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Author(s): P. J. den Boer

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Original papers

Density dependence and the stabilization of animal numbers*

3. The winter moth reconsidered

P.J. den Boer

Biological Station of the Agricultural University, Nature Conservation Department, Kampsweg 27, 9418 PD Wijster, The Netherlands

Summary. Latto and Hassell (1987) disagree with the conclusion of Den Boer (1986), that the winter moth population at Wytham Wood, studied by Varley and Gradwell, was not regulated. They attempt to demonstrate regulation by means of a simulation model. In the present paper the validity of this model is tested step by step. The fixing of the initial and final densities, as practised by Den Boer and rejected by Latto and Hassell, did not prevent population explosions and extinctions, as was assumed by Latto and Hassell. It is shown that the deterministic formulation of the density dependence of pupal predation, as used by Latto and Hassell, deviates systematically from the field data. Replacing the values of the key-factor (k_1) by random values drawn from a normal distribution (Latto and Hassell) affects the dynamics such that the ability of pupal predation to govern density is improved in the model. Changing mortalities other than the key-factor does not significantly influence the pattern of fluctuations nor the limits of density. Models should leave intact the essentials of the reality under study, while removing distracting elements (Levins 1968). As both the timing of the key-factor, and its correlation with pupal predation are essential features of the winter moth population at Wytham Wood between 1950 and 1968, the model of Latto and Hassell does not apply to this population. By simply changing \log_{10} (eggs/female) it is shown that the power of the density dependence of pupal predation to govern possible trends in density of the winter moth population at Wytham Wood is weak. On the other hand, the model of Latto and Hassell gives insight into the conditions that might favour regulation of numbers. Although the model of Poethke and Kirchberg (1987) preserves more features of the pertinent winter moth population than that of Latto and Hassell (1987) it still deviates in one essential aspect: the succession in time of both the (coupled) mortalities and the deviations from the deterministic density dependence are taken at random. Therefore, also this model is still too far from the field population to be a sound base for the statistical speculation proposed by Poethke and Kirchberg.

Key words: Winter moth – Density dependence – Regulation – Limits of density – Key-factor

The life table study of the winter moth (*Operophtera brumata* L.) between 1950 and 1968 at Wytham Wood near

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Oxford (see e.g.: Varley et al. 1973) has long been considered a classical investigation of a natural insect population regulated by density-dependent mortality. The regulating agent was inferred to be pupal mortality caused by polyphagous predators, k_5 in the key-factor analysis, which on average was responsible for 35% of total mortality per generation. Recently, Den Boer (1986) contradicted this interpretation by showing that the density dependence of pupal predation, though distinctly discernable from the data, did not keep density within narrower limits than would have occurred without density dependence. Latto and Hassell (1987) disagree with Den Boer and try to re-emphasize pupal predation as the crucial regulator of the winter moth population studied by Varley and Gradwell (1968). Here I respond to Latto and Hassell.

First, we must make clear what we understand by the term “regulation”. Varley et al. (1973, p. 19) described “a regulated population” as: “one which tends to return to an equilibrium density following any departure from this level”, and further stated (p. 112): “Density-dependent mortality serves to regulate the population and keeps it within limits”. Taken together this says: “Density-dependent mortality serves to return density to an equilibrium value following any departure from this level and keeps density within limits”. Reddingius (1971) and Bulmer (1975) translated this in mathematically tractable terms as: in a regulated population the growth rate (coefficient of net reproduction) should significantly and negatively be correlated with density. These authors developed similar tests for this, and I will use Bulmer’s first test here (see further: Den Boer and Reddingius unpublished work). Although the autoregressive model, on which this test rests, is not biologically entirely realistic the test is sufficiently robust to be useful (Reddingius 1971). As densities have usually to be estimated from samples, it should be realized, that this source of error will lead to rejecting the null hypothesis too often (Reddingius 1971: 201). But for the present discussion we will thus stay on the conservative side.

The main objection of Latto and Hassell (1987) to Den Boer (1986) is that, by keeping both initial and final density as observed, simulations of the winter moth population are unnecessarily restrained with reduced possibilities for population explosions and extinctions, and little can be learned about the role of the density-dependent pupal predation (k_5) in regulating the population. To show the regulating power of k_5 it would be necessary to let the simulated populations fluctuate freely, i.e. without the constraint of always reaching the same final density as it was observed in the field population in 1968.

