

# The upper limit for the exponent of Taylor's power law is a consequence of deterministic population growth

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## ABSTRACT

**Question:** The exponent of Taylor's power law has an apparent upper limit of two. What might produce that limit?

**Method:** I calculate Taylor's power law for data generated by three well-known single-species population dynamics models.

**Result:** Rescaling dimensionless population growth equations leads to the upper limit of two. Empirical values less than two reflect a departure from determinism. This will allow improved understanding of the combined effects of deterministic dynamics and stochasticity on population fluctuations and long-term stability.

*Keywords:* deterministic dynamics, population growth, scaling, stochasticity, Taylor's power law.

## INTRODUCTION

Taylor's power law is a well-documented relationship between the mean and variance in abundance for ecological populations. To generate Taylor's power law for empirical data, one plots log transformed variance in abundance as a function of log transformed mean abundance. Taylor first made these types of plots (Taylor, 1961) and the relationship has subsequently been documented for larger data sets and a wide range of taxa (Taylor *et al.*, 1978, 1983; Taylor and Woiwod, 1980; Taylor, 1986; Maurer and Taper, 2002; Kerkhoff and Ballantyne, 2003). Taylor's initial plots were for spatial data but temporal data have also been well characterized by power law scaling between the mean and variance of abundance (Taylor and Woiwod, 1980; Anderson *et al.*, 1982; Taylor *et al.*, 1983; Taylor, 1986; Perry, 1994; Maurer and Taper, 2002; Kerkhoff and Ballantyne, 2003). For almost all species, the exponents of Taylor's power law from temporal data fall in the interval between one and two with many towards the extremes (Anderson *et al.*, 1982; Keeling, 2000).

The existence of Taylor's power law for temporal data has prompted population ecologists to link population dynamics to the empirical patterns of abundance described

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by the power law. The first models that included population dynamics did so only in the context of spatial processes (Iwao, 1968; Taylor and Taylor, 1977; Taylor and Woiwod, 1980; Taylor, 1981), but later studies have focused on demographics and their relationship to Taylor's power law (Anderson *et al.*, 1982; Perry, 1994; Keeling, 2000; Maurer and Taper, 2002; Kilpatrick and Ives, 2003). However, the demographic models that have been related to Taylor's power law are, to a large degree, stochastic and include spatial movement or competition. Here, I show that a large class of deterministic population growth models for isolated single-species populations generate Taylor's power law with an exponent of two.

### MODELS

Single-species models of population dynamics usually take one of two forms to reflect the reproductive biology of the species, discrete or continuous in time. I consider, in detail, two common discrete-time population growth models, the familiar logistic map

$$N_{t+1} = rN_t(1 - N_t/K) \quad (1)$$

and the Ricker map (Ricker, 1954)

$$N_{t+1} = N_t e^{r(1 - N_t/K)} \quad (2)$$

and one continuous time model, the lagged logistic growth model

$$\frac{dN}{dt} = rN \left[ 1 - \frac{N(t - \tau)}{K} \right] \quad (3)$$

first proposed by Hutchinson (1948). In all models,  $r$  is the intrinsic rate of population increase and  $K$  is the carrying capacity for the environment in which the population lives. In the continuous-time model,  $\tau$  is the time delay of density dependence. All three models have been well studied in the ecological and mathematics literature because of the rich dynamics they exhibit (Jones, 1962; May, 1973; Holmgren, 1996; Kot, 2001; Murray, 2002). Most notably, as  $r$  increases, all of the models exhibit periodic solutions or limit cycles that are independent of initial conditions. There has been considerable debate in the literature as to how prevalent population cycles are, but Turchin (2003) provides compelling evidence for the existence of cycles in empirical populations. It is therefore reasonable to first study the mean–variance scaling properties of the simplest population models that produce cycles. And it is necessary that models exhibit sustained fluctuations in the current treatment so temporal variance can be calculated.

