)*AP*THATT(K,1)*TH*TOTALS(IDD,K,1)
     +          +APATT(K,2)*AP*THATT(K,2)*TH*TOTALS(IDD,K,2)
   71 DENOVP=DENOVP+APOVIP(K,1)*AP*THOVIP(K,1)*TH*TOTALS(IDD,K,1)
     +          +APOVIP(K,2)*AP*THOVIP(K,2)*TH*TOTALS(IDD,K,2)
      DENATT=1.+DENATT
      DENOVP=1.+DENOVP
C  SUM ATTACKS AND OVIPS BY PARASITE AGE GROUP FOR EACH HOST STAGE.
C  (FIRST ALLOW FOR SEX RATIO)
      PARA=AP*PSEXRT*PCOHT(IDY,2)
      DO 72 K=1,6
      PSURV(K,1)=PSURV(K,1)+APATT(K,1)*PARA/DENATT
      PSURV(K,2)=PSURV(K,2)+APATT(K,2)*PARA/DENATT
      POVIP(K,1)=POVIP(K,1)+APOVIP(K,1)*PARA/DENOVP
   72 POVIP(K,2)=POVIP(K,2)+APOVIP(K,2)*PARA/DENOVP
C  ADULT MORTALITES.
      PCOHT(IDY,2)=PCOHT(IDY,2)*(1.-PGDIS(I,2))
    7 SUM=SUM+PCOHT(IDY,2)
      TOTLP(IDD,2)=SUM
C  DISTRIBUTE ATTACKS AND OVIPS AT RANDOM WITHIN A STAGE.
      RNEW=0.
      DO 800 ISP=1,2
      DO 8 K=1,6
      PSUR=EXP(-PSURV(K,ISP))
      POVP=1.-EXP(-POVIP(K,ISP))
      RNEW=RNEW+POVP*TOTALS(IDD,K,ISP)
      IF(PSUR.GE.1.)GOTO8
      DO 81 I=1,JEND(K,ISP)
   81 COHORT(IDD-I+1,K,ISP)=PSUR*COHORT(IDD-I+1,K,ISP)
      TOTALS(IDD,K,ISP)=TOTALS(IDD,K,ISP)*PSUR
    8 CONTINUE
  800 CONTINUE
      PCOHT(IDD,1)=RNEW*PEGFRT
      TOTPRC(1)=TOTPRC(1)+RNEW
      TOTLP(IDD,1)=TOTLP(IDD,1)+PCOHT(IDD,1)
C
C END OF PARASITE SIMULATION.  END OF MODEL1 SUBROUTINE.
      RETURN
      END
C
C
      SUBROUTINE GETDIS3(DM,DSIG,N,GDIS,IGDAYS,ORIGNL,ORIGNA)
C  SUBROUTINE FOR DEFINING THE DEVELOPMENTAL DISTRIBUTION G FOR SIMULATI
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C  MODELS.  USES SKEWED DISTRIBUTION FOR FIRST N-1 INSTARS (LARVAE) AND
C  NORMAL DISTRIBUTION FOR LAST INSTAR (ADULT). T.S. BELLOWS,JR  DEC 197
C
      DIMENSION DM(N),DSIG(N),GDIS(20,N),IGDAYS(N),FDIS(20),CUMDIS(20)
C
      ORIGIN=ORIGNL
      DO 10 K=1,N
      DO 1 I=1,20
    1 GDIS(I,K)=0.
      NAD=N
C
C GET FDIS
      IF(K.EQ.NAD)ORIGIN=ORIGNA
      XU=DM(K)
      XS=DSIG(K)
      S=0.
      FDIS(1)=0.
      DO 2 I=1,20
      IF(K.EQ.N)ORIGIN=ORIGNA
      XC=FLOAT(I)-1.+ORIGIN
      IF(K.EQ.NAD)GOTO20
C  SKEWED MODEL.
      IF(XC.EQ.0..OR.XC.EQ.1.)GOTO2
      Y=(1./XC-XU)/XS
      YP=(1./(XC-1.)-XU)/XS
      S1=1.
      IF(XC.GE.1.)S1=S15ABF(YP,IFAIL)
      FDIS(I)=S1-S15ABF(Y,IFAIL)
      IF(FDIS(I).LT.1.0E-08)FDIS(I)=0.
      GOTO2
C  NORMAL MODEL.
   20 Y=(XC-XU)/XS
      YP=-XU/XS
      IF(XC.GT.1.)YP=(XC-XU-1.)/XS
      FDIS(I)=S15ABF(Y,IFAIL)-S15ABF(YP,IFAIL)
      IF(FDIS(I).LT.1.0E-08)FDIS(I)=0.
    2 S=S+FDIS(I)
C
C  FIX CUMDIS,GDIS
      FDIS(1)=FDIS(1)/S
      CUMDIS(1)=FDIS(1)
      GDIS(1,K)=FDIS(1)
      DO 10 I=2,20
      FDIS(I)=FDIS(I)/S
      CUMDIS(I)=CUMDIS(I-1)+FDIS(I)
      DUM=1.-CUMDIS(I-1)
      IF(DUM.LE.0.)GOTO3
      GDIS(I,K)=FDIS(I)/DUM
      IF(GDIS(I,K).GT.1.)GDIS(I,K)=1.
      GOTO10
    3 GDIS(I,K)=1.
   10 IF(GDIS(I,K).LT.1.)IGDAYS(K)=I
C
C  CORRECT IGDAYS
      DO 11 K=1,N
      IGDAYS(K)=IGDAYS(K)+1
   11 IF(IGDAYS(K).GT.20)IGDAYS(K)=20
C
C  END OF GETDIS3.
      RETURN
      END
C
C  END OF SIMUL2 PACKAGE.
```

C.4 DENDEP

Object: to fit density dependent models to data.

Readlist variables:

XDATA: vector of initial number of individuals.

YDATA: number of survivors at each density.

WTS: (optional) weights to be applied to the data during fitting.

X: contains estimates of the parameters a, b and d.

M: number of data points.

MODEL: values of 1, 2, 3 and 4 select models corresponding to entries 4, 5, 7 and 6 in table 2.1.

N: the number of parameters being fitted. Usually 3, but a value of 2 fits only the parameters a and b, leaving d fixed at whatever value is in the third element of X.

NAME: a four digit or smaller integer used for identifying a particular data set.

IOUT: specifies output at the terminal (=6, assumed) or on the line printer (=7).

Readlist options:

BEGIN: required initial step after input of data.

PDATA: prints the current data set.

REPS: provides analysis of replicates.

FIT: fits the data to the model specified by the parameter MODEL by a nonlinear least-squares technique.

FIT1: fits the single-parameter density independent model S = aN to the data for comparison with the fits of density dependent models.

FIT2: fits entry 6 of table 2.1 by an alternate method.

ANOVA: tabulates results of last analysis.

ANOVAS: short version of output from ANOVA.

PLOT: stores a plot of fitted results for later printing on the line printer.

DATAIN: inputs data from an optional data tape.

REWIND: rewinds the optional data tape.

END: terminates execution.

Required additional subroutines: REPANA, VB03A, MB01A, VD02A, MC03AS, CHCKF, CHCKG, ANOVA. These subroutines are included at D.7. In addition the NAG library subroutine E04CAF is used in executing the option FIT2.

Notes: If plots are required, it is necessary to include the additional programme PLOTFR (page 359) in the permanent file base and the subroutine PLOT1 in the library LIBM.

DENDEP

```
      NOTRACE
      PROGRAM DENDEP(INPUT,OUTPUT,BATCH,TAPE1,TAPE2,TAPE6=OUTPUT,
     +          TAPE7=BATCH,PLTFIL,TAPE8=PLTFIL,DATAFR,TAPE3=DATAFR)
      DIMENSION R(120),X(3),EPS(3),PLOTX(81),PLOTY(81),W(21),
     +          GSEND(120,3)
      COMMON XDATA(120),YDATA(120),EXPCTD(120),RESID(120),XJAC(120,3)
     +         ,P,T,WTS(120),MODEL,G(3),XJTJ(3,3),H(3,3)
      COMMON /CREP1/ PESS,NDFPE,SSTOT,CORSS,COR
      COMMON /CST01/ ST01(120),ST02(120)
      COMMON /CANOV1/IOUT
      COMMON /FUN1/MM
      DATA IOUT/6/,DATNAM/10H           /,X/3*1./
      DATA NAME/1/
      EXTERNAL RESFR,LSQFR
      EXTERNAL FUNHSL,MONIT
C
   20 READLIST XDATA,YDATA,WTS,X,M,MODEL,N,IPRINT,MAXCAL,G,NAME,
     +      ACCUR,RSS,EPS,P,T,IOUT,STEPMX,BEGIN=21,PDATA=22,RCPS=23,
     +            FIT=24,PLOT=25,ANOVA=27,ANOVAS=1004,DATAIN=01,END=99
     +                    ,ISTOP,FIT2=124,G,FDATAIN=91,REWIND=71
     +                          ,TITLE=61,MAKE=30,FIT1=162,SWITCH=500
C
   30 CALL MAKE(X,R,N,M)
      GOTO20
C
   61 WRITE(IOUT,126)DATNAM
  126 FORMAT(1H ,10HDATA NAME ,3X,A10)
      GOTO20
C
   21 CALL REPANA(1,D,M)
      N=3
      IPRINT=5
      MAXCAL=100
      ISTOP=1
      DO 10 I=1,N
   10 EPS(I)=X(I)*1.0E-07
      IOUT=6
      MM=M
      DO 50 I=1,M
   50 WTS(I)=1.
      STEPMX=1.0E+06
      GOTO20
C
   22 WRITE(IOUT,28)NAME
      WRITE(IOUT,100)(I,XDATA(I),YDATA(I),WTS(I),I=1,M)
  100 FORMAT(1H ,/,1H ,4HDATA,7X,1HX,15X,1HY,14X,3HWTS,/,1H ,
     +    49(1H-),100(/,1H ,I3,1X,3F15.7))
      GOTO20
C
   23 WRITE(IOUT,28)NAME
   70 FORMAT(1H ,7HMODEL   ,I4)
      CALL REPANA(2,D,M)
      GOTO20
C
   24 CONTINUE
      CALL VB03A(M,N,X,EPS,R,GSEND,STEPMX,IPRINT,MAXCAL,120,W)
      GOTO20
C
  124 IFAIL=1
      IW=N*N+3*N
      CALL E04CAF(N,X,RSS,EPS,STEPMX,ISTOP,W,IW,FUNHSL,MONIT,
     +      IPRINT,MAXCAL,IFAIL)
      PRINT 125,IFAIL
  125 FORMAT(1H ,7HIFAIL= ,I1)
      DO 62 I=1,3
      DO 62 J=1,3
      XJTJ(I,J)=0.
   62 IF(I.EQ.J)XJTJ(I,J)=1.
      GOTO20
C
   25 DX=XDATA(M)/81.
      YEST=0.
      YMAX=YDATA(1)
      DO 42 I=2,M
   42 IF(YDATA(I).GT.YMAX)YMAX=YDATA(I)
      DO 11 I=1,81
      PLOTX(I)=FLOAT(I-1)*DX
   11 PLOTY(I)=FUNFR(PLOTX(I),PLOTY(I),YEST,X(1),X(2),X(3))
      WRITE(8)NAME
      WRITE(8)M,PLOTX,PLOTY,(XDATA(I),YDATA(I),RESID(I),I=1,M),YMAX
      GOTO20
C
 1004 IPAN=1
      GOTO1005
   27 IPAN=2
 1005 WRITE(IOUT,28)NAME
   28 FORMAT(1H ,9HPROBLEM   ,I4)
      WRITE(IOUT,70)MODEL
      CALL CHCKF(M,N,X,R,RSS)
      CALL CHCKG(M,N,X,R)
      CALL ANOVA(M,N,RSS,X,IPAN)
      GOTO20
C
   98 CONTINUE
      NAME=-1
      WRITE(8)NAME
      ENDFILE 8
      STOP
C
   71 REWIND 3
      GOTO20
C
   81 READ(3,84)DATNAM,M
   84 FORMAT(A10,/,I3)
      DO 82 I=1,M
      READ(3,83)XDATA(I),YDATA(I),WTS(I)
   83 FORMAT(3F10.0)
   82 IF(WTS(I).EQ.0.)WTS(I)=1.
      GOTO20
   91 READ(3,84)DATNAM,M
      DO 92 I=1,M
      READ(3,83)YDATA(I),XDATA(I),WTS(I)
   92 IF(WTS(I).EQ.0.)WTS(I)=1.
      GOTO20
C
  162 S=0.
      SS=0.
      DO 63 I=1,M
      S=S+XDATA(I)*XDATA(I)
      SS=SS+XDATA(I)*YDATA(I)
   63 CONTINUE
      SLOPE=SS/S
      S=0.
      DO 64 I=1,M
      EXPCTD(I)=XDATA(I)*SLOPE
      RESID(I)=YDATA(I)-EXPCTD(I)
      S=S+RESID(I)*RESID(I)
```

