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RISK-DISTRIBUTION AND STABILIZATION OF ANIMAL NUMBERS

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1. INTRODUCTORY REMARKS.

1. Introduction (1.1). During the last three or four decades the problem of the apparently long-term existence of insect populations in spite of their often violently fluctuating numbers has intrigued a large number of workers. Many authors have offered "general theories" which range from the maintainance of a "balance" or "equilibrium" by a rigid "regulation"(NICHOLSON,1933;NICHOLSON and BAILEY,1935,WILBERT 1962) through a number of more or less compromising "theories" (e.g.: SOLOMON,1949;MILNE,1957,1962;BODENHEIMER,1958 and many others) to a determination of numbers in each generation by chance, i.e. by the action of a number of "non-reactive" environmental components (BODENHEIMER,1928,1930, ANDREWARTHA and BIRCH,1954).

For a number of years already I have the impression that the degree of "generality" of a "theory" on animal numbers largely depends on the kinds of animals and the kinds of environments known to the author. Since the number of possible and even of realized combinations of populations of animal species with kinds of environments must be astronomically large, I am sure that each author of a sound hypothesis on animal numbers will be able to find examples in nature which confirm his ideas (see also: BAKKER,1964). But this does not mean that his hypothesis is a "general theory". Perhaps some degree of "generality" would be shown by a "theory" based on a hypothesis which relates fluctuations in animal numbers only to the number of influences on it, without the need of specifying these influences; examples of attempts in this direction are the hypothesis of PALMGREN (1949) and COLE (1951,1954,1958) concerning populations cycles.

2. Stabilization (1.2).As an insurance company is able to flourish and to exist for a long time by distributing the risks over a great number of "factors", so an insect population must be able to run through only restricted density fluctuations and to exist for a long time by "distributing the risks" over a great number of "factors". The very number of influences on density (without specifying them in the first instance) in my opinion must have an important stabilizing effect on density fluctuations and will permit an insect population to exist for a considerable time merely by chance. Each factor irrespective its degree of density-dependence will contribute to this relative stabilization of density fluctuations, although some density-dependent factors may have special influences too.

When opposing to the models of KLOMP (1962) on the influence of a meteorological factor I was forced to demonstrate the relatively stabilizing effect of a number of meteorological factors, which gave rise to the construction of a model. Now I am grateful to KLOMP for stimulating me to elaborate these ideas.

In this paper I'll try to test the hypothesis that the fluctuations of insect numbers are relatively stabilized by the number of influences on it and to discuss how far this hypothesis may explain the different aspects of animal numbers known from nature and repeatedly mentioned in the pertaining literature.

3.Literature (1.3 etc.) ....

4.Definitions (1.4) Since the growing confusion in ecological literature is partly due to a loose and inconsistent application of terms, I feel impelled to define and discuss some of the terms which I want to use in this paper. Sometimes the difficulties are obviously connected with a kind of "holistic" reasoning (see:MULLER,1958) and its inevitable attributes (entity, super-organism, regulation,etc.) and sometimes with the contradiction between typological and population thinking (see: MAYR,1963,p.5-6). These problems will be discussed in a separate paper on the concept of "population". Here I will confine myself to mentioning of the resulting points of view.

1.4.1.
By "animal population"is understood: a more or less bounded group of individuals from which samples are taken to get acquainted with a number of quantitative properties (e.g.:relative density, activity rate, sex ratio, mortality rate, birth rate, age distribution, genetic distribution) of the group as a whole. Hence, an animal population is an ecological working-unit comparable with the statistical working-unit "population". The properties derived from an animal population by taking samples in fact are the added-up properties (statistics) of the individuals in the samples (see also:MILNE,1957, 1962 and ANDREWARTHA,1957). In my opinion an "animal population" generally can not be considered an entity comparable with an individual organism (extrapolation of analogies).

1.4.3.
There is a general feeling among population ecologists that the fluctuations of animal numbers are somehow more or less limited, since without limitation we generally expect that extinction or increase to large numbers resulting in collective suicide by exhausting the resources would be the fate of most animal populations within the course of relatively few generations. If we accept for the present the correctness of this feeling, we need a general and unloaded term to indicate this phenomenon. I propose to use the neutral term "stabilization" and to describe this assumed phenomenon: as compared with the expectation (of catastrophes) above mentioned fluctuations in animal numbers are somehow stabilized (= made more stable), without anticipating possible causes and without excluding the possibility of relative stabilization by a number of "non-reactive factors" (by chance).
Some authors have used the term "natural control" to indicate the same phenomenon (e.g.: THOMPSON,1939, 1956; UVAROV,1931; SOLOMON, 1949; MILNE,1957, 1962). In my opinion,however, the word "control" is too strongly associated with directed interference and in order to avoid unintended suggestions and another contribution to the confusion it seems better to me to abandon the term "natural control".

1.4.4.
A number of authors take the stand that animal populations must be "regulated" to be able to exist for a considerable number of generations.
By some of them (especially NICHOLSON,1933,1954,1957; NICHOLSON and BAILEY,1935; PIMENTEL,1961; WILBERT,1962) regulation is assumed to be achieved by one or more "mechanisms" which react on density increase and decrease in such a way that reproduction (and immigration) counterbalances mortality (and emigration) and only restricted fluctuations around a (constant) mean density level result (populations are "balanced", are in "equilibrium"). In the sense of these authors and taking into account 1.4.3. "regulation" should be the only possible form of the relative "stabilization" of fluctuations in animal numbers. In this meaning the term "regulation" is used (as a hypothesis !!) in concordance with its semantic significance and with its application in cybernetics and physiology.
In this paper "regulation" will be used in this way, i.e. in the sense of the operation of one or more negative feed-back mechanisms.
By most of these (and other) authors "regulation" is thought to be brought about by "density-dependent (-governing) factors" (e.g.: LACK,1954; WILBERT,1962; KLOMP,1962;NICHOLSON,1954,1957). In these cases the problem shifts to the part played by "density-dependent factors" in the relative "stabilization" (1.4.3.) of animal numbers.
Since "density-dependent (-governing) factors" can only operate through the chance of individuals to contact directly or indirectly the influence of such "factors" will always increase with growing of this chance (= rate of activity within the population per unit of area and per unit of time). Although this chance will not necessarily be a function of density (see e.g.: PETRUSEWICZ, 1963:

this chance obviously is a function of "population area" in his experiments), for the moment we will continu to speak of "density-dependent factors" (strictly speaking we should say: "factors dependent on activity rate"). If we drop for the moment the generally unimportant "positive density-dependent factors", which above a critical density- (or activity-) level may stimulate an increasing growth of density (e.g.:"conditioning factors") and which will often tend to "destabilize" the fluctuations of animal numbers, we may conclude that (negative) "density-dependent-factors" (the so-called "regulatory factors") always tend to restrict density incrasingly (above a critical density- (or activity-) level, i.e.: the density (better : the rate of activity) at which the chance of contacting between individuals becomes significant). Thus, the influence of such factors is principally one-sided (restricting) and since it is irrelevant and confusing to speak of a "one-sided regulation" or of a "one-sided negative feed-back mechanism", in these cases I prefer to use the term (density-dependent) "restriction" instead of "regulation". It must be noted that below the level of significantly contacting (other than for mating) between the individuals of a population (directly or indirectly) any "perfectly density-dependent influence" (both "positive"and "negative") becomes impossible and the fate of the population will be a matter of chance (see also: MILNE,1957,1962).

