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DETECTION OF DELAYED DENSITY DEPENDENCE: EFFECTS OF AUTOCORRELATION IN AN EXOGENOUS FACTOR

David W. Williams¹ and Andrew M. Liebhold²

Delayed density-dependent factors are important in population regulation. Mechanisms operating with time lags are abundant in nature, as exemplified by parasitoids that track host populations with a reproductive delay (Morris 1959, Varley et al. 1973). In a recent analysis of forest insect population data, Turchin (1990) detected delayed density dependence in 8 of 14 species investigated.

Delayed density dependence may be conceptualized using a linear second-order autoregressive (AR) model

$$N_{t+1} = \phi_0 N_t + \phi_1 N_{t-1} + A_t \quad (1)$$

where N_t is the logarithm of population size in generation t and A_t is a random variable (Royama 1977, 1981). Population size in the next generation depends upon the sizes of the previous two, and the parameters ϕ_0 and ϕ_1 subsume all the endogenous factors that influence population size. Thus, ϕ_0 includes the factors involved in direct density dependence, and ϕ_1 those involved in delayed density dependence. A_t summarizes exogenous factors, which influence population size but are not reciprocally affected by it (Royama 1977). Weather is the most obvious example of such a factor. Although the endogenous and exogenous factors are explicitly defined in this simple model, their separate effects may be difficult to partition through analyses of natural populations (Royama 1981). For example, demonstrating the role of weather in insect outbreaks is often difficult, despite knowledge of some specific effects of temperature and precipitation on populations (Martinat 1987).

Complications may arise in detecting density dependence if an exogenous factor is serially autocorrelated. Using simulated populations, Maelzer (1970) demonstrated that serial autocorrelation could inflate an es-

timate of direct density dependence and mask its true value. Royama (1981: Appendix 1) demonstrated that a first-order linear population model of the form

$$N_{t+1} = \phi N_t + A_t \quad (2)$$

can be transformed into a second-order equation (Eq. 1) if the exogenous term, A_t , is itself represented as a first-order AR process. Thus, a population process without explicit second-lag effects can be represented as a second-order process through change in a random exogenous factor. This clearly may affect the interpretation of delayed density dependence using a model such as Eq. 1.

We were interested to know how autocorrelation in an exogenous factor may affect the detection of delayed density dependence and give the appearance of delayed density dependence in a first-order model. We investigated this question using simulations of a simple nonlinear model with varying degrees of direct density dependence and with an exogenous factor having several levels of autocorrelation and variation. We then analyzed the simulations by the methods suggested by Turchin (1990) for detecting delayed density dependence.

Methods

As our first-order population model, we used the Ricker model (Ricker 1954, Cook 1965)

$$n_{t+1} = n_t \exp[r(1 - n_t/K)], \quad (3)$$

where n_t is population size in generation t , and the parameters r and K are the intrinsic rate of increase and the carrying capacity, respectively. The model was log-transformed for simulation and made stochastic by adding the random variable, A_t , to the log-transformed carrying capacity, K' . The resulting stochastic difference equation was

$$N_{t+1} = N_t + r(1 - \exp[N_t - (K' + A_t)]) \quad (4)$$

where N_t is $\ln n_t$. We modeled the exogenous factor as a first-order autoregressive (AR) process

$$A_{t+1} = \psi A_t + s\epsilon_t \quad (5)$$

where ψ determines the level of autocorrelation, ϵ_t is a standard normal random variable, and s scales the variation of ϵ_t .

Series of normal random deviates were generated using the Box-Muller method (Press et al. 1986). Simulation experiments involved 36 combinations of r , ψ , and s . We ran 1000 replicate simulations for each combination. The same 1000 random series were used for each parameter combination to provide a common basis for comparing scenarios.

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The model was iterated 100 times, and iterations 51–100 were used for the analyses. A series length of 50 was used because it is near the maximum for existing time series of natural populations (Turchin 1990) and near the minimum limit for which time series analysis is valid (Box and Jenkins 1976). Each simulation was initiated with $N_0 = 1$, and K' had a constant value of 2. We chose a range of 0–1 for ψ to guarantee stationarity, the relative constancy of the mean of a series over time (Box and Jenkins 1976). We set the same range for r to ensure that it would be well below the threshold (i.e., $r = 2$) at which complex behavior begins in the Ricker model (May and Oster 1976).

We analyzed the simulated series for delayed density dependence using time series analysis and multiple linear regression, as proposed by Turchin (1990). The classical approach to time series analysis entails identification of the type and order of a model using the autocorrelation function (ACF) and the partial autocorrelation function (PACF) (Box and Jenkins 1976). Delayed density dependence is characterized minimally as a second-order AR process with a significant negative second-lag coefficient in the PACF (Turchin 1990).

