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INVESTIGATION OF EXPERIMENTALLY INDUCED
POPULATION GROWTH

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I. MATERIAL, METHODS AND COURSE OF EXPERIMENTS

The laboratory mice were reared in cages of the following sizes: $38 \times 15 \times 15$ (type A), $38 \times 30 \times 15$ (M), $80 \times 80 \times 15$ (P, Z, L, D, V) and $160 \times 80 \times 15$ (B). In the $80 \times 80 \times 15$ cages there were different degrees of complication of the interior of the cage. Type P was the simplest, and type V the most complicated (Fig. 1).

A certain number of mice were placed in a cage as a population base (most often 8 ♀♀ and 3 ♂♂) and allowed to breed freely. Food, water and shavings were supplied as required. Observations were made daily of the numbers born, the number of unweaned mice, and the number of dead mice. The mice were weighed every two weeks and the young ones which had reached the age of 3 weeks were marked by clipping various combinations of toes (each litter was marked with one mark).

A total of 59 populations were founded, which jointly lived for a total of 1247 months, but for purposes of analysis only those populations which had existed for not less than 12 months were used. In this way material was obtained from 47 populations which jointly lived 1175 months.

After an „acclimatisation” period lasting from 3 to 8 weeks, during which period biting to a moderate degree was observed, the mice began to breed, reached a certain level of numbers, varying in different cases (in *P* size cages 16 — 69 individuals), then symptoms of over-crowding occurred (biting, poor coats, decrease in or disappearance of both the capacity for survival in the unweaned mice, and of fertility), then a decrease in the numbers of the population lasting for varying periods. After this, if the population

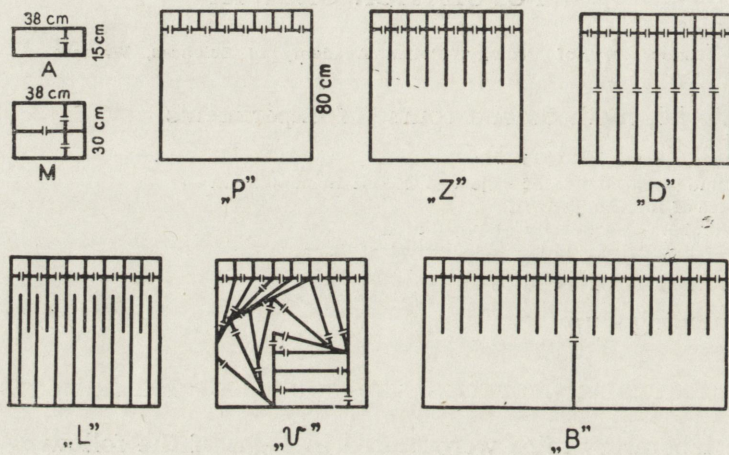


Fig. 1. Types of cages

in question did not die out, altogether, a fresh increase in numbers took place. In *P* size cages a spontaneous increase in population was observed when the numbers fell to a level of from 4 — 30 individuals (Fig. 3). This increase took place, however, after widely differing periods. It could take place immediately, or after a long period of stability in the numbers of the population, lasting for as long as 7 months. Then symptoms of over-crowding re-appeared, decrease etc. Certain typical pictures of the quantitative dynamics of the population are shown in Fig. 2.

The size of the population in which symptoms of over-crowding occurred, and in which a fresh increase began, and also the duration of the whole cycle and of its respective phases, varied greatly. It may therefore be stated that the course taken by the quantitative dynamics of our populations provide an excellent illustration of Southwick's (1955a) statement: "Population differed from population

Populations signs	Dates	Kinds of experiments	Populations state at:		Size of the population growth (in %)	Density (number of mice in 1 m ²)	Monthly birth rate:		Surviving to 3 weeks during 2 month:		Development phase of population was:
			cage change	beginning of growth			before the cage change (F)	after the cage change (F')	before (S) (in %)	after (S') (in %)	
1	2	3	4	5	6	7	8	9	10	11	12
AII	3.II.54.	A→Z	28	20	195	31	4	10	0	23	↘
AIII	3.II.54.	A→Z	27	22	132	34	11	25	0	15	→
AV	3.II.54.	A→Z	23	21	205	33	5	10	40	76	→
AVI	3.II.54.	A→Z	27	27	174	42	6	29	25	72	↗
AIX	21.XII.55.	A→Z	19	18	294	28	0	21	0	35	→
AIX	17.V.57.	D→B	34	31	131	24	5	9	0	21	↘
AX	22.II.56.	A→Z	30	26	256	40	15	48	34	36	↗
AX	17.V.57.	Z→B	34	—	—	—	33	* 0	0	*—	↘
AXI	12.VII.56.	A→Z	30	26	208	40	0	13	0	23	→
AXI	4.IV.56.	A→Z	16	—	—	—	0	18	—	* 0	↘
AXIV	4.IV.56.	A→Z	28	27	179	42	25	26	18	45	↗
AXVII	3.I.56.	A→Z	26	22	200	34	0	6	—	* 6	↘
AXVIII	26.VII.56.	A→Z	24	24	177	37	3	39	50	26	→
DI	17.V.57.	M→L	31	26	170	40	16	18	0	25	↘
VI	17.V.57.	M→Z	28	—	—	—	10	20	0	* 0	↘
ZmII	3.I.57.	M→Z	27	26	138	40	39	* 8	56	* 0	↘
ZmIII	2.III.57.	M→Z	34	27	244	42	10	29	0	15	Mx
LIV	25.VII.56.	L→B	30	—	—	—	0	* 0	0	* 0	↘
LIV	17.V.57.	Z→B	21	17	141	13	10	27	0	23	↘
ZVI	17.I.56.	Z→B	20	16	112	12	9	37	0	6	↘
LI	1.II.56.	L→P	17	16	231	25	0	9	13	28	→
LII	4.IX.56.	L→P	35	33	133	52	30	59	10	*10	↗
LIII	25.VII.56	L→P	19	18	122	28	11	14	23	26	→
LIII	8.II.56.	L→D	15	14	164	22	0	16	25	33	→
LV	25.VII.56.	L→P	9	—	—	—	6	7	0	* 0	↘
LV	1.XII.56.	P→V	11	8	175	12	16	*11	0	21	→
AIII	26.VI.57.	L→P	8	6	320	9	11	23	0	23	↘
AIII	17.I.57.	Z→L	9	6	160	9	7	* 1	0	50	↘
PI	6.IX.56.	Z→D	17	17	165	26	18	20	14	56	→
PI	3.I.57.	D→P	19	18	128	28	5	28	0	11	↘
PI	15.VI.55.	Z→Z	19	17	153	26	17	18	0	23	Mx
ZmIII	4.IX.56.	Z→D	31	30	130	47	25	30	10	18	↘
ZmIII	26.VI.57.	Z→P	36	31	110	48	13	27	0	15	↘
AIX	20.X.56.	Z→D	39	34	129	53	0	14	—	11	↘
DII	1.X.56.	D→P	28	—	—	—	13	27	0	* 0	↘
DII	26.VI.57.	P→L	28	—	—	—	4	11	0	* 0	↘
PIII	4.II.56.	P→L	9	7	500	11	7	* 0	7	21	→
PIV	1.II.56.	P→L	17	16	394	25	29	*16	10	41	↗
VII	15.IX.56.	V→P	35	—	—	—	19	* 0	0	*—	Mx
ZmII	26.VI.57.	Z→L	26	23	179	32	20	34	15	47	→
ZV	20.IX.56.	Z→V	17	17	137	26	16	41	22	* 6	→
LIV	23.I.57.	B→Z	19	16	133	25	26	*17	0	25	↘
BII	17.V.57.	B→P	25	—	—	—	17	* 4	0	* 0	↘
BIII	17.V.57.	B→Z	43	—	—	—	64	* 4	1	* 0	Mx
LV	17.V.57.	V→A	6	5	180	88	0	5	—	60	↘
LI	3.IX.56.	P→M	30	30	148	263	19	59	3	11	↘
PIII	17.V.57.	L→M	17	13	138	114	2	8	0	37	↘
PV	29.VIII.56.	P→M	20	—	—	—	0	7	0	* 0	↘
PVI	29.X.56.	P→M	17	13	223	114	23	29	0	23	↘
PVII	1.XI.56.	P→M	34	30	120	263	21	36	0	29	↘
DI	11.XII.56.	D→M	26	23	195	200	55	58	0	15	↘
VI	1.XII.57.	V→M	16	14	257	123	16	33	45	*24	↗
ZmII	29.VIII.56.	Z→M	20	13	223	114	38	39	3	25	↘
ZmIII	2.I.57.	D→M	20	20	175	175	31	*20	30	* 0	→
Average			23.6	20.1	188	57.4	14.4	20.7	8.9	21.1	

