Comment on “On the Regulation of Populations of Mammals, Birds, Fish, and Insects” II

Joshua V. Ross

Sibly et al. (Reports, 22 July 2005, p. 607) recently estimated the relationship between population size and growth rate for 1780 time series of various species. I explain why some aspects of their analysis are questionable and, therefore, why their results and estimation procedure should be used with care.

My concern with the results of Sibly et al. (1) revolves around the interpretation of their parameters. They model the per capita growth rate (pgr) of populations by the theta-logistic equation

\[ pgr = r_0 \left[ 1 - \left( \frac{N}{K} \right)^\theta \right] \] (1)

where \( N \) is the population size, \( r_0 \) is a parameter representing pgr when \( N = 0 \), \( K \) is the carrying capacity of the population, and \( \theta \) is a parameter describing the curvature of the relationship. When \( N = 0 \), the population growth rate is 0 and, therefore, \( r_0 \) should be defined as the rate of population growth at low densities, as Reynolds and Frecelton (2) did in their discussion of Sibly et al. (1), or perhaps even more accurately as the pgr of the population in the absence of density-dependent regulation. Although this clarification may appear trivial, its importance will become apparent. Also, the parameter \( \theta \) should be defined to take values (strictly) greater than 0. Sibly et al. (1) allow \( \theta \) to be negative and 0. In fact, they estimate \( \theta \) to be negative for real populations [see figure 1C in (1)]. The reason \( \theta \) should be greater than 0 can be seen by considering \( \theta \) negative in Eq. 1. In this case, we have

\[ pgr = r_0 \left[ 1 - \left( \frac{K}{N} \right)^\theta \right] \] (2)

Thus, provided \( r_0 \) is positive (which appears necessary from the above discussion), when the population is below its carrying capacity, pgr is negative, resulting in population extinction. Further, when the population is above its carrying capacity, pgr is positive, resulting in unbounded growth. Sibly et al. (1) allow \( r_0 \) to be negative. This can be seen from consideration of their analysis of the insect population Xylena vetusta [GPDD ID 6321 (3)], presented in figure 1C in (1). They estimate that \( K = 512 \) and \( \theta = -2.0 \) for this population. From the figure, we can see that when \( N \) is approximately 1200, pgr is approximately -0.5. Thus, using Eq. 1, \( r_0 \approx -0.61 \). Therefore, if \( \theta \) is allowed to take negative values, \( r_0 \) must also be negative, so its physical interpretation is lost.

Sibly et al. (1), in their Supporting Online Material (SOM), discuss two mathematical oddities in Eq. 1. They first point out that specifying the value of pgr for low \( N \) at \( N = 0 \) or at \( N > 0 \) makes a big difference, as seen by comparing their figure 2 and figure S1 when \( \theta = 0 \). In figure 2 in (1), the curves are said to be constrained to go through \((N, pgr)\) equaling \((1, 0.1)\), and in figure S1 \((0, 0.1)\) (a seemingly impossible scenario when \( \theta \leq 0 \)). When \( \theta \) is greater than 0, the curves are almost identical. The big differences occur when the parameter \( \theta \) takes negative values (and the value 0). However, this is not due to a “mathematical oddity” but is simply because pgr \( \rightarrow -\infty \) as \( N \rightarrow 0 \) when \( \theta < 0 \) and \( r_0 > 0 \), and pgr is finite when \( N = 1 \) [thus allowing Sibly et al. to choose \( r_0 (\leq 0) \) such that pgr = 0.1]. In the case \( \theta = 0 \), we need to consider the “second mathematical oddity.” Sibly et al. (1) state, “It turns out that when \( \theta \rightarrow 0 \), \( r_0 \rightarrow \infty \) in such a way that \( r_0 \theta \) assumes a finite value not equal to 0.” This cannot simply “turn out”; when \( \theta = 0 \), Eq. 1 is clearly equal to 0 for all \( N \), independent of the value of \( r_0 \), and thus the requirement that the above limiting process takes place is clearly an assumption of the authors.

My concern with the method of estimation used by Sibly et al. is as follows. They state that they fitted Eq. 1 to each of the 3296 tractable time series in the GPDD using a nonlinear least-squares procedure. However, the method for estimating \( \theta \) described in the SOM does not use a nonlinear least-squares procedure. Instead, Sibly et al. fix \( \theta \) at various values (including negative values), regress \( \log(N_{t+1}/N_t) \) on \( N_0^\theta \), and choose the value that gives the lowest residual sum of squares. The constant of this linear regression corresponds to \( r_0 \) and the coefficient of \( N_0^\theta \) corresponds to \( -r_0/K^\theta \). Although this procedure may result in a model that provides a good fit to the data [keeping in mind that \( \log(N_{t+1}/N_t) \) is only a proxy for pgr], this estimated model may not be sensible for all population sizes, and \( r_0 \) may have no physical interpretation. Considering figure 1C in (1), we can see that the model explains the data well, but this model predicts that pgr is approximately 6396 when \( N = 5 \), and approximately 159,907 when \( N = 1 \), a questionable result, and, as already discussed, \( r_0 \approx -0.61 \).

Although I do not believe the above concerns have had a major effect on the overall conclusions of Sibly et al. (1), I do believe they raise an important issue: whether we wish to model the relationship between abundance and growth only for population sizes contained in our data set [again keeping in mind that \( \log(N_{t+1}/N_t) \) is just a proxy for pgr], and thus \( r_0 \) may possibly have no physical interpretation, or to have a relationship that is sensible for all \( N \) and thus retains the physical interpretation of \( r_0 \). The latter can only be achieved with \( \theta > 0 \). In this case, a reasonable fit to the data should still be achievable [cf., Fig. 1 below with figure 2 from (1)]. If this is not the case, then the user should perhaps consider a model other than Eq. 1 to explain the relationship between abundance and growth for the population in question.

![Fig. 1. Illustration of the curves generated by the theta-logistic equation (Eq. 1) for different values of \( \theta \) when \( r_0 = 0.1 \) and \( K = 100 \).](http://science.sciencemag.org/)
References and Notes
4. The author acknowledges the support of the Australian Research Council Centre of Excellence for Mathematics and Statistics of Complex Systems and thanks M. O’Hely, P. Pollett, and D. Sirl for comments.

26 October 2005; accepted 25 January 2006
10.1126/science.1121875
Comment on "On the Regulation of Populations of Mammals, Birds, Fish, and Insects" II
Joshua V. Ross

Science 311 (5764), 1100.
DOI: 10.1126/science.1121875