

# Population dynamics of a tree-dwelling aphid: regulation and density-independent processes

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## Summary

1. A population of the Turkey-oak aphid (*Myzocallis boernerii* Stroyan) was sampled at approximately weekly intervals on two Turkey-oak trees for 19 years.
2. On one tree (A), the aphids exhibited a distinct seasonal pattern with a spring increase, summer decrease, early autumn increase, and late autumn decline. On the other tree (B) the aphids remained at low densities after the decrease in summer.
3. On tree A, significant undercompensating density dependence occurred during all periods of the seasonal population development, and their strength varied little during the course of the season. On tree B, significant density dependence compensated exactly for increase, but appeared only after the decrease in summer when the population remained at very low densities for the rest of the season.
4. Density-independent weather variables affected the population dynamics very little. Their influence was marginally significant only at very low densities when the aphids were regulated exactly by compensating density-dependent factors.
5. The results suggest a curvilinear density dependence, with strong regulation at low densities, and weak at high densities. That is, this aphid was most regulated not at the peak but at the trough densities.

*Key-words:* census data, curvilinear density dependence, *Myzocallis boernerii*, tests of density dependence, weather variables.

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## Introduction

An understanding of regulatory mechanisms based on interactions among density-dependent and density-independent factors is a central ecological issue. Identifying feedback processes that lead to population regulation is of fundamental importance: only then can such ecological applications as conservation of species (Ginzburg, Ferson & Akcakaya 1990) or pest control (May *et al.* 1981) be properly addressed in a truly scientific way (Hassell, Latto & May 1989). It is also widely accepted that these interactions have broad theoretical implications for the structure of communities, and the evolution of species (Pianka 1974; Berryman 1981; Emlen 1984).

Since Nicholson (1933), Solomon (1949), Andrewartha & Birch (1954) and Morris (1959) first studied populations there have been two trends in

interpretation. The first stresses the disturbing influence of density-independent environmental factors (Andrewartha 1957; Birch 1957; Dempster 1983; Den Boer 1988, 1990; Den Boer & Reddingius 1989) the second the stabilizing influence of density-dependent mechanisms (Varley, Gradwell & Hassell 1973; Hassell 1975; Bellows 1981; Royama 1984; Latto & Hassell 1987; Latto & Bernstein 1990; Turchin 1990), and there is an ongoing discussion between representatives of both opinions (e.g. Berryman 1987, 1991; Sinclair 1989; Wolda 1989, 1991; Holyoak & Lawton 1993; Wolda & Dennis 1993).

Three problems confound the debate: (i) a paucity of high-quality, long-term population data (Hassell *et al.* 1989; Holyoak & Lawton 1992; Woiwod & Hanski 1992); (ii) absence of a reliable method of detecting density dependence, in spite of the efforts of many authors (Varley & Gradwell 1960; Solomon 1964; Maelzer 1970; St Amant 1970; Bulmer 1975; Slade 1977; Vickery & Nudds 1984; Bernstein 1985; Gaston & Lawton 1987; Pollard, Lakhani & Rothery 1987; Reddingius & den Boer 1989; Turchin 1990; Vickery 1991; Crowley 1992; Turchin & Taylor 1992; Holyoak

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& Crowley 1993; Holyoak 1993, 1994; Dennis & Taper 1994; Holyoak, Jarošík & Novák 1997); and (iii) a preoccupation with extracting deterministic dynamics from the data, which may obscure the ultimate aim: to identify the nature of real-world dynamic processes (Kindlmann & Dixon 1995; Dixon, Kindlmann & Sequeira 1996; Sequeira & Dixon 1997).

Here the population dynamics of the Turkey-oak aphid (*Myzocallis boernerii* Stroyan), which has been monitored on two Turkey-oak trees (*Quercus cerris* L.) in Norwich, England, for 19 years (1975–93) is analysed. In the UK, *M. boernerii* is host specific and without specialized insect natural enemies. Its life cycle starts when the first generation hatches from overwintering eggs in late April. This, and the subsequent generations, are winged and parthenogenetic. Winged males and unwinged sexual females first appear in the middle of October and after mating, females lay eggs on the twigs, and the aphid life cycle ends in late November/early December. During the season, aphids show definite patterns of fluctuation in abundance, and their numbers are regulated by density-dependent processes (Dixon *et al.* 1996).