```
 64 CONTINUE
    X(1)=SLOPE
    SS=CORSS-S
    R2=100.*SS/CORSS
    WRITE(IOUT,131) SLOPE,SS,S,CORSS,R2
131 FORMAT(" ",/," ","FOR 1-PARAM LINEAR MODEL S=D*N",/," ",
   +    "D=",13X,E20.12,/," ",15HREGRESSION SS  ,E20.12,/," ",
   +           15HRESIDUAL SS    ,E20.12,/," ",15HTOT(CORR) SS   ,E20
   +.12,//,                " ",5HR2    ,10X,F10.6,/)
    MODEL=5
    GOTO20
C
500 DO 501 I=1,M
    C=XDATA(I)
    XDATA(I)=YDATA(I)
501 YDATA(I)=C
    GOTO20
C
    END
C
    SUBROUTINE CHCKF(M,N,X,R,RSS)
    DIMENSION X(N),R(M)
    COMMON XDATA(120),YDATA(120),EXPCTD(120),RESID(120),XJAC(120,3)
   +      ,P,T,WTS(120),MODEL,G(3),XJTJ(3,3),H(3,3)
    CALL RESFR(M,N,X,R)
    S=0.
    WS=0.
    DO 10 I=1,M
    S=S+RESID(I)*RESID(I)
 10 WS=WS+R(I)*R(I)
    RSS=S
    WRSS=WS
    RETURN
    END
C
    SUBROUTINE CHCKG(M,N,X,R)
    DIMENSION X(N),R(M)
    CALL LSQFR(M,N,X,R)
    RETURN
    END
C
    SUBROUTINE RESFR(M,N,XP,R)
    DIMENSION XP(N),R(M)
    COMMON XDATA(120),YDATA(120),EXPCTD(120),RESID(120),XJAC(120,3)
   +      ,P,T,WTS(120),MODEL,G(3),XJTJ(3,3),H(3,3)
    COMMON /CST01/ ST01(120),ST02(120)
    YHAT=0.
    A=XP(1)
    B=XP(2)
    C=XP(3)
    DO 3 I=1,M
    IF(I.EQ.1)GOTO11
    IF(XDATA(I).EQ.XDATA(I-1))GOTO8
 11 X=XDATA(I)
    ST02(I)=0.
    GOTO(5,6,7,8)MODEL
  5 ST02(I)=(X/A)**B
    ST01(I)=X*EXP(-ST02(I))
    YHAT=C*ST01(I)
    GOTO4
  6 ST02(I)=(X/A)**B
    ST01(I)=X/(1.+ST02(I))
    YHAT=C*ST01(I)
    GOTO4
  7 ST02(I)=EXP((X-A)/B)
    ST01(I)=X/(1.+ST02(I))
    YHAT=C*ST01(I)
    GOTO4
  8 ST01(I)=X*(1.+X/A)**(-B)
    YHAT=C*ST01(I)
    GOTO4
  9 ST01(I)=ST01(I-1)
    ST02(I)=ST02(I-1)
  4 EXPCTD(I)=YHAT
    R(I)=YDATA(I)*WTS(I)-YHAT
  3 RESID(I)=YDATA(I)-YHAT
    RETURN
    END
C
    SUBROUTINE LSQFR(M,N,XP,R)
    DIMENSION XP(N),R(M)
    COMMON XDATA(120),YDATA(120),EXPCTD(120),RESID(120),XJAC(120,3)
   +      ,P,T,WTS(120),MODEL,G(3),XJTJ(3,3),H(3,3)
    COMMON /CST01/ ST01(120),ST02(120)
    A=XP(1)
    B=XP(2)
    C=XP(3)
    DO 1 I=1,M
    IF(I.EQ.1)GOTO11
    IF(XDATA(I).EQ.XDATA(I-1))GOTO2
 11 X=XDATA(I)
    FS=ST01(I)
    GS=ST02(I)
    YHAT=EXPCTD(I)
    XJ3=-FS
    GOTO(3,4,5,6)MODEL
  3 XJ1=-B/A*YHAT*GS
    XJ2=GS*YHAT*ALOG(X/A)
    GOTO2
  4 XJ1=-B/A*GS*YHAT*FS/X
    XJ2=YHAT*FS/X*GS*ALOG(X/A)
    GOTO2
  5 XJ1=-YHAT*GS/B/(1.+GS)
    XJ2=-YHAT/(1.+GS)*GS*(X-A)/B/B
    GOTO2
  6 XJ1=-B*C*(X/A)*(X/A)*(1.+X/A)**(-B-1.)
    XJ2=YHAT*ALOG(1.+X/A)
  2 XJAC(I,1)=XJ1
    XJAC(I,2)=XJ2
  1 XJAC(I,3)=XJ3
    DO 7 I=1,N
    DO 7 J=I,N
    D=0.
    DO 8 K=1,M
  8 D=D+XJAC(K,I)*R(K)
    G(I)=2.0*D
    E=0.
    DO 10 K=1,M
 10 E=E+XJAC(K,I)*XJAC(K,J)
    XJTJ(I,J)=E
    XJTJ(J,I)=E
  7 CONTINUE
    RETURN
    END
C
    FUNCTION FUNFR(X,Y,YHAT,A,B,C)
    COMMON XDATA(120),YDATA(120),EXPCTD(120),RESID(120),XJAC(120,3)
   +      ,P,T,WTS(120),MODEL,G(3),XJTJ(3,3),H(3,3)
```

```
      COMMON /CRESF1/ ACCUR
      GOTO(1,2,3,4,5)MODEL
    1 FUNFR=C*X*EXP(-(X/A)**B)
      RETURN
    2 FUNFR=C*X/(1.+(X/A)**B)
      RETURN
    3 FUNFR=C*X/(1.+EXP((X-A)/B))
      RETURN
    4 FUNFR=C*X*(1.+X/A)**(-B)
      RETURN
    5 FUNFR=A*X
      RETURN
      END
C
      SUBROUTINE CALFG(M,N,X,F,G,IG)
      DIMENSION X(N),F(M),G(IG,N)
      COMMON XDATA(120),YDATA(120),EXPCTD(120),RESID(120),XJAC(120,3)
     +       ,P,T,WTS(120),MODEL,GC(3),XJTJ(3,3),H(3,3)
      CALL RESFR(M,N,X,F)
      CALL LSGFR(M,N,X,F)
      DO 1 I=1,M
      DO 1 J=1,N
    1 G(I,J)=XJAC(I,J)
      RETURN
      END
C
      SUBROUTINE FUNHSL(N,X,RSS)
      DIMENSION X(N)
      COMMON XDATA(120),YDATA(120),EXPCTD(120),RESID(120),XJAC(120,3)
     +       ,P,T,WTS(120),MODEL,G(3),XJTJ(3,3),H(3,3)
      COMMON /FUN1/M
      RSS=0.
      DO 1 I=1,M
      YHAT=X(3)*XDATA(I)*(1.+XDATA(I)/X(1))**(-X(2))
      EXPCTD(I)=YHAT
      RESID(I)=YDATA(I)-YHAT
    1 RSS=RSS+RESID(I)*RESID(I)
      RETURN
      END
C
      SUBROUTINE MONIT(N,X,RSS,NC)
      DIMENSION X(N)
      PRINT 11,NC,RSS
      PRINT 10,(X(I),I=1,N)
   11 FORMAT(1H ,I5,2X,E20.10)
   10 FORMAT(1H ,3E15.8,/)
      RETURN
      END
C
      SUBROUTINE MAKE(X,R,N,M)
      DIMENSION X(N),R(M)
      COMMON XDATA(120),YDATA(120),EXPCTD(120),RESID(120),XJAC(120,3)
     +       ,P,T,WTS(120),MODEL,G(3),XJTJ(3,3),H(3,3)
      DO 1 I=1,M
    1 YDATA(I)=FUNFR(XDATA(I),YDATA(I),YEST,X(1),X(2),X(3))
      RETURN
      END
C
```

C.5 LTANA

Object: to fit the cohort life-table model of chapter 4 to data.
Readlist variables:

INSTAR : the stage being considered.
ISTART : vector of first day of appearance of each stage.
IEND: vector of last day of presence of each stage.
TSMOBS: matrix containing cohort life-table data in the format of table 4.3.
MODEL: selects a fitting option. Usuall value is 2. Value of 1 assumes no mortality.
ORIGIN: the earliest possible age (in days) which an individual might have when first observed.
X: vector containing parameter estimates for μ, σ and s for the current stage.
IOUT: specifies output at the terminal (=6) or line printer (=7).
EGGDEN: the initial number of eggs.
LASTDY: last day of the sampling period.
NORMAL: specifies whether a normal (=1) or skewed (=0, assumed) developmental distribution is used.
IMAT: used for controlling output as specified below.
DISMU: vector of estimated mean developmental rates, μ.
DISSIG: vector of estimated developmental rate variance parameters, σ.
SURV: vector of estimated stage daily survival rates, s.
INSTR1: when more than one stage is being considered simultaneously, INSTR1 specifies the first instar and INSTAR specifies the last.

Readlist execution options:

BEGIN: required initial step after data input.
FIT: estimates the parameters μ, σ and s for the current instar(s).
PARMS: tabulates the estimated parameter values for development and survival.
MATOUT: Outputs the following matrices as specified by the value of the parameter IMAT : (1) predicted recruitment time series, (2) the predicted developmental distributions, (3) the predicted number of individuals in each stage on each day and (4) the input data matrix.

Notes: This programme uses the NAG library routine E04FBF.

LTANA

