

## Appropriate time scales for identifying lags in density-dependent processes

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### Introduction

In a recent paper, Woiwod & Hanski (1992) presented the analysis of 5715 time series from aphid and moth populations for density dependence. In the longer (>20 generation) series that lacked temporal trends in abundances they found non-delayed density dependence in 67–88% of moth species and 87–91% of aphids (depending on the choice of statistical test). The high frequency with which density dependence was found was taken to indicate that density dependence is pervasive and common in the year-to-year population changes of moths and aphids (Woiwod & Hanski 1992; Godfray & Hassell 1992). Surprisingly, delayed density dependence was found less frequently than would be expected by chance alone (from <5% of series) (Hanski & Woiwod 1991; Woiwod & Hanski 1992). This is in stark contrast to Turchin (1990) who found delayed (lag 2) density dependence in eight of 14 (57%) time series from forest insects using identical statistical techniques to those employed by Woiwod & Hanski (1992). Turchin (1990) found non-delayed density dependence in only a single species (7%). Woiwod & Hanski explain this difference in the frequency of delayed density dependence as being due to Turchin's choice of forest insect pests that often show cyclical dynamics, whereas their study used a more balanced sample of species. However, it seems somewhat unlikely that virtually all of the 456 species considered by Woiwod & Hanski would lack delayed density dependence. A possible alternative explanation is considered here, which stems from the temporal scale at which the species are sampled. The possibility explored here is not a *sole* explanation but is a *contribution* to explanation of Woiwod and Hanski's results.

There are many studies looking at the effects of measuring ecological processes at different spatial scales (e.g. Greig-Smith 1954; Heads & Lawton 1983; Menge & Olson 1990; Rose & Leggett 1990; Yamamura 1990; Holling 1992; Doak, Marino & Kareiva 1992; Holt 1992). A lucid review of studies of spatial scale and patterning is provided by Levin (1992). There are fewer studies that consider both spatial and temporal scales (e.g. McArdle, Gaston & Lawton 1990; Thomas 1991; Fahrig 1992; Johnson, Milne & Wiens 1992; Loreau 1992) and studies of the effects of temporal scales are even less common (e.g. Pimm & Redfearn 1988).

If we turn to the question of scale and detecting density dependence there are very few studies. In a field study of the viburnum whitefly (*Aleurotrachelus jelinekii* Frauenf.) (Southwood & Reader 1976), key factor analysis failed to reveal any source of density-dependent mortality in 16 generations of data; however, more detailed *within*-generation studies on a per leaf basis revealed that egg mortality was density-dependent (Hassell, Southwood & Reader 1987). Additionally, Hassell (1985, 1986) used simulations to demonstrate that for both parasitoids and herbivorous insect species, density dependence *within* generations did not necessarily lead to density dependence showing up *between* generations (in time series). In parasitoids, analysis at inappropriate spatial scales could lead to direct density dependence being incorrectly identified as inverse density dependence (Walde & Murdoch 1988). Furthermore, subsampling a population (a form of sampling at an inappropriate spatial scale) could mask within-generation density-dependent processes (Hassell 1987). It appears that sampling scale in both time and space is important for detecting density dependence. Since Woiwod & Hanski (1992) used only a single mean annual abundance for each species and some species have more than a single generation per year the results of their analysis for these species might be biased in some way. The purpose of this note is to demonstrate that sampling at different temporal scales has consequences for detecting delayed density dependence, but not for identifying *some* form of density dependence. I concentrate on the effects of taking the mean of more than a single generation per year on detecting density dependence.

In Woiwod & Hanski's (1992) study only annual abundances of moths and aphids were used, whereas there may have been two or more generations per year in some species. The consequence of taking the mean of more than one consecutive generation is that time series are smoothed and the amount of smoothing increases with the number of generations per year that are sampled. Aphids, in particular, typically have several generations per year (the exact number depending on temperature and nutritional state). The identity for 263 moth species is published (Taylor & Woiwod 1980) and Ian Woiwod kindly provided the names of the other species. The numbers of generations per year were obtained from Skinner (1984)

and are given in Table 1. 26% of the moth species may have more than a single generation per year, with no significant differences between families ( $P > 0.05$ ; two-way analysis of variance, logit-transforming proportions and weighting for sample size).

