

AUTOCORRELATED EXOGENOUS FACTORS AND THE DETECTION OF DELAYED DENSITY DEPENDENCE

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Abstract. Coupled trophic interactions with specialist predators or resources are thought to be primarily responsible for generating delayed density dependence. Previous theoretical studies suggest that autocorrelation in exogenous factors could generate apparent negative delayed density dependence in populations regulated only by direct density dependence. Using both linear and nonlinear models, we show that autocorrelated exogenous factors can generate the spurious appearance of not only negative, but also positive, delayed density dependence in populations regulated only by direct density dependence. Evidence for negative delayed density dependence is found mainly in populations exhibiting monotonic deterministic stability, whereas evidence for positive delayed density dependence is found mainly in populations exhibiting damped or persistent two-point cycles, or more complex deterministic dynamics. We argue that fluctuating resources (e.g., mast seeding) in bottom-up controlled communities could qualify as autocorrelated exogenous factors and cause apparent delayed density dependence in the population of their consumers.

Key words: autocorrelation; bottom-up; delayed density dependence; direct density dependence; exogenous factors; fluctuating resources; time-series models; trophic interactions.

INTRODUCTION

A central problem in population ecology is to identify the mechanisms behind the fluctuating population dynamics exhibited by many species in nature. One approach, adopted by many ecologists, is to use results from time-series analyses to infer possible mechanisms about population regulation. Delayed density dependence (hereafter DDD), an important concept recently drawing attention from population ecologists, refers to the time-delayed regulatory effect of past population densities on the reproduction and survival of individuals. DDD has been found in many cyclic populations since the seminal work of Turchin (1990) (e.g., Turchin and Taylor 1992, Hornfeldt 1994, Bjørnstad et al. 1995, Stenseth et al. 1996, Saitoh et al. 1997, 1999, Hansen et al. 1999a, b, Lima et al. 1999). When making inference, ecologists routinely interpret DDD as a sign of trophic interactions, because lagged feedback can readily arise from specialist predator–prey or consumer–resource interactions.

Most ecological time-series studies have employed statistical procedures based on autoregressive models

to detect DDD. Autoregressive models usually take the form

$$N_t = f(N_{t-1}, N_{t-2}, \dots, N_{t-k}, \varepsilon_t) \quad (1)$$

where N is the population size, k is the order of the density-dependent process, f is a linear or nonlinear function of past population sizes and represents the effects of endogenous (density-dependent) factors, and ε is a random variable representing the effects of exogenous (density-independent) factors (Royama 1992, Turchin 1995, Berryman and Turchin 2001). Because high-order processes ($k > 2$) are generally of little ecological significance, primary interest is on first-order ($k = 1$) direct density dependence, which characterizes almost all animal time series, and second-order ($k = 2$) DDD. Autoregressive models focus on the effects of endogenous factors, with the assumption that exogenous factors can always be modeled as independently distributed random variables.

Nonrandom exogenous factors may complicate the tests for DDD. Royama (1981) reported that apparent second-order DDD could arise in linear first-order models with autocorrelated exogenous factors. Williams and Liebhold (1995) demonstrated that the frequency of apparent second-order DDD increased with the degree of autocorrelation in the exogenous factors and

Manuscript received 11 September 2002; revised 29 January 2003; accepted 7 February 2003. Corresponding Editor: A. R. Ives.

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decreased with the rate of population growth in Ricker logistic models. Such apparent second-order DDD results from imposing first-order exogenous dynamics upon first-order endogenous dynamics, and lacks the dynamical feedback processes that characterize regular DDD (primarily due to coupled trophic interactions). These findings have cast a shadow on the prevailing practice of inferring DDD as the result of trophic interactions.

This paper seeks to provide a full investigation of apparent DDD caused by exogenous autocorrelation. Royama (1981) did not report what affected the frequency of apparent DDD in his models. Williams and Liebhold (1995) only studied how apparent DDD arose in populations with monotonic deterministic stability. In this study, we investigate how apparent DDD could arise in populations with a variety of deterministic dynamics. We demonstrate that exogenous autocorrelation could lead to the detection of not only apparent negative (standard) DDD, but also positive (inverse) DDD. We consider both linear and nonlinear models.

THE LINEAR MODEL

We first studied a linear population model. We acknowledge that linear models may not be adequate to capture the complex and often nonlinear population dynamics for many species. However, the main purpose of the linear model is to illustrate that apparent DDD due to exogenous autocorrelation is a common phenomenon, regardless of the structure of the deterministic skeleton (i.e., the model with $\varepsilon = 0$). The simple linear model also has the advantage of being analytically tractable.

