THE DESCRIPTIVE PROPERTIES OF SOME MODELS FOR DENSITY DEPENDENCE

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SUMMARY

(1) The descriptive abilities of several difference equation models for density dependence have been examined, first by a qualitative comparison of their flexibility and secondly by considering their ability to describe thirty sets of data on density dependent mortality.

(2) The qualitative comparison demonstrated that two of the models have forms which are particularly flexible. The quantitative comparison indicated that of these two, that due to Maynard Smith & Slatkin (1973) is better able to describe a wide range of data.

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 dynamical behaviour of such populations (May, Conway, Hassell & Southwood 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 and 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 a means of quantifying density dependence (e.g. Ullyet 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 similar ranges of dynamical behaviour, they differ widely in their ability to describe different types of density dependence. This paper examines some of the different density dependent models in the literature and compares 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 and (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 comparison begins with a consideration of different methods of graphical presentation of density dependence in data. This is

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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 are 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 effects of density dependence in single-species populations are re-examined 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.

PRESENTING DENSITY DEPENDENCE DATA

A variety of methods of graphically presenting density dependence data have appeared in the literature and a primary aim common to them all is to demonstrate whether or not the 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 dependent mortality.

The most immediate method of presenting density dependence data is to plot the number of survivors S against the initial density 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, Figs 1(a) and 7(a)) or a humped curve

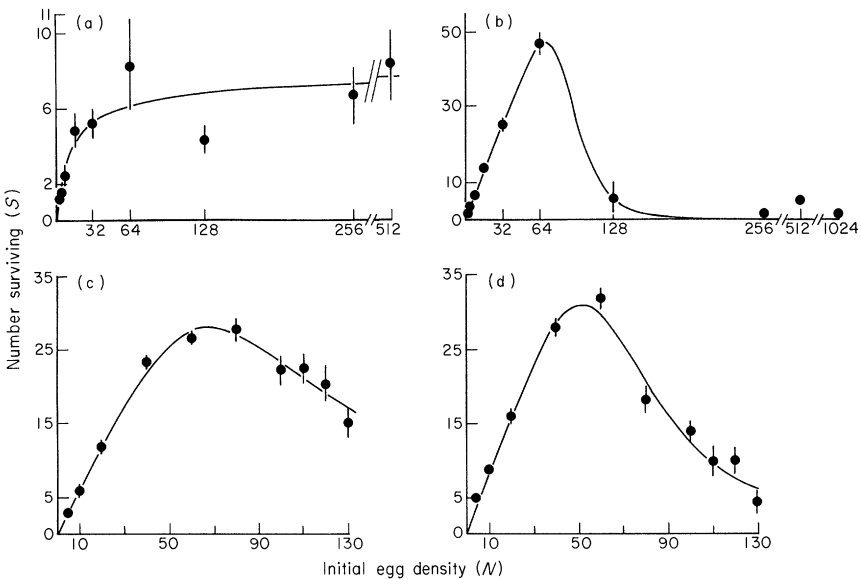FIG. 1. The relationship between number of survivors (mean ± s.e.) and density for four stored product beetles. The fitted curves are from entry 5 of Table 1, $S = dN/(1 + (aN)^b)$. (a) *Stegobium paneceum, d = 0·711, a = 0·110, b = 0·950.* (b) *Lasioderma serricorne, d = 0·806, a = 0·0114, b = 7·53.* (c) *Tribolium confusum, d = 0·610, a = 0·0116, b = 3·12.* (d) *Tribolium castaneum, d = 0·800, a = 0·0149, b = 4·21.*
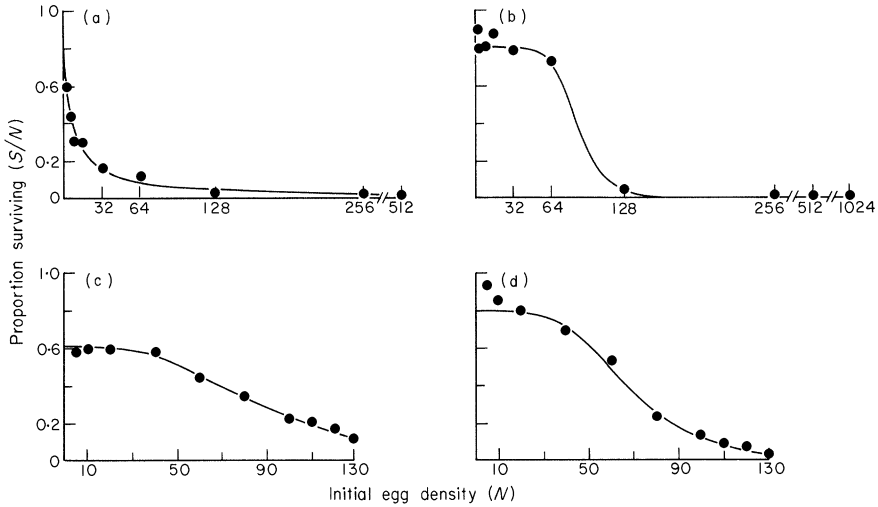
FIG. 2. The data of Fig. 1 expressed as proportion surviving (transformation on the means) against density. Fitted lines were obtained by transforming the predicted number of survivors to proportionate survival. (a) *Stegobium paneceum*. (b) *Lasioderma serricorne*. (c) *Tribolium confusum*. (d) *Tribolium castaneum*.

