

Kazimierz PETRUSEWICZ

Some Regularities in Male and Female Numerical Dynamic in Mice Populations

Niektóre prawidłowości dynamiki liczebności samców i samic w populacjach myszy

(with 11 tables and 8 figs.)

ABSTRACT. In confined populations of mice, the number of females have been found to be greater than males, and more so at periods of minimum population numbers than of maximum. Males were found to exceed females in: rate and amplitude of numerical changes, mortality, and duration of numerical stabilization. In birth rate the sexes were alike.

I. Material and methods	103
II. Numbers of males and females	105
III. The rate and amplitude of numerical changes	117
IV. Duration of numerical stabilization	122
V. Mortality and natality	123
VI. Discussion	126
VII. Summary	133
References	134
Streszczenie	135

I. MATERIAL AND METHODS

The object was to explore the regularities, if any, of males and females numerical dynamics in confined populations of laboratory white mice. Specific points were: male - to - female numerical ratio, the rate, character and amplitude of numerical changes in relation

to the phase (lows and highs) of the population, the duration of the numerical predominance of either sex, and others.

The data were obtained from populations bred in closed cages of the following types:

type *Z* (*P*, *Z*, *L*, *D*, and *V*), size: $80 \times 80 \times 15$ cm;
type *B* size: $160 \times 80 \times 15$ cm; and
type *A* size: $38 \times 15 \times 15$ cm¹⁾.

Cages of types *P*, *Z*, *L*, *D* and *V* differed in interior arrangement: *P* were the simplest and *V* the most complicated (P e t r u s e w i c z, 1957).

Some data related to type *H* populations bred in roughly 6-sq. m. enclosures after C a l h o u n (1956) with some modifications²⁾.

The populations were started by putting into particular cages some mice. In type *Z* cages the usual number was eight females and three males, either litter-mates or kept together since their early days. This precaution with males was necessary because otherwise one or two of them were almost as a rule killed within the first few days. Once a population has been started no individuals were added to it or taken away. The population's numerical status was regulated merely by natural processes within.

The animals were invariably fed and watered ad libitum, and the cages were cleaned fortnightly. Births, number of living young ones, and deaths of adults (if known) were recorded daily. Juveniles at the age of three weeks were sexed and marked with an individual number. All adults were counted and weighed half-monthly (on the 1st and 15th of each month). The analyses are based on these data.

Between 1953 and Jan. 1, 1960, the following populations were bred, and the data recorded from them analyzed:

¹⁾ In Table I and elsewhere reference may be found to populations marked *A* in type *Z* cages. This is because a population started in cage *A* was subsequently transferred to cage *Z* or *B*. In such cases analysis concerned the data and life-time of the population in the actual type of cage without changing the population's number.

²⁾ Type *H* populations have been bred by the author jointly with R. A n d r z e j e w s k i and W. W a l k o w a in Institute of Ecology P.A.Sc., who used them also for other purposes (cf. A n d r z e j e w s k i, P e t r u s e w i c z & W a l k o w a, 1959),

60	populations of size Z,	with an over-all life time of 1504 months;
7	„ B,	204 „
15	„ A,	191 „
4	„ H,	128 „

The basis for the analyses³⁾ was provided by populations of type Z (80 × 80 cm), since this type had the largest number of replications and the longest period of observation (Fig. 1 gives some examples of the numerical dynamics of Z-type populations). The data recorded from the remaining types of cages were treated in principle as material for comparisons. The statistical likelihood of the data from these populations has not always been checked, for, in this type of cages, either replications were too scant (in H — 4, in B — 7) or observation was too short (A).

For statistical analyses use was made of the data from only such type Z populations which have lived more than 12 months. The analyses concerned only the data recorded since the first peak of any given population, to eliminate from consideration the period in which the sex ratio may have been affected by the original one; as has been said, the original sex ratio was not always the same.

II. NUMBERS OF MALES AND FEMALES

For each population the time has been computed over which females out-numbered the males ($Y♀ > Y♂$), and that over which the males equalled or exceeded the females in numbers ($Y♀ ≤ Y♂$). This time was subsequently calculated in terms of per cent of the population's over-all life-time.

