

# Identifying the density-dependent structure underlying ecological time series

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A central problem in ecology is explaining the causes of population fluctuations, and an important step in the solution is determining the structure of the negative feedback (density dependent) process regulating population dynamics. The conventional way to determine the dimension or order of density dependence in a time series is to calculate the partial autocorrelation function (PACF). We maintain, however, that PACF is not designed with biological populations in mind and has the wrong null model for detecting the structure of density dependence. We suggest an alternative diagnostic, the partial rate correlation function (PRCF), which is specifically designed for biological populations and has an appropriate null model for detecting their density dependent structures. Tests with simulated data show PRCF to be superior to PACF in detecting the underlying density dependent structure of two simple mathematical models.

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Understanding the patterns and causes of temporal changes in population numbers or density is a central goal of population ecology (Royama 1977, 1992, Berryman 1989, 1999). Many critical environmental issues in conservation biology, natural resource management, and pest control cannot be resolved without such understanding. One type of data frequently available to resource and pest managers, and which contains useful information about the pattern of population fluctuations, is a time series – a record of the abundance of a particular organism living in a certain locality collected at regular intervals over a fairly long period of time (Fig. 1).

Analysis of time series data can provide insights into the relative importance of exogenous (density independent) and endogenous (density dependent) factors, whether there are systematic trends or discontinuities due to exogenous forcing, the type of endogenous dynamics (stable, periodic, or chaotic), and how accurately (as well as how far ahead) we can predict future

population numbers (Berryman 1991, 1999, Hastings et al. 1993).

The conventional way to analyze the endogenous dynamics of time series data employs an autoregressive model relating the current density of a population,  $N_t$ , to past densities,  $N_{t-1}$ ,  $N_{t-2}$ , ...,  $N_{t-d}$ , and an exogenous input composed of density-independent “random shocks”,  $\varepsilon_t$  (Royama 1977, 1981, 1992, Turchin 1990, Ellner et al. 1991, Turchin and Taylor 1992)

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

A critical problem in autoregressive modeling is to determine  $d$ , the number of terms that need to be retained in eq. (1). In the statistical literature, the quantity  $d$  is referred to as the *order* of the autoregressive process (Box and Jenkins 1976), in nonlinear dynamics theory it is the *embedding dimension* (Schaffer 1985), while in ecology it is sometimes called the maximum *time delay* in density dependent regulation (Berry-

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man et al. 1987). Correct estimation of  $d$  is critical for successful forecasting, because both underestimating and overestimating this parameter will lead to decreased accuracy of forecasts (Berryman 1992). Moreover, we can use the estimated value of  $d$  to generate hypotheses about the proximal (biological) causes driving population fluctuations (Berryman 1999, Turchin and Ellner 2000).

A second major activity in ecological time series analysis is to determine the structure of the density dependent feedback processes, for knowledge about this can lead to important inferences about the factors involved in population regulation (Berryman 1999, Turchin and Ellner 2000). One particularly important aspect of structure is the relative contribution of rapid first-order feedback (direct density dependence) and slower second and/or higher order feedback (delayed density dependence) to the determination of population dynamics.

### Ecological time series analysis

The most commonly used diagnostics in conventional time series analysis are the autocorrelation and partial autocorrelation functions. The *autocorrelation function*, or *ACF*, is estimated by calculating the correlation between pairs of log-transformed population densities  $L_t \equiv \ln N_t$  and  $L_{t-\tau}$ , where  $\tau = 1, 2, \dots, d$  is the time lag or time delay in the feedback response. The autocorrelation coefficients are then plotted against the lag to give the *ACF* (Fig. 2). By averaging over noisy data, *ACF* reveals periodic patterns more clearly than the time plot and also provides an objective estimate of the cycle period (Box and Jenkins 1976, Finerty 1980, Nisbet and Gurney 1982, Chatfield 1989, Turchin and Taylor 1992). For instance, large positive spikes in the larch budmoth *ACF* at lags 9 and 10 (Fig. 2) indicate that the population oscillates with a frequency of 9–10 yr.