If the quantitative influence of a "regulatory mechanism" or of "density-dependent factors" (negative) is "embedded" in dominant quantitative influences of "density-independent (non-reactive)factors" (as will often be the case in nature) there is spoken of a "tendency to regulate" resp.of a "tendency to restrict", in order to indicate that within the course of one or a few generations the quantitative influence of the resulting "regulation" resp."restriction" generally will not be unambiguously measurable (which does not wholly exclude a more important quantitative influence in the long run). These problems will be discussed more ample in a separate paper on the concept of "population", especially in connection with the introduction of cybernetic terms by WILBERT (1962).

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2. STABILIZING EFFECT OF THE NUMBER OF FACTORS: A MODEL.

1. Introduction (2.1). When discussing possible causes of density fluctuations in natural insect populations we have to realize that "density-independent" mortality factors (especially meteorological factors) will always be operating (see e.g. UVAROV,1931) and will generally have a quantitatively important influence- except perhaps in some tropical regions. I am not sure that the same can be said about "density-dependent"factors. This means, that in my opinion it is desirable first to form an adequate notion of the (population) dynamical influence of factors which are always at work (e.g. meteorological factors), before stating that natural insect populations always must be "regulated" (by "density-dependent" factors).

2.1.1.

KLOMP (1962) and WILBERT 1962) discussed the influence of meteorological factors on the density fluctuations of natural insect populations and they concluded that the apparently long-term existence of many insect populations can only be understood if the operation of "density-dependent (-related) factors" is assumed.
I do not exclude the possibility of the operation of "density-dependent factors" in a wide sense. Especially if density becomes high in comparison with the capacity of the resources a (density-dependent) restriction may be expected (1.4.4.)although in some cases "intolerance" (1.4.5) seems already to influence density increase at rather low densities without a noticeable depletion of resources. But this does not mean that the assumption of a continuous operation of "density-dependent factors" is a logical necessity for the understanding of density fluctuations and of the apparently long-term existence of natural insect populations. In my opinion KLOMP (1962) and WILBERT (1962) overlooked the relatively stabilizing effect of the number

of influences of density (1.2 and 1.4.3). I will try to demonstrate this effect with the help of a simple model.

2. Characteristics of fluctuations in animal numbers (2.2).
If we assume for the moment that the density of natural insect populations must be "regulated" in some way (1.4.4.), then, the fluctuations of numbers must show some quantitative characteristics which do not agree with the assumption that only "density-independent factors" are at work, i.e.: under natural conditions characteristics of the fluctuations of animal numbers would show values which would not be observed if only "density-independent factors" were operating.

2.2.1.

In spite of the fact that most ecologists are highly interested in the problem of the "regulation" resp. "non-regulation" of animal numbers, no adequate quantitative analyses of the fluctuations of animal numbers under natural conditions are known to me, except perhaps for analyses intended to prove the presence or absence of "population cycles" (e.g. ELTON,1942; PALMGREN,1949; COLE,1951, 1958 and JOURN.of WILDLIFE MAN,18, 1954). If we try "to read between the lines", we get the impression that most students defending the hypothesis of the "regulation of animal numbers" (1.4.4.) must have some notion of fluctuation-characteristics which confirm their ideas. In as close agreement as possible with these ideas,in the following sections I shall try to define some fluctuation-characteristics which should modestly enable us to describe and compare different sets of fluctuations and to study the quantitative influence of "density independent" and of "density-dependent-factors".

2.2.2.

It is often stated in the literature that animal numbers "fluctuate around a constant mean density level" (e.g. NICHOLSON,1933,1954; SMITH,1935; MORAN,1954; KLOMP,1962). In general it does not become clear from such quotations what is meant by "a constant mean density level". If this level is synonymous with the arithmetic mean the above statement is an evident tautology:each series of unranked numbers between zero and some maximum (given in this case by the absolute spacial capacity of the habitat) "fluctuates around its mean". Probably is meant: if the density-data are divided in a number of equal portions (e.g. ten generations each) and the arithmetic mean of each portion is calculated, these means do not differ significantly. But I don't know of any such test and I wonder whether "a constant mean density level" in this sense often will be found in natural insect populations. Another interpretation is given by KLOMP (pers.comm.): the geometric mean of "the net rates of reproduction" of natural populations would be close to unity. Although in my opinion this is only a useful characteristic for long series (it is highly influenced by the first and by the last density value estimated: $\sqrt[N]{\frac{\text{density in generation n}}{\text{density in generation 0}}}$

it will be used in the following as a statistic indicating the "central tendency" of the set of fluctuations (expressed as the deviation from unity of the geometric mean of the net rates of reproduction).

2.2.3.

It is often stated that natural populations generally show "only restricted fluctuations" (see also: 1.4.3.), sometimes with the addition: "as compared with the theoretical possibilities of geometric increase" (KLOMP,1962, p 69). Besides a statistic indicating "central tendency" (2.2.2.) it is therefore necessary to have a measure for "the range of fluctuation ". As such a measure may be used the range of the logarithms of the densities in the set of fluctuations, i.e.: log.highest density minus log.lowest density will be used as a statistic indicating "fluctuation-range".

2.2.4.

KLOMP (1962) wrote: "In natural populations high and low densities rarely occur in more than two or three successive generations"(p.68) and: "It has been shown in literature, that after the occurence of a population low, induced for instance by a very severe winter, the species normally recuperates the losses in a very short time"(p.106). Apparently in natural populations peaks and troughs in density (turning points) generally succeed each other with only a small number of generations between.
This means that the sum of the squares of the numbers of generations between all pairs of succeeding "turning points" (divided by the number of generations) would be an appropriate measure for this tendency, i.e.: a low sum of squares would indicate a rather high number of regularly distributed "turning points". In the following this sum of squares (not divided by 30, the number of generations) will be used as a statistic indicating the "speed" and frequency with which "turning points" use to succeed each other within a given set of fluctuations ("turning frequency"). A less appropriate statistic indicating "turning-frequency" is the number of "turning points" within a given set of fluctuations.

2.2.5.

In connection with discussions on "population cycles" (ELTON,1942; PALMGREN,1949; COLE,1951,1954,1958; and others) still another characteristic will be mentioned, viz.: the mean number of generations between succeeding peaks ("mean cycle-length").
As in the models of COLE(1951) each density-value following a lower value and followed by a lower value is called a "peak".

2.2.6.

To summarize: The following statistics will be used to characterize and compare different sets of fluctuations (see Table 3):

a. "central tendency" = deviation from unity of the geometric mean of the net rates of reproduction:

$$1-\sqrt[n]{R_1.R_2\ldots R_n} = 1-\sqrt[n]{\frac{Dn}{Do}}$$

(R = net rate of reproduction; D_n= density in generation n; D_o= starting density).

b. "fluctuation range" = logarithm of maximal density minus logarithm of minimal density: log.Dmax - log.Dmin.

c. "turning frequency" - sum of squares of the number of generations between all pairs of succeeding "turning points":

$$\sum_{i=1}^{k}(dt_i)^2$$ (not divided in this case by 30: the number of generations).

(dt_i= "distance" in number of generations between "turning point" i and "turning point" i + 1). The number of "turning points" (k) will be given too.

d. "mean cycle-length" = mean number of generations between succeeding peaks:

$$\frac{\sum_{l=1}^{m} dp_l}{m}$$

(dp_l = "peak-distance" between peak l and peak l+1; m = number of peaks).
The values of the separate "peak-distances" (dp's) will also be given in the right order to enable students on "population-cycles" to make more detailed calculations.