### Methods

To investigate how taking the mean of more than one successive generation influences detection of density dependence, time series containing delayed (lag 2) density dependence were generated using two different population models. A realistic scenario is that a specialist parasitoid is involved in the life-cycle, but only host abundances were collected because parasitism occurs in a different life-stage to that which was sampled. The Nicholson–Bailey model, as modified by May (1978) to incorporate the effects of parasitoid aggregation, and a modified form of the Ricker (1954) equation (with only delayed density dependence) were used to generate time series. Time series from these models were then analysed for both delayed (lag 2) and non-delayed (lag 1) density dependence using the tests of Turchin (1990). These tests were used despite criticisms of regression tests for density dependence (Vickery 1991, and references therein) because they were used by Woiwod & Hanski (1992) and because Turchin's test for delayed density dependence is the only technique which partials out non-delayed density dependence (which is necessary in order to test for delayed density dependence). Testing was carried out either using 20 consecutive generations or by sampling the total individuals in 2, 3, 4, 5 or 10 consecutive generations from longer series to give time series for analysis of 20 data points in length. Hence, for example, where numbers in 10 consecutive generations were cumulatively sampled, the overall simulated

time series was 200 generations in length, which yielded a series 20 data points long.

Details of the two models were as follows, the first was a modification of the Nicholson–Bailey (1935) model, described by May (1978) that introduces non-random predator search, whilst retaining the effects of predator aggregation. In this model the negative binomial distribution describes the distribution of parasitoid encounters with hosts (Hassell 1978). The model is

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

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

The parameter  $k$  (the exponent of the negative binomial distribution) describes the degree of predator/parasitoid aggregation,  $P_t$  is the number of predators/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, 0.00005) deviates. Preliminary investigations showed that the amount of stochastic variation and the way that this was added into the model influenced detection of density dependence relatively little, providing the standard deviation and variance–mean ratio of logarithmic abundance were kept within limits observed for real insect populations. A wide parameter space was explored. However, for brevity only a typical set of results is shown. Values reported here are all combinations of  $k = 0.2$  and  $0.6$ ,  $a = 0.5$  and  $r = 1.5$ ,  $2.0$  and  $2.5$ . Initial abundances were  $\ln(P_t) = 3.0$  and  $\ln(N_t) = 4.0$ ; again, preliminary work showed that these values

**Table 1.** Numbers of generations per year (Skinner 1984) for 362 species of moths that were used in Woiwod & Hanski's (1992) analysis

Number of generations per year	All moths	Noctuidae	Geometridae	Other families
1	275 (76.0%)	119 (77.3%)	115 (74.7%)	41 (75.9%)
1(2)	31 (8.6%)	16 (10.4%)	12 (7.8%)	3 (5.5%)
2(1)	26 (7.2%)	8 (5.2%)	13 (8.4%)	5 (9.3%)
2	23 (6.4%)	7 (4.5%)	11 (7.0%)	5 (9.3%)
2(3)	3 (0.8%)	2 (1.3%)	1 (0.7%)	0 (0%)
1.5(1)	1 (0.2%)	0 (0%)	1 (0.7%)	0 (0%)
Immigrants	3 (0.8%)	2 (1.3%)	1 (0.7%)	0 (0%)
Total	362	154	154	54

Percentages for each group are given in parentheses. The abbreviation 1(2) indicates that in either most years or at most localities the species usually has 1 generation, but occasionally (or at some localities) has 2 generations. Similarly 2(1) indicates that the species mainly has 2 generations, but less often has 1 generation per year, where the figure in parentheses in the first column indicates the less usual number of generations. A minority of classifications are based on judgement, bearing in mind that most of the sampling sites are in southern England, the Midlands or Wales (Taylor & Woiwod 1980).

were not important, presumably because the first 20 generations were discarded.

The second model was a modified form of the exponential model of Ricker (1954):

$$N_{t+1} = N_t \exp[r(1 - \alpha_t N_{t-1})]$$

where  $N_t$  is the abundance at time  $t$ ,  $r$  is a parameter that affects the response to increasing density (Olson 1992) and  $\alpha_t$  scales (but does not set) the size of the equilibrium abundance capacity since  $r$  also influences the equilibrium abundance (Ginzburg 1992). The parameter  $\alpha_t$  was made into a normally distributed random variate. To avoid introducing temporal trends into the time series the two initial abundances,  $N_1$  and  $N_2$ , were set close to  $1/\bar{\alpha}_t$ ; actual values of the logarithm of initial abundances were generated as evenly distributed deviates with a mean of  $1/\bar{\alpha}_t$  and a standard deviation of 0.01. Mean values of  $\alpha_t$  were set at 0.0005, 0.001 and 0.003, with the standard deviation of  $\alpha_t$  set at 0.00005 for each of these values of  $\bar{\alpha}_t$ . For all these combinations,  $r$ -values of 1.8 and 2.4 were used.

