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Source: *Oecologia*, Vol. 69, No. 4 (1986), pp. 507-512

Published by: [Springer](#) in cooperation with [International Association for Ecology](#)

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Accessed: 24/10/2014 04:01

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Density dependence and the stabilization of animal numbers*

1. The winter moth

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Summary. The claim of Varley and Gradwell that the highly density-dependent pupal predation (k_5) in the population of the winter moth in Wytham Wood, England would keep density within limits (regulate) is compared in this paper with the density limits in the null model: pupal predation causes the same mean generation mortality (35%) as in the field, but is not density-dependent, i.e. either constant or randomly fluctuating between years according to the actual frequency distribution, *ceteris paribus*. According to this null model the winter moth would have fluctuated between narrower limits than in the field; the claim of Varley & Gradwell must thus be rejected. It is more generally concluded that a regulating factor should be the key factor, but this is not a sufficient condition. It should also prevent in some way the low throughs in the time series that usually accompany the operation of a dominating density-dependent mortality factor.

During the last decade the well known debate about density dependence (Pielou 1974) appeared to have fallen out of fashion, although the opposing viewpoints continued to exist (compare e.g. Begon and Mortimer 1981 with Andrewartha and Birch 1984). Apparently, the arguments for and against density-dependent regulation, that were discussed in Oosterbeek (den Boer and Gradwell 1971), have hardly been investigated further. However, recently the interest in these still unsolved problems has revived again (Dempster and Pollard 1981; Dempster 1983; Hassell 1985; Milne 1984). Also some of my co-workers (Baars and Van Dijk 1984) observed density-related egg production in two carabid species and considered this to be an important density-limiting factor. As I did not favour the deterministic model from which their conclusion originated, I compared the variances of the different components of the net reproductive rate (Den Boer 1986). Some interesting and unexpected findings from this study have caused me to reconsider the arguments favouring "regulation", and to try to test the hypothesis that density-dependent processes keep density within limits, i.e. regulate density (Varley et al. 1973: 112). Note, that I prefer to call the general tendency for population density to stay within relatively narrow limits "stabilization", and to restrict "regulation" to those cases of stabi-

lization in which density-dependent, or more generally, feed-back processes play a decisive part (Den Boer 1968).

Our problem thus is: how to show that a density-dependent factor, which is claimed to regulate, has indeed kept density within narrower bounds than would have occurred in its absence (in the null case)? The simple regression methods often used for testing for density dependence are inadequate: the slope (b) of the least squares line fitted to the plot of N_{t+1} (or N_{t+1}/N_t) versus N_t only estimates the scatter of the points (r) (Pielou 1974: 53–58). The models proposed by Reddingius (1971: Ch. 10) and by Bulmer (1975), which test whether or not the logarithm of net reproduction depends, linearly and negatively, on log density, are close to the mark, and in fact are just what we need if we want to test whether or not regulation governs our population counts. In spite of this, these models are not generally in use. Possibly this is due to the fact that these tests result in a statistical judgement, and do not tell us what part was played by particular (e.g. density-dependent) processes.

Morris (1963) had already tried to overcome this problem by introducing "key factor analysis" to identify the factor(s) that principally determine the pattern of population fluctuations. Let us therefore consider the data for the winter moth in Wytham Wood, England, for which key factor analysis was elaborated further (Varley and Gradwell 1968). The effect of the density-dependent pupal predation by polyphagous predators (factor k_5) on the density of the winter moth is considered to be one of the landmark cases of regulation of insect numbers. Not only did East (1974) and Kowalski (1976) satisfactorily demonstrate the density dependence of pupal predation, but this supposed regulating factor appeared to be responsible for as much as 35% of total generation mortality. Moreover, the effect of mortality factors on the density of the winter moth was studied quantitatively for a considerable number of years (Varley and Gradwell 1968; Varley et al. 1973). Varley and Gradwell (1968) tried to get some insight into the pattern of density fluctuations of the winter moth by considering a model of the possible effects of the parasitoid *Cratichneumon* (k_6). As k_6 covers 8–9% of generation mortality, the effect appeared to be only small. Hassell (1980) thoroughly analyzed the regulating potential of the parasitoid *Cyzenis* (k_2), which was successfully introduced in Nova Scotia to control the winter moth. But in Wytham Wood its influence is negligibly small. Kowalski (1977) tried to evaluate the regulating influence of pupal predation (k_5).

