



Short communication

Paradoxes in the logistic equation?

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Abstract

Levins and Ginzburg raised two paradoxes concerning the logistic equation of population growth. None of them received a satisfactory answer within the frame of the original equation. Here, we propose solutions to both paradoxes.

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The logistic equation of population growth occupies a unique and fascinating position in the development of ecological thinking. Proposed in the first half of the nineteenth century by the Belgian mathematician Pierre-François Verhulst (1838) as a potential solution to the dilemma of Malthusian exponential growth, it was rediscovered and imposed to biologists as a simple model of population self-regulation in the early twentieth century by the American biologist Raymond Pearl and his colleagues (Kingsland, 1985).

The logistic equation has since inspired and stimulated much ecological work, including modeling, experimental and field research. Nowadays, the concept

of carrying capacity can hardly be dissociated from the model. It has also permeated evolutionary biology in the 1950s and the concept of r/K selection was named after its parameters in the 1970s. Finally, its remarkable fitting abilities to early datasets have also contributed to the popularity of the model (Pearl, 1925; Feller, 1940; Hutchinson, 1978). The logistic equation can be found in many biology textbooks and belongs to basic education in ecology. Independently of the status that one gives to this model, it has been and remains a cornerstone of empirical and theoretical ecology.

The logistic equation however also elicited strong attacks and vigorous criticisms, so that ecologists have developed a love-hate relationship with the logistic equation (Olson, 1992). Many legitimate criticisms address the phenomenological foundations of the model and its adequacy to describe the real world. They include for example the difficulty in the interpretation of

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its parameters (e.g., Olson, 1992; Miller et al., 2002), or its unrealistic form of density dependence (e.g., Getz, 1996; McCarthy, 1997; Courchamp et al., 1999; Etienne et al., 2002; Kent et al., 2003). Other criticisms have been raised with regard to internal contradictions. Named hereafter paradoxes, these apparent contradictions challenge the consistency of the model itself, and we shall focus here on this issue. We believe that clarifying such points might help understanding the significance and limitations of this historically and educationally important model. Our aim is to discuss two paradoxes raised respectively by Levins (Hutchinson, 1978) and Ginzburg (1992), and we show how they can be solved within the framework of the original formulation of the model (Verhulst, 1838).

1. Levins' paradox

The usual “ecological” form of the logistic equation is

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

To our knowledge, the first apparition of this ecological form goes back to Lotka (1925), with a typo in the formula. The first paradox, raised by Levins, has been exposed in Hutchinson (1978, p. 4) as follows: “ r (...) be negative, setting $N > K$, leads to an impossible result, for dN/dt is positive and increases indefinitely with N ” (it can be shown that infinity is even reached in a finite time). To avoid such a situation, Levins suggested that r should be constrained to non-negative values. If so the paradox disappears, but at the cost of excluding biologically meaningful situations, namely declining populations. Obviously, r has to be negative in sink environments (Hairston et al., 1970; Pulliam, 1988). Actually, a more sensible resolution emerges from Verhulst's original formulation (1838):

$$\frac{dN}{dt} = aN - bN^2, \quad (2)$$

where a is the Malthusian growth rate and, as such, has to admit both signs. In the second term added to avoid infinite growth, b is a friction coefficient and therefore strictly positive. Eq. (1) is derived from Eq. (2) by writ-

ing the latter as:

$$\frac{dN}{dt} = aN \left(1 - \frac{N}{a/b} \right), \quad (2')$$

and identifying $r = a$ and $K = a/b$. These relations are well known, and can be found in several textbooks. However, a simple but important consequence that, to our knowledge, has never been pointed out is that r and K must have the same sign since $b = r/K$ is positive. This constraint rules out Levin's case ($r < 0$ and $K > 0$) and therefore solves the paradox without limiting the sign of r .

It is worth emphasizing that, while a and b are two independent parameters in Verhulst's equation (Eq. (2)), K depends on r in Eq. (1). At this stage, one can see that the ecological form of the logistic (Eq. (1)) leads to two non-equivalent models, though expressed by the same equation. We call “free” logistic the model with r and K independent, and “constrained” logistic the model derived from Verhulst approach, i.e., with $r = a$, $K = a/b$, and b strictly positive.

In the constrained model, a difficulty arises with $r < 0$, since K is also negative and cannot be interpreted as a “carrying capacity”. It is easy to see that, if $r < 0$, then all the solutions with $N(0) \geq 0$ converge to 0, as expected in sink environments. The “carrying capacity” can be redefined as:

$$K_\infty = \lim_{t \rightarrow \infty} N(t), \text{ for } N(0) > 0. \quad (3)$$

As a consequence

$$K_\infty = \begin{cases} a/b = K, & \text{if } a > 0, \\ 0 & \text{if } a \leq 0. \end{cases} \quad (4)$$

A classical derivation (e.g., Begon et al., 1996) of the logistic equation assumes a linear decrease of the per capita growth rate, i.e., a negative density-dependence (see Fig. 1a). In this approach, r and K are implicitly assumed to be both positive and independent. With r negative and K positive (Fig. 1b), a linear variation of the per capita growth rate leads to a positive density-dependence (Levins' configuration). This paradoxical situation is impossible in the constraint model where r and K have always the same sign (Fig. 1a and c).

