

## Population fluctuations, power laws and mixtures of lognormal distributions

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### Abstract

A number of investigators have invoked a cascading local interaction model to account for power-law-distributed fluctuations in ecological variables. Invoking such a model requires that species be tightly coupled, and that local interactions among species influence ecosystem dynamics over a broad range of scales. Here we reanalyse bird population data used by Keitt & Stanley (1998, Dynamics of North American breeding bird populations. *Nature*, 393, 257–260) to support a cascading local interaction model. We find that the power law they report can be attributed to mixing of lognormal distributions. More tentatively, we propose that mixing of distributions accounts for other empirical power laws reported in the ecological literature.

### Keywords

Self-organised criticality, bird population dynamics, power laws.

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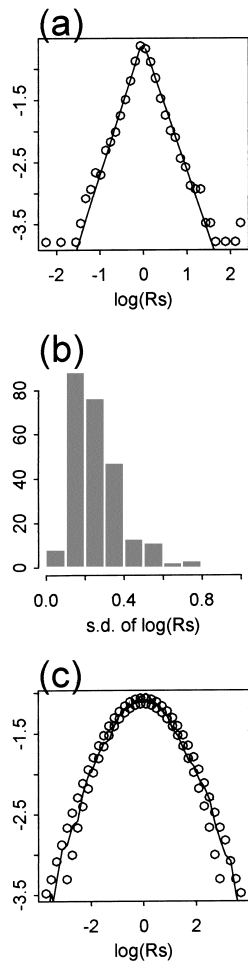
Keitt & Stanley (1998) report that year-to-year fluctuations of North American breeding bird populations adhere to a power law distribution of event sizes. Power law scaling can arise in inanimate systems as a result of local interactions among particles that propagate through space (Stanley 1995). Keitt & Stanley (1998) therefore propose that local interactions among bird species “cascade” spatially to produce power-law-distributed population fluctuations for the North American avifauna. We report here that the empirical power law they derive can be attributed to mixing of lognormal distributions.

Keitt & Stanley (1998) derive their empirical power law from abundance data collected on over 600 bird species from approximately 2500 survey routes throughout North America (data available at <http://www.mp2-pwrc.usgs.gov/bbs>). They characterise population fluctuations for each species on each survey route as  $R_s = N_s(t+1)/N_s(t)$ , where  $N_s(t)$  and  $N_s(t+1)$  are the number of individuals of species  $s$  observed on a particular route for years  $t$  and  $t+1$ . They then aggregate  $R_s$  values across all species and routes to obtain the power law  $P(R_s) \propto R_s^{\pm\alpha}$ , where  $P(R_s)$  is the probability of a fluctuation of size  $R_s$  occurring,  $\alpha = 2$  when  $R_s \leq 1$ , and  $\alpha = -2$  when  $R_s \geq 1$ .

We analyse the same data as Keitt & Stanley (1998) but, for each species, consider only one survey route that meets the following criteria: (1) it has 25 or more years of nonzero abundance data for the species of interest; (2) it has the highest geometric mean abundance among the routes meeting criterion (1) and (3) this geometric mean is  $\geq 10$  individuals. We adopt these more stringent criteria to avoid

sampling errors and indeterminacy of  $R_s$  values that occur when dividing by 0. After computing the  $R_s$  values for each species and aggregating  $R_s$  values across all species, we observe straight-line relationships between  $\log_{10}(P(R_s))$  and  $\log_{10}(R_s)$  (Fig. 1a), indicating a power law relationship between the two variables. As reported by Keitt & Stanley (1998), we find that the distribution of  $\log_{10}(R_s)$  values is symmetrical about 0, indicating that there is no discernible overall trend in population abundance.

