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On the stabilization of animal numbers. Problems of testing *

3. What do we conclude from significant test results?

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Summary. When testing census data of insect populations for regulation, and/or for overall density dependence in the course of numbers over years, certain conditions, which follow from the testing models, should be fulfilled. Even if the series of densities may be considered a piece of first-order Markov chain (a necessary condition) significant test results need not obviously point to regulation of numbers by dominant density-dependent processes. Such a case is presented by the pine looper population at “Hoge Veluwe” studied by Klomp. A drastic drop in density from 1952 to 1953, which takes 78–97% of the log-density range (LR) over all years, most probably wrongly causes significant test results. This is supported by some simulation experiments. Moreover, we cannot be sure that the population was sufficiently isolated, i.e. that dispersal of adults from surrounding populations did not importantly influence population numbers. Among 6 *Panolis*-populations studied by Schwerdtfeger during 17 years a single one scored significantly with all tests. This resulted, however, from such a drastic drop in density that it covered the entire log-density range (LR=9.39), which therefore is wider than in any of the other (non-significant) populations. Another *Panolis*-population that maintained itself during 60 years, and which also scored significantly, most probably was kept within limits by supplementation of very low densities with immigrants, on the one hand, and by restriction of high densities by defoliation caused by other species, on the other. It is discussed whether this can be considered “regulation”, or results from spreading of risk. It is concluded that the range stability of particular populations must be considered generally to be the result of stabilization by both internal and external processes among which both density-dependent and density-independent processes play a significant part, and from which the contribution of the density-dependent processes need not be separated. The most interesting aspect of the stabilization of animal

numbers is its relationship with the expected survival time of the population.

Key words: Density dependence – Regulation – Closed populations – Stabilization

The rapid decline of the diversity of life on our planet alarms increasing numbers of people (see e.g.: Ehrlich & Ehrlich 1982; Kaufman & Mallory 1986), and not only biologists. The extinction of each species occurs with the extinction of the last population of that species. Therefore, knowledge about the processes that may significantly reduce the survival time of populations is urgently needed. We not only need knowledge on destructive processes that are due to the activities of man, such as overexploitation, pollution of air, water and soil, habitat-destruction and isolation of small groups, but also knowledge about more natural processes increasing the chance of extinction of populations.

During the greater part of this century it was generally accepted that natural populations do survive rather long, for a number of centuries and often during geological periods. Because of that until the seventies of this century biologists were not so much occupied by the causes of population extinction, but more by the processes that can be expected to ensure long-term survival of populations. Populations were thought to be regulated around equilibrium densities by density-dependent (governing) processes (e.g.: Smith 1935; Nicholson 1933, 1954, 1955, 1960; Solomon 1949, 1964; and many others). However, a minority of authors called this view in question (e.g.: Uvarov 1931; Thompson 1939, 1956; Andrewartha & Birch 1954; Dempster 1975; Strong 1986). Reddingius (1971), after a critical analysis of this controversy, with theoretical and mathematical arguments concluded that the evidence favouring the regulation hypothesis is not very convincing. Nevertheless, the idea of a general population regulation survived (e.g.

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Bakker 1980; Begon & Mortimer 1981; Hassell 1986) without having been tested correctly (see e.g. Pielou 1974). Therefore, Reddingius & den Boer (1989) and Den Boer & Reddingius (1989) thought it necessary to critically discuss some appropriate tests, and to apply these to all long series of census data from the literature that met the requirements of the test models.

Among 12 insect populations that were studied during more than 10 generations and that satisfied the assumptions of the models, only a single one, the pine looper population at "Hoge Veluwe", The Netherlands (Klomp 1966), could be considered "regulated" in terms of these tests (Den Boer & Reddingius l.c.). This brings us to the question "In what relevant respects does the pine looper population studied by Klomp differ from the other populations tested?". This is the more interesting since Den Boer (1987) with another test concluded that the density-dependent factors discovered by Klomp (l.c.) did not keep density within limits. In this paper I will try to remove this contradiction.

The test conditions require that the series of census data must represent pieces of first-order Markov chain, which means that the animals should be both semelparous and univoltine (Den Boer & Reddingius 1989), which is sufficiently answered by all populations tested. Moreover, all three tests applied tacitly presuppose that the population studied was isolated from other populations of that species, i.e. especially immigration should be small enough to remain within normal estimating errors when measuring local densities. As with all statistical tests the number of data points affect the power of the test. From the power estimates in Reddingius & Den Boer (l.c.) we decided to accept only data sets with at least 11 years. However, it is quite possible that the

regulation of density by density-dependent processes will significantly manifest itself only in much longer series of census data. Therefore, we will also try to test the not very reliable data of Schwerdtfeger (e.g. 1941) on a number of forest insects (among which the pine looper), which were made available by Varley (1949). As there are no conclusive reasons to suppose that the errors necessarily made by Varley, when reconstructing Schwerdtfeger's original data from some unclear graphs, were significantly biased towards either too low or too high values, we expect that the fact that these series cover a period of 60 years will be more important in the present context than the uncertainties about the deviations from the exact density values.