*— are signed the cases when fertility and surviving was greater before the change of the cage than after

Mx—the peak

→— population is stabilised

↗— population is increased

↘— population is decreased

«temperamentally»”, in which he travested the statement made by Crew and Mirskaja (1931).

During our observations a total of 51 spontaneous increases were obtained (not counting the increase taking place in each population immediately after foundation).

During the period of existence of the populations, an experiment, consisting in transferring the whole population to another cage at a certain moment in the life of the population, was carried out 54 times. The moment of transfer was limited by the following conditions: 1) the "acclimatisation" period had to be ended, i.e. the experiment was not carried out until the first population growth began (in 48 cases, that is in the overwhelming majority of cases the change of cage was made after the conclusion of the whole of the first population development cycle); 2) the numbers of the population could not be too high in relation to the level at which spontaneous population growths were observed (not more than 45 mice). Apart from these two limiting conditions, the choice of moment was entirely optional.

Of the 54 such experiments carried out, the population was transferred from a smaller to a larger cage 20 times; to a cage of the same size, but of different type 21 times (transfer within the limits of *P*, *Z*, *D*, *L*, *V* type cages); and finally transfer to a smaller cage — 13 times (from *B* to *P*, from cages of the *P* size to *M* size, and from size *P* cage to size *A*).

The results of these experiments were as follows: in the great majority of cases population growth took place shortly after the change in cage (cf. Fig. 2). Growth was considered as having occurred if population growth took place within 2,5 months after the change in case.

The course followed by these experiments was as follows: immediately after transfer the mice were restless, and exhibited increased investigating behaviour. At the same time the amount of biting per unit of time was on the whole less than during the last 5 — 6 days before transfer. On the second, third or fourth day a slight increase in biting occurred, but never to the same extent as at peak periods¹. The mice were restless, sweated slightly, many

¹ It should be emphasised that the size of the differences in the figures illustrating the amount of biting, before and after the change in cage, in the 13 cases in which it was noted, were not statistically significant, so that the picture of biting can only be given descriptively.

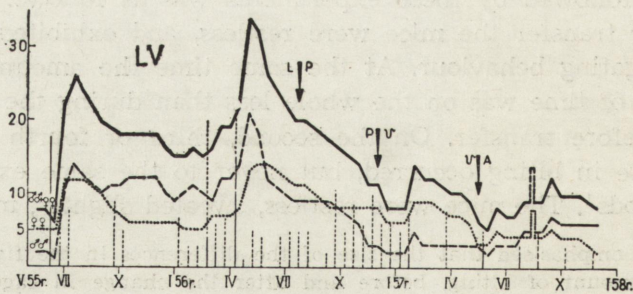
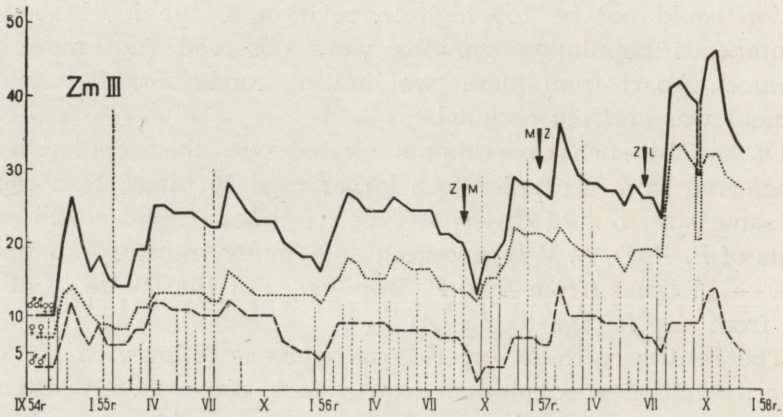
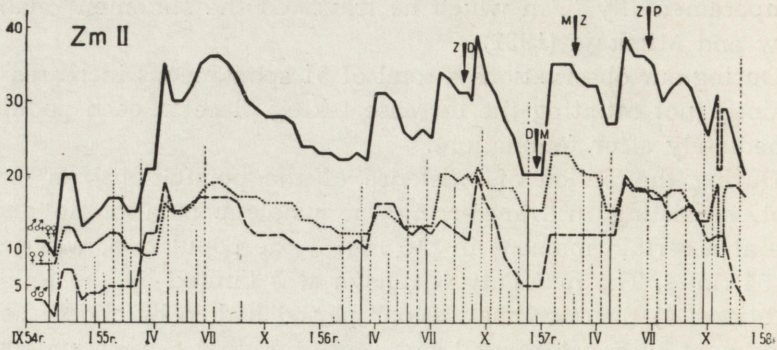


Fig. 2. ZmII, ZmIII, LV

The vertical axis indicates number of mice.

The vertical lines show of the born mice within half a month /in this the uninterrupted lines indicate the number of youngs that have lived for three weeks/.

The arrows indicate the moment of the cage change.