```
      NOTRACE
      PROGRAM LTANA(INPUT,OUTPUT,BATCH,TAPE1,TAPE2,TAPE6=OUTPUT,
     +         TAPE7=BATCH)
      DIMENSION X(18),W(3350),R(90),TOTREC(8)
      DIMENSION RSSV(7)
      COMMON ISTART(8),IEND(8),TSMOBS(35,8),TSMEXP(35,8),RECM(35,8),
     +         MODEL,INSTAR,FDIS(20),CUMDIS(20),GDIS(20,7),ORIGIN,EGGDEN,
     +                  COHORT(35,8),LASTDY,DISMU(7),DISSIG(7),SURV(7)
     +                           ,INSTR1,RECDM(20,8)
      COMMON /TEST/ NORMAL
      DATA IOUT/6/,NAME/1/,X/18*0./
      EXTERNAL LARSB,MONIT
      NORMAL=0
C
      DO 200 I=2,20
  200 RECDM(I,1)=0.
      RECDM(1,1)=1.
C
   20 READLIST ISTART,IEND,TSMOBS,TSMEXP,RECM,MODEL,INSTAR,FDIS,
     +      CUMDIS,GDIS,ORIGIN,RSS,M,N,X,R,IOUT,NAME,MAXCAL,IPRINT,DELTA,
     +           STEPMX,EGGDEN,LASTDY,BEGIN=21,CHECKF=22,FIT=23,CHDIS=2
     +4,MATOUT=25,          END=99,DISMU,DISSIG,SURV,PARMS=26
     +                           ,INSTR1,IMAT,RECDM,RSSV,PDIS=27
     +                                 ,NORMAL
C
   21 STEPMX=.05
      INSTR1=INSTAR
      IF(MODEL.LT.3)INSTR1=2
      IF(MODEL.EQ.1)N=2*(INSTAR-1)
      IF(MODEL.EQ.2)N=3*(INSTAR-1)
      IF(MODEL.EQ.3)N=2
      IF(MODEL.EQ.4)N=3
      DELTA=.000001
      MAXCAL=300
      IPRINT=20
      M=0
      DO 2 I=INSTR1,INSTAR
    2 M=M+IEND(I)-ISTART(I)+1
      EPS=1.0E-10
      GOTO20
C
   22 CALL CHLAR(M,N,X,R,RSS,LARSB)
      RSSV(INSTAR)=RSS
      GOTO20
C
   24 CALL GETDIS2
      GOTO20
C
   23 IFAIL=1
      IW=3358
      CALL E04FBF(M,N,X,R,RSS,EPS,DELTA,STEPMX,W,IW,LARSB,MONIT,
     +      IPRINT,MAXCAL,IFAIL)
      PRINT 1000,IFAIL
 1000 FORMAT(7H IFAIL=,I3)
      RSSV(INSTAR)=RSS
      GOTO20
C
   26 WRITE(IOUT,10)NAME
      WRITE(IOUT,11)MODEL
      WRITE(IOUT,16)INSTAR,(I,DISMU(I),DISSIG(I),SURV(I),RSSV(I),
     +      I=1,INSTAR)
   16 FORMAT(1H ,6HINSTAR,3X,I1,//,1H ,10HPARAMETERS,/,1H ,10(1H-),
     +   /,1H ,6HINSTAR,4X,2HMU,12X,5HSIGMA,7X,17HPROP. DAILY SURV.,/,
     +1H ,          5(1H-),7(/,1H ,I4,2X,4F15.10))
      GOTO20
C
   25 WRITE(IOUT,10)NAME
      DO 3 I=1,8
      TOTREC(I)=0.
      DO 3 J=1,LASTDY
    3 TOTREC(I)=TOTREC(I)+RECM(J,I)
      WRITE(IOUT,11)MODEL
      GOTO(251,252,253,254)IMAT
  251 WRITE(IOUT,14)
      WRITE(IOUT,13)(I,(RECM(I,J),J=1,8),I=1,LASTDY)
      WRITE(IOUT,17)(TOTREC(I),I=1,8)
      GOTO20
  252 WRITE(IOUT,9)
      WRITE(IOUT,8)(I,(RECDM(I,J),J=1,8),I=1,20)
      GOTO20
  253 WRITE(IOUT,15)
      WRITE(IOUT,13)(I,(TSMEXP(I,J),J=1,8),I=1,LASTDY)
      GOTO20
  254 WRITE(IOUT,12)
      WRITE(IOUT,13)(I,(TSMOBS(I,J),J=1,8),I=1,LASTDY)
      GOTO20
   10 FORMAT(1H ,8HPROBLEM  ,I4)
   11 FORMAT(10H MODEL     ,I4)
   12 FORMAT(1H ,//,1H ,21HNOS. PRESENT (OBS.)    )
   13 FORMAT(1H ,20(1H-),/,(1H ,I2,8F9.4))
   14 FORMAT(1H ,//,21H NOS. RECR. (PREDICT))
   15 FORMAT(1H ,//,22H NOS. PRESENT (EXPCTD))
   17 FORMAT(1H ,5HTOTAL,/,1H ,2X,8F9.4)
    9 FORMAT(1H ,//,21H RECR. DIST.(PREDICT))
    8 FORMAT(1H ,20(1H-),/,(1H ,I2,8F9.6))
C
   27 WRITE(IOUT,18)(I,FDIS(I),CUMDIS(I),GDIS(I,1),I=1,20)
   18 FORMAT(1H ,20(/,1H ,I3,2X,3F15.8))
      GOTO20
C
   99 STOP
      END
C
      SUBROUTINE CHLAR(M,N,X,R,RSS,LARSB)
      DIMENSION X(18),R(90)
      EXTERNAL LARSB
      CALL LARSB(M,N,X,R)
      RSS=0.
      DO 1 I=1,M
    1 RSS=RSS+R(I)*R(I)
      RETURN
      END
C
      SUBROUTINE LARSB(M,N,X,R)
      DIMENSION X(18),R(90),TOTAL(7)
      COMMON ISTART(8),IEND(8),TSMOBS(35,8),TSMEXP(35,8),RECM(35,8),
     +         MODEL,INSTAR,FDIS(20),CUMDIS(20),GDIS(20,7),ORIGIN,EGGDEN,
     +                  COHORT(35,8),LASTDY,DISMU(7),DISSIG(7),SURV(7)
     +                           ,INSTR1,RECDM(20,8)
C
      SURV(1)=1.
      IF(MODEL.GT.2)GOTO30
      DO 8 K=2,INSTAR
      KI=2*(K-1)
      DISMU(K)=X(KI-1)
      DISSIG(K)=X(KI)
    8 SURV(K)=1.
      IF(MODEL.EQ.1)GOTO10
```

```
      KI=2*(INSTAR-1)-1
      DO 11 K=2,INSTAR
   11 SURV(K)=X(K+KI)
      GOTO10
   30 DO 12 K=INSTR1,INSTAR
      SURV(K)=1.
      KI=2*(K-INSTR1+1)-1
      DISMU(K)=X(KI)
   12 DISSIG(K)=X(KI+1)
      IF(MODEL.EQ.3)GOTO10
      KD=1+2*(INSTAR-INSTR1+1)
      DO 13 K=INSTR1,INSTAR
   13 SURV(K)=X(K-INSTR1+KD)
   10 DO 1 K=1,8
      DO 1 J=1,35
    1 COHORT(J,K)=0.
      CALL GETDIS2
C
      COHORT(1,1)=EGGDEN
      RECM(1,1)=EGGDEN
      DO 3 J=1,LASTDY
C
      JEND=J
      IF(JEND.GT.20)JEND=20
      DO 51 K=1,INSTAR
  215 FORMAT(1H ,I2)
      DO 5 I=1,JEND
      COHORT(J,K+1)=COHORT(J,K+1)+GDIS(I,K)*COHORT(J-I+1,K)
    5 COHORT(J-I+1,K)=COHORT(J-I+1,K)*(1.-GDIS(I,K))
   51 RECM(J,K+1)=COHORT(J,K+1)
C
      DO 4 K=1,INSTAR
      SV=SURV(K)
      DO 4 I=1,JEND
    4 COHORT(J-I+1,K)=COHORT(J-I+1,K)*SV
C
      DO 6 K=1,INSTAR
      TOTAL(K)=0.
      DO 6 I=1,JEND
    6 TOTAL(K)=TOTAL(K)+COHORT(J-I+1,K)
C
      DO 7 K=1,INSTAR
    7 TSMEXP(J,K)=TOTAL(K)
      S=0.
      IF(J.GT.1)S=TSMEXP(J-1,INSTAR+1)
      TSMEXP(J,INSTAR+1)=S+RECM(J,INSTAR+1)
C
    3 CONTINUE
C
      ICNT=1
      DO 8 I=INSTR1,INSTAR
      DO 8 J=ISTART(I),IEND(I)
      R(ICNT)=TSMOBS(J,I)-TSMEXP(J,I)
      ICNT=ICNT+1
    8 CONTINUE
      RETURN
      END
C
      SUBROUTINE GETDIS2
      COMMON ISTART(8),IEND(8),TSMOBS(35,8),TSMEXPC(35,8),RECM(35,8),
     +       MODEL,INSTAR,FDIS(20),CUMDIS(20),GDIS(20,7),ORIGIN,EGGDEN,
     +            COHORT(35,8),LASTDY,DISMU(7),DISSIG(7),SURV(7)
     +                 ,INSTR1,RECOM(20,8)
      COMMON /TEST/ NORMAL
C
      DO 10 K=1,INSTAR
      DO 100 J=1,20
  100 GDIS(J,K)=0.
C  GET FDIS (SKEWED MODEL)
      XU=DISMU(K)
      XS=DISSIG(K)
      S=0.
      FDIS(1)=0.
      DO 2 I=1,20
      XC=FLOAT(I)-1.+ORIGIN
      IF(NORMAL.EQ.1)GOTO20
      IF(I.EQ.1.AND.ORIGIN.EQ.0.)GOTO2
      XC=FLOAT(I)-1.+ORIGIN
      Y=(1./XC-XU)/XS
      YP=(1./(XC-1.)-XU)/XS
      S1=1.
      IF(XC.GE.1.)S1=S15ABF(YP,IFAIL)
      FDIS(I)=S1-S15ABF(Y,IFAIL)
      IF(FDIS(I).LT.1.0E-08)FDIS(I)=0.
      GOTO2
C     (NORMAL MODEL)
   20 Y=(XC-XU)/XS
      YP=-XU/XS
      IF(XC.GT.1)YP=(XC-XU-1.)/XS
      FDIS(I)=S15ABF(Y,IFAIL)-S15ABF(YP,IFAIL)
      IF(FDIS(I).LT.1.0E-08)FDIS(I)=0.
    2 S=S+FDIS(I)
C  FIX CUMDIS,GDIS
      FDIS(1)=FDIS(1)/S
      CUMDIS(1)=FDIS(1)
      GDIS(1,K)=FDIS(1)
      DO 1 I=2,20
      FDIS(I)=FDIS(I)/S
      CUMDIS(I)=CUMDIS(I-1)+FDIS(I)
      DUM=1.-CUMDIS(I-1)
      IF(DUM.LE.0.)GOTO3
      GDIS(I,K)=FDIS(I)/DUM
      GOTO1
    3 GDIS(I,K)=1.
    1 IF(GDIS(I,K).GT.1.)GDIS(I,K)=1.
      DO 10 I=1,20
   10 RECOM(I,K+1)=FDIS(I)
      RETURN
      END
C
C  END OF LTAMA
```

C.6 FRESAN

Object: to fit functional response models to data.

Readlist variables:

XDATA: the initial prey densities.
YDATA: the number of prey attacked.
WTS: (optional) weights to be assigned to each datum during fitting.
X: the estimates of the parameters a' and T_h or b, c and T_h.
M: the number of data points.
MODEL: selects type II parasitoid model (=1), type III parasitoid model (=2), type II predator model (=3) or type III predator model (=4).
P: (optional) the number of predators (assumed 1).
T: (optional) total time of experiment (assumed 1).
IOUT: specifies the results to be printed at the terminal (=6, assumed) or at the line printer (=7).
NAME: this variable may be set equal to any four digit (or smaller) number for identifying the results of a particular data set.

Readlist execution options:

BEGIN: required initial step after input of data.
PDATA: prints the current data set.
REPS: provides analysis of replicates.
ROGERS: performs a linearized parameter estimation.
FIT: performs nonlinear least squares parameter estimation.
ANOVA: tabulates results of last analysis.
ANOVAS: short version of output from ANOVA.
PLOT: stores a plot of fitted results for later printing on the line printer.
DATAIN: inputs data from an optional data tape.
REWIND: rewinds the optional data tape.
END: terminates execution.

Required additional subroutines: REPANA, VB03A, MB01A, VD02A, MC03AS, CHCKF, CHCKG, ANOVA. All of these subroutines are included at C.7.

Notes: If plots are required, it is necessary to include the additional programme PLOTFR (page 359) in the permanent file base and the subroutine PLOT1 in the library LIBM.

FRESAN