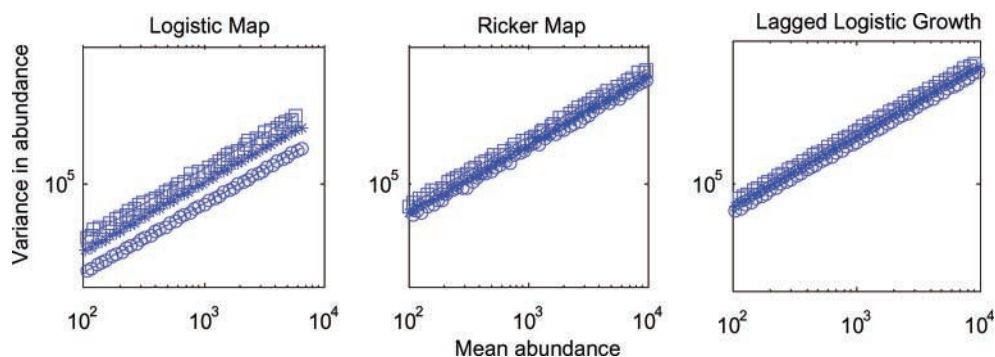
For low rates of population growth, mean abundance is a sufficient descriptor of the dynamics of the three models, but with higher population growth rates, the presence of fluctuations in abundance necessitates an additional descriptor for completeness, namely the variance. Although these models are purely deterministic and the amplitude of periodic fluctuations can sometimes be calculated (see Appendix), the variance of a time series yields essentially the same information. And because Taylor's power law is a relationship between the mean and variance of empirical data, I followed convention and calculated the mean and variance of time series generated by the above models. Additionally, once chaos occurs, the calculation of an amplitude is not possible. For completeness, however, I calculated the amplitude and the mean for the logistic map in the Appendix to show that the ratio of amplitude to mean is independent of  $K$ .

## DATA

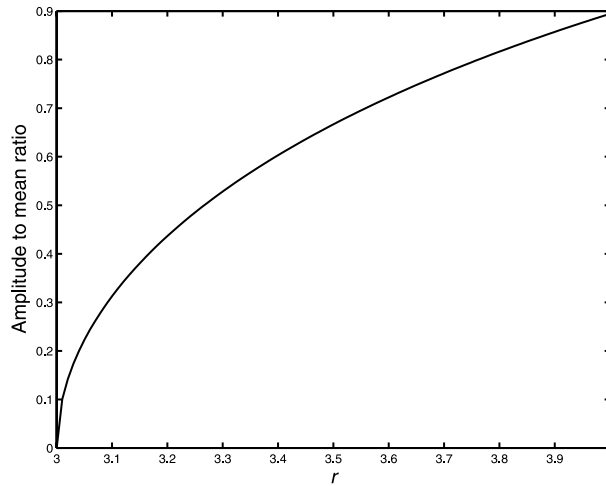
For the models considered here, growth rates below specific thresholds ( $r < 3$  for the logistic map,  $r < 2$  for the Ricker map, and  $r\tau < \pi/2$  for lagged continuous logistic growth) result in monotonic approach or damped oscillations towards a stable equilibrium, but above these thresholds all models produce sustained fluctuations (for details, see May, 1973; Kot, 2001). Therefore, it only makes sense to calculate variance for model output generated with  $r$  above the critical threshold for oscillatory dynamics. Otherwise, there is no systematic increase in variance of abundance with an increase in mean abundance because there is no variability at all.

To generate data for which Taylor's power law could be calculated, I performed simulations of the three aforementioned models with  $K$  ranging from 100 to 10,000 and  $r$  ranging from 3.1 to 3.9 (so all models produced sustained oscillations). For each combination of  $r$  and  $K$ , I iterated models (1) and (2) for 1000 time steps/units and simulated (3) using a linear spline approximation described by Hoppensteadt (1993) with  $\tau = 1$ . I then calculated the mean and the variance of the last 100 time steps for each simulation to eliminate the effects of transient dynamics. The log transformed means and variances for each simulation are plotted in Fig. 1.

