

## Identifying delayed density dependence in time-series data

Marcel Holyoak

Holyoak, M. 1994. Identifying delayed density dependence in time-series data. – *Oikos* 70: 296–304.

I investigated the ability of statistical tests to detect delayed density dependence in series of abundances per generation. I generated time series containing delayed density dependence using two simple population models (a host-parasitoid model and a version of the Ricker equation) and analysed these using the tests for delayed density dependence of Turchin (1990), the lag 2 partial autocorrelation coefficient (PACF) and a novel modification of Pollard et al's (1987) test. All tests of delayed density dependence are of low statistical power, and so any delayed density dependence that is present may frequently be overlooked, particularly with short (<25 generation) time series. The modification of Pollard et al's test was the best test for detecting delayed density dependence. The modification of Pollard et al's test has similar statistical power to Turchin's test. However, the latter test falsely detects delayed density dependence from approximately 9% of density independent random-walk series (of 20 generations), whereas only 5% of cases of false detection would be expected by chance alone. The modified version of Pollard et al's test did not identify delayed density dependence too often and it has similar power to Turchin's test. The presence of *delayed* density dependence frequently caused tests to detect *non-delayed* density dependence, despite only *delayed* density dependence being present. This was always true of Varley and Gradwell's test, frequently true of Bulmer's test, but not true of Pollard et al's test with series of 15–25 generations. The difference between tests is presumably due to variations in statistical power. Studies where large numbers of time series are analysed for density dependence may show non-delayed density dependence more frequently than it is present and show the presence of delayed density dependence less frequently than it is present.

*M. Holyoak, NERC Centre for Population Biology, Imperial College at Silwood Park, Ascot, Berks., U.K. SL5 7PY.*

This paper addresses the problem of detecting delayed density dependent processes in animal populations with discrete generations, using censuses carried out at generation intervals. Density dependence is a dependence of per capita growth rate on present and/or past population densities (Murdoch and Walde 1989, Reddingius and den Boer 1989). A single generation lag between abundance and the per capita growth rate is called non-delayed density dependence, whereas a lag of two or more generations is called delayed density dependence. The problem of detecting non-delayed density dependence and related processes from series of abundances per generation has

received much recent attention (den Boer and Reddingius 1989, Berryman 1991a, 1992, Vickery 1991, Vickery and Nudds 1991, Crowley 1992, Godfray and Hassell 1992, Holyoak and Lawton 1992, Woiwod and Hanski 1992, Dennis and Taper 1993, Holyoak 1993, Holyoak and Crowley 1993, Wolda and Dennis 1993). By contrast, delayed density dependent processes have been relatively neglected in the present literature (for exceptions see Royama 1977, Turchin 1990, Berryman 1986, 1991b, 1992, Hanski and Woiwod 1991, Woiwod and Hanski 1992) and there have been few improvements in methodology since the work of Varley and Gradwell (1960).

Accepted 12 January 1994

Copyright © OIKOS 1994

ISSN 0030-1299

Printed in Denmark – all rights reserved

Recently, several workers have used the partial autocorrelation function (PACF) to identify important lags in time series and hence whether any density dependence is delayed or not (Turchin 1990, 1991, Berryman 1992, Royama 1992, Turchin and Taylor 1992). I analyse time series from two simple population models to investigate whether these tests (and the PACF) can efficiently identify delayed density dependence. Woiwod and Hanski (1992) suggested that in aphids with several generations per year the presence of delayed density dependence leads to over-detection of non-delayed density dependence. Here, I investigate more generally whether the presence of delayed density dependence can cause non-delayed density dependence to be detected more frequently than it is present. Additionally, I question how long time series should be to accurately assess whether density dependence is present.

Woiwod and Hanski's (1992) analysis of 5715 time series from 447 aphid and moth species demonstrated that non-delayed density dependence can be detected in long time series (> 20 generations) which lack temporal trends in abundances (Godfray and Hassell 1992). Using Pollard et al.'s (1987) test, Woiwod and Hanski found non-delayed density dependence in 67% of moth series and 87% of aphid series (> 20 generations and lacking temporal trends); the first test of Bulmer (1975) gave equivalent figures of 88 and 89% respectively. In shorter insect time-series, non-delayed density dependence was found less frequently, as expected from considerations of test power. In the same time series Woiwod and Hanski (1992) (and Hanski and Woiwod 1991) found delayed density dependence in no more than the 5% of cases expected by chance alone. Conversely, Turchin (1990) reported delayed density dependence in 8 of 14 forest insect species (57% of cases), whereas non-delayed density dependence was detected in only a single species. Woiwod and Hanski (1992) attributed the difference in rates of detection of delayed density dependence to Turchin's (1990) use of series from forest insect pests, because predators and parasitoids are thought to be of particular importance in forest insect dynamics and these frequently cause delayed density dependence. An additional explanation for at least some of the taxa considered by Woiwod and Hanski (1992) is that the presence of delayed density dependence may be masked because sampling was not at generation intervals (Holyoak 1994). However, it is unclear how reliable estimates of the frequency of delayed density dependence are.

