

LETTER

Weak population regulation in ecological time series

Nicolas L. Ziebarth,^{1,2} Karen C. Abbott^{2†} and Anthony R. Ives^{2*}

¹*Department of Economics, Northwestern University, Evanston, IL 60202, USA*

²*Department of Zoology, University of Wisconsin – Madison, Madison, WI 53706, USA*

*Correspondence:

E-mail: arives@wisc.edu

†Present address: Department of Ecology, Evolution and Organismal Biology, Iowa State University, Ames IA 50011, USA.

Abstract

How strongly natural populations are regulated has a long history of debate in ecology. Here, we discuss concepts of population regulation appropriate for stochastic population dynamics. We then analyse two large collections of data sets with autoregressive-moving average (ARMA) models, using model selection techniques to find best-fitting models. We estimated two metrics of population regulation: the characteristic return rate of populations to stationarity and the variability of the stationary distribution (the long-term distribution of population abundance). Empirically, longer time series were more likely to show weakly regulated population dynamics. For data sets of length ≥ 20 , more than 35% had characteristic return times > 6 years, and more than 29% had stationary distributions whose coefficients of variation were more than two times greater than would be the case if they were maximally regulated. These results suggest that many natural populations are weakly regulated.

Keywords

Autoregressive-moving average, autoregressive model, Global Population Dynamics Database, linear model, non-stationarity, population regulation, return to equilibrium, time-series analysis.

Ecology Letters (2010) 13: 21–31

INTRODUCTION

How strongly are the dynamics of natural populations regulated? This has proved to be a remarkably long-lived and contentious question. More than 50 years ago, Nicholson (1933, 1954) emphasized the importance of density-dependent processes – changes in birth and death rates with changes in density – for regulating populations. Per capita population growth rates must decrease as population densities increase to stop populations from expanding in an unbounded exponential way. Nicholson's emphasis on density-dependent processes was contested by Andrewartha & Birch (1954). They noted that for many populations, density was a poor predictor of per capita population growth rates. Therefore, emphasis should be placed on environmental processes that affect populations. This debate between emphasizing density-dependent, intrinsic processes vs. extrinsic, environmental processes has persisted to today (e.g. Hunter & Price 1998, 2000; Turchin & Berryman 2000).

We believe there are three broad and related conceptual issues that need to be addressed in studies of population regulation. First, density dependence of some form is essential for population regulation to stop populations from

exhibiting a random walk behaviour, expanding indefinitely or declining to certain extinction (Nicholson 1954; Berryman 2003); density dependence is required to bound populations so the variance in the population distribution does not become infinite. Nonetheless, not only can density dependence bound population variability, density dependence can also generate intrinsic population variability. For example, delayed nonlinear density dependence can drive stable limit cycles in the absence of any stochastic variation (May *et al.* 1974), and severe overcompensating density dependence can lead to chaos through period doubling (May & Oster 1976). Density dependence has multifarious effects on population dynamics that make it difficult to equate density dependence to any specific definition of population regulation. Therefore, it is not always clear what information the detection of density dependence gives to our understanding of population regulation.

Second, while older literature focused on the detection of density dependence, treating density independence as a null hypothesis (Bulmer 1975; Pollard *et al.* 1987; Den Boer & Reddingius 1989; Reddingius & Den Boer 1989), most recent literature has assumed density dependence exists and focused on estimating its strength. This requires specifying a statistical model or suite of statistical models that are fit to

time-series data (Zeng *et al.* 1998; Osenberg *et al.* 2002; Turchin 2003; Brook & Bradshaw 2006). When a particular model or suite of models is fit to time series, the range of possible conclusions about population regulation is limited by the range of dynamics possible in the models. For example, if only models without time lags are fit to data showing clear cyclicity (that is not caused by simple period-doubling), then the estimates of population regulation must be incomplete; such cyclicity can only be caused by time lags, and single-species models that do not incorporate time lags will be incapable of fitting the cyclicity of the data. Therefore, studying population regulation must involve model selection from a broad range of models that encompass the possible dynamics observed in the data (Shenk *et al.* 1998; Zeng *et al.* 1998; Kendall *et al.* 1999; de Valpine & Hastings 2002).

Third, there are different possible definitions of population regulation (Turchin 1995). Much of the original debate between Nicholson (1954) and Andrewartha & Birch (1954) stemmed from a fundamental disagreement about what is the most important feature of population dynamics. Nicholson was primarily interested in long-term patterns, with a well-regulated population being one that remained within tight bounds for extended periods. Andrewartha and Birch were interested in explaining the short-term fluctuations of species; they focused on predicting changes in population densities and equated regulation with predictability from known effects of the environment. With this disagreement about the question, it is not surprising that they had different answers. Nonetheless, we believe that much of their disagreement can be resolved by simultaneously investigating both long-term and short-term patterns in population dynamics and applying a concept of population regulation that is explicitly stochastic.

Here, we first describe two metrics of population regulation designed for stochastic systems and relate these metrics to the broader concepts of population regulation championed by Nicholson (1954) and Andrewartha & Birch (1954). We then analyse 1633 time series from a wide range of animal species using autoregressive moving average (ARMA) models and model selection techniques to identify the best-fitting model. From the fitted models we use the two metrics to assess the strength of population regulation. In contrast to previous surveys of data sets that overlap with those we analysed (Sibly *et al.* 2005, 2007; Brook & Bradshaw 2006), we found that, for the metrics we use, population regulation is weak for a substantial portion of populations.

Return rates and variability of the stationary distribution

Both to illustrate our measure of population regulation and to analyse our time-series data, we will use the ARMA(p, q) model (Box *et al.* 1994)

$$(x_t - \bar{x}_\infty) = \sum_{i=1}^p \beta_i (x_{t-i} - \bar{x}_\infty) + \sum_{j=0}^q \alpha_j \varepsilon_{t-j}, \quad (1)$$

where x_t is a measure of population density at sample t , \bar{x}_∞ is the long-term mean of the stochastic process, parameters β_i ($i = 1, \dots, p$) are the coefficients for an autoregressive (AR) process of order p , ε_t is a temporally independent normal random variable, and α_j ($j = 1, \dots, q$) are the coefficients of a moving average (MA) process of order q . Both generally and in our specific analyses, population densities are log-transformed for analyses, so that eqn 1 is a log-linear model of population dynamics.

Although ecological time series are unlikely to be linear, by the Wold Representation Theorem (Wold 1938) any stochastic process can be represented by an infinite-order MA process. Furthermore, under mild restrictions a pure MA process can be written as an ARMA process, and the AR component of the ARMA may absorb much of the higher-order MA lags (Box *et al.* 1994). Therefore, although eqn 1 is linear, it can nonetheless be used to approximate any nonlinear stochastic process.