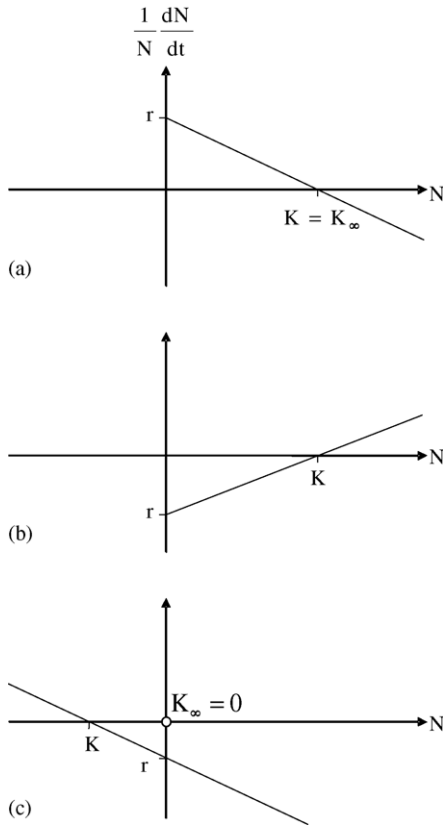


Fig. 1. Per capita growth rate as a function of population density N for the logistic model: (a) usual configuration with r and K positive, K_∞ as a new definition of the carrying capacity (see Eq. (4)); (b) Levins’ situation leading to an inverse density dependence; (c) constrained model with r negative.

2. Ginzburg’s paradox

Ginzburg (1992) considered incorporating additional mortality into the logistic equation without changing any other aspects of the environment, and proposed two ways to do so. Firstly

$$\frac{dN}{dt} = rN \left(1 - \frac{N}{K} \right) - \mu N, \tag{5}$$

where μN ($\mu > 0$) is the additional mortality term. The new equilibrium density is $K(r - \mu)/r$ ($\mu < r$). Ginzburg rejected this approach because it “disagrees with our intuition about unchanging equilibrium”. He claimed that, as the resources do not change, the population with higher mortality might attain the same K , but more slowly. This point is obviously disputable. Like all pop-

ulation equations, the logistic is a conservation or balance equation, i.e., the size variation over a time interval is the difference between input and output over that interval. In any case, it is admissible to act on such an equation by adding a term reflecting increased mortality, e.g., by harvesting a constant fraction of the population per unit of time. If one’s intuition is puzzled by the consequences of such a change, one must either adapt or reject the whole model, i.e., the logistic itself. Moreover, our own intuition is not hurt by the decrease of the equilibrium density: with additional mortality, individuals are continuously removed from the population, and thus the population might never reach K again. Such a behaviour is ultimately dictated by the model, and not the intuition.

Secondly, Ginzburg proposed, as an alternative solution, to introduce additional mortality in r only:

$$\frac{dN}{dt} = (r - \mu)N \left(1 - \frac{N}{K} \right) = rN \left(1 - \frac{N}{K} \right) - \mu N \left(1 - \frac{N}{K} \right), \tag{6}$$

which does not change K . But Ginzburg stated that the additional term $-\mu N(1 - N/K)$ cannot represent mortality since it is positive for $N > K$ (note that it is valid only for $K > 0$, i.e. $\mu < r$).

This paradoxical situation fostered a lively debate on equations of population growth in the issues of September 1992 and February 1993 of *Trends in Ecology and Evolution*. Most of these answers were based on models different from the logistic one and we will not tackle them, because our aim is to solve the paradox internally to the logistic equation. Only Young (1992) and Berryman (1992) replied within the framework of the logistic, but their answers are unsatisfactory. Indeed, Young’s (1992) and Ginzburg’s (1992) second approach (Eq. (6)) are mathematically equivalent (set $p = 1 - \mu/r$ in Eq. (7) of Young (1992)), and therefore deserve the same analysis given below. With regard to Berryman, although we share his conclusions (Berryman, 1992), we cannot adopt his line of reasoning. He tackled the problem by decomposing the model into two density dependent linear birth and death rates leading to the following form of the logistic equation: $dN/N dt = (n - vN) - (s + \sigma N)$; n and s are the intrinsic birth and death rates, v and σ the density dependent birth and death coefficients (Fig. 2). Such a derivation