We consider a simple linear first-order density-dependent model

$$N_{t+1} = (1 + a_1)N_t + a_0 \quad (2)$$

where N_t is the population density at time t , a_1 measures the strength of direct density dependence, and a_0 is a constant that affects population size but not population dynamics (the steady state point $N^* = -a_0/a_1$). The dynamics of Eq. 2 are entirely determined by a_1 (Royama 1992). In the absence of noise, N_t would converge monotonically to the steady state point N^* when $-1 < a_1 < 0$, and would converge to N^* with oscillatory two-point dynamics when $-2 < a_1 < -1$. We restrict our attention to these stable cases, because unstable populations ($-2 > a_1$ or $a_1 > 0$) do not persist.

Adding an exogenous factor (noise) e_t into Eq. 2, we obtain the stochastic model

$$N_{t+1} = (1 + a_1)N_t + a_0 + e_t. \quad (3)$$

To simulate autocorrelated noise, we model e_t as a first-order autoregressive process

$$e_t = be_{t-1} + \varepsilon_t \quad (4)$$

where b is the autoregressive coefficient, and ε_t is drawn from a standard normal distribution. We limit our attention to positively autocorrelated noise (i.e., $0 < b < 1$), which is much more common than negative correlation in nature. After algebraic manipulations, we can rewrite Eq. 3 as

$$N_{t+1} = (1 + a_1 + b)N_t - b(1 + a_1)N_{t-1} + a_0(1 - b) + \varepsilon_t. \quad (5)$$

Similar forms of Eq. 5 are described in Royama (1981: Appendix 1) and in Ives (1995). It can be shown that Eq. 5 depicts a stationary second-order process when both Eqs. 3 and 4 are stationary, i.e., if $-2 < a_1 < 0$ and $-1 < b < 1$. We used the partial autocorrelation coefficient function (PACF) to characterize DDD (Box and Jenkins 1970, Turchin 1990). Here the PACF two time steps apart (Royama 1992) is

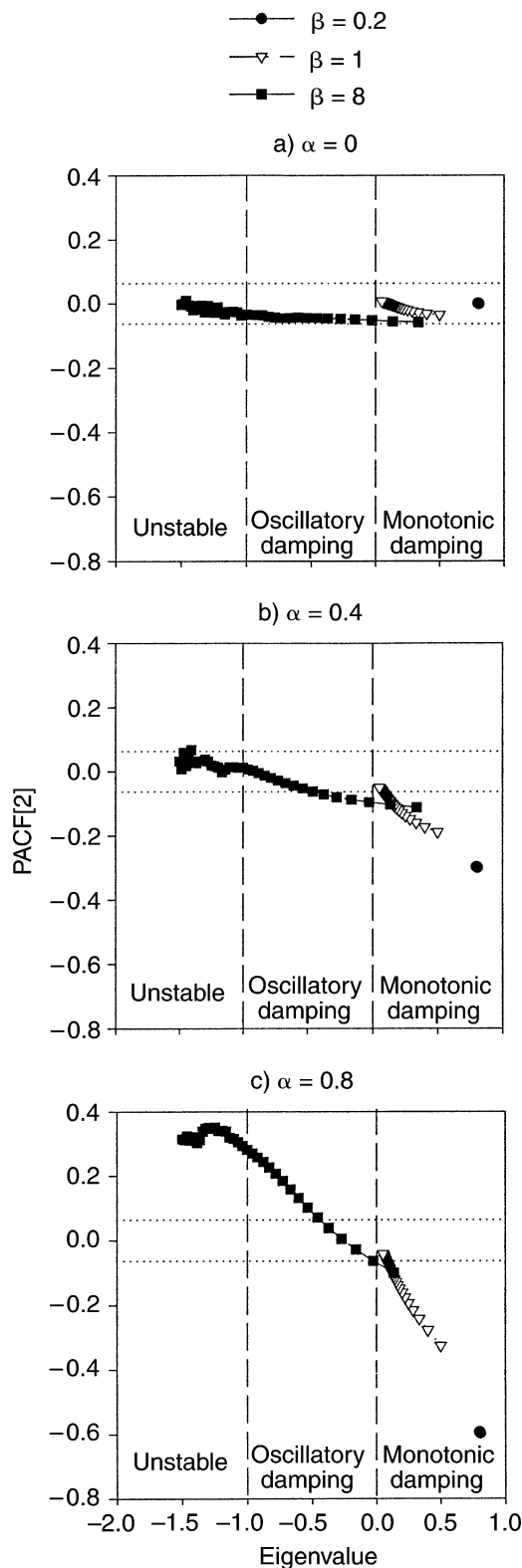
$$\text{PACF}[2] = -b(1 + a_1). \quad (6)$$