Delayed density dependence can arise from a wide range of biological mechanisms. However, there is little information on which mechanisms are more frequent. A specialist parasitoid attacking a host population may cause delayed density dependence, the delay arising because of the generation time lag between parasitoid eggs being laid and adult parasitoids attacking hosts (Nicholson and Bailey 1935). This assumes that the host and parasitoid populations are free of control from other factors. Similarly, a specialist predator may increase in

abundance from eating hosts, the predator population takes a generation to mature, causing any density dependence to be delayed. Some insects undergo facultative diapause, causing delays in development; for example in some sawflies (Hymenoptera: Symphyta) a proportion of adults emerge in the first year and the remainder in the second year. In some forest insects changes in host plant quality may influence survival, such that a year (or generation) with high numbers of pests would stimulate production of many secondary chemicals by plants, reducing survival in the next generation; causing mortality to act a generation after the reproduction bringing about the levels of mortality, thereby making any density dependence delayed. Additionally, changes in host plant quantity (not quality) may potentially bring about delayed density dependence; for example in the pine beauty moth (*Panolis flammea* (Lepidoptera: Noctuidae)) attacking mature pine trees, large populations are followed by trees remaining partially defoliated and of similar nutritional quality to the previous year (Watt et al. 1991). In the next generation, moths either leave the area or starve (Watt et al. 1989), reducing populations levels and introducing a delay into the population dynamics, although if moths disperse any density dependence may be apparent rather than real.

To reliably identify lag 2 processes, such as delayed density dependence, it is necessary that tests allow for the influence of any lag 1 processes (such as non-delayed density dependence and reproduction), which would distort the signal from any delayed density dependence (Berryman 1992, Royama 1992). Turchin's (1990) test for delayed density dependence does this by partialling out lag 1 density dependence. However, regression tests (such as Turchin's test and Varley and Gradwell's test) are problematic because they detect density dependence too frequently when it is absent (Maelzer 1970, St Amant 1970, Kuno 1971, Itô 1972, Vickery and Nudds 1984, Latto 1989, Vickery 1991, Dennis and Taper 1993, Holyoak 1993a). Studies of bias in regression tests are based on non-delayed density dependence, but the problem is identical with delayed density dependence. Results of Varley and Gradwell's test are presented here solely to allow comparison with other published studies, whereas the extent of the problem is investigated with Turchin's test. Unlike regression tests, randomization techniques (such as Pollard et al.'s (1987) test for non-delayed density dependence) protect against false detection of density dependence when it is absent (Dennis and Taper 1993, Holyoak and Crowley 1993). Because Pollard et al.'s test is the most reliable test of non-delayed density dependence available (Vickery and Nudds 1991, Woiwod and Hanski 1992, Holyoak 1993, Holyoak and Crowley 1993), I here modify this method to make it into a test for *delayed* density dependence. Dennis and Taper (1993) have proposed a number of tests for density dependence which they suggest may be modified to test for delayed density dependence; however in order to test for a lag of 2 generations it is necessary to partial out any lag 1 correla-

tions (Royama 1992), which is not done in Dennis and Taper's tests. For this reason I do not consider any of Dennis and Taper's (1993) tests.

The only other published statistical method which has been used to identify delayed density dependence is the partial autocorrelation coefficient (PACF) for a lag of 2 generations (Turchin 1990, 1991, Berryman 1992, Royama 1992, Turchin and Taylor 1992). The PACF provides a measure of the correlation between observations in a time series which are separated by a lag of a given number of generations, and where the effects of any intermediate (smaller) lags have been partialled out. It is well known (Chatfield 1989, Royama 1992) that with autoregressive models a plot of the PACF against lag number (called a correlogram) truncates at the lag which is acting; this property is also expected to follow for cases of non-linear density dependence, although the precise form of the correlogram will vary. The shape of a correlogram will be a characteristic of the type of population dynamics that generated the process, be it a random-walk, a density dependent process with a fixed equilibrium, cycles or chaotic behaviour, and be it stationary or with a temporal trend in abundances. All of these factors combine to produce useful patterns in correlograms; Chatfield (1989) and Royama (1992) give practical advice on how to interpret this information. Most importantly, values of the PACF for a lag of 2 generations (in series lacking temporal trends) which are significantly negative indicate delayed density dependence. A way of testing the significance of values of the PACF is given in the Methods section.

Three questions are addressed in this paper:

- (1) Do tests for delayed density dependence detect it too frequently when it is absent? Density independent random-walk data and series containing only non-delayed density dependence were analysed using the tests of Turchin (1990), the PACF and a novel form of Pollard et al's (1987) test.
- (2) How good are tests for delayed density dependence and which is the most reliable test? Time series containing delayed density dependence were simulated using two widely differing models; a modification of the discrete exponential logistic equation of Ricker (1954) (also Cook 1965 and May 1974) and a modified form of the Nicholson-Bailey host-parasitoid model. The length of time series was varied to investigate how many generations are needed for tests of delayed density dependence to be reliable.
- (3) Does the presence of delayed density dependence cause tests for non-delayed density dependence to detect the process when it is absent? The tests of Bulmer (1975) and Pollard et al. (1987) were used to test for non-delayed density dependence.

The choice of two widely differing models containing delayed density dependence is a compromise between the

wish to make results as general as possible and having a set of simulations of manageable size.