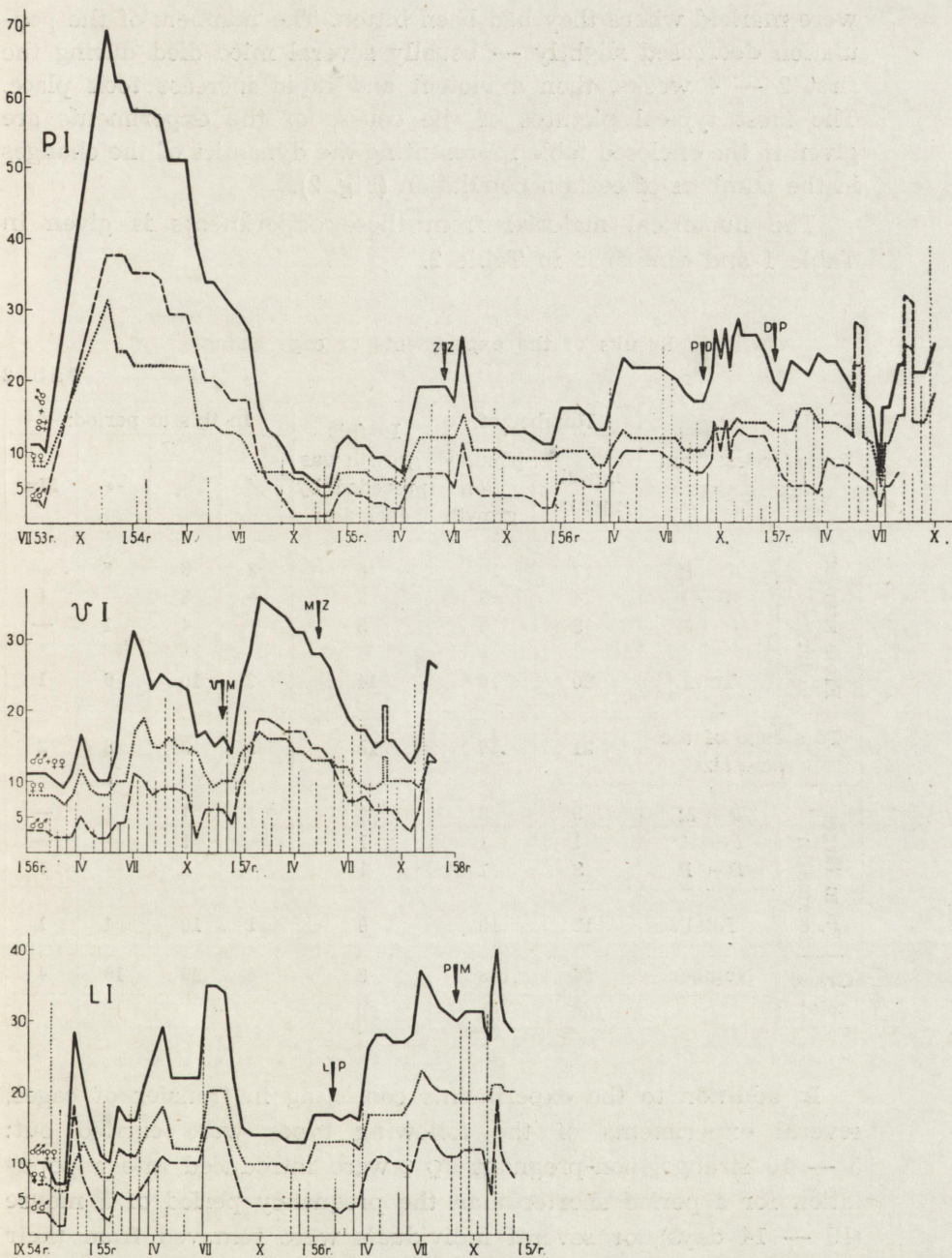


Fig. 2 PI, VI, LI

were marked where they had been bitten. The numbers of the population decreased slightly — usually several mice died during the first 2 — 4 weeks, then a violent and rapid increase took place. The most typical pictures of the course of the experiments are given in the enclosed table representing the dynamics of the changes in the numbers of certain population (Fig. 2).

The numerical material from these experiments is given in Table 1 and compared in Table 2.

Results of the experiments of cage change

Tab. 2

Transferring from cage to cage		Number of:		In this growth was preceded by decrease:	In this at period:			
		experiments	population growth		↗	↘	→	Mx
From smaller to larger	A → P	11	10	8	3	3	5	—
	M → P	4	3	3	—	3	—	1
	P → B	5	3	3	—	4	1	—
	Total	20	16	14	2	10	6	1
To a cage of the same size		21	17	15	2	9	8	2
From larger to smaller	P → M	9	8	7	1	7	1	—
	P → A	1	1	1	—	1	—	—
	B → P	3	1	1	—	2	—	1
	Total	13	10	9	1	10	1	1
Grand total	Number	54	43	38	6	29	15	4
		100	80	70				

In addition to the experiments consisting in transfer of cages, several experiments of the following types were carried out: 5 — 10 strange, non-pregnant ♀♀ were introduced into a population for a period shorter than the pregnancy period of a mouse (10 — 14 days), or several individuals were removed from their population for 5 — 10 days, keeping the ♂♂ separate from the ♀♀. Thirteen such experiments were carried out up to the end of 1957.

In 8 cases the population reacted by an increase, in 3 cases no increase took place, and in 2 cases no result is yet available. These experiments can only be regarded as started, and the mention made here of them, as a record of the fact.

II. ANALYSIS OF MATERIAL

A total of 54 experiments was made, consisting in transferring populations to different cages. Numerical results: in 43 cases (80% of cases) the population reacted by increase; in 38 of the cases (70%) the increase was preceded by a decrease (Table 1 and 2).

The reaction by increase lies outside the limits of error, and

is not the result of chance, since $\frac{(P_1 - P_2)}{\sigma} = 7.6 > 3; P_1 = \frac{43}{54}$,

$P_2 = \frac{11}{54}$, σ is standard deviation and $\sigma = \sqrt{\frac{2P_1 \cdot P_2}{n}}$ n — number

of observations, i.e. 54. Also the number of increase responses preceded by a decrease (38 cases) is so great, that, it is statistically significant, since

$$\frac{(P_1 - P_2)}{\sigma} = 5.2 > 3.$$

In spite of the fact that the participation of increase responses is statistically significant, the question should be carefully considered as to whether the results of the experiment illustrate a chance happening, since no control experiments were carried out and there is no possibility of setting any up. The position is that we accepted that the population reacts by increase, if within 2.5 months from its transfer to another cage, quantitative population increase begins. It is, however, impossible to be completely certain whether, during this 2.5 months period, which is a comparatively long one in the life of the population, a spontaneous increase in the numbers of the population would not take place even if the change of cage had not taken place. It is true that it is possible to foresee, with a considerable degree of probability, the direction that the development of a given population will take, on the basis of such data as the previous tendency of the population dynamics (increase, decrease or stabilisation period), greater or

lesser amount of biting, the condition of the mice in the population (treated fairly subjectively), numbers of the population, in particular the numbers of the males. Such forecasting however, must always of necessity be probable only, since the quantitative dynamics of the population are both variable and irregular. The numbers of a population in which growth takes place vary considerably. If a large number of cases are taken into consideration, it may be stated that there is a certain level of numbers at which spontaneous increase most often takes place (see Fig. 2). For a given particular population, however, this number may vary within comparatively wide limits. Also the length of time from the peak moment to the new spontaneous increase again varies greatly. Increase may begin immediately after a decrease (e.g. population PIV in May 1955, or LI in January 1955 — Fig. 2), or after a long period, even of several months, of quantitative stabilisation (see, e. g., Table 1 : PV 1.X.55 — 15.II.56, AIII 1.VIII.55 — 1.III.56, ZVI 15.XII.54 — 15.VI.55, LI 1.IX.55 — 1.II.56 and others). Symptoms of overcrowding such as poor condition of individuals in the population, and large amount of biting may tell us that there will be no increase in the nearest future (1/2 — 1 month). Contrary symptoms however, do not by any means necessarily indicate that an increase is about to take place, since, as we said before, the period of stabilisation is of varying duration. Some indication is given by the increasing fertility of the population. An increase in the population is nearly always preceded by a marked increase in fertility. But again population increase does not take place after every increase in fertility and sometimes the population may increase rapidly after one or a few more litters immediately following each other (e.g. large increase, 22 to 35 individuals forming an increase in the LI population in June 1955).