Several important conclusions can be drawn from Eq. 6. First, given constant a_1 , the magnitude of $\text{PACF}[2]$ should increase with b , implying that apparent DDD should be more frequently detected as autocorrelation in the exogenous factors becomes stronger. Second, only *negative* DDD emerges if populations are regulated by weak direct density dependence ($-1 < a_1 < 0$), i.e., when the population monotonically approaches N^* in the absence of noise. Only *positive* DDD is present if direct density dependence is strong ($-2 < a_1 < -1$), i.e., when the population approaches N^* with two-point cycles in the absence of noise. Finally, given constant b , the frequency of negative DDD declines as the strength of direct density dependence increases ($-1 \leftarrow a_1$), and the frequency of positive DDD increases as the strength of direct density dependence increases further ($-2 \leftarrow a_1$).

THE NONLINEAR MODEL

The merits of the linear models just analyzed lie in their simplicity, but in the absence of noise, they lack the ability to produce dynamics other than stable equilibria. By contrast, nonlinear deterministic models can yield a variety of dynamics, including stable equilibria, limit cycles, and chaos (May 1981). We build on the work of Williams and Liebhold (1995) to study how exogenous autocorrelation can give rise to apparent DDD in nonlinear models.

Williams and Liebhold's (1995) results were based on Ricker logistic models, which implicitly assume that strong direct density dependence operates in populations. Their analyses were also restricted to populations with deterministic monotonic stability (i.e., populations with small growth rates). Hence, their results



might not be applicable to populations characterized by other dynamics. More general conclusions can be achieved by using more generalized models that allow both the strength of density dependence and the rate of population growth to be varied. Here, we study such a model, originally formulated by Hassell (1975):

$$N_{t+1} = \frac{\lambda N_t}{(1 + N_t/K_t)^\beta} \quad (7)$$

Here, λ is the geometric growth rate, β affects the strength of direct density dependence, and K_t is a surrogate for carrying capacity.

We added an exogenous factor (noise) to K_t , as in Williams and Liebhold (1995). At each time step,

$$K_t = K_0 + \phi_t \quad (8)$$

where K_0 is a constant, and the exogenous factor, ϕ_t , was drawn from a first-order autoregressive process. The autoregressive process was created serially as

$$\phi_t = \alpha \phi_{t-1} + c(1 - \alpha^2)^{1/2} \varepsilon_t \quad (9)$$

where α defines the strength of autocorrelation and ranges from 0 to 1 (again we focus on positive autocorrelation), ε_t is a standard normal variable, and c is a constant defining the amplitude of noise variation (Ripa and Lundberg 1996). We subjected all the raw noise series created by Eq. 9 to a procedure called spectral mimicry (Cohen et al. 1999, Petchey 2000) to ensure that all noise series had identical variance and all K_t remained positive.

The nonlinearity in the models prevented analytical solutions, so we used numerical simulation. For each combination of parameter values, we iterated the model for 2000 time steps. Such long time series, presumably approximating a stationary distribution, allowed us to estimate the statistical properties (i.e., the structure and strength of density dependence) of the simulated pro-

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FIG. 1. The value of PACF[2] (lag-2 partial autocorrelation coefficient function) at three levels of autocorrelation strength (α) as a function of the eigenvalue of the nonlinear Eq. 7 for different combinations of β (the strength of density dependence) and λ (the geometric growth rate). Eqs. 7–9 were used to generate the time series. The constant for carrying capacity is $K_0 = 2$ in Eq. 8; the constant defining noise variation amplitude is $c = 1$ in Eq. 9. β was varied from 0.2 to 10 in all simulations, but only three values of β are shown for clarity: undercompensation ($\beta = 0.2$, solid circles), exact compensation ($\beta = 1$, open inverted triangles), and overcompensation ($\beta = 8$, solid squares). For each value of β , λ was increased from 2 to 20, causing the reduction of the eigenvalue. Note that eigenvalues changed little in the case of $\beta = 0.2$, indicated by the single filled dot. The vertical lines separate regions with different stability properties. The two horizontal dotted lines represent the Bartlett bands outside which DDD (delayed density dependence) is significant.

cess with more precision. We discarded the first 1000 points to remove transient dynamics, and log-transformed the data before statistical analysis. To test for DDD, we applied both PACF and linear autoregressive models to simulated data (Turchin 1990). We report the results only from PACF because the two approaches yielded very similar results. Significant DDD was indicated by lag-2 partial autocorrelation coefficients (PACF[2]) outside the Bartlett bands (Royama 1992).