The shape of the ACF is also important in characterizing ecological processes (Turchin and Taylor 1992). The ACFs reported by Turchin (1990) from natural populations displaying delayed density dependence were primarily in the form of a damped sine wave, which indicates oscillatory behavior in the second-order AR process. To avoid visual inspection of thousands of ACFs we estimated the autoregressive parameters for the second-order AR model for each simulation and examined the properties of the fitted model. The second-order AR model fitted was Eq. 1, with the addition of a mean term. Parameters were estimated by the method of conditional least squares (Box and Jenkins 1976). When both ϕ_0 and ϕ_1 were significant ($P < 0.05$), they were used to assess the stationarity and periodic behavior of the simulated series. Periodic behavior was identified for stationary second-order models by the condition, $\phi_0^2 + 4\phi_1 < 0$ (Box and Jenkins 1976).

The second method for assessing delayed density dependence followed Turchin (1990), who modified a different form of the Ricker equation to include time lags

$$n_{t+1} = n_t \exp[r_0 + \alpha_1 n_t + \alpha_2 n_{t-1} + \epsilon_t], \quad (6)$$

where n_t is the untransformed population size (i.e., $N_t = \ln n_t$) in generation t . The parameters, r_0 , α_1 , and α_2 , were estimated by log-transforming the equation and regressing the rate of population change, $R_t = N_{t+1} - N_t$, on the lagged population sizes according to the regression equation

TABLE 1. The number of significant second-order models per 1000 simulations for the Ricker model (Ricker 1954, Cook 1965) under 36 combinations of the parameters, r , s , and ψ , using two analyses. r = the intrinsic rate of population increase; s = constant scaling the variation of the random variable, ϵ_t , of the exogenous factor; ψ = the autoregressive parameter of the exogenous factor.

s	ψ	Time series analysis			Regression analysis		
		r			r		
		0.1	0.4	0.7	0.1	0.4	0.7
0.3	0.0	32	25	27	36	31	27
	0.1	89	55	44	127	78	46
	0.3	320	220	78	446	261	106
	0.5	592	454	155	835	527	187
	0.7	678	658	244	977	767	288
	0.9	433	635	254	883	894	341
0.6	0.0	24	17	19	40	28	18
	0.1	74	28	26	111	60	31
	0.3	227	121	46	361	189	82
	0.5	483	264	75	731	379	130
	0.7	587	425	110	925	561	180
	0.9	400	431	106	929	617	186

$$R_t = r_0 + \alpha_1 n_t + \alpha_2 n_{t-1} + \epsilon_t \quad (7)$$

A significant t value for α_2 ($P < 0.05$) indicated delayed density dependence in a simulated population.

Results and Discussion

Time series analysis revealed numerous cases of significant negative second-lag partial autocorrelations for the 36 combinations of r , ψ , and s (Table 1). Frequency of second-order models generally increased with increasing autocorrelation in the exogenous factor (ψ). However, there were fewer significant cases at $\psi = 0.9$ than at 0.7 for r values of 0.1 and 0.4. This result is likely explained by the closeness of 0.9 to 1.0, at which value the first-order process simulates a random walk (Renshaw 1991). As ψ approaches 1.0, we expect to find more purely random behavior and a lower detection of AR (autoregressive) processes. The number of significant second-order cases generally decreased as r increased. Because r determines the strength of direct density dependence, increasing it probably masked more subtle second-order effects in this nonlinear model. Doubling s resulted in lower numbers of significant cases, presumably because increasing variation in the random disturbance obscured the higher order effect.

Trends were similar for the regression analysis (Table 1), although the number of significant second-order cases was uniformly higher than with time series analysis. The nonlinear regression technique was apparently quite sensitive in detecting second-order effects in series generated by the nonlinear first-order model to which it was very similar.

Proceeding to the second component in diagnosing delayed density dependence, the form of the ACF (au-

TABLE 2. The number of simulations of the Ricker model (per 1000) showing periodic behavior under 36 combinations of the parameters, r , s , and ψ . The number of simulations for which the estimated second-order lag parameter, ϕ_1 , was negative and significant ($P < 0.05$) is given in parentheses.

s	ψ	r		
		0.1	0.4	0.7
0.3	0.0	15 (35)	26 (26)	31 (31)
	0.1	37 (105)	63 (63)	51 (51)
	0.3	127 (407)	231 (244)	93 (93)
	0.5	204 (799)	413 (497)	166 (168)
	0.7	299 (901)	391 (751)	224 (260)
	0.9	267 (665)	214 (863)	83 (326)
0.6	0.0	14 (29)	16 (16)	20 (20)
	0.1	30 (89)	30 (31)	26 (26)
	0.3	97 (309)	119 (132)	49 (49)
	0.5	152 (655)	240 (299)	82 (83)
	0.7	202 (847)	232 (510)	93 (113)
	0.9	180 (733)	99 (665)	34 (141)

tocorrelation function), we show the number of stationary second-order simulations with periodic behavior in Table 2. Many simulations showed periodic behavior, and the trends along parameter values were similar to those for significant second-order models (cf. Table 1). Note that the number of significant second-order models diagnosed by this estimation method (in parentheses) generally lay between those for the other two techniques. Typical ACFs for simulations with periodic behavior (Fig. 1) were in the characteristic form of a damped sine wave. Periodic behavior and ACFs like those in Fig. 1 were also observed in another set of simulations not reported here, which used the linear first-order population model (Eq. 2) and an autocorrelated exogenous factor (Eq. 5).

