

Short communications

Comment arising from a paper by Wolda and Dennis: using and interpreting the results of tests for density dependence

M. Holyoak, J.H. Lawton

N.E.R.C. Centre for Population Biology, Imperial College at Silwood Park, Ascot, Berks, SL57PY, UK

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Abstract. We argue that tests for density dependence are useful in analyses of population dynamics and suggest guide lines for their use and interpretation of results which avoid many of the problems discussed by Wolda and Dennis (1993). Processes other than density dependence *per se* can cause statistical tests to indicate the presence of density dependence (Wolda and Dennis 1993 and unpublished simulations). Tests for density dependence cannot reveal the mechanism of regulation, but they do indicate the nature of long-term population dynamics. Tests for density dependence give misleading results if sampling is not at generation intervals; however, this problem is avoided if we only use tests on data collected in each generation (Holyoak 1993a). Similarly, species should be semelparous. Non-delayed density dependence should not be considered without looking for delayed density dependence, since the presence of delayed density dependence can lead to over-detection of non-delayed density dependence (Woiwod and Hanski 1992; Holyoak 1993b). The partial autocorrelation function and knowledge of life-history are more useful than tests for density dependence for indicating whether any density dependence is delayed or not (Royama 1992; Holyoak 1993b). Estimation error with a constant upper size limit causes tests for density dependence to overestimate the frequency of delayed density dependence; however we do not know whether estimation error is bounded in real populations. Work in progress suggests that 20–40 generations (depending on the nature of population dynamics) gives a moderate level of accuracy with tests for density dependence, and >40 generations are necessary for tests to be accurate in their assessment of the strength of density dependence. We conclude that tests are useful indicators of whether density dependence, or other feedback mechanisms are likely to be acting.

Key words: Delayed density dependence – Estimation error – Persistence – Time Series

What do tests for density dependence show?

Tests for density dependence in time series data are formulated so that they rarely indicate the presence of density dependence when it is absent ($\leq 5\%$ of cases with random-walk data: e.g. Bulmer 1975; Vickery and Nudds 1984; Pollard et al. 1987; Reddingius and den Boer 1989). Regression tests for density dependence in time series data are generally not reliable in this way and should be avoided (see Vickery 1991 and references therein). Other mechanisms which cause abundances to remain within (narrow) bounds can fool tests of density dependence into indicating the presence of density dependence. Solow (1990) showed that certain kinds of secondary autocorrelation caused Bulmer's (1975) first test to frequently indicate the presence of density dependence. This was because secondary autocorrelation was translated into negative first-order autocorrelation, which is equivalent to direct density dependence (Reddingius 1990).

Wolda and Dennis (1993) suggest that a series of density independent identically distributed random variables is typically described better by a density-dependent model than by the null (density-independent) model. As Royama (1992) (and others before him) pointed out, real populations are extremely unlikely to remain within the bounds typically observed in field populations if they follow a random walk. We agree that *spreading the risk* of extinction (Reddingius 1971) might permit populations to persist for some time; however for such a scenario to occur and to be detected by biologists requires mechanisms to bring subpopulations together at the time of sampling, followed by desynchronization of individual subpopulations. In at least some taxa, widespread environmental influences cause *synchronous* fluctuations in local populations (e.g. Pollard 1991; Pollard et al. 1993), ruling out the possibility of asynchronous subpopulations and also, incidentally, providing additional evidence for regulation (see Royama 1992).

Tests for density dependence should only be applied to appropriate data

Tests for density dependence assume that series of abundances represent a first-order Markovian chain (Reddingius 1971; Bulmer 1975; Royama 1981; Reddingius and den Boer 1989; Wolda and Dennis 1993). This means that species tested must have discrete generations, be sampled at generation intervals and be semelparous. Most of the moth species investigated by Woiwod and Hanski (1992), in the most extensive study of density dependence published, have discrete generations, although this is not true of the aphid species. Some taxa in Woiwod and Hanski's study were not sampled at generation intervals, which would make delayed density dependence less likely to be found and non-delayed density dependence more likely to be found compared to sampling at generation intervals (Holyoak 1993a). However, this problem of sampling at intervals of more than a generation is minor; correction of Woiwod and Hanski's moth results for the likely bias still leads us to conclude that non-delayed density dependence (or similar feedback processes) occurs very frequently and delayed density dependence is infrequent (Holyoak 1993a). The effects of departures from semelparity are not known. In the bird data used by Wolda and Dennis the longevity of many of the species would make annual censuses strongly autocorrelated and pseudo-replicated (because the same individuals would be sampled in more than one year) which would be expected to increase the frequency with which density dependence is detected; clearly these kinds of data are inappropriate for analysis using tests for density dependence that assume semelparity.