## Methods

All testing was carried out in Turbo Pascal (version 5.5 Borland International Inc.) using the Random function as a source of uniform deviates. To avoid problems of numerical overflow and under-flow all abundances were logarithmically transformed before testing. Only direct density dependence (be this delayed or not) was considered in the present analyses.

### Tests of delayed density dependence

- (1) Turchin's (1990) test is a regression of  $k$ -value [ $\text{Ln}(N_t) - \text{Ln}(N_{t-1})$ ] on  $N_{t-2}$ , whilst partialling out  $N_{t-1}$ , where  $N_t$  is the abundance in generation  $t$ . I use a Student's  $t$ -test to check the significance of the slope. Significantly negative slopes indicate direct density dependence (which is delayed), whereas positive slopes show inverse density dependence (which is delayed).
- (2) A modification of Pollard et al.'s (1987) test to analyse series for delayed (lag 2) density dependence consists of the following:
  - a. From the observed census data calculate the test statistic as the correlation coefficient between observed  $k$ -value and the natural logarithm of population size,  $\text{Ln}(N_{t-2})$ , whilst partialling out  $\text{Ln}(N_{t-1})$ .
  - b. Calculate  $\chi_i = X_i$ , where  $\chi_i$  ( $1 < i < (n-1)$ ) is used to denote the natural logarithm of abundance in a randomized data set at time  $i$  and  $X_i$  is the natural logarithm of abundance at time  $t$  in the observed time series.
  - c. Calculate  $d_i = X_{i+1} - X_i$ . These values are then randomly shuffled using evenly distributed random deviates as positions in the series, such that the new positions in the sequence are called  $i$  for the  $d_i$  values. Following Manly (1991), a total of 25000 simulated time series were used.
  - d. Construct randomized data sets using  $\kappa_{i+1} = \chi_i + d_i$  and calculate the test statistic for each randomized data set.
  - e. Calculate the proportion of values of the test statistic which is larger or equal to the value for the observed census data. This proportion is the conditional probability of delayed (and direct) density independence.
- (3) The partial autocorrelation coefficient (PACF) for a lag of 2 generations. I calculate partial autocorrelation coefficients, which collectively make up the partial autocorrelation function, using the autocorrelation coefficients ( $\rho_K$ , where  $K$  is the lag). I calculate autocorrelation functions using the following formula:

$$\rho_k = \frac{\sum_{t=1}^{T-k} \left\{ (N_t - \bar{N})(N_{t+k} - \bar{N}) \right\}}{\sum_{t=1}^T (N_t - \bar{N})^2}$$

Where  $T$  is the total number of generations and  $N_t$  is the abundance at time  $t$ . For lag 1 the PACF is identical to  $\rho_1$ , the autocorrelation coefficient for lag 1. The PACF for lag 2 is calculated in the following way (Royama 1992):

$$\frac{\rho_2 - \rho_1^2}{1 - \rho_1^2}$$

I calculate confidence limits as  $-1/T \pm 2/\sqrt{T}$ , which is appropriate for short time series (Chatfield 1989).

### Tests of non-delayed density dependence

- (4) Varley and Gradwell's (1960) test for non-delayed density dependence consists of a least-squares regression of  $k$ -value,  $\text{Ln}(N_t/N_{t-1})$ , against  $N_{t-1}$  (Varley and Gradwell 1960). I used F-tests to judge significance at  $p \leq 0.05$  and then test the slope against a slope of zero using a Student's  $t$ -test. Errors in the ordinate are assumed to be normally distributed.
- (5) Pollard et al.'s (1987) test for non-delayed density dependence is identical to the modified form of it (test 2, above), however the test statistic is the correlation coefficient between  $k$ -value and  $\text{Ln}(N_{t-1})$ , not  $\text{Ln}(N_{t-2})$ .
- (6) Bulmer's (1975) first test is carried out using the formulae given by Bulmer (1975), which are summarized in Holyoak and Lawton (1992).

### Types of data analysed

The first model was the exponential form of the logistic equation (Ricker 1954, Cook 1965, May 1974), see eq. 1, below, which was modified by making the parameter  $r_t$  a normal deviate. The addition of stochastic variation (noise) allowed time series to be produced that visually, at least, resemble real population data. Hanski and Woivod (1993) showed that making the intrinsic growth rate,  $r$ , stochastic is a realistic way to generate mean-related variability in simulated population data.

Time series had a range of logarithmic variance-mean ratios that encompass all natural variation (ranging from less than 0.1 to over 3.0) and realistic values of the standard deviation of the natural logarithm of abundance (0.2–2.8). For each parameter combination of each model, 100 time series of 10, 15, 20, 25, 30, 35, 40, 45 and 50 generations in length were analysed for density dependence. In all cases 2000 generations were generated

before the time series, these initial generations were then discarded to eliminate any effects of the size of the initial abundance. A wide range of parameter values was chosen to minimize the risk of placing too much emphasis on individual combinations and limiting the range of parameter values to those that are thought to be typical of insect populations.

