Original papers

On the stabilization of animal numbers. Problems of testing*
2. Confrontation with data from the field

P.J. den Boer and J. Reddingius
Biological Station LUW, Kampsweg 27, 9418 PD Wijster, The Netherlands

Summary. When testing for regulation of population numbers, rather than using Bulmer's second test in cases where population numbers are estimated instead of measured, we prefer to correct Bulmer's first test for estimation error. A correction method is expounded, discussed, and applied to two series of census data: the pine looper of Klomp and the garden chafer of Milne. In neither case the tentative conclusion from using the uncorrected test was changed after correction. Therefore, in practice Bulmer's first test without correction can be used well as a first orientation. Twelve long series (more than 10 years) of census data of both univoltine and semelparous (a necessary condition) insects were tested for significant density dependence in the fluctuations of numbers with the randomization test of Pollard et al. None of the series, all we could find to meet the necessary condition as well as being longer than 10 years, showed significant density dependence at the 0.05 level, though the pine looper of Klomp did so at the 0.1 level. Next, the same series were tested for regulation in the sense of "keeping density within limits" with both the first test of Bulmer and the permutation test of Reddingius and Den Boer. Only Klomp's pine looper population at "Hoge Veluwe" scored significantly. In a following paper this population will be considered more closely, in order to enable understanding of this test result.

Key words: Density dependence – Census data – Trends – Regulation

In the first part of this paper (Reddingius and Den Boer 1989) we compared and discussed two tests that might be used to detect the existence of regulation of population numbers: the parametric first test of Bulmer and the nonparametric permutation test. As in most population studies densities are not exactly measured but estimated by taking samples, a parametric "regulation"-test should take into account the possible effect of estimation error. Rather than using Bulmer's second test (1975), which hardly has any power, we proposed to correct the test statistic of Bulmer's first test for estimation error. We noted, that if U^* and V^* are the uncorrected estimates of Bulmer's U and V respectively, R^{**}, the imperfect test statistic based on density

estimates, can be expressed as $R^{**} = (V + n\sigma_d^2)/[U + 2(n-1)\sigma_d^2]$, by which Bulmer's $R = U/V$ can be approximated as $R \approx (V^* - n\sigma_d^2)/[U^* - 2(n-1)\sigma_d^2]$. If a reasonable estimate can be obtained for the sample variance of the density estimates σ_d^2, S_d^2, say, the corrected test statistic can be computed as $R^c = (V^* - nS_d^2)/[U^* - 2(n-1)S_d^2]$.

At the time we prepared the present paper, Pollard et al. (1987) published an interesting test for detecting density dependence in the variation of population numbers without the necessary condition that it should have to contribute to "regulation", i.e. to "keeping between limits", of density. For this "randomization" test, as it is called, they independently used the same method of taking samples from the collection of all possible permutations of the values of net reproduction ($Y_t = X_{t+1} - X_t = \ln R_t$, where $X_t = \ln N_t$, and N_t is population size or density in year t), as was presented by Reddingius and Den Boer (1989) for the permutation test. The randomization test uses the product-moment correlation coefficient between population density (or size) and the next population change (net reproduction). By randomly permuting the values for net reproduction of the original time series many times, and each time calculating the matching densities, population change is made independent of density. Therefore, the currently computed correlation coefficients define the probability distribution of this coefficient under the null hypothesis, with which the coefficient of the original series can be compared in the way it was described by Reddingius and Den Boer (1989) for Log-Range values. The interesting point with this test of Pollard et al. (1987) is that the outcome is independent of whether or not there is a marked trend in the data.

In the following we will expound how to correct the test statistic of Bulmer's first test for estimation errors, after which we will try to find out how much difference it makes in practice whether one uses the corrected statistic, R^c, or the uncorrected one, R^{**}. Next, we will apply the randomization test of Pollard et al. (1987) to a number of long series of published population data to see whether or not significant density dependence can be detected in these series. With this knowledge we can adequately test the same series with Bulmer's first test and the permutation test to get some idea of the evidence that actually supports the regulation hypothesis. Unfortunately, we will have to restrict our explorations to insects that are both univoltine and semelparous, because a basic assumption of these tests – especially of the parametric one, but also in an unbiased use of the permutation and randomization tests – is that the sequence

of population densities can be considered a piece of first-order Markov chain. Because of this we could not test some of the best series of census data, such as on the great tit of Kluyver (1951), on muskrats and bobwhite quail of Errington (1957), and on the many series of carabid species available at the Biological Station, Wijster. New tests that also cover higher-order Markov chains will have to be developed for that.

Methods

Correcting for the effect of density estimates

Suppose, in a given year the estimate of density is based on k independent random samples of size a, and let N_i denote the number of animals in the i-th sample. The obvious estimator of the density then will be the arithmetic average of the numbers per unit area, i.e. $\bar{N}/a = \sum_{i=1}^{k} N_i/(ka)$. Let N be the real population density, and σ^2 the variance among samples. Let $S^2 = \sum_{i=1}^{k} (N_i - \bar{N})^2/(k-1)$ be the sample variance, used as an estimator for σ^2. The problem we will consider is how to estimate the variance of $X^* = \log(\bar{N}/a)$. That this is an intricate problem will be realized if one is aware of the fact that the variance of the logarithm of a variable depends on the expected value (mean) as well as on the variance of that variable (see Fig. 1, where this is illustrated for normally distributed variables). Moreover, since $X^* = \log(\sum N_i) - \log(k) - \log(a)$, we have $\mathrm{var}(X^*) = \mathrm{var}[\log(\sum N_i)]$. In general, increasing k will not decrease the variance of X^*, although it does decrease the variance of $\bar{N}$. In what follows, we will suppose $a=1$. We can think of four ways to approach our problem.

