

DENSITY DEPENDENCE AND THE STABILIZATION OF ANIMAL NUMBERS

2. THE PINE LOOPER*

by

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SUMMARY

To test the hypothesis that the density-dependent mortality of advanced larvae of the pine looper kept density within limits (i.e. "regulated"), the fluctuations of numbers in the field population studied by Klomp are compared with those in the null model in which, on average, this mortality of older larvae is kept at the field level, but the density dependence is removed. It is concluded that the density-dependent mortality of advanced larvae, whether or not in concert with the following density-dependent reduction of fecundity, did not regulate density, but rather had a somewhat destabilizing influence by increasing the chance that very low densities are reached. In an earlier paper the same effect was shown to occur in the winter moth population studied by Varley and Gradwell. It is suggested that this destabilizing tendency may result from the fact that the action of a significantly density-dependent factor can be frustrated by correlations with other, more independent and mutually non-randomly interrelated, mortality factors, by which the potentially stabilizing effect can get lost, and may even turn into the reverse.

INTRODUCTION

This article is published in memory of Herman Klomp with whom in the course of about twenty years, I frequently and thoroughly discussed problems concerning the persistence of populations. We were both convinced that significant evolution results from continuing selection processes, which we agreed will occur only in long-persisting populations. Klomp thought that populations could only persist long enough for this to happen, if density was kept—"regulated"—within safe limits by powerful density-dependent processes. Otherwise, density would rapidly "random-walk", either to extinction or to catastrophically high values (KLOMP, 1962). In particular, I did not agree with the latter statement. In my opinion, the trend of density will depend on the parameters of the frequency distribution of the multiplication factors (R = net reproduction), which determine the

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random walk of densities. Also, I could imagine random walks that would let density fluctuate within restricted bounds, for hundreds of years. Such favourable distributions of R-values might result, for instance, from a large number of factors, each independently affecting density, because there is, then, a good chance that the influence of one factor will be levelled, or even nullified, by the effects of others (DEN BOER, 1966). Klomp, however, objected that it can hardly be expected that the effects of such "non-reactive" factors would balance one another, so that mean $\ln R$ would be kept very close to zero, a necessary condition to avoid a significant trend of numbers. My answer was that populations which do not conform to this condition—which in my opinion is less critical than supposed by Klomp—would have a low chance of being observed (especially if mean $\ln R < 0$), because they would rapidly become extinct. In other words, the populations we study form a biased sample with respect to distributions of R-values.

This controversy dominated the meetings of the "Discussion group for population dynamics" (founded in 1962 by Klomp and Kluyver) for some years, and led me to formulate the concept of "spreading of risk" (DEN BOER, 1968). Although it could be shown (REDDINGIUS & DEN BOER, 1970) that spreading of risk may significantly contribute to the stabilization of animal numbers, and thus could be an alternative to regulation of numbers, it was not possible to prove which of these two (or possibly other) principles was generally responsible for the supposed persistence of natural populations. REDDINGIUS (1971), who thoroughly examined this question, concluded that the regulation hypothesis loses much of its deterministic rigidity, and probably also much of its appeal to many population ecologists, when it is generalized to a more realistic, *i.e.* probabilistic, model. On the other hand, however, "spreading of risk" is modelled in probabilistic terms, quite naturally. Therefore, he advised that population hypotheses should be formulated in probabilistic terms, and he recognized the potential role of spreading of risk in the stabilization of numbers. However, this is not to say that regulation of numbers may not play a part in the persistence of natural populations. Therefore, Klomp had good reasons to continue his search for the "regulating mechanism" of the pine looper (*Bupalus piniarius*) population, which he studied for many years.

In the following I will try to evaluate the stabilizing influence of the density-dependent processes found by Klomp, and which he expected to make some contribution to the "regulation of numbers" of this pine looper population.

THE PINE LOOPER

In his monograph on the dynamics of the pine looper population of "Hoge Veluwe" (near Otterlo, The Netherlands) KLOMP (1966) carefully discussed all aspects of his investigation. We will only be engaged here with his key-factor analysis, as described by VARLEY & GRADWELL (1960), which he adopted to evaluate the influence of density-dependent factors on the pattern of density fluctuations. The relevant data on densities in successive stages of the life cycle are brought together in table I. I could use only the data from 1953 onwards, because only in that year did Klomp discriminate between the mortality of older larvae in September and October (k_4 and k_5 respectively), which appears to be distinctly density-dependent, and the mortality of nymphs in November (k_6), which is not density-dependent. In table II the densities of four stages, *viz.* pupae in April, reproducing females, eggs, and older larvae in September, are presented as \log_{10} -values, together with the values (k) of the different mortality factors, which are the differences between the \log_{10} -values of two succeeding stages in table I (*e.g.* $k_8 + k_9$ in 1956 = $\log_{10}(2.58) - \log_{10}(1.52) = 0.4116 - 0.1818 = 0.230$).