The problems addressed in this paper are: (i) to what extent are the population dynamics driven by density dependent factors? (ii) what effect do density-independent factors have on the population dynamics? (iii) how do the density-dependent and density-independent factors interact? These questions are answered by determining: (a) the influence of population density on changes in aphid numbers between successive sampling dates; (b) the influence of weather variables after the effect of density-dependent factors have been filtered out; and (c) a synthesis of the findings.

### Materials and methods

The populations were sampled each year at approximately weekly intervals, from the beginning to the end of the aphid life cycle. Each week, 10 leaves were selected at random at each of eight fixed sampling points around the circumference of each of the trees, and the numbers of the various life stages recorded. For each year and each tree, the seasonal pattern in aphid abundance was divided into: (i) spring increase; (ii) summer decrease; (iii) early autumn increase; and (iv) late autumn decline.

In 1976 and 1977, daily reproduction was assessed by clip caging adult aphids on leaves (Dixon 1966) from spring (late May–early June) to summer (late July–August). The daily production of offspring was converted into per capita rate of increase, and for the same period  $R$  was calculated from changes in aphid numbers,  $N$ , on successive sampling dates,  $N(t)$  and  $N(t-1)$ , as:

$$R(t) = [N(t) - N(t-1)]/N(t-1).$$

For tests of density dependence, changes in aphid

numbers between successive sampling dates were expressed as  $k$ -values,  $\ln[N(t)] - \ln[N(t-1)]$ . To obtain census data in equidistant intervals, for each season and each tree the  $k$ -values within each period of the seasonal pattern (spring increase, summer decrease, early autumn increase, late autumn decline) were ordered from the onset to the end of the period. Density dependences were detected, separately for each tree, by Pollard *et al.* (1987) and Varley & Gradwell (1960) regression tests, using in each successive analysis a single  $k$ -value from each season. Consequently, each regression test of  $k$ -value on log of population density,  $N$ , was based on  $n \leq 19$  points, because although the total number of evaluated seasons was 19 there was not always the same number of census points in a particular period.

The aphid's lifetime, of 2–3 weeks, is longer than the weekly sampling interval. Individuals from one generation may thus be included in the following one or two weekly estimates of population density. This introduces pseudoreplication because the  $k$ -values within a season are not statistically independent. It is an unavoidable consequence of aphid biology: parthenogenetic generations overlap, and individuals are born at different, but close, instants of time. Consequently, it is impossible to avoid pseudoreplication using a sampling interval that spans a generation. In an attempt to overcome this problem, only the significant results of density-dependence tests that are two or more weeks apart are presented.

To detect an effect of weather variables, natural logarithms of seasonal totals of aphids were regressed on standardized (zero mean, variance one) seasonal averages of daily temperature, precipitation and run of wind. To detect an effect of density-independent factors after the variation explained by density-dependent factors has been accounted for, standardized residuals of significant density-dependence tests determined by the Varley & Gradwell (1960) method were regressed on standardized averages of factor scores of corresponding weather variables for each sampling period. The factor scores of weather variables were determined by principal component analysis. The principal component analysis was used to find independent weather variables, because the weather variables are known to be correlated with each other, and show complex temporal autocorrelations (M. Holyoak, personal communication). Weather data were obtained in a meteorological station placed 14 km south-west from the trees.

### Results

On tree A, the aphids exhibited a distinct seasonal pattern of abundance with a period of spring increase, summer decrease, early autumn increase, and late autumn decline (Fig. 1A). On tree B, the average population densities were lower (one-way ANOVA:  $F_{1,61} = 4.579$ ,  $P < 0.05$ ), and the seasonal pattern