```
      NOTRACE
      PROGRAM FRESAN(INPUT,OUTPUT,BATCH,TAPE1,TAPE2,TAPE6=OUTPUT,
     +        TAPE7=BATCH,PLTFIL,TAPE8=PLTFIL,DATAFR,TAPE3=DATAFR)
C
C  FITS FUNCTIONAL RESPONSE DATA TO VARIOUS MODELS BY EITHER
C  A LEAST SQUARES METHOD OR LINEARIZATION (ROGERS METHOD).
C  T.S. BELLOWS,JR.  OCT 1970
      DIMENSION A(100),X(3),EPS(3),PLOTX(81),PLOTY(81),W(21),
     +        GSEND(100,3)
      COMMON XDATA(120),YDATA(120),EXPCTD(120),RESID(120),XJAC(120,3)
     +        ,P,T,WTS(120),MODEL,G(3),XJTJ(3,3),H(3,3)
      DATA NAME/1/,IOUT/6/,X/3*1./
      COMMON /CRESF1/ ACCUR
      COMMON /CST01/ ST01(100),ST02(100)
      COMMON /CANOV1/IOUT
      EXTERNAL RESFR,LSQFR
C
      DO 1 I=1,100
    1 WTS(I)=1.
      P=1.
      T=1.
C
   20 READLIST XDATA,YDATA,WTS,X,M,MODEL,N,IPRINT,MAXCAL,G,NAME,
     +     ACCUR,RSS,EPS,P,T,IOUT,STEPMX,BEGIN=21,PDATA=22,REPS=23,ROGER
     +S=26,        FIT=24,PLOT=25,ANOVA=27,ANOVAS=1004,DATAIN=81,REWIND=
     +71,END=99
C
   21 CALL REPANA(1,0,M)
      N=2
      IF(MODEL.EQ.2.OR.MODEL.EQ.4)N=3
      IPRINT=5
      MAXCAL=100
      IF(N.EQ.2)X(3)=0.
      ACCUR=1.0E-08
      DO 10 I=1,N
   10 EPS(I)=X(I)*1.0E-07
      STEPMX=1.0E+06
      GOTO20
C
   22 WRITE(IOUT,28)NAME
      WRITE(IOUT,100)(I,XDATA(I),YDATA(I),WTS(I),I=1,M)
  100 FORMAT(1H ,/,1H ,4HDATA,7X,1HX,15X,1HY,14X,3HWTS,/,1H ,
     +    49(1H-),100(/,1H ,I3,1X,3F15.7))
      GOTO20
C
   23 WRITE(IOUT,28)NAME
   70 FORMAT(1H ,7HMODEL   ,I4)
      CALL REPANA(2,0,M)
      GOTO20
C
   24 NSAVE=N
      CALL VB03A(M,N,X,EPS,R,GSEND,STEPMX,IPRINT,MAXCAL,100,W)
      N=NSAVE
      GOTO20
C
   26 GOTO(106,103,106,103)MODEL
  106 WRITE(IOUT,28)NAME
      CALL ROGERS(X,N,M)
      GOTO20
  103 WRITE(6,105)
  105 FORMAT(1H ,24H ANALYSIS NOT AVAILABLE.)
      GOTO20
C
   25 DX=XDATA(M)/81.
      YEST=0.
      YMAX=YDATA(1)
      DO 42 I=2,M
   42 IF(YDATA(I).GT.YMAX)YMAX=YDATA(I)
      DO 11 I=1,81
      PLOTX(I)=FLOAT(I-1)*DX
   11 PLOTY(I)=FUNFR(PLOTX(I),PLOTY(I),YEST,X(1),X(2),X(3))
      WRITE(8)NAME
      WRITE(8)M,PLOTX,PLOTY,(XDATA(I),YDATA(I),RESID(I),I=1,M),YMAX
      GOTO20
C
 1004 IPAN=1
      GOTO1005
   27 IPAN=2
 1005 WRITE(IOUT,28)NAME
   28 FORMAT(1H ,9HPROBLEM  ,I4)
      WRITE(IOUT,70)MODEL
      CALL CHCKF(M,N,X,R,RSS,RESFR)
      CALL CHCKG(M,N,X,R,LSQFR)
      CALL ANOVA(M,N,RSS,X,IPAN)
      GOTO20
C
C
   71 REWIND 3
      GOTO20
C
   81 CONTINUE
      READ(3,84)M
   84 FORMAT(I5)
      DO 82 I=1,M
      READ(3,83)XDATA(I),YDATA(I),WTS(I)
   83 FORMAT(3F10.0)
   82 IF(WTS(I).EQ.0.)WTS(I)=1.
      GOTO20
C
   99 NAME=-1
      WRITE(8)NAME
      ENDFILE 8
      STOP
      END
C
      SUBROUTINE RESFR(M,N,XP,R)
C  MAIN FRESAN
C  DEFINES EXPECTED AND RESIDUAL VALUES FOR FUNC. RES. MODELS.
      DIMENSION XP(N),R(M)
      COMMON XDATA(120),YDATA(120),EXPCTD(120),RESID(120),XJAC(120,3)
     +        ,P,T,WTS(120),MODEL,G(3),XJTJ(3,3),H(3,3)
      COMMON /CRESF1/ ACCUR
      COMMON /CST01/ ST01(100),ST02(100)
      YHAT=0.
      A=XP(1)
      B=XP(2)
      C=XP(3)
      DO 3 I=1,M
      IF(I.EQ.1)GOTO11
      IF(XDATA(I).EQ.XDATA(I-1))GOTO9
   11 X=XDATA(I)
      ST02(I)=0.
      GOTO(5,6,7,8)MODEL
    5 ST01(I)=P*T/(1.+A*B**C)
      ST02(I)=X*EXP(-A*ST01(I))
      YHAT=X-ST02(I)
      GOTO4
    6 ST01(I)=P*T**C/(1.+B*X+A*C**C)
```

```
      ST02(I)=X*EXP(-A*ST01(I))
      YHAT=X-ST02(I)
      GOTO4
    7 YOLD=YHAT
      F=X*EXP(A*B*YOLD-A*P*T)
      YHAT=YOLD-(YOLD-X+F)/(1.+A*B*F)
      IF(ABS(YOLD-YHAT)-ACCUR)17,17,7
   17 ST01(I)=X*EXP(A*B*YHAT-A*P*T)
      GOTO4
    8 YOLD=YHAT
      F=X*EXP((A*C**2*YOLD-A**2*P*T)/(1.+B**2)
      YHAT=YOLD-(YOLD-X+F)/(1.+A*C**2*F/(1.+B**2)
      IF(ABS(YOLD-YHAT)-ACCUR)10,10,8
   18 ST01(I)=X*EXP((A*C**2*YHAT-A**2*P*T)/(1.+B**2)
      GOTO4
    9 ST01(I)=ST01(I-1)
      ST02(I)=ST02(I-1)
    4 EXPCTD(I)=YHAT
      R(I)=YDATA(I)*WTS(I)-YHAT
    3 RESID(I)=YDATA(I)-YHAT
      RETURN
      END
C
      SUBROUTINE LSQFR(M,N,XP,R)
C  MAIN FRESAN
C  DEFINES JACOBIAN MATRIX (=FIRST PARTIAL DERIVATIVES) OF
C  RESIDUALS FOR FUNCTIONAL RESPONSE MODELS.
      DIMENSION XP(N),R(M)
      COMMON XDATA(120),YDATA(120),EXPCTD(120),RESID(120),XJAC(120,3)
     +       ,P,T,WTS(120),MODEL,G(3),XJTJ(3,3),H(3,3)
      COMMON /CST01/ ST01(100),ST02(100)
      A=XP(1)
      B=XP(2)
      C=XP(3)
      DO 1 I=1,M
      IF(I.EQ.1)GOTO11
      IF(XDATA(I).EQ.XDATA(I-1))GOTO2
   11 X=XDATA(I)
      GS=ST01(I)
      FS=ST02(I)
      YHAT=EXPCTD(I)
      XJ3=0.
      GOTO(3,4,5,6)MODEL
    3 D=A*X*GS*GS/P/T
      XJ1=FS*(B*D-GS)
      XJ2=FS*A*D
      GOTO2
    4 D=A*X*GS*GS/P/T
      XJ1=FS*(C*D-GS)
      XJ2=FS*D/X
      XJ3=FS*A*D
      GOTO2
    5 D=1.+A*B*P*GS
      XJ1=(B*P*YHAT-P*T)*GS/D
      XJ2=A*P*YHAT*GS/D
      GOTO2
    6 D=X*P/(1.+B**2)
      E=1.+GS*A*C*D
      XJ1=GS*((C*YHAT-T)*D)/E
      XJ2=GS*(B*D/P*A*(T-C*YHAT))/E
      XJ3=GS*A*YHAT*D/E
    2 XJAC(I,1)=XJ1
      XJAC(I,2)=XJ2
    1 XJAC(I,3)=XJ3
      DO 7 I=1,N
      DO 7 J=I,N
      D=0.
      DO 8 K=1,M
    8 D=D+XJAC(K,I)*R(K)
      G(I)=2.D*D
      E=0.
      DO 10 K=1,M
   10 E=E+XJAC(K,I)*XJAC(K,J)
      XJTJ(I,J)=E
      XJTJ(J,I)=E
    7 CONTINUE
      RETURN
      END
C
      FUNCTION FUNFR(X,Y,YHAT,A,B,C)
C  MAIN FRESAN
C  GIVES EXPECTED NUMBER ATTACKED (FUNFR) FOR FOUR FUNCTIONAL
C  RESPONSE MODELS, USED BY FRESAN IN PLOTTING PREDICTED VALUES.
C  USES NEWTON INTERATIONS TO FIND NUMBER ATTACKED FOR PREDATION
C  (EXPLOITATIVE) MODELS TO ABSOLUTE ACCURACY OF ACCUR.
      COMMON XDATA(120),YDATA(120),EXPCTD(120),RESID(120),XJAC(120,3)
     +       ,P,T,WTS(120),MODEL,G(3),XJTJ(3,3),H(3,3)
      COMMON /CRESF1/ ACCUR
      GOTO(1,2,3,4)MODEL
    1 YHAT=X*(1.-EXP(-A*P*T/(1.+A*B*X)))
      GOTO5
    2 YHAT=X*(1.-EXP(-A*P*T*X/(1.+B*X+C*A*X**2)))
    5 FUNFR=YHAT
      RETURN
    3 YOLD=YHAT
      F=X*EXP(A*B*P*YOLD-A*P*T)
      YHAT=YOLD-(YOLD-X+F)/(1.+A*B*P*F)
      IF(ABS(YOLD-YHAT)-ACCUR)5,5,3
    4 YOLD=YHAT
      F=X*EXP((A*C**2*P*YOLD-A**2*T*X)/(1.+B*X))
      YHAT=YOLD-(YOLD-X+F)/(1.+A*C**2*X/(1.+B*X)*F)
      IF(ABS(YOLD-YHAT)-ACCUR)5,5,4
      END
C
      SUBROUTINE CALFG(M,N,X,F,G,IG)
C  MAIN FRESAN
C  REQUIRED SUBROUTINE FOR USE OF MINIMIZATION ROUTINE VA03A TO
C  OBTAIN VECTOR OF RESIDUALS AND JACOBIAN MATRIX.
      DIMENSION X(N),F(M),G(IG,N)
      COMMON XDATA(120),YDATA(120),EXPCTD(120),RESID(120),XJAC(120,3)
     +       ,P,T,WTS(120),MODEL,GC(3),XJTJ(3,3),H(3,3)
      CALL RESFR(M,N,X,F)
      CALL LSQFR(M,N,X,F)
      DO 1 I=1,M
      DO 1 J=1,N
    1 G(I,J)=XJAC(I,J)
      RETURN
      END
C
      SUBROUTINE ROGERS(X,N,M)
C  MAIN FRESAN
C  SUBROUTINE TO PROVIDE ESTIMATES OF A AND TH FOR FUNC. RES. MODELS
C  BY THE LINEARIZATION TECHNIQUE SUGGESTED BY ROGERS.
C
      DIMENSION X(N)
      COMMON /CANGV1/ IOUT
      COMMON XDATA(120),YDATA(120),EXPCTD(120),RESID(120),XJAC(120,3)
     +       ,P,T,WTS(120),MODEL,G(3),XJTJ(3,3),H(3,3)
```