1. One might work with logarithms from the very start and estimate $X = \log(N)$ by $\bar{X} = \sum_{i=1}^{k} \log(N_i)/k = \sum X_i/k$, say, and use the sample variance of this mean by $\sum(X_i - \bar{X})^2/[k(k-1)]$. This approach seems straightforward but there are some objections to be raised against it. In the first place, the density itself, $N = \exp(X)$, is now estimated as the geometric average of the N_i's, suggesting a multiplicative rather than an additive relationship between samples. This does not seem very plausible. In the second place, some N_i's may be zero, in which cases the corresponding X_i's are undefined, although, of course, the zeroes must be included in our density estimate. Adding a constant such as 0.5 or 0.375 may be useful if the data are to be treated by ANOVA or regression analysis, but in the present case this is not relevant. We have to estimate $X = \log(N)$ not $\log(N + 0.375)$, or something like that. It follows from what was said above concerning the moments of logarithms of variables that the (arbitrary) choice of which constant is added will influence the variance.

2. One might postulate a certain type of probability distribution for the sample sizes. Rather often, a Negative Binomial distribution will fit the data rather well, for example. We might then estimate the parameters of this distribution from the data and numerically compute the variance of the logarithm of the sum of k variables with the fitted distribution. The probability that this sum will be zero must be zero or at least negligibly small.
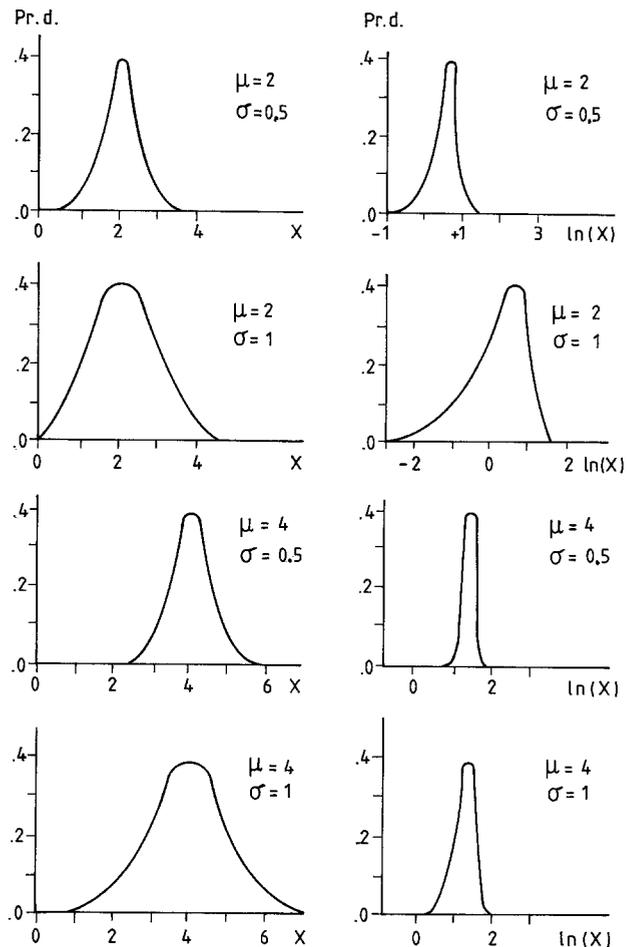

Fig. 1. Probability densities of a normally distributed variable X, in the graphs at left plotted as X, and in those at right plotted as $\ln(X)$

3. We may try to estimate $\mathrm{var}(X^*)$ using a series development, which may be valid if the variance is small compared to the mean. Suppose $\bar{N}$ is an unbiased estimator of N. We write

$$\ln(\bar{N}) = \ln(N) + (\bar{N} - N)/N - (\bar{N} - N)^2/(2N^2) + \ldots$$
$$\ln^2(\bar{N}) = [\ln(\bar{N})]^2 = \ln^2(N) + (\bar{N} - N)^2/(N^2)$$
$$+ 2\ln(N)\cdot(\bar{N} - N)/N$$
$$- 2\ln(N)\cdot(\bar{N} - N)^2/(2N^2) - \ldots + \ldots$$

Neclecting higher order terms, we obtain

$$\mathscr{E}\ln(\bar{N}) \approx \ln(N) - \mathrm{var}(\bar{N})/(2N^2) \quad (\text{because } \mathscr{E}(\bar{N} - N) = 0)$$
$$\mathscr{E}(\ln^2(\bar{N})) \approx \ln^2(N) + [1 - \ln(N)]\,\mathrm{var}(\bar{N})/(N^2)$$

whence

$$\mathrm{var}\ln(\bar{N}) = \mathscr{E}\ln^2(\bar{N}) - [\mathscr{E}\ln(N)]^2$$
$$= \mathrm{var}(\bar{N})[1 - \{\mathrm{var}(\bar{N})/(4N^2)\}]/N^2.$$

So as an estimator of $\mathrm{var}\ln(\bar{N})$ we might use

$$S^2[1 - \{S^2/(4k\bar{N}^2)\}]/(k\bar{N}^2), \quad \text{as } \mathrm{var}(\bar{N}) = \sigma^2/k.$$

This formula is valid provided the higher order terms may indeed be neglected, i.e. for example $\mathscr{E}(\bar{N} - N)^3/(3N^3)$ must

be small compared to $\mathrm{var}(\bar{N})/(2N^2)$. This means that $\bar{N}$ with a high probability must be close to N.