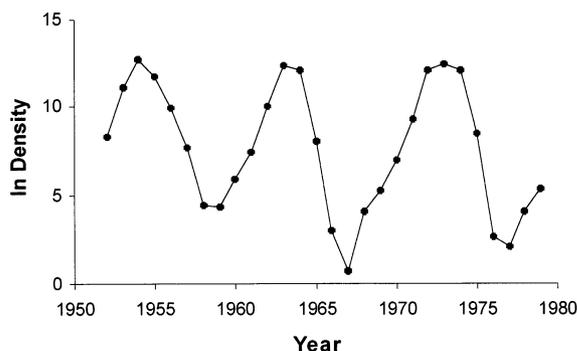


Fig. 1. Natural logarithm of the number of larch budmoth (*Zeiraphera diniana*) larvae per 1000 kg larch foliage (data from Baltensweiler 1989).

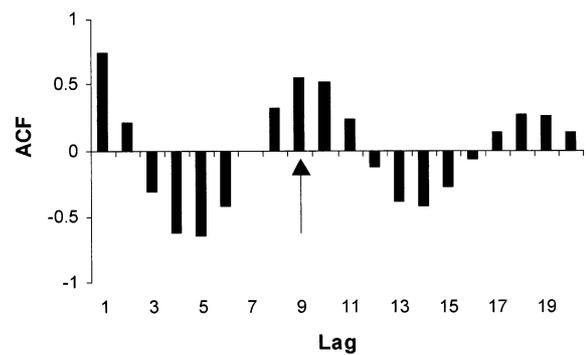


Fig. 2. Autocorrelation function (*ACF*) for the larch budmoth time series.

While *ACF* may be a useful tool for detecting the period of time series data, it cannot tell us much about the dimension or structure of density dependent feedback. For example, a significant autocorrelation at lag 9 in Fig. 2 does not necessarily mean that there is a direct effect of larch budmoth density 9 yr ago on present density, since it is much more likely that  $N_{t-9}$  is correlated with  $N_t$  through intermediate effects. For example, a model with only two lags [say  $N_{t-1}$  and  $N_{t-2}$  in eq. (1)] can generate cycles that have significant autocorrelation at lags 9 and 10, even though the maximum time delay in the density dependence is only 2. Therefore, *ACF* cannot detect the dimension of the feedback processes operating on the population, or the number of lags that should be included in a population model. The problem is analogous to that of deciding on the number of terms to include in a multiple regression equation (Box and Jenkins 1976).

To solve this problem, Box and Jenkins (1976) recommend the use of the partial autocorrelation function (*PACF*). Constructing a *PACF* is equivalent to performing stepwise regression. First,  $L_t$  is regressed on  $L_{t-1}$  and the correlation coefficient gives us *PACF*[1] which, naturally, is the same as *ACF*[1]. Next,  $L_t$  is regressed on  $L_{t-1}$  and  $L_{t-2}$  and *PACF*[2] is the *partial* correlation coefficient between  $L_t$  and  $L_{t-2}$  given that  $L_{t-1}$  is already in the model. *PACF*[2] squared measures how much the second term increases the proportion of variance explained by regression. To estimate *PACF*[3] we add  $L_{t-3}$  to the model, and so on. Partial autocorrelations are usually plotted against lag to provide a *PACF* histogram or partial autocorrelation function (Fig. 3).

If the dynamics of a system can be at least approximated by a linear (in logs) autoregressive process of order  $d$ , with  $\varepsilon_t$  again representing the exogenous component and  $a_i$  the constants of regression, then the autoregressive process is described by the linear model

$$L_t = a_0 + a_1 L_{t-1} + a_2 L_{t-2} + \dots + a_d L_{t-d} + \varepsilon_t. \quad (2)$$

The theoretical *PACF* for such a model will have non-zero correlations at lags less than or equal to  $d$  and zero correlations at lags greater than  $d$ . This observation suggests the following practical rule (Box and Jenkins 1976): If *PACF* has correlations significantly different from zero at lags of  $d$  or less while correlations at higher lags are non-significant, then a reasonable model for that system is an autoregressive process of order  $d$  (significance can be roughly assessed by Bartlett's criterion  $2\sqrt{n}$ , with  $n$  the length of the time series). For example, the *PACF* for the larch budmoth (Fig. 3) indicates a second order autoregressive process ( $d = 2$ ) because the absolute value

$$|PACF[2]| = 0.79 > 2/\sqrt{28} = 0.38$$

while all higher order correlation coefficients (absolute values) are less than this value. Notice that  $PACF[1] = 0.75$  is also significant but in this case the correlation coefficient is positive which indicates the presence of positive feedback at lag 1. As we will see, this is the heart of the problem with *PACF* as a diagnostic tool.

