Short communication

A note on density dependence in population models

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ABSTRACT

One of the most studied phenomena in ecology is density dependent regulation. The model most frequently used to study this behaviour is the theta-logistic model. However, disagreement has developed within the ecology community pertaining to the interpretation of this model’s parameters, and thus as to appropriate values for the parameters to assume. In particular, the parameter \( \theta \) has been allowed to take negative values, resulting in the ‘growth rate parameter’ estimated to be negative for species which are extant and exhibit no signs of becoming extinct in the short-term. Here we explain this phenomenon by formulating the theta-logistic model in the manner in which the original logistic model was formulated by Verhulst (1838), in doing so providing a simple interpretation of model parameters and thus restrictions on values the parameters may assume. We conclude that \( \theta \) should (almost always) be restricted to values greater than – 1. This has implications for studies assessing the form of density dependence from data. Additionally, another model appearing in the literature is presented which provides a more flexible model of density dependence at the expense of only one additional parameter.

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1. Introduction

As a population grows competition for resources amongst its individuals typically increases. This competition slows the growth in population abundance, until the population is reduced to a level at which resources are more readily accessible. The relationship between abundance and growth that emerges is one of the central issues of ecology. Studies of such density dependent regulation abound, typically highlighting its fundamental importance on population dynamics (Verhulst, 1838; Pearl and Reed, 1920; Gilpin and Ayala, 1973; Getz, 1996; Turchin, 2003; Sibly et al., 2005; Stacey and Taper, 1992; Clutton-Brock et al., 1997; Sæther et al., 2000, 2002; Sinclair, 2003; Gerber et al., 2004; Chamaillé-Jammes et al., 2008).

The classical model of population dynamics, the logistic equation (Verhulst, 1838), incorporates density dependent regulation, but in a restrictive way, as it implies that the per-capita growth rate (PGR) of the population declines linearly with population size:

\[
PGR = \frac{1}{n} \frac{dn}{dt} = r \left[ 1 - \left( \frac{n}{K} \right) \right].
\]  

(1)

The parameter \( r \) is a growth rate parameter and \( K \) is the carrying capacity of the population (i.e. the stable equilibrium point of the model in the case \( r > 0 \)).

A model developed to allow more freedom in the form of density dependence is the theta-logistic equation (Gilpin and Ayala, 1973)

\[
\frac{dn}{dt} = r n \left[ 1 - \left( \frac{n}{K} \right) ^{\theta} \right].
\]  

(2)

where \( \theta \) is a parameter describing the curvature of the relationship. When \( \theta < 1 \) there is a concave relationship between abundance and PGR and when \( \theta > 1 \) a convex relationship exists (see Fig. 1).

The theta-logistic model has been applied to several species including acorn woodpecker (inter alia Melanerpes formicivorus) (Stacey and Taper, 1992) and several other populations of birds (Sæther et al., 2000, 2002, 2008), sea otters (Enhydra lutris) off the coast of Washington State, U.S.A. (Gerber et al., 2004), and elephant (Loxodonta africana) in Hwange National Park, Zimbabwe (Chamaillé-Jammes et al., 2008). In fact, it has been used in the largest study of density dependence undertaken to date, in which it was fitted to a large number of population time series from the Global Population Dynamics Database (GPDD; NERC, 1999) to determine if any general patterns of density dependence could be found for mammals, birds, fish and insects (Sibly et al., 2005).

In a number of these studies the parameter \( \theta \) has been allowed to take negative values. Consequently the growth rate parameter \( r \) has been estimated to be negative for species which are extant and exhibit no signs of becoming extinct in the short-term. These studies have created disagreement in the ecology community as to whether such values for parameters are realistic and confusion over the true interpretation of parameters. The purpose of this note is to address these issues and thus hopefully settle any disagreement as to the interpretation of parameters in the theta-logistic model and...
the values appropriate for parameters to assume. Additionally an alternative more general model of density dependence is discussed.