The pine looper population at "Hoge Veluwe"

Den Boer & Reddingius (1989: Table 3) showed that in particular with Bulmer's first test the pine looper at "Hoge Veluwe" (Klomp 1966) scored significantly in a series of 15 years (1950-'64): Table 1A, whereas especially the adults suggest that the variation of numbers might indeed be influenced by density dependence: randomization test of Pollard et al. (1987), $P = 0.06$ (Table 1A). However, only from 1953 onwards could Klomp (l.c.) separate the density-dependent mortality of advanced larvae, $k_4 + k_5$, from the non-density-dependent mortality of nymphs after November, k_6 . Therefore, when testing the hypothesis whether or not the density-dependent processes regulated density, Den Boer (1987) could only make use of the period 1953-'64. Thus it seems appropriate, now also to test this 12-year period with both Bulmer's first test, the permutation

Table 1. The pine looper population at "Hoge Veluwe" (Klomp 1966). n.s. = not significant; # : $P < 0.05$. Perm. test = Permutation test, Rand. test = Randomization test (Pollard et al. 1987). (further explanations in Reddingius and Den Boer 1989)

Developmental stage	Bulmer's first test	Perm. test	Rand. test
A. The period 1950-'64 (15 years); see Den Boer & Reddingius (1989)			
Larvae in August	$U^* = 18.345$, $V^* = 11.373$ $R^{**} = 0.620 < R_{0.05} (= 0.726)$ #	$P = 0.030$ #	$P = 0.100$
Larvae in September	$U^* = 25.204$, $V^* = 15.790$ $R^{**} = 0.626 < R_{0.05} (= 0.726)$ #	$P = 0.060$	$P = 0.126$
Pupae in April	$U^* = 16.768$, $V^* = 13.564$ $R^{**} = 0.809 > R_{0.05} (= 0.689)$ n.s.	$P = 0.475$	$P = 0.246$
Adults in June	$U^* = 22.364$, $V^* = 13.002$ $R^{**} = 0.581 < R_{0.05} (= 0.689)$ #	$P = 0.076$	$P = 0.060$
B. The period 1953-'64 (12 years) that was studied by Den Boer (1987)			
Larvae in August	$U^* = 9.134$, $V^* = 7.493$ $R^{**} = 0.820 > R_{0.05} (= 6.16)$ n.s.	$P = 0.392$	$P = 0.333$
Larvae in September	$U^* = 14.419$, $V^* = 11.617$ $R^{**} = 0.806 > R_{0.05} (= 6.16)$ n.s.	$P = 0.451$	$P = 0.393$
Pupae in April	$U^* = 14.058$, $V^* = 11.932$ $R^{**} = 0.849 > R_{0.05} (= 0.616)$ n.s.	$P = 0.411$	$P = 0.391$
Adults in June	$U^* = 15.251$, $V^* = 11.150$ $R^{**} = 0.731 > R_{0.05} (= 0.616)$ n.s.	$P = 0.138$	$P = 0.054$

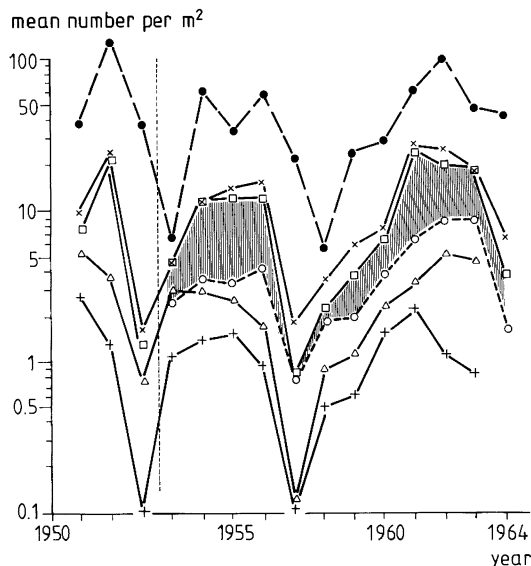


Fig. 1. Fluctuations of numbers in different stages of development of the pine looper at "Hoge Veluwe". Vertically hatched area: density-dependent mortality of advanced larvae in September and October ($k_4 + k_5$). Modified from: Klomp (1966). ● = eggs (July); × = larvae in August; □ = larvae in September; ○ = nymphs (November); △ = pupae in April (next year); + = adults in June (next year)

test and the randomization test. Then it appears that none of the four stages tested by Den Boer & Reddingius (l.c.) gives a significant result: Table 1 B.

