

parameters that define the form of density dependence. This equation has a number of advantages over the logistic equation, not least of which is that it makes no assumptions about the ultimate size of a population. It is also possible to estimate the parameters readily from field and laboratory data. For this equation the equilibrium population size is

$$N^* = \frac{(\lambda - 1)^{1/b}}{a} \quad (3)$$

Clearly, N^* is determined in part by the nature of the density-dependent feedback (a, b) and in part by the finite rate of population increase (λ). Consequently, the population size can be expected to be susceptible to variation in the numbers of births and deaths, irrespective of the level of resource availability. It is this result that fits in with my intuition and that I have argued for previously⁴. Population size is determined by the interaction of the density-independent and density-dependent processes that influence the number of births, deaths, immigrants and emigrants in a population. This is the belief commonly expressed in many modern ecology texts⁵, often on a graphical basis following Williamson⁶.

Are there situations in which one might expect to alter λ and not affect the equilibrium population size as Ginzburg² suggests? If the value of b in the above equation is set to infinity, the equilibrium population size becomes $N^* = 1/a$. A high value of b represents scramble competition but it should be noted that such values are likely to produce complex dynamical behavior⁷. Most of the evidence from annual plants⁸ and insects⁷, however, points toward values of b that are much closer to unity. Moreover, for annual plants there is evidence that the values of λ and a are correlated⁹, and also that the time at which density-independent mortality occurs has the potential to modify equilibrium population size¹⁰.

While variations in λ can often be expected to produce a change in the equilibrium population size, there are situations among annual plants, at least, where an alteration of λ only changes the speed at which equilibrium is reached. Watkinson and Davy¹¹ have illustrated this point using a model of the form

$$N_{t+1} = \frac{\lambda N_t}{(1 + aN_t)^b + m\lambda N_t} \quad (4)$$

where m is a self-thinning parameter. Assuming for simplicity that

$b = 1$, then at equilibrium

$$N^* = \frac{\lambda - 1}{\lambda m + a} \quad (5)$$

Given that the value of a is generally significantly less than 1.0 (Ref. 11), then if λ is large, self-thinning can be expected to produce equilibrium population sizes that approximate to $1/m$. However, as λ decreases N^* will become increasingly sensitive to variations in λ . I would therefore argue that, for annual plants, only populations that show considerable self-thinning can be expected to have an equilibrium population size independent of λ . Ironically, an increase in the level of resources in this case will decrease, rather than increase, the size of the equilibrium population, because an increase in the biomass of plants will be concomitant with a decrease in plant density.

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Ginzburg² notes two shortcomings in the standard logistic equation: first, it implies an independence between the rate of increase and the equilibrium population size, and secondly the addition of a mortality term to r results in lower mortality when N is above the carrying capacity.

Above, Watkinson expounds the virtues of the difference equation of Maynard Smith and Slatkin¹² (Eqn 4) in overcoming the problem of independence between growth rate and population size. He does not indicate that this equation also escapes the constraint of a strict equality between the rate of population decline above the carrying capacity and the growth rate.

The paradoxical effect of the incorporation of the mortality factor is due to the nature of the time constant (or what May¹³ calls the 'return time') of the logistic equation – it is $1/r$. The logistic thus states that rate of return of a population displaced from equilibrium will be slower if r is low. It is difficult to place any biologically meaningful interpretation on the notion that populations with high rates of increase will plummet from a given density towards the carrying capacity more rapidly than similar populations with lower rates of increase.

This undesirable feature is not entirely eliminated from the Maynard Smith and Slatkin model, but the rate of return to the equilibrium population size becomes less depen-

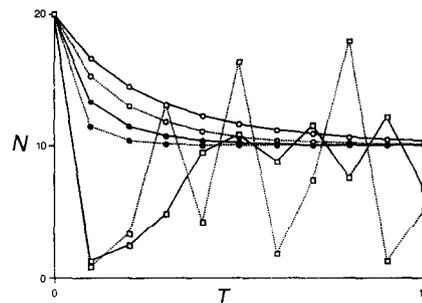


Fig. 1. Simulated populations following Eqn 4, showing effects of b and λ on rate of return to equilibrium. Solid lines, $\lambda=2$; dashed lines, $\lambda=4$; open circles, $b=0.5$; closed circles, $b=1$; open squares, $b=5$; equilibrium population size=10, throughout.

dent on λ as the severity of the density dependence b increases. The time constant of the equation is difficult to derive analytically, but this pattern is clearly demonstrated by simulation results (see Fig. 1). The very similar, but mathematically more tractable model

$$N_{t+1} = \frac{\lambda N_t}{(1 + aN_t)^b} \quad (6)$$

has a rate constant of $1/[b(1 - \lambda)^{-1/b}]$ (Ref. 13), which exhibits the same properties.

It is clear that the two theoretical weaknesses Ginzburg finds in the logistic are overcome by the Maynard Smith and Slatkin model: rate of increase is not independent of the equilibrium population density; and population contraction is not wholly dependent on the rate of increase. This model has also been fêted as the best available descriptor of density-dependent processes in real data³. It doubtless deserves wider recognition and use.