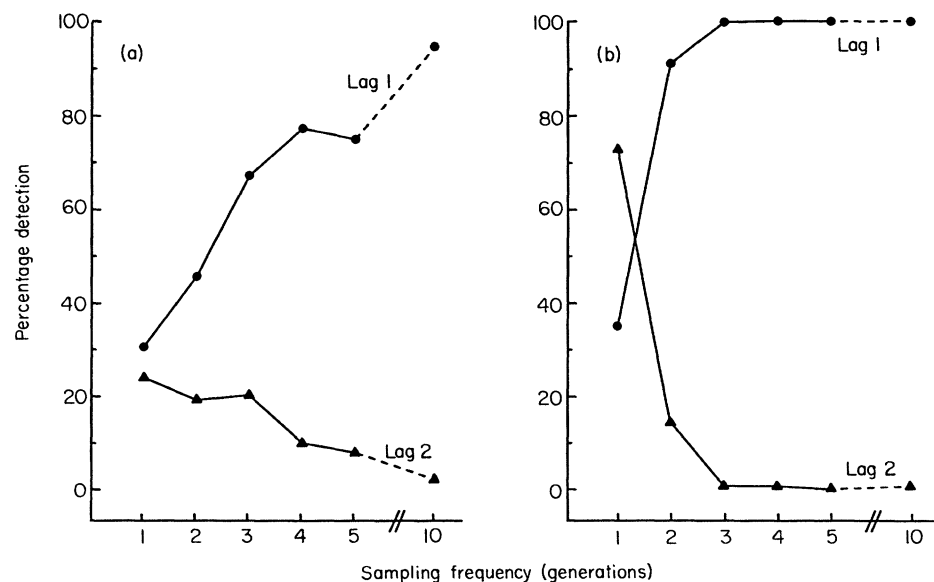
## Results

The frequency of detection of density dependence from time series generated using the host-parasitoid model are given in Fig. 1 and those for the Ricker

model are given in Fig. 2. In all cases the analysis of time series for non-delayed density dependence produced rates of detection (at  $P \leq 0.05$ ) much greater than the commonly accepted 5% of spurious cases, despite the presence of only delayed (lag 2) density dependence. Conversely, overall rates of correct identification of delayed (lag 2) density dependence (Figs 1 & 2) did not exceed 76% in these simulations, a figure that falls far below the 95% level which would be needed to be statistically certain of finding delayed density dependence if it was present.

Different degrees of aggregation of parasitoids (compare Fig. 1a and b) produced quantitatively different patterns in detection from series generated using the mean of different numbers of consecutive generations; however, patterns were qualitatively similar. The more generations that were sampled for each data point in the time series (the more time series were smoothed) the lower the rate of detection of delayed (lag 2) density dependence (Figs 1 & 2). Conversely, taking the mean of more than a single generation for each abundance (smoothing time series) lead to non-delayed density dependence being found more frequently.

Smoothing had a slightly more complicated effect on data generated by the Ricker model (Fig. 2). Sampling of up to three consecutive generations led to increases in detection of non-delayed density



**Fig. 1.** The frequency of detection of delayed (lag 2) and non-delayed (lag 1) density dependence from time series containing lag 2 delayed density dependence that were generated using the Nicholson-Bailey model as modified by May (1978) to include parasitoid aggregation. In (a) the value of  $k$  of the negative binomial distribution was 0.2 and in (b) it was 0.6. Only host densities were analysed. Other parameters were  $\lambda = 1.5, 2.0$  and  $2.5$ ,  $a = 0.5$  and  $Z_t = 0.00005$ . 100 series of each of these three-parameter combinations were used for each point on each graph. All series analysed were of 20 data points in length and the mean was taken of various numbers of generations (shown on the x-axis). Density independence was rejected in favour of density dependence if  $P \leq 0.05$  in Turchin's (1990) tests. Other details are given in the text.