Table 1. Field data of the winter moth at Wytham Wood near Oxford between 1950 and 1968 (all data are given as \log_{10} -values)

year	\log_{10} larvae ^a	k_2	k_3	k_4	k_{2-4}	PDB ^b	k_5	k_6	k_1	K	$K - k_5$
1	2.05	0.11	0.04	0.05	0.20	1.85	0.69	0.29	0.56	1.74	1.05
2	2.06	0.01	0.02	0.03	0.06	2.00	0.77	0.10	1.14	2.07	1.30
3	1.74	0.003	0.06	0.05	0.113	1.627	0.75	0.03	1.33	2.223	1.473
4	1.267	0.01	0.02	0.04	0.07	1.197	0.34	0.16	0.24	0.81	0.47
5	2.207	0.004	0.03	0.06	0.094	2.113	0.73	0.07	1.16	2.054	1.324
6	1.903	0.003	0.03	0.04	0.073	1.83	0.65	0.09	0.83	1.643	0.993
7	2.01	0.03	0.01	0.02	0.06	1.95	0.47	0.28	0.48	1.29	0.82
8	2.47	0.02	0.01	0.05	0.08	2.39	0.79	0.20	0.83	1.90	1.11
9	2.32	0.07	0.02	0.04	0.13	2.19	0.82	0.16	1.15	2.26	1.44
10	1.81	0.10	0.04	0.02	0.16	1.65	0.66	0.15	1.21	2.18	1.52
11	1.38	0.02	0.06	0.03	0.11	1.27	0.72	0.45	0.91	2.19	1.47
12	0.94	0.0	0.06	0.04	0.10	0.84	0.22	0.08	1.09	1.49	1.27
13	1.20	0.02	0.06	0.03	0.11	1.09	0.24	0.06	0.85	1.26	1.02
14	1.69	0.0	0.04	0.01	0.05	1.64	0.40	0.12	0.66	1.23	0.83
15	2.21	0.005	0.01	0.01	0.025	2.185	0.74	0.14	0.52	1.425	0.685
16	2.535	0.03	0.01	0.01	0.05	2.485	0.87	0.13	1.42	2.47	1.60
17	1.815	0.04	0.005	0.02	0.065	1.75	0.86	0.33	1.20	2.455	1.595
18	1.11	0.01	0.03	0.0	0.04	1.07	0.50	0.0	1.19	1.73	1.23
19	1.13										
Log-Range (LR) = 2.535 - 0.94 = 1.595											
mean	1.78	0.027	0.031	0.031	0.088	1.73	0.623	0.158	0.932	1.88	1.18
s.d.	0.487	0.033	0.019	0.017	0.044	0.477	0.209	0.115	0.332	0.475	0.328

^a All values are calculated from the start value in 1950 (=2.05). Following densities are obtained by adding 1.75 (= \log_{10} (eggs/female) which is considered constant) and subtracting the K-value given at the same line. For instance: \log_{10} (larvae) in year 2 = 2.05 + 1.75 - 1.74 = 2.06, and in year 3 = 2.06 + 1.75 - 2.07 = 1.74, etc.; k-values from Varley et al. (1973: Table F), see also Den Boer (1986 Table 1a). As these k-values were rounded off, in the present table most values of \log_{10} (larvae) deviate somewhat from the field values (see Table 2)

^b PDB = Pupal Density Before (predation) = \log_{10} (larval density) - $k_2 - k_3 - k_4$. These values are used to calculate density-dependent effects of k_5 (see further Table 2)

I believe that this argument is incorrect: by merely permutating the coefficients of net reproduction (R) from the field population (Den Boer 1986: Table 1b) the "Logarithmic Range" [$LR = \log_{10}$ (highest density) minus \log_{10} (lowest density)] can vary between 1.05 and 4.12, i.e. the highest density need not be greater than about 10 times the smallest one, but at the other extreme it can be more than 10000 times the smallest density. In the latter case the lowest density in particular simulations is 0.008 ($\log_{10} = -2.07$), i.e. a single larva at 125 m² of canopy, which would have brought the population to extinction; in other simulations, the highest density is 131 734 ($\log_{10} = 5.12$) larvae per m² which can safely be called an "explosion". Hence, in these simulations a long string of 108 subtractions (mortalities) and 18 additions (egg production) between 2.05 (start) and 1.00 (end) can follow sufficiently different paths to demonstrate the possibly regulating role of the density-dependent pupal predation.

In order to keep his simulation experiments as close as possible to the field data Den Boer (1986) changed only a single variable, the density dependence of pupal predation, and carefully kept all other variables at the field values. In other words, he was especially interested in the actual effect of that kind of density dependence in the real winter moth population at Wytham Wood between 1950 and 1968, and less in the manifold ways in which density-dependent regulation can be modelled in more or less theoretical populations. Because, on the one hand, it is not difficult to model regulated populations, but on the other,

field populations generally do not resemble such modelled populations in many respects (see e.g. Murdoch 1979; Strong 1986), it was considered necessary to mimic the field population as carefully as possible before executing simulation experiments. Then, changing only one variable at a time maximizes comparability.

In the model of Latto and Hassell (1987), on the one hand, many features of the winter moth population at Wytham Wood are taken up, but on the other many variables have been changed simultaneously, by which they interfere with convincingly supporting their conclusion that "Pupal predation is crucial to the population regulation of the winter moth at Wytham Wood". Therefore, in the following we will investigate, step by step, the effects of the different deviations from the field population they jointly introduced into their model.