* Communication No. 264 of the Biological Station, Wijster

He did not test, however, the density dependence of k_5 against the relevant null case. In the following I will try to do the latter.

Methods and results

The limits between which density fluctuates during some observation period will be given by the "logarithmic range" (LR): i.e. \log_{10} (highest density) minus \log_{10} (lowest density), as proposed by Reddingius and Den Boer (1970), Den Boer (1971). From the data on the winter moth in Table 1 a, $LR(\text{larvae}) = 1.56$ and $LR(\text{adults}) = 1.33$. If we assume that pupal predation did not show density dependence, but still accounted for the same average mortality, the values of k_5 in Table 1 a can be replaced by its mean value, or by random values with the same mean and variance as k_5 . This enables us to compare the density changes of the winter moth with and without the density-dependent effects of pupal predation (k_5). Such a comparison can be made in two different ways:

1. For each generation separately, i.e. starting from the actual larval density in year t (N_t), larval density in the next year is computed with k_5 fixed at its expected (= mean) value (0.623). For each generation this calculated value ($N_{p_{t+1}}$) is compared with the value (N_{t+1}) actually observed (Fig. 1A). This plot shows whether or not density dependence resulted in a general limitation of potentially high and/or low densities: if potentially high densities are restricted $N_{p_{t+1}} > N_{t+1}$ (black dots above the mean), if potentially low densities are limited $N_{t+1} > N_{p_{t+1}}$ (black dots below mean). The test for symmetry of Wilcoxon (Van Eeden and Benard 1956) enables us to check whether these effects can be considered significant: Table 2.

The same procedure can be applied with all mortality factors, except k_5 , fixed at their expected (= mean) values (Table 1a). Comparing these $N_{p_{t+1}}$'s with the observed N_{t+1} 's gives an idea of the maximal power of the density dependence of k_5 (Fig. 1B; Table 2), i.e. in an otherwise constant environment.

Figure 1B shows that the density dependence of k_5 has indeed the potential to regulate, as suggested by Varley et al. (1973): the highest densities would be reduced by about 9%, and low densities would even be increased by some 20% (Table 2: (2)). Such effects might be expected to keep density within limits (Varley et al. 1973: 112), if no other variables interfered significantly. However, in each generation larval density of the winter moth is affected by other variables too, and Fig. 1A shows that, in the field, not much is left of the promising "regulatory" tendency of k_5 . Extreme densities may sometimes even be pushed into a still more extreme direction by the density dependence of k_5 , though not significantly so (Table 2: (1)).

Hence, in practice density cannot be expected to be kept within limits by the density dependence of k_5 . Note, that this is different from alleging that k_5 would not be a powerful density-dependent factor. The latter can be checked by comparing $\text{Var } \log_{10}(N_{t+1}, \text{ adults})$ as found in the field (= 0.140), i.e. after the density-dependent effect of k_5 , with $\text{Var } \log_{10}(N_{p_{t+1}}, \text{ adults})$ after the fixed influence of k_5 (= 0.235). The variance of adult density is importantly (though not significantly, $P \sim 0.30$) reduced by the density-dependent effect of k_5 . After further stages in the life-cycle have passed this effect has largely disappeared, which be-

Table 1 a, b. Population dynamics of the winter moth (modified from: Varley et al. 1973: Table F, p. 201).