The standard deviation of  $\log_{10}(R_s)$  varies considerably among the 250 species we analysed (Fig. 1b). If we separately standardise the distribution of  $\log_{10}(R_s)$  for each species with respect to mean ( $= 0$ ) and variance ( $= 1$ ) and then aggregate the standardised values across all species, the empirical frequencies lie within the 95% confidence intervals of those estimated for the corresponding lognormal distribution (Fig. 1c). Moreover, if we sample 25 values [same as our criterion (1)] from each of 250 lognormal distributions, all with a mean of  $\log_{10}(R_s) = 0$ , but with standard deviations distributed as in Fig. 1(b), the aggregate distribution of simulated  $R_s$  values is a power law identical to that in Fig. 1(a) and to that reported by Keitt & Stanley (1998). The power law they report can therefore be attributed to mixing of lognormal distributions, a result consistent with that of Hsu *et al.* (1974). We cannot, however, reject other explanations for this power law (e.g. Embrechts *et al.* 1998; Podobnik *et al.* 2000; see Appendix) because 25 data points is a small sample for investigating behaviour at the tails of a distribution.



**Figure 1** (a) Frequency distribution of  $\log_{10}(R_s)$  for 250 species combined. Frequencies are computed as proportions of data points whose values fall within each of 40 bins of equal width on a  $\log_{10}$ -scale. The slopes of the power law fits are identical to those of Keitt & Stanley (1998) ( $\pm 2$ ), although we observe more scatter near the tails owing to a much reduced sample size. (b) Frequency distribution of the standard deviations of  $\log_{10}(R_s)$  for the 250 species analysed. (c) The line represents the frequency distribution of  $\log_{10}(R_s)$  for all species combined after separately standardising values for each species with respect to mean ( $= 0$ ) and variance ( $= 1$ ). Dots delineate 95% confidence intervals of frequency estimates (computed separately for each bin) for the corresponding normal distribution of  $\log_{10}(R_s)$ . Data are binned as in (a) to compute frequencies.

The lognormal distribution can be justified theoretically because population growth is a multiplicative process (Dennis & Patil 1988). The probability density function (PDF) that results from mixing  $k$  lognormal distributions can be expressed as

$$P(x) = \sum_{i=1}^k \hat{\omega}_i f_i(x)$$

where  $f_i(x)$  is a lognormal PDF and  $\hat{\omega}_i$  is the proportion of points contributed by  $f_i(x)$  to  $P(x)$  with  $\sum \hat{\omega}_i = 1$ . The PDF of the mixed distribution thus depends on the form of the  $k$  underlying lognormal distributions and their relative contributions to the mix. Mixing lognormal distributions does not always yield a power law but if, as here, means are identical but variances vary among distributions contributing to the mix, the resulting distribution will be fat-tailed compared to the lognormal (Titterton *et al.* 1985).

Ecological systems are composed of heterogeneous units that are influenced by a variety of processes that vary in the scale and magnitude of their effects. Mixing of distributions may therefore account for many, if not most, empirical power laws reported in the ecological literature [see Sole *et al.* (1999) for a review]. For the North American avifauna, we find that the standard deviations of the  $\log_{10}(R_i)$  distributions are significantly correlated with bird body mass ( $r = 0.46$ ,  $P < 0.0001$ ), which here varies among species by over 3 orders of magnitude. Species differences thus contribute to differences in the magnitudes of bird population fluctuations which, in turn, produces a power law when fluctuation data are aggregated across multiple species.

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#### BIOSKETCH

Mr Allen is presently pursuing a PhD in Biology at the University of New Mexico. His current research involves developing analytical models to predict landscape and community dynamics, and designing and implementing microcosm experiments to test predictions of these models.

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#### APPENDIX

In response to this paper, Keitt and Stanley (personal communication) state that Keitt and Stanley (1998) also present metapopulation dynamics as a potential explanation for this power law. Keitt and Stanley (personal communication) also point out that mixing of locally exponential distributions is what generates power laws in cascading local interaction models and in the metapopulation model they propose. Here we present a third possible mechanism by which mixing of distributions can occur to generate this power law. In contrast to the mechanisms proposed by Keitt and Stanley (1998), our mechanism does not involve species interactions and assumes only that the magnitudes of population fluctuations varies among species. Keitt and Stanley are currently testing other predictions of their metapopulation model in an attempt to determine the extent to which metapopulation dynamics and species differences contribute to this power law. The issues raised here demonstrate that interpreting power laws requires careful consideration of precisely how mixing of distributions occurs.