The density-dependent process

Latto and Hassell (1987) expressed the density-dependent pupal predation as $k_5 = 0.374 \cdot \text{PDB}$ (Pupal Density Before (predation)); cf Table 1) being a function of the least squares line of PDB on k_5 estimated from the field data (Table 1). Although in some years the value from this deterministic function closely approaches the field value of k_5 , in other years it deviates appreciably from the latter: Table 2 (DIFF). Surprisingly, negative and positive deviations show a distinct pattern; they appear in runs such that positive deviations (mortality from k_5 higher than expected) occur

Table 2. Calculation of a density-dependent process for k_5 that both closely mimics the field values and can be used to simulate situations that deviate from the conditions for the winter moth at Wytham Wood 1950–1968

year	k_5		coefficient to correct expected value of k_5		corrected value of k_5 (=0.374*PDB + 0.374*PDB/CORR)	corrected values of \log_{10} (larvae) between brackets (field values)
	field values from Table 1	expected from 0.374*PDB	DIFF ^a (=field k_5 - expected)	CORR ^b (=correction)		
1	0.69	0.692	-0.002	-200.0	0.688	2.062 (2.07)
2	0.77	0.748	0.022	30.0	0.774	1.738 (1.74)
3	0.75	0.608	0.142	4.3	0.749	1.266 (1.26)
4	0.34	0.448	-0.108	-4.2	0.341	2.205 (2.20)
5	0.73	0.790	-0.060	-15.0	0.737	1.894 (1.89)
6	0.65	0.684	-0.034	-25.0	0.654	1.997 (1.98)
7	0.47	0.729	-0.259	-3.0	0.483	2.444 (2.44)
8	0.79	0.894	-0.104	-10.0	0.796	2.288 (2.28)
9	0.82	0.819	0.001	40.0	0.827	1.771 (1.76)
10	0.66	0.617	0.043	9.3	0.667	1.334 (1.33)
11	0.72	0.475	0.245	1.7	0.727	0.887 (0.88)
12	0.22	0.314	-0.094	-4.0	0.221	1.146 (1.13)
13	0.24	0.408	-0.168	-3.0	0.258	1.618 (1.61)
14	0.40	0.613	-0.213	-3.5	0.419	2.119 (2.12)
15	0.74	0.817	-0.077	-20.0	0.744	2.440 (2.43)
16	0.87	0.929	-0.059	-44.2	0.874	1.716 (1.71)
17	0.86	0.655	0.205	2.5	0.865	1.007 (0.99)
18	0.50	0.400	0.100	2.5	0.506	1.021 (1.00)

Log-Range (LR) = 2.444 - 0.887 = 1.557 (1.56)

^a The signs of the deviations occur in runs (almost significantly at 5%, run test Sokal & Rohlf 1969), and each deviation is significantly correlated with the following value of the key-factor (k_1), ρ (Spearman) = +0.65 ($P=0.0076$, 2-sided)

^b By some trial and error the corrections of the expected values of k_5 are chosen such that in the results both the field values of k_5 (first column) and the next field values of \log_{10} (larval density) (last column: between brackets; compare the first column of Table 1) are approached as good as possible. This is reached by adding 0.374*PDB/CORR (which approaches DIFF) to the value expected from 0.374*PDB

at relatively low values of PDB, whereas negative deviations (mortality from k_5 lower than expected) occur at high values (Mann-Whitney: $P=0.0065$, two-sided). As well, the field values of k_5 tend to decrease with increasing PDB: ρ (Spearman) = -0.73 ($P=0.003$, two-sided). I have tried to mimic this pattern as closely as possible in the following simulations, i.e. as it is shown in Table 2.

The above pattern might be explicable by (unpublished) observations on the behaviour of predatory (carabid) beetles: the longer such beetles feed on the same kind of prey, the more they are inclined to look for another kind of prey. Tinbergen (1960) discovered the same phenomenon in the great tit. In carabids such switching appears to stimulate egg production. At high densities of winter moth pupae, such behaviour of polyphagous predators feeding on pupae may lead to a loosening of the predation pressure. This would be in accordance with the conclusions and suggestions of Kowalski (1977) concerning the predatory beetle *Philonthus decorus*. However, this effect will vary as a result of independent changes of the densities of some or all of these predators in different years. Therefore, such density dependence cannot be predicted exactly. Predation by polyphagous predators will always involve a great deal of variation.