(scramble competition, Figs 1(b), (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 N (Figs 2(b), (c)). Here there is a region of low density where proportionate survival is nearly constant at some density independent level, after which proportionate survival

FIG. 3. The data of Fig. 1 expressed as k-value (transformation on the means) against log 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) *Tribolium 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 Fig. 1(b).)
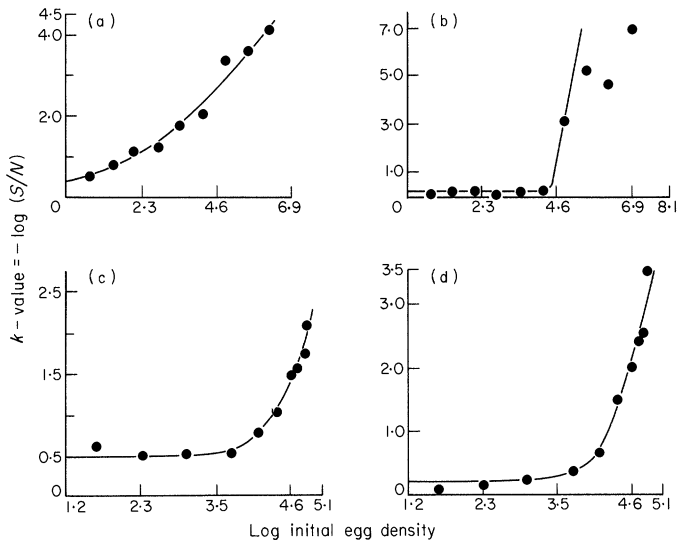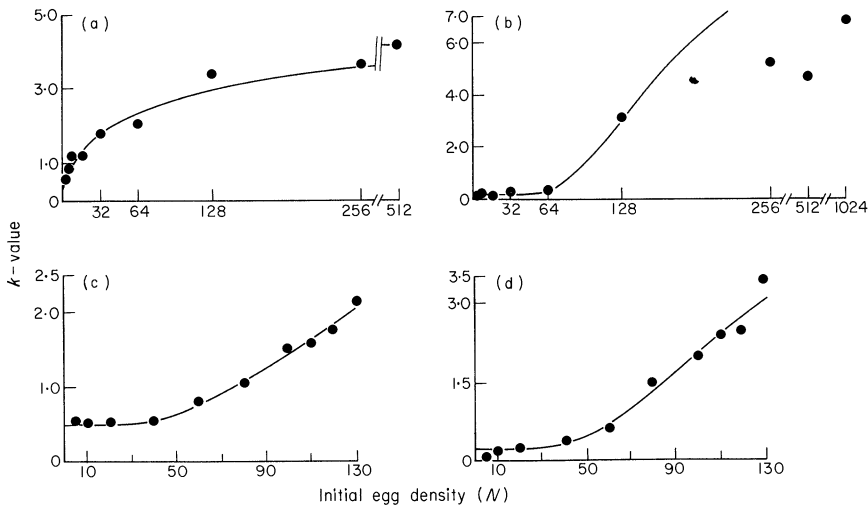
FIG. 4. The data of Fig. 1 expressed as k-value against density. Fitted lines were obtained by transforming the predicted number of survivors to k-value. (a) *Stegobium paneceum*. (b) *Lasioderma serricorne*. (c) *Tribolium confusum*. (d) *Tribolium castaneum*. (N.B. See note in legend of Fig. 3.)

drops sharply. The density at which survival suddenly decreases has been termed the 'critical density' by Hassell (1975). Proportionate survival may also decrease monotonically with density (Figs 2(a) and 5(a)). In a plot of proportionate survival against density, deviation from a line with zero slope indicates density dependence, but there is no simple interpretation of these plots which distinguishes between contest and scramble competition. Two further methods of presenting density dependence data are based on plotting proportionate survival on logarithmic scales (the k-value of Haldane (1949) and Varley & Gradwell (1960)). When k-value ($= -\log(S/N)$, where log indicates natural logarithms) is plotted against log 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 (Figs 3 and 5(b)). 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 (Figs 4(a) and 5(c)) or exponentially (Figs 4(b), (c), (d)) increasing 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.