The problem with using *PACF* in ecology is that the autoregressive model (2) is not well suited to biological systems. This is because changes in biological populations are brought about by changes in *individual* organisms; i.e., individuals reproduce, die and move. Thus, a better general regression model for biological populations is (Royama 1977, 1992, Berryman et al. 1987, Berryman 1999, Turchin and Taylor 1992, Huffaker et al. 1998)

$$N_t = N_{t-1}F'(N_{t-1}, N_{t-2}, \dots, N_{t-d}, \varepsilon_t), \quad (3)$$

where the function  $F'(\dots)$  now represents the realized *per-capita* rate of population change.

This model suggests that, instead of  $L_t$ , we should use the replacement rate  $N_t/N_{t-1}$  or, better still, the logarithmic *per-capita* rate of change  $R_t = \ln(N_t/N_{t-1})$  as the dependent variable in the stepwise regression (log-transforming the replacement rate linearizes the growth

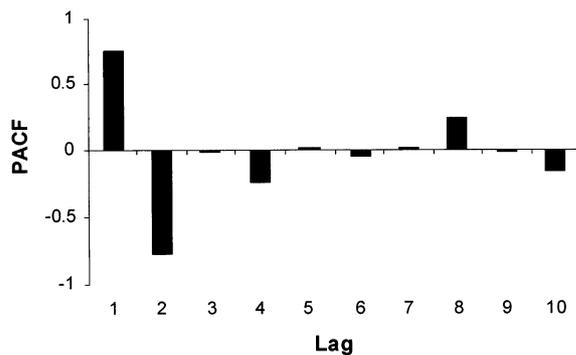


Fig. 3. Partial autocorrelation function (*PACF*) for the larch budmoth time series.

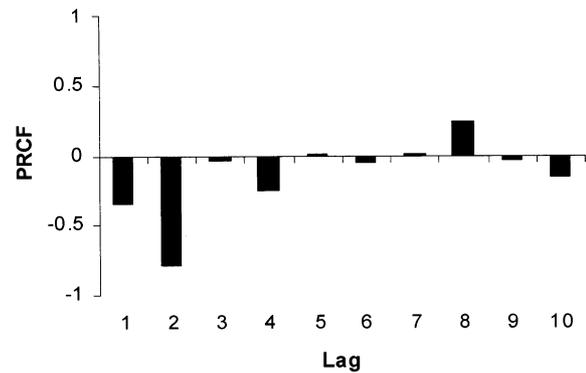


Fig. 4. Partial rate correlation function (*PRCF*) for the larch budmoth time series.

process and makes the statistical estimation procedure better behaved). Assuming again linear relationships between dependent and independent variables, we have the model

$$R_t = L_t - L_{t-1} = a_0 + a_1L_{t-1} + a_2L_{t-2} + \dots + a_dL_{t-d} + \varepsilon_t. \quad (4)$$

In this model we regress the differenced series ( $R_t = L_t - L_{t-1}$ ) against lagged population densities ( $L_{t-1}, L_{t-2}, \dots$ ) to give what we call the partial rate correlation function, or *PRCF* (Fig. 4). Like *PACF*, the partial rate correlation function shows how the addition of a term to the model increases the coefficient of multiple determination. It is important to notice that the larch budmoth *PRCF* has a negative correlation coefficient at lag 1, indicating the presence of direct density dependence, while *PACF* shows no such effect.