```
C
      WRITE(IOUT,101)MODEL
      XM=M
      SX=0.
      SY=0.
      SXX=0.
      SXY=0.
      GOTO(1,2,3,2)MODEL
    1 DO 4 I=1,M
      XD=XDATA(I)
      Y=YDATA(I)
      IF(XD.LE.Y.OR.Y.LE.0.)GOTO14
      SX=SX+XD
      SXX=SXX+XD*XD
      Y=1./ALOG((XD-Y)/XD)
      SY=SY+Y
      SXY=SXY+XD*Y
      GOTO4
   14 WRITE(IOUT,109)XD,Y
  109 FORMAT(1H ,2F10.5)
      XM=M-1.
    4 CONTINUE
   10 SLOPE=(SXY-SX*SY/XM)/(SXX-SX*SX/XM)
      XINTCP=(SY-SLOPE*SX)/XM
      IF(MODEL.EQ.3)GOTO9
      X(2)=-T*P*SLOPE
      X(1)=-1./T/P/XINTCP
      GOTO6
    3 DO 7 I=1,M
      XD=XDATA(I)
      Y=YDATA(I)
      IF(XD.LE.Y.OR.Y.LT.0.)GOTO8
      Y=ALOG((XD-Y)/XD)
      XD=YDATA(I)/P
      SX=SX+XD
      SXX=SXX+XD*XD
      SY=SY+Y
      SXY=SXY+XD*Y
      GOTO7
    8 WRITE(IOUT,109)XD,Y
      XM=XM-1.
    7 CONTINUE
      GOTO10
    9 X(1)=-XINTCP/T/P
      X(2)=SLOPE/X(1)/P
    6 WRITE(IOUT,110)X(1),X(2)
  101 FORMAT(1H ,25HROGERS ANALYSIS FOR MODEL ,I2,1H.,/,1H ,
     +    32HDATA EXCLUDED FROM ANALYSIS ARE ,/,1H ,5X,1HN,8X,2HNA)
  110 FORMAT(1H ,/,1H ,32HESTIMATES OF THE PARAMETERS ARE ,/,1H ,
     +    5X,3HA= ,F15.7,/,1H ,5X,3HTH=,F15.7)
    2 RETURN
      END
C
C  END OF FRESAN
```

PLOTFR

```
      PROGRAM PLOTFR(INPUT,OUTPUT,PLTFIL,BATCH1,TAPE9=PLTFIL,
     +               TAPE10=BATCH1)
      COMMON /CPLOT1/IPLTOT
      DIMENSION XPLT(81),YPLT(81),X(100),Y(100),R(100)
      DATA PLUS/1H+/,ZERO/1HO/,STAR/1H*/,RESLT/8HN ATTCKD/
      DATA DENS/8HN INIT  /,RESDL/8H RESID  /
      IPLTOT=10
      REWIND 9
      IHINT=0
      WRITE(IPLTOT,52)
   52 FORMAT(1H )
    1 READ(9)NAME
      IF(NAME.LT.0)GOTO15
      READ(9)M,XPLT,YPLT,(X(I),Y(I),R(I),I=1,M),YMAX
      IF(IHINT.EQ.0)GOTO50
      WRITE(IPLTOT,51)
   51 FORMAT(1H ,19(/))
   50 IHINT=1
      WRITE(IPLTOT,41)NAME
   41 FORMAT(1H ,9HPROBLEM  ,I4,5X,15HPLOT OF RESULTS,/)
      CALL PLOT1(XPLT,YPLT,81,80,40.3,X(M),0.,3,YMAX,0.,0,11,
     +           PLUS,2,1,0,0.,0.)
      CALL PLOT1(X,Y,M,80,40,3,X(M),0.,3,YMAX,0.,1,11,ZERO,
     +           2,0,1,DENS,RESLT)
      WRITE(IPLTOT,42)NAME
   42 FORMAT(1H ,20(/),1H ,9HPROBLEM  ,I4,5X,17HPLOT OF RESIDUALS,/)
      CALL PLOT1(X,R,M,80,40,3,X(M),0.,0,0.,0.,0,11,
     +           STAR,2,0,1,DENS,RESDL)
      GOTO1
   15 ENDFILE 10
      STOP
      END
```

C.7 Subroutines.

These subroutines are required by the data fitting programmes DENDEP and FRESAN and were stored in the binary library LIBM. The first four subroutines (V803A, M801A, VD02A, and MC03AS) are part of the Harwell Subroutine Library (Hopper 1973) and are included here by the kind permission of Mr. S. Marlow of the Atomic Energy Research Establishment, Harwell, Berkshire.

```
      NOTRACE
      SUBROUTINE V903A(M,N,X,E,F,G,ESCALE,IPRINT,MAXIT,IG,W)
      DIMENSION X(N),E(N),F(M),W(1),G(IG,1).
      NN=N
      K=N
      IMAX=0
      IA=2
      GOTO41
   37 DO 2 I=1,NN
      DO 3 J=1,NN
      K=K+1
      SUM=0.
      DO 4 L=1,M
      SUM=SUM+G(L,I)*G(L,J)
    4 CONTINUE
      W(K)=2.*SUM
    3 CONTINUE
    2 CONTINUE
      NNP1=N+1
      CALL MB01A(W(NNP1),N,N)
      IA=1
      N1=K
      N2=NN+K
      N3=NN+N2
      ICOUNT=0
      ISPR=1
      IF(IPRINT)1,1,26
   26 PRINT 46,FX,(X(I),I=1,NN)
    1 IF(IMAX-MAXIT)58,59,59
   58 EMAX=0.
      IMAX=IMAX+1
      K=NN
      DO 5 I=1,NN
      K1=N1+I
      K2=N2+I
      SUM=0.
      DO 6 J=1,NN
      K=K+1
      SUM=W(K)*W(J)+SUM
    6 CONTINUE
      W(K2)=W(I)
      A=ABS(SUM/E(I))
      W(K1)=-SUM
      IF(EMAX-A)7,5,5
    7 EMAX=A
    5 CONTINUE
      IS=2
    8 GC=0.
      DO 9 I=1,NN
      K1=N1+I
      GC=W(I)*W(K1)+GC
    9 CONTINUE
      GOTO(11,10)IS
   10 IF(GC)14,14,13
   13 N=0
      PRINT 15
   15 FORMAT(5X,30HERROR DUE TO ROUNDING IN V903A)
      IA=3
      GOTO41
   14 IS=1
      GA=GC
      FMIN=FX
      YP=0.
      XSTEP=AMIN1(1.,ESCALE/EMAX)
   65 XP=0.
      ITEST=3
   17 CALL V902A(ITEST,YP,FX,GC,6,0.1/EMAX,0.1,XSTEP)
      GOTO(18,19,19,19,19)ITEST
   18 YS=YP-XP
      XP=YP
      DO 20 I=1,NN
      K1=N1+I
      X(I)=X(I)+YS*W(K1)
   20 CONTINUE
   41 CALL CALFG(M,NN,X,F,G,IG)
      FX=0.
      DO 61 I=1,M
      FX=FX+F(I)*F(I)
   61 CONTINUE
      DO 38 J=1,N
      SUM=0.
      DO 39 I=1,M
      SUM=SUM+F(I)*G(I,J)
   39 CONTINUE
      W(J)=2.*SUM
   38 CONTINUE
      GOTO(8,37,24),IA
   24 ISPR=2
      IF(IPRINT)66,66,45
   66 RETURN
   11 IF(FX-FMIN)22,17,17
   22 FMIN=FX
      DO 23 I=1,NN
      K3=N3+I
      W(K3)=W(I)
   23 CONTINUE
      GOTO17
   19 IF(YP*EMAX-0.1)16,16,35
   16 YS=YP-XP
      DO 62 I=1,NN
      K1=N1+I
      X(I)=X(I)+YS*W(K1)
   62 CONTINUE
      IA=3
      IF(YP)63,63,41
   63 IF(XSTEP*EMAX-1.)41,41,64
   64 XSTEP=0.1*XSTEP
      IA=1
      GOTO65
   35 YS=XP-YP
      DO 21 I=1,NN
      K1=N1+I
      K2=N2+I
      K3=N3+I
      X(I)=X(I)-YS*W(K1)
      W(I)=W(K3)
      W(K2)=W(I)-W(K2)
   21 CONTINUE
      IF(IPRINT)44,44,43
   43 ICOUNT=ICOUNT+1
      IF(IPRINT-ICOUNT)44,45,44
   45 PRINT 46,FX,(X(I),I=1,NN)
   46 FORMAT(/,E14.6,/,(8E14.6))
      ICOUNT=0
      GOTO(44,66)ISPR
   44 A=YP/(GC-GA)
      IF(A)1,1,48
   48 K=NN
```