The model of Latto and Hassell

Latto and Hassell (1987) treated all mortalities (k_1 to k_6 , k_5 included) as independent random variables taken from

normal distributions with mean and standard deviation (s.d.) as calculated from the field data, and compared these with similar cases where k_5 was deterministically density-dependent according to 0.374*PDB (compare the preceding section). It must be noted, however, that in the field data (Table 1) the different mortalities are neither normally distributed, randomly changing in time, nor independent of each other. As a result of this the Latto and Hassell model considerably departs from the winter moth dynamics at Wytham Wood between 1950 and 1968. The frequencies of the mortalities in 7 equal classes (from low to high) are: k_1 : 1, 3, 1, 4, 6, 2, 2; k_{2-4} : 4, 6, 3, 3, 1, 1, 1; k_6 : 3, 5, 5, 1, 2, 1, 1; the distribution in time of values above (+) and below (-) the median (0) is:

k_1 : + - + + - + - - - + + + 0 - - - + + + ;

k_{2-4} : + - + - + 0 - + + + + + - - - - - ;

k_6 : + - - + - - + + + + - - - + 0 + - - ;

and these values show a highly significant concordance within years (Kendall 1962): $W=0.475$ ($P<0.001$).

Nevertheless, from a purely theoretical point of view it is interesting to do similar simulations, but step by step, and not only with k_5 deterministically density-dependent, but also with k_5 density-dependent according to 0.374*PDB + 0.374*PDB/CORR (Table 2). In each of these simulations, first, all 18 normally distributed values for k_2 are taken randomly from the distribution defined by mean and s.d. (at the foot of Table 1), next those for k_3 are taken, etc. (including those for k_5). Thereupon, the same simulation is executed with only k_5 density-dependent (i.e. all

Table 3. Paired simulations with k_5 either density-dependent or independent, and one or more of the other mortalities normally distributed (mean and s.d. at the foot of Table 1). Compared are the mean Logarithmic Ranges (LR), and the number from 100 coupled simulations in which the case with k_5 independent shows narrower (or equal) limits of density than the case with k_5 density-dependent. Final density is not fixed

normal distributions according to mean and s.d. at the foot of Table 1	LR with k_5 density-dependent		LR with k_5 independently and normally distributed 3	% simulations in which LR of the independent case \leq LR of the coupled density-dependent case. Compared:	
	k_5 corrected (Table 2) 1	$k_5 = 0.374 * PDB$ 2		1 and 3	2 and 3
standard of comparison (only k_5 density-dependent or indep.)	1.56	1.13	1.88	33	3
also k_{2-4} normally distributed	1.52	1.11	1.92	22	1
k_6 normally distributed	1.62	1.21	1.95	32	9
k_{2-4} and k_6 normally distributed	1.61	1.24	2.02	26	4
k_1 normally distributed	1.72	1.43	2.49	15**	6
k_1 and k_{2-4} normally distributed	1.71	1.43	2.49	20*	10*
k_1 and k_6 normally distributed	1.64	1.42	2.60	10***	4
all mortalities normally distributed	1.65	1.42	2.54	12***	8

% of simulations significantly different from standard of comparison (Chi-square):

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

other mortalities have the same values, in the same order, as in the coupled simulation with k_5 independent of density). In the first step, normally distributed values for only k_{2-4} are introduced, in the next step, values for only k_6 , in the third step, values for both k_{2-4} and k_6 , and so on. Each step is executed 100 times, each time with different pseudo-random numbers (listings of the program can be sent on request).

The results of these simulations are given in Table 3. In general, the density-dependent cases (1, 2) seem to do "better" as regarded to regulation than the density-independent one (3), though there are distinct differences between simulations in which the actual density-dependent process is closely mimicked (1, from Table 2), and those with the deterministic version (2). In particular, in the paired comparisons the deterministic version appears to be superior over the field process of pupal predation (last two columns of Table 3). Whether the values of k_{2-4} , or those of k_6 , or both, are normalized, makes little difference to the density-dependent cases, or the independent one (upper part of Table 3). However, if the field values of the key-factor (k_1) are replaced by normally distributed ones (lower part of Table 3), this picture is disturbed.

Table 3 shows, that the deterministic version of pupal predation may have some stabilizing effect, compared with independent k_5 -values, both in the field population and under changed conditions (paired comparisons). But we cannot necessarily say the same about the actual process of pupal predation. The results from these simulations are very sensitive to particular parameter values, which is shown by introducing an only small change: replacing the value 1.75 for $EGGS = \log_{10}(\text{eggs/female})$ by 1.80. Then, the %'s of coupled simulations in which LR of the independent case \leq LR of the dependent one (comparing 1 and 3, Table 3) alter into 49, 38, 40, 41, 25, 20, 19 and 17 respectively, where again the last four values (with k_1 normally distributed) differ significantly ($P < 0.001$) from the standard of comparison (49). This demonstrates that a favourable effect of pupal predation can easily disappear under an only slightly different set of conditions: with $EGGS = 1.80$ (instead of 1.75) in the standard of comparison (49,

above) and in the three following cases the above frequencies (38, 40, 41) do not or hardly differ from the expected value (50) under the null hypothesis "no effect of density dependence" (compare Table 3).