### Null models

In order to understand the difference between *PACF* and *PRCF* it is necessary to look at their null models. First consider the null model of *PACF*. In the null model the dependent variable is unaffected by the independent variables so that the parameters associated with the independent variables in eq. (2) are zero (i.e.,  $a_1 = a_2 = \dots = a_d = 0$ ). Thus the null model of *PACF* is

$$L_t = a_0 + \varepsilon_t. \quad (5)$$

An important property of this model is that, when random disturbances are removed (i.e.,  $\varepsilon_t = 0$ ), the system goes immediately to the fixed point  $a_0$ . This property of dynamic systems is called perfect compensation. Compensation refers to the speed with which a system returns to equilibrium following a perturbation (Varley and Gradwell 1960, Royama 1977). Under-compensated systems return slowly and smoothly to equi-

librium while over-compensated ones return quickly and tend to overshoot equilibrium. Perfectly compensated systems, on the other hand, return exactly to equilibrium in a single time step and generally operate on a fast time scale relative to the interval of observation.

Now consider the null model underlying *PRCF*. As before, the parameters on the independent variables in eq. (4) will be zero under the null model so that we have

$$R_t = a_0 + \varepsilon_t$$

or

$$L_t = L_{t-1} + a_0 + \varepsilon_t. \quad (6)$$

If random disturbances are removed from this model, the population either grows continuously if  $a_0 > 0$ , declines continuously if  $a_0 < 0$ , or remains at its previous value if  $a_0 = 0$ . In other words it is a model for exponential growth and, therefore, does not have an equilibrium point and does not fluctuate around a particular mean value. In a randomly varying environment, the null model generates an “unbiased random walk” if  $a_0 = 0$  or a “random walk with drift” if  $a_0 \neq 0$ .

Clearly, the null models underlying *PACF* and *PRCF* are fundamentally different; i.e., perfect compensation in the case of *PACF* versus unregulated or uncompensated population dynamics in the case of *PRCF*. The question is, which is the more useful null model in ecology? A major goal of ecological time series analyses is to deduce the structure of the stabilizing density dependent negative feedback process(es) regulating population dynamics. Because these processes are by definition compensatory, it will be difficult (or impossible) to detect their presence against a null model for perfect compensation. In fact, as we saw with the larch budmoth, *PACF* can mislead one about the effect of direct density dependence. This is because *PACF* can have a strong *positive* spike at lag 1, even in unregulated populations, due to the usual positive relationship between population densities at two consecutive points in time; i.e., years with large populations are invariably followed by large populations and vice versa. This trivial positive correlation can obscure the effects of negative feedback caused by direct density dependence (Berryman 1999). Even systems under strong direct density dependent control can have a positive *PACF*[1] when regulation is under-compensated, while in over-compensated systems, where *PACF*[1] may give the correct negative signal, it may severely underestimate the negative feedback effect.

In contrast, the “unregulated” null model underlying *PRCF* seems to be a logical starting point for an

ecological investigation because *PRCF*[1] provides a direct indication of the presence of feedback at lag 1 (i.e., direct density dependence when *PRCF*[1] < 0 and inverse density dependence when *PRCF*[1] > 0), as well as the relative strength of that feedback in comparison to higher-order effects. For example, the larch budmoth *PRCF* (Fig. 4) indicates the presence of weak negative feedback at lag 1 (*PRCF*[1] = 0.12) and quite strong negative feedback at lag 2 (*PRCF*[2] = 0.61). This kind of comparative information about the underlying feedback structure cannot be obtained from *PACF*.

For lags greater than 1, *PACF* and *PRCF* give similar information. In fact the correlation coefficients are identical if calculated by partial regression of  $R_t$  on  $L_{t-d}$ . In other words, both *PACF* and *PRCF* give the same information on the maximum dimension of the dynamic system as long as the dimension is two or greater. However, the critical ability of *PRCF* to quantitatively compare the influence of the first lag (direct density dependence) to that of longer time delays (delayed density dependence), or to identify the nontrivial feedback structure of the dynamic system, is not available with *PACF* (Berryman 1999). For these reasons we believe *PRCF* to be a more useful diagnostic tool for evaluating the density dependent structure of ecological time series.

