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DENSITY-DEPENDENCE IN SINGLE-SPECIES POPULATIONS

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INTRODUCTION

Models for population growth in a limited environment are based on two fundamental premises: that populations have the potential to increase exponentially and that there is density-dependent feedback that progressively reduces the actual rate of increase. The most familiar of these models is the logistic equation of Verhulst (1838) and Pearl & Reed (1920). A recent paper by May *et al.* (1974) has explored several other continuous and discrete models and shown the general relationship between time delays in a continuous (differential) model and the density-dependence in a discrete (difference) model.

In this paper the form of density-dependent relationships is examined with particular reference to insects, a new discrete model is presented and its stability properties described.

SOME OBSERVED RELATIONSHIPS AND THEIR DESCRIPTION

The examples in Fig. 1 show several density-dependent relationships arising from intra-specific competition for a fixed amount of food. In each case the mortality is expressed as $\log(N_t/N_s)$ (the k -value of Haldane (1949) and Varley & Gradwell (1960)) where N_t is the original population density and N_s is the density of survivors. The significant features of these are that (1) there is pronounced density-dependence at high population densities which becomes negligible as density decreases and (2) the density-dependence at high populations is either characterized by a fixed slope (b) or this slope increases rapidly with increasing density as in Fig. 1a. These properties should be part of a general model describing density-dependent relationships.

A familiar model that is the basis for the tests for density-dependence of Varley & Gradwell (1970) and Morris (1959) may be expressed as

$$N_s = \frac{1}{\alpha} N_t^{(1-b)} \quad (1)$$

where α and b are constants that define the relationship between mortality, or natality, (this qualification is assumed throughout) and density. In logarithmic form and on rearranging, we have the linear equation

$$\text{Log } \frac{N_t}{N_s} = \log \alpha + b \log N_t. \quad (2)$$

This is now in the same units as the observed data in Fig. 1. Clearly equation (2) is only adequate in describing those parts of the overall relationships in Fig. 1 which tend to be linear.

Density-dependence in single-species populations

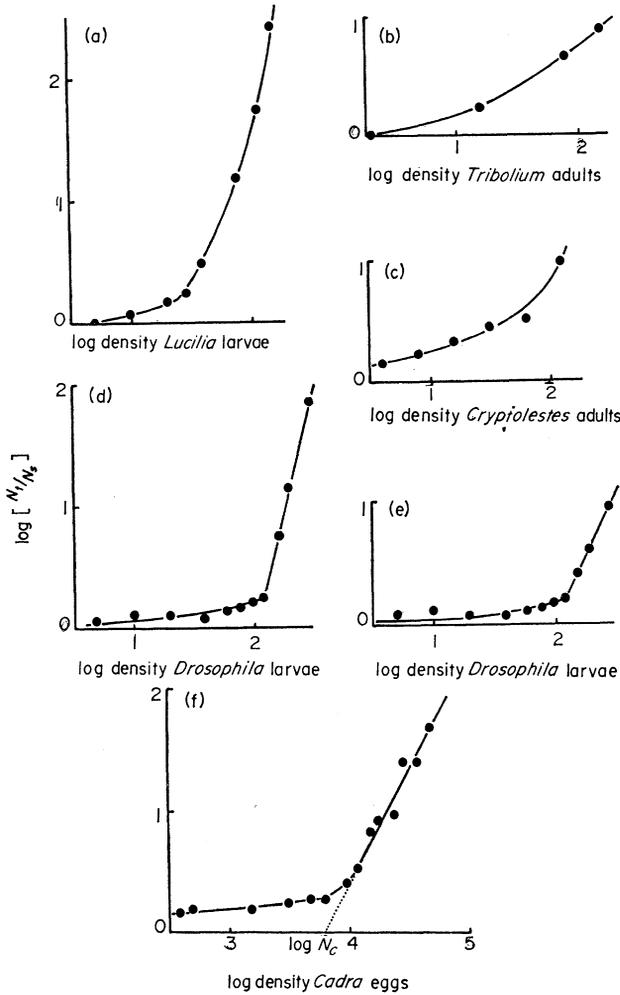


FIG. 1. Some density-dependent relationships due to intraspecific competition. In each case mortality, or reduced natality, is expressed as a k -value ($\log N_t/N_s$) and plotted against the log initial density ($\log N_t$). Figs 1a to 1e, after Varley *et al.* (1973); Fig. 1f, after Rogers (1970). All curves fitted by eye. (a) Mortality of *Lucilia cuprina* (Meig.) between larval and adult stages (data from Nicholson 1954). (b) Reduced fecundity of *Tribolium castaneum* (Herbst) (data from Birch, Park & Frank 1951). (c) Reduced fecundity of *Cryptolestes*. (d) Mortality of *Drosophila simulans* Meig. between larval and adult stages (data from Miller 1964). (e) Mortality of *D. melanogaster* Meig. between larval and adult stages (data from Miller 1964). (f) Mortality of *Cadra cautella* Walk. between egg and pupal stages.