To discover the key factor (MORRIS, 1963), *i.e.* the mortality factor with the greatest variation in effect between years, and which therefore is expected to govern the pattern of density fluctuations, the changes in time of each mortality factor, distinguished by Klomp, are compared with changes in the total generation mortality (K): fig. 1. It will be obvious that k_{1-3} , egg mortality (k_1) + juvenile mortality of larvae I (k_2) and of larvae II/III (k_3), can be considered the key factor, because the variation in total generation mortality ($K = k_1 + k_2 + \dots + k_{12}$) mainly results from that in k_{1-3} (correlation(Pearson) \bar{K}/k_{1-3} : $r = +0.78$, $P = 0.006$); compare table III, from which will be clear that also $k_1 + k_2$ can be considered the key factor. Figure 1 next shows that $k_4 + k_5$ has some tendency (though not significantly so: $r = +0.13$) to be low when the values of K are highest. This results from the density-dependent relationship between the magnitude of this mortality and the density of the larvae in September, on which it acts: ρ (Spearman) = $+0.77$ ($P = 0.01$). Curiously enough, high densities of larvae in September not only coincide with a high mortality of these larvae ($k_4 + k_5$), but also with a relatively high reduction of fecundity (k_{12}) of the moths that develop from the surviving larvae: $\rho = +0.76$ ($P = 0.016$). See also table III. On average $k_4 + k_5 + k_{12}$ is responsible for 18.3% of generation mortality (K), but the variation in this mortality from year to year is high (table IV: between 1.4 and 34.0%). The correlation of larvae Sept. to $k_4 + k_5 + k_{12}$ is $\rho = +0.78$

TABLE I
Population dynamics of the pine looper (*Bupalus piniarius* L.). From tabulated data of Klomp (1966).

Mean number/m ²	1953	1954	1955	1956	1957	1958	1959	1960	1961	1962	1963	1964	Mortality factors
pupae in April (from Table VIII)	0.73	3.00	3.00	2.58	1.67	0.12	0.87	1.13	2.25	3.38	5.04	4.63	$k_8 + k_9$
moths in June (from Table X)	0.10	1.05	1.42	1.52	0.90	0.10	0.48	0.58	1.50	2.13	1.08	0.83	$k_{10} = \text{sex ratio}$
female moths (from Table XXIII)	0.04	0.52	0.61	0.67	0.47	0.04	0.21	0.28	0.79	0.86	0.54	0.44	k_{11}
reproducing females (calculated from Table XXIII)	0.0355	0.296	0.192	0.35	0.136	0.025	0.114	0.145	0.311	0.59	0.26	0.24	$k_{12} = \text{reduction of fecundity}$
fecundity/female (Table XXIII)	178	205	172	166	161	216	210	192	196	168	181	175	
eggs in July (from Table III)	6.3	61	33	58	22	5.4	24	28	61	99	47	42	$k_1 + k_2$
larvae in August (from Table IV)	4.5	11.5	13.9	15.1	1.8	3.6	5.8	7.5	26.3	24.8	18.3	6.5	k_3
larvae in September (Table XXIII)	4.5	11.5	12.0	12.2	0.8	2.2	3.7	6.5	25.6	(20.1)	18.3	3.7	k_4
larvae in October (Table XXIII)	4.6	9.0	7.4	8.7	0.8	2.5	2.9	-	-	14.8	12.5	2.3	k_5
nymphs in November (from Table V)	2.5	3.46	3.23	4.13	0.73	1.84	1.92	3.64	6.22	8.36	8.58	1.62	k_6
pupae in December (Table XXIII)	3.0	3.3	2.7	1.8	0.13	1.0	1.2	2.3	3.5	5.5	4.9		k_7
(pupae in April of next year)	(3.0)	(3.0)	(2.58)	(1.67)	(0.12)	(0.87)	(1.13)	(2.25)	(3.38)	(5.04)	(4.63)		

The mortality- (k -) factor is that factor by which the density in some stage has to be divided to get the density in the next stage, expressed as logarithms at base 10. For example: to get the density of moths in June 1953, *i.e.* 0.10, the density of pupae in April 1953, *i.e.* 0.73, has to be divided by 7.3, or \log_{10} (pupae in April) ($= -0.137$) has to be diminished by 0.863 ($= k_8 + k_9$) to get at \log_{10} (moths in June) ($= -1.0$); see table II. In the same way is k_{10} (sex ratio) $\log_{10}[1/(\text{fraction females})]$, *e.g.* in 1954 $k_{10} = \log_{10}$ (moths in June) $= 0.021$ minus \log_{10} (female moths) $= -0.284$, *i.e.* 0.305 (table II). $k_{12} = \text{reduction of fecundity}$ as compared with the highest value of mean fecundity estimated in the study, *i.e.* 216 in 1958; thus *e.g.* in 1955 $k_{12} = \log_{10}(216) - \log_{10}(172) = 2.3345 - 2.2344 = 0.099$ (table II).

