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

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Stochasticity in time series explains concave responses of per capita growth rate to population size. The gradients with the natural log of population size have more biological importance because they measure strength of density compensation. Its weakening with increasing body size across taxa (Sibly et al., Reports, 22 July 2005, p. 607) is consistent with slower responses in ascent than descent toward carrying capacity. Time series therefore suggest that populations of large-bodied animals underfill their environments.

Sibly et al. (1) analyzed a large number of time series for the influence of population size at time t (Nt) on per capita growth rate (pgr). Their principal finding is a predominating deviation from the much-used logistic model of a linear decline in pgr, with Nt (characterized by θ = 1) toward a concave decline (θ < 1, and often negative). However, a concave response is precisely the expectation for any independently distributed sequence (2). The effect arises from the definition of pgr = ln(Nt+1) - ln(Nt). Any sequence in which Nt+1 is independent of Nt will have an average linear regression for the relation of pgr to ln(Nt) given by the equation

\[ \text{average}[\ln(N_{t+1}) - \ln(N_t)] = -1 \times \ln(N_t) + \ln(N_0) \]  

(1)

The regression slope of pgr, to ln(Nt) thus takes a gradient of −1, and its intercept is at the within-series average [ln(Nt+1)]. The corresponding plot of pgr, against raw (unlogged) population size is therefore inherently concave, with a between-series average θ = 0. The universality of θ < 1 is an example of the illusory patterns that can arise from regressing variables against themselves (3). The between-series average θ = 0 observed in real data sets (1) suggests only a strong component of stochasticity in the time series, be it caused by fluctuations in the quality of the environment or by measurement error. Equation 1 nevertheless fails to explain why several animal classes have regression slopes of pgr, on ln(Nt) typically much shallower than −1, and this failure has been used to justify ruling out measurement error as causing the concave relation of pgr, to Nt (1). Here, I show that these shallow gradients are logically explained by under-compensating density dependence, without ruling out stochasticity as the sole cause of θ < 1.

The negative slope of pgr, to ln(Nt) has a magnitude γ that measures the strength of density dependence (4). In the presence of undercompensating density dependence, pgr decreases with ln(Nt) at a rate γ < 1 (or equally, the “killing power” (5): [γ = ln(Nt) - ln(Nt+1)] increases with ln(Nt) at rate γ < 1). In effect, undercompensation causes ln(Nt+1) to deviate from the average population size in direct proportion to the deviations of ln(Nt), although less strongly (unless density has negligible effect, in which case the rate = 0). Perfectly compensating density dependence gives γ = 1, when ln(Nt+1) fluctuates independently of ln(Nt) or is invariant in the absence of stochasticity. Density overcompensation causes ln(Nt+1) to deviate in inverse proportion to ln(Nt) as it overshoots the returns toward the average, and it yields γ > 1. Simulations in Fig. 1 show how stochasticity induces the concave relation of pgr, to Nt and how density undercompensation independently sets the slope of pgr, to ln(Nt) shallower than −1 (i.e., γ < 1). The empirical observation of shallower slopes with larger body size across taxa (1) is consistent with increasingly undercompensating responses from slower vital rates.

Because any stochastic contributions to time series will force θ < 1, its value reveals little about deviations from carrying capacity. Yet Sibly et al. (1) interpreted the observed predominance of θ < 1 to mean generally slower descents than ascents toward equilibrium which, in combination with an extended right-hand tail typifying the frequency distribution of Nt, led them to conclude that “many animals may...

Fig. 1. Hypothetical time series of population size N over time t simulated by the model (6) Nt+1 = Nt · exp(rt) / (1 + (a · Nt)β). (A) Regressions of fitted θ = 0.3, 0.7, 1.8, and 2.1 from most concave to most convex line, resulting from weak to strong density dependence given by, respectively, b = 0.5 (monotonic damping), 1.0 (logistic), 3.0 (damped oscillations), and 4.0 (stable limit cycles), all with maximum net rate of increase, r0 = 1.1, a = 0.01, and N0 = 1. These regressions all become markedly concave (θ = 0 for all) in the presence of stochasticity. A stochastic contribution is added to the model by calculating each Nt+1 from an Nt that has fluctuated on a normal distribution with SD = 1 either side of the loge of its calculated value. (B) An example of a sharply concave relation of pgr, to Nt, with fitted θ = 0.8, r0 = 1.1, and a = 0.01. This stochasticity linearizes the relation of pgr, to ln(Nt) in (D). Its linear regression explains 26% of the variation in pgr, and its slope of −0.523 reveals the density undercompensation that results from setting b = 0.1. With negligible stochasticity and Nt close to K, the model will give a slope of pgr, to ln(Nt) = −b if r0 is large (γ → b as r0 → ∞). Alternatively, if Nt+1 is set only by the stochastic variation, the linear regression of pgr, explains approx. 50% of the variation in ln(Nt) regardless of SD and has gradient γ = −1 (consistent with Eq. 1).
spend most of their time at or above carrying capacity.” An extended tail will result from any $N_t$ constrained to positive values, however, and descent appears slower only because $p_{gr_t}$ is measured in logarithmic units. The nature of exponential growth dictates that time spent ascending from a finite negative deviation always exceeds time descending from a positive deviation of equal magnitude, particularly with weak density compensation (confirmed for Fig. 1A simulations). Only the small-bodied insects, with slopes of $p_{gr_t}$ to ln($N_t$) observed steeper than $-1$ ($I$), may have sufficient density overcompensation to determine some time spent cycling above carrying capacity. The shallower slopes observed for larger-bodied animals indicate their tendency to under-fill environments, with consequent dynamic stability and vulnerability to habitat loss both relevant to population management.

The regression slopes of $p_{gr_t}$ to ln($N_t$) reveal much more about regulation than $\theta$ because their estimates of density compensation are not confounded with the presence of stochasticity. The principle challenge for interpreting their slopes is to resolve time-lagged contributions to the strength of density compensation ($\hat{\theta}$), whereas the challenge for interpreting variation around the regressions is to partition out stochastic measurement error from the deterministic component given by the population tracking stochastic fluctuations in its carrying capacity.

References and Notes


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