By introducing a finite nett rate of increase (λ), we have the population model

$$N_{t+1} = \frac{\lambda}{\alpha} N_t^{(1-b)} \tag{3}$$

where N_{t+1} and N_t are population sizes in successive generations. The stability conditions of this model have been discussed by May *et al.* (1974). Stability is governed by the parameter b alone, the population being stable when

$$2 > b > 0.$$

When $1 > b > 0$, a perturbed population returns smoothly to the point equilibrium, but if $2 > b > 1$ the population 'overcompensates' and exhibits damped oscillations about the equilibrium. When $b > 2$, equation (3) predicts oscillations of increasing amplitude (see below).

This model is well suited to describe the density-dependence occurring at high population densities (Fig. 1). It has the severe limitation, however, of being linear on logarithmic scales, intercepting the abscissa. This implies a threshold population density (N_c , see Fig. 1f) below which the mortality ($\log N_t/N_s$) becomes negative: there are more survivors (N_s) than initial numbers present (N_t)! This could only occur when immigration or reproduction intervenes before the survivors are sampled. This linearity alone is responsible for the oscillations of increasing amplitude in population size when $b > 2$. Varley, Gradwell & Hassell (1973), realizing this, made the simplest kind of correction, namely

$$\begin{aligned} N_{t+1} &= \frac{\lambda}{\alpha} N_t^{(1-b)} \quad \text{when } N_t > N_c \\ N_{t+1} &= \lambda N_t \quad \text{when } N_t < N_c. \end{aligned} \quad (4)$$

There is either density-dependence defined by the linear eqn (2) or no mortality at all (exponential growth). This discontinuity at N_c effectively reduces the objection of $N_s > N_t$ when $N_t < N_c$. However, when $b > 2$ in this model, the population oscillates irregularly about the equilibrium with a pattern that varies with the initial value of N_t . This, too, is an unsatisfactory result. Such oscillations are akin to the neutrally stable cycles of the Lotka-Volterra predator-prey models where the system always 'remembers' its starting conditions. They are not to be expected under natural conditions.

The more likely general outcome is one of stable limit cycles when $b > 2$. This only occurs when some 'smoothing' is introduced in the region of the threshold (N_c) (May *et al.* 1974), which leads us to the generalized model

$$N_{t+1} = (\lambda N_t^{-f(N_t)}) N_t \quad (5)$$

where the function, $f(N_t)$, now replaces the density-dependence term, b . This function is given the limiting forms

$$\begin{aligned} f(N_t) &\rightarrow 0 \quad \text{when } N_t \ll N_c \\ f(N_t) &\rightarrow b \quad \text{when } N_t \gg N_c. \end{aligned} \quad (6)$$

SCRAMBLE AND CONTEST

Nicholson's (1954) terms, 'scramble' and 'contest', distinguish between two quite different kinds of intraspecific competition.

Ideally, scramble involves the exactly equal partitioning of the resource such that there is an abrupt change from complete survival to 100% mortality when there is just insufficient resource to maintain any individual. This is shown in idealized form in Fig. 2a where

$$\begin{aligned} b &= 0 \quad \text{when } N_t < N_c \\ b &= \infty \quad \text{when } N_t > N_c. \end{aligned} \quad (7)$$

'In *contest* each successful animal gets all it requires, the unsuccessful animals get insufficient for survival or reproduction' (Varley *et al.* 1973). The classic example usually

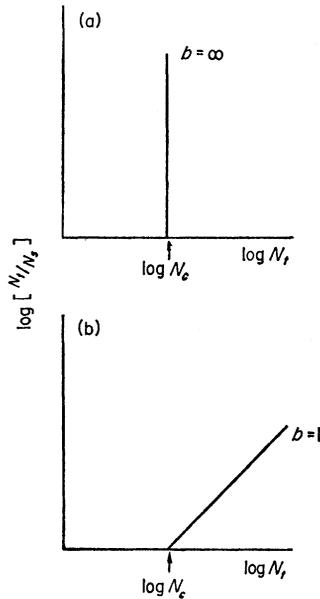


FIG. 2. The density-dependent relationships arising from two extremes of intraspecific competition: (a) scramble; (b) contest. Axes as in Fig. 1. (After Varley *et al.* 1973.)

quoted is where there is competition for a fixed number of refuges. As density increases the number surviving remains constant. In idealized form this leads to density-dependence as shown in Fig. 2b where

$$\begin{aligned} b &= 0 \text{ when } N_t < N_c \\ b &= 1 \text{ when } N_t > N_c. \end{aligned} \quad (8)$$

A model that approaches this situation is the logistic equation. This conforms to conditions (8) except for a smooth transition in the region of N_c .