To sum up: no indicators were found, which at a given moment would permit of foreseeing the future quantitative dynamics of a population. Hence there is no certainty as to whether, after the moment of changing the population's cage, increase would not have occurred spontaneously, even if the population had not been transferred to another cage.

For this reason we have devoted a good deal of space in the discussion of results, to proofs that a change of cage induces quantitative increase of population.

1. Time from change of cages to increase in population

In order to be able to acknowledge that increase in population took place under the influence of the "transfer of cage" stimulus, it is necessary to define exactly the period during which a quantitative population increase occurring after transfer of cage may be attributed to the influence of this stimulus. For this purpose the period after which population increase took place was calculated for all the experiments. From the enclosed table (Table 3) a period limited to 2.5 months emerges fairly clearly. Hence it was accepted that the population reacted by increase to the change of cage, if this increase began not later than 2.5 months after carrying out the experiment.

Period of time (in months) from change of cage population growth

Tab. 3

Time	0.1 — 0.5	0.6 — 1.0	1.1 — 1.5	1.6 — 2.0	2.1 — 2.5	2.6 — 3.0	3.1 — 3.5	3.5 — 3.6	Died out
Number of cases	5	20	11	5	2	0	1	8	2

In order to attempt to reply to the questions arising as to whether this increase would have taken place even if no change of cage had been made, or whether it is in fact evoked by the change of cage, calculation was made of the length of the period during which each population lived in conditions under which spontaneous increase might take place. It was accepted, on the basis of an analysis of diagrams giving the quantitative population dynamics, that increase could not take place: during the period of the first cycle; at a time when the numbers were higher than 30 individuals (the greatest spontaneous increase took place when the numbers were 25-30- cf. Fig. 3); in periods of induced growth and at peak periods with distinct symptoms of overcrowding. Adding up periods in the life of the population during which spontaneous increase might take place, a total figure of 531 months was obtained. During this period a total of 51 spontaneous increases took place, i.e. on an average 1 increase per $531 : 51 = 10.4$ months. 54 experiments were carried out and observations continued for

a period of 2.5 months after each experiment, that is, jointly $54 \cdot 2.5 = 135$ months. If increase after transfer of cage occurred not as the result of the transfer of cage, but spontaneously, we ought to obtain a total number of increases $135 : 10.4 = 13$, whereas within 2.5 months after each of the 54 experiments we in fact obtained 43 increases. This is a considerable difference and it is

statistically significant, since $\frac{(P_1 - P_2)}{\sigma} = 6.95 > 3$ where $P_1 = \frac{43}{54}$,

$P_2 = \frac{13}{54}$ and σ is standard deviation. It indicates that the number of increases in population during the period of 2.5 months after the transfers of cage was not subject to the same rules as the ordinary spontaneous increases, and it may therefore be presumed that the stimulus was the change of cage.

In order to check the value of the above calculations the following further calculations were made. On the axis of time of the diagrams showing the quantitative dynamics of population, during the periods in which increase might take place (cf. above) 230 points were chosen at random, then a check was made to ascertain how many times within 2.5 months increase took place after the point chosen at random. Such increase occurred

41 times. Theoretically however, it should take place $\frac{230 \cdot 2.5}{10.4} = 55.3$ times. The difference lies within the limits of error, since

$$\frac{(P_1 - P_2)}{\sigma} = 1.64 < 3.$$

2. Size of induced growth

The size of the population growth following on the transfer of cage fluctuates within wide limits. If calculated in percentages from the starting point, it varies from 110% to 500% — the most frequent size being 130% to 200%. Average increase for all the experiments is 188%. The size of the induced growths was compared with spontaneous increases (Table 4). The size of the induced growths proved to be slightly less than the spontaneous (Table 4), but statistical analysis showed that the extent of the difference between spontaneous and induced growths is not statistically significant.

Sizes of spontaneous and induced populations growth

Tab. 4

Size of population growth in %	100 — 150	151 — 200	201 — 250	251 — 300	301 — 350	351 — 400	401 — 450	451 — 500	501 — 550	551 — 600	≥ 600	Average
Induced growth in %	37	34	14	7	2	2	2	2	0	0	0	188
Spontaneous growth in %	25	30	25	12	2	2	0	0	2	0	2	216

Interesting data are obtained from an analysis of the size of increase depending on the population phase during which the experiment of change of cage was carried out.

Allowing for a certain amount of simplification, the following phases in the life of the population were distinguished:

1. Peak periods with distinct symptoms of overcrowding.
2. Periods of decrease in numbers — a fall in the numbers of adult mice of not less than 2 individuals per month.
3. Periods of stabilisation — periods during which the increase or decrease in numbers of adult mice was not greater than 1 mouse per month.
4. Periods of growth — the growth in numbers is not less than 2 mice per month, with a total amount of increase of not less than 5 individuals.

Results of experiments depending on phase of population

Tab. 5

Phase of population	Number of experiments	No growth		Time from cage change to population growth	Size of growth in %
		number	%		
Peak period	4	2	50	1.3	198
Decrease period	29	9	31	1.18	164
Stabilization period	15	0	0	1.03	203
Growth period	6	0	0	0.6	292

The enclosed comparative table (Table 5) indicates that the time between the change of cage and start of growth, the size of the growth itself and the very fact of the existence or absence of growth depends on the population phase during which the experiment is carried out. It is true that the figures illustrating this are too small to permit of making a statistical analysis of their reliability, and it is therefore only possible to use the trends of these variations as guides. For this purpose the population phases were set out in Table 5 in the following order: peak period, decrease period, stabilisation period, growth period. This order illustrates the increasing chances of the existence of further growth. The least chance that further growth will take place is encountered during peak periods. Points of time within the growth

periods give us the greatest chance of further growth. Now the average sizes of growth, the average length of time from the change of cage to start of growth when arranged in this same order exhibit the tendencies foreseen. Growth takes place the latest when the experiment was made during the peak period, and the population reacted by growth most rapidly when the change of cage was made during the growth period. The highest average growth is also obtained from experiments carried out during the growth period. In experiments made during stabilisation and the growth periods, the population always reacted by growth, whereas all cases of absence of growth after change of cage occur when the experiments were carried out during peak periods or periods of decrease.