DENSITY DEPENDENCE IN MODELS

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

$$S = Nf(N) \tag{1}$$
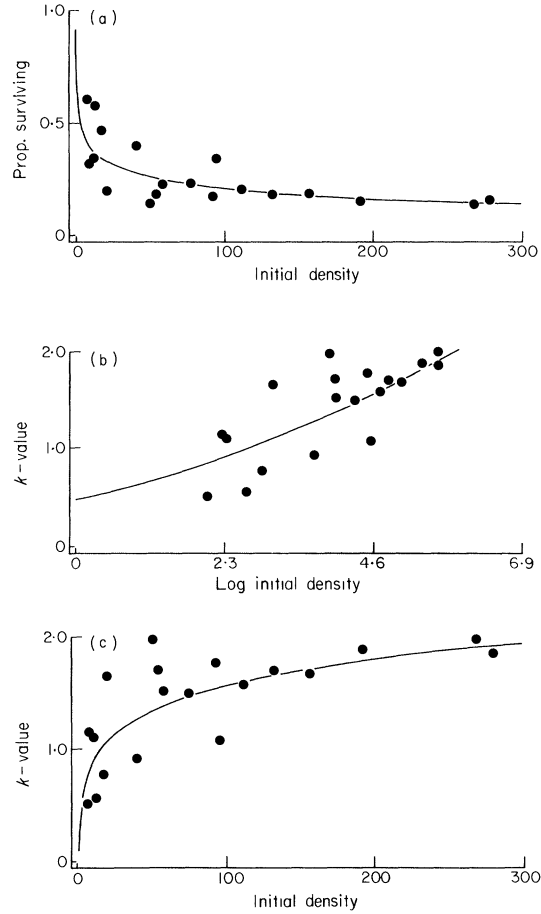
FIG. 5. The plots of (a) proportionate survival against density, (b) k-value against log density and (c) k-value against density for *Operophtera brumata* (L.) (data from Varley & Gradwell 1968). The fitted curves were obtained by transforming the predicted number of survivors (see Fig. 7(a)) to these measures of mortality.

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.

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

$$\frac{dN}{dt} = -N\mu(N) \qquad (2)$$

where N is the population size and $\mu(N)$ is a function relating mortality rate to density. A homologous discrete time formulation of eqn (2) may be constructed by integrating at a fixed density, say N_o, to give

$$N_t = N_o \exp(-\mu(N_o)t). \qquad (3)$$

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, eqn (3) may be written in the form of eqn (1),

$$S = N \exp(-\mu(N)), \qquad (4)$$

where $S = N_t$, $N = N_o$ and $f(N) = \exp(-\mu(N))$. Isolating the mortality rate ($\mu(N)$) from eqn (4) gives

$$\mu(N) = \log(N/S), \qquad (5)$$

which is the familiar k-value for mortality of Haldane (1949) and Varley & Gradwell (1960).

A variety of models have been proposed in the literature with $\mu(N)$ taking the different forms shown in Table 1. Only entry 4 has not been previously considered, although a homologous differential equation has been discussed by Goel, Maitra & Montroll (1971). Entry 4 arises when the following general relationship between mortality rate and density is postulated:

$$\mu(N) = c + aN^b; \, a, b > 0, c \geqslant 0. \qquad (6)$$

Substituting eqn (6) into eqn (4) now gives the model

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

or

$$S = dN \exp(-aN^b), \, d = \exp(-c). \qquad (7)$$

The parameters in eqn (7) are restricted such that $0 \leqslant d \leqslant 1$ and $a, b > 0$. The function $f(N)$ is now given by $f(N) = d \exp(-aN^b)$.

Although eqn (7) has three parameters, the parameter d only determines the level of density independent mortality. The density dependent form of the curve is solely 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, while the parameter b determines the severity of the density dependence. Thus, increasing values of b imply movement along the continuum of contest-scramble competition towards more severe scramble. The precise relationship between these parameters and the type of competition implied is more easily discussed for the related model (see below) of entry 5 in Table 1. In this model the roles of the parameters a and b are the same as in eqn (7) but, in addition, a plot of k-value against log density is linear at high densities and reaches an asymptotic slope of b, thus providing a readily interpretable relationship between this parameter and the type of competition implied (Varley, Gradwell & Hassell 1973; Hassell 1975, 1976). This relationship is more complex for eqn (7) as discussed more fully below.