4. If k is large, $\bar{N}$ is approximately normally distributed. This approximation may be used only if $\mathscr{E}(\bar{N})$ is large compared to $\sqrt{\mathrm{var}(\bar{N})}$, because the probability of the approximating variable's being less than or equal to zero must be negligible. But if $\bar{N}$ is large enough, we may estimate its expectation and variance, and compute the expectation and variance of the logarithm of a variable with the fitted normal distribution using numerical integration. For example, a simple way of calculating the expectation is the following. If $\mathscr{E}\log(\bar{N})=\mu$, $\mathrm{var}\log(\bar{N})=\sigma^2$, one chooses a large a and a small h, and, putting

$$k=a/h: \mathscr{E}\log(N)\approx \sum_{j=1}^{k}[\log(jh)\,e^{-\frac{1}{2}[(jh-\mu)/\sigma]^2}]\cdot h.$$

In our calculations, we chose a sequence of decreasing values of h until the successive results no longer differed in their two or three most significant digits. If μ is not large in comparison to σ, this procedure fails because the inproper integral

$$(1/\sigma\sqrt{2\pi})\int_{0}^{\infty}\log(X)\,e^{-\frac{1}{2}[(x-\mu)/\sigma]^2}\cdot dx$$

$$=\lim_{\varepsilon\to 0}(1/\sigma\sqrt{2\pi})\int_{\varepsilon}^{\infty}\log(X)\,e^{-\frac{1}{2}[(x-\mu)/\sigma]^2}\cdot dx$$

does not converge. Formally we should divide the result by $1-(1/\sigma\sqrt{2\pi})\int_{-\infty}^{0}e^{-\frac{1}{2}[(x-\mu)/\sigma]^2}\cdot dx$, but if μ is large enough in comparison to σ, this quantity is almost 1.

Results

Correction for estimation errors

We tried to apply these ideas to two cases: larval density of the Pine Looper according to Klomp (1966), using data on sample sizes from his Table I, and larval density of the Garden Chafer from Milne (1984) using Table 1a from Appendix 1. However, we dropped the second approach; although it may seem the most exact one, it was not feasible to fit probability distributions that were numerically tractable.

A. *Bupalus* larvae.
1. Variance of $\log_{10}$ (number of larvae/number of shoots)
    August, 9 samples: 0.00429
    September, 9 samples: 0.001071
3. August: $\bar{N}=0.025072$ $S^2=0.00010373$ $k=9$
    estimate of var $\ln(\bar{N})=0.018251$
    estimate of var $\log_{10}(\bar{N})=0.018251/[\ln(10)]^2$
                           $=0.0034424$
    September: $\bar{N}=0.025238$ $S^2=0.000033980$ $k=9$
    estimate of var $\ln(\bar{N})=0.0059188$
    estimate of var $\log_{10}(\bar{N})=0.0011164$
4. August: estimate of var $\ln(\bar{N})=0.019254$
         estimate of var $\log_{10}(\bar{N})=0.0036315$
    September: estimate of var $\ln(\bar{N})=0.0060692$
          estimate of var $\log_{10}(\bar{N})=0.0011447$
The results agree fairly well.

In Table IV, Klomp (l.c.) gives estimates of larval density for the years 1950–1964 ($n=15$). Using logarithms to the base 10 of the densities per shoot in August, we calculated

$$U^*=3.492 \quad V^*=2.154, \text{ hence } R^{**}=0.617$$

$$R_{L;\,0.05}=0.25+13\times 0.0366=0.7258,$$

so R^{**} would be considered significant at the 0.05 level.

If we assume $\sigma_d^2=0.004$, we obtain $R^c=0.6195$, which is still significant at the 0.05 level. So, unless sampling errors on the average were much worse than they were in 1954, the year on which Table I was based, these data do support the hypothesis that net reproduction is negatively density-dependent.

B. *Garden Chafer* larvae.
1. Method 1 could not be applied because there were many zeroes.
3. Data for 1949:
    number of larvae   0   1   2   3
    number of samples   303   28   6   1
    $\bar{N}=0.12722$ $S^2=0.16478$ $k=338$
    estimate of var $\ln(\bar{N})=0.029895$
    estimate of var $\log_{10}(\bar{N})=0.0056385$
    Data for 1975:
    number of larvae   0   1   2   3   4   5   6 7
    number of samples   213   42   20   13   19   10   11 5
                                8   9   10   11   12
                                1   2   0   1   1
    $\bar{N}=1.17456$ $S^2=4.32849$ $k=338$
    estimate of var $\ln(\bar{N})=0.0092611$
    estimate of var $\log_{10}(\bar{N})=0.0017467$
4. Data for 1949:
    estimate of var $\ln(\bar{N})=0.032750$
    estimate of var $\log_{10}(\bar{N})=0.0061770$
    Data for 1975:
    estimate of var $\ln(\bar{N})=0.0095071$
    estimate of var $\log_{10}(\bar{N})=0.0017931$.