2.2.7.

It will be evident that a set of fluctuations with a strong "central tendency" (a.) and a great "turning frequency" (c.) will show a high degree of stability, i.e. the chance of reaching extremely high or extremely low values will be relatively small. The same can be said about a set of fluctuations with a small "fluctuation range" (b.) and a great "turning frequency" (c.).
Many ecologists are obviously impressed if in insect populations in the field one of these combinations of "fluctuations-characteristics" is found, which naturally contributed to the conviction (from theoretical considerations) that natural insect populations must be "regulated" (1.4.4.).
In the following I shall try to make an attempt in testing this conviction.

3. Construction of comparable sets of fluctuations (2.3.)

2.3.1.

If during a number of generations (e.g. 30) we had studied the density of a natural insect population, a set of density-fluctuations would result. For each generation we can calculate the factor by which the density has to be multiplied to get the density of the following generation. These R-values (net rates of reproduction) estimated from our field-data will vary between a lowest value (e.g. 1/6) and a highest value (e.g.6) and can be ranged into a number of classes. We can also calculate the fluctuation-characteristics discussed in 2.2., but we don't know the number of weather factors actually involved, neither their quantitative influence.
Now, suppose that the varying value of R is exclusively due to the influence of one varying meteorological factor (M_1). We would be able to test this hypothesis by ranging the values of the meteorological factor into the same number of classes as used in the R-values; by awarding subsequently the corresponding R-value to each "meteorological class"; next by calculating in the original succession the set of fluctuations based now on these "meteorological" R-values and by comparing the fluctuation-characteristics(2.2.) of this hypothetic set with those of the original one. In the same way another meteorological factor (M_2) can be tested, and still another (M_3), etc.
Let us now assume that $M_1$and M_2 in concert influence the varying value of R. For each generation the influence of M_1 can be combined with those of M_2 by multiplying each R_1-value with the corresponding R_2-value, but the frequency-distribution of these $R_1.R_2$ -values will not cover the same range as those of the R-values of our natural population (e.g. 1/6 - 6). To be able to test our hypothesis and to compare adequately the influence of M_1 and M_2 in concert with that of a single factor (M_1 or M_2 separately), we will have to modify the range of the frequency-distribution of $R_1.R_2$ in such a way that the modified $R_1.R_2$ -values cover about the same range as R in our natural population (1/6 - 6) for this range of R is the datum from which we started. The desired conversion-method will be given in 2.3.5. Next, the new set of fluctuations can be calculated and its fluctuation-characteristics can be adequately compared with those of the original set and/or with those of the sets based on a single meteorological factor.
In the same way other combinations of meteorological factors can be tested and compared, not only combinations of two factors but also of three, four, etc.factors.

2.3.2.

KLOMP (1962, p.86) gives the R-range of a number of natural populations of phytophagous insects. From these data it was concluded that it would be reasonable to assume that within a set of 30 generations R covers the range 1/6 (0.167) - 6.

We will study now what the fluctuation-characteristics (2.2.) are like for sets of fluctuations of 30 generations in which R varies between about 1/6 and 6, if density is influenced by one, by two, by three, by four, by five, by six or by ten meteorological factors.

2.3.3.

For the 30 years 1901-1930 the values of ten meteorological factors have been arbitrarily taken from tables of the Meteorological Station De Bilt (Holland), viz.:

1. air-temperature in June.
2. number of hours of sunshine in May.
3. air-temperature in July.
4. number of hours of sunshine in April.
5. soil-temperature in December.
6. evaporation in April.
7. amount of precipitation in August.
8. evaporation in June.
9. amount of precipitation in September.
10. air-temperature in September.

To fix the mind, a phytophagous insect may be imagined which comes across with one or a number of following density-independent factors: the winged adults hatch from the soil in April (4,6) and move about in May to copulate and to deposit eggs (2); the larvae hatch on the trees in June (1,8) and grow up in July and August (3,7); the full-grown larvae migrate from the trees and burrow into the soil in September (9,10) and the pupae fall into diapause in December (5).

2.3.4.

The range of the values of each meteorological factor was divided into 11 classes with the same class interval each, To each class a value of R was awarded, viz.:1:1/6; 2:1/5; 3:1/4; 4:1/3; 5:1/2; 6:1; 7:2; 8:3; 9:4; 10:5 and 11:6.(since R is a multiplication factor the scale of R must be logarithmic around unity(see 2.4.3, Table 5). The frequency distributions of the R-values thus derived from the 10 meteorological factors are given in Table 1.

TABLE 1. Frequency distributions of R-values.

R-values / Factor(M)	1/6	1/5	1/4	1/3	1/2	1	2	3	4	5	6	Total
1	1	1	-	4	9	4	6	2	1	1	1	30
2	1	-	4	4	2	5	5	4	1	3	1	30
3	2	-	2	3	3	4	3	3	3	4	3	30
4	1	4	4	5	3	3	3	3	2	1	1	30
5	1	-	1	4	5	8	6	2	1	1	1	30
6	-	3	3	3	4	8	2	2	1	3	1	30
7	3	2	4	5	1	5	5	2	1	-	2	30
8	1	3	1	3	1	6	7	2	3	1	2	30
9	-	2	3	10	1	3	2	-	4	3	2	30
10	1	-	1	1	4	8	5	5	3	1	1	30
Total	11	15	23	42	33	54	44	25	20	18	15	300

To construct adequate frequency distributions of R-values, the values of real meteorological factors are prefered here above "random numbers". In the first place since we do not know how close a frequency distribution of "random numbers" resembles that of the values of a meteorological factor. In the second place since values of different meteorological factors may show unknown correlations and it did not seem desirable to leave such possible correlations out of consideration (we may be sure, for instance, that there will be a correlations between factors 1 and 8, 4 and 6, 9 and 10 and perhaps between others too).
A provisional trial with "random numbers" indicated, however, that with "random numbers" our conclusions would have been about the same (2.5.1.).

2.3.5.

Starting with a density of, say, 500 individuals in 1900, the density in 1901, in 1902, etc. can now be calculated, assuming that it is influenced by a single meteorological factor (2.3.3. and 2,3.4). Ten sets of fluctuations of 30 generations (1901-1930) based on a single meteorological factor each, thus were obtained and the corresponding "fluctuation-characteristics" were calculated (Table 3.).
To be able to compare adequately the influence of two factors in concert with that of a single factor we have to convert the range of the frequency distribution of the combined R-values ($R_i.R_j$) to about the original limits (see 2.3.1.). Table 1 shows that the relative frequency of R = 1/6 is 11/300 on the average and that R = 6 is 15/300 on the average, whereas in most separate frequency distributions the relative frequency of R = 1/6 and /or R = 6 is 1/30 (in 5 out of 10 distributions both the relative frequency of R = 1/6 and of R = 6 is 1/30, in 2 out of 10 one of the frequencies is 1/30). Hence, it seemed reasonable to convert the range of the combined R-values (R_c)in such a way that the probability of $R_c \leq 1/6$ is 1/30 and that of $R_c \geq 6$ is 1/30), (the fact that these probabilities are a little too small on the average - especially $P (R_c \geq 6)$ -is compensated in the course of the calculation).
After combining two frequency distributions of R we can estimate the probability of $R_i.R_j = 1/36$, that of $R_i.R_j = 1/30$, that of $R_i.R_j = 1/25$ etc. (Under the assumption that the factors are independently combined) and at the other side the probability of $R_i.R_j = 36$, that of $R_i.R_j = 30$, that of $R_i.R_j = 25$ etc. Now, two values of $R_i.R_j$ (l and h) can be empirically found in such a way that at l the sum of the probabilities of the lowest $R_i.R_j$-values ($\sum P (R_i.R_j)$ reaches 1/30 and that at h the sum of the probabilities of the highest $R_i.R_j$-values ($\sum P (R_i.R_j)$ reaches 1/30. Often l and h are at about equal logarithmic distances from R=1 and in the cases where they are not, they are provisionally fixed at equal distances from R=1 for reasons of calculation (see below).
The estimation of l and h is demonstrated in Table 2. for the combination of factors 1 and 2.