Figure 6 shows how changes in the parameters a and b in model 5 of Table 1 affect the shape of the plot of survivors against density and the plots of k-value against density and log density. When $b = 1$ (curves I) the number of survivors increases monotonically with density to an asymptotic maximum of $1/a$ (Fig. 6(a)), k-value increases logarithmically with density (Fig. 6(b)) and k-value increases exponentially with log density reaching an asymptotic slope of $b = 1$ (Fig. 6(c)), all of which imply contest competition. For values of $b \gg 1$ (curves II and III), scramble competition is implied with mortality overcompensating at high densities, resulting in few survivors (Fig. 6(a)). The plot of k-value against density now shows an initial exponential increase which changes to a

logarithmic increase at high densities (Fig. 6(b)), and the plot of k-value against log density increases exponentially, again reaching an asymptotic slope of b. Varying the parameter a effectively changes the scale of density on which the mortality acts (compare curves II and III); 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 50% mortality when the initial density is $1/a$.

Similar interpretations can be made for eqn (7) concerning the effect of the parameters a and b. Thus contest competition is indicated by values of $b \simeq 1$ and scramble competition by values $b \gg 1$. However, the slope of a plot of k-value against log density for this model increases without bound as density increases, and consequently the distinction between contest and scramble is not as sharply defined as in the model discussed above. Even for values of $b < 1$, sufficiently high values of N (density) in eqn (7) can cause a reduction in the number of survivors, a phenomenon usually associated with scramble competition.

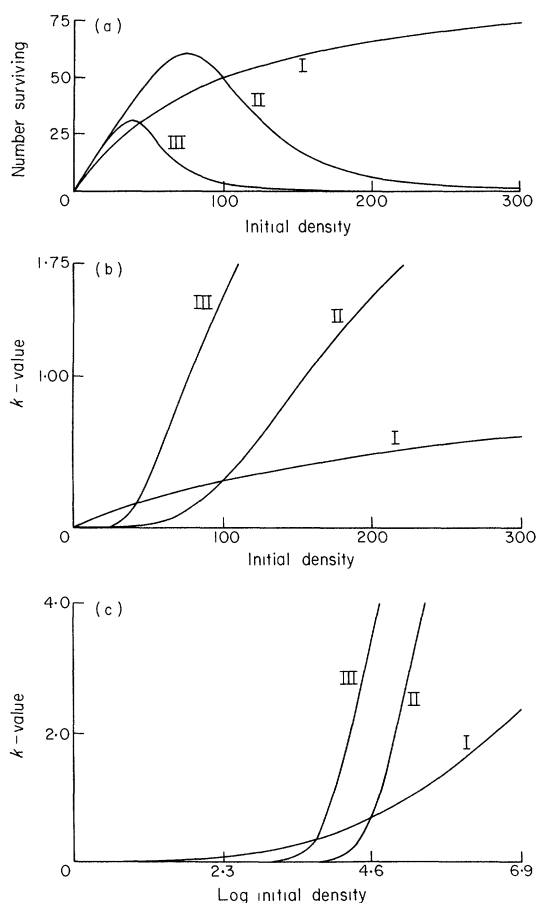FIG. 6. The effects of the parameters a and b in the density dependent model entry 5 of Table 1. Curves I ($a = 0.01$, $b = 1$) indicate contest competition and curves II and III ($b = 5$) indicate scramble competition. In curve II, $a = 0.01$ so that density dependent mortality is 50% at $N = 1/a = 100$. In curve III, $a = 0.02$ and density-dependent mortality is 50% at $N = 50$. See text for further discussion.

In order to more fully understand the descriptive abilities of the models in Table 1 it is useful to relate them to each other via eqn (1). Thus entry 4 (eqn 7) may 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 of Table 1 are less clearly related to the general model of entry 4. Entry 1 is a linear model on logarithmic scales of density and proportionate survival and arises from the linear k-value analysis for density dependence of Varley & Gradwell (1963). In order to overcome some of the restrictions of this particular model, Hassell (1975) introduced entry 6. Entry 7 has been used to describe symmetric sigmoid curves of proportionate survival against density (e.g. Ullyett 1950; Pennycuik, Compton & Beckingham 1968).