We have selected ARMA models because they give a flexible structure that can accommodate implicitly many dynamical features that occur in ecological time series (see Ives *et al.* 2009). AR lags can be generated if populations are age or stage structured so that, for example, juveniles produced in 1 year do not reproduce until several years hence (Fromentin *et al.* 2001; Lande 2002; Murdoch *et al.* 2002). AR lags can also be generated through species interactions. If, for example, there are p interacting species with no time lags, then the dynamics of the entire system can be captured in a single-species model with at most $2p + 1$ AR lags (Stark 1999, 2000); for linear systems, this reduces to p AR lags (Royama 1992; Reinsel 1997; Abbott *et al.* 2009). MA lags can similarly be created by species interactions, with p interacting species generating at most $2p$ MA lags, or $p-1$ MA lags for linear systems. MA lags can also be caused by measurement error, with a pure AR(p) process contaminated by measurement error generating an ARMA($p, p-1$) process (Staudenmayer & Buonaccorsi 2005). Finally, the environmental variables generating population variability may in fact be autocorrelated, and this autocorrelation will be captured in the MA component of the process. As described below, much of the dynamical characterization of time series depends on the AR component of the ARMA model, and therefore the MA component serves to absorb the 'nuisance' correlations caused by species interactions, measurement error or environmental variables.

We have written the ARMA model assuming that the population dynamics depend only on population densities x_t and unknown sources of stochastic variability ε_t . We do this only because time-series data typically lack additional

information on possible environmental or other extrinsic variables that might affect population dynamics. When additional information is available, it can be incorporated directly into the model (Rothery *et al.* 1997; Ives *et al.* 2003), often providing better estimates of other model parameters (e.g. better estimates of β_i) and greater understanding of the system under study (Dennis & Otten 2000). However, even if environmental variables can help to explain population fluctuations, when the environmental variables are themselves unpredictable, they can be incorporated into the stochastic terms ε_t for the sake of characterizing the population dynamics.

Stochastic populations that persist for long periods have stationary distributions describing the mean, variance, autocovariance, and higher statistical moments of the long-term dynamics (Dennis & Taper 1994; Turchin 1995). To illustrate the stationary distribution, Fig. 1 shows trajectories from four AR(2) processes as they approach stationarity. The time-dependent distribution of trajectories from a given point to the stationary distribution is called the transition distribution (e.g. Feller 1968). Return to the stationary distribution is measured by the asymptotic rates at which the mean, variance and other moments of the

transition distribution approach the stationary distribution. This is closely related to the more familiar concept of the return rate of deterministic systems to a fixed equilibrium point. A common technique in the analyses of deterministic models is to identify a stable equilibrium point, approximate the model around the fixed point by linearizing it, and then determining the characteristic return rate to the equilibrium point from the eigenvalue of the linear model approximation (e.g. May 1974). Our approach using ARMA models is similar, in that we use the ARMA model as a linear approximation to a stochastic process and then measure the return rate for this approximation (Ives *et al.* 2003; p. 305); our method is analogous to standard approaches in nonlinear stochastic models such as small noise perturbation methods (e.g. Gardiner 1990, Ch. 6), although applied to data rather than stochastic equations.

To correspond to the common measure of return time in discrete-time deterministic systems (the magnitude of the dominant eigenvalue of the linearized model), we will measure the characteristic return time to stationarity by $\|\lambda\|$, the magnitude of the inverse of the minimum root of the characteristic equation of eqn 1 (Box *et al.* 1994; see also Appendix S1). $\|\lambda\|$ depends solely on the AR component

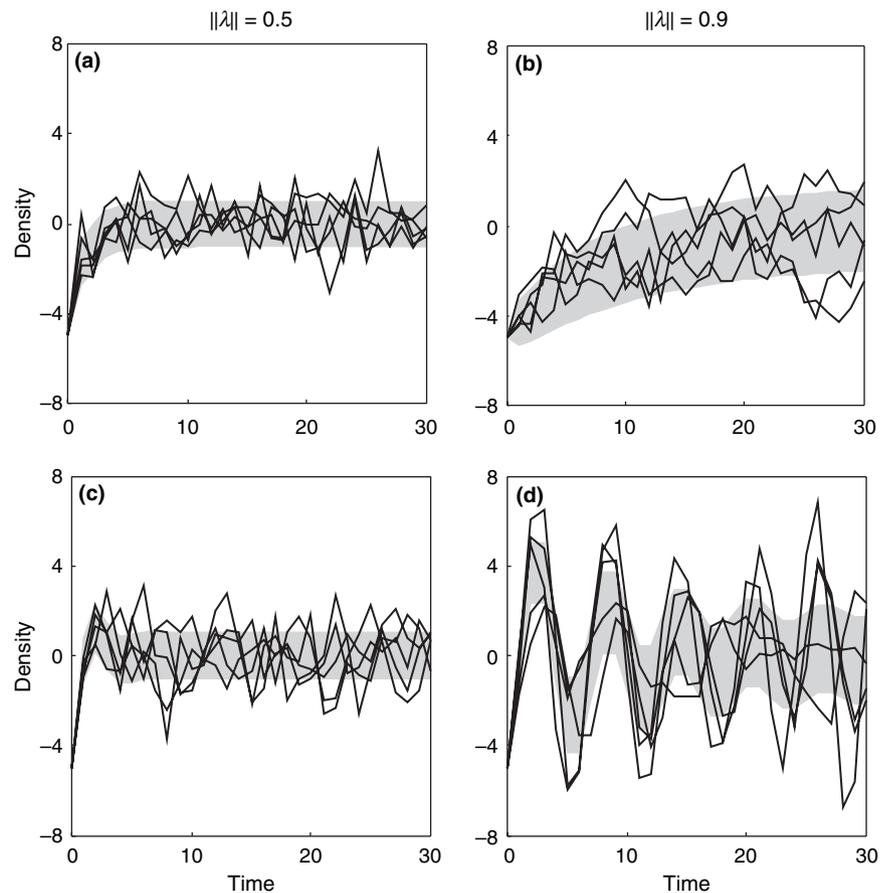


Figure 1 Example trajectories approaching the stationary distributions for AR(2) processes showing monotonic (a and b) and cyclic (c and d) approaches to stationarity. Five trajectories are shown in each panel, and the transition distributions are shown by the grey regions that bound ± 1 SD around the mean. The return rate to stationarity is given by $\|\lambda\| = 0.5$ in (a) and (c), and $\|\lambda\| = 0.9$ in (b) and (d). Parameter values are (a) $\beta_1 = 0.2$ and $\beta_2 = 0.15$, (b) $\beta_1 = 0.57$ and $\beta_2 = 0.3$, (c) $\beta_1 = 0.3$ and $\beta_2 = -0.25$ and (d) $\beta_1 = 0.9$ and $\beta_2 = -0.81$; in all panels $\sigma_E = 1$.

of an ARMA model. For the case in which λ is real, the asymptotic rate at which the mean of the transition distribution, \bar{x}_t , approaches the mean of the stationary distribution, \bar{x}_∞ , is given by $\bar{x}_t - \bar{x}_\infty = \lambda(\bar{x}_{t-1} - \bar{x}_\infty)$, and the asymptotic rate at which the standard deviation σ_t approaches the standard deviation of the stationary distribution, σ_∞ , is $\sigma_t - \sigma_\infty = \|\lambda\|(\sigma_{t-1} - \sigma_\infty)$. Thus, if $\|\lambda\| = 0$ the return to the stationary distribution is immediate, whereas as $\|\lambda\|$ approaches 1 the rate of return drops to zero. For $\|\lambda\| \geq 1$, the process is non-stationary, that is, the stationary distribution does not exist. The case in which λ is complex is analogous, although oscillatory dynamics are laid over the trajectories converging to the stationary distribution. The panels in Fig. 1 show both fast ($\|\lambda\| = 0.5$, Fig. 1a,c) and slow ($\|\lambda\| = 0.9$, Fig. 1b,d) rates of return to stationarity.