The results for a given year agree fairly well, but the sampling variance was much larger in 1949 than it was in 1975. We considered all years in which $\bar{N}$ was at least 4.5 times as large as its standard error, i.e. 12 out of 29 cases. For these we estimated $\mathrm{var}\ln(\bar{N})$ by Method 4. The weighted avarage, weighted according to k-value, of these variances is 0.023755. Converted to logarithms to the base 10, this is 0.0044804. These results suggest tentatively that putting $\sigma_d^2=0.01$ may be conservative.

Using natural logarithms, we obtained $V^*=42.1703$, $U^*=20.9015$, $k=29$, hence $R^{**}=2.018$. With $R_{L;\,0.05}=1.238$, this is not significant at 0.05 level. Converted to logarithms to the base 10, we have $V^*=7.9538$, $U^*=3.9423$. With $\sigma_d^2=0.01$ we then obtain $R^c=2.2659$, which is, of course, not significant.

An approach which may also be useful in certain cases is to calculate for which value of σ_d^2 a "significant" R^{**} would be transformed into a non-significant R^c. Suppose $R^{**}=V^*/U^*<R_L$; we now ask for which value of σ_d^2 we have $(V^*-n\sigma_d^2)/(U^*-2(n-1)\sigma_d^2)>R_L$. The answer one obtains after some algebra is $\sigma_d^2>(R_L U^*-V^*)/[2(n-1)R_L-n]$.

For example, for the data on moth density of Klomp (l.c. Table X), we obtained, using logarithms to the base 10:

$$U^*=4.218 \quad V^*=2.452 \quad k=14$$

Table 1. Population densities or population sizes (N_t) with natural logarithm (ln) of the density range (LR) in a number of longterm population counts in univoltine insect species, i.e. populations for which the yearly densities may be considered terms of a first-order Markov chain

Species, area, period, and source of data	N_t-values	LR (ln)
Winter moth, Wytham Wood, Oxford UK, 19 years (1950–1968), Varley et al. (1973, Table F, p 201). Larvae per m² of canopy	112.2; 117.5; 55.0; 18.2; 158.5; 77.6; 95.5; 275.4; 190.55 57.54; 21.4; 7.6; 13.5; 40.7; 131.8; 269.15; 51.3; 9.8; 10.0	3.59
Winter moth, 19 years (1950–1968) Adults converted per m²	7.4; 13.8; 7.03; 4.9; 20.23; 11.94; 14.8; 23.44; 14.8; 6.17; 1.12; 3.02; 5.25; 10.965; 16.4; 24.0; 2.85; 2.82; 3.02	3.06
Pine looper, Hoge Veluwe, Netherlands, 15 years (1950–1964), Klomp (1966, Table XXIII, pp 268–270). Larvae in August per m² of canopy	9.5; 24.4; 1.6; 4.5; 11.5; 13.9; 15.1; 1.8; 3.6; 5.8; 7.5; 26.3; 24.8; 18.3; 6.5	2.80
Pine looper, 15 years (1950–1964) Larvae in September per m²	7.7; 22.4; 1.3; 4.5; 11.5; 12.0; 12.2; 0.8; 2.2; 3.7; 6.5; 25.6; 20.1; 18.3; 3.7	3.47
Pine looper, 14 years (1950–1963) Pupae in April per m²	5.4; 3.6; 0.73; 3.0; 3.0; 2.6; 1.7; 0.12; 0.87; 1.1; 2.3; 3.4; 5.0; 4.6	3.81
Pine looper, 14 years (1950–1963) Adults converted per m²	2.7; 1.3; 0.10; 1.1; 1.4; 1.5; 0.99; 0.10; 0.48; 0.58; 1.5; 2.1; 1.1; 0.83	3.29
Pine looper at Cannock, Staffordshire UK, 13 years (period unknown); read from Fig. 8.3 (p 139) of Varley et al. (1973) Pupae per m²	7.94; 40.74; 30.9; 26.92; 89.13; 6.31; 2.34; 1.58; 6.31; 15.85; 20.42; 12.3; 3.31	4.03
Garden chafer, Rydal Farm, Ambleside UK, 29 years (1947–1975), Milne (1984, Appendix 1, p 195) Third instar larvae (in 338 samples of 4 × 4 in./year)	136; 83; 43; 139; 161; 307; 251; 140; 22; 8; 4; 43; 21; 35; 19; 23; 11; 16; 11; 11; 14; 11; 46; 22; 44; 49; 63; 260; 397	4.60
Garden chafer, Hawes End Farm, Keswick UK, 18 years (1951–1968), Milne (1984, p 196) Third instar larvae (in 85 samples of 4 × 4 in./year)	159; 184; 43; 39; 13; 10; 9; 17; 14; 38; 15; 17; 17; 15; 10; 12; 2; 2; 6	4.52
Grey larch bud moth, Upper Engadin, Switzerland, 20 years (1949–1968), Van den Bos and Rabbinge (1976, Table 4, p 57). Larvae per 7.5 kg of branches	0.13; 0.62; 3.37; 31.3; 516.0; 2488.0; 949.0; 160.0; 16.8; 0.63; 0.59; 2.12; 12.3; 172.0; 1866.0; 1382.0; 23.4; 0.15; 0.015; 1.5	12.02
Spruce budworm, New Brunswick, Canada, 15 years, (1945–1959), Morris (1963, Fig. 28.1, p 177) Third instar larvae per 10 feet², Plot G4	0.056; 0.071; 0.427; 3.236; 3.981; 56.23; 51.29; 44.67; 25.7; 63.1; 12.3; 6.31; 19.95; 2.818; 0.331	7.03
Spruce budworm, 14 years (1946–1959) Third instar larvae per 10 feet², Plot G5	0.04; 0.048; 1.072; 1.585; 5.248; 5.623; 2.291; 12.59; 54.95; 4.476; 2.884; 6.31; 1.778; 0.302	7.23
Viburnum whitefly, Silwood Park, London UK, 12 years (1962–1973), Southwood and Reader (1976, Table 1, p 318) Fourth instar larvae in entire population 1	13190; 1937; 3904; 13919; 27562; 34136; 31110; 50658; 78943; 164027; 300583; 3303390	5.14
Viburnum whitefly, 12 years (1962–1973) Fourth instar larvae in entire population 2	708; 168; 195; 144; 134; 582; 1021; 2640; 6209; 12236; 6957; 6756	4.51
Viburnum whitefly, 12 years (1962–1973) Fourth instar larvae in entire population 3	597; 146; 115; 9; 25; 28; 27; 97; 348; 152; 48; 75	4.19
Nebria brevicollis (carabid), Wijster, The Netherlands, 11 years (1968–1978), Nelemans and Den Boer Young adults per 1000 m²	268; 341; 238; 784; 396; 604; 626; 1641; 1281; 1006; 645	1.93