Table 2. Estimation of l and h for factors 1 and 2.

R-value (Table 1).	1/6	1/5	1/4	1/3	1/2	1	2	3	4	5	6
frequency factor 1.	1	1	-	4	9	4	6	2	1	1	1
frequency factor 2.	1	-	4	4	2	5	5	4	1	3	1
Combinations of factors 1 and 2.											
$R_1.R_2$.(lowest)	1/36	1/30	1/24	1/20	1/18	1/15	1/12	etc.			
estimated frequency	1	1	4	4	8	4	27	etc.			
$P(R_1.R_2)$lowest	1/900	1/900	4/900	4/900	8/900	4/900	27/900	etc.			
$\sum P(R_1.R_2)$	1/900	2/900	6/900	10/900	18/900	22/900	49/900	etc.			
For $R_1.R_2$= 1/12 $\sum P(R_1.R_2)$ goes from 23/900 to 49/900. Hence, l=1/12											
$R_1.R_2$(highest)	36	30	25	24	20	18	16	15	etc.		
estimated frequency	1	4	3	2	4	6	1	10	etc.		
$P(R_1.R_2)$ highest	1/900	4/900	3/900	2/900	4/900	6/900	1/900	10/900	etc.		
$\sum P(R_1.R_2)$	1/900	5/900	8/900	10/900	14/900	20/900	21/900	31/900	etc.		
For $R_1.R_2$=15 $\sum P(R_1.R_2)$goes from 22/900 to 31/900. Hence, h≠15, but close to 12.											

Generally l and h are fixed as close to unity as the estimation permits in order to prevent too strong a reduction of the range of $R_i.R_j$ (see below) and to compensate for the probabilities of $R_c \leq 1/6$ and of $R_c \geq 6$ fixed a little too small (see above).
In the case of Table 2 l and h were fixed at 1/12 and 12. They must be fixed at equal (logarithmic) distances from R=1 to enable the realization of only one "conversion-coëfficient"(c) for all $R_i.R_j$-values of a given set of fluctuations, but this does not influence of course the "(a)symmetry" of the frequency distribution of the new R-values (R_c), see: 2.4.3.(Fig.1).
The relation between the estimated values l and h (e.g.Table 2) and the desired values R_t(1/6 or 6) is given by $l=R_t^c$ (c= conversion-coëfficient) or $h= R_t^c$; $c\,|\log R_t| = |\log l| = |\log h|$; $c=\frac{\log l}{\log R_t}$
$c=\frac{\log l}{\log R_t} = \frac{\log h}{\log R_t}$ (1). In the case of Table 2 equation (1) gives $c = 1.39$

Each $R_i.R_j$. can now be converted to the desired R_c by: $R_c=\sqrt[c]{R_i.R_j}$ (2) or $\log R_c=\frac{\log R_i.R_j}{c}$ (3) (for each c, this last equation (3) gives one straight line on log.-log.-paper).

2.3.6.

With the conversion method described in 2.3.5 ten sets of fluctuations were constructed, in each of which two of the meteorological factors given in Table 1 in concert determined Rc between about the same limits as in the "one-factor-sets" (1/6 and 6). The "fluctuation-characteristics" (2.2.6.) are calculated again and compared with those of the "one-factor-sets" (Table 3). The factors were combined at random, with the proviso that each of the ten factors was used the same number of times in the ten sets; thus, two times in the "two-factor-sets", three times in the "three-factor sets", four times in the "four-factor-sets", etc.and all 10 together in one "ten-factor-set".
To construct "three-factor-sets" one "two-factor-set" was combined with a "one-factor-set" after which the range of $R_i.R_j.R_k$ was converted in the same way and to the same limits as described in 2.3.5. Ten of such sets were constructed and also ten "four-factor-sets" by combining each time two "two-factor-sets"(see 2.3.5.). In the same way ten "six-factor-sets" were constructed by combining each time two "three-factor-sets".
Also two "five-factor-sets" were constructed (by combining a "two-factor-set" with a "three-factor-set") in such a way that the sets had no factors in common and could again be combined to one "ten-factor-set". Although the conversion method described in 2.3.5. is somewhat "primitive", it comes up to expectations as is shown by 2.4.3.: Table 5(class-∞ + class-5 and class +∞ + class + 5 give about the same frequencies in the "more-factor-sets" as in the "one-factor-sets") and Table 6. For all sets the "fluctuation-characteristics were calculated (2.2.6.). The results are given in Table 3 and discussed in 2.4.

4. The relative stabilizing effect of a number of meteorological factors. (2.4.)

2.4.1.

When studying the fluctuations-characteristics given in Table 3 we have to realize that only the ten "one-factor-sets" are completely comparable with the one "ten-factor-set", since the latter is the only possible combination of the ten separate factors. All other sets of ten are samples taken from the "population of possible combinations" and thus give no complete ground for comparison.
Generally, the number of combinations of x objects at a time chosen from a group of n objects is

$$c_x^n = \frac{n!}{x!\,(n-x)!}$$

Hence, the ten "two-factor-sets" is a sample taken from 45 possible combinations (22%), the "three-factor-sets" is a sample taken from 120 possible combinations (8.3%) and the "four-factor-sets" as well as the "six-factor-sets" are samples taken from 210 possible combinations (4.8 %).

The averaged fluctuation-characteristics (Table 4) of such samples will inevitably deviate from the general trend in the effect of the number of meteorological factors; some samples will be "too favourable" others "too unfavourable". For the moment, however, this simple approximation will suffice to indicate the relatively stabilizing effect of the number of meteorological factors. It will be evident that the absolute values of the fluctuation-characteristics of all sets are equally influenced by the weather factors chosen, by the awarded range of R and by the "number of generations". Hence, it would be pointless to discuss the absolute values of the fluctuation-characteristics. The only intention of the model is to show the relatively stabilizing effect of the number of factors. We may be sure that the number of factors involved in natural animal populations will have a comparable stabilizing effect, although the absolute values of the fluctuation-characteristics estimated from field data generally will be different. For this reason picturing of some of the constructed fluctuation-sets is considered unnecessary and even confusing.

Table 3. Fluctuation-characteristics of comparable sets (see 2.2.6).