```
      B=0.
      DO 51 I=1,NN
      K3=N3+I
      SUM=0.
      DO 52 J=1,NN
      K2=N2+J
      K=K+1
      SUM=W(K)*W(K2)+SUM
   52 CONTINUE
      K2=N2+I
      W(K3)=SUM
      B=W(K2)*SUM+B
   51 CONTINUE
      B=-1./B
   53 K=NN
      DO 54 I=1,NN
      K1=N1+I
      K3=N3+I
      A1=A*W(K1)
      B1=B*W(K3)
      DO 55 J=1,NN
      K1=N1+J
      K3=N3+J
      K=K+1
      W(K)=A1*W(K1)+B1*W(K3)+W(K)
   55 CONTINUE
   54 CONTINUE
      GOTO1
   59 PRINT 60,IMAX
   60 FORMAT(I10,21H ITERATIONS COMPLETED)
      N=0
      GOTO16
      END
C
      SUBROUTINE MB01A(A,M,IA)
      DIMENSION A(IA,2),IND(100),C(100)
      IF(M-1)99,2,3
    2 IF(A(1,1).NE.D.)A(1,1)=1./A(1,1)
      GOTO99
    3 M1=M-1
      AMAX=0.
      DO 32 I=1,M
      IND(I)=I
      IF(ABS(A(I,1))-ABS(AMAX))32,32,31
   31 AMAX=A(I,1)
      IMAX=I
   32 CONTINUE
      ASSIGN 38 TO JUMP
      DO 41 J=1,M1
      IF(IMAX-J)35,35,33
   33 IW=IND(IMAX)
      IND(IMAX)=IND(J)
      IND(J)=IW
      DO 34 K=1,M
      W=A(IMAX,K)
      A(IMAX,K)=A(J,K)
      A(J,K)=W
   34 CONTINUE
   35 J1=J+1
      GO TO JUMP,(36,38)
   36 DO 37 I=J1,M
      CALL MC03AS(A(J,1),A(J,2),A(1,I),A(2,I),A(J,I),A(J,I),J-1,1)
   37 CONTINUE
   38 DIV=AMAX
      AMAX=0.
      ASSIGN 36 TO JUMP
      DO 40 I=J1,M
      A(I,J)=A(I,J)/DIV
      CALL MC03AS(A(I,1),A(I,2),A(1,J+1),A(2,J+1),A(I,J+1),A(I,J+1),J,1)
      IF(ABS(A(I,J1))-ABS(AMAX))40,40,39
   39 AMAX=A(I,J1)
      IMAX=I
   40 CONTINUE
   41 CONTINUE
      DO 13 I1=1,M1
      I=M+1-I1
      I2=I-1
      DO 11 J1=1,I2
      J=I2+1-J1
      J2=J+1
      W1=-A(I,J)
      IF(I2-J2)10,9,9
    9 CALL MC03AS(A(J2,J),A(J2+1,J),C(J2),C(J2+1),W1,W1,I2-J2+1,1)
   10 C(J)=W1
   11 CONTINUE
      DO 12 K=1,I2
      A(I,K)=C(K)
   12 CONTINUE
   13 CONTINUE
      DO 22 I1=1,M
      I=M+1-I1
      I2=I+1
      W=A(I,I)
      DO 20 J=1,M
      IF(I-J)14,15,16
   14 W1=0.
      GOTO17
   15 W1=1.0
      GOTO17
   16 W1=A(I,J)
   17 IF(I1-1)19,19,18
   18 CALL MC03AS(A(I,I2),A(I,I2+1),A(I2,J),A(I2+1,J),W1,W1,M-I2+1,1)
   19 C(J)=W1
   20 CONTINUE
      DO 21 J=1,M
      A(I,J)=C(J)/W
   21 CONTINUE
   22 CONTINUE
      DO 26 I=1,M
   23 IF(IND(I)-I)24,26,24
   24 J=IND(I)
      DO 25 K=1,M
      STO=A(K,I)
      A(K,I)=A(K,J)
      A(K,J)=STO
   25 CONTINUE
      ISTO=IND(J)
      IND(J)=J
      IND(I)=ISTO
      GOTO23
   26 CONTINUE
   99 RETURN
      END
C
      SUBROUTINE VD02A(ITEST,X,F,G,MAXFUN,ABSACC,RELACC,XSTEP)
      GOTO(1,2,2),ITEST
    2 IS=ITEST
      ITEST=1
```

```
      IINC=1
      XINC=XSTEP
      MC=1
      GOTO(4,4,10),IS
    3 MC=MC+1
      IF(MC-MAXFUN)4,4,5
    5 ITEST=4
   11 F=FA
      X=XA
      G=GA
    4 RETURN
   10 IS=2
      MC=0
    1 IF(G)6,7,6
    7 ITEST=5
      GOTO4
    6 GOTO(8,9),IS
    9 XA=X
      FA=F
      GA=G
      IS=1
   12 X=XA-SIGN(XINC,GA)
      XINC=XINC+XINC
      GOTO3
    8 IF(F-FA)13,13,14
   13 DUM=FA
      FA=F
      F=DUM
      DUM=GA
      GA=G
      G=DUM
      DUM=XA
      XA=X
      X=DUM
   14 IF(GA*(X-XA))15,16,16
   15 IINC=2
      XINC=X
   16 Z=3.*(FA-F)/(X-XA)+G+GA
      W=Z*Z-G*GA
      IF(W)20,20,17
   17 W=SIGN(SQRT(W),X-XA)
      XP=X-(X-XA)*(G+W-Z)/(G-GA+W+W)
      IF((XP-XA)*GA)18,19,20
   18 GOTO(21,22),IINC
   21 IF(ABS(XP-XA)-ABS(XINC))23,23,12
   22 IF(ABS(XP-XA)-ABS(XINC-XP))23,23,24
   24 X=0.5*(XINC+XA)
      IF((X-XA)*(XINC-X))25,25,3
   25 ITEST=3
      GOTO11
   20 GOTO(12,24),IINC
   23 X=XP
      IF(ABS(XP-XA)-ABS(ABSACC))19,19,26
   26 IF(ABS(XP-XA)-ABS(XP*RELACC))19,19,3
   19 ITEST=2
      GOTO11
      END
```

```
      NOTRACE
      SUBROUTINE MCO3AS(A1,A2,B1,B2,X,SUM,N,IFLAG)
C THIS IS A FORTRAN VERSION OF THE ORIGINAL IBM-360 ASSEMBLY LANGUAGE
C ROUTINE TO CALCULATE THE SCALER PRODUCT OF TWO VECTORS.
C CALL MCO3AS(A1,A2,B1,B2,X,SUM,N,IFLAG)
C SETS SUM = SCALER PRODUCT OF (A1,A2,...) WITH (B1,B2,...) PLUS OR
C MINUS X WHERE N GIVES THE NUMBER OF TERMS IN THE PRODUCT
C THUS TO COMPUTE THE SCALER PRODUCT OF THE ITH ROW OF MATRIX A AND THE
C JTH COLUMN OF MATRIX B (BOTH N BY N) -
C       CALL MCO3AS(A(I,1),A(I,2),B(1,J),B(2,J),0,SUM,N,IFLAG)
C IFLAG IS AN INDICATOR WHICH CAN BE SET WITH A VALUE OF 0 TO 7 -
C     IFLAG          SIGN OF X          SIGN OF SCALAR PRODUCT
C     0 OR 4             +                      +
C     1 OR 5             +                      -
C     2 OR 6             +                      +
C     3 OR 7             -                      -
C NOTE THAT IN THE 360 ASSEMBLY LANGUAGE VERSION, RESULTS WOULD BE
C ROUNDED IF IFLAG HAD A VALUE OF 4 - 7 AND UNROUNDED FOR IFLAG OF 0-3.
      DIMENSION A1(1),B1(1)
      I1=LOCF(A1)
      I2=LOCF(A2)
      J1=LOCF(B1)
      J2=LOCF(B2)
      KSTA=1
      KSTB=1
      I2=I2-I1
      J2=J2-J1
      DSUM=0.0
      DO 1 I=1,N
      DSUM=DSUM+A1(KSTA)*B1(KSTB)
      KSTA=KSTA+I2
      KSTB=KSTB+J2
    1 CONTINUE
      IFL=IFLAG+1
      GO TO (10,11,12,13,10,11,12,13),IFL
   10 SUM=DSUM+X
      RETURN
   11 SUM=X-DSUM
      RETURN
   12 SUM=DSUM-X
      RETURN
   13 SUM=-(X+DSUM)
      RETURN
      END
```