Such scramble and contest are the two extremes of competition. Normally, some element of contest is always likely since some individuals will be more successful than others. In terms of the parameter, b , the condition

$$1 > b > 0 \text{ when } N_t > N_c$$

represents different degrees of contest alone, while the condition

$$\infty > b > 1 \text{ when } N_t > N_c$$

represents varying combinations of scramble and contest. This range is well illustrated from Fig. 1. Scramble is most marked in Figs 1a and 1d, while contest is better seen in Fig. 1b. Of course, in all cases the sharp discontinuity at N_c contained in eqns (4), (7) and (8) gives way to a smoother transition.

A model that is well suited to describe the extremes of scramble has been discussed by May (1974) as a limiting case of a model for a population of periodical cicadas (see also Cook (1965), May *et al.* (1974) and Southwood *et al.* (1975)). It has the form

$$N_{t+1} = \lambda N_t e^{-aN_t}. \quad (9)$$

The mortality term ($\log N_t/N_s$) here increases exponentially with $\log N_t$ giving the limiting forms of $f(N_t)$ from equation (5) of

$$\begin{aligned} f(N_t) &\rightarrow 0 \quad \text{when } N_t \ll N_c \\ f(N_t) &\rightarrow \infty \quad \text{when } N_t \gg N_c. \end{aligned} \quad (10)$$

The stability properties of this model (May 1974) are governed by the nett rate of increase (λ) alone, and not by any specific density-dependence term. The population exhibits exponential damping towards the equilibrium, damped oscillations and stable limit cycle behaviour, respectively, as the value of λ increases. Its disadvantage as a general description for density-dependence is that it does not cater well for the cases where the density-dependence is linear (characterized by b) at high population densities.

A NEW MODEL

The following model satisfies the conditions (6) on page 285 and has the further obvious constraint that $\log N_t/N_s \rightarrow 0$ when $N_t \rightarrow 0$

$$N_{t+1} = [\lambda(1 + aN_t)^{-b}]N_t \quad (11)$$

where λ and b are as previously defined and a is a constant defining the threshold density ($N_c = 1/a$). Fig. 3 shows the form of the density-dependent function from the model, again expressed as mortality ($\log N_t/N_s$) plotted against \log population density ($\log N_t$) (cf. Fig. 1). The curve is described by the equation,

$$\log \frac{N_t}{N_s} = b \log (1 + aN_t). \quad (12)$$

Note that b is a constant representing the slope of the relationship attained at high population densities (at lower values of N_t , the slope is *not* constant). In the particular example in Fig. 3, $b = 1.0$ and $a = 0.01$ (i.e. $N_c = 100$). By varying b and a , a wide range of curves is obtained of the same general form as the examples in Fig. 1.

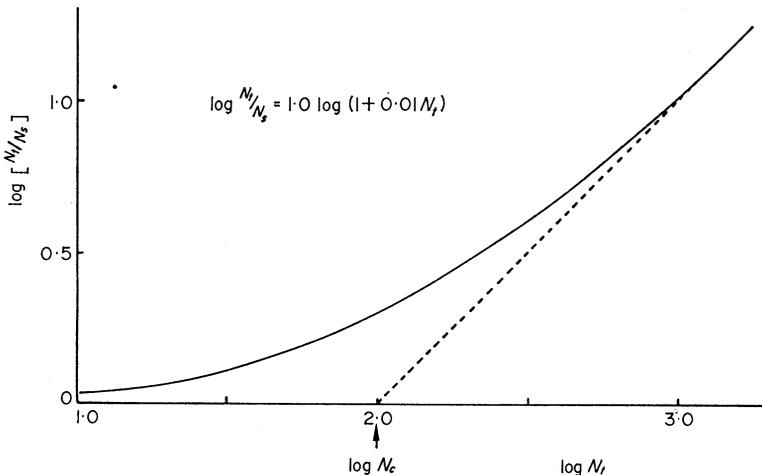


FIG. 3. A density-dependent relationship from equation (11) where $a = 0.01$ and $b = 1.0$.

The stability properties of this model are shown in the section below and the extent to which the model describes actual data sets is considered in the Discussion.