Larvae, both in August and in September, and adults show an exceptionally deep drop in density from the second (1952) to the third year (with values of net reproduction of 0.066, 0.058 and 0.077 respectively): Fig. 1 (see also: Den Boer & Reddingius (l.c.): Table 1). As a consequence, when changing over from 12 to 15 years, U^* , the uncorrected estimate of U = the sum of the squared ln-values of net reproduction (Reddingius &

Den Boer 1989: 2), increases up to twice as much (with 50–100%) as V^* , the uncorrected estimate of V = the sum of the squared deviations of $\ln N_t$ from mean $\ln N_t$ (Table 1), by which R^{**} (the approximation of the test statistic of Bulmer as proposed by Reddingius & Den Boer 1989: 6) = V^*/U^* is importantly decreased. Curiously enough, this does not occur in pupae in April (net reproduction is 0.203), where V^* and U^* increase to about the same extent (14 and 19%), and R^{**} hardly changes (Table 1). The deep drop in density, mentioned above, also affects the permutation test, because it covers 97% of the total log-range (LR = the difference between the natural logarithm of the highest and that of the lowest density in the time series) of larvae in August, 82% of LR of larvae in September, and 78% of LR of adults, but only 42% of LR of pupae in April (from Den Boer & Reddingius, 1989: Table 1). This highly restricts the possibilities of permuted series to show smaller log-ranges than the field series, by which the permutation test produced one significant result (larvae in August) and two nearly significant ones (larvae in September, and adults): Table 1 A. These (nearly) significant results disappear completely when considering the shorter period 1953–'64: Table 1 B. The second drop in density (Fig. 1: from 1956 to 1957) apparently is not sufficient to give an effect comparable to that of the drop from 1952 to 1953. Perhaps, 12 years is too short a period to allow significance. Only in the shorter series of the adults is there a suggestion of some overall density-dependent process (Table 1 B: Randomization test).

The above illustrates: (1) In a time series of 15 years a single exceptional drop in density can make all the difference. To reduce the chance of such irrelevant effects at an acceptable level in their study Den Boer & Reddingius (1989) only included series of 11–12 years or longer. Nevertheless, it occurred in one of 12 populations; (2) The change from significant (Table 1 A) into not-significant (Table 1 B) shows that for short series of years

Table 2. More information on the stabilization of the pine looper at "Hoge Veluwe" (Klomp 1966). n.s. = not significant, # : $P < 0.05$; LR = log-range

Developmental stage	Bulmer's first test	Permutation test
A The period 1950–'64^a after fixing $k_4 + k_5$ at its mean value		
Larvae in September	$R^{**} = 0.572 < R_{0.05} (= 0.726)$ #	$P = 0.026$ #
Pupae in April	$R^{**} = 0.800 > R_{0.05} (= 0.689)$ n.s.	$P = 0.230$
B The period 1950–'64^a after fixing $k_4 + k_5 + k_{12}$ at its mean value		
Larvae in September	$R^{**} = 0.569 < R_{0.05} (= 0.726)$ #	$P = 0.044$ #
Pupae in April	$R^{**} = 0.785 > R_{0.05} (= 0.689)$ n.s.	$P = 0.176$
C The period 1950–'64^a. the values of $k_4 + k_5$ are randomly permuted over years, after which the new densities are tested. This is repeated 500 times		
Larvae in August	392 significant (108 not)	94 < field LR ($P = 0.188$)
Larvae in September	425 significant (75 not)	357 < field LR ($P = 0.713$)
Pupae in April	114 significant (386 not)	176 < field LR ($P = 0.351$)
Adults in June	285 significant (215 not)	0 < field LR ($P < 0.002$) #

^a In 1950, 1951 and 1952 Klomp did not discriminate between $k_4 + k_5$, which is density-dependent, and k_6 , which is not. Therefore, for these 3 years we preserved the densities as given by Klomp in order to keep the series as in Table 1 A at 15(14) years

the tests are not very powerful. The fact that the pupae do not participate in this change only accentuates this unreliability (see Den Boer 1987: Table V).

To test the hypothesis whether or not density-dependent processes actually determine the regulation of density, we are thus reduced to simple simulations, such as those used by Den Boer (1987). In two stages, a significant (larvae in September) and a non-significant one (pupae in April), we removed the density dependence of $k_4 + k_5$ by fixing it at its mean value. Next, we recalculated the densities in these series and tested anew. Table 2A shows that not much changed: the significant stage is still significant, even somewhat better ($R^{**} = R_{0.01}$), with also the permutation test giving a significant value now, and the non-significant stage stays non-significant (compare Table 1A). We get a similar result if we also fix the small density-dependent effect (around 3%) on fecundity, k_{12} (Den Boer 1987: Table IV): Table 2B. As $k_4 + k_5$ is only significantly coupled to k_{12} (Den Boer 1987: Table III) the latter simulation will not importantly disturb other relationships between k -factors, which means that the result given in Table 2B will indeed be unaffected by density-dependent processes. In other words, the significant test results for larvae in September apparently may be reached without the intervention of some density-dependent (governing) processes. Clearly, the deep fall of density in 1952–'53 is still responsible for that: net reproduction is 0.058, the natural logarithm of which covers 94% of $LR = 3.02$.

Fixing some k -factors might reduce the range of variation of density, which could more or less compensate for the loss of density dependence (Den Boer 1987). Therefore, it seems advisable to permute their values over years (see Reddingius & Den Boer 1989, Appendix). The 11 values for $k_4 + k_5$ (see Den Boer 1987: Table II) were permuted 500 times, and for each permutation the densities were recalculated and tested. As far as Bulmer's test is concerned not much changes: in the three significant stages the majority of the 500 tests is also significant, least evidently so in the adults (Table 2C). But the permutation test gives a curious result: whereas in three stages too many of these randomized "populations" (with permuted values) fluctuated between narrower limits than did the field population, for the adults the field population is the best one, all permuted populations showing a higher log-range.