log ₁₀ factor or log ₁₀ density	Densities and mortality factors																	Variance	Expected value (\hat{E})			
	1950	1951	1952	1953	1954	1955	1956	1957	1958	1959	1960	1961	1962	1963	1964	1965	1966		1967	1968	larvae	adults
k_1	1.59	0.56	1.14	1.33	0.24	1.16	0.83	0.48	0.83	1.15	1.21	0.91	1.09	0.85	0.66	0.52	1.42	1.20	1.19	0.127	0.932	0.932
larvae	2.05	2.07	1.74	1.26	2.20	1.89	1.98	2.44	2.28	1.76	1.33	0.88	1.13	1.61	2.12	2.43	1.71	0.99	1.00	0.252	1.7295	1.7295
$k_2 + k_3 + k_4$	0.20	0.06	0.113	0.07	0.094	0.073	0.06	0.08	0.13	0.16	0.11	0.10	0.11	0.05	0.025	0.05	0.065	0.04	0.04	0.002	0.088	0.079
k_5	0.69	0.77	0.75	0.34	0.73	0.65	0.47	0.79	0.82	0.66	0.72	0.22	0.24	0.40	0.74	0.87	0.86	0.50	0.48	0.042	0.623	0.612
k_6	0.29	0.10	0.03	0.16	0.07	0.09	0.28	0.20	0.16	0.15	0.45	0.08	0.06	0.12	0.14	0.13	0.33	-	-	0.014	0.158	0.142
K	2.77	1.49	2.033	1.90	1.134	1.973	1.64	1.55	1.94	2.12	2.49	1.31	1.50	1.42	1.565	1.57	2.675	1.74	1.71	0.201	1.8174	1.8174
adults	0.87	1.14	0.847	0.69	1.306	1.077	1.17	1.37	1.17	0.79	0.05	0.48	0.72	1.04	1.215	1.38	0.455	0.45	0.48	0.140	-	-
b Coefficients of net reproduction (larvae): R																						
field data	1.05	0.47	0.33	8.71	0.49	1.23	2.88	0.69	0.30	0.37	0.36	1.78	3.02	3.24	2.04	0.19	0.19	1.02	0.226			
k_5 fixed	1.19	0.67	0.45	4.54	0.64	1.36	2.03	1.04	0.49	0.41	0.45	0.72	1.28	1.98	2.77	0.34	0.34	0.75	0.107			

* $\log_{10} \text{ eggs} = \log_{10}(\text{adults} * 0.5 * 150.00) = \log_{10} \text{ adults} + 1.75$; $\hat{E}(k_5)$ for larvae is the mean over 1950 until and including 1967, whereas $\hat{E}(k_5)$ for adults is the mean over 1951 until and including 1968. The same applies to $k_2 + k_3 + k_4$ and to k_6 . As densities and mortalities are given as \log_{10} -values the density changes from year to year are transformed into subtractions and additions, e.g.: $\log_{10}(\text{larvae '51}) = \log_{10}(\text{larvae '50}) - (k_2 + k_3 + k_4)('50) - k_5('50) + 1.75 - k_1('51) = 2.05 - 0.20 - 0.69 - 0.29 + 1.75 - 0.56 = 2.06$ (Varley et al. (1973) mention 2.07). Further information about life tables and key factor analysis in Varley et al. (1973)