This conclusion is confirmed by the first test of Bulmer (1975): the field population does not show a significant (negative) correlation between net reproduction and density. Among the simulations in the upper part of Table 3 only about 5% of the density-dependent cases (1) show a significant test result, but since also 5–7% of the independent cases (3) score significantly, this will only be a casual and not a real result. As could be expected, the deterministic version (2) scores better: about 15% of the simulations in the upper part of Table 3 give a significant test result.

It is interesting to note that, for both the deterministic version and the field process of pupal predation, taking the values of the key-factor (k_1) randomly from a normal distribution, and thus disturbing the actual pattern in time, as well as the correlations with pupal predation (Table 2, and Den Boer 1986: 510), results in a higher likelihood of detecting regulation: about 25% of the density-dependent simulations (1, 2) of the lower part of Table 3 score significantly with Bulmer's test (and again about 5% of the independent cases). Note that, because of the still high proportion of insignificant cases, on average this does not necessarily coincide with narrower limits of density. Hence, as was already concluded by Den Boer (1986), the key-factor dominates the pattern of fluctuations in the field population, and thus controls the limits of density to such a degree that pupal predation cannot govern it significantly.

This dominance of the key-factor is most clearly illustrated by the mean LR-values of the independent case (3 in Table 3): the values in the lower part of Table 3 are much higher than those in the upper part. Replacing the k_1 -values by normally distributed ones has two important effects: (a) the relations between the different mortalities as well as the pattern in time of this combined effect ($K - k_5$) will be disturbed, and the chance that values of $K - k_5$ (Table 1) above (+) and below (-) the median alternate in time will increase (in the field population these occur in the order - + + - + - - - + + + - - - + + -),

Table 4. Simulations with different values for egg production to compare under different (induced) trends of density the effect on the Logarithmic Range (LR) of (1) the density dependence of k_5 (extreme densities in last two columns); (2) k_5 fixed at its mean value, and (3) independent values of k_5 (the values from A resp. B randomly permuted). Also is given: the number from 100 permutations of k_5 -values in which LR is smaller than (or equal to) LR in cases A or B

\log_{10} (eggs/ female)	LR with k_5 density-dependent		LR with k_5 fixed at its mean value (between brackets)		k_5 -values of either A or B randomly permuted: mean LR, and % permutations with LR of indep. case \leq LR of coupled dependent case (\leq LR with k_5 fixed)				Extreme density (number of larvae/m ² of canopy) with k_5 density-dependent	
	A k_5 as in Table 2	B $k_5 =$ 0.374*PDB	A	B	LR	A	LR	B	A	B
									<i>highest density</i>	
3.00	4.14	3.56	2.27 (1.73)	3.03 (1.68)	3.49	78 (6)	3.30	70 (25)	1559553	402717
2.80	2.80	3.02	1.99 (1.56)	2.58 (1.51)	3.04	78 (8)	2.82	61 (29)	390841	117761
2.50	2.50	2.22	1.56 (1.29)	2.00 (1.25)	2.41	65 (10)	2.15	53 (32)	49204	18621
2.30	2.06	1.69	1.28 (1.11)	1.64 (1.08)	2.06	49 (6)	1.77	(40)	12331	5433
2.20	1.97	1.42	1.15 (1.03)	1.46 (1.00)	1.92	53 (3)	1.60	24 (29)	6180	2938
2.10	1.88	1.15	1.09 (0.94)	1.28 (0.91)	1.82	59 (2)	1.46	7 (20)	3097	1589
2.00	1.78	1.13	1.16 (0.85)	1.14 (0.83)	1.75	53 (4)	1.36	12 (14)	1552	859
1.90	1.69	1.13	1.28 (0.76)	1.09 (0.74)	1.72	50 (6)	1.35	10 (8)	776	465
1.85	1.65	1.13	1.34 (0.72)	1.17 (0.70)	1.73	47 (14)	1.38	6 (16)	551	341
1.80	1.60	1.13	1.39 (0.67)	1.24 (0.66)	1.74	41 (14)	1.42	10 (21)	391	251
									<i>lowest density</i>	
1.75*	1.56	1.13	1.45 (0.63)	1.32 (0.62)	1.77	31 (22)	1.48	7 (26)	A	B
1.70	1.51	1.13	1.51 (0.59)	1.39 (0.57)	1.80	24 (24)	1.56	4 (25)	6.1	10.2
1.65	1.47	1.18	1.57 (0.54)	1.46 (0.53)	1.85	14 (22)	1.64	2 (24)	4.8	9.4
1.60	1.47	1.31	1.64 (0.50)	1.54 (0.49)	1.90	10 (23)	1.73	6 (24)	3.8	5.5
1.50	1.68	1.57	1.77 (0.41)	1.70 (0.40)	2.02	17 (25)	1.91	14 (24)	2.3	3.0
1.40	1.89	1.84	1.90 (0.32)	1.86 (0.32)	2.17	19 (19)	2.12	18 (23)	1.4	1.6
1.30	2.12	2.11	2.03 (0.23)	2.03 (0.23)	2.35	24 (13)	2.33	24 (16)	0.9	0.9
1.20	2.35	2.37	2.21 (0.15)	2.37 (0.15)	2.53	29 (15)	2.57	28 (17)	0.5	0.5
1.00	2.83	2.90	2.63 (-0.03)	2.79 (-0.02)	2.94	45 (16)	3.05	33 (21)	0.2	0.2