hence $R^{**} = 0.581$. As $R_{L;0.05} = 0.6892$, this is "significant" at the 0.05 level. The result would not be significant, however, if

$$\sigma_d^2 > (0.6892 \times 4.11970 - 2.45048)/(26 \times 0.6892 - 14.0) = 0.09921.$$

Moth density was minimal in the years 1953 and 1958. In both cases it was 0.1 moths/m², and the 0.95 confidence interval given by Klomp was 0.02–0.18. The 0.95 confidence interval for the logarithm of the moth density then would be -1.699 to -0.745. This interval has a width of 0.954. Moth density was maximal, i.e. 2.71 moths/m² in 1951. The confidence interval was 2.09–3.33. Converted to logarithms this is 0.320–0.522, with a width of 0.202. If we assume the width of a 0.95 confidence interval to be about 4 times the standard deviation (as Klomp did), then σ_d might be somewhere between 0.05 and 0.24, and σ_d^2 accordingly between 0.0025 and 0.058. It seems reasonable, therefore, to reject the null hypothesis.

The cases in which we tried to correct for possible errors from estimating instead of measuring densities, the pine looper of Klomp and the garden chafer of Milne, both illustrate that the difference between R^{**} and R^c cannot be expected to play a decisive role in the detection of the ex-

istence of regulation of population numbers. In neither case was the tentative conclusion from R^{**} changed after correction. Therefore, in practice Bulmer's first test without correction often will do. Because R^{**} always will be smaller than R^c, by restricting the search for regulation to testing of the significance of R^{**} will lead to accepting the regulation hypothesis a little bit too often, but the error in the significance level stated will usually be small.

Density dependence in long series of census data

In Table 1 we bring together from the literature a number of series of population data that may tentatively be considered pieces of first-order Markov chain. This means that we could not use data from species with more, generally overlapping generations per year, such as those of 16 generations of *Epiphyas postvittana* (Danthanarayana 1983) and of many other moths, or data from univoltine insects for which a sizeable fraction of individuals reproduce in more than one year, such as in most carabid beetles (Van Dijk 1982). We further restricted ourselves to series of at least 11–12 years. Since we intend also to apply "regulation" tests, strictly speaking, we should have excluded the grey larch bud moth and the spruce budworm, because in the first the sequence of densities is highly affected by a self-induced and cyclical change in food quality and quantity (Bos and Rabbinge 1976), and in the second by trends in the overall weather conditions over years (Greenbank in Morris 1963; Andrewartha and Birch 1984). Den Boer (1987:233) showed that in the pine looper of Klomp (1966) the effect of the supposed regulating factor may be different in different developmental stages of the same population. Therefore, in Table 1 we included four stages of the pine looper, to detect in what stage a possibly density-dependent process might be most effective. For comparison, we added another pine looper series in which densities were much higher. Adults of the winter moth are included in addition to larvae, because the winter moth at Wytham Wood has long been considered a classical example of regulation, in which the density-dependent pupal predation was responsible for a mean generation mortality of 35%. For the other species in Table 1 regulation of numbers has hardly been considered seriously, although most of the authors were in search for density-dependent processes. So far, *Nebria brevicollis* is the only carabid species studied by us that is virtually semelparous (Den Boer 1979), and like the majority of carabid species it is also univoltine (Nelemans 1987). Within the context of the present paper this species is particularly interesting, because, in the population studied, the number of recruits per female tended to be negatively correlated with the number of reproducing females: $\rho = -0.55$ ($p = 0.048$, one-sided); Nelemans et al. (unpublished work).