TABLE II
Key-factor analysis of the pine looper on the data of table I

	1953	1954	1955	1956	1957	1958	1959	1960	1961	1962	1963	1964	Var.	mean values larvae	Q	Q
log ₁₀ pupae	-0.137	0.477	0.477	0.41	0.223	-0.92	-0.060	0.053	0.352	0.529	0.702	0.666	0.204	0.264		
k ₈ + k ₉	0.863	0.456	0.325	0.230	0.268	0.08	0.258	0.29	0.176	0.201	0.669	0.747	0.062	0.336		
k ₁₀	0.398	0.305	0.367	0.356	0.282	0.398	0.359	0.316	0.278	0.394	0.301	0.276	0.0023	0.33		
k ₁₁	0.052	0.245	0.502	0.282	0.539	0.204	0.265	0.286	0.405	0.164	0.317	0.263	0.0186	0.316		
log ₁₀ repr. Q	-1.45	-0.53	-0.717	-0.456	-0.866	-1.602	-0.943	-0.839	-0.507	-0.229	-0.585	-0.62	0.161	-0.718	-0.779	
k ₁₂	0.084	0.0227	0.099	0.114	0.1276	0.	0.012	0.051	0.042	0.109	0.076	0.091	0.0018	0.068	0.067	
log ₁₀ eggs	0.799	1.785	1.52	1.763	1.34	0.732	1.38	1.447	1.785	2.00	1.672	1.623	0.150	1.55	1.487	
k ₁ + k ₂	0.146	0.725	0.375	0.584	1.087	0.176	0.617	0.572	0.365	0.601	0.41	0.81	0.071	0.575	0.514	
k ₃	0.	0.	0.064	0.093	0.352	0.214	0.195	0.062	0.012	0.091	0.	0.245	0.013	0.121	0.098	
log ₁₀ larvae	0.653	1.06	1.08	1.086	-0.097	0.342	0.568	0.813	1.408	1.303	1.262	0.568	0.199	0.837		
k ₄ + k ₅	0.248	0.5216	0.57	0.47	0.04	0.078	0.285	0.252	0.614	0.381	0.329	(0.359)	0.0325	0.3444		
k ₆	-0.072	0.02	0.078	0.361	0.749	0.265	0.204	0.199	0.25	0.182	0.243	0.045	0.045	0.225		
k ₇	0.	0.041	0.02	0.033	0.035	0.06	0.026	0.01	0.015	0.038	0.025	0.0003	0.0003	0.0275		
log ₁₀ pupae (next year: above)	(0.477)	(0.477)	(0.41)	(0.223)	(-0.92)	(-0.06)	(0.053)	(0.352)	(0.529)	(0.702)	(0.666)					
K: generation mort.	1.35	2.60	2.09	2.76	2.945	1.69	2.27	2.00	2.124	2.66	2.38		0.228	2.26		

As densities and mortalities are given in this table as log₁₀-values density changes from year to year are transformed into subtractions and additions, e.g. log₁₀ (larvae '54) = log₁₀(larvae '53) - (k₄ + k₅)('53) - k₆('53) - k₇('53) - (k₈ + k₉)('54) - k₁₀('54) - k₁₁('54) + log₁₀(210) - k₁₂('54) - (k₁ + k₂)('54) - k₃('54) = 0.653 - 0.248 - (-0.072) - 0. - 0.456 - 0.305 - 0.245 + 2.3345 - 0.0227 - 0.725 - 0. = 1.06. This also means that in calculations on the dynamics of larvae in the mean values of mortality factors the values of k₈ + k₉, k₁₀, k₁₁, k₁₂, k₁ + k₂, k₃ for 1953, and of k₄ + k₅ for 1964, are not included (see column: mean values, larvae).

In the same way log₁₀ (repr. Q '54) = log₁₀ (repr. Q '53) + log₁₀ (216) - k₁₂('53) - (k₁ + k₂) ('53) - k₃('53) - k₄('53) - k₅('53) - k₆('53) - k₇('53) - (k₈ + k₉)('54) - k₁₀('54) - k₁₁('54) = -1.45 + 2.3345 - 0.084 - 0.146 - 0. - 0.248 - (-0.072) - 0. - 0.456 - 0.305 - 0.245 = -0.53. In calculations on the dynamics of reproducing females in the mean values of mortality factors the values of k₈ + k₉, k₁₀ and k₁₁ for 1953, and of k₁₂, k₁ + k₂, k₃ and k₄ + k₅ for 1964, are not included (see column: mean values, Q Q).

Var. = Variances, which are calculated over all values. Note that K (generation mort.) = k₁ + k₂ +k₁₂.

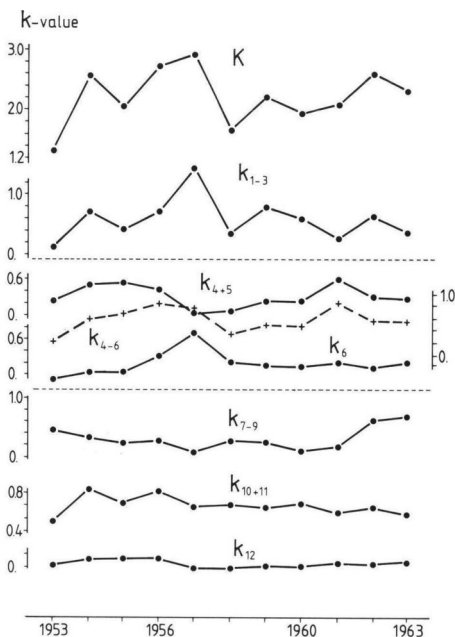


Fig. 1. Key-factor analysis of the pine looper population at "Hoge Veluwe" (The Netherlands). Modified from KLOMP (1966). For further expansion see the tables I and II.

($P = 0.014$). No other k -factors showed significant correlations with the densities on which they act.