Combination of factors (Table 1)	"central tendency" $1-\sqrt[n]{\frac{D_n}{D_o}}$	"fluctuation range" log.Dmax-log.Dmin.	"turning frequency" $\sum_{i=1}^{k}(dt_i)^2$	k	"peak distances" (dp) in right order	"mean cycle length" $\frac{\sum_{l=1}^{m} dp_l}{m}$
1	+ 0.1525	3.15776	100	14	3,3,4,3,2,5	3.3
2	- 0.0700	3.77815	141	11	10,11,3,2,2	5.6
3	-0.3490	3.95134	103	14	5,2,4,2,4,3	3.3
4	+ 0.2865	4.55630	159	7	5.10.7	7.3
5	+ 0.0255	1.85673	80	12	5.10.3.3.2.5	4.7
6	+ 0.1094	5.28398	157	7	9,4,9	7.3
7	+ 0.2767	4.22167	63	16	3,2,4,3,5,3,4,4	3.5
8	- 0.2500	3.36248	122	11	5,4,7,3,5	4.8
9	+ 0.1094	5.09377	129	12	2,9,2,4,9	5.2
10	- 0.4820	5.12722	140	11	8,10,3,3,3	5.4
1.2	+ 0.0672	2.48572	93	12	4,6,4,7,3,6	5.0
3.4	+ 0.0168	2.10037	81	15	5,6,3,6,2,3,3	4.0
1.3	- 0.0900	1.65896	83	14	5,2,4,3,2,4	3.3
2.4	+ 0.1486	3.00561	173	9	5,11,2,3	5.3
5.6	+ 0.0970	4.18327	131	9	5,3,6,7	5.3
7.8	+ 0.1068	3.28443	61	17	5,4,3,3,2,3,5,3	3.5
7.10	+ 0.0070	2.20140	114	10	6,8,3,4	5.3
8.9	- 0.0150	2.14922	92	12	5,2,6,4,3	4.0
5.9	+ 0.1010	3.41847	87	14	4,7,3,3,4,5	4.3
6.10	- 0.1670	3.88338	110	12	3,7,3,7,5	5.0
1.2.5	+ 0.0660	2.24055	79	15	4,6,4,4,3,2,6	4.1
1.2.6	+ 0.0680	2.74507	101	13	5,6,3,3,4,8	4.8
3.4.5	+ 0.0300	2.55509	67	15	5,6,3,3,5,3,3	4.0
1.3.4	+ 0.1400	2.71933	69	16	5,2,4,3,2,4,4	3.4
6.7.10	+ 0.1191	3.54370	83	14	3,3,3,5,7,4	4.2
5.7.10	+ 0.0263	1.75967	96	12	3,4,3,6,6	4.4
7.8.9	+ 0.1472	3.23274	61	17	2,4,3,5,3,5,3	3.6
3.8.9	- 0.3050	3.46805	81	16	5,2,4,2,4,3,7	3.9
2.4.10	- 0.1440	3.43185	63	19	2,3,5,6,2,3,2,3,2	3.1
6.8.9	+ 0.0545	4.58488	93	14	5,4,2,2,8,3	4.0
1.2.3.4	+ 0.0264	2.05308	71	15	4,7,3,2,5,3,4	4.0
1.2.7.10	+ 0.0506	2.28780	59	16	2,6,4,2,3,4,3	3.4
7.8.9.10	+ 0.0023	3.07954	57	16	2,4,3,6,2,5,2	3.4
3.4.5.6	+ 0.0749	3.81921	77	15	5,3,3,3,6,2,5	3.9
5.6.9.10	- 0.0355	1.96858	61	18	5,3,3,2,4,4,2,2	3.1
1.3.7.8	+ 0.0165	2.33041	48	18	3,3,4,3,2,4,4,3	3.3
2.4.8.9	+ 0.1031	2.24797	105	12	11,4,3,4,3	5.0
1.2.6.10	- 0.1248	2.58092	81	16	2,2,6,4,2,2,3	3.0
3.4.5.9	+ 0.0838	2.88874	91	12	5,6,3,3,9	5.2
5.6.7.8	+ 0.1300	4.15806	76	16	4,3,3,3,2,7,4	3.7
1.2.6.8.9	+ 0.0510	3.43838	76	14	4,5,2,6,4,3	4.0
3.4.5.7.10	+ 0.0272	2.02531	53	19	5,3,3,3,2,4,3,2,3	3.1
1.2.3.5.8.9	- 0.1273	2.03743	57	16	4,3,4,3,3,4,3	3.4
1.2.5.6.7.10	+ 0.0824	2.88480	61	16	4,4,3,3,3,4,2,4	3.4
1.2.6.7.8.9	+ 0.1411	3.48387	59	18	2,2,5,2,3,3,4,3	3.0
1.3.4.5.7.10	+ 0.1187	2.73320	60	16	3,3,4,3,2,4,3	3.1
1.2.5.6.8.9	+ 0.0985	3.23274	73	14	4,7,3,3,4,3	4.0
1.3.4.6.7.10	+ 0.1267	4.04883	58	16	4,3,3,3,2,4,3	3.1
2.4.6.8.9.10	- 0.0370	2.25042	75	16	2,3,6,3,2,5,2	3.3
2.3.4.8.9.10	- 0.2915	3.34674	73	16	2,3,3,3,6,4,5	3.7
3.4.5.6.7.10	+ 0.1595	3.68215	59	17	5,3,3,3,2,4,3,5	3.5
3.4.5.7.8.9	+ 0.1190	2.29667	51	18	4,4,3,3,3,3,4,3	3.4
1.2.3.4.5.6.7.8.9.10	+ 0.0499	2.41664	63	16	5,3,3,3,3,4,3	3.4

2.4.2.

Table 3 shows that the fluctuation-characteristics of the different "one-factor-sets" diverge noticeably, i.e. some factors obviously give a relatively "unstable" set of fluctuations (e.g. 10,4 and 6) and others a "rather stable" one (e.g.5); see also 2.2.7.
The combination of all ten factors in one comparable set of fluctuations gives a very important improvement of stability(Table 4), not only a "favourable central tendency" and "fluctuation-range" but also a high "turning frequency".
The fluctuation-characteristics of the "more-factor-sets" of the same sample also diverge noticeably (Table 3.), although less than those of the "one-factor-sets" and generally less when more factors are involved.

Table 4. Averaged fluctuation-characteristics of comparable sets (see 2.4).

number of factors (Table 3).	"central tendency"	"fluctuation range"	"turning frequency"		"mean cycle length"	number of fluctuation sets
1	0.2111	4.03894	119.4	11.5	4.7	10
2	0.0844	2.83708	102.5	12.4	4.4	sample of 10
3	0.1070	3.02809	79.3	15.1	3.9	sample of 10
4	0.0648	2.74143	72.6	15.4	3.7	sample of 10
5	0.0391	2.73184	64.5	16.5	3.5	2(no factors in common)
6	0.1302	2.99959	62.6	16.3	3.4	sample of 10
--	--	--	--	--	--	--
10	0.0499	2.41664	63.0	16.0	3.4	1(all 10 factors combined)

Although the averaged fluctuation-characteristics of the samples of "more-factor-sets" show some irregularities (see 2.4.1.), they range well between those of the "one-factor-sets" and those of the "ten-factor-set" (Table 4.). Since the effect on the fluctuation-characteristics increases with the logarithm of the number of factors the improvement of stability can be best judged if sets with doubling of the number of factors are compared (Table 4.).
All fluctuation-characteristics discussed in 2.2. obviously alter towards increasing stability of the fluctuation-set when the number of meteorological factors determining R (2.3.1.) increases:
a. the geometric mean of the net rates of reproduction draws nearer to unity (central tendency).
b. the logarithmic range of density decreases (fluctuation range).
c. "turning points" tend to succeed each other more regularly and more frequently (turning frequency).
d. the mean number of generations between succeeding peaks decreases (mean cycle length) and nears to three.

2.4.3.