Unfortunately, we failed to discover more published data on densities in populations of insects that are both semelparous and univoltine, and which, moreover, were uninterruptedly studied for 11–12 years or longer.

The results of the randomization test are given in Table 2. It will be seen that, at the 0.05 level, none of the series shows significant density dependence in the variation of population numbers, and at the 0.1 level only the pine looper of Klomp (1966) scores significantly for adults and marginally so for larvae in August. So far as the winter moth at Wytham Wood is concerned, the results are in

Table 2. Test results of the randomization test of Pollard et al. (1987), when applied to the census data of Table 1. Given are: (1) the product-moment correlation coefficient r_{dx} between the density estimates ($\log_e$-values) and the next coefficient of net reproduction ($\log_e$-values), (2) mean and standard deviation (S.d.) of the 500 correlation coefficients (r_p) of the permutated series, (3) the number of permutated series (out of 500) in which the correlation coefficient was less than or equal to (L.E.) r_{dx}, and (4) the latter number divided by 501 being an estimate of P, the chance to accept the density dependence hypothesis wrongly

Population counts (Table 1)	r_{dx}	$r_p \pm$ S.d.	L.E. r_{dx}	P-value
Winter moth; larvae	−0.434	−0.39±0.15	208	0.415
Winter moth; adults	−0.496	−0.43±0.11	137	0.274
Pine looper; larvae August	−0.635	−0.49±0.11	50	0.100
Pine looper; larvae Sept.	−0.630	−0.49±0.11	63	0.126
Pine looper; pupae April	−0.584	−0.51±0.11	123	0.246
Pine looper; adults	−0.699	−0.49±0.13	30	0.060
Pine looper; UK, pupae	−0.484	−0.51±0.12	279	0.557
Garden chafer; Rydal Farm	−0.307	−0.34±0.10	306	0.611
Garden chafer; Hawes End	−0.501	−0.31±0.19	79	0.158
Grey larch bud moth	−0.412	−0.42±0.11	260	0.519
Spruce budworm; Plot G4	−0.459	−0.47±0.13	261	0.521
Spruce budworm; Plot G5	−0.553	−0.46±0.14	145	0.289
Viburnum whitefly; pop. 1	−0.086	−0.34±0.22	415	0.828
Viburnum whitefly; pop. 2	−0.115	−0.39±0.21	449	0.896
Viburnum whitefly; pop. 3	−0.637	−0.48±0.16	93	0.186
Nebria brevicollis; adults	−0.536	−0.50±0.16	180	0.359

accordance with the conclusions of Den Boer (1986): the density-dependent process is apparently counterbalanced by the key factor to such a degree that no density dependence can be discovered in the variation of population numbers. The results for the pine looper at Hoge Veluwe are somewhat better than could be expected from the analysis by Den Boer (1987). The other time series tested did not give cause to expect significant density dependence in the fluctuations of numbers, so that the results of the randomization test are perhaps not surprising. For instance, there are other reasons (Nelemans et al., unpublished work) to suppose that the negative correlation between recruitment and number of females in *Nebria brevicollis* (above) will not result in significant density dependence.

Note that the strikingly low correlation coefficients (r_{dx}), which might suggest negative density dependence, are importantly biased, because the highest density in such a series is necessarily followed by a net reproduction below unity, whereas the lowest density by definition is always followed by a net reproduction above unity. Although less stringently so, something similar can be stated about other very high and very low densities in the series. Reddingius (1971:8.2) has already shown that this phenomenon can be expected to lower correlation and regression coefficients considerably

Table 3. Test results of Bulmer's first test and of the Permutation test when applied to the population counts of Table 1. Given are: Bulmer's first test, with the uncorrected test statistic $R^{**} = V^*/U^*$ (based on natural logarithms) as compared with $R_{0.05}$; Permutation test, test statistic $r/(k+1)[=P]$ for k (number of permutations) = 500. n.s. = not significant