We are thus left with two interesting questions concerning the regulation of the numbers of the pine looper:

- (1) What are the causes of the density-dependent relationship between larval mortality in September ($k_4 + k_5$) and the subsequent fecundity (k_{12})?
- (2) Can the population be "regulated" by only 18% of generation mortality, in spite of the fact that the variance of $k_4 + k_5$ (table II: 0.0325) is smaller than that of the key factor (table II: 0.071)?

TABLE III

Product-moment (Pearson) correlations (r) between total mortality (K) and composing mortality factors (k), as well as between the different mortality factors mutually; $100r^2 =$ % variation "explained" by that variable.

	$k_1 + k_2$	k_3	$k_4 + k_5$	k_6	k_7	$k_8 + k_9$	k_{10}	k_{11}	k_{12}
K	0.854	0.326	0.128	0.521	0.386	-0.018	0.107	0.338	0.312
$100r^2$	72.89	10.60	1.63	27.11	14.91	0.03	1.15	11.14	9.74
$k_1 + k_2$	1	0.526	-0.162	0.658	0.219	-0.300	0.232	0.220	-0.086
k_3		1	-0.701	0.783	0.486	-0.476	0.374	-0.251	-0.618
$k_4 + k_5$			1	-0.462	-0.261	0.102	0.035	0.273	0.927
k_6				1	0.347	-0.386	0.305	-0.195	-0.290
k_7					1	-0.013	0.282	0.204	-0.094
$k_8 + k_9$						1	-0.568	-0.013	0.203
k_{10}							1	-0.424	-0.142
k_{11}								1	0.417
k_{12}									1

Note: Correlations between mortality factors are taken in the normal time order only, e.g. $k_1 + k_2$ with the $k_8 + k_9$ -values following in time (next year). If $|r| \geq 0.602$ the correlation is significant at 5%.

TABLE IV

Proportional share (%) of the different mortality factors in total mortality (K) in different years.

	1953	1954	1955	1956	1957	1958	1959	1960	1961	1962	1963	1964	mean
$k_1 + k_2$	10.8	27.9	17.9	21.2	36.9	10.4	27.2	30.9	17.2	22.6	17.2		22.8
k_3	0	0	3.1	3.4	11.9	12.7	8.6	3.1	0.6	3.4	0		4.4
$k_4 + k_5$	18.4	20.1	27.3	17.0	1.4	4.6	12.6	12.6	28.9	14.3	13.8		15.3
k_6	-5.3	0.8	3.7	13.1	25.4	15.7	9.0	10.0	11.8	6.8	10.2		10.0
k_7	0	1.6	1.0	1.2	1.2	3.6	1.1	0.5	0.7	1.4	1.1		1.2
$k_8 + k_9$		33.8	12.5	11.0	9.7	2.7	15.3	12.8	8.8	9.5	25.2	31.4	14.9
k_{10}		22.6	14.1	17.0	10.2	13.5	21.2	13.9	13.9	18.5	11.3	11.6	14.7
k_{11}		18.1	19.3	13.5	19.5	6.9	15.7	12.6	20.3	7.7	11.9	11.1	14.0
k_{12}		1.7	3.8	5.5	4.6	0	0.7	2.2	2.1	5.1	2.9	3.8	3.0
$k_4 + k_5 +$													
k_{12}		20.1	23.9	32.8	21.6	1.4	5.3	14.8	14.7	34.0	17.2	17.6	18.3

Note: $K = k_1 + k_2 + k_3 + k_4 + k_5 + k_6 + k_7$ of year(t) + $k_8 + k_9 + k_{10} + k_{11} + k_{12}$ of year(t+1).

The first question was studied by GRUYS (1970, 1971). He found that advanced larvae which make contact during the night will regurgitate gut fluid, and transmit it to each other. Because of this, growth is reduced, and this results in smaller moths with lowered fecundity. However, larval and pupal mortality, longevity of the adults, and viability of the progeny are all unaffected by these nocturnal encounters of older larvae. It had already been shown by KLOMP (1958) that the density-related reduction of fecundity (k_{12}) cannot regulate population density. He rightly concluded that the range of reduction is much too small for that (KLOMP, 1966); see also table II ($\text{Var} = 0.0018$) and table IV. This is confirmed by fig. 2: over the entire range of densities a higher density of reproducing females results in a nearly proportional increase in the density of eggs (*i.e.* the regression coefficient hardly differs from unity). GRUYS (1971) suggested that the smaller moths, which result from the density-related growth reduction of advanced larvae, might have an increased likelihood of dispersal from the population (because of a more favourable wing-loading), and that this would restrict density in the next generation. However, BOTTERWEG (1978) showed that this hypothesis also has to be rejected, because dispersal is low, and neither density-related nor dependent on moth size. KLOMP (1966) supposed that, because of the nearly perfect concealment of the older larvae, mutual interference among them might result in spacing them out, so that they would be more difficult to find by bird predators, that hunt by sight. However, if this supposition is right the spacing behaviour cannot be very effective, because $k_4 + k_5$, which results from bird predation and from disease, is still highly density-dependent. Moreover, GRUYS (1971) did not find indications that grouped larvae showed any increased tendency to space out. What then might be the biological function—if any—of the remarkable “territorial behaviour” of the advanced larvae?