Stability analysis

It is now widely appreciated that density-dependent factors need not invariably lead to the damping of population fluctuations. The work of May in particular (1972, 1973, 1974 and May *et al.* 1974) has illustrated how density-dependent relationships can lead to a similar range of exponential and oscillatory damping and stable limit cycle behaviour as found in some predator-prey models. This range of stability properties is also obtained from the model in equation (11). The procedure for determining the boundaries between the different stability conditions follows that outlined in May *et al.* (1974).

Firstly, equation (11) is written in the general form

$$N_{t+1} = [f(N_t)]N_t \quad (13)$$

where $f(N_t)$ is the density-dependent nett growth rate from generation to generation. At equilibrium, $N_{t+1} = N_t = N^*$, which occurs when

$$f(N^*) = 1. \quad (14)$$

The stability of this equilibrium depends on the effective density-dependence (henceforth called \tilde{b}) evaluated by plotting $\log N_t/N_{t+1}$ against N_t and determining the slope of the relationship at the equilibrium point, N^* (see Fig. 6 below). It therefore encompasses the density-dependent mortality, $\log N_t/N_s$, and the growth rate of the population, λ . In general terms this density-dependent term, \tilde{b} , may be defined from

$$\tilde{b} = -\left[\frac{d \log f(N)}{d \log N}\right]^* = -N^*\left[\frac{df}{dN}\right]^* \quad (15)$$

As discussed in May *et al.* (1974), neighbourhood stability now depends on the condition $2 > \tilde{b} > 0$. We thus need to evaluate equation (15) for our specific model, equation (11).

Equilibrium is now defined as

$$f(N^*) = \lambda(1 + aN^*)^{-b} = 1. \quad (16)$$

From equation (15), \tilde{b} is given by

$$\tilde{b} = N^* ab \lambda(1 + aN^*)^{-b-1} \quad (17)$$

which, by combining with equation (16), gives

$$\tilde{b} = b \left[\frac{aN^*}{1 + aN^*} \right] \quad (18)$$

or

$$\tilde{b} = b(1 - \lambda^{-1/b}) = b \left[1 - \exp\left(\frac{-\ln \lambda}{b}\right) \right]. \quad (19)$$

By combining this expression for \tilde{b} with the equilibrium relationship (15), the stability criterion $2 > \tilde{b} > 0$ leads to a relationship between b and λ that affects stability. Fig. 4 displays the stability boundaries as functions of b and λ . Notice that the condition $\tilde{b} = 1$ divides exponential and oscillatory damping, and $\tilde{b} = 2$ divides neighbourhood stability from limit cycle behaviour. Fig. 5 shows some numerical examples of these different kinds of stability achieved by varying λ as shown.

Equation (18) shows there to be only two parameters affecting stability, the 'slope' of

the density-dependence, b , manifest at high population densities and the growth rate of the population λ . The parameter, a , is important in affecting the equilibrium, N^* , but has no effect on stability. This is made clearer from Fig. 6a. The density-dependent functions are plotted for two models where a varies (0.1 and 0.01) while b and λ are kept constant. Although the equilibria are very different, the values of \tilde{b} at the equilibria are

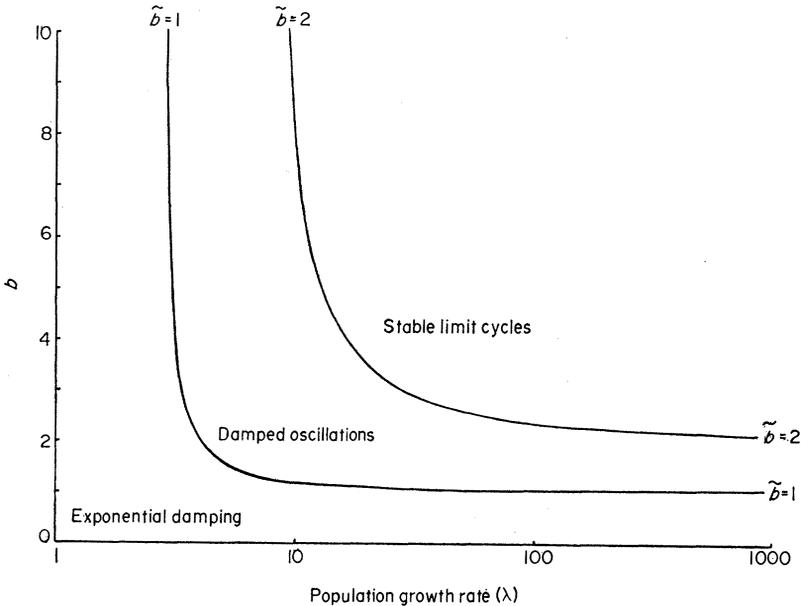


FIG. 4. Stability boundaries between the parameters, b and λ , from equation (11). See text for further explanation.

the same and hence stability unaffected. Contrast this with Fig. 6b where a and b are held constant but λ varied. Here the value of \tilde{b} clearly increases as λ increases and consequently the stability properties will change.