A QUALITATIVE COMPARISON OF THE MODELS

To evaluate the general descriptive abilities of these models one should consider the different types of density dependent curves that they can 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 (Figs 2(a) and 5(a)) or as a non-symmetric sigmoid curve (Figs 2(b), (c)). A simple mathematical way to express the difference between these two types of curves is to consider the second derivative of (S/N) with respect to N (i.e. $d^2(S/N)/dN^2$). 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. Thus, a general model for density dependence would have a form such that $d^2f(N)/dN^2$ could either be positive for all values of N or could change from negative to positive as N increased. Table 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

TABLE 1. Some density dependent functions $f(N)$ (eqn (1)) and their related functions, $\mu(N)$ (eqn 5), and their second derivatives. A more complete list of references concerning each model is given by May & Oster (1976)

Entry	$f(N)$	$\mu(N) = k$-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	MacFadyen (1963); Cook (1965); May *et al.* (1974); May (1975, 1976)
3	$(1 + aN)^{-1}$	$\ln(1 + aN)$	$+$	$-$	Skellam (1951); Pielou (1969)
4	$\exp(-aN^b)$	aN^b	$+ -$	$+ -$	This paper
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	$(1 + \exp(bN - a))^{-1}$	$\ln(1 + \exp(bN - a))$	$+ -$	$+$	Ullyett (1950); Pennycuik, Compton & Beckingham (1968); Usher (1972)

this derivative is always positive, and consequently can only describe monotonically decreasing curves of proportionate survival against density. 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 curves that increase both logarithmically (Figs 4(a) and 5(c)) and exponentially (Figs 4(b), (c), (d)). Expressed mathematically, the second derivative $d^2\mu/dN^2$ may be either negative or positive. Table 1 also gives the potential signs of these derivatives. Only 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 entry 7 describes only exponential increase for $\mu(N)$.

A QUANTITATIVE COMPARISON OF THE MODELS

The discussion above indicates that two of the models in Table 1 (entries 4 and 5) have forms which are particularly flexible, being able to describe a wide range of forms of density dependence. Differences in the descriptive ability of the various models may be further clarified 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 carried out as part of this study.

The data may be divided into two categories. The first set of data (Table 2) arises from experiments in which varying numbers of individuals, usually in an early developmental stage such as eggs or larvae, have been confined with a fixed amount of food, and at some later stage or time the survivors scored. The experiments conducted here on *Stegobium paneceum* L., *Lasioderma serricorne* (F.), *Tribolium castaneum* (Herbst.) and *Tribolium confusum* Duval are typical examples. Eggs were collected by sieving flour from oviposition chambers at 24-h intervals. Varying numbers of 0–24-h-old eggs

TABLE 2. Some experimental laboratory studies on the effect of density on survival in insects

Species	Author(s)
Coleoptera	
1. *Lasioderma serricorne* (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 kuhniella* Zell.	Ullyett & van der Merwe (1947)
8. *Plodia interpunctella* Hubn.	Snyman (1949)
9. *Sitotroga cerealella* (Oliv.)	Crombie (1944)
Diptera	
10. *Chrysomyia albiceps* Wied.	Ullyett (1950)
11. *Chrysomyia chloropyga* Wied.	Ullyett (1950)
12. *Drosophila melanogaster* Mg.	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 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 model 5 of Table 1 to the data. Numbers correspond to the numbered points in Fig. 9

Species	λ	$d\lambda$	b	Author(s)
Hemiptera				
1. *Anthocorus confusus* (Reuter)	1·6	1·0	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. *Saccharosydne saccharivora* (Ww.)	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 aQ	37·5	29·5	1·6	Fujii (1967)
8. *Leptinotarsa decemlineata* (Say)	75·0	75·0	4·8	Harcourt (1971)
Lepidoptera				
9. *Acleris variana* (Fern.)	13·0	3·5	2·7	Morris (1959)
10. *Anagasta kuhniella* (Zell.)	8·6	1·1	2·4	Hassell & Huffaker (1969)
11. *Erannis defoliaria* (Clerk)	3·0	1·8	2·0	Ekanayake (1967)
12. *Hyphantria cunea* Drury	1·7	1·7	1·3	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)

were then isolated in glass tubes (2·2 × 7 cm) with 0·5 g medium (commercial fine white flour with added yeast, 10% by weight) and the glass tubes closed with cotton wool and kept at either 28·5 °C, 70% relative humidity (*Stegobium paneceum* and *Lasioderma serricorne*) or 30 °C, 70% relative humidity (*Tribolium* species). After the adults eclosed, the total number of survivors in each tube were scored. The second set of data (Table 3) was compiled from long-term censuses of insect populations and is abbreviated from a similar list given by Hassell, Lawton & May (1976). The examples come both from field studies and studies of populations maintained in the laboratory and include only those cases which demonstrated density dependence when analysed by the method discussed below.