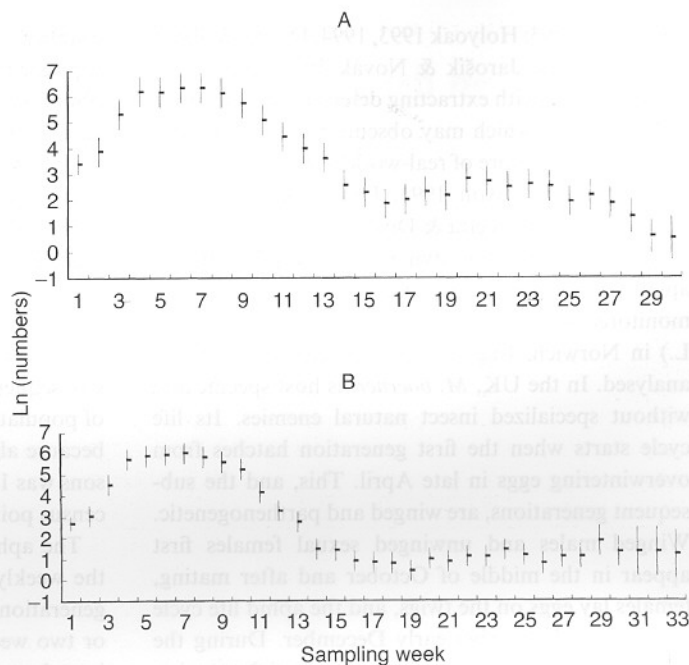


Fig. 1. Population dynamics of the Turkey-oak aphid (*Myzocallis boernerii*), monitored on two Turkey-oak trees (A, B) in Norwich, England, for 19 years (1975–93). Means  $\pm$  SE for weekly samples from early May to late November.

differed in that the aphids remained at low densities after the summer decrease (Fig. 1B). The low numbers in summer were associated with negative values in the weekly per capita rate of increase, and low but positive values for the reproductive rates obtained by caging adults on the same trees (Fig. 2).

Varley and Gradwell's conventional regression tests for density dependence gave very similar outcomes to Pollard *et al.*'s randomization tests (Table 1). On tree A the tests detected significant ( $P < 0.05$ ) density dependences during all periods of the population

development. In the Varley and Gradwell test the slopes varied little with seasonal changes in abundance, and indicated undercompensating density dependences that did not differ significantly from a regression slope  $-0.25$ . On tree B significant density dependences were recorded only late on in the season when the populations were at very low densities of about 4–5 aphids per sample. In the Varley and Gradwell test the regression slopes were not significantly different from  $-1$ , indicating exact compensating density dependence, and the regression

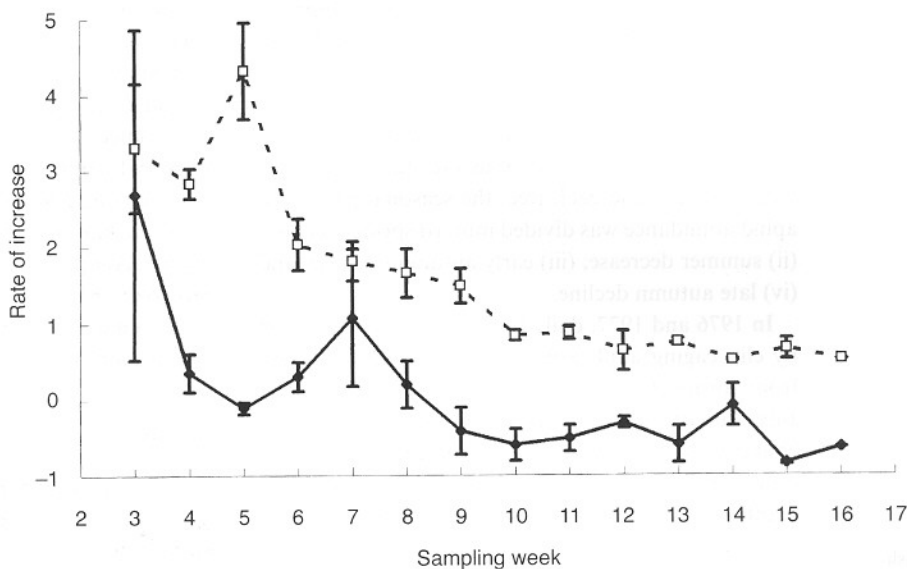


Fig. 2. The per capita rate of increase of the Turkey-oak aphid (*Myzocallis boernerii*) assessed from the daily production of offspring in cages (---), and from population changes (—). Means  $\pm$  SE for weekly samples from the beginning of the spring peak (late May–early June) throughout the summer (late July–August) in 1976 and 1977.