DISCUSSION

Description of data

To be useful in more than a theoretical sense, a general model for density-dependence should describe adequately the full range of relationships known to occur from available data. We have seen from Fig. 1 that laboratory competition experiments lead to similar outcomes characterized by low- and high-density behaviours. These density-dependent relationships may either rise almost exponentially as in Fig. 1a ($b \rightarrow \infty$) or tend to become linear at high population densities as shown in Figs 1d, e, f. Data from the field are usually collected over a smaller range of densities than contrived in the laboratory and thus only a segment of the relationships are apparent.

The data shown in Fig. 1 have one feature that cannot be described by equation (12): the fairly abrupt transition in the region of N_c . Fig. 7 shows this using the data from

Density-dependence in single-species populations

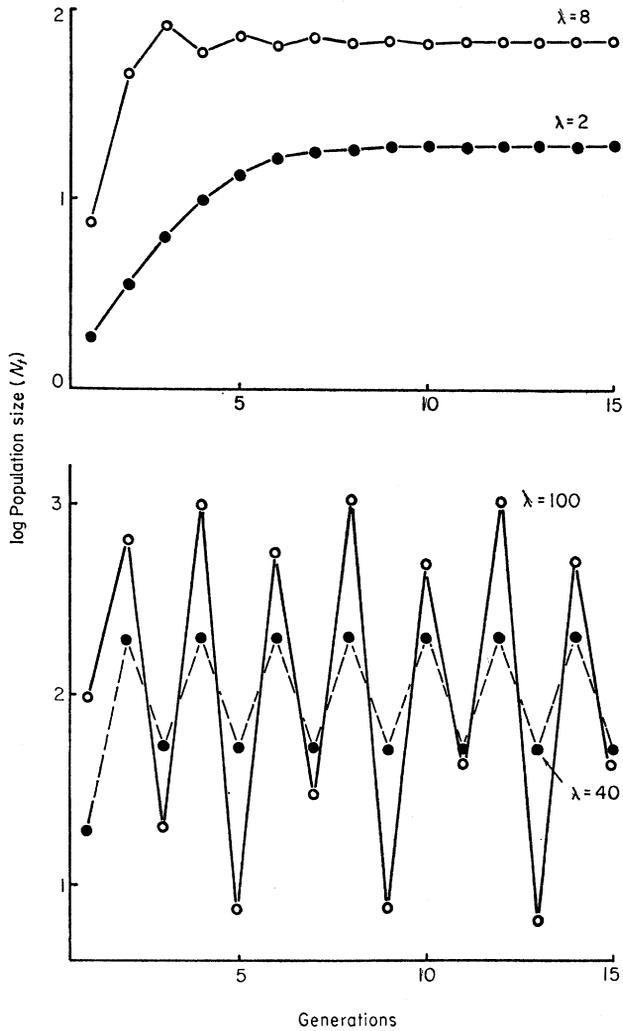


FIG. 5. Population changes calculated from equation (11), where $a = 0.01$, $b = 4.0$ and λ varies as shown.

Fig. 1a and a further example from a competition experiment between larvae of the moth *Plodia interpunctella* (Hübner)*. The fit of the model is poorest where the transition is most abrupt (as in Fig. 1f), which also leads to inadequate estimates of the 'slope', b . The inclusion in the model of further parameters would improve these fits but, unfortunately, with such parameter proliferation goes an increased unwieldiness. Of course, in the extreme case where there is a sharp discontinuity at N_c , only two distinct equations could adequately describe the data.

Fortunately, the model produces more encouraging results using field data. Under field conditions, such sharp discontinuities as seen in Fig. 1 are much less likely. Six

* The parameters a and b in these examples (and also from Fig. 8 below) were estimated by a least squares technique. A copy of the computer programme is available on request.