For future reference, we note here that \( \frac{dn}{dt} \) denotes the population growth rate, whilst \( \frac{1}{n}(dn/dt) \) denotes the per-capita growth rate. Additionally, we will consider the population growth rate to consist of a population birth rate minus a population death rate; each of these components, when divided by the population size \( n \), will be referred to as the per-capita birth rate and per-capita death rate, respectively.

2. Density dependence

The logistic model was first formulated in the literature by Verhulst in 1838 (Verhulst, 1838; Gabriel et al., 2005). He proposed the equation

\[
\frac{dn}{dt} = an - bn^2,
\]

where \( a \) is the per-capita birth rate and \( b \) is a positive ‘friction’ coefficient which influences the rate of density dependent regulation. This equation may be expressed in its now more common form (cf. 1) as

\[
\frac{dn}{dt} = an \left[ 1 - \left( \frac{n}{a/b} \right) \right],
\]

so that \( r = a \) and \( K = a/b \).

Following this original formulation, the theta-logistic model can be written

\[
\frac{dn}{dt} = an - bn^{\gamma},
\]

where \( \gamma \) allows more flexibility in the form of density dependence, and it must be larger than 1 to serve its purpose of population regulation if \( a \) and \( b \) are to retain their original interpretations. Expressing this equation in its more ubiquitous form (cf. 2), we have

\[
\frac{dn}{dt} = an \left[ 1 - \left( \frac{n}{(a/b)^{1/(\gamma - 1)}} \right)^{\gamma - 1} \right],
\]

so that \( r = a, K = (a/b)^{1/(\gamma - 1)} \) and \( \theta = \gamma - 1 \). Thus, from this line of reasoning, the parameter \( \theta \) must be greater than 0.

The confusion that arises in the literature, and amongst some of the ecology community, is that Eq. (5) (unlike Eq. (3)) can capture density dependent regulation with parameters having different interpretations. In particular, the model

\[
\frac{dn}{dt} = cn^{\gamma} - dn
\]

also displays density dependence, in the sense that the population growth rate is positive for small population sizes and negative for large population sizes, when \( \gamma < 1 \). This can be incorporated in the previous framework (5) by setting \( a = -d \) and \( b = -c \). Thus if \( \gamma < 1 \), then \( a \) and \( b \) can both be chosen to be negative and the resulting model displays density dependent regulation:

\[
\frac{dn}{dt} = |b|n^{\gamma} - |a|n.
\]

Note that PGR approaches \( a \) as the population size \( n \to \infty \). Thus, the parameter \( \theta \) may assume negative values, but in such a case the parameter \( r \) is no longer the per-capita birth rate, but is the per-capita growth rate as the population size \( n \) tends to infinity.

Closer inspection shows that in (5) the dynamics are composed of a constant per-capita birth rate \( a \) (and thus linear population birth rate), and a population death rate which increases with population size like \( n^\gamma \), whereas in (8) the dynamics are composed of a constant per-capita death rate \( |a| \) (and thus linear population death rate), and a population birth rate which changes with population size like \( n^{\gamma} \). In the former we have both the rate of birth and death increasing with population size \( n \), but death increasing at a faster rate than birth (super-linear population death rate compared to linear population birth rate). In the latter, for \( 0 < \gamma < 1 \) we have, once again, both birth and death increasing with population size, and death increasing at a faster rate than birth; this is due to population birth rate increasing at a sub-linear rate (with death rate remaining linear). However, when \( \gamma < 0 \), we no longer have the population birth rate increasing with population size—it is **always decreasing** with increasing population size \( n \). To be emphatic, if \( \gamma < 0 \) a population with \( n = 4 \) individuals always has a smaller population birth rate than one with \( n = 2 \) individuals. It can be seen from this argument that the assumptions required for use of the model with \( \gamma < 0 \) will rarely (if ever) be satisfied in reality. For this reason care needs to be taken when fitting the model to data—the model with \( \gamma < 0 \) estimated to be less than 0 may provide a ‘best’ fit to the particular data available (typically observations of the population close to the carrying capacity) but the physical properties required for use of such a model will almost never be satisfied for the species from which the data was collected; in such a case estimation should be performed with \( \gamma \) restricted to positive values.