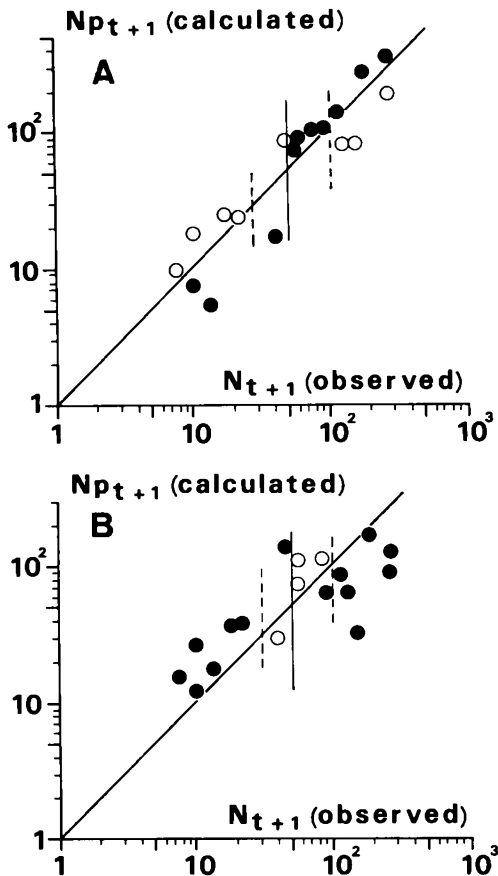


Fig. 1A, B. Possible effects of the density dependence of pupal predation (k_5) on the larval density of the winter moth in separate generations (section 2.1). **A** The real effect of k_5 in the field: in each generation actual larval density (N_{t+1}) is plotted against the value that is calculated after having put k_5 at its mean value (Np_{t+1}). Test results in Table 2 (1). Black dots: observed densities less extreme than calculated values (i.e. k_5 had a stabilizing effect); open circles: observed densities more extreme than calculated values (k_5 had a destabilizing effect). **B** The maximum possible effect of k_5 : for each year the observed value of larval density (N_{t+1}) is plotted against the value that is calculated after having fixed all mortality factors – except k_5 – at their respective mean values (Np_{t+1}): Table 1a. Test results in Table 2 (2). Black dots: calculated values more stabilizing than observed densities; open circles: calculated values less stabilizing than observed densities.

Vertical line: mean value of $\log_{10}(N_{t+1})$; the dotted lines divide the observed densities into 3 equal groups of 6, the left and the right groups giving information on possible regulatory effects

comes clear if we compare $\text{Var} \log_{10}(N_{t+1}, \text{larvae})$ as found in the field ($=0.260$), i.e. before the density-dependent influence of k_5 , with $\text{Var} \log_{10}(Np_{t+1}, \text{larvae})$ before the fixed influence of k_5 ($=0.296$). Although k_5 appears to counteract somewhat (but not significantly so) the possibly unbalancing effects of $k_2 + k_3 + k_4 + k_6$ (Table 2 (3)) its influence is apparently swamped by that of k_1 : Table 2 (4). We thus conclude that a powerful density-dependent factor, which governs 35% of generation mortality and which is highly and significantly correlated with the preceding larval density ($\rho(\text{Spearman}) = +0.74$; $P = 0.0017$), need not be regulatory. Apparently each case has to be considered separately.

The above test may be objected to on the grounds that only separate generations are considered. Not much can

be changed in one generation, and each test value is derived from a field value of N_t , which is itself already affected by the density-dependent process (k_5) during many generations. It is possible that the small net effects of the density dependence of k_5 in separate generations accumulate in such a way over years that eventually density is kept between narrower limits than without density dependence. Therefore, it seems more informative to compare entire time series.

2. For the whole time series, i.e. starting from larval (or adult) density in 1950, all other densities are consecutively calculated anew from the data in Table 1a, but now with k_5 fixed at its expected (mean) value. To avoid unnecessary accumulation in time of small, but inevitable, inaccuracies, it is preferable first to calculate for each generation anew the coefficient of net reproduction R (Table 1b), then to multiply the successive R -values, and thus to establish the densities in the new time series (Fig. 2). Comparison of the “logarithmic range” (LR) of this new time series with that of the field data allows us to test whether the density dependence of k_5 “regulated” density (i.e. kept it within narrower limits than without density dependence).

It will be evident from Fig. 2 (and from Table 3) that the density dependence of k_5 did not keep the larval density of the winter moth within limits. The range of density fluctuations was even wider (LR = 1.56) with than without (LR = 1.39) density dependence. The density dependence of k_5 was especially responsible for very low densities at the troughs of the fluctuation pattern (1953, 1961, 1967), whereas it did not always reduce the high densities (e.g. not in 1964 and 1965). This kind of effect of density-dependent mortality acting in a time series was predicted by Den Boer (1968: 184): “Moreover, each limitation of density after one or more generations will necessarily be followed by an accordingly low trough, by which the chance the population runs of becoming extinct may be increased”. At that time only Milne (1962) had recognized this consequence of density-dependent mortality.