I analysed random-walk data identical to Holyoak (1993a) to check levels of spurious detection; for brevity I do not report the methodology for these simulations in any more detail. May (1974), Bellows (1981) and Olson (1992) discuss the mathematical properties of the non-delayed model for density dependent populations and Hassell (1978) and May (1978) discuss these properties for the host-parasitoid model. I generated the data using the following methods:

#### *Non-delayed density dependent data generated using the exponential logistic model*

As indicated, I used a modified form of the exponential model of Ricker (1954):

$$N_{t+1} = N_t \exp[r_t(1 - \alpha N_t)] \quad (1)$$

where  $N_t$  is the abundance at time  $t$ ,  $r_t$  is a parameter that affects the response to increasing density (Olson 1992) and  $\alpha$  scales the mean abundance (however, the mean abundance is not independent of  $r_t$  (Ginzburg 1992)). The parameter  $r_t$  was a normally distributed random variate. I set the initial abundance,  $N_1$  at  $1/\alpha$ . I used values of  $\alpha$  of 0.0005, 0.001, and 0.003. Mean values of  $r_t$  were set at 1.0, 1.5 and 2.0, with the standard deviation of  $r_t$  set at 0.075.

#### *Delayed density dependent (lag 2) data generated using the exponential logistic model*

These simulations were identical to those for the non-delayed model (above) except the model was

$$N_{t+2} = N_{t+1} \exp[r_t(1 - \alpha N_t)] \quad (2)$$

and the initial two abundances were set at  $1/\alpha$ .

#### *Delayed density dependent (lag 2) data generated using a host-parasitoid model*

There is a wealth of evidence from the biological control literature (e.g. Beddington et al. 1978) that specific parasitoids are important influences in insect population dynamics and this is further supported by Stiling (1987) who reviews the evidence of density dependence in insect host-parasitoid systems. Hence, I used a modification of the Nicholson-Bailey (1935) model, described by May (1978) that introduces non-random parasitoid search, whilst retaining the effects of parasitoid aggregation. In this model the negative binomial distribution describes the distribution of parasitoid encounters with hosts (Hassell 1978). The model is

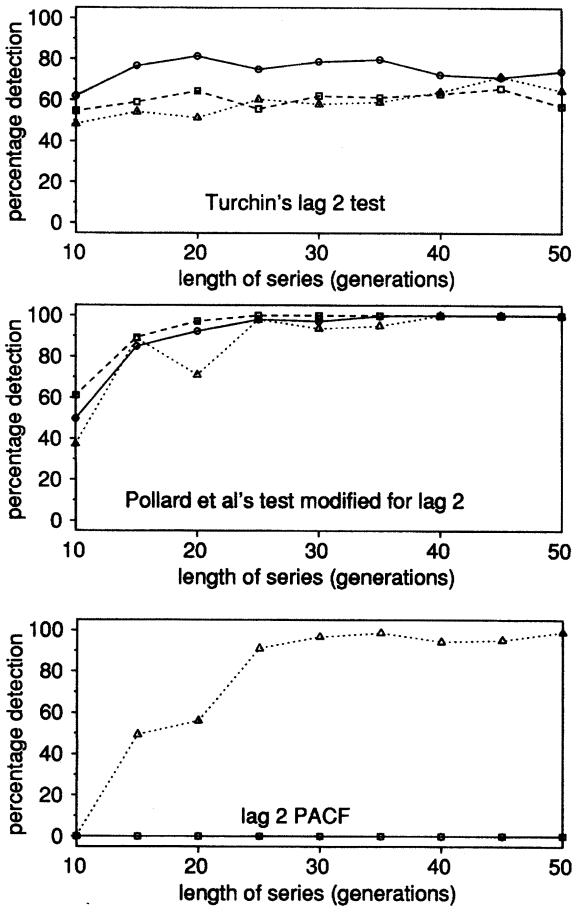


Fig. 1. The frequency of detection of delayed density dependence (at  $p \leq 0.05$ ) from time series of different lengths containing delayed density dependence generated using a logistic model (see eq. 2). Each point on the graph represents the mean % detection from 100 series with  $\alpha = 0.0005, 0.001$  and  $0.003$ . Circular symbols (and solid lines) represent  $\bar{r}_t = 1.0$ , square symbols (and dashed lines) represent  $\bar{r}_t = 1.5$  and triangular symbols (and dotted lines) represent  $\bar{r}_t = 2.0$ . Details of the model and the abbreviations are described in the Methods.

$$N_{t+1} = \lambda N_t \left[ 1 + \frac{aP_t}{k} \right]^{-k} Z_t \quad (3A)$$

$$P_{t+1} = N_t \left[ 1 - \left( 1 + \frac{aP_t}{k} \right)^{-k} \right]. \quad (3B)$$

The parameter  $k$  (the exponent of the negative binomial distribution) describes the degree of parasitoid aggregation.  $P_t$  is the number of parasitoids at time  $t$ ,  $N_t$  is the number of hosts at time  $t$ ,  $\lambda$  is the net rate of increase of prey per generation and  $a$  is the predator searching efficiency. A stochastic parameter  $Z_t$  was added, where  $Z_t$ -values were independent log-normal (0,1) deviates. Values reported here are all combinations of  $k = 0.2, 0.4$  and

$0.6$ ,  $a = 0.5$  and  $\lambda = 2.71, 4.48$  and  $7.39$  (equivalent to the  $r_t$ -values used in eqs 1 and 2). Initial abundances were  $\ln(P_t) = 3.0$  and  $\ln(N_t) = 4.0$ . Data are analysed just for the host (prey) population, because for most real insect populations, time series for both a host and its parasitoids are not available (e.g. many of those in the analyses of Woivod and Hanski 1992 and Holyoak and Crowley 1993).