Concerning the second question, KLOMP (1966) had serious doubts himself (p. 292), and did not reach any conclusion about the possible regulating effects of the density-dependent mortality of advanced larvae ($k_4 + k_5$), whether or not in concert with the following reduction of fecundity (k_{12}). It, therefore, seems useful to apply the test that was developed for the winter moth in Wytham Wood (DEN BOER, 1986a) to the data for the pine looper at “Hoge Veluwe”, to investigate the likely effects of the density-dependent factors.

METHODS AND RESULTS

VARLEY *et al* (1973: 19) defined “a regulated population” to be: “one which tends to return to an equilibrium density following any depar-

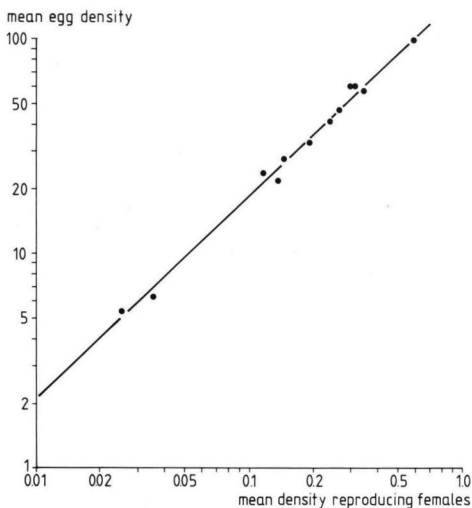


Fig. 2. Relationship between $\log_{10}(\text{mean density of reproducing females}) = X$ and $\log_{10}(\text{mean egg density}) = Y$ to show the effect of the density-dependent reduction of fecundity in the pine looper at "Hoge Veluwe". Productmoment corr.(r) = +0.95 (n = 12), ρ (Spearman) = +0.97 (P = 0.001); line of least squares $Y = a + bX = 2.23366 + 0.9587X$.

ture from this level". This is thought to be brought about by density-dependent processes: "Density dependent mortality serves to regulate the population density and keeps it within limits" (VARLEY *et al.*, 1973: 112). Therefore, I will compare the limits of density as LR (Logarithmic Range: DEN BOER, 1971) = $\log_{10}(\text{highest density}) - \log_{10}(\text{lowest density})$, with and without the density-dependent effects (*ceteris paribus*). To be sure that the density-dependent effect of $k_4 + k_5$ is not made ineffective by factors operating on stages which follow, and is not lost before the next generation, I will mainly apply the test to the density of advanced larvae in September, *i.e.* just before the operation of $k_4 + k_5$.

Before applying the test I will first consider separate generations, with and without density dependence. Starting from the actual larval

density in year t (N_t), larval density in year $t + 1$ is computed with $k_4 + k_5$ fixed at its mean value (0.3444; table II). For each generation, this calculated value $N_{i,t+1}$ —from which density dependence is thus removed—is plotted against the observed value N_{t+1} fig. 3A. This figure shows whether or not density dependence resulted in a direct and general limitation of high densities ($N_{i,t+1} > N_{t+1}$, *i.e.* black dots above vertical bar = mean) or low densities ($N_{t+1} > N_{i,t+1}$, *i.e.* black dots below the mean). It appears from these data that the density dependence of $k_4 + k_5$ has indeed some effect on the density of larvae in the next generation: high densities (except for the highest one!) are somewhat restricted, and low densities (except for the lowest one!) are increased.

If we fix all k -values, except $k_4 + k_5$, at their mean values (table II), comparison of the $N_{i,t+1}$'s, then computed, with the observed N_{t+1} 's will give some idea of the maximum possible power of the density dependence of $k_4 + k_5$ in separate generations (fig. 3B), *i.e.* if *Bupalus* exists in an otherwise (demographically) constant environment. Figure 3B shows that potentially the density dependence of $k_4 + k_5$ is not powerless: on average, high densities are reduced by about 19%, and low densities increased by as much as 68%! Although such effects cannot be expected to operate each year (not in 3 out of 11 years: open circles), they most probably would keep density within limits. However, in each generation, the density of advanced larvae of the pine looper is also affected, of course, by other powerful variables, *e.g.*—apart from the key factor—by $k_8 + k_9$ (pupal mortality between December and April from predators, parasitoids and disease). This is responsible for an average mortality of 15% (table IV), and shows a higher variance (table II: 0.062) than $k_4 + k_5$. Nevertheless, even under field conditions, the density dependence of $k_4 + k_5$ might still have some effect in the next generation: on average high densities are restricted by about 6.7% and low densities increased by 24.8% (fig. 3A).

In spite of this encouraging result, we still do not know whether $k_4 + k_5$ indeed kept the density of advanced larvae of the pine looper within limits. To show that, we have to demonstrate that the net effects of $k_4 + k_5$ in separate generations accumulated in such a way that, during the eleven years of the study, density was kept within narrower limits with, than it would have been without, density dependence. Therefore we have to consider the entire time series.