It is interesting and significant that the null model for *PACF* [eq. (5)] also describes the dynamic behavior of a random variable drawn from a statistical distribution with mean  $a_0$ . For this reason, a sequence of numbers chosen at random from a statistical distribution will behave exactly like a perfectly compensated system operating in a noisy environment. There is no contradiction here since a sequence of random numbers taken from a statistical distribution has a well-defined equilibrium, the mean of the distribution. Unfortunately, this property of randomly distributed numbers is sometimes used as an argument against models like eq. (4). The argument goes something like this: If the per-capita rate of change ( $R_t = L_t - L_{t-1}$ ) is calculated from a series of numbers chosen at random from a statistical distribution, a strong negative correlation will be obtained between  $R_t$  and  $L_{t-1}$ , which leads to the claim that *PRCF*[1] cannot distinguish between a density dependent process and a random process. Of course, the answer to this criticism is simple, for randomly distributed numbers are actually generated by a perfectly compensated “density dependent” system and are expected to have a strong negative correlation at *PRCF*[1]. In other words, perfect compensation is the wrong null model for detecting direct density dependence. The appropriate null model is, of course, unregulated population growth [eq. (6)] (Huffaker et al. 1998).

## Testing *PRCF* with simulated data

We tested the ability of *PRCF* to provide qualitative insights into the feedback structure of population systems by generating “pseudo-data”. Data were generated by two ecological models of known dynamic characteristics but different mathematical structure from the theoretical model underlying *PRCF*:

1. A single-species equation (Hassell 1975) was used to model direct (first order) density dependence

$$N_t = \lambda N_{t-1} (1 + \theta N_{t-1})^{-b}. \quad (7)$$

The parameters  $\theta$  and  $b$  were kept constant ( $b = 1/\theta = 3$ ) while  $\lambda$  was varied to change the dynamic properties of the model ( $\lambda = 5, 10$  and  $20$ ).

2. A discrete version of a two-species predator-prey equation (Leslie 1948, May 1973) was used to model delayed (second order) density dependence

$$\begin{aligned} N_t &= N_{t-1} \exp[r(1 - N_{t-1}/K) - gP_{t-1}] \\ P_t &= P_{t-1} \exp[s(1 - hP_{t-1}/N_{t-1})]. \end{aligned} \quad (8)$$

Parameters  $K$  and  $h$  in (8) were set to unity, effectively making  $N_t$  and  $P_t$  the scaled densities of prey and predator populations, respectively; i.e., prey density was expressed in units of prey carrying capacity, and predator density in units of prey abundance. Parameters  $g$  and  $s$  were kept constant ( $s = 1, g = 4$ ) while  $r$  was varied to affect the dynamic properties of the model ( $r = 0.5, 1$  and  $2$ ).

The model output (“data”) was influenced by dynamic noise (environmental stochasticity) and measurement error. Dynamic noise was introduced by perturbing parameters; i.e., each parameter  $p$  was considered to be a random, normally distributed variable, with mean  $\bar{p}$  and variance  $\sigma_p^2$

$$p_t = \bar{p} + \sigma_p N(0, 1) \quad (9)$$

where  $N(0,1)$  is a normally distributed random variable with mean zero and variance one. This was done for all parameters except  $\theta$ , which was set to  $1/b$ , and  $K$  and  $h$ , which were constants.

Observation errors were introduced by analyzing  $L'_t$  obtained by adding a random normal variable with mean zero and variance  $\sigma_{obs}^2$  to values of  $L_t$  generated by the models. Unlike dynamic noise, observation errors do not affect the “real” population trajectory, but only the data used in the analysis. Noise was generated with  $\sigma_p^2 = 0.5$  and  $\sigma_{obs}^2 = 0.1$ .

Each simulation was initiated at a randomly chosen point in phase space and the model iterated for 30 time steps to eliminate transients. The model was then iterated for an additional  $n = 16, 30$  or  $100$  time steps to generate sample data. One thousand simula-

tions were generated for each value of  $n$  and  $\lambda$  (or  $r$ ). *PACF* and *PRCF* was calculated for lags 1 through 5 for each simulated data set (only prey data were used from the two-species model) and the value of each correlation coefficient was checked for the correct sign (i.e., its value should be negative to detect density dependence), and whether its absolute value exceeded Bartlett’s criterion (our intention here is not to test the significance of the coefficient but to have a basis for comparison). The per cent of the cases where *PACF* and *PRCF* detected density dependent negative feedback at lags 1 and 2 was used as a measure their power in detecting the feedback structure of the model.