The two parameter models of Table 1 (entries 4, 5, 6 and 7) have been fitted to these data. The models were used in the form of eqn (1) with the addition of a parameter for density independent mortality, d, so that

$$S = dNf(N). \tag{8}$$

As before, d is constrained such that $0 \leqslant d \leqslant 1$. 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 present. These models are intrinsically non-linear as they cannot be manipulated into forms which are linear in the parameters. Indeed, even the one-parameter models in Table 1 may be considered intrinsically non-linear as they may not be transformed to linear forms without the use of ratios such as S/N or N/S. These ratios may be subject to considerable biases, particularly when the initial density is estimated from data (Atchley, Gaskins & Anderson 1976). Consequently, the fitting procedure involved minimizing a residual sum of squares of a non-linear model, and the descent method of Fletcher & Powell (1963) was used. This iterative method gave rapid

convergence and appeared generally robust when applied to all the models except model 6, where it was subject to rounding errors. To overcome this problem the conjugant gradient method of Powell (1964) for minimizing a general function was used with model 6 to find the minimum residual sum of squares. In all cases, the fitting was by unweighted least squares so that each observation was treated equally. A copy of the computer programme used is available on request.

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 set of data. In linear regression analysis this is usually done by considering the parameter r^2,

$$r^2 = 100 \left(1 - \frac{\text{residual sum of squares}}{\text{sum of squares about the mean}}\right). \tag{9}$$

The sum of squares in the denominator of the fraction in eqn (9) 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:

$$H_0 : Y = \bar{Y}. \tag{10}$$

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

$$H_0 : S = pN. \tag{11}$$

Consequently, an appropriate measure of the percent variance explained by the various density dependent models is

$$r' = 100 \left(1 - \frac{\text{residual sum of squares}}{\text{sum of squares about the line } pN}\right). \tag{12}$$

The sum of squares in the denominator of the fraction in eqn (12) is the residual sum of squares from a straight line through the origin fitted to the data, and the numerator is the residual sum of squares obtained by fitting a density dependent model to the data. The values for percent variances explained shown in Tables 4 and 5 have been computed in this way.

The definition of the null hypothesis in eqn (11) provides a method for determining whether or not a particular data set demonstrates density dependence (Fig. 7). The null hypothesis model, $S = pN$, may be fitted to the data and the residuals plotted against the densities at which they occur. If the plot of residuals shows no systematic pattern (Fig. 7(d)), 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 (Fig. 7(b)), 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 3.

The values of percent variance explained given in Tables 4 and 5 shows that all four models usually explained a similar amount of variance; for some data sets there was practically no distinction between some of the models. Models 4 and 5 gave better fits to most of the data than did 6 and 7. Model 5 provided the best fit to 19 of the data sets, model 4 best described five data sets, and models 6 and 7 best described one and five data sets respectively.
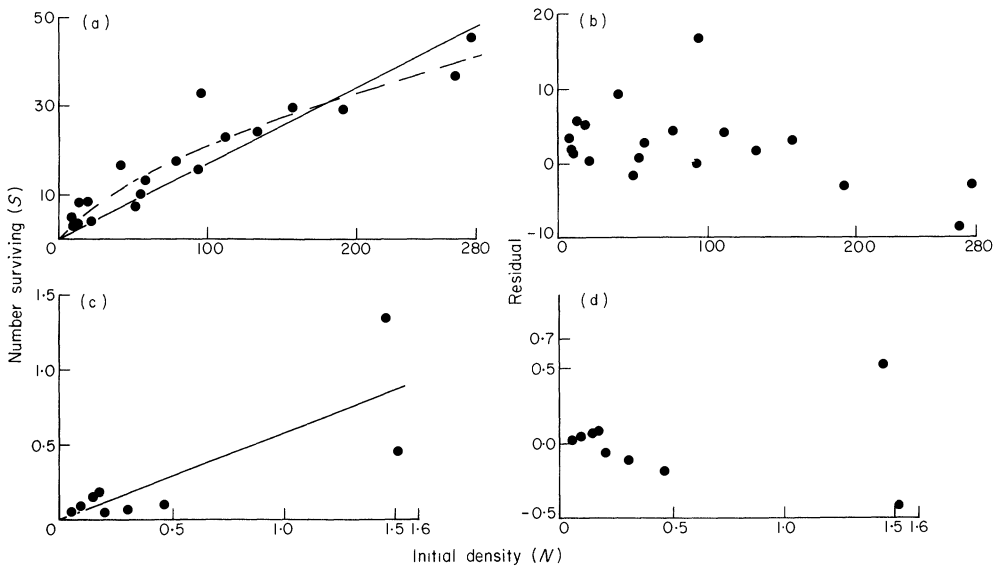
FIG. 7. A test for density dependence applied to two sets of data. (a) and (b) are for pupal predation of *Operophtera brumata* (Varley & Gradwell 1968); (c) and (d) are for parasitism of third instar *Parlatoria oleae* (Colvee) by *Aphytus maculicornis* (Masi) (Huffaker & Kennett 1966). After fitting 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 in (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 1 ($d = 0.913, a = 0.174, b = 0.428$).