So far I cannot completely exclude that the pine looper population at "Hoge Veluwe" was "regulated" in the sense of Reddingius & Den Boer (1989) and Den Boer & Reddingius (1989), but only if the whole period 1950–'64 is taken into account. A small value of Bulmer's first test statistic means that deviations from mean density are smaller than can be expected in a random walk of densities. Although one might attribute this to density-dependent processes this is not a necessary conclusion. Small deviations from a non-regulated, and non-trendy course of densities can also result by chance. Especially if such equable conditions persist over many years, this might result in unlikely small log-ranges, which may promote significant values for the permutation test, as well as for Bulmer's first test. This

occurs in particular when the population is not sufficiently isolated, i.e. when there is significant dispersal of individuals from surrounding (sub)populations. Often such a situation importantly increases the chance of survival of the local population, and in some way it may even contribute to the persistence of these equable conditions. See Reddingius & Den Boer (1970: Table 9), Den Boer (1986a: Fig. 7), and Van der Eijk (1987: Ch. VIII).

All tests for density dependence or regulation are based on the tacit assumption that the population is an entity, i.e. is isolated from other populations of the same species, because "regulation" was originally imagined to be an internal process (self-regulation, e.g. Nicholson 1954, 1958, 1960) that worked as a feedback loop (e.g. Wilbert 1971), i.e. a property of the population; but see Bakker (1971). Whereas emigration may be – but not necessarily so – a density-dependent reaction to high densities, and thus be included in a feedback loop, immigration, especially in insect populations below carrying capacity, mostly will be independent of the density of the receiving population, individuals usually immigrating separately. This means that, if a population is not sufficiently isolated, these tests are not applicable, or at least one should realize that a significant test result might be caused by too much immigration. To return to the pine looper population at "Hoge Veluwe": Klomp (1966) sampled 6–8 ha of pine forest in the centre of a larger pine forest (20 ha), which was situated again in an area with many such forests. Therefore, in spite of the apparently not very high mobility of the adults (Botterweg 1978), we cannot be sure that the test results were not significantly influenced by dispersal of adults between the investigation area and surrounding pine forest.

Thus, we are still left with the question: is the pine looper population of Klomp (1966) "regulated", or not? On the one hand, density-dependent processes are clearly involved, as is distinctly shown by the hatched area in Fig. 1. Also, the pine looper of Klomp is the only population so far known to me where an effective density-dependent mortality ($k_4 + k_5$) is supported by a density-dependent fecundity (k_{12}), so that a feedback loop might indeed be approached. k_{12} has an only small effect, however, so that Klomp (1958, 1966) himself thought it to be ineffective. Fig. 1 shows that Klomp was right: neither the fall of density from 1952 to 1953, nor that from 1956 to 1957 was sufficiently compensated by a higher egg production in 1954 or 1958 respectively; see also Den Boer (1987: Fig. 2). On the other hand, an effective influence of the density-dependent factors is favoured by the absence of significant correlations of these possibly "regulating" factors with other factors (Den Boer 1987: Table III). However, the density-dependent effects are relatively small, e.g. as compared with those in the winter moth (Den Boer 1986b), so that taking these away hardly changes the outcome of the tests (Table 2). Moreover, the fact that so many series (out of 500) with permuted $k_4 + k_5$ -values give significant results with Bulmer's first test (Table 2C), in spite that in most series density dependence have been effectively randomized away is difficult to explain. Because of this, I am more

inclined to believe that between 1950 and 1964 the densities of this population were kept within reasonable limits by a variety of factors, among which dispersal of adults from surrounding pine forest may have played a significant part.

Populations of moths in East-European pine forests

The most sizeable census work on univoltine insects was done by the German State Forests Company between 1880 and 1940 in large areas of pine forest in Eastern Germany (at present mainly Poland). Each year in December in many forest districts the numbers of pupae of 3 species of moth, and the larvae of a fourth one, were counted in quadrates of surface soil. During the second world war, however, the majority of this data was lost. Varley (1949: Fig. 1) tried to replot at a logarithmic scale the data from the graphs on a linear scale in publications of Schwerdtfeger. He assumed that his inaccuracies of reading, especially of low densities, were not greater than the statistical errors made when estimating low densities from quadrates in the field. I read the densities from an enlarged version of his plot. These data, for two of the species pictured in Fig. 2, are used for the calculations in Tables 3 A and B. The calculations in Table 3 C could directly be based on densities in "Tabelle" 1 of Schwerdtfeger (1941). Three of the four graphs in Varley's Fig. 1 (1949) are each interrupted once by arrows pointing downward. Neither from Varley (1949), nor from Schwerdtfeger (1941) did it become clear whether this indicates that density was estimated to be zero, or that it was too low to be plotted in Varley's graphs. Therefore, in Table 3 A we tested the two periods separately, whereas in Table 3 B we connected these time series by an extremely low density (one pupa per ha). Only *Panolis*, the pine beauty, gave uninterrupted counts over 60 years (Fig. 2).