This gave the time (in per cent) of predominance for females:

$$TD♀ = 100 \cdot \frac{\text{time over which } Y♀ > Y♂}{T = \text{population's life-time}}, \text{ and for males:}$$

$$TD♂ = 100 \cdot \frac{\text{time over which } Y♀ ≤ Y♂}{T = \text{population's life-time}}, (TD♂ = 100\% - TD♀ \text{ — see}$$

Table 1, column 5).

An analysis of the $TD♂$ score (Table 3) for populations bred in type Z cages (80 × 80 cm) shows that the number of populations where

$$TD♀ > TD♂ \text{ was } 48 (80\% = P_1), \text{ and where}$$

$$TD♀ ≤ TD♂ \text{ was } 12 (20\% = P_2).$$

³⁾ For help with the statistical analyses of the material the autor is greatly indebted to Mrs. T. Wierzbowska (Instytut of Ecology P. A. Sc.),

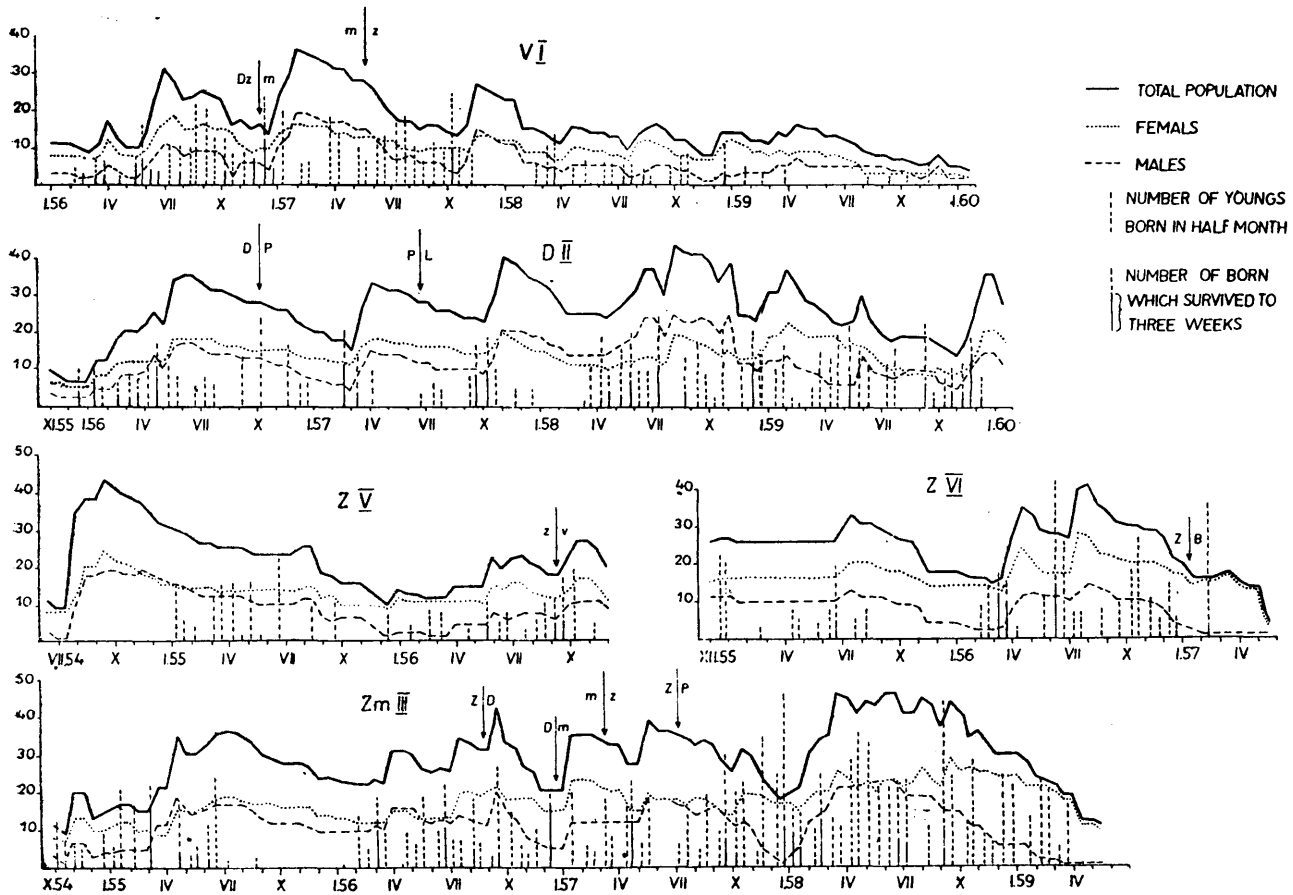


Fig. 1. Population dynamics (examples).