As a second measure of population regulation, we use the variability of the stationary distribution relative to the variability of the unexplained environmental variability (Ives 1995; Ives *et al.* 2003). Specifically, we use the ratio σ_∞/σ_E where σ_E is the standard deviation in the MA component of the model,

$$\sigma_E = \sigma_\varepsilon \left(\sum_{j=0}^q \alpha_j^2 \right)^{1/2}$$

and σ_ε is the standard deviation of ε_t (eqn 1). A value of $\sigma_\infty/\sigma_E = 1$ represents strong population regulation; in this case, the standard deviation of the (log) population density equals the standard deviation of the environmental variation driving population fluctuations. As population regulation becomes weaker, σ_∞/σ_E increases because populations are only weakly drawn back to the mean of the stationary distribution. Standardizing by σ_E factors out differences in the

environmental severity experienced by different populations, measured by the year-to-year shocks in population densities contained within σ_ε . Because the MA component of the ARMA model may contain variability that is driven by intrinsic factors (such as interactions among species, see above), σ_E may overestimate the true environmental variability experienced by a population; this will cause σ_∞/σ_E to underestimate the true impact of intrinsic factors on population variability and hence overestimate the strength of population regulation.

For linear models there is a close mathematical relationship between the return rate to stationarity and the variability of the stationary distribution (Ives 1995); in comparing stochastic processes with the same degree of extrinsic stochasticity (σ_E), rapid return rates will be associated with stationary distributions having low values of σ_∞ . This is because the same processes that cause populations to return rapidly to the stationary distribution will also act to narrowly bound the stochastic fluctuations of the population at stationarity. This is shown in Fig. 2a, in which σ_∞/σ_E for three ARMA processes are plotted against $\|\lambda\|$. Although different ARMA(p, q) processes have different values of σ_∞/σ_E for the same value of $\|\lambda\|$, they all show an increase in σ_∞/σ_E as $\|\lambda\|$ increases, and as $\|\lambda\|$ approaches 1, σ_∞/σ_E approaches infinity.

It is instructive to compare our two metrics of population regulation with both Nicholson's (1933, 1954) and Andrewartha & Birch's (1954) views on population regulation. Nicholson viewed regulated populations as those that are quickly drawn towards an equilibrium, thus having low values of $\|\lambda\|$. This then causes populations to be more tightly bounded, thereby having lower values of σ_∞/σ_E . Thus, Nicholson's views of population regulation are closely allied to both of our measures.

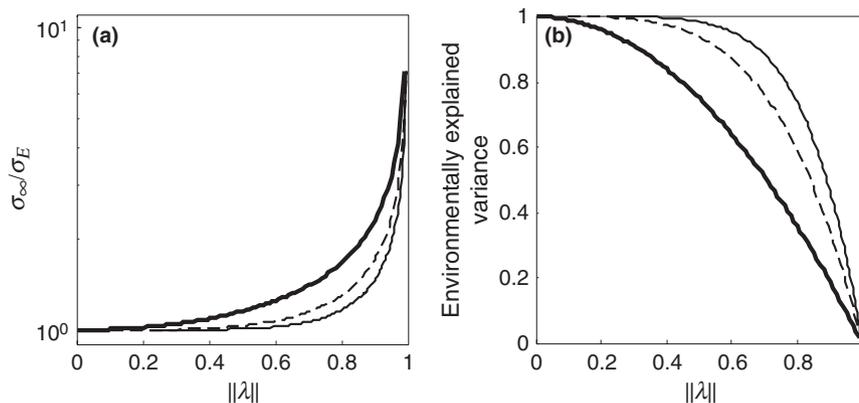


Figure 2 Relationship between the return rate to stationarity determined by $\|\lambda\|$ and (a) the standard deviation of the stationary distribution relative to the environmental variability, σ_∞/σ_E , and (b) the proportion of the variance in the stationary distribution σ_∞^2 that is explained by the environmental variance σ_E^2 (i.e. $\sigma_E^2/\sigma_\infty^2$). In each panel results for an AR(1) (thick line), an AR(2) (dashed line) and an AR(3) (thin line) are shown. $\|\lambda\|$ is varied by changing β_1, β_2 and β_3 in the AR(1), AR(2) and AR(3) models, respectively, and the other autoregressive coefficients are set to zero. Setting the other coefficients to zero caused the differences between AR(1), AR(2) and AR(3) models to be large.

Andrewartha and Birch focused on explaining short-term (year-to-year) population fluctuations in terms of environmental factors. In their classic study on thrips, *Thrips imaginis* (Andrewartha & Birch 1954, pp. 568–583), they regressed yearly peak thrips density in a rose hedge against temperature and rainfall variables; these environmental variables explained almost 80% in the annual variance in peak log densities. This analysis is comparable with applying eqn 1 while setting the AR coefficients β_i to zero and using the ε_t terms to represent the influence of the environment on density; their analysis regresses ε_t against environmental variables. Although for the general case we consider here we do not have direct measurements of the environment, we can use eqn 1 to ask what proportion of the temporal variance in population densities at the stationary distribution can be explained solely by ε_t excluding information on past densities, x_{t-1} , x_{t-2} , etc.; this is consistent with Andrewartha and Birch's view that population densities have little predictive power in explaining population fluctuations. Figure 2b shows the environmental variance scaled by the population variance, $\sigma_E^2/\sigma_\infty^2$, graphed vs. $\|\lambda\|$ for AR(1), AR(2) and AR(3) processes. When the rate of return to stationarity is rapid ($\|\lambda\|$ is close to zero), most of the temporal variance in population density is driven solely by environmental factors. This occurs because the density at a given time is only weakly determined by the previous densities, so the only remaining source of variation is environmental. Since Andrewartha & Birch's (1954) regression study found that a very high proportion of the variance in population density could be explained by environmental factors, their work suggests a high $\sigma_E^2/\sigma_\infty^2$ for their thrips.