In summary, both tests suggested by Turchin (1990) as diagnostics for delayed density dependence showed significant negative second-lag effects over the range of parameter values examined. Our simulations suggested, as did the theoretical results of Royama (1981), that the appearance of delayed density dependence may arise from autocorrelation in an exogenous factor. In addition, we commonly observed ACFs in the form of a damped sine wave, the prevalent pattern for forest insect time series diagnosed as delayed density dependent (Turchin 1990).

What are examples of real world phenomena that might serve as autocorrelated exogenous factors? Among biotic entities, the most likely are generalist predators. For insect populations, generalist predators may include insectivorous birds, small mammals, or web-spinning spiders. We expect to find serial autocorrelation in predator populations because of its frequent occurrence in animal populations (Bulmer 1975, Turchin 1990).

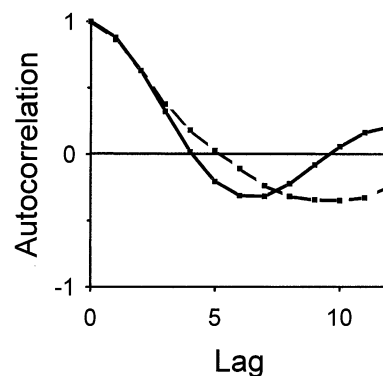


FIG. 1. Two examples of autocorrelation functions from simulated time series with periodic behavior.

Among abiotic phenomena, weather is the most likely exogenous factor. Daily weather, including temperature and precipitation, is often modeled using first-order AR (autoregressive) processes (Leith 1973, Madden 1979). In general, AR processes provide good models up to a scale of weeks. However, at time scales approaching a year, weather shows little autocorrelation, as evidenced by our inability to predict it on such scales (Madden and Shea 1978). Thus, it is not clear how weather might function as an autocorrelated exogenous factor for univoltine populations. Evidence of weather cycles at scales of >1 yr and <10 yr is relatively recent (Burroughs 1992). Phenomena such as the "quasi-biennial oscillation" may provide autocorrelations, implying higher order processes for exogenous factors driving populations at an annual time scale. In addition, with impending climatic change from greenhouse warming, weather patterns may exhibit an increase in autocorrelation (Mearns et al. 1984).

In conclusion, our simulations show that autocorrelation in an exogenous factor may mimic the second-order effects identified as delayed density dependence using available techniques, thereby confounding the interpretation of population regulation. Future development of statistical procedures that explicitly accommodate a serially correlated disturbance term may produce tests that distinguish delayed density dependence from second-order effects resulting from autocorrelation in an exogenous process. Using current methodologies, however, diagnosis of the underlying causes of dynamics from single-species population censuses is at best tenuous and may be impossible. In addition to their use in diagnosis, simple single-species models with time delays have been proposed to predict population dynamics (Berryman 1991). Such models may incorporate delayed density dependence through an endogenous factor. Because our findings suggest that ex-

ogenous factors may affect population dynamics while giving the appearance of delayed density dependence, we urge caution in the use of such models for prediction. To understand regulation and predict populations, we clearly need more information on the factors, both endogenous and exogenous, that influence population density than is contained in censuses of individual species.

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PREDATOR-INDUCED DIAPAUSE IN DAPHNIA

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Diapause is generally believed to be an adaptation to allow temporal avoidance of adverse conditions (Cohen 1966, Levins 1968, Venable and Lawlor 1980, Ellner 1985, Venable and Brown 1988). Passive dis-

persion of dormant stages can also enable a spatial escape from local adversity (Janzen 1970) and colonization of a new territory (Platt 1976, Howe and Smallwood 1982). Dormant stages are usually better equipped to withstand harsh environmental conditions than active individuals (Danks 1987, Schwartz and Hebert 1987). Diapause typically occurs before living conditions deteriorate (Taylor 1980, Hairston and Munns 1984). This anticipation is achieved by responding to token environmental stimuli that do not necessarily themselves influence fitness, but that are reliable predictors of future environmental change. Photoperiod and temperature are the most commonly recognized cues controlling diapause, which avoids adverse periods correlated with the seasons (Danks 1987, Stross 1987). The timing of seasonal dormancy is usually a species- and place-specific feature and in

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