```
      NOTRACE
      SUBROUTINE ANOVA(M,N,RSS,X,IPRINT)
C  GENERAL SUBROUTINE FOR TABULAR OUTPUT OF RESULTS OF REGRESSION
C  ANALYSIS.  IPRINT=1 PROVIDES TABLE OF REGRESSION ESTIMATES
C  AND ANOVA TABLE. IPRINT=0 PROVIDES ADDITIONAL TABLE OF OBSERVED
C  GENERAL SUBROUTINE REPANA.  ALSO REQUIRES VALUES IN THE COMMON
C  VECTORS XDATA,YDATA,EXPCTD,RESID,G (THE GRADIENT AT THE SOLUTION),
C  AND XJTJ (THE JACOBIAN CROSS PRODUCT MATRIX).  ARGUMENTS ARE
C  M=NO. OF DATA POINTS, N=NO. OF VARIABLES, RSS=RESIDUAL SUM OF
C  SQUARES, X=VECTOR OF PARAMETER ESTIMATES, AND PRINT AS DEFINED
C  ABOVE. CALLING PROGRAM MUST ALSO HAVE A NAMED COMMON /CANOV1/
C  TO DEFINE OUTPUT TAPE (IOUT).  T.S. BELLOWS,JR.  OCT 1970
      DIMENSION SE(3),X(N)
      COMMON XDATA(120),YDATA(120),EXPCTD(120),RESID(120),XJAC(120,3)
     +      ,P,T,WTS(120),MODEL,G(3),XJTJ(3,3),H(3,3)
      COMMON /CREP1/ PESS,NDFPE,SSTOT,CORSS,COR
      COMMON /CANOV1/IOUT
C
      CALL MB01A(XJTJ,N,3)
      DO 1 I=1,N
    1 SE(I)=RSS/FLOAT(M-N)*SQRT(XJTJ(I,I))
      WRITE(IOUT,10) (I,X(I),SE(I),G(I),I=1,N)
   10 FORMAT(1H ,/,8H RESULTS,//,11H PARAMETERS,/,1H ,10X,
     +     5HVALUE,15X,4HS.E.,16X,4HGRAD,/,1H ,63(1H-),3(/,1H ,I2,
     +            1X,3E20.10))
      N1=M-N
      N3=M-1
      N2=N-1
      F=-1.
      REGSS=CORSS-RSS
      REGMS=REGSS/FLOAT(N2)
      RMS=RSS/FLOAT(N1)
      IF(RMS.EQ.0.)GOTO4
      F=REGMS/RMS
    4 CONTINUE
      WRITE(IOUT,11)REGSS,N2,REGMS,F,RSS,N1,RMS,CORSS,N3
   11 FORMAT(1H ,/,6H ANOVA,/,1H ,2X,6HSOURCE,8X,2HSS,9X,
     +     2HDF,7X,2HMS,12X,1HF,/,1H ,55(1H-),/,11H REGRESSION,
     +            F15.9,I4,1X,F15.9,1X,F9.4,/,11H RESIDUAL  ,F15.9,I4,
     +                  1X,F15.9,/,11H TOTAL(COR),F15.9,I4)
      IF(NDFPE.EQ.0)GOTO2
      F=-1.
      SSLOF=RSS-PESS
      NLOF=N1-NDFPE
      PEMS=PESS/FLOAT(NDFPE)
      SMLOF=SSLOF/FLOAT(NLOF)
      IF(PEMS.EQ.0.)GOTO3
      F=SMLOF/PEMS
    3 CONTINUE
      WRITE(IOUT,12)SSLOF,NLOF,SMLOF,F,PESS,NDFPE,PEMS
   12 FORMAT(1H ,/,11H LACK FIT  ,F15.9,I4,1X,F15.9,1X,F9.4,
     +     /,11H PURE ERR  ,F15.9,I4,1X,F15.9)
    2 CONTINUE
      R2=REGSS/CORSS*100.
      WRITE(IOUT,13)R2
   13 FORMAT(1H ,55(1H-),//,27H PERCENT VARIANCE EXPLAINED,
     +     13H (R-SQUARED) ,F9.4)
      IF(IPRINT.EQ.1)RETURN
      WRITE(IOUT,14)(I,XDATA(I),YDATA(I),EXPCTD(I),RESID(I),WTS(I),
     +      I=1,M)
   14 FORMAT(1H ,//,1H ,9X,1HX,7X,6HY(OBS),4X,6HEXPCTD,4X,
     +     5HRESID,6X,3HWTS,/,1H ,55(1H-),100(/,1H ,I3,2X,5F10.4))
      RETURN
      END
C
      SUBROUTINE REPANA(INOUT,ISORT,M)
C  GENERAL SUBROUTINE TO FIND THE PURE ERROR SUM OF SQUARES OF A
C  SET OF DATA.  OUTPUT INCLUDES MEANS, VARIANCES, SUMS OF SQUARES,
C  AND STANDARD ERRORS OF THE DEPENDENT VARIABLE (YDATA) AT EACH
C  VALUE OF THE INDEPENDENT VARIABLE XDATA.  ARGUMENTS ARE M= NO.
C  OF DATA POINTS, INOUT=0 PROVIDES ANALYSIS AND OUTPUT OF RESULTS,
C  INOUT=1 PROVIDES ANALYSIS BUT NO OUTPUT, INOUT=2 PROVIDES OUTPUT
C  FROM A PREVIOUS CALL WITH INOUT=1 OR 0, ISORT=0 SORTS THE DATA
C  (ASCENDING) BEFORE ANALYSIS, ISORT=1 DOES NOT.  THE FIRST M
C  ELEMENTS OF COMMON VECTORS XDATA AND YDATA MUST BE SET BEFORE
C  CALLING.  REQUIRES A BLANK COMMON AS DEFINED AND A NAMED COMMON
C  /CANOV1/ TO DEFINE OUTPUT TAPE (IOUT)
C  ADDITIONALLY, ENTRY WITH INOUT=3 FINDS TOTAL SUM OF SQUARES
C  WITHOUT REPLICATE ANALYSIS.
C  T.S. BELLOWS,JR.  OCT 1978.
      DIMENSION XS(120),YAVE(120),YSS(120),NS(120),YSE(120)
     +         ,NDF(120),VAR(120)
      COMMON XDATA(120),YDATA(120),EXPCTD(120),RESID(120),XJAC(120,3)
     +      ,P,T,WTS(120),MODEL,G(3),XJTJ(3,3),H(3,3)
      COMMON /CREP1/ PESS,NDFPE,SSTOT,CORSS,COR
      COMMON /CANOV1/IOUT
C
      IF(M.EQ.1)RETURN
      IF(INOUT.EQ.2)GOTO11
C
      YAVE(1)=0.
      YSS(1)=0.
      SSTOT=YDATA(1)*YDATA(1)
      COR=YDATA(1)
      DO 10 I=2,M
      YAVE(I)=0.
      YSS(I)=0.
      SSTOT=SSTOT+YDATA(I)*YDATA(I)
   10 COR=COR+YDATA(I)
C
      IF(ISORT.EQ.1)GOTO20
      DO 1 I=2,M
      DO 1 J=I,M
      IF(XDATA(I-1).LE.XDATA(J))GOTO1
      C=XDATA(I-1)
      XDATA(I-1)=XDATA(J)
      XDATA(J)=C
      C=YDATA(I-1)
      YDATA(I-1)=YDATA(J)
      YDATA(J)=C
      C=WTS(I-1)
      WTS(I-1)=WTS(I)
      WTS(I)=C
    1 CONTINUE
C
   20 PESS=0.
      NDFPE=0
      COR=COR*COR/FLOAT(M)
      CORSS=SSTOT-COR
      IF(INOUT.EQ.3)RETURN
      IS=1
      I=1
      ICHECK=0
    9 CNS=1.
      XS(IS)=XDATA(I)
    6 YAVE(IS)=YAVE(IS)+YDATA(I)
      YSS(IS)=YSS(IS)+YDATA(I)*YDATA(I)
      IF(I.EQ.M)GOTO5
```