* Standard of comparison: in these simulations of the field population the actual values of k_5 are either closely mimicked according to the calculation given in Table 2 (A), or estimated according to the deterministic equation $k_5 = 0.374 * PDB$ (B), without fixing final density

and the same can be expected to occur with the coefficients of net reproduction (R); (b) also the chance will increase that in the string of values between \log_{10} (initial density) and \log_{10} (final density) (see section 1) the sum of subtractions (mortalities) appreciably deviates from the sum of additions (fixed at 18 times 1.75), i.e. population density will more often show a significant trend in time. Both phenomena are nicely illustrated by Fig.'s 2a and 4a of Latto and Hassell (1987). The first phenomenon, a higher frequency of turning points in the trend of density, is responsible for the above mentioned higher likelihood of detecting regulation. But, in spite of the theoretical interest of this phenomenon, it does not apply to the winter moth population at Wytham Wood (compare Fig. 1 of Latto and Hassell 1987, in which the fluctuation pattern is dominated by the key-factor).

The inability of the density dependence of pupal predation to keep the field population within limits has been shown by the model of Den Boer (1986), and is confirmed by the present analysis of the model of Latto and Hassell.

The governing of trends in density

To further increase our insight into the winter moth population at Wytham Wood without fixing final density, but in a more adequate way than was done by Latto and Has-

sell, we will induce trends in time by changing only \log_{10} (eggs/female) = EGGS, without disturbing the general pattern of density fluctuations as it occurs in the field.

The results from simulations of the winter moth population at Wytham Wood between 1950 and 1968, in which different values of EGGS = \log_{10} (eggs/female) were introduced, and in which the density dependence of pupal predation was represented in one of two forms: A, according to the calculation in Table 2, and B, deterministically according to 0.374*PDB, are presented in Table 4. All other mortalities were kept unaltered (values as in Table 1). Each simulation was executed in 3 versions: (1) with k_5 density-dependent; (2) with k_5 fixed at its mean value; and (3) with the k_5 -values randomly permuted. The latter version was repeated 100 times with different independently chosen permutations, and the number of times that the limits of density (LR) were narrower than, or equal to, those of the versions (1) or (2) respectively was determined (listings of the program can be sent on request).

Table 4 shows that changing EGGS generally results in widening of the limits of density (LR). Only between about EGGS = 1.60 and 2.10 are the changes not consistent, and clearly different in the different versions. With the deterministic version (B) of density dependence, within this range LR remained at about the same value (but with different extreme densities, last column of Table 4), a value that

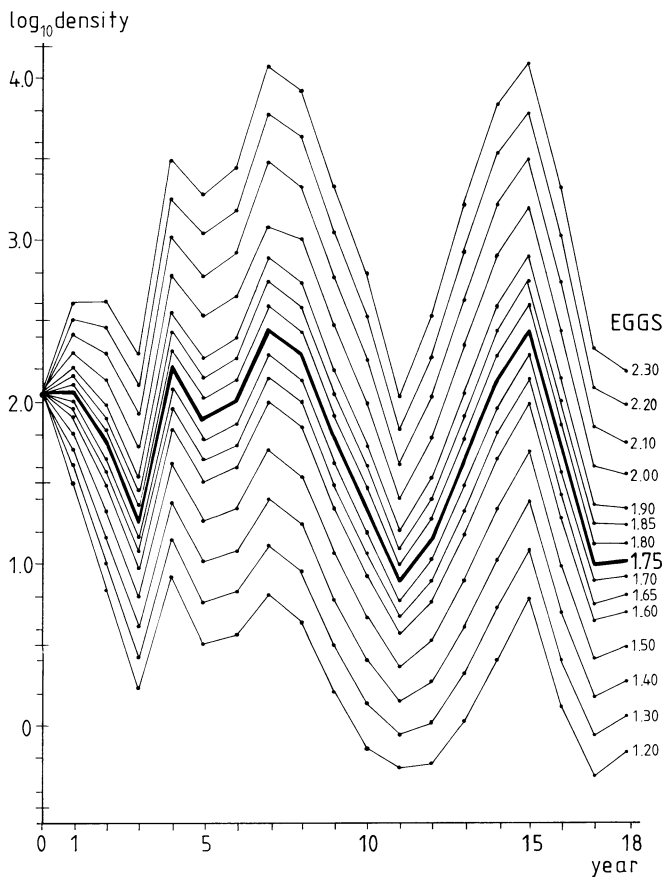


Fig. 1. Fluctuation of larval density in the winter moth population at Wytham Wood between 1950 and 1968 (fat line) compared with densities from models in which only $\log_{10}(\text{eggs/female}) = \text{EGGS}$ is changed. The density-dependent process is mimicked according to the calculation given in Table 2