**Table 1.** Significant results (probability  $\leq 5\%$ ) in tests of density dependence two or more sampling weeks apart in census data of the Turkey-oak aphid (*Myzocallis boernerii*) monitored on two trees (A, B) by weekly samples for 19 seasons.  $n$  = number of evaluated seasons on a particular tree ( $n < 19$  is caused by there not always being the same number of census points in a particular period of population development each year)

Tree	$n$	Period of population development	Test of density dependence Varley & Gradwell (1960)				Explained variance (%)	Probability (F-test, %)	Pollard <i>et al.</i> (1987)
			Slope	SE	Intercept	SE			Probability (% points for absolute regression coefficients)
A	19	Spring increase	-0.26	0.12	2.44	0.54	22.2	4.16	4.68
A	17	Spring increase	-0.27	0.11	2.30	0.59	28.0	2.89	3.36
A	13	Spring increase	-0.26	0.06	1.89	0.37	63.6	0.11	0.26
A	17	Summer decrease	-0.29	0.11	0.75	0.49	29.9	2.32	2.68
B	13	Early autumn	-1.06	0.31	1.58	0.50	51.6	0.57	0.56
B	9	Early autumn	-0.95	0.36	1.59	0.58	49.7	3.38	4.24
A	8	Early autumn	-0.24	0.12	1.32	0.12	90.6	0.03	0.08
A	17	Late autumn	-0.19	0.07	0.55	0.27	29.3	2.33	2.52

equations predicted zero change in aphid numbers when the observed abundances were of the order of 4–5 aphids.

There was no significant relationship between seasonal totals of aphids and seasonal averages of any meteorological variable. An influence of weather variables, after the effect of density-dependent factors had been filtered out, appeared only at the lower population densities, and it was only marginally significant (Table 2). Thus density-independent factors may have a destabilizing effect when aphids are present in low numbers in late summer and autumn (Fig. 1B).

## Discussion

The test developed by Pollard *et al.* (1987) is among the most reliable tests of density dependence (Holyoak 1993). Because it is a randomization test, its test statistic, the correlation coefficient between observed  $k$ -value and the natural logarithm of observed population size,  $\ln[N(t-1)]$ , is equivalent to a regression

coefficient (Pollard *et al.* 1987; Manly 1991). Consequently, this test statistic is equal to Varley & Gradwell's (1960) density-dependence test, the conventional least-square regression of  $k$ -value against  $\ln[N(t-1)]$ , with errors in the ordinate assumed to be normally distributed.

Despite the criticisms of the Varley and Gradwell test (Maelzer 1970; St Amant 1970; Slade 1977; Vickery & Nudds 1984; Vickery 1991; Holyoak 1993), it continues to be widely used (see Hassell *et al.* 1989). As the Varley and Gradwell conventional regression test, and the Pollard *et al.* randomization test gave similar results, the use of the conventional regression in our analysis was justified, because the data looked as if it came from a normal distribution. In this case, a classical, conventional parametric test can be thought of as an approximation for a randomization test (see Manly 1991, p. 17). The similar outcome of both tests also justified the use of standardized residuals about a conventional linear regression for detecting an effect of density-independent factors after

**Table 2.** Multiple regressions of standardized residuals of the significant (probability  $\leq 5\%$ ) density-dependence tests two or more sampling weeks apart on standardized factor scores of corresponding average temperatures, precipitation, and runs of wind over the sampling interval.  $n$  = number of evaluated seasons on a particular tree ( $n < 19$  is caused by there not always being the same number of census points in a particular period of population development each year)

Tree	$n$	Period of population development	Mean square			Probability (%)
			Regression	Error	F-ratio	
A	19	Spring increase	0.33	1.32	0.248	78.35
A	17	Spring increase	0.63	0.60	1.057	37.20
A	13	Spring increase	0.04	0.08	0.477	63.31
A	17	Summer decrease	0.31	0.64	0.483	62.59
B	13	Early autumn	1.56	0.71	2.194	15.78
B	9	Early autumn	1.98	0.42	4.665	5.16
A	8	Early autumn	0.02	0.03	0.665	54.82
A	17	Late autumn	0.02	0.01	1.660	21.71

the variation explained by density-dependent factors had been accounted for.