Results of experiments depending on kind of experiment

Tab. 6

Kind of experiment	Number of experiments	No growth		Time from cage change to population growth in %	Size of growth in %
		num-ber	%		
From smaller to larger	20	4	20	1.24	185
To a cage of the same size	21	4	19	0.86	196
From larger to smaller	13	3	23	1.00	179

The above considerations permit us to presume that certain tendencies existing in the population before the change of cage remain after the change of cage, and the change of phase evoked by the change of cage. It must be emphasised that population growth occurring after the change of cage in the growth period is not just a simple continuation of the previous growth. The population growth is in fact interrupted after the change of cage, a slight decrease in the number of adult mice follows, then a fresh increase (by accepting young mice into the population). We have the same picture when the experiments are carried out during the stabilisation period. Growth usually takes place, not directly after the stabilisation period, but the stabilisation period passes into a short period of decrease, after which growth occurs again.

Data obtained from an analysis of the phase in which the experiments were carried out were compared with data illustrating the influence of the category of experiment. The same indicators were set out in Table 6 in the following order: transfer from small to larger cage, to a cage of the same size, from larger to smaller. Figures illustrating the indicators examined do not exhibit any regular tendency. It may be concluded from this that the change of cage acts as such only, and that no particular influence is exerted by transfer from a smaller to larger cage, and by the consequent increase in living space (reduction of density of population).

3. Numbers and density of population at which growth occurs

Numbers of population. In order to check if change of cage is a stimulus inducing population growth, the numbers of population at which spontaneous growth takes place were compared with the numbers of population at the moment of transfer to another cage, and with the numbers of population at the time of start of population growth after change of cage (Table 1, columns 4 and 5). Only those experiments after which growth took place were considered for purposes of analysis, i. e. 43 cases, and not all 54 experiments — cf. Table 1.

An increase of not less than 5 individuals within a month was accepted as spontaneous population growth. In calculating spontaneous population growths, the first increase after founding the population was not taken into consideration, as the numbers of the population during these first population growths were not spontaneously formed, but were allotted by the experimenter as a population base. During the observations carried out, 51 spontaneous quantitative population growths took place (not counting the first growth).

Comparison of these three collections of figures (Fig. 3) showed that:

1. Numbers of population at which spontaneous growth takes place form a regular curve (Fig. 3). This curve differs distinctly from curves representing the numbers of population at the moment of experiment, and at the moment of beginning of experimental growth. It may be supposed that the numbers of population at the

moments of spontaneous growth reflect some biological rules. We have a marked preference for numbers of from 6-20 individuals. 82% of the numbers of population growth fall within the limits of these numbers.

2. The arrangement of the size of the populations at the moments when transfer is made to another cage, and the arrangement of the size of the populations at the moment of start of population growth is made, and when growth follows (evoked by the experiment) are growth after the change of cage are very similar. They present an irregular curve with many vertices (Fig. 3). It may be presumed that these numbers are not governed by the same biological rules which shape the arrangement of the numbers of the population at the moment of spontaneous growth, but that they were chosen fortuitously.

3. Numbers of population at the moments when change of cage clearly greater than the numbers at which spontaneous population growth took place (Fig. 3). In the first case the classes of 16 — 20

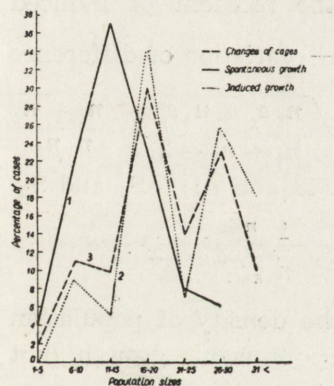


Fig. 3. Plan of population sizes at the moments of the beginning of spontaneous and induced growth and cages change

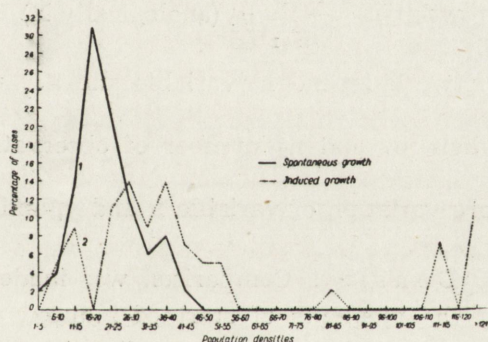


Fig. 4. Plan of population densities (number of mice in 1 m²) at the moments of the beginning of induced and spontaneous population growth

and 26 — 30 individuals are represented in the greatest numbers, whereas with spontaneous growth the great majority (82%) of the cases occurs where the numbers are 6 — 20 individuals. Also, the

averages from all the cases are less for spontaneous growth (14.7) than at the moments of experiment (23.6) and at moments of induced growth (20.1).

It may therefore be considered that:

a) the moments at which the experiments were made were not specially pre-destined for growth; if however, growth took place afterwards, it was evoked by the change of cage;

b) by means of the "change of cage" stimulus it proved possible to force the population to increase when the numbers are those at which spontaneous growth would not have taken place.

As a check, a statistical analysis was made of the numbers of population at moments of spontaneous and induced growth (Table 1, columns 4 and 5). The difference between these numbers

proved to be statistically significant, since $\frac{(\bar{y} - \bar{x})}{S_{xy}} = 3.18 > 3$,

where y — numbers of population at the moment of spontaneous growth, x — numbers of population at the moment of induced

growth, $\bar{y} = \frac{1}{n_1} \sum_{k=1}^{n_1} y_k$ (analogically \bar{x}), S_{xy} — variation of difference

of two independent variable and $S_{xy} = \sqrt{\frac{n_1 s_1^2 + n_2 s_2^2}{n_1 + n_2 - 2}} \sqrt{\frac{n_1 + n_2}{n_1 n_2}}$

where n_1 and n_2 number of observations (43 and 51) S_1 and S_2

are variation of variable x and y , and $S_1^2 = \frac{1}{n} \sum_{k=1}^n x_k^2 - \bar{x}^2$.

Density. Comparison was made of the density of population at the moments of start of induced and spontaneous growth (not counting the first growth after founding of population). The number of mice per 1 m^2 was accepted as the measure of density.

Comparison (Fig. 4) shows that population density where induced growth takes place is clearly greater than in the case of spontaneous growth. The majority (78%) of cases of spontaneous growth take place where the density is 11 — 30 mice per 1 m^2 . Cases of population growth where the density is greater or less are less frequent, so that the arrangement of densities with spontaneous population growth form a regular curve. Densities where induced population growths took place present an irregular curve. Induced

growth may take place at markedly greater densities. 26% of the cases of induced population growth take place where the densities are greater than 51 mice per sq. m. (greatest is 263 mice per 1 sq. m.), whilst the highest density at which spontaneous growth may still be observed was 44 mice per 1 m². Average density for all cases of spontaneous population growth is 21.9 mice per sq. m, whereas for induced growth the average is 57.4 mice per sq. m.

Attention must also be drawn to the great range of densities at which growth is observed. This range is considerably greater than the range of population numbers at which population growth is observed. Density at which spontaneous growth is observed varies from 4 to 44 mice per sq. m, i.e. the maximum density is 11 times as great as the minimum observed. Numbers varied from 4 to 29 (7.5 times as much). In the case of induced growth the differences are even greater, since the numbers vary from 5 to 39 (7.8 times), and the densities at which induced growth took place are from 9 to 263, that is, the greatest density at which it proved possible to evoke growth is 19.2 times as great as the minimum observed.