## Results

### Spurious detection of delayed density dependence

Regression tests (Varley and Gradwell 1960, Turchin 1990) detect *both* delayed and non-delayed density dependence too frequently when it is absent. Simulations identical to those in Holyoak (1993) confirmed that this was true of Turchin's test, which gave a rate of detection of delayed density dependence from density independent random-walk data of 9% for series of 20 generations, which is significantly greater ( $p < 0.001$  in a G-test) than the generally accepted 5% level of erroneous detection.

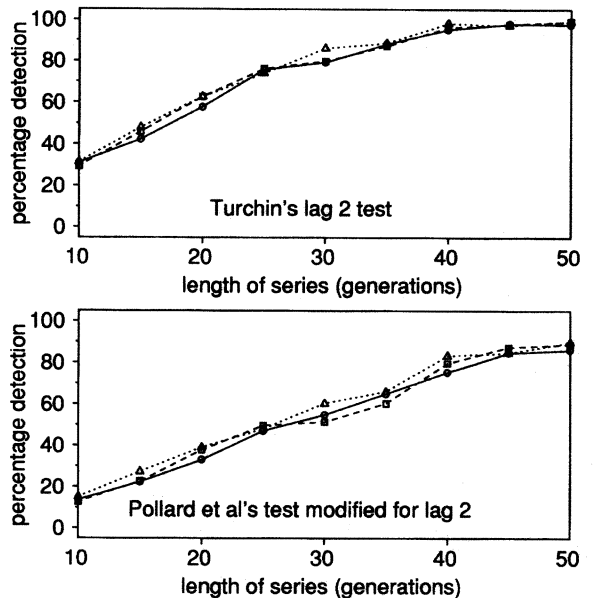


Fig. 2. The frequency of detection of delayed density dependence (at  $p \leq 0.05$ ) from time series of different lengths containing delayed density dependence generated using a modification of the Nicholson-Bailey host-parasitoid model (see eqs 3A and 3B). Each point on the graph represents the mean % detection from 100 series with  $k = 0.2, 0.4$  and  $0.6$ . Circular symbols (and solid lines) represent  $\gamma = 2.72$ , square symbols (and dashed lines) represent  $\gamma = 4.48$  and triangular symbols (and dotted lines) represent  $\gamma = 7.39$ . Details of the model and the abbreviations are described in the Methods. Only host abundances were analysed.

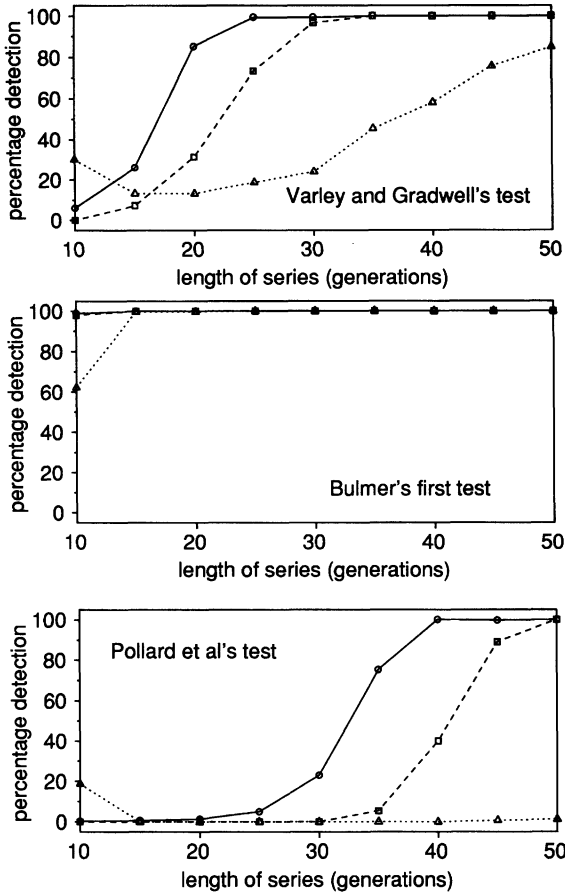


Fig. 3. The frequency of detection of non-delayed density dependence (at  $p \leq 0.05$ ) from time series of different lengths containing delayed density dependence generated using a logistic model (see eq. 2). Each point on the graph represents the mean % detection from 100 series with  $\alpha = 0.0005, 0.001$  and  $0.003$ . Circular symbols (and solid lines) represent  $\bar{r}_i = 1.0$ , square symbols (and dashed lines) represent  $\bar{r}_i = 1.5$  and triangular symbols (and dotted lines) represent  $\bar{r}_i = 2.0$ . Details of the model and the abbreviations are described in the Methods.