```
      I=I+1
      IF(XDATA(I).NE.XDATA(I-1))GOTO5
      CNS=CNS+1.
      GOTO6
    5 IF(CNS.EQ.1.)GOTO7
      YSS(IS)=YSS(IS)-YAVE(IS)*YAVE(IS)/CNS
      VAR(IS)=YSS(IS)/(CNS-1.)
      YSE(IS)=SQRT(VAR(IS)/CNS)
      YAVE(IS)=YAVE(IS)/CNS
      NS(IS)=CNS
      NDF(IS)=CNS-1.
      GOTO8
    7 YSS(IS)=0.
      VAR(IS)=0.
      YSE(IS)=0.
      NS(IS)=1
      NDF(IS)=0
    8 PESS=PESS+YSS(IS)
      NDFPE=NDFPE+NDF(IS)
      IF(I.LT.M)GOTO13
      IF(I.EQ.M.AND.XDATA(I).EQ.XDATA(I-1))GOTO11
      IF(ICHECK.EQ.1)GOTO11
      ICHECK=1
   13 IS=IS+1
      GOTO9
C
   11 IF(INOUT.EQ.1)RETURN
      WRITE(IOUT,17)
      WRITE(IOUT,18)(XS(I),YAVE(I),YSS(I),VAR(I),YSE(I),NS(I),NDF(I),
     +          I=1,IS)
      YMS=0.
      IF(NDFPE.EQ.0)GOTO12
      YMS=PESS/FLOAT(NDFPE)
   12 WRITE(IOUT,19)PESS,M,NDFPE,YMS
      RETURN
   17 FORMAT(1H ,//,1H ,18HREPLICATE ANALYSIS,//,1H ,18(1H-),//
     +      ,1H ,6X,1HX,9X,5HAVE Y,7X,5HSS(Y),6X,6HVAR(Y),7X,5HSE(Y),
     +            7X,1HN,3X,2HDF,/,1H ,70(1H-))
   18 FORMAT(1H ,5F12.5,2I5)
   19 FORMAT(1H ,70(1H-),//,1H ,6HTOTALS,18X,F12.5,24X,2I5,//,
     +     1H ,24HPURE ERROR MEAN SQUARE  ,F12.5,//)
      END
C
      SUBROUTINE CHCKF(M,N,X,R,RSS,FSUB)
C  GENERAL. DESIGNED FOR USE WITH LEAST SQUARES FITTING ROUTINES.
C  CALLS THE SUBROUTINE FSUB WHICH SHOULD DEFINE RESIDUALS IN COMMON
C  VECTOR RESID. RETURNS RESIDUAL SUM OF SQUARES IN RSS.
      DIMENSION X(N),R(M)
      COMMON XDATA(120),YDATA(120),EXPCTD(120),RESID(120),XJAC(120,3)
     +      ,P,T,WTS(120),MODEL,G(3),XJTJ(3,3),H(3,3)
      EXTERNAL FSUB
      CALL FSUB(M,N,X,R)
      S=0.
      DO 10 I=1,M
   10 S=S+RESID(I)*RESID(I)
      RSS=S
      RETURN
      END
C
      SUBROUTINE CHCKG(M,N,X,R,GSUB)
C  GENERAL. DESIGNED FOR USE WITH LEAST SQUARES FITTING ROUTINES.
C  CALLS THE SUBROUTINE GSUB WHICH SHOULD DEFINE THE JACOBIAN
C  MATRIX IN THE COMMON MATRIX XJAC.
      DIMENSION X(N),R(M)
      EXTERNAL GSUB
      CALL GSUB(M,N,X,R)
      RETURN
      END
C
C
      SUBROUTINE MONIT(M,N,X,R,RSS,NC)
C  GENERAL. OUTPUT SUBRTNE USED BY NAG FITTING
C  ROUTINE E04FBF.
      DIMENSION X(N),R(M)
      WRITE(6,1)NC,RSS
      WRITE(6,2)(X(I),I=1,N)
    1 FORMAT(1H ,/,1H ,I5,E20.8)
    2 FORMAT(1H ,3E15.7)
      RETURN
      END
C
      SUBROUTINE PLOT1(X,Y,NS,IXSIZS,IYSIZS,IXCODS,XMAXS,XMINS,IYCODS,
     +YMAXS,YMINS,ICLEAR,ISYMBS,SYMBLS,IRANGE,IPRINT,ITITLE,XTITLE,
     +YTITLE)
C  GENERAL PLOT ROUTINE.  OPTIONS AND PARAMETERS DESCRIBED BELOW.
C  X= VECTOR SIZE N WITH X VALUES
C  Y= VECTOR SIZE N WITH Y VALUES.
C  N= NUMBER OF POINTS
C  IXSIZE= WIDTH OF PLOT IN SPACES. DEFAULT WHEN =0 IS 120.
C  IYSIZE= HIGHT OF PLOT IN LINES. DEFAULT WHEN =0 IS 70
C  IXCODE= FLAG FOR DECISION ON MAX AND MIN VALUES FOR ABSCISSA-
C     =0 FOR USE MIN AND MAX VALUES OF X-VECTOR
C     =1 FOR FIND MIN OF X-VECTOR, USE PASSED ARGUMENT FOR XMAX
C     =2 FOR FIND MAX OF X-VECTOR, USE ARGUMENT PASSED FOR XMIN
C     =3 FOR USE PASSED ARGUMENTS FOR XMIN AND XMAX
C  XMAX=MAX VALUE OF X-AXIS. WILL BE DEFINED OR MAY BE SENT( SEE IXCODE)
C  XMIN= MIN VALUE FOR X-AXIS ,AS FOR XMAX.
C  IYCODE =AS ABOVE FOR IXCODE
C  YMAX,YMIN = AS ABOVE FOR Y-AXIS
C  ICLEAR= SET TO 0 WILL CLEAR PLOT BEFORE USE, SET TO 1 WILL NOT CLEAR
C     PLOT. SHOULD BE SET TO 0 ON FIRST CALL.
C  ISYMBL= NUMBER OF SYMBOL IN VECTOR "SYMBLE" TO BE USED FOR PLOTTING.
C     MAY BE SET TO 1-10 FOR ROUTINE DEFINED SYMBOLS. SET TO 11 FOR USER
C     DEFINED SUMBOL IN PARAMETER "SYMBOL". SET TO 0 ON FIRST CALL USES
C     ROUTINE CHOSEN SYMBOLS IN ORDER ON SUBSEQUENT CALLS PROVIDED
C     RETURNED VALUE OF ISYMBL IS NOT CHANGED.
C  SYMBOL= ON ENTRY MAY BE SET TO USER DESIRED SUMBOL (REAL,A1) FOR
C     PLOTTING. RETURNS PLOTTED SYMBOL.
C  IRANGE= KEY FOR HANDLING OUT OF RANGE POINTS. POINTS WILL BE HANDLED
C     ACCORDING TO -
C     0=POINTS OUT OF RANGE NOT PLOTTED, BUT WARNING IS WRITTEN
C     1=POINTS WILL BE PLOTTED AT EDGE OF PLOT, NO WARNING
C     2= POINTS IGNORED
C     THIS PARAMETER IS NOT USED IF IXCODE AND IYCODE =0
C  IPRINT=0 FOR PLOT TO BE PRINTED.=1 FOR PLOT NOT PRINTED.
C  ITITLE=0 FOR NO AXIS TITLES.=1 OTHERWISE(USER MIST SUPPLY TITLES
C     FOR BOTH AXES IF ITITLE=1)
C  XTITLE=A8 TITLE FOR X AXIS, IGNORED IF ITITLE =0
C  YTITLE=A8 TITLE FOR Y AXIS, IGNORED IF ITITLE=0
C     IF TITLES ARE PRINTED, PLOT REQUIES ADDITIONAL 2 LINES ON PAGE.
C
C  T BELLOWS,JR.  AUG 77
C
      DIMENSION X(NS),Y(NS)
      DIMENSION PLOT(71,121),SYMBLE(11),XSCALE(14),YSCALE(8),SPACE(16)
      DATA SYMBLE/"0","1","2","3","4","5","6","7","8","9","*"/
      DATA SPACE/16*"    "/,BLANK/" "/,XLINE/"I"/,DASH/"-"/,PLUS/"+"/
      DATA TTLBLK/"        "/,TTLLNE/"————————"/,BLNK10/"          "/
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```
      DATA IOUT/6/
      COMMON /CPLOT1/ IOUT
C
      N=NS
      IXCODE=IXCODS
      XMAX=XMAXS
      XMIN=XMINS
      IYCODE=IYCODS
      YMAX=YMAXS
      YMIN=YMINS
      ISYMBL=ISYMBS
      SYMBOL=SYMBLS
      IXSIZE=IXSIZS
      IYSIZE=IYSIZS
C
C  FIX SIZE
      IXSIZE=FLOAT(IXSIZE)/10.+.5
      IXSIZE=IXSIZE*10
      IF(IXSIZE.GT.120.OR.IXSIZE.LE.0) IXSIZE=120
      IYSIZE=FLOAT(IYSIZE)/10.+.5
      IYSIZE=IYSIZE*10
      IF(IYSIZE.GT.70.OR.IYSIZE.LE.0) IYSIZE=70
      IXSZE1=IXSIZE+1
      IYSZE1=IYSIZE+1
      RXSIZE=IXSIZE
      RYSIZE=IYSIZE
C
C  CLEAR MATRIX PLOT
      IF(ICLEAR.NE.0) GOTO10
      DO 11 I=2,IXSZE1
      PLOT(1,I)=DASH
      DO 11 J=2,IYSZE1
   11 PLOT(J,I)=BLANK
      DO 12 J=1,IYSZE1
   12 PLOT(J,1)=XLINE
      PLOT(1,1)=PLUS
      DO 13 I=11,IXSZE1,10
   13 PLOT(1,I)=PLUS
      DO 14 J=11,IYSZE1,10
   14 PLOT(J,1)=PLUS
C
C  FIND SYMBOL
   10 IF(ISYMBL.EQ.0) ISYMBL=1
      IF(ICLEAR.NE.0.AND.ISYMBL.LE.9) ISYMBL=ISYMBL+1
      IF(ICLEAR.NE.0.AND.ISYMBL.EQ.10) ISYMBL=1
      IF(ISYMBL.EQ.1) SYMBLE(11)=SYMBOL
      SYMBOL=SYMBLE(ISYMBL)
C
C  FIX XMAX,XMIN
      IPLTLP=-1
      IF(IXCODE.EQ.3) GOTO20
      IPLTLP=0
      IF(IXCODE.EQ.2) XSAVE=XMIN
      IF(IXCODE.EQ.1) XSAVE=XMAX
      XMAX=X(1)
      XMIN=XMAX
      DO 21 I=2,N
      IF(XMAX.LT.X(I)) XMAX=X(I)
   21 IF(XMIN.GT.X(I)) XMIN=X(I)
      IF(IXCODE.EQ.1) XMAX=XSAVE
      IF(IXCODE.EQ.2) XMIN=XSAVE
C
C  FIX YMAX,YMIN
   20 IF(IYCODE.EQ.3) GOTO30
      IPLTLP=IPLTLP+1
      IF(IYCODE.EQ.1) YSAVE=YMAX
      IF(IYCODE.EQ.2) YSAVE=YMIN
      YMAX=Y(1)
      YMIN=YMAX
      DO 31 I=2,N
      IF(YMAX.LT.Y(I)) YMAX=Y(I)
   31 IF(YMIN.GT.Y(I)) YMIN=Y(I)
      IF(IYCODE.EQ.1) YMAX=YSAVE
      IF(IYCODE.EQ.2) YMIN=YSAVE
C
C  INSERT POINTS
   30 XSPRED=XMAX-XMIN
      IF(XSPRED) 101,101,32
   32 YSPRED=YMAX-YMIN
      IF(YSPRED) 101,101,33
   33 IPLTLP=IPLTLP-IXCODE-IYCODE
      IF(IPLTLP.EQ.1) GOTO70
      IF(IRANGE-1) 40,50,60
C
C  WRITE WARNINGS BUT DONT PLOT POINTS OUT OF RANGE
   40 IPNTCN=0
      WRITE(IOUT,43)
   43 FORMAT(1H ,19HPOINTS OUT OF RANGE)
      DO 41 K=1,N
      XN=X(K)
      YN=Y(K)
      IF(XN.GT.XMAX.OR.XN.LT.XMIN) GOTO42
      IF(YN.GT.YMAX.OR.YN.LT.YMIN) GOTO42
      I=(XN-XMIN)/XSPRED*RXSIZE+1.5
      J=(YN-YMIN)/YSPRED*RYSIZE+1.5
      PLOT(J,I)=SYMBOL
      GOTO41
   42 WRITE(IOUT,44) K,XN,YN
   44 FORMAT(1H ,I5,3X,3HX= ,E14.6,4H Y= ,E14.6)
      IPNTCN=1
   41 CONTINUE
      IF(IPNTCN.EQ.1) GOTO80
      WRITE(IOUT,46)
   46 FORMAT(10H       NONE)
      GOTO80
C
C  PLOT OUT OF RANGE POINTS AT EDGE OF PLOT,NO WARNING
   50 DO 51 K=1,N
      I=(X(K)-XMIN)/XSPRED*RXSIZE+1.5
      IF(I.GT.IXSZE1) I=IXSZE1
      IF(I.LT.1) I=1
      J=(Y(K)-YMIN)/YSPRED*RYSIZE+1.5
      IF(J.GT.IYSZE1) J=IYSZE1
      IF(J.LT.1) J=1
   51 PLOT(J,I)=SYMBOL
      GOTO80
C
C  IGNORE OUT OF RANGE POINTS
   60 DO 61 K=1,N
      I=(X(K)-XMIN)/XSPRED*RXSIZE+1.5
      IF(I.GT.IXSZE1.OR.I.LT.1) GOTO61
      J=(Y(K)-YMIN)/YSPRED*RYSIZE+1.5
      IF(J.GT.IYSZE1.OR.J.LT.1) GOTO61
      PLOT(J,I)=SYMBOL
   61 CONTINUE
      GOTO80
C
C  MAXIMUM EFFICIENCY LOOP IF ROUTINE FOUND MAX-MIN VALUES FOR BOTH AXES
```

```
   70 DO 71 K=1,N
      I=(X(K)-XMIN)/XSPRED*RXSIZE+1.5
      J=(Y(K)-YMIN)/YSPRED*RYSIZE+1.5
   71 PLOT(J,I)=SYMBOL
C
C  CHECK FOR PLOT TO BE PRINTED
   80 IF(IPRINT.NE.0)GOTO100
C
C  FIX SCALE PRINT VECTORS
      IXS=IXSIZE/10+1
      IYS=IYSIZE/10+1
      XS=IXS-1
      YS=IYS-1
      XSPACE=XSPRED/XS
      YSPACE=YSPRED/YS
      DO 81 I=1,IXS
      XI=I-1
   81 XSCALE(I)=XI*XSPACE+XMIN
      DO 82 I=1,IYS
      YI=I-1
   82 YSCALE(I)=YI*YSPACE+YMIN
C
C  CHECK FOR TITLES
      UNORLN=TTLLNE
      IF(ITITLE.NE.0)GOTO90
      YTITLE=TTLBLK
      UNORLN=TTLBLK
   90 WRITE(IOUT,92)YSCALE(IYS),(PLOT(IYSIZE1,J),J=1,IXSIZE1)
   92 FORMAT(" ",E10.3,121A1)
      WRITE(IOUT,93)YTITLE,(PLOT(IYSIZE1-1,J),J=1,IXSIZE1)
   93 FORMAT(" ",A8,2X,121A1)
      WRITE(IOUT,93)UNORLN,(PLOT(IYSIZE1-2,J),J=1,IXSIZE1)
      DO 91 K=1,7
      KK=IYSIZE1-K-2
   91 WRITE(IOUT,94) (PLOT(KK,J),J=1,IXSIZE1)
   94 FORMAT(" ",10X,121A1)
      IF(IYSIZE1.EQ.11)GOTO100
      K=IYS-2
      DO 95 K=1,IYS
      KK=IYS-K+1
      K10=KK*10+1
      KKYSC=KK+1
      WRITE(IOUT,92)YSCALE(KKYSC),(PLOT(K10,J),J=1,IXSIZE1)
      DO 96 KKK=1,9
      KKJ=K10-KKK
   96 WRITE(IOUT,94) (PLOT(KKJ,J),J=1,IXSIZE1)
   95 CONTINUE
  100 WRITE(IOUT,92)YSCALE(1),(PLOT(1,J),J=1,IXSIZE1)
      WRITE(IOUT,98) (XSCALE(J),J=1,IXS)
   98 FORMAT(" ",6X,13E10.3)
      IF(ITITLE.EQ.0)RETURN
      K=IXSIZE/10-1
      WRITE(IOUT,97) (BLNK10,I=1,K),XTITLE
      WRITE(IOUT,97) (BLNK10,I=1,K),UNORLN
   97 FORMAT(" ",12A10)
  180 ISYMBS=ISYMBL
      SYMBLS=SYMBOL
      RETURN
  101 WRITE(IOUT,102)
  102  FORMAT(1H ,18HNO SPREAD TO DATA.)
      GOTO180
      END
C
```

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