Starting from the density of larvae in September 1953, *i.e.* 4.5 (table I; $\log_{10} = 0.653$, table II), all other larval densities were calculated anew, in a single run from the data in table II, but now with $k_4 + k_5$ fixed at its mean value (= 0.3444) in each generation. To avoid the

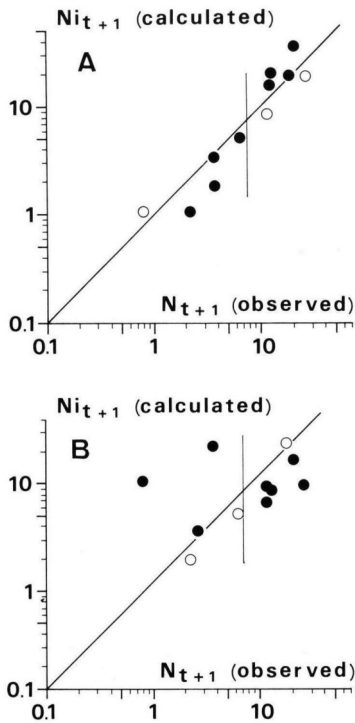


Fig. 3. Possible effects of the density-dependent mortality of advanced larvae ($k_4 + k_5$) on larval density in the next generation of the pine looper at "Hoge Veluwe". **A.** The effect of $k_4 + k_5$ in the field: for each generation actual larval density (N_{t+1}) is plotted against the value calculated after having fixed $k_4 + k_5$ at its mean value ($N_{i,t+1}$). Black dots: observed densities less extreme than calculated ($k_4 + k_5$ had a stabilizing effect); open circles: observed densities more extreme than calculated ($k_4 + k_5$ had a destabilizing effect). **B.** Maximally possible effect of $k_4 + k_5$: for each generation the field value of larval density (N_{t+1}) is plotted against the value computed after having fixed all k -values—except $k_4 + k_5$ —at their respective mean values ($N_{i,t+1}$). Black dots: calculated values more stabilizing than field data; open circles: calculated values less stabilizing than observed densities.

Vertical line: mean value of $\log_{10}(N_{t+1})$.

accumulation of small inaccuracies in this long computation, it is best first to calculate for each generation the new coefficient of net reproduction R'_t according to $\log_{10}R'_t = \log_{10}N'_{t+1} - \log_{10}N_t$ if $\log_{10}N'_{t+1} = \log_{10}N_{t+1} + [(k_4 + k_5)_t - 0.3444]$, and $R'_t = \text{antilog}(\log_{10}R'_t)$. For instance, $\log_{10}N'_{54} = 1.06 + (0.248 - 0.3444) = 0.9636$, by which $\log_{10}R'_{53} = 0.9636 - 0.653 = 0.3106$, and $R'_{53} = 2.045$. By multiplying the successive R' -values (starting from 4.5), the successive densities in the new time series can be simulated: fig. 4. Comparison of the "Logarithmic Range" (LR) of the new time series with that of the field data will tell us whether the density dependence of $k_4 + k_5$ kept density within narrower limits than without density dependence.

It is clear from fig. 4 that the density dependence of $k_4 + k_5$ did not keep larval density in September within limits. The density range was even wider (LR = 1.51) with, than without (LR = 1.06), density dependence (table V). Although the density dependence of $k_4 + k_5$ restricted density in 1956, it was at the same time responsible for the dangerously low density in 1957, and it also resulted in a very high density in 1961. Apparently, positive effects in separate generations (such as in fig. 3) do not necessarily predict the course of density in the whole time series, as was pointed out previously by MILNE (1962) and by DEN BOER (1968). It may be suggested that this contradiction could have something to do with the imperfection of the density-dependent relationship under field conditions. If we replace the values of $k_4 + k_5$ by $0.381164 \cdot \log_{10}(\text{larval density in Sept.})$ —from the least squares line of $k_4 + k_5$ on $\log_{10}(\text{larval density in Sept.})$ —we remove this imperfection by making $k_4 + k_5$ "deterministically" density-dependent, without changing the average mortality. Figure 4 shows that this does not solve the above problem: the density in 1956 is more extreme and that in 1957 somewhat less extreme than in the field, but neither is any better than in the case without any density dependence: LR = 1.32, *i.e.* intermediate between cases (1) and (2) of table V.

Hence, even if the density dependence of $k_4 + k_5$ exerted its full power, it would not have kept larval density in September within narrower limits than without any density dependence in this mortality, *i.e.* $k_4 + k_5$ could not regulate density. This becomes even more obvious if we apply our test to other stages of the life cycle: whether $k_4 + k_5$ is density-dependent or not does not appreciably influence the limits of density of either reproducing females, or eggs, or pupae in April, table V, (1) and (2). This may partly be caused by k_6 , being somewhat antagonistic to $k_4 + k_5$ ($r = -0.46$, table III), see also fig. 1. In some years k_6 will immediately nullify the effect of $k_4 + k_5$; compare table V, (2) and (4). Also taking into account the density

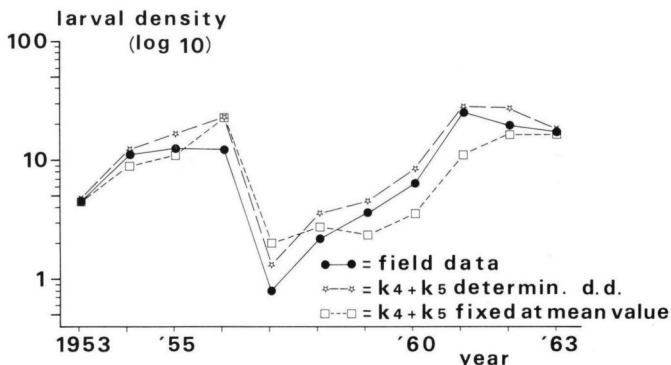


Fig. 4. Pattern of density fluctuations of advanced larvae of the pine looper in time series. The fluctuations of numbers in the field data ($LR = 1.51$) are compared with those of the series with $k_4 + k_5$ deterministically density-dependent ($LR = 1.32$), and with the fluctuations in the series with the density dependence removed, *i.e.* $k_4 + k_5$ fixed at its mean value ($LR = 1.06$). See table III, (1) and (2).

dependence of the reduction of fecundity (k_{12}) does not change the results of our test: table V, (3).

