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

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Sibly *et al.* (Reports, 22 July 2005, p. 607) concluded that density dependence acts far below the carrying capacity in most animal populations. We argue that the authors confused discrete and continuous models, that their best-fit models cannot explain observed oscillations, and that their estimation procedures appear biased. They also neglected trophic and migratory processes, which we demonstrate could underlie their empirical findings.

Sibly *et al.* (1) presented an impressively broad analysis of population data sets with the potential to upend the way ecologists think about the onset of density dependence in regulating population growth (2). They analyzed 1780 time series from the global population dynamics database (GPDD) to assess the relation between the population per capita growth rate (*pgr*) and current population size ( $N_t$ ). This comprehensive effort yields unexpected empirical results. Unfortunately, they misinterpret their analysis, do not discuss the dynamic consequences of their results or potential bias due to known processes, and do not reconcile differences between their results and previous studies.

The empirical analysis anchoring the Sibly *et al.* study is based on computing the *pgr* at each time step using the formula

$$pgr = \ln(N_{t+1}/N_t) = G(N_t) \quad (1)$$

This definition is mathematically equivalent to the difference model

$$N_{t+1} = N_t e^{G(N_t)} \quad (2)$$

Sibly *et al.* mistakenly interpret their results in the context of differential equation models, where *pgr* is defined as an instantaneous rate

$$pgr_{inst} = \frac{1}{N} \frac{dN}{dt} = G(N) \quad (3)$$

They fit the theta-logistic form

$$G(N) = r_0 \left[ 1 - (N/K)^\theta \right] \quad (4)$$

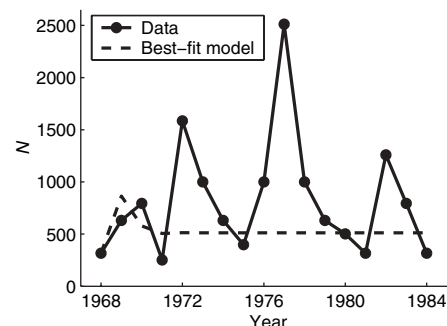
to *pgr* values obtained from the data using Eq. 1, finding the value of  $\theta$  that minimizes squared

residuals without regard for the estimated values of the carrying capacity  $K$  or intrinsic growth rate  $r_0$ . They conclude that birds, mammals, fish, and insects most often exhibit concave up ( $\theta < 1$ ) rather than the expected concave down [or convex (1)] ( $\theta > 1$ ) density dependence.

First, our distinction between *pgr* and *pgr*<sub>inst</sub> is important, because many of the populations experience several-fold changes in  $N$  from one time-step to the next. The discrete-time *pgr* used to fit data is an average value related to *pgr*<sub>inst</sub> through integration of  $G(N)$  over  $(t, t+1)$ . The authors should have interpreted their results in terms of the discrete equation (Eq. 2) that, in the context of Eq. 4, yields the  $\theta$ -Ricker model (3)

$$N_{t+1} = N_t e^{r_0 \left( 1 - \left( \frac{N_t}{K} \right)^\theta \right)} \quad (5)$$

For  $\theta > 1$ , this model is initially (small  $N$ ) concave down and, hence, has the potential to exhibit chaotic behavior (4), whereas the continuous-time  $\theta$  logistic generates very stable trajectories. For  $\theta < 1$ , density dependence is immediate and initially precipitous, thereby yielding biologically implausible predictions: for parameters es-

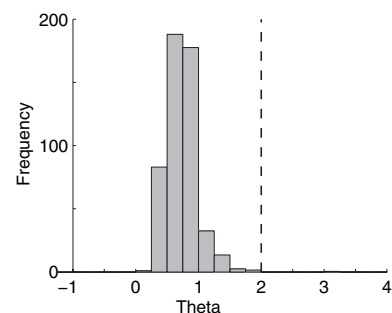


**Fig. 1.** Dynamics of *X. vetusta* (GPDD ID 6321) from figure 1C in (1), superimposed with the dynamics predicted by the best-fit model parameters from Sibly *et al.* Model parameters were  $K = 512$  and  $r_0 = -0.62$ , derived from the regression parameters when  $\theta = -2$ .

timated for *Xylena vetusta* (Fig. 1),  $N_t = 1 \Rightarrow N_{t+1}/N_t = e^{1.6 \times 10^7}$  (extremely large),  $N_t = K/20 \Rightarrow N_{t+1}/N_t = e^{247}$  (a googol, still vast), and  $N_t = K/2 \Rightarrow N_{t+1}/N_t = 6.4$ .