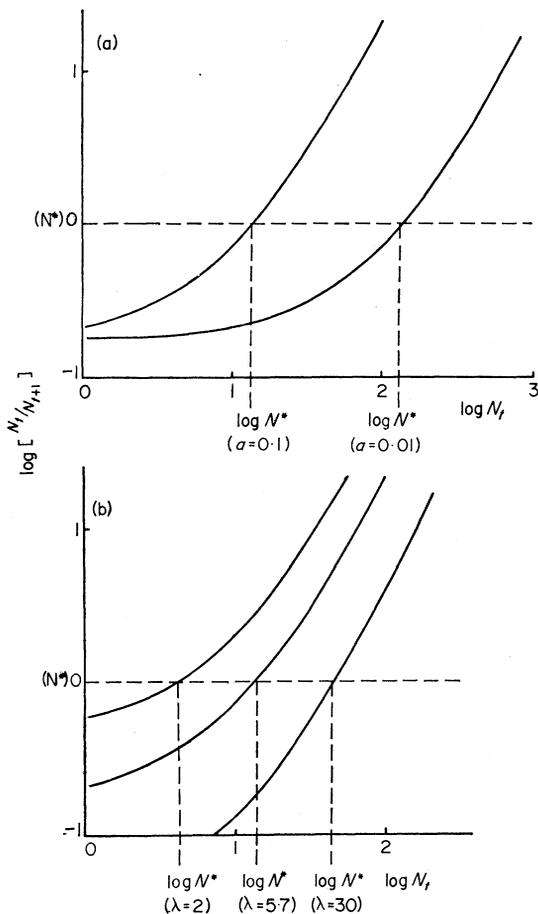


FIG. 6. Density-dependent relationships from equation (11), where the trend index (expressed as $\log N_t/N_{t+1}$) is plotted against population density ($\log N_t$). (a) $b = 2$, $\lambda = 5.75$ and a varied as shown. The slopes of the relationships (\tilde{b}) at the equilibrium (N^*) are the same in both cases, giving the same stability properties. (b) $a = 0.1$, $b = 2$ and λ varied as shown. The values of \tilde{b} at equilibrium are now different in each case, leading to different stability properties.

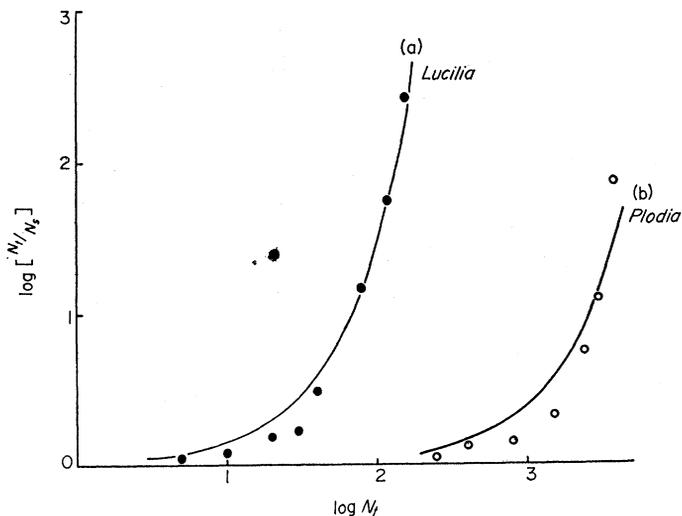


FIG. 7. Data from two laboratory competition experiments and their description based on equation (12). In both cases the least squares estimates of b and a converge to very high and low values respectively. (a) *Lucilia cuprina* as in Fig. 1a. (b) Mortality of *Plodia interpunctella* (Hübner) between egg and pupal stages plotted against \log egg density (after Rogers 1970, data from Snyman 1949).

examples of density-dependent relationships from census data are shown in Fig. 8. Some of the examples embrace a sufficient range of densities to show clearly the curvilinear nature of the relationships. In particular, the data for disease amongst larch bud moth larvae (Fig. 8c) and larval starvation in Colorado potato beetles (Fig. 8f) are cases where