If we replace the values of k_5 by $0.374 * \log_{10}(\text{old larvae})$, from the least squares line of $\log_{10}(\text{pupating larvae})$ on k_5 (see note to Table 3), we make k_5 “deterministically” density-dependent without changing $\bar{E}(k_5)$, i.e. the average mortality from pupal predation is kept the same as in the field (Fig. 2). Although this does increase the limiting influence on high densities (e.g. in 1957, 1958 and in 1964, 1965), it does not prevent the low troughs, and the variation in density (LR = 1.39) is not different from that without any density dependence of k_5 (LR = 1.39). Hence, even in a time series of 19 years, the density dependence of k_5 did not result in regulation of density, and it would not have regulated even if it could have exerted its full power.

The objection may possibly be made, that fixing k_5 at its mean value is not realistic; since even if pupal predation had not been density-dependent, it would still have varied between years. Therefore, it seems useful to allocate to k_5 random values in time, either according to a fitted normal distribution, or according to the frequency distribution of the actual k_5 -values (program-sections for this kind of job are mentioned in Den Boer (1981: Appendix (A)3)), in such a way that the sum of these simulated k_5 -values does not deviate more than 1% (say) from the sum of the actual values of k_5 ($=11.22$). One can also randomly permute the actual k_5 -values a number of times and study the frequency distribution of LR that results (this approach is

Table 2. Possible effects of the density-dependence of k_5 in separate generations

(all probabilities one-sided) (expected values in Table 1a)	limiting high larval densities		increasing low larval densities	
	all high densities	6 highest densities	all low densities	6 lowest densities
(1) only k_5 fixed at $\hat{E}(k_5)$, as compared with field densities: Fig. 1 A	1.1%; $T = +7$ ($P = 0.38$)	-2.1%; $T = -7$ ($P = 0.28$) (effect in unfavourable direction)	1.1%; $T = 0$ ($P = 0.53$)	-0.4%; $T = +3$ ($P = 0.42$) (effect in unfavourable direction)
(2) only k_5 varies (other factors fixed at mean values), as compared with field densities: Fig. 1 B.	reduction 7.6%; $T = +27$ ($P = 0.097$)	reduction 9.4%; $T = +21$ ($P = 0.016$)	increase 19.2%; $T = -30$ ($P = 0.02$)	increase 24.4%; $T = -21$ ($P = 0.016$)
(3) k_1 fixed at $\hat{E}(k_1)$ and k_5 fixed at $\hat{E}(k_5)$, as compared with only k_1 fixed at $\hat{E}(k_1)$	3.8%; $T = +19$ ($P = 0.15$)	5.8%; $T = +15$ ($P = 0.08$)	4.5%; $T = -11$ ($P = 0.29$)	10.5%; $T = -13$ ($P = 0.13$)
(4) only k_1 and k_5 vary (other factors fixed) compared with only k_1 varies (all other factors fixed)	-0.5%; $T = -1$ ($P = 0.50$) (effects in unfavourable direction)	-2.7%; $T = -9$ ($P = 0.22$) (effects in unfavourable direction)	-1.0%; $T = +3$ ($P = 0.46$) (effects in unfavourable direction)	-1.4%; $T = +1$ ($P = 0.50$) (effects in unfavourable direction)

Comparisons with Wilcoxon's test for symmetry (Van Eeden and Benard 1956), which is essentially similar to Wilcoxon's signed-ranks test as described in e.g. Sokal and Rohlf (1969), and which gives exactly the same probabilities. As an example (1): for all $\log_{10}(N_{t+1})$ above the expected value (1.7295: Table 1a) the (absolute) values of $|\log_{10}(N_{t+1}) - \log_{10}(N_{t+1})|$ are ranked after which the relevant sign is added again; T , being the difference between the sum of positive ranks and that of negative ranks is expected to be positive in this case ($T = +7$). The same is done for all $\log_{10}(N_{t+1})$ below the expected value; then T is expected to be negative ($T = 0$, in this case)