Although there are slight quantitative differences associated with the dynamics of the models, the qualitative patterns in Fig. 1 are the same. All three models generate Taylor's power law with an exponent of two when  $r$  is large enough to produce indefinite oscillations. The differences in the normalization constants (analogous to the y-intercept) of the power laws reflect different population growth rates. Growth rate has a greater influence on the normalization constant for the logistic map than for the Ricker map or continuous logistic growth with a time lag. Coefficients of variation of dimensionless growth equations determine the normalization constants of Taylor's power law in general (see below) and the amplitude to mean ratio for a particular  $r$  value determines the normalization constant, when the ratio can be calculated (see equation A5 in the Appendix). In Fig. 2, the amplitude to mean ratio for period two orbits of the logistic map is plotted as a function of  $r$ . Clearly, increasing  $r$  increases the normalization constant of Taylor's power law.



**Fig. 1.** Taylor power laws for simulated data from the logistic map, the Ricker map and the continuous logistic equation with a time lag. Growth rates ( $r$ ) correspond to the same symbols in all three panels (3.1 =  $\circ$ , 3.5 =  $*$ , 3.9 =  $\square$ ). The slopes of the least squares regressions for simulations with growth rates (3.1, 3.5, 3.9) are (2.003, 1.9995, 2.0208) for the logistic map, (2.0014, 1.9943, 1.9898) for the Ricker map and (2.000, 1.9927, 2.0059) for the lagged continuous logistic equation respectively.



**Fig. 2.** Amplitude to mean ratio (equation A5) for the logistic map (equation 1) changes as a function of population growth rate  $r$ . Period two orbits occur for  $r > 3$ . Higher growth rates result in larger fluctuations in abundance.

### VARIANCE SCALING

The fact that these particular population growth models all generate power laws is compelling, but a more general statement about population growth is possible; a population growth process that yields a dimensionless description through a linear change of variables will generate Taylor's power law with an exponent of two if fluctuations in population size persist and the population growth rate remains constant through time. This is a consequence of the properties of mathematical expectation. To produce populations with differing carrying capacities, one multiplies a dimensionless population growth equation by the appropriate scale factor ( $\kappa$ ) to obtain a specific carrying capacity. For example, to rescale the dimensionless logistic map,  $X_{t+1} = rX_t(1 - X_t)$  in which  $X_t = N_t/\kappa$ , to a particular carrying capacity  $\kappa$ ,  $X_t$  is multiplied by  $\kappa$  to recover  $N_t$ . Subsequent calculation of the mean ( $E(N)$ ) and the variance ( $V(N)$ ) of the population trajectory introduce the scale factor in a linear fashion ( $E(\kappa N) = \kappa E(N)$ ) and a quadratic fashion ( $V(\kappa N) = \kappa^2 V(N)$ ) respectively. The variance of a population growth process meeting the above assumptions scales as a function of the mean of the process in the following way:

$$V(\kappa N) = \kappa^2 V(N) = [E(\kappa N)]^2 \frac{V(N)}{[E(N)]^2} \quad (4)$$

where  $N$  is the number of individuals in the population. Therefore, a linear increase in mean abundance results in a quadratic increase in variance of abundance with the normalization constant of Taylor's power law given by the square of the coefficient of variation ( $CV = \sqrt{V(N)}/E(N)$ ) of the dimensionless population growth equation. This is seen by taking logarithms of both sides of (4) to get

$$\log[V(\kappa N)] = 2\log[E(\kappa N)] + \log\left[\frac{V(N)}{E(N)^2}\right] \quad (5)$$

In (5),  $\kappa$  is the only parameter so long as the dimensionless growth process does not change ( $E(N)$  and  $V(N)$  constant). Taylor's power law generated by models that fit the above criteria will have a constant exponent of two throughout the entire range of mean abundance. The quantity  $\log \left[ \frac{V(N)}{E(N)^2} \right]$  is independent of  $\kappa$  and determines the normalization constant.

## DISCUSSION

The value of two for the exponent of Taylor's power law is, in a sense, a null expectation that has been proposed before, albeit on different grounds. Gillis *et al.* (1986) showed that Taylor's power law with an exponent of two is a direct consequence of the ideal free distribution proposed by Fretwell and Lucas (1970), but this argument is based on the movement of individuals between patches, not on any population growth process. Anderson *et al.* (1982) and Keeling (2000) have shown that two is the upper limit for the slope of Taylor power laws generated by population growth models with some degree of stochasticity and some spatial dynamics. Kilpatrick and Ives (2003) have also concluded from models of interspecific competition that two appears to be an upper limit for the exponent of Taylor's power law. I have shown that Taylor's power law with an exponent of two is the result of purely deterministic population dynamics without any spatial movement. This analysis also suggests that the exact form of density dependence operating in a population may not be extremely important because all deterministic population growth models that can be non-dimensionalized generate Taylor's power law with an exponent of two.