This comparison between Nicholson's emphasis on long-term population variability and Andrewartha and Birch's emphasis on short-term variability shows a simple resolution to their disagreement about population regulation. Long-term population variance is reduced when return rates to stationarity are rapid (Fig. 2a). Furthermore, environmental factors have their strongest effect, and density has its weakest effect, when return rates are rapid (Fig. 2b; Rothery *et al.* 1997; Dennis & Otten 2000; Brook & Bradshaw 2006). Therefore, Nicholson's conclusion that populations are strongly regulated is completely consistent with Andrewartha and Birch's conclusion that environmental factors explain year-to-year fluctuations in population densities. If populations were not strongly regulated ($\|\lambda\|$ far from zero), then previous population densities would be stronger predictors of year-to-year fluctuations. In summary, there is no conflict between Nicholson, and Andrewartha and Birch; return rates to stationarity must be rapid both for long-term population fluctuations to be narrowly bounded and for most of the year-to-year fluctuations to be explained by environmental variables rather than previous population densities.

Many studies on population regulation have investigated the strength of density dependence (e.g. Turchin 1990; Holyoak 1992; Woiwod & Hanski 1992; Saether *et al.* 2005; Sibly *et al.* 2005; Brook & Bradshaw 2006). Therefore, it is useful to relate our metrics of population regulation to density dependence. Unfortunately, the relationship between the return rate to the stationary distribution and the strength of direct (non-lagged) or lagged density dependence is complex for all but the simplest models. The strength of direct density dependence can be described by how the change in density between successive samples, $\Delta x_t = x_t - x_{t-1}$, depends on the initial density x_{t-1} (Fig. 3). For an AR(1) model this slope is simply given by $\beta_1 - 1 = \lambda - 1$, so that increasing the rate of return to stationarity (decreasing $\beta_1 = \lambda$) corresponds to stronger density dependence provided $\beta_1 > 0$ (Fig. 3a,b). In contrast, for models of higher order the relationship between return rates and direct density dependence is more complex, and direct density dependence can decrease with increasing rates of return to stationarity (Fig. 3c,d). This example illustrates the difficulty with equating density dependence with population regulation in all but the simplest cases when there are no time lags.

We should note that our metrics of population regulation assume that a stationary distribution exists. This assumption makes the metrics inappropriate for application to situations in which populations are possibly declining to extinction, as in population viability analyses, or situations in which populations are increasing exponentially, as for some invasive species. Nonetheless, fitting ARMA models may often detect non-stationary processes as those giving estimates of $\|\lambda\|$ equal to one.

Finally, issues also arise when the metrics are applied to highly nonlinear processes that could generate sustained population fluctuations even in the absence of environmental stochasticity, for example stable limit cycles or chaotic dynamics. The metrics are based on approximating the stochastic process with a linear model that is incapable of producing such sustained, internally driven fluctuations. In these situations, however, the metrics will likely be conservative, in the sense that they will indicate stronger population regulation than might be the case. This is easy to show for the metric σ_∞/σ_E . In this metric, σ_∞^2 can be thought of as the total variance of the stochastic process and σ_E^2 as the variance that is unexplained by the linear model. If there are strong nonlinearities, then σ_E^2 will overestimate the true environmental variance by attributing to the environment the variability in the residuals that cannot be explained by the linear model. Therefore, σ_∞/σ_E will underestimate the variability of the stationary distribution relative to the environmental variability (Ives 1995). (We should note, however, that this argument applies only if a single model is fit to the data; if model selection is used to

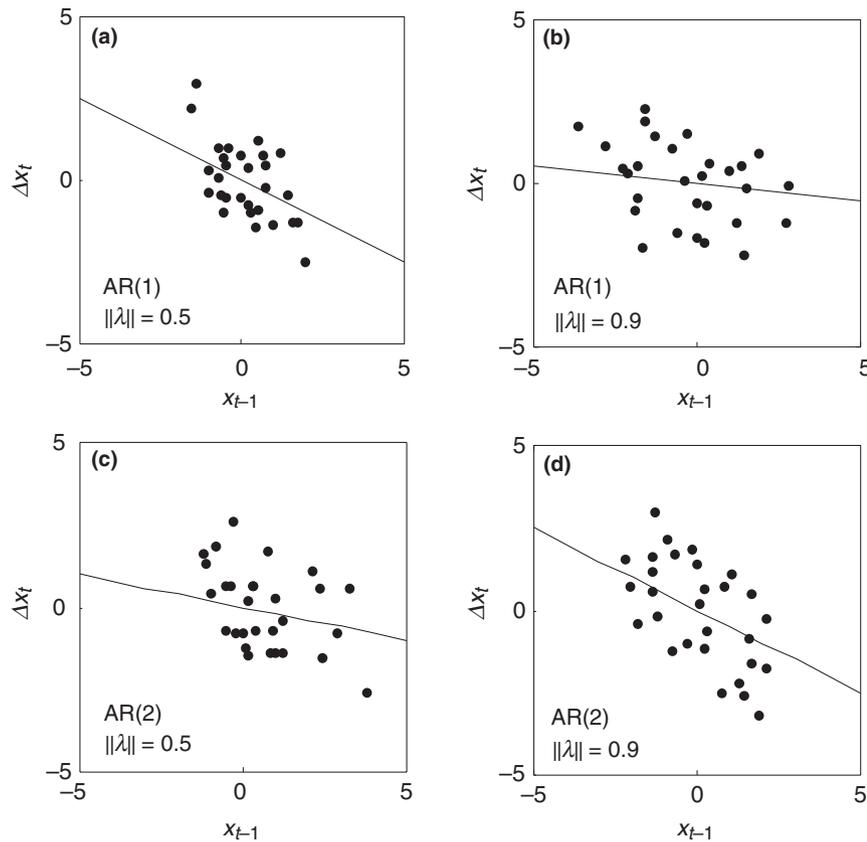


Figure 3 Strength of density dependence in AR(1) (a, b) and AR(2) (c, d) processes for different rates of return to stationarity, $\|\lambda\|$. Density dependence is measured by the relationship between the change in densities between samples $t-1$ and t , $\Delta x_t = x_t - x_{t-1}$, and the density at sample $t-1$, x_{t-1} ; the steeper the slope (i.e. the more negative), the stronger is density dependence. Each panel gives a representative time series of length 30, and the line gives the theoretical relationship between Δx_t and x_{t-1} at the stationary distribution, calculated as the expectation of Δx_t conditional on the value of x_{t-1} . Model parameters are: (a) $\beta_1 = 0.5$, (b) $\beta_1 = 0.9$, (c) $\beta_1 = 1$ and $\beta_2 = -0.25$, and (d) $\beta_1 = 0.9$ and $\beta_2 = -0.81$; in all panels $\sigma_E = 1$.

identify the AR and MA lags, p and q , then nonlinearities may affect which model is selected and hence the estimate of σ_∞/σ_E . Because σ_∞/σ_E will likely be an underestimate, we suspect that in most cases the metric $\|\lambda\|$ will also be an underestimate, predicting more rapid return times for the nonlinear case than actually occurs. Nonetheless, at present this is only a conjecture, and the transition distribution for nonlinear processes can show complex behaviours (e.g. Yao & Tong 1994) that make generalizations risky. The main difficulty limiting the assessment of population regulation in highly nonlinear population processes is determining the strength and character of the nonlinearities given the short length of typical ecological time series; ecological time series will rarely allow the rigorous validation on any specific nonlinear model. In the face of this difficulty, a prudent approach is to use a linear approximation that likely leads to conservative conclusions.