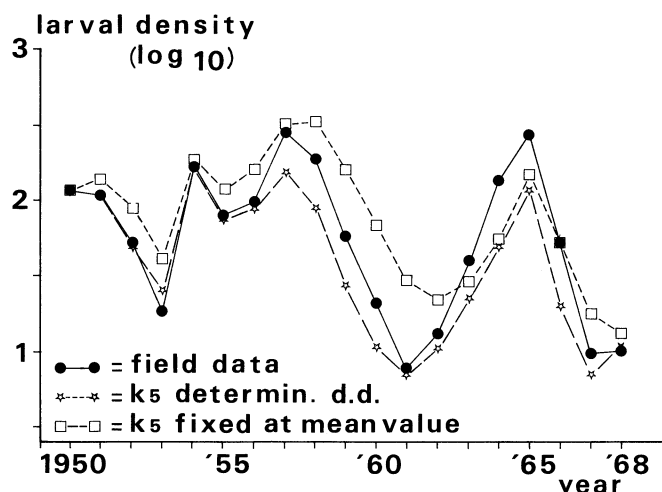


Fig. 2. Pattern of larval density fluctuations of the winter moth in a time series. The fluctuations in density in the field data ($LR = 1.56$) are compared with those when k_5 is deterministically density-dependent ($LR = 1.39$), and when the density dependence of k_5 has been removed ($LR = 1.39$); see Table 3, the cases (1), (2) and (3) respectively

worked out by Reddingius and Den Boer, and a paper is in preparation).

If we randomly allocate values for k_5 according to a normal distribution fitted to the field data (only simulations with the summed k_5 -values (Table 1a) between 11.15 and 11.29 are taken into account), LR (larvae) is greater than in the field (1.56) in 69 cases, and is smaller or equal in 87 cases ($\chi^2 = 2.08$, $P \sim 0.16$). Simulations of a frequency distribution that accurately fits that of the field data of k_5 (7 classes of 0.103 between 0.152 and 0.873 with frequencies 2, 1, 1, 2, 2, 5 and 5 respectively; compare Table 1a)

results in 71 cases with $LR > 1.56$ and 44 cases with $LR \leq 1.56$ ($\chi^2 = 6.34$, $P \sim 0.02$). In other, still closer, fitting simulations these numbers of cases were 31 and 31 respectively. Two hundred random permutations in time of the actual k_5 -values (Table 1a) gave 123 cases with $LR > 1.56$ and 77 cases with $LR \leq 1.56$ ($P = 0.383$). All these simulations taken together tell us that values of pupal predation randomly allocated in time – i.e. no longer dependent on density – within the same range, and with about (or even exactly) the same variation as in the field, do not give density limits that are significantly wider than that observed in the actual sequence of 19 years. It must be noted that all simulations also produced some very favourable cases with LR -values around 1.00, which indicates that, under certain circumstances, randomly allocated values may result in much smaller density ranges than the density-dependent values. In such cases the density fluctuations are apparently favoured by the levelling effect of the number of factors (Reddingius and Den Boer 1970). Just as Varley and Gradwell (1968) in the above models we worked with larval densities, but we satisfied ourselves that all results stay essentially the same when adult densities are used.

These surprising effects of a density-dependent factor in a time series are not exceptional, they can be expected for many kinds of factors when a number of variables together determine the successive values of the time series. In the case of the winter moth, the effects are partly caused by each k_5 being followed by mortality from the key factor (k_1) with a three times greater variance (Table 1a), and with which it is positively correlated ($\rho = +0.50$, $P = 0.04$). This means that in some years the limiting effect of k_5 is excessively repeated by k_1 , and this will accentuate the fluctuations of numbers. This is also illustrated in Table 3. When only the key factor k_1 varies (all other factors fixed at their mean values), both the variance of $\log_{10}R$ and of \log_{10} density, as well as the range of fluctuations (LR) of

Table 3. Influence of the different mortality factors on the fluctuation pattern of larvae and adults of the winter moth, i.e. as incorporated in the time series