Although statistically significant, the difference between 9% and 5% erroneous detection is small. For the lag 2 PACF and the modification of Pollard et al's test (for delayed density dependence) detection rates were similar to the expected 5% level ( $0.05 < p < 0.95$  in a G-test) and so were acceptable.

The presence in time series of *non-delayed* density dependence did not cause tests of *delayed* density dependence to detect *delayed* density dependence too frequently when it is absent. That is, rates of detection of delayed density dependence from series containing only non-delayed density dependence were less than 5% for all 3 of the testing methods used (with series of between 10 and 50 generations), and so were acceptable.

## The best test for delayed density dependence

Rates of correct identification of delayed density dependence were most consistently high for the modification of Pollard et al's test with data from the lag 2 exponential logistic model (for most series > 10 generations), as shown in Fig. 1. Conversely, for series from the host-parasitoid model (Fig. 2), Turchin's test always identified delayed density dependence more frequently than the modification of Pollard et al's test and the lag 2 PACF. With series from the host-parasitoid model time-series, at least 40 generations were required to be 95% certain of detecting delayed density dependence with Turchin's test. Conversely, with data from the logistic equation this

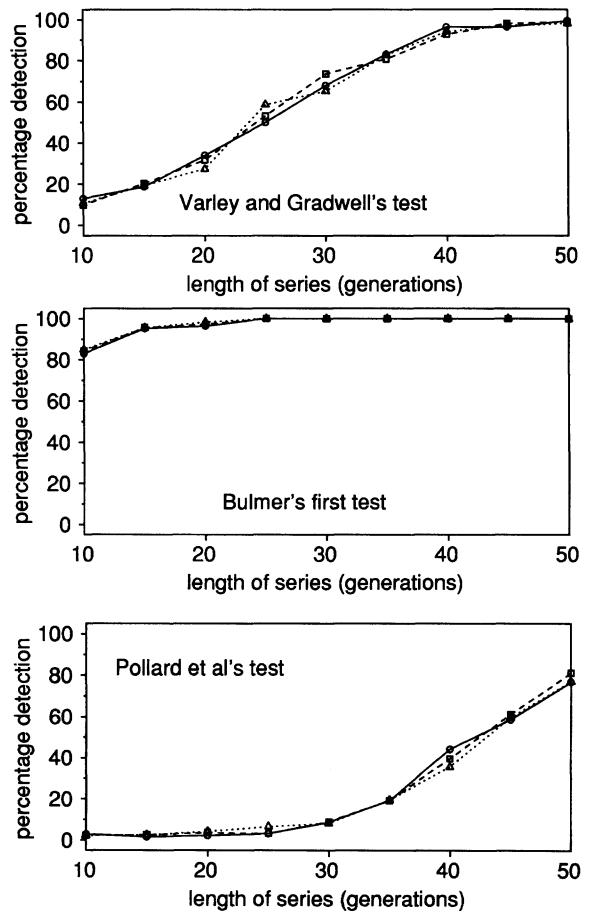


Fig. 4. The frequency of detection of non-delayed density dependence (at  $p \leq 0.05$ ) from time series of different lengths containing delayed density dependence generated using a modification of the Nicholson-Bailey host-parasitoid model (see eqs 3A and 3B). Each point on the graph represents the mean % detection from 100 series with  $k = 0.2, 0.4$  and  $0.6$ . Circular symbols (and solid lines) represent  $\lambda = 2.72$ , square symbols (and dashed lines) represent  $\lambda = 4.48$  and triangular symbols (and dotted lines) represent  $\lambda = 7.39$ . Details of the model and the abbreviations are described in the Methods. Only host abundances were analysed.

figure was not approached for Turchin's test even with 50 generations. The modified version of Pollard et al's test detected delayed density dependence in 95% of cases from 25 (or more) generations, whereas this was not true even for series of 50 generations from the host parasitoid model. With time series from the logistic equation containing delayed density dependence, the frequency of detection from the lag 2 PACF was very variable (Fig. 2). However, this test failed to find delayed density dependence in any host-parasitoid series and in the lag 2 exponential logistic series with the two lowest intrinsic growth rates (Fig. 1). For series of 20 or more generations in length, the suggested modification of Pollard et al's test (to test for delayed density dependence) is a conservative test, 5% spurious detection was not exceeded and power is broadly similar to Turchin's test.

### **Over-detection of non-delayed density dependence from data containing only delayed density dependence**

The presence of certain types of delayed density dependence causes tests to detect non-delayed density dependence too frequently when it is absent. This problem was most extreme for Bulmer's test, and occurred with all lengths of series investigated for series from both the lag 2 logistic equation (Fig. 3) and the host-parasitoid model (Fig. 4). For Varley and Gradwell's test this problem occurred with all series except some of the series of 10 generations in length (Figs 3 and 4). Pollard et al's test (for non-delayed density dependence) showed this problem less frequently than Varley and Gradwell's test and Bulmer's test (Figs 3 and 4); detection rates were always  $\leq 5\%$  for series of between 15 and 25 generations in length. However, rates of detection were greater than 5% for almost all longer time series examined.