Population counts (Table 1)	Bulmer's first test	Permutation test
Winter moth; larvae	$R^{**} = 1.160 > R_{0.05}(=0.872)$ n.s.	$P = 0.064$
Winter moth; adults	$R^{**} = 0.952 > R_{0.05}(=0.872)$ n.s.	$P = 0.164$
Pine looper; larvae August	$R^{**} = 0.620 < R_{0.05}(=0.726)^*$	$P = 0.030^*$
Pine looper; larvae Sept.	$R^{**} = 0.626 < R_{0.05}(=0.726)^*$	$P = 0.060$
Pine looper; pupae April	$R^{**} = 0.809 > R_{0.05}(=0.689)$ n.s.	$P = 0.475$
Pine looper; adults	$R^{**} = 0.581 < R_{0.05}(=0.689)^*$	$P = 0.076$
Pine looper; UK, pupae	$R^{**} = 0.979 > R_{0.05}(=0.653)$ n.s.	$P = 0.461$
Garden chafer; Rydal Farm	$R^{**} = 2.018 > R_{0.05}(=1.238)$ n.s.	$P = 0.377$
Garden chafer; Hawes End	$R^{**} = 1.896 > R_{0.05}(=0.836)$ n.s.	$P = 0.551$
Grey larch bud moth	$R^{**} = 1.932 > R_{0.05}(=0.909)$ n.s.	$P = 0.533$
Spruce budworm; Plot G4	$R^{**} = 2.816 > R_{0.05}(=0.726)$ n.s.	$P = 0.842$
Spruce budworm; Plot G5	$R^{**} = 1.781 > R_{0.05}(=0.689)$ n.s.	$P = 0.850$
Viburnum whitefly; pop. 1	$R^{**} = 3.646 > R_{0.05}(=0.616)$ n.s.	$P = 0.812$
Viburnum whitefly; pop. 2	$R^{**} = 4.516 > R_{0.05}(=0.616)$ n.s.	$P = 0.946$
Viburnum whitefly; pop. 3	$R^{**} = 1.046 > R_{0.05}(=0.616)$ n.s.	$P = 0.451$
Nebria brevicollis; adults	$R^{**} = 1.123 > R_{0.05}(=0.579)$ n.s.	$P = 0.437$

*: $P < 0.05$

(e.g. those in Table 2) in still longer time series, without the operation of negative feedback processes (e.g. in series with random increments). As this applies equally well to the permuted series (r_p), the test is not invalidated by this bias.

Evidence favouring the regulation hypothesis

After our experiences with the randomization test we can hardly expect to detect significant regulation in the census data of Table 1. However, Table 3, which contains the results of both Bulmer's first test and the permutation test, deviates somewhat from this expectation in that three of the four stages of the pine looper at Hoge Veluwe (Klomp 1966), in a series of 15 years (1950–1964), score significantly with Bulmer's first test. One of these stages, larvae in August, was also the only case for which the permutation test gives a significant result. This is not in accordance with the conclusions of Den Boer (1987), but it was already foreshadowed by Table 2. Again, the results of the winter moth, though suggestive, do not reach the significance level of 0.05, neither for Bulmer's first test, nor for the permutation test. This is in agreement with Den Boer (1986) in spite of the interesting critisisms of Latto and Hassell (1987) and of Poethke and Kirchberg (1987), which were, however, refuted by Den Boer (1988). The results of the Viburnum whitefly are in accordance with the conclusions of Southwood and Reader (1988). The students of most other species, i.e. the garden chafer (Milne), the grey larch bud moth (Baltensweiler 1968), and the spruce budworm (Morris 1963), did not expect regulation of numbers in the strict sense of "keeping density within limits". This is not surprising, because these three species are potential pest insects which reached peak numbers within the census periods (see Table 1).

Discussion

Throughout most of this century, theories to explain the supposedly rather stable density levels of animal popula-

tions have dominated the attention of population ecologists. After some decades of both population research and connected controversies, Nicholson (1958) could still state: "Probably the most contentious question concerning animal ecology at the present time is whether animal populations are self-regulated or not. ... It is important that every effort should be made to resolve it unequivocally, for confused ideas upon this subject have bedevilled ecological theory for many years". Nicholson himself, was convinced that "density-induced governing reaction" adjusted populations to their environments.

Reddingius (1971), after an extensive study of the literature, tried to formulate the different ideas in mathematical terms, and discussed the mathematical and biological difficulties that are connected with the current deterministic regulation models. Therefore, he preferred to consider and formulate the course of population density through time as a stochastic process. This provided a basis for developing a statistical method for testing the "governed density hypothesis", using census data from populations that may be considered as pieces of first-order Markov chain. However, neither this test, nor the nearly identical first test of Bulmer (1975), seemed to stimulate population ecologists to answer Nicholson's appeal (above); see further Reddingius and Den Boer (1989). Instead they confined themselves to agreeing that the view of Andrewartha and Birch (1954), who almost completely denied an important role of density-dependent processes, must be wrong (see e.g. Bakker 1980; Itô 1980). Although many ecologists admit that the controversies are not yet resolved, they are no longer heavily involved in these controversies, and generally seem to believe that, in some way or another, the "governed density (regulation) hypothesis" will appear to be the right one (see e.g. Williamson 1972; Begon and Mortimer 1981). Because of this attitude of resignation during the last twenty years, population theory has arrived at an impasse. Highly interesting population studies continue to be done, but they are no longer explicitly connected with realistic concepts on the long-term survival of populations.

As knowledge about the processes that may significantly influence the long-term survival of populations is urgently needed, we thought it useful to reopen the discussions about whether or not the long-term survival of animal populations may be favoured by regulating processes. In the present paper, as a continuation of Reddingius and Den Boer (1989), in the 12 population series that met the necessary condition of being pieces of first-order Markov chain, with the exception of the pine looper population at "Hoge Veluwe" (Klomp l.c.), neither governing of population densities by density dependence, nor their significant being kept within limits could be statistically detected. It may be objected that the series presented in Table 1 are still too short to expect significant results, even if regulating processes were at work. Although this is quite possible, no longer series are available for the moment. On the other hand, Figs. 4 and 5 of Reddingius and Den Boer (1989) show that, with census data of about 20 years, the power of both regulation tests seems to be sufficient, whereas the only significant series, the pine looper of Klomp, has been studied during a comparatively low number of years (15). In any case, for the present series we cannot generally reject the null hypothesis. Be this as it may, so far we have no arguments to expect much from regulating processes, or from density-dependent processes in general, for the long-term survival of animal populations.