Mortality factor(s) manipulated fixed at expected value(s): (Table 1 a)	larvae LR	larvae variance of: log ₁₀ density		adults LR	adults variance of: log ₁₀ density		No.
		log ₁₀ R	log ₁₀ R		log ₁₀ R	log ₁₀ R	
no change: field data	1.56	0.260	0.226	1.34	0.140	0.159	(1)
<i>k</i> ₅ deterministically dens.- dependent (<i>k</i> ₅ = 0.374 * log ₁₀ (pupating larvae) ^a)	1.39	0.214	0.154	1.03	0.098	0.124	(2)
<i>k</i> ₅ fixed at mean value	1.39	0.176	0.107	1.03	0.128	0.142	(3)
all factors except <i>k</i> ₁ fixed	1.39	0.129	0.110	1.08	0.090	0.111	(4)
<i>k</i> ₂ + <i>k</i> ₃ + <i>k</i> ₄ + <i>k</i> ₆ fixed (only <i>k</i> ₁ and <i>k</i> ₅ vary)	1.53	0.192	0.215	1.02	0.088	0.116	(5)
<i>k</i> ₂ + <i>k</i> ₃ + <i>k</i> ₅ fixed	1.53	0.228	0.218	1.29	0.126	0.150	(6)
only <i>k</i> ₆ fixed	1.42	0.197	0.203	1.21	0.098	0.117	(7)
only <i>k</i> ₁ fixed	1.52	0.141	0.076	1.22	0.116	0.077	(8)

The time series (1), (2), and (3) are pictured in Fig. 2

^a The value 0.374 differs from 0.35 as given by Varley et al. (1973, p. 123 Fig. 7.4). Perhaps Varley et al. plotted *k*₅ against log density (young larvae) – i.e. before the influence of *k*₂ + *k*₃ + *k*₄. In the present case *k*₅ was considered a mortality factor of pupating larvae and pupae – working i.e. after the influence of *k*₂ + *k*₃ + *k*₄

the larvae are smaller (4) than when *k*₁ and *k*₅ together determine the pattern of fluctuations (5). Curiously enough, this does not apply to the adults, but this is exactly the kind of contradiction that can be expected to occur in a time series with manifold relations among a number of variables. This is also illustrated by the fact that fixing only the key factor *k*₁ (8, in Table 3) does not greatly improve LR, even though it greatly diminishes the variance of log₁₀R. Note, that the field data are less favourable in all respects than any of the other cases, and that the cases from which the density dependence of *k*₅ has been removed ((3) and (4) in Table 3) are among the least variable patterns when judged by LR.

Varley et al. (1973: 90–92) suggest that a difference in density range between different stages of the life-cycle points to the action of a powerful density-dependent factor. In all cases LR was therefore estimated for both larvae and adults. Table 3 shows that, in all cases, LR(adults) is smaller than LR(larvae). Contrary to the obvious expectations of Varley et al. (1973) this difference was not related to the density dependence of *k*₅; e.g. in case (3) in which *k*₅ is fixed the difference between LR(larvae) and LR(adults) is not smaller than in case (2) with *k*₅ deterministically density-dependent, and greater than in case (1) the field data. This also means that the explanation given by Varley et al. (1973: 89–92) for the *Thrips imaginis* data of Davidson and Andrewartha (1948) is unconvincing.

Discussion

The hypothesis that “the density dependence of pupal predation (*k*₅) kept the density of the winter moth within limits (i.e. regulated density)” is not corroborated by the tests described in section 2. The possibilities of *k*₅ to vary are much too small, and so its compensatory power is insufficient to regulate (compare Table 2, (3) and (4)), even if it could have exerted its full power (compare Table 3, (2) and (3)). Note, that a greater effect of *k*₅ (e.g. 0.6 * log₁₀ (pupating larvae)) would have brought the population to