Objection may still be made, that fixing $k_4 + k_5$ at its mean value takes away part of the variation of mortality, which may reduce the range of variation in density. However, the likelihood that fixing a variable, which operates in the midst of other variables with the same or greater variances, would reduce overall variability, will not be very high. Nevertheless, it seems useful to allocate to $k_4 + k_5$ random values in time, either according to a fitted normal distribution, or—which is much better—according to the frequency distribution of the actual $k_4 + k_5$ -values, in such a way that the sum of the simulated $k_4 + k_5$ -values does not deviate more than 2% (say) from the sum of the field values (table II). If we repeatedly allocate random values to $k_4 + k_5$ according to a normal distribution fitted to the field data, LR of advanced larvae in September is greater than in the field (1.51) in only 11 cases, and smaller or equal in 87 cases ($\chi^2 = 58.9$, $P < 0.001$; mean $LR = 1.24$). When simulating a frequency distribution that accurately fits that of the field data for $k_4 + k_5$ (*i.e.* with 6 classes of 0.10 between 0.03 and 0.63, and with frequencies 2,0,3,2,2,2 respectively, table II) we get only 5 cases with $LR > 1.51$ and 79 cases with $LR < 1.51$ ($\chi^2 = 65.2$, $P < 0.001$; mean $LR = 1.24$), and in another simulation mean $LR = 1.17$ (in all cases $LR < 1.51$).

TABLE V

Influence of the different mortality factors on the fluctuation pattern of numbers in different stages of the pine looper as expressed by the limits of density, *i.e.* LR [$= \log_{10}$ (highest density)— \log_{10} (lowest density)] of the pertinent time series.

	<i>larvae in Sept.</i>	<i>repr. ♀ ♀</i>	<i>eggs</i>	<i>pupae in April</i>	
no change: field data	1.51	1.37	1.26	1.62	(1)
$k_4 + k_5$ fixed at mean value	1.06	1.34	1.27	1.51	(2)
$k_4 + k_5 + k_{12}$ fixed	1.03	1.31	1.30	1.40	(3)
$k_4 + k_5 + k_6$ fixed	1.49	1.24	1.21	1.48	(4)
$k_1 + k_2 + k_3$ fixed	1.12	1.35	1.34	1.46	(5)
$k_8 + k_9$ fixed	1.48	1.69	1.67	1.68	(6)

The above simulations tell us the same as before: the density dependence of $k_4 + k_5$ did not contribute to regulation of density—in the sense of “keeping the population within limits”. On the contrary, in all cases, the limits of density were wider—or more often wider—with than without density dependence. We have already seen (table V) that something similar can be said of other stages of the life cycle. In this respect, $k_4 + k_5$ does not differ from other, non-density-dependent, mortality factors: table V, (4), (5), (6). This remarkable “insensitivity” of the density range to the removal of the variance of one or other mortality factors probably results from these variances (and/or averages) not being very different from each other: $\text{Var}(k_{4-6}) = 0.044$ (mean 0.57), $\text{Var}(k_8 + k_9) = 0.062$ (mean 0.336), $\text{Var}(k_{1-3}) = 0.12$ (mean 0.67)—see also table II—by which none of these factors, not even the “key factor” k_{1-3} , will conspicuously dominate total mortality K ($\text{Var} = 0.228$, $\text{mean} = 2.26$; table II). Otherwise is it not clear why the density range of larvae in September “reacts” most to fixing just one of the mortality factors. It seems unlikely that this is because this density is reached just after the action of k_{1-3} (the key factor), and just before that of $k_4 + k_5$, since $k_1 + k_2$ is not correlated with $k_4 + k_5$ (table III), as it appeared to be the case in the winter moth (DEN BOER, 1986a). Note that k_3 , which shows an interesting correlation with $k_4 + k_5$ (table III) has a too small effect (table IV) to have any appreciable influence.

The conclusion from these tests is, that if a density-dependent process acts on the same numbers—though not in the same stage of the life cycle—as other variables with similar, or greater, variances, the resulting pattern of density fluctuations will be unpredictable, or at least not more predictable than the effect of these other variables on density (compare the problems concerning weather-forecasts for more than one or two days ahead). In the present case of the pine looper at “Hoge Veluwe” this means that the doubts expressed by KLOMP (1966) were justified: the density dependent processes found operating were insufficient to keep density within limits.