Translating the above arguments into restrictions on the parameter \( \theta \), we can see that it will typically be necessary to restrict \( \theta > -1 \). We note that this is the parameter region considered by Saether et al. (2008), and is less restrictive than that suggested in earlier comments on this subject (Ross, 2006). Saether et al. (2008) comment (page 1203) that this restriction on \( \theta \) results in estimates of \( r \) that can be considered biologically plausible; the current study explains their finding. A summary of the form of the population...
birth and death rates, and interpretation of \( r \), for different values of \( \theta \) is provided in Table 1.

With respect to the theta-logistic model, finally we note that the case \( \gamma = 1 \) (equivalently \( \theta = 0 \)) results in exponential growth or decay depending upon whether \( a - b \) is positive or negative, respectively, and thus implies no density dependence. Whereas with formulation (2) the case \( \theta = 0 \) appears to result in no change to population size \( (dn/dt = 0) \), using formulation (5) we can see that in this case the dynamics are governed by the equation \( dn/dt = (a - b)n \). This is because (2) ignores the dependence of the carrying capacity \( K \) on the parameters \( a, b, \) and \( \gamma \); thus, with respect to estimation of model parameters, the crux of assessing density dependence, it may be useful to estimate these parameters, as opposed to \( r, K, \) and \( \theta \); in any case, estimates of \( K \) tell us important information about the species characteristics \( (b) \).

As discussed above, the theta-logistic model imposes linear growth in either the population birth or population death rate. A more flexible model would allow for non-linear growth in both of these rates. This may be achieved with a model of the same ilk as those previously considered:

\[
dn/dt = an^\theta_1 - bn^\gamma,
\]

where \( a \) and \( b \) are both positive and \( \theta_1 < \gamma \); for the same reasons as \( \gamma > 0 \) is almost always a requirement for use of the theta-logistic model, we will have \( \theta_1 > 0 \). This is the so-called ‘basic’ model of Savageau, derived from similar considerations as here in formulating models from their underlying determinants (Savageau, 1979, 1980; Tsoularis and Wallace, 2002). Reformulating the model into a form more analogous to the theta-logistic model, we have

\[
dn/dt = rn^\theta_1 \left[ 1 - \left( \frac{n}{K} \right)^\theta_2 \right],
\]

where \( r = a, K = (a/b)^{1/\theta_1} \) and \( \theta_2 = \gamma - \theta_1 \).

The basic-Savageau model provides a more flexible and realistic framework in which to study density dependent regulation, allowing for simultaneous non-linear effects of population size on population birth and death rates. Whilst this model certainly allows for a wider range of behaviours than the theta-logistic model, it will obviously still remain inadequate for many populations where factors such as habitat destruction, the Allee effect, and harvesting are present.

3. Summary

Through formulating the theta-logistic model in a manner analogous to Verhulst’s original formulation of the logistic model we have clearly determined the interpretation of model parameters and thus have determined appropriate values to allow the parameters of the theta-logistic model to assume. It appears necessary to require \( \theta > -1 \). In the case \( \theta > 0 \) the parameter \( r \) is the per-capita birth rate, whilst when \( \theta < 0 \) the parameter \( r \) is the per-capita growth rate of the population as the population size tends to infinity. Formulating the theta-logistic model in this manner also elucidates the behaviour of the model in the case \( \theta = 0 \) (see Table 1). Of course one may ignore the formulation provided herein and use the theta-logistic model without constraint; however, the relationship between the model and the population it is proposing to model may be lost. Finally, a more flexible model of density dependence was discussed, the basic-Savageau model (see (9) or (10)), which will hopefully aid in gaining a better understanding of the density dependent regulation of populations.

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References