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 4 and 5. When this occurred for models 6 and 7 it was often a result of the forms of these models being inappropriate for describing a particular data set (i.e. applying model 6 to data which showed an exponential plot of k-value against density or model 7 to data which showed a logarithmic plot of k-value against density). The form of model 6 also caused unreasonable estimates of the parameters a and b when the data indicated an exponential curve of k-value against density. In these cases, the estimated value of the parameter b was very high (>1000) and the value for a was very small (<10^{-6}), resulting in an approximately linear relationship between k-value and density for this model.

The fit of the four models to the data on survival of *Stegobium paneceum* and *Tribolium castaneum* are shown in Fig. 8 in terms of the number of survivors against density (Figs 8(a) and (c)) and as k-value against density (Figs 8(b) and (d)). Models 4 and 5 described both sets of data well and there was little difference in their predicted curves. Model 6 described the *Stegobium* data well but did not give a good description of the *Tribolium* data. Model 7 provided a poor description of the *Stegobium* data but described the *Tribolium* data well.

Following Hassell, Lawton & May (1976), the fitted parameters from the data in Table 3 may be used to characterize the nature of the population dynamics shown by

TABLE 4. The percent of the variance explained by the four two-parameter density dependent models of Table 1 applied to the data from the sources given in Table 2

Species	Model (entry in Table 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 kuhniella*	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*	99·82	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 serricata*	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	2	10	1	3

* Best fit occurred when $d = 1$.
† Best fit occurred at unreasonable parameter values for *a* and *b*.

TABLE 5. The percent of the variance explained by the four two-parameter density dependent models applied to the data from the sources given in Table 3

Species	Model (entry in Table 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. *Saccharosydne 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 defoliara*	47·02	47·22	46·64†	46·98*
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	3	9	0	2

* Best fit occurred when $d = 1$.
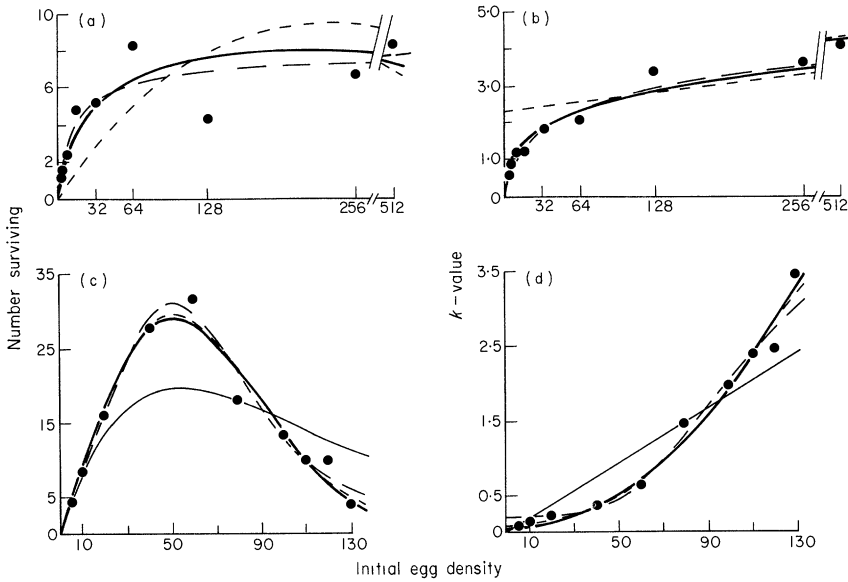† Best fit occurred at unreasonable parameter values for *a* and *b*.

FIG. 8. The predicted curves of the four two-parameter models of Table 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 the estimated parameter values were used to provide the curves in (b) and (d). Model 4 (———): (a) $d = 1.00$, $a = 0.676$, $b = 0.295$; (c) $d = 0.925$, $a = 0.000160$, $b = 2.04$. Model 5 (——): (a) $d = 0.711$, $a = 0.110$, $b = 0.950$; (c) $d = 0.800$, 0.0149, $b = 4.21$. Model 6 (———): (a) $d = 0.691$, $a = 0.113$, $b = 0.936$ (note that in (a) and (b) the predicted curves for models 5 and 6 are coincident); (c) $d = 1.00$, $a = 1.65 \times 10^{-8}$, $b = 1.13 \times 10^{6}$. Model 7 (– – –): (a) $d = 1.00$, $a = -2.21$, $b = 0.00409$; (c) $d = 1.00$, $a = 2.61$, $b = 0.0448$.

these species. Figure 9 shows the regions of dynamical behaviour of the population model (from entry 5 of Table 1)

$$N_{t+1} = d\lambda N_t (1 + (aN_t)^b)^{-1}. \tag{13}$$

The boundaries between the regions were found by a linearized stability analysis of eqn (13) using the method of May *et al.* (1974). 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 in Fig. 9. Ten of the fourteen species were placed in the region of monotonic damping. 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.