The fact that two is more of an upper limit for the exponent of both empirically and theoretically derived power laws (Taylor and Woivod, 1980; Keeling, 2000; Maurer and Taper, 2002; Kilpatrick and Ives, 2003) suggests that deterministic density dependence, stochasticity and movement are conspiring to generate the mean to variance ratios observed for real-world populations. Some empirically calculated power laws have exponents slightly greater than two, but it is unclear whether this is the result of sampling error or is indicative of processes of deeper significance. As of now, I am in general agreement with other authors (Anderson *et al.*, 1982; Keeling, 2000; Kilpatrick and Ives, 2003) that two is an intuitive upper limit for the exponent of Taylor's power law because of strong theoretical support and insufficient empirical evidence to reject a large body of theory.

In general, Taylor's power law with an exponent of two implies that population dynamics are invariant with respect to carrying capacity (Keeling, 2000). This can be seen by noting that the coefficient of variation of abundance equals one irrespective of mean abundance,

$$CV = \frac{\sqrt{V(N)}}{E(N)} \propto \frac{\sqrt{E(N)^2}}{E(N)} = 1 \quad (6)$$

and that the ratio of amplitude to mean is independent of  $K$  (see Appendix). Thus, when the exponent of Taylor's power law is two, we are justified in removing mean abundance from the discussion of population fluctuations (Keeling, 2000). This means that for deterministic models of the sort discussed here, the non-dimensional growth form captures all possible dynamics. Therefore, an exponent of two for Taylor's power law generated by empirical data

may indicate that the population growth is invariant with respect to carrying capacity or abundance. This is significant because it means that the relative magnitude of fluctuations in abundance is not affected by mean population size. In other words, there is no buffering against population decline or increased stability with increased abundance.

If deterministic population dynamics are thought to be well described by a model that generates Taylor's power law with an exponent of two, then an exponent of less than two for an empirically derived power law indicates that population dynamics depend on population size. Stochastic effects and the intrinsic rate of population increase may both be influenced by abundance. Keeling (2000) has shown that the form of stochasticity determines, to a large degree, the exponent of mean to variance ratios for models incorporating stochasticity. However, the influence of stochasticity is only realized for a limited range of mean abundance. The underlying deterministic density dependence is more influential over the remaining range of mean abundance (Keeling, 2000). In contrast, purely deterministic dynamics of the sort presented here have constant influence for the entire range of mean abundance. This tells us that we do not fully understand mean–variance scaling, but also that the interplay between determinism and stochasticity is critical for our understanding of population fluctuations.

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#### REFERENCES

- Anderson, R.M., Gordon, D.M., Crawley, M.J. and Hassell, M.P. 1982. Variability in the abundance of animal and plant species. *Nature*, **296**: 245–248.
- Fretwell, S.D. and Lucas, H.L. 1970. On territorial behavior and other factors influencing habitat distribution in birds. I. Theoretical development. *Acta Biotheor.*, **19**: 16–36.
- Gillis, D.M., Kramer, D.L. and Bell, G. 1986. Taylor's power law as a consequence of Fretwell's ideal free distribution. *J. Theor. Biol.*, **123**: 281–287.
- Holmgren, R.A. 1996. *A First Course in Discrete Dynamical Systems*. New York: Springer.
- Hoppensteadt, F.C. 1993. *Analysis and Simulation of Chaotic Systems*. New York: Springer.
- Hutchinson, G.E. 1948. Circular causal systems in ecology. *Ann. NY Acad. Sci.*, **50**: 221–246.
- Iwao, S. 1968. A new regression method for analyzing the aggregation pattern of animal populations. *Res. Popul. Ecol.*, **10**: 1–20.
- Jones, G.S. 1962. On the nonlinear differential difference equation  $f'(x) = -af(x-1)[1+f(x)]$ . *J. Math. Anal. Appl.*, **4**: 440–469.
- Keeling, M.J. 2000. Simple stochastic models and their power-law type behaviour. *Theor. Popul. Biol.*, **58**: 21–31.
- Kerkhoff, A.J. and Ballantyne, F. 2003. The scaling of reproductive variability in trees. *Ecol. Lett.*, **6**: 850–856.
- Kilpatrick, A.M. and Ives, A.R. 2003. Species interactions can explain Taylor's power law for ecological time series. *Nature*, **422**: 65–68.
- Kot, M. 2001. *Elements of Mathematical Ecology*. Cambridge: Cambridge University Press.
- Maurer, B. and Taper, M.L. 2002. Connecting geographical distributions with population processes. *Ecol. Lett.*, **5**: 223–231.
- May, R.M. 1973. *Stability and Complexity in Model Ecosystems*. Princeton, NJ: Princeton University Press.