While discussing density at which growth takes place, we would like to draw attention to one other thing. In cages of size *P* and *B* directly the numbers fell, a fresh increase takes place, so that the population can exist for an indefinite period. In cages of size *A* and *M*, after the first increase following foundation of the population, not once was increase observed to occur. The mice after reaching the first peak gradually died. The length of life of the population was the length of the physiological life of the mice. These populations were kept for about 2 years, fertility was only rarely observed, but the unweaned mice were never observed to survive as long as three weeks. It would seem that cages *A* and *M* were too small for the populations to develop normally in them². On the other hand the population transferred from a different cage (larger, since type *P*) to cage *M* or *A*, increased.

² It is interesting to compare these data with the results of other work (Petrusewicz, 1958). It was proved that during encounters between the male mice in type *A* cages, a smaller percentage of fights was statistically real than in the case of encounters in cages *Z*, despite the fact that in a small cage the chances of an encounter between the males are of course greater.

To sum up, we may state that the data given above are evidence that:

1. Population growth may take place within a wide range of size and density of population. The range of density is far greater (from 8 — 263 mice per 1 sq. m) than the range of size (from 4 — 43 individuals).

2. After the change of cage, increase may follow at distinctly greater density and numbers of population, than the density and numbers of population at which spontaneous growth was observed to take place.

3. The number of cases, falling into the various classes of size and density, in which spontaneous growth is observed to take place, form a regular curve (Fig. 3 and 4), whereas the size and density in the cases of induced growth observed, form an irregular broken curve.

4. Taking the statement given at 2 and 3 as a basis, we may consider that the growths which could be observed after the change of cage are caused by just that change.

5. By using the stimulus of transferring a population to another cage, it proved possible to force the population to increase under conditions of density and size under which spontaneous growth was never observed.

4. Fertility of population and survival of litters

Fertility of the population. The number of young mice born in a population within one month was accepted as the measure of its fertility. The fertility of the population was calculated for the month immediately preceding the change of cage (F), and for the first month after the change (F').

As will be seen from comparison (Table 7) fertility after the change of cage is distinctly greater. Before the change of cage in 41 cases (i.e. 78%), the fertility is 0 — 20 young mice per month, whereas after the change in cage the fertility most frequently occurring is 11 — 30 young mice per month. The average fertility for all the experiments before change of cage is 14.4, and after the change 20.7.

Comparison of fertility (number of young born in one month) before (F) and after (F') the cage change

Tab. 7

Size of fertility		0	1—10	11—20	21—30	31—40	41—50	50	Average fertility
Number of cases	F	10	15	16	7	4	0	2	14.4
	F'	4	11	14	14	6	2	3	20.7

Comparing the rate of fertility before and after the change of cage for each of the experiments, it was confirmed that $F \geq F'$ in 12 cases (22%), whereas $F' > F$ in 42 cases (78%) which is statistically significant since:

$$\frac{P_1 - P_2}{\sigma} = 7.2 > 3, \text{ where } P_1 = \frac{42}{54}, P_2 = \frac{12}{54},$$

$$\sigma = \sqrt{\frac{2 \cdot P_1 \cdot P_2}{n}} \text{ and } n = 54 \text{ (number of experiments).}$$

For purposes of control 230 points chosen at random were selected on the axis of diagrams of numerical dynamic of all the populations. Fertility during one month was calculated before (F_1) and after (F'_1), a point chosen at random. This showed that $F_1 \geq F'_1$ 116 times (in this $F_1 = F'_1 = 8.42$ times), whereas $F'_1 > F_1$ 114 times, that is, the difference in fertility before and after points chosen at random lies within the limits of error.

In the light of the above data, we have grounds for considering that in our experiments the increase in fertility was caused by transferring the population to another cage, and not accidentally.

Survival of litters. The percentage of young mice which survived up to 3 weeks, i.e. to the time when they definitely leave the nest and their mothers, and become self-sufficient component members of the population, was accepted as an indicator of their capacity for survival. The researches of Southwick (1955), Brown (1953), which were also confirmed by our investigations show that the greatest mortality among the unweaned mice takes place during the first two days of life, and that the majority of the individuals which survived for 2 weeks become members of the population.

Calculation was made of the capacity to survive of the young mice born during the first 2 months after the change of cage (S'), and during the two months immediately preceding the change of

cage (S). From the enclosed comparison (Table 8) it can be seen that before the change of cage, in 33 cases (61%), the capacity to survive was 0% (including 4 cases in which fertility during the last two months was 0).

Comparison of survival (percentage of youngs surviving to 3 weeks) during 2 months before (S) and after (S') the cage change

Tab. 8

Survival (percentage)								Average survival	
	0	1-10	11-20	21-30	31-40	41-50	50		
Number of cases	S	33	7	4	5	2	2	1	8.9
	S'	13	4	8	17	4	4	4	21.1

So large a percentage of cases in which there was no survival of the young ones, is evidence that the moments at which the population of the cage was changed, were not moments destined for increase. Since, however, growth did take place, it may be assumed that it was the result of the "change of cage" stimulus.

After the exchange of cage, fertility is distinctly greater. The most numerous class is that with a percentage of 21% — 30% survival (17 cases). Average survival in all experiments before change of cage is $\bar{S} = 8.9\%$, after the change of cage $\bar{S}' = 21.1\%$ (Table 8). Comparing for each particular experiment the survival before transfer (S) and after transfer (S') to a new cage (Table 1), it was confirmed that $S \geq S'$ 17 times (31% of cases), whereas $S' > S$ 37 times (69%). The difference in number of cases where $S \geq S'$ from number of cases where $S' > S$ is statistically significant since

$$\frac{P_1 - P_2}{\sigma} = 4.16 > 3.$$

Survival for 2 months before (S₁) and after (S'₁) at 230 points chosen at random was: S₁ ≥ S'₁ 112 times (with S'₁ = S'₁ = 0 78 times), and S'₁ > S₁ 118 times. Comparison of capacity for survival before and after the change of cage with survival before and after points chosen at random proves that an increase in capacity for survival after the change of cage is subject to different rules than that after points chosen at random, and is the result of the stimulus given by the change of cage.

III. DISCUSSION OF RESULTS

Analysing the data obtained from the experiments carried out, we have shown that after transferring the population to another cage we obtained a rise in the fertility of the population, an increase in the capacity for survival of the young mice, and in consequence, a quantitative growth of the population. When comparing at the same time the density and size of the population during the periods of the experiments and spontaneous increases, frequency of cases of population growth, fertility and capacity for survival of the young mice, we showed that the number of cases where the population reacts by growth to the stimulus provided by the "change of cage" lies beyond the limits of error and is statistically significant.

The picture of induced growth was, as we have stated, as follows: after the change of cage, a slight decrease in the numbers of the population usually took place, then the mortality among the adult mice ceased. At the same time it was usually possible to observe an increase of fertility, and increase in the capacity for survival of the unweaned mice. Then, owing to the absence of/or very low mortality among the adult mice, and the capacity for survival of the young mice, population growth followed. Most frequently (in 30 cases — 56%) an increase in both fertility and in capacity for survival followed.