Both apparent negative and positive DDD emerged. As in the linear models, the strength of apparent DDD increased as autocorrelation in the exogenous factor increased (Fig. 1). When exogenous autocorrelation was absent ($\alpha = 0$), PACF[2] values lay well within the Bartlett bands and therefore no significant DDD was present (Fig. 1a). Significant DDD, especially negative DDD, emerged with moderate exogenous autocorrelation ($\alpha = 0.4$; Fig. 1b). Further increases in the degree of exogenous autocorrelation resulted in more frequent occurrence of both negative and positive DDD ($\alpha = 0.8$; Fig. 1c).

The incidence of apparent positive and negative DDD also depends on the parameter values of β and λ (Fig. 1). For populations regulated by undercompensatory ($\beta = 0.2$) or exact-compensatory ($\beta = 1$) direct density dependence, only apparent negative DDD was present regardless of λ . In contrast, for populations regulated by overcompensatory ($\beta = 8$) direct density dependence, both apparent negative and positive DDD were detected, and increasing λ tended to reduce the incidence of negative DDD, but to increase the incidence of positive DDD.

It can be shown that the stability of the nonlinear Eq. 7 depends on only β and λ . Specifically, populations described by Eq. 7 are always stable and return monotonically to equilibrium states after perturbation (i.e., eigenvalue between 0 and 1) if they are governed by exact- or undercompensatory direct density dependence (i.e., $\beta \leq 1$), regardless of the value of λ . Conversely, populations regulated by overcompensation ($\beta > 1$) can show various types of dynamics, including monotonic damping (eigenvalue between 0 and 1), oscillatory damping (eigenvalue between -1 and 0), and unstable population oscillation such as limit cycles or chaos (eigenvalue less than -1). A simple pattern emerged when the values of PACF[2] were plotted against the eigenvalues of the nonlinear model for different combinations of β and λ : apparent negative DDD was only found in the region of monotonic damping, and apparent positive DDD was only found in regions of oscillatory damping or unstable dynamics (Fig. 1). This simple relationship applies to several other nonlinear models that we explored, and is consistent with the finding from the linear model, Eq. 3, for which the eigenvalue equals $1 + a_1$.

DISCUSSION

In addition to apparent negative DDD, our investigation clearly demonstrated that autocorrelation in exogenous factors can also lead to the spurious appearance of positive DDD, in populations regulated only by direct density dependence. Evidence for apparent negative DDD was primarily observed in populations with deterministic monotonic stability, and apparent positive DDD was found in populations with deterministic damped or sustained two-point oscillations, or more complex dynamics.

The results of our models depend, of course, upon the critical question: do autocorrelated exogenous factors exist in the real world? We wish to focus on terrestrial environments and univoltine species, for which most population time series have been collected. It is important to note, however, that temporal autocorrelation in environmental variables (e.g., temperature) often exists in marine habitats, due to the large thermal capacity of the ocean (Steele 1985). For terrestrial environments, Williams and Liebhold (1995, 1997) argued that weather and generalist predators might serve as autocorrelated exogenous factors, whereas Berryman and Turchin (1997) contended that annual weather patterns show little autocorrelation between years and that generalist predators are more likely to impose direct density dependence on their prey populations. We agree with Berryman and Turchin in their assertions. Weather variables are generally autocorrelated on very large time scales, but seem uncorrelated on the time scale of <50 years (Steele 1985, Halley 1996). Because most ecological time series are shorter than 50 years, weather seems unlikely to cause apparent DDD in most observed time series on univoltine species. Generalist predators often respond to prey density instantaneously via switching or migratory behavior, resulting in direct density dependence rather than delayed density dependence (Hassell 1978, 2000, Hanski et al. 1991, 2001).