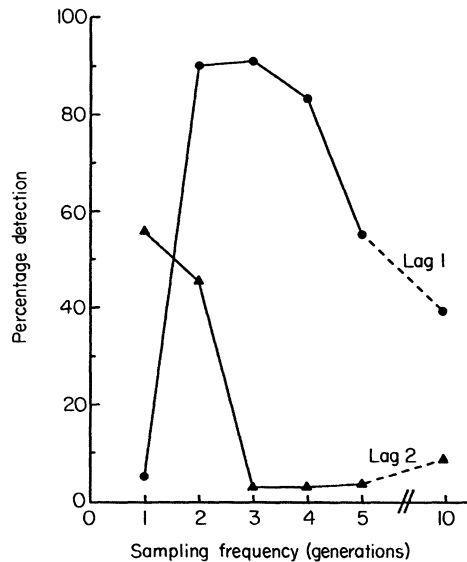


Fig. 2. The frequency of detection of non-delayed (lag 1) and delayed (lag 2) density dependence from time series containing a lag of two generations. Series were generated using a modified form of the logistic equation,  $N_{t+2} = N_{t+1} \exp[r(1 - \alpha_t N_t)]$ , where  $N_t$  is the abundance at time  $t$ ,  $\alpha_t$  is usually called  $1/\text{carrying capacity}$  and  $r$  is called the intrinsic growth rate. The parameter  $\alpha_t$  was a normal deviate with a mean of 0.00005, 0.001, or 0.003 and a standard deviation of 0.00005,  $r$  was set at 1.8 or 2.4 for each of these values of  $\alpha_t$ . Each percentage is the mean of 100 series of 20 data points in length from each of the six parameter combinations. Density independence was rejected in favour of density dependence if  $P \leq 0.05$  in Turchin's (1990) tests.

dependence and declines in the rate of detection of delayed density dependence. However, as the number of generations sampled increased beyond three the rate of detection of delayed density dependence increased and non-delayed density dependence declined in frequency.

### Discussion

Smoothing time series by sampling over time scales of longer than a generation influences our assessment of density dependence in these series in complex ways. However, it is clear that smoothing series hides delayed density dependence, and makes it more likely to misidentify delayed density dependence as non-delayed density dependence. These analyses therefore suggest that delayed (lag 2) density dependence may have been overlooked in the study of Woiwod & Hanski (1992), and non-delayed density dependence detected too frequently if delayed density dependence is present. If series had more than a single generation per year then the sampling procedure used by Woiwod & Hanski (1992) would cause delayed (lag 2) density dependence to be overlooked in the majority of cases. These problems could apply to all of the aphids considered by Woiwod & Hanski and

up to 24% of the moths, which had  $>1$  generation per year.

The problem is, however, complicated. For example, although all aphids have more than one generation per year, delayed density dependence in aphid populations may be generated by predators that have a single generation a year, and whose numbers build up during the season in response to cumulative aphid numbers over several generations (Ian Woiwod, personal communication). Other aphid natural enemies (parasitoids, diseases and different species of predators) may respond in a delayed density-dependent manner to individual aphid generations. It is therefore unclear exactly how sampling cumulative aphid numbers and smoothing the time series will obscure delayed density dependence, but we may deduce with reasonable confidence that Woiwod and Hanski's method must have obscured some delayed density dependence in British aphid populations. Similar remarks apply to the 24% of moth species with more than a generation per year. Their methods are very likely again to have under-estimated the prevalence of delayed density dependence.

This leaves at least 76% of moth series in Woiwod & Hanski's study where the sampling method was suitable. Delayed density dependence (at  $P \leq 0.05$ ) was detected from 22–72% of simulated series of 20 generations in length (Figs 1 & 2). This leads to delayed density dependence being expected from between 16.7 ( $=76/100 \times 22/100$ ) and 54.7% ( $=76/100 \times 72/100$ ) of series of 20 generations in length that contain delayed density dependence, compared with the actual figure of 3.3% for moth series ( $>20$  generations and which lacked temporal trends). Hence, Woiwod & Hanski found delayed density dependence in moths significantly less frequently ( $P < 0.001$  in a  $G$ -test) than any of the three types of simulated series used here, even when we exclude those series where sampling may have been inappropriate. This is important because it does suggest that delayed density dependence is genuinely infrequent in the moth species which they considered.

Summarizing, the analyses of Woiwod & Hanski (1992) probably detect delayed density dependence *less* frequently than it is actually present and detect non-delayed density dependence *more* frequently than it is actually present. This is because non-delayed density dependence is detected when only delayed density dependence is present and combining data from several generations tends to cause even more frequent detection of delayed density dependence. However, for moth species with only a single generation per year, delayed density dependence was found by Woiwod and Hanski much less often than would be expected if it was present. Why British moths have such a low incidence of delayed density dependence compared with Turchin's forest insects is unknown, but Woiwod and Hanski may well be correct that delayed density dependence is more common in

pest/outbreak species. What the present paper shows is that we are more likely to correctly identify delayed density dependence if analyses are carried out on individual generations, rather than combined generations.

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