Time-series analyses

We analysed two collections of time-series data sets to estimate the two metrics of population regulation, $\|\lambda\|$ and σ_∞/σ_E . First, we used 49 data sets from the Global Population Dynamics Database (GPDD; NERC Centre for Population Biology 1999) and one data set from the United

States Forest Service (2007) that were analysed by Abbott *et al.* (2009). These 50 data sets consist of abundances collected annually for 35–157 years, with a mean length of 60.9 years, and each represents a unique species. From the GPDD's very large collection of time series, we chose these data sets haphazardly with the goal of selecting long time series with few missing data points. We will refer to these 50 data sets as collection A. Second, collection B consists of 1583 data sets from the GPDD that were assembled by Sibly *et al.* (2005, 2007); they provided us with 1780 time series from which we removed 195 data sets of length < 10 and two additional data sets for which our ARMA fitting procedure failed to converge. Because relatively few long ecological time series exist, collection B contains many shorter time series, with an average length of 22.1 years. Not only did we analyse all 1583 data sets in collection B, but we also analysed the subset of 567 data sets having length at least 20; this subset had an average length of 35.9 years.

We fit ARMA(p, q) models to each data set using restricted maximum likelihood estimation (REML) following the procedure of Ives *et al.* (2009). We considered AR lags of $p = 1-3$ years and MA lags $q = 0-2$ years. We then computed $\|\lambda\|$ and σ_∞/σ_E for the best-fitting model, where we selected the best-fitting model as that with the lowest small-sample-size-corrected Akaike's Information

Criterion (AIC_c) value; in a simulation study, Malgras & Debouzie (1997) found the performance of AIC_c superior to common alternatives. Our procedure has three sources of bias that generally lead to underestimates of $\|\lambda\|$ and σ_∞/σ_E (Ives *et al.* 2009), and hence overestimates of the strength of population regulation. First, the REML parameter estimates obtained from a given model tend to be biased (McGilchrist 1989; Cheang & Reinsel 2003). Second, bias arises in the model selection process; when the incorrect model is selected, it is more likely to give lower estimates of $\|\lambda\|$ and σ_∞/σ_E than the correct model (Ives *et al.* 2009). Third, although the MA structure of the models can absorb some effects of measurement error on the estimates of $\|\lambda\|$ and σ_∞/σ_E , measurement error nonetheless will often lead to underestimates (Staudenmayer & Buonaccorsi 2005). These sources of bias make our analyses conservative, in the sense that they decrease the chances of identifying weakly regulated populations.

Because we are analyzing a large number of data sets, we are more concerned with bias in the estimates than with their precision (e.g. the width of confidence intervals of $\|\lambda\|$ and σ_∞/σ_E). Even though precision may be low, especially for short time series (Ives *et al.* 2009), precision in the estimates for individual time series will not greatly affect our summary descriptions of a large collection of data sets, for example, that a certain percentage of data sets have $\|\lambda\| > 0.9$. The precision of our summary descriptions is determined more by the number of time series in the collections of data sets than the precision in the estimates for each time series.

Considering the 567 data sets in collection B having length at least 20, the estimates of $\|\lambda\|$ and σ_∞/σ_E for both collections A and B had similar distributions (Fig. 4). Here, for discussion we select $\|\lambda\| > 0.9$ and $\sigma_\infty/\sigma_E > 2$ to represent weak population regulation, recognizing that the full distributions of values of $\|\lambda\|$ and σ_∞/σ_E in Fig. 4 give more complete pictures of the results. For collection A, 42% of the time series had $\|\lambda\| > 0.9$, and 40% had $\sigma_\infty/\sigma_E > 2$, while for collection B (for data sets of length ≥ 20), 35% of the time series had $\|\lambda\| > 0.9$, and 28% had $\sigma_\infty/\sigma_E > 2$. (A similar histogram for $\|\lambda\|$ for all 1583 data sets in collection B is given in Fig. S1.) In the analyses, we also distinguished between estimates from best-fitting models that were AR(1) models (black histograms) and those from ARMA(p, q) models with $p > 1$ and/or $q > 0$. Those data sets giving high estimates of $\|\lambda\|$ and σ_∞/σ_E were more often more-complex models (i.e. higher values of p and/or q) than those giving lower estimates of $\|\lambda\|$ and σ_∞/σ_E , suggesting that data sets with more complex, higher-order dynamics are also likely to be weakly regulated.

The lower estimates of $\|\lambda\|$ and σ_∞/σ_E for collection B relative to collection A are likely due in part to the known downward bias in the estimates that are exaggerated for smaller sample sizes (Appendix S2). Considering all 1583 data sets in collection B with length ≥ 10 , there is a strong increase in the estimates of $\|\lambda\|$ with increasing time series length (Fig. 5a). Furthermore, the complexity of the best-fitting model, measured by $p + q$, increases with increasing length of the time series (Fig. 5b). These increases in $\|\lambda\|$ and $p + q$ with time series length show no signs of reaching

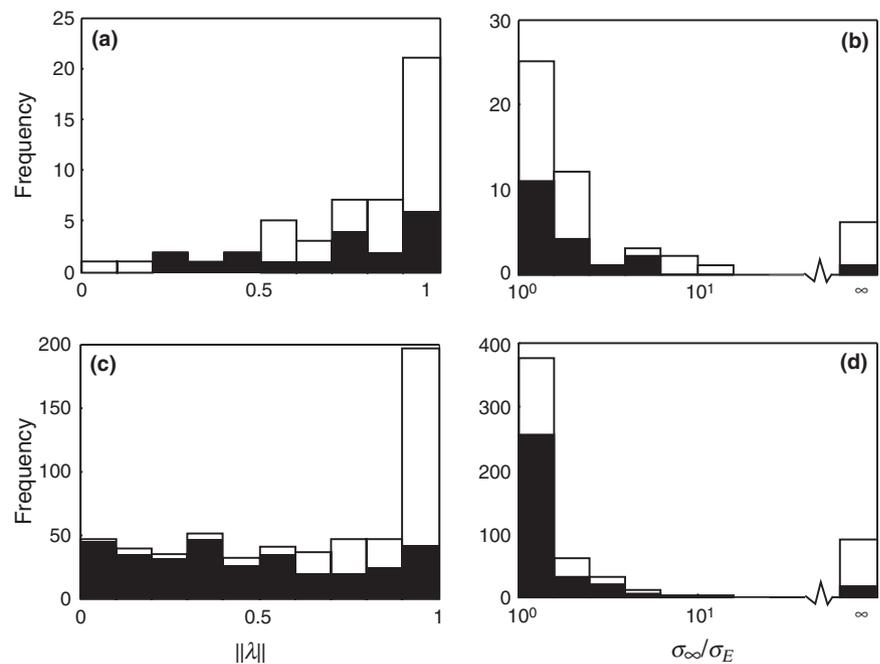


Figure 4 The distribution of estimates of $\|\lambda\|$ calculated from the corrected Akaike’s Information Criterion (AIC_c) best-fitting ARMA(p, q) models for (a) the 50 data sets in collection A, and (c) the 567 data sets in collection B with length ≥ 20 . (b) and (d) give, for the same collections of data sets, the distributions of the estimates of standard deviation of the stationary distribution relative to the environmental variability, σ_∞/σ_E . The black bars give the data sets for which the best-fitting model was an AR(1).