Murray, J.D. 2002. *Mathematical Biology*. New York: Springer.  
 Perry, J.N. 1994. Chaotic dynamics can generate Taylor's power law. *Proc. R. Soc. Lond. B*, **257**: 221–226.  
 Ricker, W.E. 1954. Stock and recruitment. *J. Fish. Res. Board Can.*, **11**: 559–623.  
 Taylor, L.R. 1961. Aggregation, variance and the mean. *Nature*, **189**: 732–735.  
 Taylor, L.R. 1986. Synoptic dynamics, migration and the Rothamsted insect survey. *J. Anim. Ecol.*, **55**: 1–38.  
 Taylor, L.R. and Taylor, R.A.J. 1977. Aggregation, migration and population mechanics. *Nature*, **265**: 415–421.  
 Taylor, L.R. and Woivod, I.P. Temporal stability as a density-dependent species characteristic. *J. Anim. Ecol.*, **49**: 209–224.  
 Taylor, L.R., Woivod, I.P. and Perry, J.N. 1978. The density-dependence of spatial behaviour and the rarity of randomness. *J. Anim. Ecol.*, **47**: 383–406.  
 Taylor, L.R., Taylor, R.A.J., Woivod, I.P. and Perry, J.N. 1983. Behavioural dynamics. *Nature*, **303**: 801–804.  
 Taylor, R.A.J. 1981. The behavioural basis of redistribution. 1. The delta-model concept. *J. Anim. Ecol.*, **50**: 573–586.  
 Turchin, P. 2003. *Complex Population Dynamics*. Princeton, NJ: Princeton University Press.

**APPENDIX**

For any discrete map  $f(x)$ , fixed points are calculated by solving  $f(x) = x$ . Values for period two orbits are calculated by solving  $f^2(x) = x$ . Higher-order orbit values are calculated similarly by solving  $f^n(x) = x$ . For the logistic map,  $f^2(x)$  is given by

$$r^2 N(1 - N/K) \left[ 1 - \frac{rN(1 - N/K)}{K} \right] \tag{A1}$$

Solving (6) for values  $N^*$  of the period two orbit yields the non-trivial solutions

$$N^* = \begin{cases} \frac{K(r-1)}{r} & (a) \\ \frac{K}{r} \left[ \frac{1}{2} + \frac{r}{2} + \frac{\sqrt{r^2 - 2r - 3}}{2} \right] & (b) \\ \frac{K}{r} \left[ \frac{1}{2} + \frac{r}{2} - \frac{\sqrt{r^2 - 2r - 3}}{2} \right] & (c) \end{cases} \tag{A2}$$

The first solution (a) is a fixed point which is obviously a two-orbit solution and the second two solutions (b and c) are the non-degenerate two-orbit values. Their difference

$$\frac{K}{r} \sqrt{r^2 - 2r - 3} \tag{A3}$$

is the amplitude of the period two orbit. The mean value of the trajectory through time is

$$K \frac{(r+1)}{2r} \tag{A4}$$

Therefore, the ratio of amplitude to mean is

$$\frac{2\sqrt{r^2 - 2r - 3}}{(r + 1)} \quad (\text{A5})$$

This ratio is an increasing function of  $r$  and is analogous to the coefficient of variation. It is obviously independent of  $K$ , so relative fluctuations are independent of population size as discussed in the text. The same result holds for higher-order periodic orbits as well.