## **Discussion**

Overall, it is unclear whether Turchin's test or the modification of Pollard et al's test is the most reliable test for delayed density dependence currently available. If data from a host-parasitoid model was analysed then Turchin's test found delayed density more frequently than the modified form of Pollard et al's test (Fig. 2). However, this situation was reversed with data from the lag 2 logistic model (Fig. 1). The test of Turchin has a problem that delayed density dependence was misidentified in 9% of density independent random-walk series (of 20 generations), which is greater than the 5% false detection rate expected by chance alone. This suggests that there is no clear cost of the greater reliability of the modification of Pollard et al's test, since this method appears to have similar statistical power to Turchin's test and does not detect delayed density dependence more frequently than

in the 5% of cases expected from density independent random-walk data.

Tests for delayed density dependence are markedly poorer than tests for non-delayed density dependence (as shown by a comparison with Holyoak 1993) because their power is lower. This does not however apply to regression tests, which are of generally lower power than other techniques. Detection of delayed density dependence requires long time series (at least 25 to 40 generations; depending on the source of series and testing method) to make detection of the process occur with  $>95\%$  probability. However, even with such long time series, there is no guarantee that we are certain of finding delayed density dependence if it is present. Even when time series are long (Figs 1 and 2), the failure of a test to indicate the presence of delayed density dependence cannot be taken as an indication of absence of the process. The extremely low power of the PACF is probably a result of the difference in linearity of the delayed density dependence which is present compared with that being tested for.

The presence of delayed density dependence can cause tests to indicate the presence of non-delayed density dependence when it is absent. This is true of the tests of Varley and Gradwell (1960), Bulmer (1975) and Pollard et al. (1987) with series from both kinds of models of delayed density dependence that were investigated (Figs 3 and 4). Detection rates of non-delayed density dependence from series containing delayed density dependence were greater in longer time series. This problem of over-detection of non-delayed density dependence was absent with Pollard et al's test for series of between 15 and 25 generations (Figs 3 and 4), presumably because of the shortness of time series. In general, significant detection of *non-delayed* density dependence must be taken as an indication of the presence of either *delayed* or *non-delayed* density dependence, unless short time series (15–25 generations) were analysed with Pollard et al's test. This has implications for studies of large numbers of time series, such as those carried out by Woiwod and Hanski (1992) or Holyoak and Crowley (1993), where the detection of non-delayed density dependence must be taken as an indication of either delayed or non-delayed density dependence in the majority of time series. Even though Woiwod and Hanski (1992) tested for both delayed and non-delayed density dependence the low power of tests for delayed density dependence means that delayed density dependence may have been over-looked. Furthermore, if delayed density dependence is present in time series (but over-looked) this still might give increased rates of detection of non-delayed density dependence. However, the series analysed by Woiwod and Hanski were mainly between 15 and 25 generations, so that over-detection of non-delayed density dependence is unlikely to be a problem in this study.

In summary I find that the suggested modification of Pollard et al's test is the best test for delayed density dependence currently available. Its power is similar to

that of Turchin's test. However, the modification of Pollard et al's test is more reliable than Turchin's test at not showing the presence of delayed density dependence when it is absent. Both of these testing methods showed detection rates of less than 50–80% (depending on the choice of model and test), so that delayed density dependence might be frequently overlooked in time series of the lengths typically collected. Turchin's test would be expected to give a spurious result from approximately 1 in 11 cases with series of 20 generations in length. The presence of delayed density dependence causes over-detection of non-delayed density dependence (except for Pollard et al's test with series of 15–25 generations) and so the results of tests for non-delayed density dependence must be treated with caution.

*Acknowledgements* – I wish to thank I. Hanski, M. Crawley, P. Crowley, J. Lawton, M. Hassell, M. Rees, Simon Leather, and Sharon Lawler for their helpful comments during the preparation of this manuscript. This study was financed by core-funding from NERC to the Centre for Population Biology.