The results of simulation experiments with the single-species model (7) are shown in Table 1. Notice that the *PRCF* correctly identified first order negative feedback (direct density dependence) in all but 1 of 9000 cases, and that its power was unaffected by the growth parameter or the length of the time series. On the other hand, the power of *PACF* to detect first order density dependence was severely constrained by short time series and small rates of increase. Both methods incorrectly identified second order negative feedback (delayed density dependence) in 4–10% of the simulations (Table 1).

The analysis of all data generated by the two-species model (8) is summarized in Table 2. Notice that *PACF* is basically useless for detecting the presence of first order density dependence in these data while *PRCF* is relatively good, particularly for long time series. Both models are fairly good at detecting second order feedback, but their power is weakened by short time series and low values of the growth parameter.

Table 1. Per cent of 1000 simulations where the partial autocorrelation function, *PACF*, and partial rate correlation function, *PRCF*, detected first- and second-order negative feedback ( $r < -2/\sqrt{n}$ ) in data generated by model (7) with different sample sizes,  $n$ , and per-capita rates of change,  $r$ . N.B. *PACF*[2] = *PRCF*[2].

	$r = 5$	$r = 10$	$r = 20$
<i>PACF</i> [1]			
$n = 16$	9.5	35.8	68.9
$n = 30$	17.4	68.5	95.3
$n = 100$	45.8	99.8	100
<i>PRCF</i> [1]			
$r = 5$			
$n = 16$	99.9	100	100
$n = 30$	100	100	100
$n = 100$	100	100	100
<i>PRCF</i> [2]			
$r = 5$			
$n = 16$	7.7	10.4	6.2
$n = 30$	5.5	6.5	4.3
$n = 100$	5.6	9.3	3.8

Table 2. Per cent of 1000 simulations where the partial autocorrelation function, *PACF*, and partial rate correlation function, *PRCF*, detected first- and second-order negative feedback ( $r < -2/\sqrt{n}$ ) in data generated by model (8) with different sample sizes,  $n$ , and per-capita rates of change,  $r$ . N.B.  $PACF[2] = PRCF[2]$ .

	$r = 0.5$	$r = 1$	$r = 2$
<i>PACF</i> [1]			
$n = 16$	0	0	0.2
$n = 30$	0.1	0	0
$n = 100$	0	0.2	0
<i>PRCF</i> [1]	$r = 0.5$	$r = 1$	$r = 2$
$n = 16$	33.1	37.1	48.8
$n = 30$	68.1	79.8	88.2
$n = 100$	96.2	98.8	98.1
<i>PRCF</i> [2]	$r = 0.5$	$r = 1$	$r = 2$
$n = 16$	35.2	66.1	70.1
$n = 30$	55.0	87.9	88.1
$n = 100$	91.3	97.4	96.0

## Conclusions

One of the major problems in animal ecology is explaining the causes of population fluctuations (Royama 1992, Berryman 1999). Determining the order and structure of the negative feedback processes generating observed population fluctuations is a critical step towards this explanation. Our contention is that the partial rate correlation function, *PRCF*, is the most useful diagnostic tool for making inferences about the structure of the density dependent feedback processes governing an observed population trajectory. This is because *PRCF* is designed specifically for ecological systems analysis, and its null model is an appropriate background for detecting density dependent feedback. Tests with simulated data show that *PRCF* provides a better description of the feedback structure of population dynamics, although both methods are equally good for determining its *dimension*. The primary limitation of *PRCF* is that it is based on a linear model while real population dynamics can be highly nonlinear (Royama 1981, 1992, Berryman 1991, 1999, Turchin and Millstein 1993). For this reason, its proper role in ecological time series analysis is for diagnosis rather than modeling. Finally, lest we be misunderstood yet again, we repeat that time series analysis should be used with intelligence and caution. It is particularly important that the time series be stationary and that the likelihood of exogenous causal factors have been ruled out. Time series analysis is not an end in itself but rather a starting point for detecting the causes of population fluctuations.

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