Usually, therefore, the population growth took place together with an increase in capacity to survive. In 5 cases, however, i.e. in the experiments carried out with the following populations: AXVIII 26.VII.57, LII 4.IX.54, ZV 20.IX.56, VI 1.XII.56 and ZmIII 2.I.57, the population growth took place while the capacity to survive decreased, although it did not disappear (Table 1).

Most of the increase occurred as the result of the survival of the unweaned mice born after the change of cage. In certain cases, however (especially those carried out during the increase period) the young mice born before the change of cage also survived, but in one case (ZmIII 2.I.57) capacity to survive after the change of cage was nil, while the population growth took place only owing to the survival to an adult age of the young mice born before the cage change.

From the above data it can be seen that population growth took place owing to the different co-operation of the increase in fertility and especially of the increase in the capacity for survival.

It is interesting to try to find the answer to the question as to what caused the increase in the capacity to survive of the young mice, and the consequent increase in the size of the population. This population growth takes place after the change in the living environment, yet it is difficult to assign this to the direct influence of the new environment on the organism. If indeed the growth in numbers of the population following on transfer to a larger cage may be explained simply by the increase in living space and consequent decrease in density, this explanation is completely inadequate in cases of population growth after transfer to a cage of the same size, although differently arranged, and even more so in the cases of population growth after transfer to a smaller cage.

These last experiments are deserving of special notice. Population growth was obtained after the population was transferred from cage *V* to *A*, that is, to a cage 11.2 times smaller, and in 8 times out of 9 experiments after transfer from *P* size cage to *M*, that is, to a cage 5.7 times smaller (Table 2).

The picture of population growth in this type of experiment is often characteristic, E.g. population *ZmII* was reared for 23.5 months in a type *Z* cage, reaching at its highest level 28 individuals. After transfer to an *M* type cage, that is, more than 5 times smaller, the population reached a level of 29 individuals, i.e. greater than the highest level attained during the 23.5 months the population had lived in a large cage (Fig. 2, *ZmII*). Similarly population *LI* lived in type *L* and *P* cages (that is, cages measuring $80 \times 80 \times 15$) for 25 months, reaching during that time 5 peaks, of which the greatest spontaneous peak was 35 individuals, whereas the peak reached after transfer from *L* to *P* was 37 individuals. After transfer to cage *M* (dimensions $38 \times 30 \times 15$) the population attained a level of 40 individuals, that is, a higher level than hitherto, during the period of more than 2 years spent in cages 5.7 times larger (Fig. 2, *LI*). Also, population *VI* after transfer from *V* to *M* attained a level of 36 individuals, whereas previously the highest level reached was 30 (in a larger cage) (Fig. 2, *VI*).

A picture exhibiting the same trends is supplied by *PIV* in which during a period of 18 months we have two practically identical cycles, with peaks of 35 and 33 individuals. After transfer to an *L* type cage, the population increases to 63 individuals, that is, to a level almost twice as high.

Attention should also be paid to the density of population of mice in which population growth takes place. The greatest density during which spontaneous growth was observed was 44 mice per 1 sq.m. On the other hand growth induced by the change of cage was obtained in LV and PVII with a density of 263 mice per 1 sq.m. (Table 1).

Of course it should not be concluded from the data given above that density does not influence population at all. The regularity of the curve of densities during which spontaneous growth takes place, bears witness to the fact that density exerts a powerful influence. On the basis of the data discussed above, however, it is possible to confirm that it is not only density which decides population growth.

From an analysis of the experiments presented, it may be stated that they confirm and expressly emphasise Southwick's opinion (1955a), since he, in discussing the factors limiting populations of mice, states that they "were related to crowding and confinement, but not to density *per se*".

This thesis is confirmed by the above data, resulting from an analysis of the numbers of populations during spontaneous growth. The point is that population growth takes place at greatly varying levels of size and density of population. Also spontaneous decrease in population began at a peak point, when symptoms of over-crowding could be observed, such as a large amount of biting, poor coats, fall in fertility of population, increase of mortality among the adult mice and a complete absence of the capacity to survive among the young mice (most often the unweaned mice died or were eaten on the first or second day after birth). After a certain time, however, the symptoms of over-crowding disappeared, while the decrease in population continued, or sometimes a long-lasting period of stabilisation followed, during which the new generations were not permitted to become adults.

All these data confirm the thesis well known from the ecological papers, that among members of populations certain relations are created (generalisations of this thesis can be found e.g. in Allee 1942, Park 1942, Allee and oth. 1949, Naumov 1955 etc.). Some structure of population then arises the elements of which are: the density, relations and dependencies created among individuals etc. We may therefore suppose, that the population phases, and the

tendency to quantitative stabilisation decrease or increase of population connected with this phases, depends not only on the degree of density itself, but on the relations created by this density between the individuals of the population, i.e. on the population structure.

The structure once created (mutual relations between the mice) has a certain inertia, and lasts for a certain period after the stimulus which evoked the over-crowding has ceased to act. It changes after a certain low level has been reached, and the mice then began to breed, while the capacity to survive increases. Again we have a picture of a certain inertia of the population structure (of the relations between the individuals favouring the survival of the unweaned mice). The numbers of the population are indeed often greater than 30 individuals (the highest numbers at which the beginning of population growth was observed in size P cages), but growth continues. This means that growth, once it has begun, may continue even with a density of population which precludes the start of population growth.

The hypothesis that capability of growth depends on the population structure formed between individuals makes it possible to explain population growth taking place after change of cage. The relations between individuals were formed in a given cage. The relations formed between individuals in a given environment are destroyed by a stimulus such as a change of environment. Relations are formed between the mice in the new cage similar to those prevailing in a newly-founded population. And a newly-founded population, after a certain period during which a slight amount of biting, and often a slight fall in numbers, takes place, always increases.

Finally one general remark. T. Park (1942) in summing up and generalising on the many ecological investigations carried out, and giving a more precise formulation to Smith's statement (1935), based on the earlier suggestions of Howard and Fiske (1911), divides "ecological factors capable of controlling population size by affecting reproduction and mortality fall into two categories: density-independent and density-dependent factors". This very simple division has a deep ecological sense, and supplies the key to the understanding of many important ecological problems, such as the population as a whole, compensating processes within the pop-

ulation etc. There are however numerous ecological works which state that often the density of a population is not directly responsible for the growth or decrease of a population, that is, not the density itself as such. For instance we quoted Southwick's statement (1955a) above, that the behaviour of the mice causing a high mortality rate among the unweaned mice is dependent on density, but not on "density per se". In another work Southwick (1955b) gives a comprehensive discussion of the relations between the mice causing mortality among the unweaned mice, and even explains the mechanism of their actions. Strecker and Emlen (1953) connect the decrease in fertility not only with the lack of food, but also consider it as dependent on social factors. Calhoun (1956) in describing the difference between strains of mice, gives the differences in social behaviour influencing population growth. Finally, the experiments detailed above, which can be explained if we accept that the tendency to increase or decrease in population numbers depends on the relations formed between the mice.