To understand the relatively stabilizing effect shown in the Tables 3 and 4 (2.4.2.) we have firstly to realize that generally: the more (more or less independent) factors work upon the continuous variable values of a quantity the more these values will tend to be distributed "normally" (ignoring some special cases and sometimes only after an adequate "transformation" of course).
In our case we may expect: the more meteorological factors work upon R the more the frequency distribution of R (classes plotted upon a logarithmic scale:Table 5) will tend to be "normal".

Table 5. Averaged frequency distributions (10 sets) of R-values

class notation	- ∞	-5	-4	-3	-2	-1	0	+1	+2	+3	+4	+5	+ ∞
class interval of R-values	< 0.1538	0.1538- 0.1818	0.1818- 0.222	0.222- 0.2857	0.2857- 0.400	0.400- 0.666	0.666- 1.5	1.5- 2.5	2.5- 3.5	3.5- 4.5	4.5- 5.5	5.5- 6.5	> 6.5
class centre		1/6	1/5	1/4	1/3	1/2	1	2	3	4	5	6	
log. of class centre	< -0.813	-0.778	-0.699	-0.602	-0.477	-0.301	0	0.301	0.477	0.602	0.699	0.778	> 0.813
one factor	--	1.1	1.5	2.3	4.2	3.3	5.4	4.4	2.5	2.0	1.8	1.5	--
2 factors	0.5	0.7	1.1	1.3	2.4	5.6	7.9	4.2	2.9	1.3	1.0	0.4	0.7
3 factors	1.0	0.5	0.7	1.2	2.4	4.5	9.3	5.2	2.2	1.5	0.5	0.3	0.7
4 factors	0.8	0.6	0.7	1.2	2.7	5.6	8.2	5.6	0.9	1.5	0.5	0.6	1.1
6 factors	1.1	0.6	0.7	1.4	2.1	4.9	9.3	4.6	2.4	1.1	0.8	0.3	0.7
"best fitting normal distr." (approximated with probit-paper).	~ 0	0.5	0.6	1.3	2.3	4.9	8.8	4.9	2.3	1.3	0.6	0.5	1.0

Table 5 and Fig.1 show that this tendency is indeed present. As compared with the situation in the "one-factor-set" (Table 5 and 1) in the "more-factor-sets" a higher number of values (about two-third) is concentrated in the central classes (-1,0 and +1), whereas the tails are more flattened out with a number of values beyond the classes -5 and +5. Since in a normal distribution the tails are rather extended we may expect that with an increasing number of factors the extreme R-values will become more extreme on the average (up till a limit of course). In Table 6 the values falling into the classes −∞ and +∞ are given with the corresponding mean values, which shows that the expected tendency is generally present.

Table 6. R-values falling into the classes −∞ and +∞ .

	in class −∞	Average	in class +∞	Average
2 factors	0.0761;0.1115;0.1355; 0.1445;0.149	0.1233	7.38;7.66;7.78;8.65; 9.25;10.1;11.54.	8.91
3 factors	0.0711;0.0815;0.10; 0.1092;0.1168;0.1216; 0.131;0.1383;0.1383; 0.150	0.1158	6.52;6.55;6.73;6.89; 6.96;7.482;10.12	7.32
4 factors	0.1026;0.1069;0.1084; 0.1094;0.1094;0.113; 0.1282;0.1391.	0.1146	7.039;7.261;8.356; 8.954;9.058;10.74; 11.78;12.39;12.595; 12.66;19.15	10.907
6 factors	0.0638;0.069;0.0777; 0.088;0.092;0.0938; 0.095;0.1115;0.118; 0.119;0.128.	0.0959	7.2;7.9;8.06;8.78; 8.79;12.5;13.65	9.55

The relatively stabilizing effect of the R-values becoming distributed more "normally" with more factors involved, is thus due to an increasing concentration of R-values in the central classes of the frequency distribution, viz. to a decreasing chanceof R to deviate much from unity. Although the chance of R to reach extreme values decreases with the number of factors these extremes obviously have an increased chance to be more extreme (Table 6). Hence, a situation may be reached in which relatively long periods with small fluctuations are interrupted by an extreme fluctuation.

2.4.4.

In his paper of 1962, KLOMP criticizes my idea of a relative stabilization of density fluctuations by the influence of a higher number of factors (his 3.2.4.) by stating:"...with a higher number of weather factors involved, the range of R increases and, consequently,the mean change of density generation by generation will increase as well". The same conclusion is reached by WILBERT (1962).
Both KLOMP(1962) and WILBERT(1962) could reach this conclusion by unconsciously deviating from their original purpose: trying to explain the relatively stable density fluctuations in natural insect populations, hence, in populations of which the range of R is known, but of which the number of weather factors actually involved, is unknown!
In my opinion the possible influence of the (unknown) number of weather factors can only be critically analyzed by comparing sets of fluctuations with the same (known) range of R but with different numbers of weather factors involved, as is expounded in 2.3.1.
If analyzed in this way the relatively stabilizing effect of the number of weather factors will be evident; 2.4.2.(Table 4).

2.4.5.

But even in the case of comparing "one-factor-sets" with "more-factor-sets" with a much wider range of R (as is done by WILBERT,1962 and KLOMP,1962), the effect of the widening of the R-range may be much less "unfavourable" than is obviously expected by these authors.
In Table 7 the averaged "fluctuation-characteristics" of the ten

"one-factor-sets" are compared with those of the ten "two-factor-sets" when the range of R is not converted to the original limits. In that case for the lowest values $\sum P(R_i.R_j)$ reaches 1/30 at $R_i.R_j$ = 1/12 on the average and for the highest values at $R_i.R_j$ = 18 (see 2.3.5) thus, l and h are now about 1/15 and 15 on the average inst. of 1/6 and 6. For comparison the averaged "fluctuation-characteristics" of the converted "two-factor-sets" are mentioned too in Table 7.

Table 7. Averaged fluctuations-characteristics in three cases (compare: Table 4).

number of factors	"central tendency"	"fluctuation range"	"turning frequency"		P=1/30 at about		number of fluctuation sets.
one factor	0.2111	4.03894	119.4	11.5	R=1/6	R=6	10
two factors (not converted).	0.1206	4.17629	102.5	12.4	R≤1/15	R≥15	sample of 10
two factors (converted)	0.0844	2.83708	102.5	12.4	R≤1/6	R≥6	sample of 10

Table 7 shows that in spite of the much wider range of R, unconverted "two-factor-sets" are not necessarily less stable than "one-factor-sets"; in the case of Table 7 the unconverted "two-factor-sets" by chance are even more stable. Nevertheless the conclusion of KLOMP (1962,p.94):"...with a higher number of weather factors involved,... the mean change of density generation by generation will increase.." in my opinion must generally be right in the special (although inadequate: 2.4.4.)case that the averaged frequency distribution of R in the "one-factor-sets" is compared with those in the unconverted "two-factor-sets" (Table 8).