rapid extinction: after 5 years larval density would have been already <1.00, and after 11 years even <0.0004. Nevertheless, *k*₅ seems to affect the net reproductive rate (R) in the expected way ($\rho = -0.82$, $P = 0.001$), which appears to be confirmed by permutating the R-values repeatedly: the actual range of densities (LR = 1.56) is just significantly narrower ($P = 0.05$) than the ranges of permutated time series. However, the latter effect does not necessarily result from a regulatory influence of *k*₅. Serious doubt is especially entertained by the fact that the key factor (*k*₁), which is neither correlated with the preceding adult density ($\rho = -0.07$, n.s.) nor with the preceding larval density ($\rho = +0.066$, n.s.), shows exactly the same relationship with net reproduction ($\rho = -0.83$, $P = 0.009$) as *k*₅. As *k*₁ has both a greater mean influence (52% of generation mortality), and a three times higher variance than *k*₅, *k*₁ (the key factor) will actually determine the net rate of reproduction, whereas *k*₅ may only add to this through the correlation between *k*₅ and *k*₁ (see 2.2). We need not consider delayed effects, because the lack of any correlation between *k*₁ and preceding stages (above) prevents any transfer of regulatory effects from one generation to the next: *k*₁ sets the level, which can be modified somewhat by *k*₅ (in a density-dependent way, but in fact this is not very important in this case).

Although *k*₁ apparently greatly affects the succession of the values of net reproduction, and this sequence is not especially unfavourable (see above), these R-values themselves cause rather wide fluctuations of density. Table 3 shows that nearly every change in the mortality factors considered here improves the variance of log₁₀R, and with it the range of density fluctuations (LR). Among the factors that increase Var log₁₀R (and LR) *k*₅ plays a prominent part; compare Table 3, (3) and (4) with (1) and (2).

Pupal predation of the winter moth may just be an unfortunate case, however, in which the “regulation” is made ineffective by the key factor. It need not be representative of the regulatory significance of density-dependent factors in general. More cases will have to be investigated in this

way in order to check whether the winter moth is the exception or the rule. But compare Den Boer (1981). Two generalisations can be made. First, the range of variation of any supposed regulating factor should be as great, or at least nearly as great, as the range of variation of all other factors together influencing density, i.e. it should be the key factor. Although this is a necessary condition it need not be a sufficient one (compare e.g. *Tyria jacobaeae* in Dempster 1983). Under very restrictive, and thus rather improbable, conditions only an undercompensating density-dependent factor can be expected to have an overall regulatory influence on the range of density fluctuations (Den Boer 1986; and compare the three lines in Fig. 2)¹. Secondly, even if regulation can be expected to occur from a density-dependent mortality factor, one should make sure that the low troughs, that will inevitably result from such a process (Den Boer 1968: 184; compare Fig. 2), do not endanger the survival of the population (above). Although the latter need not apply to the winter moth at Wytham Wood, in general it may be important, because my experiences with carabid populations suggest that the main question of population dynamics should not be: "Which processes keep high densities low?", but: "Which processes lower the chance of "underpopulation" (Andrewartha and Birch 1954, Ch. 9) and thus extinction?" (Den Boer 1985).

Acknowledgements. I wish to thank all colleagues who in the course of more than fifteen years, helped me to develop my thoughts by discussing this critical subject, but in the first place my late friend Herman Klomp, who continuously challenged me by never agreeing with me. I especially thank Hans Reddingius, Henk Wolda, Mous Sabelis, Robert van der Eijk, Jack Dempster, Bob Kowalski, Martin Luff, Mike Hassell, Heinrich Kaiser, H.J. Poethke, who criticized earlier drafts of this paper. As I did not always follow their advice the present text is my responsibility alone. Reindert de Fluiter prepared the figures.

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Received February 25, 1986

¹ In general, a (mortality) factor with a lower mean effect will also show a lower variance: if one (mortality) factor (x) on average has a 5 times smaller effect than another (*ceteris paribus*) the variance of the latter will be 25 times greater than the variance of the first factor, for $\Sigma(5x_i - 5\bar{x})^2 / (n-1) = 25\Sigma(x_i - \bar{x})^2 / (n-1)$.