an asymptote but instead continue to rise even for data sets over length 30. We performed a simulation study to investigate whether this pattern could be due solely to bias in fitting ARMA models to data (Appendix S2). This study showed that the results depend on the underlying population process; a model giving oscillatory dynamics led to better estimates of $\|\lambda\|$ and $p + q$ for shorter time series than a model giving non-oscillatory dynamics (Fig. S3). Nonetheless, both models showed strong effects of the length of the time series simulated, consistent with our empirical observations (Fig. 5).

DISCUSSION

A large proportion of the data sets we analysed is weakly regulated. We obtained these results even though the methods we used likely gave underestimates of $\|\lambda\|$ and

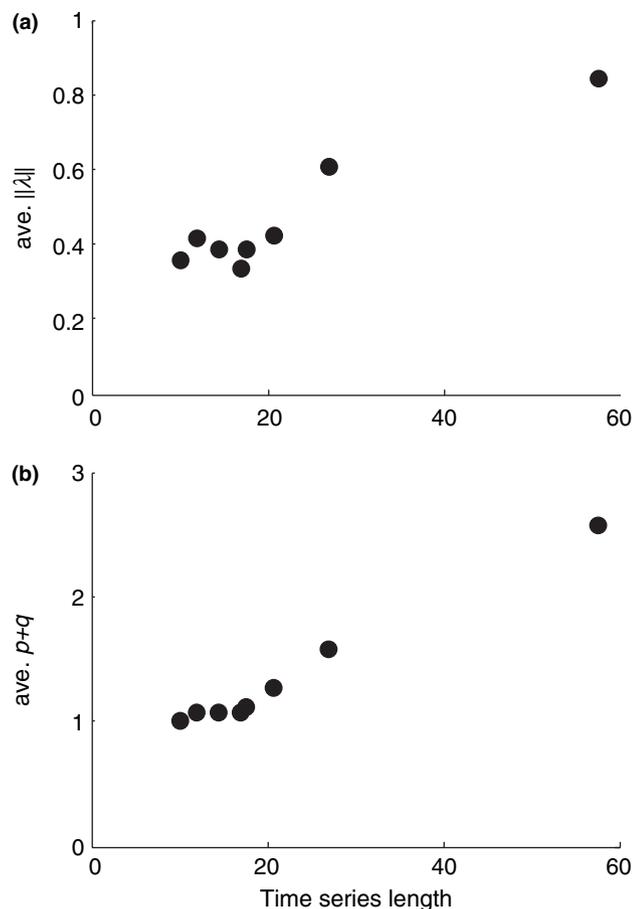


Figure 5 For collection B (all 1583 data sets), the average of estimates of $\|\lambda\|$ calculated from the best-fitting ARMA(p, q) model, and the average value of $p + q$ used as a measure of complexity of the best-fitting model. Data sets were binned into eight equally sized groups, and the points represent the average of each group.

σ_∞/σ_E ; that is, regulation is likely even weaker than our estimates. We measured population regulation by $\|\lambda\|$ that gives the rate of return of a population to its stationary distribution. If we use a threshold of $0.9 < \|\lambda\|$ to categorize weakly regulated populations, 42% and 35% of the populations from collections A (50 longer data sets) and B (567 data sets from Sibly *et al.* (2005) with length ≥ 20), respectively, were weakly regulated (Fig. 4). A value of $\|\lambda\| = 0.9$ corresponds to a characteristic population return time of roughly 6 years ($0.9^6 \approx 0.5$) when populations are measured on a log scale; for a population that is some distance away from the mean of its stationary distribution, it takes 6 years for the expected log population density to halve that distance. Thus, the weakly regulated population ‘remembers’ past densities.

We also assessed the strength of population regulation in terms of the standard deviation of the population stationary distribution relative to the distribution of environmental variability, σ_∞/σ_E ; this measure generally increases in tandem with $\|\lambda\|$ (Fig. 2a). For collections A and B (with length ≥ 20), respectively, 40% and 28% had values of $\sigma_\infty/\sigma_E > 2$. For log-transformed population densities, σ_∞ approximates (but underestimates) the coefficient of variation of the untransformed population densities (Stuart & Ord 1987); the threshold of $\sigma_\infty/\sigma_E = 2$ therefore corresponds to a coefficient of variation that is two times greater than the case of strong population regulation when $\sigma_\infty/\sigma_E = 1$. Thus, a large proportion of populations were weakly regulated as measured by their variability.

A striking methodological finding in our analyses is that longer time series were more likely to give estimates of $\|\lambda\|$ indicating weak population regulation, and were more likely to reveal more-complex dynamics (Fig. 5; Appendix S2). As data sets in collection B increased in length from 30 to 60 years, the mean estimates of $\|\lambda\|$ increased from 0.6 to 0.85, and the average complexity (measured by $p + q$) increased from 1.6 to 2.6. This problem represents a serious challenge for studies of population dynamics. Very long ecological time series are rare, and our results suggest that even data sets of length 60 years may be too short to reliably characterize the population dynamics.

Our conclusions about prevalence of weak population regulation in collection B differ markedly from those of Sibly *et al.* (2007) who analysed a subset of the same initial collection of 1780 data sets from Sibly *et al.* (2005). This contrast is caused by three differences between our analyses (Appendix S2). First, while starting with 1780 data sets, Sibly *et al.* (2007) applied a series of filters that reduced the number of data sets to 524, and these data sets were on average shorter than the data sets we analysed. The mean length of the 524 data sets was 17.5 years compared with a mean of 22.1 for collection B, and 35.9 for the subset of collection B with length ≥ 20 (Fig. 4). Shorter time series are

more likely to give estimates of stronger population regulation (Fig. 5a), and the filtering procedure used by Sibly *et al.* (2007) caused a large decrease in the proportion of time series with $\|\lambda\| > 0.9$ (Appendix S2). Second, Sibly *et al.* (2007) only fit models without time lags. In our analyses, models with longer time lags (higher p and/or q) were more likely to give larger estimates of $\|\lambda\|$, and therefore by ignoring time lags Sibly *et al.* (2007) were more likely to infer stronger population regulation. Third, the conditional least squares estimation procedure that Sibly *et al.* (2007) used produces downwards bias in $\|\lambda\|$ and hence overestimates of the strength of population regulation. Although our estimation procedure (REML) also produces downwards bias, this bias is less severe than conditional least squares. Of these three differences, the first – filtering in a way that removes long data sets – is responsible for most of the contrast between our results and those of Sibly *et al.* (2007).