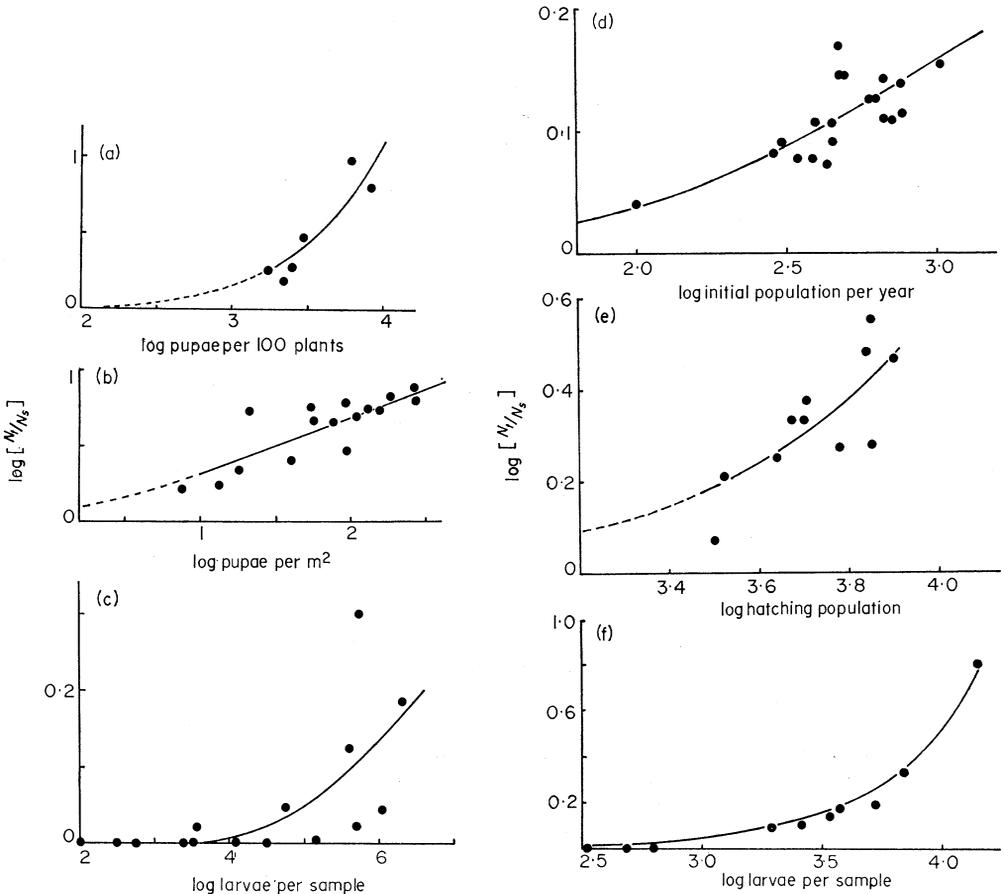


FIG. 8. Density-dependent relationships from field data and their description based on equation (12). (a) Cabbage root fly (*Erioischia brassicae* (Bouché)) pupal mortality. $a = 0.00011$, $b = 3.16$ (data from Benson 1973). (b) Winter moth (*Operophtera brumata* (L.)) pupal mortality. $a = 0.6$, $b = 0.38$ (data from Varley & Gradwell 1968). (c) Larch tortrix (*Zeiraphera diniana* Gn.) larval disease. $a = 0.000018$, $b = 0.11$ (data from Varley & Gradwell 1970, after Auer 1968). (d) Clutch size reduction in the great tit (*Parus major* L.) plotted against log maximum clutch size ($\log N_t$). $a = 0.0064$, $b = 0.18$ (after Krebs 1970). (e) Chick mortality in the partridge (*Perdix perdix* L.) plotted against log hatching population ($\log N_t$). $a < 0.000005$, $b > 28.58$ (after Blank *et al.* 1967). (f) Larval starvation in the Colorado potato beetle (*Leptinotarsa decemlineata* (Say)) plotted against log larval density ($\log N_t$). $a = 0.00007$, $b = 30.95$ (data from Harcourt 1971).

there is a wide range of sampled population densities above and below the transition region (N_c). In the remaining examples, data comes from a relatively restricted range of densities over which the relationships appear more or less linear. The model performs well in both categories.

Some implications

The stability analysis and Fig. 4 show that the rate of increase, λ , can have a marked effect on stability. Only when the value of the parameter, b , is less than unity is its effect small: there is then always exponential damping ($\bar{b} < 1$). However, if b is greater than unity, the stability properties depend critically on the magnitude of λ . If λ is large, the equilibrium population, N^* , is also large and hence the effective density-dependence, \bar{b} (slope at N^*), approaches the value of b . This will lead to decreasing oscillations or stable limit cycles as shown in Fig. 4. If λ is small, however, the equilibrium value N^* will be in the region of low density-dependence ($\bar{b} < 1$) leading to exponential damping. Thus, the contribution to stability of several of the relationships in Fig. 1 would depend very much on the assumed values for λ .

In a multiple age class population where the density-dependence acts on a given stage, the value of λ is most unlikely to be the same as the fecundity per adult. The estimate of λ should be the rate of increase of the population, having taken into account all other mortalities acting during the life cycle. Consider the simplest example where the stages of the life cycle are discrete and density-dependence acts on a single stage (e.g. the pupae):

$$\log \text{Adults } (t+1) = \log \text{Adults } (t) + \log \text{Fec} = \left[\log \frac{\text{Eggs } (t)}{\text{Larvae } (t)} \right] - \left[\log \frac{\text{Larvae } (t)}{\text{Pupae } (t)} \right] - [b \log(1 + a \text{Pupae } (t))]. \quad (20)$$

The value of λ in this example is given by

$$\log \lambda = \log \text{Fec} - \left[\log \frac{\text{Eggs}(t)}{\text{Larvae}(t)} \right] - \left[\log \frac{\text{Larvae}(t)}{\text{Pupae}(t)} \right] \quad (21)$$

This emphasizes that the appropriate value of λ for a stability analysis may be considerably less than the *potential* rate of increase of the adult population.