Plausible autocorrelated exogenous factors in terrestrial habitats, however, are likely to be biotic factors that are inherently autocorrelated and yet dynamically independent. For example, for species involved in asymmetric competition, the little-affected species may be regarded as the autocorrelated exogenous factor for the species more affected by competition. Here we wish to emphasize that important autocorrelated exogenous factors in terrestrial environments are fluctuating biotic resources in bottom-up controlled communities. Communities characterized by mast seeding or pulsed primary production are often bottom-up controlled (Ostfeld and Keesing 2000). In these communities, the production of biotic resources (i.e., seed crops, plant growth) often dominantly determines, but seems unaffected by, the dynamics of species that consume the

resources (Wolff 1996, McShea 2000, Ostfeld and Keesing 2000). Temporal autocorrelation often exists in resource production between years in these bottom-up communities (e.g., Sork et al. 1993, Koenig and Knops 2000). We thus hypothesize that apparent DDD may frequently arise in consumers residing in bottom-up communities with variable resource production. One possible example is the leaf-eared mouse (*Phyllotis darwini*) in semiarid Chile, where primary production varies considerably from year to year. Lima et al. (1999) detected DDD in the rodent time series and speculated that trophic interactions were its sources. We, however, would like to argue that the rodent's fluctuating resources, as the autocorrelated exogenous factor, might have caused the spurious appearance of DDD. We await further studies to unravel the mechanisms behind DDD in the rodent populations.

The finding of apparent positive DDD deserves further attention. Few biological mechanisms are known for positive DDD. Here we report that autocorrelated exogenous factors could generate the appearance of positive DDD. Saitoh et al. (1999) compared the pattern of density dependence between the grey-sided vole (*Clethrionomys rufocanus*) and two wood mouse species (*Apodemus speciosus* and *Apodemus argenteus*) in Hokkaido, Japan. The grey-sided voles feed primarily on green plants and are vulnerable to predation, whereas wood mice feed mainly on insects and seeds, and are less vulnerable to predation because of their greater mobility (Saitoh et al. 1999). The incidence of negative DDD was significantly higher in the vole populations than in the mouse populations. Interestingly, Saitoh et al. (1999) found 27 out of 28 significant DDDs in the wood mice time series to be positive ($P \approx 10^{-7}$, assuming that positive and negative DDD are equally likely), which they attributed to the inability of their statistical tests to completely partial out the effects of direct density dependence. Our models suggest, however, that seeds and insects might have served as autocorrelated exogenous factors, producing apparent positive DDD. The apparent DDD hypothesis gains further support from the finding that positive DDD was generally associated with mouse populations regulated by strong direct density dependence.

Our simulations demonstrate that apparent negative DDD is associated with populations characterized with monotonic stability, whereas apparent positive DDD is associated with populations characterized by oscillatory or complex dynamics. These results suggest that knowledge of deterministic dynamics is important for predicting the sign of apparent DDD for populations residing in autocorrelated environments. In a classic study, Hassell et al. (1976) examined 24 field insect populations, using Eq. 7, and found the majority of them to be monotonically stable. If the models did

correctly capture the essence of population dynamics for these species, we would expect to find apparent negative DDD in their populations when subjected to autocorrelated exogenous environments.

In practice, apparent DDD (negative or positive) may either strengthen or weaken DDD (negative) due to trophic interactions. Under this circumstance, confounding the two types of DDD and failing to recognize their relative contributions to observed population dynamics may result in erroneous interpretation of population regulation mechanisms. Although the sign of apparent DDD can be predicted, without any prior knowledge about exogenous factors, it is extremely difficult to statistically distinguish the effects of endogenous factors from autocorrelated exogenous factors (Ives 1995, Jonzen et al. 2002). Consequently, we caution against an uncritical interpretation of findings of DDD in natural populations as the result of coupled trophic interactions. We, in agreement with other authors (Berryman and Turchin 1997, 2001), advocate that the best use of time-series models should be as diagnostic tools to generate mechanistic hypotheses, which can then be tested by manipulative experiments (Turchin et al. 1999, Korpimäki et al. 2002).

ACKNOWLEDGMENTS

We thank A. Berryman, T. Casey, A. Ives, C. Kaunzinger, Z. Long, T. McPhearson, P. Morin, O. Petchey, J. Price, J. Ripa, E. Schaubert, P. Smouse, C. Steiner, H. Stevens, P. Turchin, and one anonymous reviewer for their helpful comments on the manuscript. We are grateful to P. Turchin for his advice on the analyses. This research was supported in part by Rutgers Bevier dissertation fellowship awarded to L. Jiang.

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