As all four species are pest insects, that at times reached damage levels during the census periods, it was not expected that any of the time series in Table 3 A would score significantly. Nevertheless, *Bupalus*, the pine looper, especially in the first period of 30 years (1881–1910), gave almost significant results with both tests, in spite of the fact that it was the most serious pest of the pines (Schwerdtfeger 1941), with a number of heavy outbreaks (gradations) in each of the census periods (Fig. 2). It must be noted that these gradations go with very extreme coefficients of net reproduction (in the first period e.g.: 11.7, 16.7, 15.6, 11.3, and also 0.02, 0.021, 0.022). Such extreme values all increase U^* considerably, but although an extremely high value (corresponding with pest densities within a range of 3–30 pupae/m²) also importantly contributes to V^* , an extremely low value (corresponding to densities within a range of 0.003–0.03 pupae/m²), which usually follows a pest density, only moderately increases V^* . Therefore, one or a few extremely low coefficients of net reproduction in such a series of census data may give effects such as those in Table 1 A as compared with Table 1 B for *Bupalus* at "Hoge Veluwe" (compare previous section).

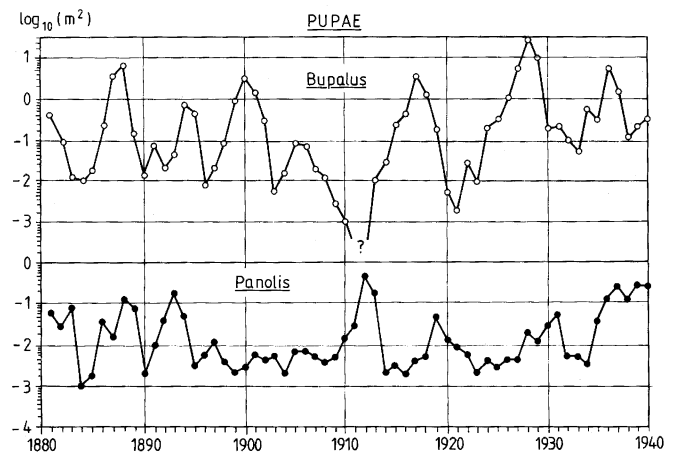


Fig. 2. Fluctuations of the number of pupae per m² of soil in two forest pests at Letzlingen. Reconstructed from a graph by Varley (1949), who replotted data of Schwerdtfeger (1941) at a logarithmic scale

The shorter series of *Panolis* (17 years) did not score significantly (Table 3 C), with the only exception of Neubrücke. This is a special case, however, because the first two densities are the highest and the lowest one respectively of the whole series (359 and 0.03 pupae per 100 m²), which results in a coefficient of net reproduction of 0.000084! As the highest density also was one of the highest observed in *Panolis* in the area, and the lowest density one of the lowest noted (compare Fig. 2) all other densities were within this range (LR = 9.39). This range (\log_e) was the widest among these six (Table 3 C). Therefore, the significant score of Neubrücke clearly is an undesirable effect of the structure of the testing model: Whereas V^* (= 79.4) is within the range of the other series (between 47 and 85) U^* (= 112.8) is far outside the range of the other 6 U^* -values of Table 3 C (20.9–74.7), and this causes $R^{**} = V^*/U^*$ to be importantly decreased. At the same time, series with permuted values of net reproduction (among which the value 0.000084!) never can reach smaller log-range values than the (high) field value of 9.39 (above), by which the permutation test necessarily scores highly significantly. This high density in the first year, followed by the extremely low value of net reproduction also contributed to the significance of the randomization test, because disconnecting this extreme coefficient of net reproduction from the preceding very high density takes away the principal feature of density dependence of the series. Moreover, the *Panolis*-series of Neubrücke cannot be considered "regulated", because it fluctuates between wider limits than any of the other (not significant) series of Table 3 C, which does not promote its chance of survival.

This case of *Panolis* at Neubrücke nicely illustrates, as did the less evident case of the pine looper at Hoge Veluwe (previous section), that significant results from our three tests do not necessarily point to a "regulated" series, because "keeping within limits" of density need not be connected with "regulation" (see Reddingius &

Table 3. Results of the three tests (compare Table 1) applied to population counts of Schwerdtfeger (1941) of 4 species of moth in pine forests at Letzlingen, Germany during 60 years (1881–1940), and of one of the species at 6 sites during the same 17 years (1924–'40). Numbers of pupae (or overwintering larvae of *Dendrolimus*) in December per m² of soil. A Two series separated by one or two immeasurably low densities (compare Fig. 2: *Bupalus*. B One series of 60 years; the series of A are (arbitrarily) connected by the extremely low density of one pupa (or larva) per ha. C *Panolis* in 6 forest districts (1924–'40); from Schwerdtfeger (1941: Tabelle 1): Pütt was not treated separately because of zero densities in 2 years, but it could be included in the average; n.s. = not significant; #: $P < 0.05$