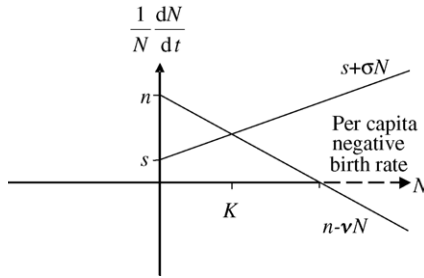


Fig. 2. Kostitzin’s derivation of the logistic leading to negative birth rates for large N .

can be found in contemporary textbooks of ecology (e.g., Krebs, 2001; Gotelli, 2001) and was already proposed in Kostitzin (1937, p. 15). A first difficulty is that the number of parameters is different in Ginzburg’s and Berryman’s equations, leading to problems with their identification. A more fundamental problem lies in the linear birth term with a negative slope, since it becomes negative for large values of N . This is conceptually unsatisfactory since it requires a limitation in the values of N and thus leads to an additional model different from Verhulst’s logistic equation. In our opinion, one should abandon this approach and rather stick to Verhulst’s derivation, which does not contain this awkward feature.

Again, returning to Verhulst framework (Eq. (2)) solves Ginzburg’s paradox. In the constrained logistic model, the only way of maintaining K fixed and respecting the equalities $r = a$ and $K = a/b$ is to act on b . If a becomes $a - \mu$ ($0 < \mu < a$ to preserve $K > 0$) then b must be replaced by $b - \delta$ ($0 < \delta < b$), so that $K = a/b = (a - \mu)/(b - \delta)$. Solving for δ , we get $\delta = \mu b/a$, and Eq. (2) becomes

$$\begin{aligned} \frac{dN}{dt} &= (a - \mu)N - (b - \delta)N^2 \\ &= aN - bN^2 - \mu N + \frac{\mu b}{a}N^2. \end{aligned} \tag{7}$$

It is now apparent that the paradoxical mortality term of Eq. (6) (i.e., $-\mu N(1 - N/K)$) is composed of the losses due to increased mortality $-\mu N$ and of $(\mu b/a)N^2$, a correction of the second order friction term. The first term is always negative and the second always positive since K , and hence a , are positive. Clearly, $(\mu b/a)N^2 = (N/K)\mu N$ is larger than μN when $N > K$, and the total contribution is positive. This means that the

gain obtained by the reduction in the quadratic friction term overcomes the loss due to the linear mortality term. There is no paradox in this, and we want to illustrate it with an example. Let us consider an animal population with cannibalism (e.g. a hypothetical spider population): let a denote the difference between intrinsic birth and death rates (cannibalism excluded); the brake bN^2 is due only to cannibalism, assumed to be proportional to the number of meetings per unit time; a predator is added to the system, and removes μN spiders per unit time. If one decrees that the equilibrium density must remain constant, then the only choice is to act on b (except increasing trivially a). The intensity of cannibalism must be weakened, and the number of individuals saved in this way per unit time is δN^2 ($\delta = \mu b/a$). For large values of N ($N > K$), the number δN^2 of individuals escaping cannibalism overcomes the number μN of individuals killed by the additional predator. Clearly, Ginzburg’s paradoxical term does not reflect mortality only. Again, returning to the historical formulation of Verhulst puts a constraint on parameters r and K , which also solves Ginzburg’s paradox.

3. Discussion

We would like to stress some important issues raised in this paper. Firstly, we showed that two paradoxes or apparent contradictions appear only in the free logistic model, but disappear in the constrained one. Other “paradoxes” can be produced, e.g. by increasing r without changing K , or by decreasing the carrying capacity with $r < 0$ and $K > 0$. In both cases, the additional terms have the “wrong” sign. Again, these “paradoxes” do not persist in the constraint model. Secondly, it is important to be aware that the choice of the derivation is not innocuous. The approach proposed in Kostitzin (1937) and used in Berryman’s reply (1992) is an example. In the same vein, following Lotka’s (1924) derivation based on Taylor’s expansion (e.g. in Hutchinson, 1978) leads to the same difficulty because there is no sign constraint on the quadratic term. Thirdly, the phenomenological identification of the parameters requires additional knowledge in each particular situation. This implies describing how the model can be implemented in the real world, i.e. how energy or matter is used, enters and leaves the system (Saucy and Gabriel, 1999). We will address this challenging question in a

forthcoming paper. Finally, although our goal is neither to rescue nor to dismiss the model, we observe that the logistic equation is of historical importance and of educational significance. For this reason we think valuable to clarify its conceptual framework and its limitations. Clinging to the historical formulation of Verhulst puts a constraint on the parameters r and K . Of course, one remains free to reject this constraint, but would have to face impossible configurations.

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