Our analyses reveal that a considerable proportion of data sets shows weak population regulation, and populations that are weakly regulated present several ecological challenges. For a weakly regulated population, it can be difficult to determine even its simplest property, its mean value. For example, consider a data set of length 100 years for a strongly regulated population ($\|\lambda\| = 0$) governed by an AR(1) process, and suppose the year-to-year variance in log population density is 1. Then the standard error of the estimate of the mean log population density is 0.1. If there were another population with $\|\lambda\| = 0.9$ that experienced the same impact of environmental fluctuations on its per capita population growth rate, then 1891 years of data would be required to achieve the same precision in the estimate of the mean.

Even though properties of the stationary distribution (e.g. the long-term mean or variance of the population) are more difficult to estimate for weakly regulated populations, the same populations are simultaneously more predictable in the short term, as population densities in the future are more strongly determined by present and past population densities (Fig. 2b). Thus, for a population with $\|\lambda\| = 0$, information about the population density this year gives no information about the density next year; for the hypothetical population described in the last paragraph, the standard error of the estimate of the predicted population density will be 1. On the other hand, for the population with $\|\lambda\| = 0.9$, knowing the density this year will reduce the standard error of the prediction for next year to 0.44 when scaled by the standard deviation of the stationary distribution, σ_∞ . Thus, from the practical standpoint of what can be learned about populations, the strength of population regulation makes a large difference.

Ecologists have used the strength of population regulation to infer ecological mechanisms driving population

dynamical processes. For example, strong regulation might imply intraspecific competition, with populations maintained close to their carrying capacities set by food availability. Conversely, weakly regulated populations might be sensitive to environmental fluctuations or predators that keep densities well below carrying capacity. We argue strongly against trying to infer mechanisms from the strength of population regulation. It is easy to produce counter-examples for any supposed relationship between the strength of population regulation and some ecological mechanism. For example, the dipteran seed predator *Euphranta connexa* experiences strong intraspecific competition; in a 22-year study, the predation rate by *E. connexa* on host plant seed pods was $> 90\%$ in 11 of the 22 years (Solbreck & Ives 2007). Nonetheless, *E. connexa* populations fluctuated over two orders of magnitude due to two-orders-of-magnitude fluctuations in seed abundance; while they could be viewed as remaining close to carrying capacity, their carrying capacity fluctuated. Similarly, weak population regulation cannot be associated with strong effects of environmental fluctuations. In fact, the predictive power of environmental variables for the future density of thrips found by Andrewartha & Birch (1954) is only possible for strongly regulated populations for which current population density has no predictive power for future densities.

While we caution against inferring mechanisms from patterns of population regulation, we nonetheless think that the strength of population regulation is a fundamental property exhibited by populations. It is as fundamental as the mean or the variance of the stationary distribution. As a descriptor of population dynamics, population regulation provides the context in which mechanisms driving population dynamics should be investigated.

ACKNOWLEDGEMENTS

We sincerely thank Richard Sibly and Daniel Barker for sending us their data sets and helping to pinpoint how our analyses differ. Funding for this work was provided by NSF grants MSPA-CSE 0434329, DEB 0415670, and DEB 0816613 to ARI.

REFERENCES

- Abbott, K.C., Ripa, J. & Ives, A.R. (2009). Environmental variation in ecological communities and inferences from single-species data. *Ecology*, 90, 1268–1278.
- Andrewartha, H.G. & Birch, L.C. (1954). *The Distribution and Abundance of Species*. Chicago University Press, Chicago.
- Berryman, A.A. (2003). On principles, laws and theory in population ecology. *Oikos*, 103, 695–701.
- Box, G.E.P., Jenkins, G.M. & Reinsel, G.C. (1994). *Time Series Analysis: Forecasting and Control*, 3rd edn. Prentice Hall, Englewood Cliffs, NJ.