The general picture arising from this analysis supports precisely the conclusions reached by Hassell, Lawton & May (1976), namely that where density dependence occurs in insect populations, it usually acts in an undercompensatory manner. Although eqn (13) is probably a better descriptive form than that used by Hassell, Lawton & May (1976), there is little difference in the stability diagrams for the two models (compare Fig. 9
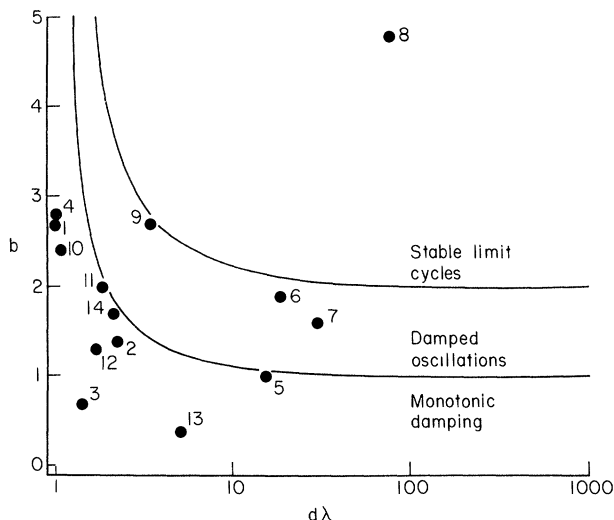
FIG. 9. The boundaries separating regions of different dynamical behaviours as functions of the density dependent parameter b and the effective rate of increase $d\lambda$ for the population model of eqn (13). The numbered points correspond to the data sets of Table 3. See text for discussion.

with their Fig. 2). The notable similarity of this analysis to that of Hassell, Lawton and May is further emphasized by the similar placement of the species in the two diagrams.

CONCLUDING REMARKS

The one-parameter models of Table 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 these models do not have general forms, they may be useful in describing data when their forms are appropriate, such as describing logarithmic curves of k-value against density (model 6) or symmetric sigmoid curves of proportionate survival against density (model 7). Two of the models in Table 1 (models 4 and 5) 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 independent survival than model 4. In addition, model 5 describes a relationship between k-value and log density which is approximately linear at high densities. This may play an important role in the description of data in light of the view of some authors that such plots are linear at high densities (Varley, Gradwell & Hassell 1973; Hassell 1975; Stubbs 1977).

One of the major uses of the models in Table 1 is in describing the affects of density in processes affecting biological populations, and often this is an initial step in the development of a population model. The value of this inductive approach was recognized by Varley & Gradwell (1968) and Hassell & Huffaker (1969), and these studies led to further modelling efforts by Benson (1974) and Podoler (1974). In addition to this descriptive use, the simple algebraic forms of the models in Table 1 lend themselves well to analytical investigations of their properties while still encapsulating the requisite range of density dependent responses. This property has been of enormous value in furthering the understanding of the consequences of density dependence both in single-species

populations (e.g. May *et al.* 1974; Hassell, Lawton & May 1976; May & Oster 1976) and in more general multispecies situations (e.g. Hassell & Comins 1976; Comins & Hassell 1976; Southwood & Comins 1976). The analytical nature of these models also permits the dynamical behaviour of populations to be predicted from estimated parameters (e.g. Hassell, Lawton & May 1976) without resource to lengthy simulation. Hence, they are admirably suited for use in understanding the dynamics of a variety of populations where, although the mechanisms involved may not be clearly understood, data on the effect of density on mortality or reproductive success is available.

In any investigation, the use of a general form (such as model 5) is particularly important where the model is to be applied to species with notably different density dependent responses. This provides easy comparisons between species in terms of descriptive parameters and is also important during the development of population models for the species. Any differences in model behaviour may, therefore, be attributed to actual species differences and not to biases in the descriptive ability of the model. Such an approach has recently been undertaken in the development of single-species and two-species models for laboratory populations of two stored-product beetles, *Callosobruchus chinensis* (L.) and *C. maculatus*, and the results of these studies will be reported in future publications.

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