## References

- Beddington, J. R., Free C. A. and Lawton, J. H. 1978. Characteristics of successful natural enemies in models of biological control of insect pests. – *Nature* 273: 513–519.
- Bellows, Jr. T. S. 1981. The descriptive properties of some models for density dependence. – *J. Anim. Ecol.* 50: 139–156.
- Berryman, A. A. 1986. On the dynamics of blackheaded budworm populations. – *Can. Entomol.* 118: 775–779.
- 1991a. Vague notions of density dependence. – *Oikos* 62: 252–254.
- 1991b. Population theory: an essential ingredient in pest prediction, management, and policy-making. – *Am. Entomol.* 37: 138–142.
- 1992. On choosing models for describing and analysing ecological time series. – *Ecology* 73: 694–698.
- Bulmer, M. G. 1975. The statistical analysis of density dependence. – *Biometrika* 31: 901–911.
- Chatfield, C. 1989. The analysis of time series: an introduction. – Chapman and Hall, London.
- Cook, L. M. 1965. Oscillations in the simple logistic growth model. – *Nature* 207: 316.
- Crowley, P. H. 1992. Density dependence, boundedness and attraction: detecting stability in stochastic systems. – *Oecologia* 90: 246–254.
- den Boer, P. J. and 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. and Taper, M. 1993. Density dependence in time series observations of natural populations: estimation and testing. – *Ecology*, in press.
- Ginzburg, L. R. 1992. Evolutionary consequences of basic growth equations. – *Trends Ecol. Evol.* 7: 133.
- Godfray, H. C. J. and Hassell, M. P. 1992. Long time series reveal density dependence. – *Nature* 359: 673–674.
- Hanski, I. and Woiwod, I. 1991. Delayed density dependence. – *Nature* 350: 28.
- and Woiwod, I. P. 1993. Mean-related stochasticity and population variability. – *Oikos* 67: 29–39.
- Hassell, M. P. 1978. The dynamics of arthropod predator-prey systems. Monographs in population biology 13. – Princeton Univ. Press, Princeton, NJ.
- Holyoak, M. 1993. New insights into testing for density dependence. – *Oecologia* 93: 435–444.
- 1994. Comment: appropriate time scales for identifying lags in density dependent processes. – *J. Anim. Ecol.*, in press.
- and Lawton, J. H. 1992. Detection of density dependence from annual censuses of bracken-feeding insects. – *Oecologia* 91: 425–430.
- and Crowley, P. H. 1993. Avoiding erroneously high levels of detection in combinations of semi-independent tests: an application to testing for density dependence. – *Oecologia* 95: 103–114.
- Itô, Y. 1972. On the methods for determining density dependence by means of regression. – *Oecologia* 10: 347–372.
- Kuno, E. 1971. Sampling error as a misleading artefact of key-factor analysis. – *Res. Popul. Ecol.* 13: 28–45.
- Latto, J. 1989. The analysis of density dependence in insect populations. – Unpublished PhD thesis, Imperial College, Univ. of London.
- Maelzer, D. A. 1970. The regression of  $\log(N_{n+1})$  on  $\log(N_n)$  as a test of density-dependence: an exercise with computer constructed density-independent populations. – *Ecology* 51: 810–822.
- Manly, B. F. J. 1991. Randomization and Monte Carlo methods in biology. – Chapman and Hall, London.
- May, R. M. 1974. Biological populations with non-overlapping generations: stable points, stable cycles and chaos. – *Science* 186: 645–647.
- 1978. Host-parasitoid systems in patchy environments: a phenomenological model. – *J. Anim. Ecol.* 47: 833–844.
- Murdoch, W. W. and Walde, S. J. 1989. Analysis of insect population dynamics. – In: Grubb, P. J. and Whittaker, J. B. (eds), *Toward a more exact ecology*. Blackwell, Oxford, pp. 113–140.
- Nicholson, A. J. and Bailey, V. A. 1935. The balance of animal populations. Part 1. – *Proc. Zool. Soc. Lond.* 3: 551–598.
- Olson, M. H. 1992. Intuition and the logistic equation. – *Trends Ecol. Evol.* 7: 314.
- Pollard, E., Lakhani, K. H. and Rothery, P. 1987. The detection of density dependence from a series of annual censuses. – *Ecology* 68: 2046–2055.
- Reddingius, J. and den Boer, P. J. 1989. On the stabilization of animal numbers. Problems of testing. 1. Power estimates and estimation errors. – *Oecologia* 78: 1–8.
- Ricker, W. E. 1954. Stock and recruitment. – *J. Fish. Res. Board Can.* 11: 942–949.
- Royama, T. 1977. Population persistence and density dependence. – *Ecol. Monogr.* 47: 1–35.
- 1992. Analytical population dynamics. – Chapman and Hall, London.
- St Amant, J. L. S. 1970. The detection of regulation in animal populations. – *Ecology* 51: 823–828.
- Stiling, P. D. 1987. The frequency of density dependence in insect host-parasitoid systems. – *Ecology* 68: 844–856.
- Turchin, P. 1990. Rarity of density dependence or population regulation with lags? – *Nature* 344: 660–663.
- 1991. Reconstructing endogenous dynamics of a laboratory *Drosophila* population. – *J. Anim. Ecol.* 60: 1091–1098.
- and Taylor, A. D. 1992. Complex dynamics in ecological time series. – *Ecology* 73: 289–305.
- Varley, G. C. and Gradwell, G. R. 1960. Key factors in population studies. – *J. Anim. Ecol.* 29: 399–401.
- Vickery, W. L. 1991. An evaluation of bias in k-factor analysis. – *Oecologia* 85: 413–418.
- and Nudds, T. D. 1984. Detection of density dependent effects in annual duck censuses. – *Ecology* 65: 96–104.
- and Nudds, T. D. 1991. Testing for density-dependent effects in sequential censuses. – *Oecologia* 85: 419–423.
- Watt, A. D., Leather, S. R. and Stoakley, J. T. 1989. Site susceptibility, population development and dispersal of the pine beauty moth in a lodgepole pine forest in northern Scotland. – *J. Appl. Entomol.* 26: 147–157.
- , Leather, S. R. and Forrest, G. I. 1991. The effect of



- previous defoliation of pole-stage lodgepole pine on plant chemistry, and on the growth and survival of pine beauty moth (*Panolis flammea*) larvae. – *Oecologia* 86: 31–35.
- Woiwod, I. P. and Hanski, I. 1992. Patterns of density dependence in moths and aphids. – *J. Anim. Ecol.* 61: 619–629.
- Wolda, H. and Dennis, B. 1993. Density dependence tests, are they? – *Oecologia* 95: 581–591.