Turchin's (1990) test for delayed density dependence, which is the best test we have for delayed density dependence, is not capable of distinguishing reliably between delayed and non-delayed density dependence (Holyoak 1993b). In order to do this we must turn to other analytical methods, such as the partial autocorrelation function or knowledge of life-history (Royama 1992). It is necessary to distinguish between delayed and non-delayed density dependence because, as Woiwod and Hanski (1992) suggest, the presence of delayed density dependence can lead to over-detection of non-delayed density dependence (Holyoak 1993b).

How long should time series be?

Unpublished work indicates that for the test of Pollard et al. (1987) (with time series generated using a variety of density dependent population models) the power of the test becomes close to its maximum at between 20 and 40 generations (the exact figure depends on the nature of the population dynamics). Approximately 40 generations are necessary to be certain of the test of Pollard et al. having its maximum power. Similarly estimations of the strength of density dependence using the test of Pollard et al. become accurate at between 20 and 40 generations (depending on the nature of dynamics).

The test of Dennis and Taper (1993), which Wolda and Dennis (1993) used, is unusual in that it appears to be influenced little by the length of time series which are analysed. Conversely, Woiwod and Hanski (1992) found strong effects of the length of time series on detection using the tests of Varley and Gradwell (1960), Bulmer (1975) and Pollard et al. (1987). Analyses of simulated density-dependent data confirm that these tests [and those of Reddingius and den Boer (1989) and Crowley (1992)] are strongly influenced by the length of time-series (in series of up to 20 generations) (Solow and Steele 1990; Holyoak 1993c). Hence, evidence that tests are unreliable because they fail to respond to the length of time series (with either simulated or real data) is limited to the test used by Wolda and Dennis (1993) and Bulmer's second test (Holyoak 1993c). A comparison of power curves observed with simulated time-series with curves from real insect time-series is of little value in judging how good tests for density dependence are because power curves vary enormously depending on the parameter values of the models used to generate data for analysis; almost any power curve is possible with extreme enough parameter values.

The best test?

In preliminary analyses (discussed in Holyoak 1993b) to investigate how frequently the tests proposed by Dennis and Taper (1993) detect density dependence, the test used by Wolda and Dennis (1993) identified density dependence less frequently with a variety of insect time series than that of Pollard et al. (1987). This is probably because Monte-Carlo shuffling tests, such as that of Pollard et al., allow for temporal trends in time series. Temporal trends in abundances would be most important when they are too weak to be quantified (e.g., by a regression test) and so cannot be allowed for in analyses. Analyses of time series generated using three different density dependent population models show that the test of Pollard et al. is affected far less by deviations from the density dependent model with which the test was formulated than a variety of other tests (Holyoak 1993c); unpublished work (similar to that in Holyoak 1993c and discussed in Holyoak 1993b) shows that Dennis and Taper's test is less general than that of Pollard et al. (1987).

Effects of sampling error on detecting density dependence

The presence of error in the estimation of abundances which has a fixed upper limit causes tests for density dependence to erroneously indicate that density dependence is present. This has been shown for regression tests (Kuno 1971; Itô 1972), Bulmer's first test (Bulmer 1975; Pollard et al. 1987; Reddingius and den Boer 1989) and Dennis and Taper's test (Dennis and Taper 1993; Wolda and Dennis 1993). This is because sampling error is strictly bounded, so that large sampling errors are likely to be followed by small sampling errors and vice versa.

However, with the kind of data that comes from light traps, pitfall traps, suction traps (all of which are very variable in time), or the typically small samples from patchily distributed populations (which vary greatly from one location to another), sampling error is extremely difficult to predict, and any effects it may have on the detection of density dependence are, at best, unpredictable. We are unconvinced by Wolda and Dennis's attempts to rank data sets by the likely size of estimation error; hence, because of the difficulty in judging the size of sampling error, it is inappropriate to dismiss tests for density dependence based solely on evidence from field populations. This is particularly true in the case of Wolda and Dennis's study, because the effect of sampling error is confounded with other problems such as the degree of voltinism and semelparity, and the possibility that density dependence is delayed.

In sum, Wolda and Dennis's analysis is based on a single test for density dependence, which appears to be unrepresentative of other well studied tests in the literature. It ignores the assumption of these tests, by using data from species with inappropriate life histories, and it uses a ranking of population variability that is at best subjective and difficult to quantify.

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