Second, the authors neglect to mention that their best-fit models are incapable of generating time series similar to the data sets from which the estimates were drawn (Fig. 1). It could be argued that this discrepancy is resolvable by making model parameters stochastic. This overlooks the obvious influence of population processes such as trophic interactions or migration among subpopulations in a metapopulation. In the latter case, we expect population growth to be greatly inflated when  $N_t$  is small. An analysis with synthesized data reveals that migration appreciably biases estimates of  $\theta$  downward (Fig. 2).

Third, the authors summarily dismiss incorporating trophic interactions using time delays because of the need to fit additional parameters. However, such interactions are particularly germane for many of their data sets, including Canada lynx (*Lynx canadensis*) and snowshoe hares (*Lepus americanus*), whose population cycles are influenced by strong predator-prey interactions (5). For the lynx, 17 of 20 estimates of  $\theta$  posted in the GPDD are negative and all are  $< 0.5$ , whereas for the hare, 4 of 5



**Fig. 2.** We used Eq. 5, with modifications below, to generate 1000 different time series, each of 20 data points, under the following assumptions. Density dependence was sigmoidal, corresponding to  $\theta = 2$ . We introduced environmental stochasticity by making  $r_0$  a uniform random variable (URV) on  $[0.75, 2.75]$  and  $K$  a URV on  $[250, 750]$ . Finally, we included a migration effect by assuming that a proportion  $P = 0.1$  of individuals emigrate at the end of each time period to an external migration pool (as could exist under a metapopulation structure), while  $c$  individuals immigrate back into the population from this pool; we treated  $c$  as a URV on  $[40, 60]$ . The full model is therefore  $N_{t+1} = N_t(1 - p)e^{r_0(1 - (N_t/K)^\theta)} + c$ . Of 1000 estimated  $\theta$  values, 999 were  $< 2$  (median 0.7), and in only 7.1% of cases did the 95% confidence interval for  $\theta$  include 2. This is due to migration rather than stochasticity because, without migration, 522 of 1000 estimated  $\theta$  values were  $< 2$  (median 1.9), and 62.9% of 95% confidence intervals included 2.

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estimates of  $\theta$  are negative and all are  $<1$ . Sibly *et al.* should not have dismissed interspecific interactions without using synthesized data to demonstrate that this is a legitimate simplification.

Fourth, the authors' *pgr* regression method appears to yield lower estimates of  $\theta$  than the more sophisticated approach of Saether *et al.* (6), which incorporated environmental stochasticity. For the one data set that appears in both reports (*Accipiter nisus*, GPDD ID 3253), Saether *et al.* estimated  $\theta = 2.57$  (SD, 0.69), whereas the Sibly *et al.* method (applied to the same period, 1975 to 1989) yields an estimate of  $\theta = -3.98$  (95% confidence interval,  $-15.8$  to

6.31). Sibly *et al.* refer to Saether *et al.* but fail to point out this difference. We suspect that the *pgr* regression method may be biased: Using the continuous logistic equation to generate artificial data by calculating  $N_{t+\Delta t}$  for different initial conditions  $N_t$ , the *pgr* versus  $N_t$  curve is concave up rather than linear.

Sibly *et al.* are to be lauded for unearthing an unexpectedly strong signal of concavity in the *pgr* generated using Eq. 1 for a wide array of species, but their interpretation of concavity in intraspecific density dependence is far from proven. Other explanations, such as migration, trophic interactions, or autocorrelations in environmental factors, appear to be more plau-

sible, particularly because their method appears to be biased.

#### References and Notes

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