DISCUSSION

Just as in the winter moth (DEN BOER, 1986a), in the pine looper the density-dependent mortality did not keep density within limits, but rather has a destabilizing influence on the density of larvae. This destabilizing effect resulted in a higher $\text{Var}(\log_{10}R) = 0.363$ of field data than in a series with $k_4 + k_5$ fixed at its mean value ($\text{Var}(\log_{10}R') = 0.211$). The same was found in the winter moth: $\text{Var}(\log_{10}R) = 0.226$, $\text{Var}(\log_{10}R') = 0.107$ (DEN BOER, 1986a; table 3). Because of this, the density ranges of (500) time series with permuted R-values (from the field data) are generally wider than those of time series with permuted R'-values (from the series with $k_4 + k_5$ fixed). The chance of the density of a permuted time series staying within the range of the field data ($LR = 1.51$) in the first case is only 0.082 (or 0.080 for reproducing females), in the latter case 0.59. In the winter moth these chances were 0.052 (or 0.046) and 0.37 respectively. This means that, in both species, the density dependence of part of mortality increased the chance of reaching extreme (especially low; see fig. 4, and DEN BOER, 1986a: fig. 2) densities, instead of “keeping density within limits” (compare: DEN BOER, 1968: 184). As in the winter moth, the density-dependent pupal mortality makes up a greater part of total mortality (35% on average) than mortality of advanced larvae in the pine looper (15% on average), it is understandable why in the winter moth the destabilizing effect of the density dependence extends over other stages of the life cycle as well (see table 3, (1), (2) and (3) in DEN BOER, 1986a), whereas in the pine looper it does not: table V, (1) and (2).

Why does the density dependence of larval(pupal) mortality have a destabilizing, rather than a stabilizing effect in both species? In my opinion, this results from the fact that density is influenced by a number of different mortality factors that are both mutually correlated to different extents (table III) and have quantitative effects that are not

less than those of $k_4 + k_5$ in most years (table IV). This also means, that if these mortality factors would have been differently—especially less—correlated mutually, and/or the more independent factors would have formed a lower part of total mortality, the density dependence of larval(pupal) mortality might not necessarily have had a destabilizing but possibly even a favourable effect (see also: DEN BOER, *in prep.*). However, such a more favourable effect of density-dependent mortality does not imply that it would have “regulated” the population. Moreover, such speculations do not apply to the reality under consideration: the pine looper at “Hoge Veluwe”, or the winter moth at Wytham Wood. Each case will have to be considered separately. More generally, we may expect that only if the density-dependent factor also is the key factor may it govern the complex of other factors and thus also the range of densities, although even then this is not necessarily so.

Does this mean that in most cases the persistence of populations is only a matter of good luck? I don't know, because much depends on what is meant by “population”. For instance, if a species occupies a large and demographically heterogeneous area, the risk of extinction will be spread over the different population units (subpopulations), and will thus be diminished. DEN BOER (1981) showed that, because of this risk spreading, the carabid beetle *Pterostichus versicolor* can be expected to survive at the Heath of Kralo and Dwingeloo (1200 ha) for many thousands of years (*ceteris paribus*). Is that merely a matter of good luck? Not more and not less than adaptation as a result of natural selection is only a matter of “good luck” (see *e.g.* EHRLICH & HOLM, 1963: 120-122). Be that as it may, it at least makes the persistence of natural populations and species comprehensible; see also: DEN BOER (1986b).

But can it be expected that a number of “non-reactive” factors will balance one another, without any feedback, such that mean $\ln R$ will keep close to zero? This was the main objection of Klomp to my ideas. As far as I can see, we indeed cannot expect this generally to occur. In population units (interaction groups: DEN BOER, 1981) of the carabid species studied, mean $\ln R$ varied widely, on average between +0.1 and -0.1 in only 50% of 62 species, between +0.2 and -0.2 in 84%, and between +0.3 and -0.3 in 90% of the species (DEN BOER, 1985, fig. 5). At the same time, this means that most population units will not survive for very long: on average less than 10 years in 31% of 65 carabid species, in 54% < 20 years, in 77% < 50 years, and in 88% < 100 years (DEN BOER, 1985, fig. 3).

However, if such population units are parts of a multipartite population (ANDREWARTHA & BIRCH, 1984), with exchange of

individuals between subpopulations, such short-lived units will not usually endanger the persistence of the (natural) whole population, because not all units will die out in the same generation, and refounding of subpopulations will occur with relative ease. With the help of stochastic modelling, under very broad conditions I could show (unpublished) that multipartite populations, consisting of about a hundred units, which die out and are refounded randomly with on average similar frequency, will survive for some geological periods (*ceteris paribus*). It is expected that the same will also apply to many multipartite populations, that consist of less than a hundred units, especially if the mean survival times of subpopulations are in the order of decades instead of years (compare: DEN BOER, 1981). In fact, in my opinion, this solves the problem of the persistence of natural populations, because these generally will be multipartite: ANDREWARTHA & BIRCH (1984). However, this also means that if such a multipartite population is considered as a single and uniform population, *i.e.* if samples from different subpopulations are considered similar and thus put together (as often will be done), density will appear to be surprisingly stable, and the mean $\ln R$ will often be very close to zero (see DEN BOER, 1986b). However, usually this stability will not have much to do with "regulation", because the latter rests on significant interactions between individuals and therefore by definition operates within population units (interaction groups). This stability will result from spreading the risk of extinction over population units (DEN BOER, 1968, 1981). This means that the controversies about population "regulation" partly result from an inappropriate use of the concept "population". The study of each problem asks for the use of adequate units.

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