It would therefore appear that in the light of data of this kind, Park's division into "density-independent and density-dependent factors" should be slightly modified. Ecological factors capable of exerting an influence on population growth or decrease should be divided into ecological factors dependent on and independent of population structure. This would be an extension of the division into density-dependent and density-independent ecological factors. In this case density would be one of the elements of the structure. Such a division would, in any case be in complete accord with the intentions of Park (1942), who writes elsewhere in the work discussed: "A population cannot be thought of as a grouping of organisms in which each individual is isolated in a particular environmental capsule and immune to the pressure of contiguous capsules and neighbouring organisms. This might be a convenient logical conception but it is biologically fallacious. Actually, as we have seen, the population members influence each other — i.e. their biotic environment — and in turn are influenced reciprocally by their physical environment... At this moment the group has a particular size because of a specific ecologic and genetic past-history which has created the present increase and decrease pressures".

These words contain the idea that the relations formed between the individuals of this population, that is, the population structure, are responsible for the quantitative dynamics of the population.

IV. SUMMING - UP

Observations were made of 47 freely reproducing populations. 54 experiments were carried out, consisting in transferring an entire population to a different cage (20 times to a larger cage, 21 times to a cage of the same size, and 13 times to a smaller cage).

1. It was confirmed that during a period of 2.5 months after transfer, increase took place in the fertility of the population (78% of cases), and capacity of the unweaned mice to survive (69% of cases), which in consequence resulted in increase of the whole population. Increase took place even after transfer to cages 5.7 and 11.2 times smaller.

2. The number of increases in population after change of cage was statistically actually greater than the spontaneous increase anticipated on the basis of probability.

3. After the change in cage, population growth was attained where size and density were statistically actually greater than the size and density of populations in which spontaneous growth was observed.

4. The size of population growth and rapidity of reaction by growth are dependent on the population phase prevailing at the time of the experiment.

5. On the basis of data from literature and from experiments carried out, the presumption was expressed that tendencies to increase, or absence of increase are dependent not only on density but also on relations between the members of the population, which had been formed in the given cage. By changing the cage, the population structure created was disturbed, which brought about increase in population.

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DOŚWIADCZALNIE WYWOŁANY WZROST POPULACJI

Streszczenie

Myszy hodowano w klatkach o wielkości: $38 \times 15 \times 15$ (typ A), $38 \times 30 \times 15$ (M), $80 \times 80 \times 15$ (P, Z, L, D, V) i $160 \times 80 \times 15$ (B). W klatkach wielkości $80 \times 80 \times 15$ był różny stopień komplikowania wnętrza klatki: typ P najprostsze, V najbardziej skomplikowane (fig. 1). Po umieszczeniu w klatce pewnej ilości myszy jako bazy populacyjnej (nacząściej 8 ♀♀ i 3 ♂♂) pozwalano im mnożyć się swobodnie. Pokarm, woda i strużki były w nadmiarze. Do analizy wzięto populacje, które żyły nie krócej niż 12 miesięcy. Otrzymano w ten sposób materiał z 47 populacji, które łącznie żyły 1175 miesięcy.

Ogółem otrzymano w czasie obserwacji 51 samorzutnych wzrostów populacji (nie licząc pierwszego po założeniu wzrostu w każdej populacji).

W czasie trwania hodowli przeprowadzono 54 razy eksperyment, polegający na przełożeniu w pewnym momencie życia populacji całej populacji do innej klatki. Z klatki mniejszej do większej przekładano populację 20 razy; 21 razy populację przekładano do klatki tej samej wielkości tylko innego typu (przekładanie w obrębie klatek typu: P, Z, D, L, V); wreszcie 13 razy przekładano do klatki mniejszej (z B do P , z klatki wielkości P do M i z wielkości P do A).

Rezultaty tych eksperymentów były następujące: wkrótce po zmianie klatki w ogromnej większości wypadków następował wzrost populacji (por. tab. 1 i 2). Uznano, że wzrost nastąpił, jeżeli w ciągu 2,5 miesięcy po zmianie klatki rozpoczął się wzrost populacji.

Przebieg tych eksperymentów był następujący: zaraz po przełożeniu myszy były niespokojne, przejawiały wzmożony instynkt poszukiwawczy, ilość walk była mała. Po paru dniach ilość walk lekko wzrastała. W ciągu miesiąca lub dwóch wyraźnie wzrastała ilość urodzeń i przeżywalność młodych, po czym w okresie do 2,5 miesięcy następował wzrost liczebności populacji.

Na podkreślenie zasługuje, że udało się osiągnąć wzrost przy przełożeniu populacji z klatki typu P do A , a więc do pomieszczenia 11 razy mniejszego. Z 13 eksperymentów polegających na przełożeniu do klatki mniejszej, w 10 przypadkach nastąpił wzrost populacji.

Porównano płodność w ciągu ostatniego miesiąca przed zmianą klatki (F) i pierwszego miesiąca po zmianie (F'). Okazało się (tab. 7), że $F \geq F'$ 12 razy (22%), zaś $F < F'$ 44 razy (78%). Porównano też przeżywalność młodych do 3 tygodni w okresie 2 miesięcy przed eksperymentem — S i po — S' . Analiza (tab. 8) dała: $S \geq S'$ w 17 przypadkach (31%) i $S < S'$ 37 razy (69%). Różnica w obu wypadkach jest statystycznie istotna. Dla kontroli porównywano płodność i przeżywalność przed i po losowo wybranych 230 punktach. Obliczenia dały: $F \geq F'$ 116 i $F < F'$ 114 razy; $S \geq S'$ 112 i $S < S'$ 118 razy.

Eksperymentu zmiany klatek dokonywano na różnym poziomie wysokości i w różnych fazach populacyjnych.

Na ogół, jeżeli eksperyment był wykonany w okresie wzrostu — populacja natychmiast gwałtownie wzrastała. Gdy zmiana klatki odbywała się w okresie spadku, odpowiedź wzrostem odbywała się po pewnym czasie (1,5 — 2 miesiące). Tak samo szybciej następował wzrost po przełożeniu, jeśli populacja była mało liczna (tab. 5 i 6).

Porównanie wielkości populacji: w momencie samorzutnego wzrostu, dokonywania eksperymentu, oraz momentu indukowanego wzrostu (fig. 3) wskazuje, że przy pomocy zmiany klatki zmuszono populację do wzrostu przy większych wysokościach. Ten sam obraz otrzymano przez porównanie zagęszczeń (ilość myszy na 1 m² — fig. 4).

Prawdopodobne wyjaśnienie: w nowozałożonej populacji po okresie przyzwyczajania się do miejsca następuje jej wzrost. Po osiągnięciu szczytu z objawami przegęszczenia, między osobnikami populacji wytwarzają się takie stosunki, że populacja nie dopuszcza do siebie nowych osobników. Rozrodczość spada lub zanika (nieraz na kilka miesięcy), przeżywalność młodych zupełnie ustaje. Stan taki trwa do czasu, gdy populacja osiągnie bardzo niski poziom (najczęściej 10 lub mniej osobników). Zmieniając klatkę burzymy ustaloną strukturę populacji. Populacja zachowuje się podobnie do nowozałożonej hodowli: pojawia się gryzienie, niepokój, wzmoczenie płodności, dopuszczanie młodych — następuje wzrost populacji.