Population counts of	Bulmer's first test	Perm. test	Rand. test
A <i>Dendrolimus</i> ; 42 years	$R^{**} = 3.188 > R_{0.05} (= 1.714)$ n.s.	$P = 0.349$	$P = 0.313$
<i>Dendrolimus</i> ; 17 years	$R^{**} = 1.263 > R_{0.05} (= 0.799)$ n.s.	$P = 0.437$	$P = 0.413$
<i>Hyloicus</i> ; 31 years	$R^{**} = 2.600 > R_{0.05} (= 1.311)$ n.s.	$P = 0.186$	$P = 0.453$
<i>Hyloicus</i> ; 18 years	$R^{**} = 2.338 > R_{0.05} (= 0.836)$ n.s.	$P = 0.767$	$P = 0.874$
<i>Bupalus</i> ; 30 years	$R^{**} = 1.340 > R_{0.05} (= 1.275)$ n.s.	$P = 0.074$	$P = 0.254$
<i>Bupalus</i> ; 28 years	$R^{**} = 1.485 > R_{0.05} (= 1.202)$ n.s.	$P = 0.285$	$P = 0.162$
B <i>Panolis</i> ; 60 years	$R^{**} = 1.091 < R_{0.05} (= 2.373)$ #	$P < 0.002$ #	$P = 0.002$ #
<i>Bupalus</i> ; 60 years	$R^{**} = 1.803 < R_{0.05} (= 2.373)$ #	$P = 0.132$	$P = 0.064$
<i>Dendrolimus</i> ; 60 years	$R^{**} = 2.266 < R_{0.05} (= 2.373)$ #	$P = 0.200$	$P = 0.062$
<i>Hyloicus</i> ; 50 years	$R^{**} = 1.598 < R_{0.05} (= 2.007)$ #	$P = 0.321$	$P = 0.060$
C Neuendorf; 17 years	$R^{**} = 1.142 > R_{0.05} (= 0.799)$ n.s.	$P = 0.258$	$P = 0.198$
Tütz; 17 years	$R^{**} = 1.572 > R_{0.05} (= 0.799)$ n.s.	$P = 0.733$	$P = 0.609$
Rohrwiese; 17 years	$R^{**} = 1.586 > R_{0.05} (= 0.799)$ n.s.	$P = 0.655$	$P = 0.399$
Neubrück; 17 years	$R^{**} = 0.704 < R_{0.05} (= 0.799)$ #	$P < 0.002$ #	$P = 0.01$ #
Hohenbrück; 17 years	$R^{**} = 1.036 > R_{0.05} (= 0.799)$ n.s.	$P = 0.691$	$P = 0.345$
Letzlingen; 17 years	$R^{**} = 2.252 > R_{0.05} (= 0.799)$ n.s.	$P = 0.116$	$P = 0.641$
mean of 7 sites;	$R^{**} = 0.964 > R_{0.05} (= 0.799)$ n.s.	$P = 0.291$	$P = 0.148$

Den Boer 1989:1). These tests just give useful hints which must be evaluated, as I did above.

In this connection it is of special interest that the 60-year series of *Panolis* (Table 3B; Fig. 2) scores highly significantly with all three tests. We cannot exclude the possibility that the drop in density from 1913 to 1914 by a factor of 100, 73% of LR (Fig. 2), played an important part (see above). But I am inclined to consider the absence of a distinct trend in densities over these 60 years important. This is because in 500 simulations of random density walks, obtained from the not significantly deviating ($P \approx 0.70$) lognormal curve fitted to the 59 coefficients of net reproduction (for methods see: Den Boer 1985), the impossibly wide limits of 0.00039 pupae/100 m², and of 610518 pupae/100 m², were rapidly reached (the latter in 495 of 500 simulations), usually within 40 years. Apparently, in the field population there are powerful trend-compensating forces. These might be negative feedback processes, of course, but, as was discussed in the previous section, this is not a necessary conclusion (see below).

Panolis generally occurred in lower numbers than the other 3 species, especially than *Bupalus* (Fig. 2). This implies that *Panolis* is frequently more or less "manipulated" by outbreaks of other species, which are often, in particular those of *Bupalus*, accompanied by defoliation. But *Panolis* adults are known to readily leave defoliating areas (Varley 1949), so that the species will continue its existence elsewhere in this huge area of pine forests. Schwerdtfeger (1941) himself strongly emphasized that in each of the species density fluctuations in different areas are not completely synchronized. For the areas of Table 3C I could confirm this. Although there was a tendency for peaks and troughs to coincide, in

none of the years did this apply to all areas: W (coefficient of concordance, Kendall 1962) = 0.67, which means that overall there is about 33% discordance in density changes. This produces the following picture: In years of outbreak *Panolis* adults will leave defoliating areas and spread over neighbouring, less damaged areas. Therefore, very low local densities are frequently replenished by dispersing adults, which are the more effective the lower density. As entire forest districts were the units of study the chance that *Panolis* disappeared from some series of census data was low, so that a non-zero lower limit of density has to be expected. On the other hand, the chance of reaching high densities was restricted by the frequent occurrence of outbreaks, usually of other species. Only in 1912 at Letzlingen *Panolis* may have had a "gradation" of itself when *Bupalus*, and also *Hyloicus*, seemed to have temporarily disappeared: Fig. 2 (see also Schwerdtfeger 1941: Abb. 1).