Because the effective density-dependence changes with population density, tending towards zero when densities are low, the response of a population to perturbations can depend on whether the population is moved above or below the equilibrium, N^* . In particular, this is important if the value of b is greater than unity but λ is small. We are now in the domain of exponential damping shown in Fig. 4. Consider the case illustrated in Fig. 9a, where there is overcompensation at high population densities ($b = 2$). If perturbed markedly above the equilibrium (to N_1), a very high mortality occurs forcing the population to a low level (N_2). There is now much reduced mortality and weak density-dependence so that the population moves smoothly back to the equilibrium as illustrated in Fig. 9b (hollow circles). This is quite different from the oscillatory behaviour normally associated with overcompensation and which tends to occur with larger values of λ . It is also in accord with field examples where population crashes from very high densities are *not* followed by marked oscillations (e.g. *Dendrolimus pini* L. and other moth species in German coniferous forests (Schwertfeger 1941)). Of course, if the initial perturbation is markedly downwards, there is simple exponential damping back to the equilibrium. These differences do *not* apply if the value of b is less than unity. There will now *always* be exponential damping irrespective of the direction of the perturbation (Fig. 9b, solid circles).

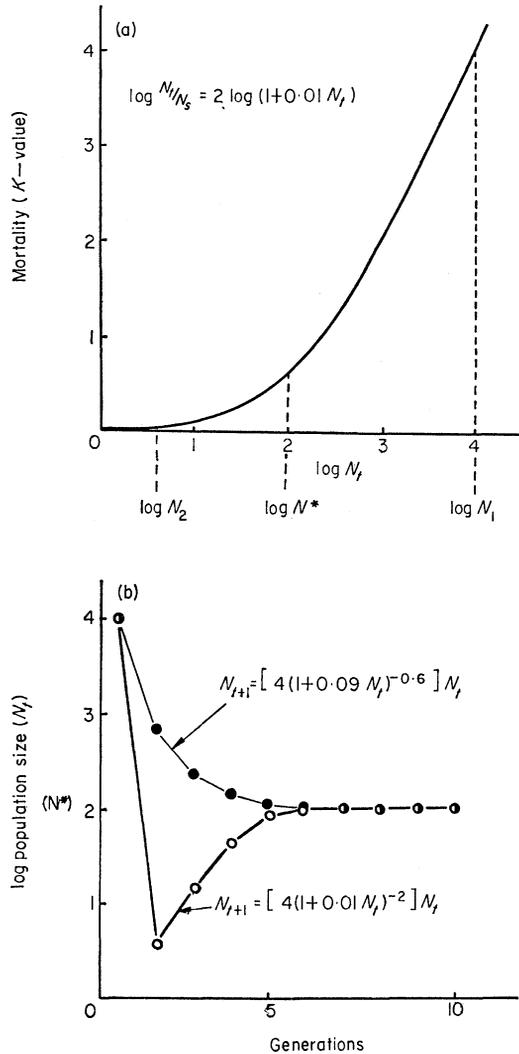


FIG. 9. (a) Density-dependent relationship calculated from equation (12) where mortality (expressed as a k -value) is plotted against \log population density ($\log N_t$). See text for further explanation. (b) Population changes calculated from eqn. (11) following displacement from the equilibrium ($N^* = 100$). ○: $a = 0.01$, $b = 2$ and $\lambda = 4$ (as in Fig. 9a). Overshooting when displaced above N^* as shown; exponential damping when displaced below. ●: $a = 0.09$, $b = 0.6$ and $\lambda = 4$. Exponential damping when displaced above or below N^* .

ACKNOWLEDGMENTS

It is my great pleasure to acknowledge the help of Professor Robert May. He suggested an improved form of the model which is used in this paper and also outlined its stability analysis. I am also grateful to Mr N. Small of the Environmental Resource Management Research Unit at Silwood Park who provided me with a least squares programme for estimating the parameters in equation (12).

SUMMARY

(1) The general form of density-dependent relationships is discussed and illustrated with examples. These are compared with the relationships predicted from two other models for density-dependence.

(2) A new model is proposed which has the properties that (1) at high population densities, the relationship between mortality, or natality (expressed as k -values), and the log density is characterized by a constant slope (b) and (2) the degree of density-dependence decreases as population density falls.

(3) The stability properties of this model are discussed. A population may exhibit exponential damping, oscillatory damping, or stable limit cycle behaviour, depending upon the parameter (b) and the effective rate of increase of the population (λ).

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