is significantly surpassed if the k_5 -values are randomly permuted. The A-version of pupal predation is less powerful: at the higher values of EGGs (but below 2.10) the LR-values from the permutations are not significantly different from those of the density-dependent cases (frequencies of $\text{LR} \leq \text{LR}$ in dependent cases do not differ from the expectation 50-50 under the null hypothesis). Taking away density dependence by fixing k_5 at its mean value is generally favourable in the A-version (except at lower values of EGGs), but usually not in the B-version, which again demonstrates the deviating "behaviour" of a deterministic formulation of density dependence. At more extreme values of EGGs (above 2.10, or below 1.60) the regulating power of pupal predation rapidly breaks down, as it does in the deterministic version. In none of the simulations with k_5 density-dependent (first two columns of Table 4) the first test of Bulmer (1975) scored significantly.

Whether EGGs is increased or decreased, a characteristic pattern of density fluctuations is seen that is imposed by the key-factor (k_1): Figure 1 (compare Fig. 7.3 (p. 121) of Varley et al. 1973). Such a pattern can hardly be that of a "regulated population", i.e. "one which tends to return to an equilibrium density following any departure from this level" (Varley et al. 1973:19). The continued decrease of density in generation 7 through to 11 (Fig. 1), and the continued increase in density in generation 11 through to 15

refute this. Because of this the values of \log_{10} (larval density) above (+) and below (−) the median (0, Table 1:1.815) occur in too few runs: + + − − + + + + − − − − + + 0 − − (6 runs, which is significantly too low at 5%, Sokal & Rohlf 1969). Fig. 1 illustrates that, when conditions change, the power of the density dependence of pupal predation to keep density within limits is not very impressive. Indeed, there are reasons to suppose that the picture given by Fig. 1 might be too optimistic: as discussed in the second section the density-dependent process would imply that with $\text{EGGS} > 1.75$ more densities will belong to the group "high densities" (above about $\log_{10} = 2.0$), where the mortality from k_5 is lower than expected according to $0.374 \cdot \text{PDB}$ (Table 2). On the other hand, with $\text{EGGS} < 1.75$ more densities will belong to the group "relatively low densities" (between about $\log_{10} = 0.8$ and $\log_{10} = 1.5$) where the mortality from k_5 is generally higher than expected (Table 2). Added to this we don't know how polyphagous predators will react above $\log_{10}(\text{density}) = 2.5$ or below $\log_{10}(\text{density}) = 0.5$.

Even if we assume that the density-dependent process, as calculated in Table 2, will stay about the same at densities outside those observed between 1950 and 1968 (as we did in this section), the expected survival time of the winter moth population studied by Varley et al. (1973) would not be very long (*ceteris paribus*). If we suppose that the pattern of fluctuations as observed between 1950 and 1968 would be simply repeated several times after 1968 (starting from the density in 1968), after 49 years (in 1999) the density would be 0.06 ($\log_{10} = -1.22$), and after 68 years it would be 0.005 ($\log_{10} = -2.27$), i.e. a single larva at 186 m² of canopy. It is likely that the population would have become extinct before such a low density was reached. If we assume that the R (net reproduction)-values (cf Den Boer 1986: Table 1b) are lognormally distributed, as often occurs among carabid beetles (Den Boer 1985), we can, after having estimated the moments of this lognormal distribution, adequately simulate fluctuation patterns of density. In the field, the most favourable sequences of R-values, as far as survival times are concerned, appear to be random sequences taken from the fitted lognormal distribution (at least for carabid beetles: Den Boer 1985). Therefore, we did not try to calculate and incorporate autocorrelations between R-values. Just as did Latto and Hassell (1987), we accepted a single larva at 10 m² as the lower (extinction) limit, and 100 000 larvae per m² as the upper (selfdestruction) limit of density. Starting from the density in 1950 (112.2 larvae/m²), and assuming randomly succeeding R-values, 500 simulations resulted in: 318 "populations" surpassing the lower limit, after an average of 59.7 years, and 182 "populations" surpassing the upper limit, after 64.6 years. Even if we had fixed the lower limit at a single larva at 100 m², 299 "populations" would have "become extinct" after 84.7 years on average.