Apparently, these external influences (degradation of resources by other species and immigration) generally affected the fluctuation pattern of this *Panolis*-population in such a way that a sequence of net reproduction values emerged, which reduced the deviations from mean density (Bulmer's first test), as well as Log-Range (permutation test), and also affected the correlation of net reproduction with the preceding density (randomization test). Thus, within these 60 years this population stayed "within limits". One might call such an arrangement regulation, but then it should be kept in mind that such a "regulation" did not result from an internal feedback loop (a property of the population itself; see Bakker 1971), but is imposed on the population from outside. Such a situation was called "stabilization" by Den Boer (1968), and was shown to improve survival very well,

both in models (Reddingius & Den Boer 1970), and in field populations (Den Boer 1981, 1986a). It is obviously necessary to distinguish between range stability resulting from governing processes (self-regulation), and range stability that results from spreading of risk (stabilization); see Reddingius & Den Boer (1989).

I thus concluded that the *Panolis*-population of Fig. 2 approached a kind of stationary state in terms of conditional probabilities or expectations, which had nothing to do with the existence of some internal "negative feedback mechanism" tending to "force population density back to equilibrium" when it has departed from it (Reddingius 1971: 77). There simply was a lower non-zero limit to the density because of frequent immigration, as well as an upper limit set by defoliation, usually by other species. This does neither exclude the possibility that the population may become extinct, nor does it mean that density-dependent processes are involved.

For the other three species in Table 3B we connected the two parts of the census data (see Fig. 2: *Bupalus*), as given in Table 3A, to reach significance with Bulmer's first test. In part, this significance results from the very low densities ($0.0001/m^2$) we used to connect these series (see above). If we simply had added the time series (e.g. in *Bupalus* the density of 0.001 in 1910 would have been directly followed by 0.01 in 1913: Fig. 2), only *Bupalus* would have stayed significant, *Dendrolimus* would just have reached $R_{0,05}$, and *Hyloicus* would have lost significance. As *Bupalus* adults also show dispersal (Botterweg 1978: until 50 m/day, but adults can even be caught at 35 km from the nearest pine forest) an alternative explanation of the significant result can also be reached along the lines given for *Panolis*, though less compelling so: high densities are eventually restricted by defoliation of the pines, and low densities will to a certain extent be replenished by dispersal. However, connecting the two time series, would give room to ascribe a significant function to "regulating" process(es). In *Bupalus* random walks of density (see above) surpass all limits ($145 \cdot 10^6$) after 18 years (in 499 of 500 simulations).

I have to emphasize that the above results can hardly have been caused by inaccuracies of the density estimates, made by unexperienced people, possibly, confounded by the readings of Varley (above). When I introduced "errors" in the data, by multiplying each density estimate by a randomly chosen value between 0.38 and 2.62, and then applied the same tests to these changed values, all significant results given in Table 3 stay significant, and all non-significant results stay insignificant. Apparently, the overall course of density through time is more important for the results in Table 3 than the exact density values.

Discussion

Like in any statistical test, the tests proposed by Reddingius & Den Boer (1989), Den Boer & Reddingius (1989), and Pollard et al. (1987), are limited by the assumptions basic to the testing models. The most restrictive assumption of the present models is that the census

data at least closely approach a piece of first-order Markov chain, which limits application to data of animals that are both semelparous and univoltine (Den Boer & Reddingius 1989). But it must also be assumed that the series of densities strictly concerns one and the same population, which implies that especially dispersal to that population has to be quantitatively unimportant. We mentioned already that it is doubtful whether the pine looper population studied by Klomp (1966) sufficiently answered this condition, and we advanced convincing arguments why this will surely not apply to the *Panolis*-population at Letzlingen (Table 3B).

A quite unexpected restriction appeared to be, that a single, extremely low coefficient of net reproduction can frustrate adequate testing. Looking back, this is not surprising, because such an almost catastrophic reduction of a very high density in fact represents a powerful expression of density dependence. Ecologists, however, do not think of regulation as a single density-dependent catastrophe each 10–50 years, or so (compare Reddingius & Den Boer 1970: 3.5), but rather as a more or less continuous negative feedback process, i.e. as a "mechanism". The present tests, however, cannot distinguish between these two possibilities, though in the computer programs there can easily be taken up a warning for almost catastrophic reductions of density. One might argue that such a catastrophe-type of density-dependent mortality is mainly a feature of some pest insects, such as *Bupalus*, and more exceptionally *Panolis* (e.g. Neubrücke), which are not the most obvious objects to show regulation of numbers, so that a more general use of these tests need not be seriously limited. However, such a catastrophe can be the result of highly unfavourable weather conditions, and not only in pest insects. For instance, in the forest trichopteron *Enoicyla pusilla*, in 1959 excessive drought caused a dramatic fall of the density of an isolated population, which resulted in a coefficient of net reproduction of 0.0006 (many other populations of this species became extinct), and gave $P < 0.002$ for the permutation test (8 years); see Den Boer (1986c: Fig. 1). But excluding populations with such an extremely low value of net reproduction from testing would mean that, so far, no example of a clearly regulated insect population is known, which does not mean, of course, that such a population will not be found in the future.