In a following paper we will try to explain why the pine looper population studied by Klomp (1966) gave significant results, and what may be the consequences of that. Then, we will also apply the tests used in this paper to the data of a number of forest insects published by Schwerdtfeger (1941), and made mangeable by Varley (1949). Although these data are not very reliable, they cover a period of 60 years, so that we may hope to learn something about the behaviour of a long series of census data.

References

Andrewartha HG, Birch LC (1954) The distribution and abundance of animals. Univ of Chicago Press, Chicago London

Andrewartha HG, Birch LC (1984) The ecological web. More on the distribution and abundance of animals. Univ of Chicago Press, Chicago London

Bakker K (1980) A place on the planet; some reflections on population ecology. Neth J Zool 30:151–160

Baltensweiler W (1968) The cyclic population dynamics of the Grey Larch Tortrix, *Zeiraphera griseana* Hübner (= *Semasiana diniana* Guenée) (Lepidoptera: Tortricidae). Symp R Ent Soc Lond 4:88–97

Begon M, Mortimer M (1981) Population ecology. Blackwell, Oxford London

Bulmer MG (1975) The statistical analysis of density dependence. Biometrics 31:901–911

Danthanarayana W (1983) Population ecology of the light brown apple moth, *Epiphyas postvittana* (Walker) (Lepidoptera, Tortricidae). J Anim Ecol 52:1–33

Den Boer PJ (1979) The individual behaviour and population dynamics of some carabid beetles of forests. Miscell Papers LH Wageningen 18:151–166

Den Boer PJ (1986) Density dependence and the stabilization of animal numbers. 1. The winter moth. Oecologia 69:507–512

Den Boer PJ (1987) Density dependence and the stabilization of animal numbers. 2. The pine looper. Neth J Zool 37:220–237

Den Boer PJ (1988) Density dependence and the stabilization of animal numbers. 3. The winter moth reconsidered. Oecologia 75:161–168

Errington PL (1957) Of population cycles and unknowns. Cold Spring Harbor Symp Quant Biol 22:287–300

Itô Y (1980) Comparative ecology. Cambridge Univ Press, Cambridge

Klomp H (1966) The dynamics of a field population of the pine looper *Bupalus piniarius* L. (Lep. Geom) Adv ecol Res 3:207–305

Kluyver HN (1951) The population ecology of the great tit, *Parus m. major* L. Ardea 38:99–135

Latto J, Hassell MP (1987) Do pupal predators regulate the winter moth? Oecologia 74:153–155

Milne A (1984) Fluctuations and natural control of animal populations, as examplified in the garden chafer *Phyllopertha horticula* (L.). Proc R Soc Edinburgh 82B:145–199

Morris RF (ed) (1963) The dynamics of epidemic spruce budworm populations. Mem Entom Soc Can 31

Nelemans MNE (1987) On the life-history of the carabid beetle *Nebria brevicollis* (F.). Neth J Zool 37:26–42

Nicholson AJ (1958) Dynamics of insect populations. A Rev Ent 3:107–136

Poethke HJ, Kirchberg M (1987) On the stabilizing effect of density-dependent mortality factors. Oecologia 74:156–158

Pollard E, Lakhani KH, Rothery P (1987) The detection of density dependence from a series of animal censuses. Ecology 68:2046–2055

Reddingius J (1971) Gambling for existence. A discussion of some theoretical problems in animal population ecology. Acta Biotheor (Leiden) 20:(Suppl): 1–208

Reddingius J, Den Boer PJ (1989) On the stabilization of animal numbers. Problems of testing. 1. Power estimates and estimation errors. Oecologia 78:1–8

Schwerdtfeger F (1941) Ueber die Ursachen des Massenwechsels der Insekten. Z Angew Ent 28:254–303

Southwood TRE, Reader PM (1976) Population census data and key factor analysis for the Viburnum whitefly, *Aleurotrachelus jelinekii* (Frauenf.) on three bushes. J Anim Ecol 45:313–325

Southwood TRE, Reader PM (1988) The impact of predation on the Viburnum whitefly (*Aleurotrachelus jelenikii*). Oecologia 74:566–570

Van den Bos J, Rabbinge R (1976) Simulation of the fluctuations of the grey larch bud moth. Simulation Monogr PUDOC, Wageningen

Van Dijk ThS (1982) Individual variability and its significance for the survival of animal populations. In: Mossakowski D, Roth G (eds) Environmental adaptation and evolution. Gustav Fischer, Stuttgart New York, pp 233–251

Varley GC (1949) Population changes in German forest pests. J Anim Ecol 18:117–122

Varley GC, Gradwell GR, Hassell MP (1973) Insect population ecology, an analytical approach. Blackwell, Oxford London

Williamson M (1972) The analysis of biological populations. Edward Arnold, London