The seasonal fluctuation in abundance is known to follow changes in host plant quality (Dixon 1970). By virtue of short generation time and programmed anticipation of seasonal trends, aphids track changes in habitat quality very closely (Dixon 1985). A possible reason why density-independent weather variables had very little effect on the population dynamics is that meteorological factors, similar to density-dependent factors (Sequeira & Dixon 1996; Dixon *et al.* 1996), manifest themselves, not directly but through their effect on plant quality.

Migration is the most important factor determining the summer decline in abundance (Kindlmann & Dixon 1995). This is also revealed by the negative values of the per capita rate of increase derived from the weekly samples, compared to the positive values obtained by monitoring reproduction in cages during the summer decline. Intraspecific competition for resources in summer results in immediate size-related reduction in recruitment, and increase in the tendency to migrate (Dixon *et al.* 1996).

If the population dynamics were driven by density-dependent factors — with the density dependences linear over all values of densities — an increase in the adverse effect of density should occur when populations increase in spring and early autumn, because a directly density-dependent factor which increases linearly should proportionally increase in strength when operating at high population density. Conversely, a significant decline in the adverse effect of density on the rate of increase should be found in summer when the populations decline, and in late autumn when densities decrease at the end of the season, because a directly density-dependent factor with linear density dependence is expected to be proportionally weaker when operating at low density.

For tree A, which has a higher average density than tree B, the results indicated: little effect of population numbers; weak density dependences, which caused on a logarithmic scale only about a quarter of the decrease in aphid numbers compared to a population without any density dependence. On tree B density dependences appeared only late in the season when populations occurred at very low densities but these density dependences were exactly compensating. This result suggests a curvilinear density dependence (Sinclair 1989), so that at low densities the regulation is strong, and at higher densities weak. In this case, it is not the peak size that a population can achieve that is most obviously regulated, but the trough size to which it repeatedly falls (cf. Richards & Waloff 1954; Whitaker 1971; Elliot 1984, 1987).

It is remarkable that exactly compensating density dependence operates over a very short period of the year, and acts most strongly on the population when it is at its lowest density. This pattern is enabled by changes in host plant quality during the season and

by clonal polymorphism and telescoping of aphid generations. Polymorphism and telescoping are life-history traits of aphids that provide an efficient tool for tracking trends in habitat quality and rapid changes in population density (Dixon 1985).

The slightly different seasonal pattern of abundance on the two trees can be a consequence of differences in phenology of the trees. Tree A always breaks its buds and senesces before tree B (Dixon 1990). It may increase population stability, as trees and aphids do not always break bud and hatch in synchrony, and the scatter of bud opening increases environmental heterogeneity at the onset of seasonal development of the aphid.

Because density dependence is difficult to measure, the weak density dependence at higher densities may be a consequence of other facts, e.g. that the test statistic used does not match the dynamics of the populations studied as a result of their complex dynamic behaviour (cf. Turchin & Taylor 1992; Sequeira & Dixon 1997) or 'ensemble dynamics', in which case it may be detectable only at a particular spatial scale (e.g. Strong 1988; Murdoch & Walde 1989).

However, the existence of a curvilinear density dependence is supported by the analysis of the effect of the density-independent factors on population dynamics after the effect of density-dependent factors have been removed. The reason that density-independent weather variables appeared important only on tree B, when the aphids were regulated by exactly compensating density-dependent factors, may be because the detection of a density-independent factor is much more difficult when the density-dependent factor is weak, than when the density-dependent factor is exactly compensating (see Varley *et al.* 1973, p. 91–2). Moreover, Sequeira & Dixon (1997), who used time series analysis on the same weekly census data, also discovered that the declining phase of density in summer on tree B is longer, and subject to more stochastic disturbances than on tree A.

Because the disturbing influence of a density-independent factor is weaker when density dependence is strong (Sinclair 1989), the disturbing influence of weather variables did not affect population persistence. With the population dynamics limited mainly by host plant quality, and regulated by exactly compensating density-dependent processes acting at low densities, migration plays an important role in shaping the population dynamics by maintaining a small but viable population through exactly compensating dispersal by winged adults.

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