Let us return to the generally accepted definition of "regulation", e.g. that given by Varley et al. (1973), p. 19: "a regulated population (is) ... one which tends to return to an equilibrium density following any departure from this level", and p. 112: "Density-dependent mortality serves to regulate the population and keeps it within limits". It is clear that the catastrophe-type of "regulation" does not fit this definition, because this kind of (density-dependent) mortality does not "keep density within limits". On the contrary, it often leads to exceptionally wide Log-Ranges, e.g. in *Enoicyla pusilla* $LR = 7.36$, or in *Panolis* in Neubrücke, which shows the highest LR (9.39) among the 6 populations tested (Table 3C). Moreover, within the 4 "gradations" in the six *Panolis*-populations of Table 3C density continued

to increase from mean density ($\approx \mathcal{E}(\ln N)$ as an estimate of “equilibrium density”), which is somewhere between 2 and 5 pupae/100 m², during 4–6 years before a density of more than 300 pupae/100 m² (the start density in Neubrück) was reached, which is not a tendency “to return to an equilibrium density following any departure from this level”.

When trying to sensibly distinguish regulation from other kinds of stabilization, as in this paper, it seems advisable to follow Den Boer (1968: III), and to call a population a “stabilized” one, when the density stays within narrower limits than could have been expected from a random walk of densities. The permutation test can be used, or adapted, to give the desired information; see further Den Boer (1985, 1986b, 1987, 1988). To give an example, the multipartite population (Andrewartha & Birch 1984: 9.2) of the carabid *Pterostichus versicolor*, composed of 10 subpopulations (Den Boer 1986a: Fig. 7, upper graph), is considered stabilized, because during 23 years density fluctuated at the same level (now, 7 more years later – in 1988 – it still fluctuates at that level), by which the permutation test gave an interesting value ($P=0.078$); compare the values in Table 3A. This stabilization results from continuous movement of beetles between these differently fluctuating subpopulations (Kendall 1962: $W=0.54$), which highly levels local differences in density. Most probably, this situation is not very different from that in the *Panolis*-population at Letzlingen (Fig. 2). Such a high range stability may hide some element of density dependence, e.g. because immigration can be expected to be quantitatively the more important the lower density. But, the amount of immigration itself most probably is independent of the density of the receiving population, and can only be considered density-dependent when erroneously correlated with the density of the receiving population. This has nothing to do, however, with “feedback mechanisms” or with “regulation”. In these, and comparable cases it is hardly interesting whether or not in some, or in all subpopulations more explicitly density-dependent processes occur (see: Baars & Van Dijk 1984, but also: Den Boer 1986d), because these special, local effects, just as all other effects, are levelled by dispersal between subpopulations (Den Boer 1968: III.3). In general, as soon as populations are evidently not isolated concepts such as “density dependence” and “regulation” lose their *raison d'être* and should no longer be used.

In more isolated populations, on the other hand, especially in spatially homogeneous ones, density-dependent processes may significantly contribute to the range stability of the population. For instance, although pupal predation appears not to regulate the density of the winter moth at Wytham Wood (Den Boer 1986b), it may still have some stabilizing influence, because it may retard a rapid growth to high densities (Den Boer 1988: Discussion). Also in the pine looper population at “Hoge Veluwe” the density dependence of $k_4 + k_5$ may have some stabilizing effect (Fig. 1), in spite of the data in Tables 1 and 2, which show that strict regulation seems not very probable. In both cases, however, the price for these restrictions of high densities is an in-

creased chance to reach dangerously low densities in following years, by which “keeping within limits” becomes wishful thinking; see Den Boer (1968: III.4), and Den Boer (1986b, 1987). It will only exceptionally be possible to satisfactorily separate such density-dependent effects from other influences on density (see also Strong 1986), because the density of a population is not the result of a single cause that dominates all others, but the result of many causes at the same time, the relative effects of which will differ in space and will change in time (Hilborn & Stearns 1982). But as we saw above, such a separation between density-dependent and density-independent effects is hardly necessary to understand survival. Therefore, even in isolated populations stabilization of numbers by spreading of the risk of extinction over different kinds of local groups and/or over different kinds of individuals (genotypes, age-classes) will usually be more effective than a theoretically possible – but so far not demonstrable objectively – “regulating mechanism” (Den Boer 1968; Reddingius & Den Boer 1970; Reddingius 1971).

To conclude: because knowledge about the expected survival times of populations under more or less natural conditions is badly needed, we should pay attention to all conditions that contribute to stabilization of animal numbers, and not just to the density-dependent ones. By directly estimating range stability in long series of census data we can approach the expected survival times of populations (*ceteris paribus*); for methods see Den Boer (1985) and Den Boer (1990).

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