Discussion

The model which Latto and Hassell (1987) constructed to refute the conclusions of Den Boer (1986) deviates in some essential aspects from the winter moth population at Wytham Wood between 1950 and 1968 (Varley et al. 1973). I agree with Levins (1968) that, because of its complexity, we can only try to reconstruct nature in models which leave intact the essential aspects of the reality under study, while

removing distracting elements. Essential aspects of the winter moth population are (a) the key-factor, and (b) pupal predation and possibly its density dependence. I hope to have shown (the third section, Table 3) that, by replacing the key-factor by values randomly taken from the relevant normal distribution, Latto and Hassell not only set free the final density, but also changed the most essential feature of the fluctuation pattern. As a result, their conclusion "pupal predation is crucial to the population regulation of the winter moth at Wytham Wood" cannot be supported by that model. Moreover, the deterministic formulation of the density dependence of pupal predation appears to deviate sufficiently from reality (second section, Table 2) to give an overoptimistic impression of the power of the density dependence of pupal predation. If both the key-factor and the density dependence of pupal predation are preserved, as they were observed in the field, pupal predation appeared not to regulate, either in the sense of "keeping density within limits" (fourth section, Table 4) or according to the first test of Bulmer (1975), thus supporting the conclusion of Den Boer (1986).

Although pupal predation appears not to regulate density, under specified conditions it may still have some stabilizing influence. Table 2 shows that the greatest power of the density dependence of pupal predation can be expected between the densities 6.3 and 31.6 larvae/m² (log₁₀ between 0.8 and 1.5), and somewhat less evident until about 100 larvae/m² (log₁₀ = 2.0). This could imply that, within this density range, predation by polyphagous predators will sometimes retard a rapid growth to still higher densities, but this will increase the chance of the population falling to dangerously low densities, when conditions turn worse (see Den Boer 1968). In both the winter moth (Den Boer 1986) and the pine looper (Den Boer 1987) density-dependent predation by polyphagous predators is indeed connected with the occurrence of very low densities. In general, if they are sufficiently numerous, predation by polyphagous predators will sometimes contribute to the restriction of the densities of a number of prey species for some time. However, they will generally not prevent the density of one or more of these prey species from growing rapidly under favourable conditions, nor can they prevent the prey populations reaching dangerously low densities under adverse conditions. Therefore, this is not "regulation of numbers", because the limits of density are not necessarily narrowed. Instead, density is shifted to a lower level, and in addition, the relationship between net reproduction and density will generally be different within different ranges of density, and therefore usually not significant. Compare Den Boer (1986, 1987).

To conclude: the model of Latto and Hassell (1987) demonstrates that regulation of numbers may be favoured if density fluctuations with many turning points (e.g. random fluctuations) are combined with a powerful density-dependent process. In the third section, with a similar model, we showed that under such circumstances (lower part of Table 3) the chance that the population is regulated (Bulmer 1975) may be about 25%. However, such model situations differ in essential aspects from the winter moth at Wytham Wood between 1950 and 1968, and therefore do not say much about the role of the density-dependent pupal predation as a possible regulator of that population.

This also answers the comments of Poethke and Kirchberg (1987). Although they kept the mortalities of the same

year together, and thus saved the mutual relationships, the succession of these coupled mortalities over years was taken at random, which distinctly deviates from the winter moth at Wytham Wood between 1950 and 1968, as we showed in the third section. Moreover, the density-dependent process, either conceived deterministically, or deterministically with a stochastic residual, deviates clearly from the field data (compare second section). At first, we also simulated k_5 deterministically with an adequate stochastic residual; the results were intermediate between those of the cases 1 and 2 of Table 3, and between those of A and B of Table 4, but generally closer to the deterministic case than to the actual field process. Therefore, the model of Poethke and Kirchberg is still too far from the field data to be a reliable base for the statistical speculation they suggest. On the other hand, I now agree with Poethke and Kirchberg in that the density-dependent process need not always be the key-factor in order to "regulate". However, in populations such as the winter moth of Wytham Wood I expect it to be a necessary condition: only if the influences of other mortalities change about randomly from year to year, thus resulting in comparatively many turning points in the fluctuation pattern of density, a not dominating, but still quantitatively important, density-dependent process may contribute to an actual "regulation" of numbers (=keeping within limits). Hence, Poethke and Kirchberg (1987) were right so far as their simulations are concerned, but most probably not for the case of the winter moth at Wytham Wood.

I more and more get convinced that random sequences are not the rule in time series from the field (compare Den Boer 1985), and sometimes the deviations may be so significant that simulations with random sequences will give a highly erroneous impression of the process under consideration. This is evidently the case with both the density-dependent process and the key-factor in the winter moth at Wytham Wood, which clearly appears from a comparison of the estimated survival times of this population by Latto and Hassell and by Poethke and Kirchberg respectively with those of the present author (fourth section).

It should also be realized that a density-dependent mortality, even if it is quantitatively important, such as in the winter moth, in itself will not form a feedback circuit (or only under specified conditions). Convincing cases of regulation of numbers can be expected if reproduction is also density-dependent to a sufficient degree, so that together with density-dependent mortality an effective feedback circuit may be maintained. Klomp (1958, 1966) found such a favourable combination of density-dependent processes in the pine looper population he studied at "Hoge Veluwe", but he rightly concluded that the density-dependent variation of fecundity was insufficient to contribute significantly to a possible regulation of numbers. This conclusion was confirmed by Den Boer (1987). See further: Den Boer and Reddingius (unpublished work).

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