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Ginzburg² has suggested that the logistic equation is 'one of the greatest disservices to theoretical ecology', in part because he finds it unable to characterize the 'r-independence of equilibria'. He asks whether the logistic equation of population growth can be used to show that a population with higher mortality reaches the same equilibrium as a population with lower mortality, only more slowly. He shows that introducing increased mortality to the logistic equation as a value to be subtracted (from r or dN/dt) produces inherently contradictory results, and suggests that this is the fault of the logistic model. I suggest that is rather the fault of the modeller. Different levels of mortality can

readily be incorporated into the logistic equation as a value p between zero and unity

$$\frac{dN}{dt} = prN \left(1 - \frac{N}{K}\right) \quad (7)$$

This formulation allows populations with different survivorships (proportional to p) to reach similar equilibria at different rates, an intuitively satisfying result. I too tend to side with intuition over equations, but when equations break with intuition, it is usually due to the modeller, not the model.

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Ginzburg² argues that the classical logistic equation is illogical because, by adding a constant death rate $-\mu$ to the value of r , the maximum instantaneous rate of growth,

$$\frac{dN}{dt} = (r - \mu)N \left(1 - \frac{N}{K}\right) \quad (8)$$

he obtains

$$\frac{dN}{dt} = rN \left(1 - \frac{N}{K}\right) - \mu N \left(1 - \frac{N}{K}\right) \quad (9)$$

in which the second term 'cannot reflect mortality since it changes sign to positive when $N > K$, signifying addition rather than subtraction'. He concludes that either his 'intuition or the equation is wrong' and prefers 'to side with intuition'.

If we think about the logistic equation in terms of density-dependent birth and death rates, then we can write the general per capita equation

$$\frac{dN}{Ndt} = b(N) - d(N) = r(N), \quad (10)$$

with b a decreasing and d an increasing function of population density, N . Inserting simple linear relationships for these birth and death functions we have

$$\frac{dN}{Ndt} = (r - sN) - (\mu + vN) \quad (11)$$

$$\text{or } \frac{dN}{Ndt} = (r - \mu) - N(s + v) \quad (12)$$

Solving these equations gives the equilibrium density

$$K = \frac{(r - \mu)}{(s + v)} \quad (13)$$

Substituting $(r - \mu)/K$ for $(s + v)$ in Eqn 12 and rearranging we get Eqn 8. However, we can now see that Ginzburg's intuition rather than the equation is wrong, for it is plain from Eqn 11 that the mortality term, $-(\mu + vN)$, can never be positive as

long as $N > 0$. Obviously, the second term in Eqn 9 does not reflect mortality at all. This is because the equilibrium density, K , is determined by the composite per capita growth rate $(r - \mu)$ not by r and μ in isolation (see Eqn 13).

Ginzburg is correct in asserting that first order equations like the logistic have difficulty in describing r -independent equilibrium points; i.e. K is always dependent on r , as in Eqn 13. However, it is not clear if population equilibria should, in reality, be dependent on r or not. If one considers the mortality imposed by harvesting a resource or controlling a pest, then there is considerable empirical evidence to suggest that a constant and regular mortality will indeed lower the equilibrium density of the affected population; i.e. K should be r -dependent. On the other hand, placing nest boxes out for birds should raise K but should not really affect the per capita birth rate; i.e. K should be r -independent. Adding nest boxes, however, should affect the density-dependent coefficients s and v on which K also depends (see Eqn 13).

Perhaps the problem is in our interpretation of K as the 'carrying capacity' of the environment when, in fact, K of the logistic contains no real information about the environment at all, but is simply the equilibrium density of a population under density-dependent negative feedback. As Ginzburg notes, higher-order models may be required to represent the influence of other environmental factors, such as food, predators and nesting sites. In the meantime, however, there is a pressing need for practical models for use in resource and pest management decision making. In many of these situations, data are only available on a single species, and it is therefore impossible to define parameters for higher order equations. It is here that the logistic family of equations, with time lags acting as surrogates for dimension and theta-coefficients forgiving the linear assumptions, may be the best models available for analysing and predicting population change¹⁴⁻¹⁷.

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Reply from L. Ginzburg

I agree with Olson that most confusion arises from the interpretation of model parameters. His reinterpretation of r is quite complex, which in my view stresses the need for a better theory. Young's formulation effectively introduces exponential rather than constant mortality, which misses the point of the discussion. Berryman's comments appear inconsistent: on the one hand he presents computations that show the equilibrium to be growth-rate dependent, while on the other he admits the possibility of the invariance. Watkinson and Mackenzie disagree with my intuition about the relationship between equilibrium and mortality. This is a well-entrenched view which I attempt to question. Watkinson also presents a case for approximate invariance in special cases. Such devices were invented for other shortcomings of the first-order equations. I fail to see why we should hold on to this inadequate framework. First-order (whether continuous or discrete) models fundamentally do not allow a possibility for equilibria to be invariant with respect to a population growth rate. This is not the property of the logistic but rather of all first-order models. Instead of continuing the debate, I would like to give a brief draft of an alternative theory.

I start by questioning the basic assumption of direct density