Table 8. Averaged frequency distributions (10 sets) of R-values in three cases (compare: Table 5).

class notation	−∞	-5	-4	-3	-2	-1	o	+1	+2	+3	+4	+5	+∞
1 factor	-	1.1	1.5	2.3	4.2	3.3	5.4	4.4	2.5	2.0	1.8	1.5	-
2 factors (not converted)	3.3	1.3	0.7	1.5	2.4	3.3	6.1	3.5	1.3	0.8	1.4	1.5	2.9
2 factors (converted)	0.5	0.7	1.1	1.3	2.4	5.6	7.9	4.2	2.9	1.3	1.0	0.4	0.7

In the unconverted "two-factor-sets" the concentration of R-values in the central classes (-1,0 and +1) is about the same as in the "one-factor-sets", whereas the remaining R-values are much more extreme in the unconverted "two-factor-sets" (even R-values as extreme as 1/30 and 30 were noted), as a consequence of the "flattening out of the tails" of the distribution (2.4.3.).
The very "unfavourable" distribution of R-values in the unconverted "two-factor-sets" (Table 8) is apparently completely counterbalanced by other effects of an increase of the number of factors involved (Table 7), which nicely illustrates the important stabilizing influence of these effects.
In my opinion this important compensating effect is mainly brought about by an increase of "turning frequency" with the number of factors, the more so since "turning frequency" is uninfluenced of course, whether the range of R is converted or not (Table 7). Especially the tendency of the increasing number of turning-points to become more regularly distributed with the number of factors (expressed as $\sum_{t=1}^{k} (dt_i)^2$: 2.2.6.,c), decreases the chance of the fluctuations to

reach extreme values and may apparently be able even to compensate for a very "unfavourable" frequency distribution of R-values (Table 8). In fact "turning frequency" tends to result in a "mean cycle length" of about 3-4 generations with 6-10 factors involved (Table 4). Although in my opinion COLE(1951) does not work with a comparable model - the concordance between his results and my Table 4 is striking. Hence, when KLOMP(1962,p.68) states: "In natural populations high and low densities rarely occur in more than two or three successive generations", this may be the result of the number of density-independent-factors involved.

2.4.6.

An increase of "central tendency" (decrease of $1 - \sqrt[n]{R_1.R_2...R_n}$:2.2.6,a) points to an increasing tendency of R-values smaller than unity to be counterbalanced by R-values greater than unity.
Hence, Table 4 generally shows that the more factors are involved, the greater the chance that small R-values are counterbalanced by high R-values, viz. the more the frequency distribution of R-values will tend to be symmetrically around unity (Table 5).
The increase of "central tendency" with a higher number of factors, thus is a consequence of the frequency distribution of R becoming more concentrated around its mean (2.4.3.).
It will be evident now, that the populations, pictured by KLOMP(1962) in his Figs.10 (p.89) and 13(p.92) and showing a clear drift of population density, have a very small "central tendency" (= a high value of $1-\sqrt[n]{\frac{D_n}{D_o}}$, since D_n is many times smaller than D_o: 2.2.2.).

The influence of the number of factors on "central tendency" may thus be formulated: the chance of population density to drift decreases with the number of factors involved. I get the impression that this effect of a great number of factors (absence of a drift of population density) by many authors is called: "a constant mean density level" (see: 2.2.2.). The irregularities in "central tendency" shown in Table 4 in my opinion are due to the fact that the deviation from unity of the geometric mean of the net rates of reproduction in short series (e.g. series of only 30 generations: see 2.2.2.), is a rather "unstable" characteristic for "central tendency", not to mention the inevitable "sample errors", which play a part of course in all "fluctuation-characteristics" estimated (2.4.1.).

2.4.7.

For reasons of calculation the construction of the model discussed in this chapter was started with giving each factor about equal importance (about the same range of R: 2.3.4.,Table 1). It may be argued that this is an unrealistic starting-point for understanding of the influence of the number of factors on the density fluctuations of natural insect populations, since "natural factors" never will have equal importance. In nature we may expect a small number of "master-factors" (Key factors":VARLEY and GRADWELL,1960) and a great number of "minor factors" of different importance. Moreover the importance of a special factor will be different in different combinations of factors, in different populations of the same species and possibly in different times in the "history" of the same population. It seemed a difficult task to me to construct an unbiased model on this base. To avoid each form of bias in the "awarding of importance" to factors, it was preferred for the moment to give each factor about equal importance.
To get some idea of the influence of combinations of factors with unequal importance, ten "two-factor-sets" were constructed in which one factor had the "normal" R-range of 1/6 - 6 (R_i) and the other a reduced one of 1/3 - 3 (R_j) (converted from the usual "one-factor-sets" with c = 1.63: see 2.3.5.). The new $R_i.R_j$-values were converted as usual to the limits of about 1/6 - 6 in the way as described in 2.3.5., after which the sets could be calculated and the fluctuation-characteristics estimated. The following sets were calculated in this way: <u>1</u>,2, 3.<u>4</u>, 1.<u>3</u>, <u>2</u>.4, <u>5</u>.6, <u>7</u>.8, 7.<u>10</u>, <u>8</u>,9, 5.<u>9</u> and <u>6</u>.10, in which the factor with the reduced R-range is underlined (compare the "two-factor-sets" in Table 3).

Now we are able to compare the fluctuation-characteristics of ten "two-factor-sets" in which one factor is much more "important" than the other with the same "two-factor-sets" in which both factors are of about "equal importance" (Table 3). In Table 9 the averaged fluctuation-characteristics and the averaged frequency distributions of R-values in both cases are given.

Table 9. Averaged fluctuation-characteristics and averaged frequency distributions of R-values in "two-factor-sets" with factors of equal and of unequal importance.

fluctuation-characteristics	"central tendency"	"fluctuation range"	"turning frequency"		number of fluctuation sets
with "equal" factors	0.0844	2.83708	102.5	12.4	sample of ten
with "unequal" factors	0.0930	2.80959	91.1	14.2	sample of ten

frequency distribution of R-values (class-notation).	-∞	-5	-4	-3	-2	-1	0	+1	+2	+3	+4	+5	+∞
with "equal" factors	0.5	0.7	1.1	1.3	2.4	5.6	7.9	4.2	2.9	1.3	1.0	0.4	0.7
with "unequal" factors	0.4	0.6	0.7	1.5	3.0	5.5	8.2	3.7	3.0	1.1	0.9	0.5	0.9

Table 9 shows that the "unequality" of the factors involved does not "unfavourably" influence the relative stability of the fluctuations-sets. If some real difference between the cases is present the case with "unequal" factors is a little more "favourable" than the case with "equal" factors (greater "turning frequency" and perhaps a more "favourable" distribution of R-values), but I am sure that these are only "chance-effects": 4 of the 10 sets with "unequal" factors have more "favourable", 3 more "unfavourable" and 3 about the same fluctuation-characteristics than the corresponding sets with "equal" factors.
Hence, even rather considerable differences in the quantitative "importance" of the weather factors involved obviously do not significantly influence the relatively stabilizing effect of the number of factors, as it is demonstrated in our model (Tables 4 and 5).
If the differences in quantitative "importance" of the weather factors are still many times greater than in the case of Table 9 we may be sure, of course, that the "small" factors will contribute less to the relative stabilization than the "master" factors, but probably more than would be expected at first sight. Generally: each density-independent factor (not only meteorological factors) will more or less contribute to the relative stabilization of density fluctuations and since the number of such factors generally will be very high (especially "minor" factors) the rate of stabilization to be expected in natural insect populations often may be very significant (see also chapter 3).

2.4.8.

The frequency distributions of the R-values of the factors used in the model are such - although not strictly symmetrical around R = 1 - that both R-values above unity and R-values below unity are represented (2.3.4.:Table 1). Although the influence upon R of many weather factors may be adequately represented in such a way, there will undoubtedly be other factors which will chiefly have an increasing influence upon R and still other factors with a mainly decreasing influence upon R.
If in e.g. a "six-factor-set" (Table 3) the R-values of one factor are multiplied by 4 we have constructed a factor with a highly increasing influence upon R_c. If in the same set the R-values of two

other factors are multiplied by ½ we have constructed two factors with a moderately decreasing influence upon R_c. It will be evident that in this case the promoting and the two checking factors are completely counterbalanced and that the fluctuation-set with its fluctuation-characteristics will not be altered at all by these substitutions.
Generally: the greater the number of independent factors that influence density, the more probable that promoting and checking factors are counterbalanced and thus contribute to the relative stabilization of density fluctuations (see also: SCHWERDTFEGER (1958) and 1.3.3.).