- Brook, B.W. & Bradshaw, C.J.A. (2006). Strength of evidence for density dependence in abundance time series of 1198 species. *Ecology*, 87, 1445–1451.
- Bulmer, M.G. (1975). Statistical analysis of density dependence. *Biometrics*, 31, 901–911.
- Cheang, W.K. & Reinsel, G.C. (2003). Finite sample properties of ML and REML estimators in time series regression models with long memory noise. *J. Stat. Comput. Simul.*, 73, 233–259.
- Den Boer, P.J. & Reddingius, J. (1989). On the stabilization of animal numbers. Problems of testing. 2. Confrontation with data from the field. *Oecologia*, 79, 143–149.
- Dennis, B. & Otten, M.R.M. (2000). Joint effects of density dependence and rainfall on abundance of San Joaquin kit fox. *J. Wildl. Manage.*, 64, 388–400.
- Dennis, B. & Taper, B. (1994). Density dependence in time series observations of natural populations: estimation and testing. *Ecol. Monogr.*, 64, 205–224.
- Feller, W. (1968). *An Introduction to Probability Theory and its Applications*, Vol. 1. John Wiley & Sons, New York, NY.
- Fromentin, J.M., Myers, R.A., Bjornstad, O.N., Stenseth, N.C., Gjosaeter, J. & Christie, H. (2001). Effects of density-dependent and stochastic processes on the regulation of cod populations. *Ecology*, 82, 567–579.
- Gardiner, C.W. (1990). *Handbook of Stochastic Methods for Physics, Chemistry and the Natural Sciences*, 2nd edn. Springer-Verlag, Berlin.
- Holyoak, M. (1992). Detection of density dependence from annual censuses of bracken-feeding insects. *Oecologia*, 91, 425–430.
- Hunter, M.D. & Price, P.W. (1998). Cycles in insect populations: delayed density dependence or exogenous driving variables?. *Ecol. Entomol.*, 23, 216–222.
- Hunter, M.D. & Price, P.W. (2000). Detecting cycles and delayed density dependence: a reply to Turchin and Berryman. *Ecol. Entomol.*, 25, 122–124.
- Ives, A.R. (1995). Measuring resilience in stochastic systems. *Ecol. Monogr.*, 65, 217–233.
- Ives, A.R., Dennis, B., Cottingham, K.L. & Carpenter, S.R. (2003). Estimating community stability and ecological interactions from time-series data. *Ecol. Monogr.*, 73, 301–330.
- Ives, A.R., Abbott, K.C. & Ziebarth, N.L. (2009). Statistical evaluation of density dependence using ARMA models. *Ecology*, in press.
- Kendall, B.E., Briggs, C.J., Murdoch, W.W., Turchin, P., Ellner, S.P., McCauley, E. *et al.* (1999). Why do populations cycle? A synthesis of statistical and mechanistic modeling approaches. *Ecology*, 80, 1789–1805.
- Lande, R. (2002). Estimating density dependence in time-series of age-structured populations. *Philos. Transact. R. Soc. Lond. B Biol. Sci.*, 357, 1179–1184.
- Malgras, J. & Debouzie, D. (1997). Can ARMA models be used reliably in ecology?. *Acta Oecol. Int. J. Ecol.*, 18, 427–447.
- May, R.M. (1974). *Stability and Complexity in Model Ecosystems*, 2nd edn. Princeton University Press, Princeton, NJ.
- May, R.M. & Oster, G.F. (1976). Bifurcations and dynamic complexity in simply ecological models. *Am. Nat.*, 110, 573–599.
- May, R.M., Conway, G.R., Hassell, M.P. & Southwood, T.R.E. (1974). Time delays, density-dependence and single-species oscillations. *J. Anim. Ecol.*, 43, 747–770.
- McGilchrist, C.A. (1989). Bias of ML and REML estimators in regression models with ARMA errors. *J. Stat. Comput. Simul.*, 32, 127–136.
- Murdoch, W.W., Kendall, B.E., Nisbet, R.M., Briggs, C.J., McCauley, E. & Bolser, R. (2002). Single-species models for many-species food webs. *Nature*, 417, 541–543.
- NERC Centre for Population Biology (1999). *The Global Population Dynamics Database*. Available at: <http://www.sw.ic.ac.uk/cpb/cpb/gpdd.html>.
- Nicholson, A.J. (1933). The balance of animal populations. *J. Anim. Ecol.*, 2, 132–178.
- Nicholson, A.J. (1954). An outline of the dynamics of animal populations. *Aust. J. Zool.*, 2, 9–65.
- Osenberg, C.W., St Mary, C.M., Schmitt, R.J., Holbrook, S.J., Chesson, P. & Byrne, B. (2002). Rethinking ecological inference: density dependence in reef fishes. *Ecol. Lett.*, 5, 715–721.
- Pollard, E., Lakhani, K.H. & Rothery, P. (1987). The detection of density-dependence from a series of annual censuses. *Ecology*, 68, 2046–2055.
- Reddingius, J. & Den Boer, P.J. (1989). On the stabilization of animal numbers. Problems of testing. 1. Power estimates and estimation errors. *Oecologia*, 78, 1–8.
- Reinsel, G.C. (1997). *Elements of Multivariate Time Series Analysis*, 2nd edn. Springer, New York.
- Rothery, P., Newton, I., Dale, L. & Wesolowski, T. (1997). Testing for density dependence allowing for weather effects. *Oecologia*, 112, 518–523.
- Royama, T. (1992). *Analytical Population Dynamics*. Chapman and Hall, London.
- Saether, B.E., Lande, R., Engen, S., Weimerskirch, H., Lillegard, M., Altwegg, R. *et al.* (2005). Generation time and temporal scaling of bird population dynamics. *Nature*, 436, 99–102.
- Shenk, T.M., White, G.C. & Burnham, K.P. (1998). Sampling variance effects on detecting density dependence from temporal trends in natural populations. *Ecol. Monogr.*, 68, 445–463.
- Sibly, R.M., Barker, D., Denham, M.C., Hone, J. & Pagel, M. (2005). On the regulation of populations of mammals, birds, fish, and insects. *Science*, 309, 607–610.
- Sibly, R.M., Barker, D., Hone, J. & Pagel, M. (2007). On the stability of populations of mammals, birds, fish and insects. *Ecol. Lett.*, 10, 970–976.
- Solbreck, C. & Ives, A.R. (2007). Density dependence vs. independence, and irregular population dynamics of a swallow-wort fruit fly. *Ecology*, 88, 1466–1475.
- Stark, J. (1999). Delay embeddings for forced systems. I. Deterministic forcing. *J. Nonlinear Sci.*, 9, 255–332.
- Stark, J. (2000). Observing complexity, seeing simplicity. *Philos. Transact. R. Soc. Lond. A Math. Phys. Eng. Sci.*, 358, 41–61.
- Staudenmayer, J. & Buonaccorsi, J.R. (2005). Measurement error in linear autoregressive models. *J. Am. Stat. Assoc.*, 100, 841–852.
- Stuart, A. & Ord, J.K. (1987). *Kendall's Advanced Theory of Statistics, Vol. 1: Distribution Theory*. Oxford University Press, New York, NY.
- Turchin, P. (1990). Rarity of density dependence or population regulation with lags?. *Nature*, 344, 660–663.
- Turchin, P. (1995). Population regulation: old arguments and a new synthesis. In: *Population Dynamics: New Approaches and Synthesis* (eds Cappuccino, N. & Price, P.W.). Academic Press, San Diego, pp. 19–40.
- Turchin, P. (2003). Dynamical effects of plant quality and parasitism on population cycles of larch budmoth. *Ecology*, 84, 1207–1214.

- Turchin, P. & Berryman, A.A. (2000). Detecting cycles and delayed density dependence: a comment on Hunter & Price (1998). *Ecol. Entomol.*, 25, 119–121.
- United States Forest Service (2007). *Gypsy Moth Digest*. Available at: <http://www.na.fs.fed.us/fhp/gm/defoliation/index.shtml>.
- de Valpine, P. & Hastings, A. (2002). Fitting population models incorporating process noise and observation error. *Ecol. Monogr.*, 72, 57–76.
- Woiwod, I.P. & Hanski, I. (1992). Patterns of density dependence in moths and aphids. *J. Anim. Ecol.*, 61, 619–629.
- Wold, H. (1938). *A Study in the Analysis of Stationary Time Series*. Almqvist & Wiksells, Uppsala, Sweden.
- Yao, Q.W. & Tong, H. (1994). On prediction and chaos in stochastic systems. *Philos. Transact. R. Soc. Lond. A Math. Phys. Eng. Sci.*, 348, 357–369.
- Zeng, Z., Nowierski, R.M., Taper, M.L., Dennis, B. & Kemp, W.P. (1998). Complex population dynamics in the real world: modeling the influence of time-varying parameters and time lags. *Ecology*, 79, 2193–2209.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Figure S1 Estimates of $\|\lambda\|$ calculated for collection B for different filtering steps and analyses used by Sibly *et al.* (2007).

Figure S2 Distribution of (a) $\|\lambda\|$ and (b) $p + q$ for collection B (only data sets with length ≥ 20) when model selection is performed including models with linear detrending.

Figure S3 Simulation study of the effects of time series length on the estimates of (a) $\|\lambda\|$ and (b) $p + q$.

Appendix S1 Mathematical properties of ARMA models.

Appendix S2 Comparison with Sibly *et al.* (2007).

As a service to our authors and readers, this journal provides supporting information supplied by the authors. Such materials are peer-reviewed and may be re-organized for online delivery, but are not copy-edited or typeset. Technical support issues arising from supporting information (other than missing files) should be addressed to the authors.

Editor, Jean-Michel Gaillard

Manuscript received 8 May 2009

First decision made 17 June 2009

Second decision made 30 July 2009

Manuscript accepted 3 September 2009