5. Conclusions (2.5.)

2.5.1.

Summarizing: If we test the influence of the number of weather factors on comparable sets of density fluctuations (= sets with about the same range of R: 2.4.4.) in a model as adequate as possible, we are forced to the following conclusions:

a. the frequency distribution of R will tend the more to "normality" the higher the number of factors involved (2.4.3.:Table 5):part of the R-values concentrating into the central classes and part spreading out into the "tails" and sometimes reaching extreme values (2.4.3.:Table 6).
b. As a consequence of a the geometric mean of R-values will draw nearer to unity with a higher number of factors involved (central tendency):Table 4, and hence, there will be a tendency to reach a "constant mean density level" (2.2.2. and 2.4.6.).
c. The number of "turning points" increases and they tend to become distributed more regularly with a higher number of factors: Table 4; this means that high or low densities will rarely occur in more than a few successive generations (2.4.5.) and "mean cycle length" will near to three generations: Table 4.
d. As a consequence of b. and c. density will only show "restricted" fluctuations": "fluctuation range" will decrease with a higher number of factors involved: Table 4.
e. As a consequence of a. and c. important deviations from the "mean density level" will not often be permanent and will generally be "compensated" in a short time; this may give an explanation for the often mentioned phenomenon of populations "recuperating severe losses in a short time" (e.g. KLOMP,1962,p.106).
f. Within a number of fluctuation-sets with the same number of factors involved, the variation of the values of the fluctuation-characteristics is smaller the more factors are involved (2.4.2., Table 3), viz. the chance of a fluctuation-set to have "unfavourable" fluctuation-characteristics decreases when more independent factors are involved.
g. Each density-independent factor (also "minor" factors and not only weather factors) will more or less contribute to the relative stabilization of density fluctuations (2.4.7.).
h. The greater the number of independent factors that influence density, the greater the chance that promoting and checking factors are counterbalanced and thus contribute to the relative stabilization of density fluctuations (2.4.8. and e.g.:SCHWERDTFEGER,1958).
i. As a consequence of a - h there is no logical necessity for the assumption of a continuous operation of "density-dependent factors", although I do not exclude the possibility of the operation of some kind of "density-dependent-factors" in some natural insect populations (see 2.1.1.).

2.5.2.

The relatively stabilizing effect of the number of independent ("nonreactive") factors, as discussed in this chapter and demonstrated by the model, must be considered a special case of the phenomenon of risk-distribution (1.2.), which plays a dominant part in the dynamics of natural populations: By the "risk" of reaching "unfavourable" densities being "distributed" over a great number of factors, density-fluctuations will be relatively stabilized and the chance of the population to survive will be increased.

Many other forms of "risk-distribution" can be demonstrated to operate in natural populations and to contribute to the relative stabilization of density fluctuations.
These foms of "risk-distribution" will be discussed in the following chapter.

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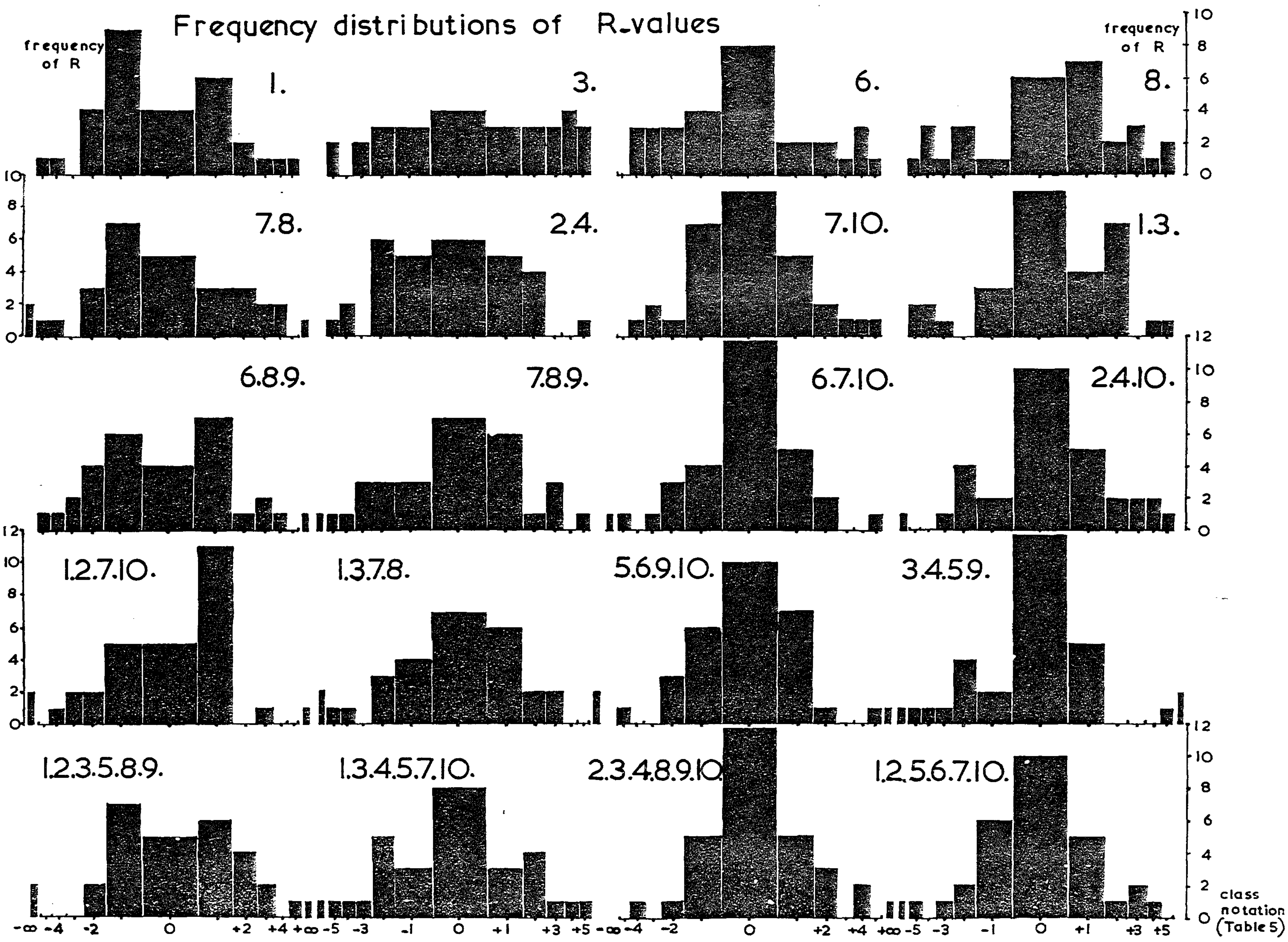

Frequency distributions of R-values
frequency of R
1.
3.
6.
8.
7.8.
2.4.
7.10.
1.3.
6.8.9.
7.8.9.
6.7.10.
2.4.10.
1.2.7.10.
1.3.7.8.
5.6.9.10.
3.4.5.9.
1.2.3.5.8.9.
1.3.4.5.7.10.
2.3.4.8.9.10.
1.2.5.6.7.10.
class notation (Table 5)

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