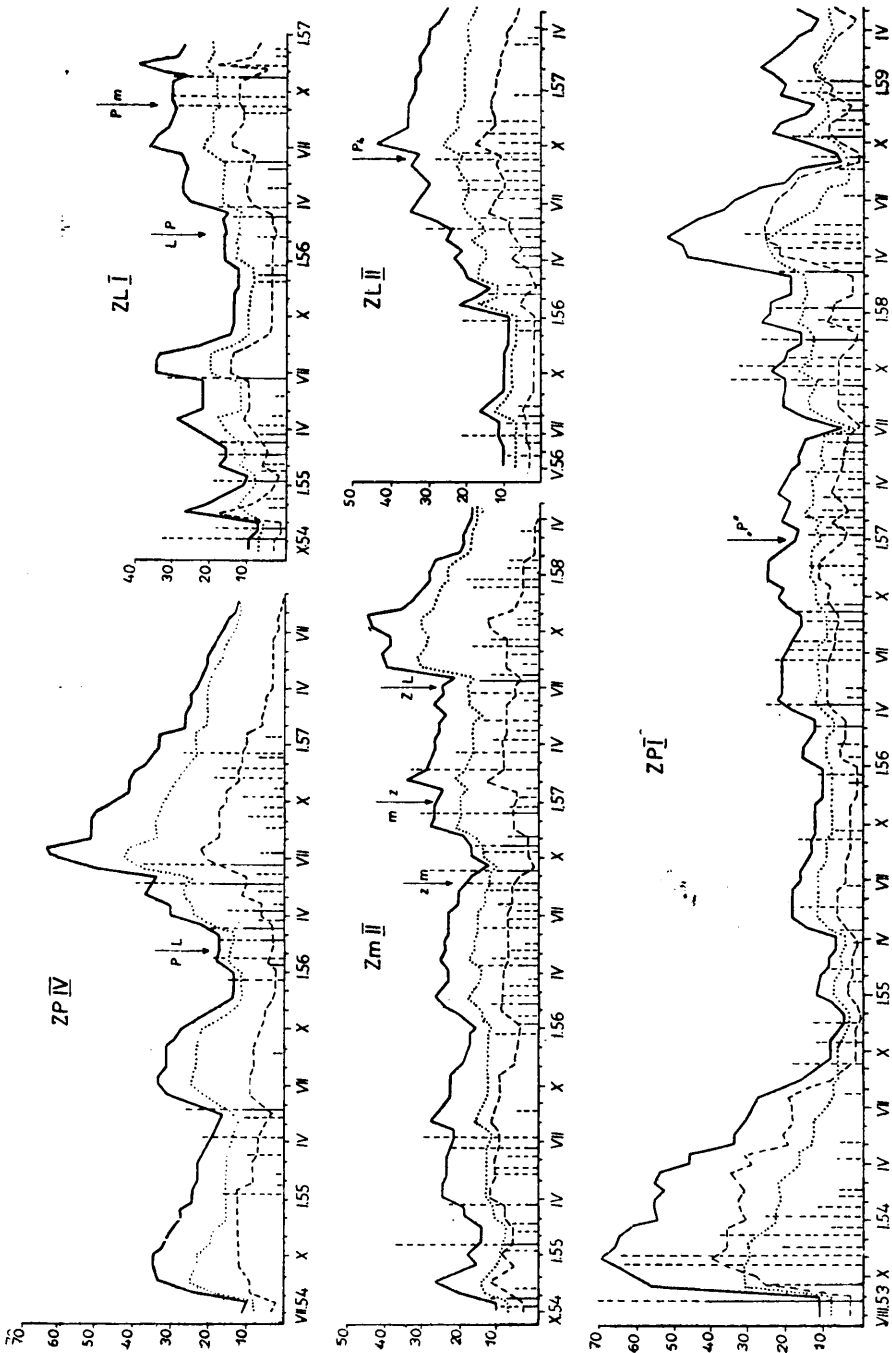


Fig. 1 (continued).

Table 1.

Numerical data relating to populations bred in size Z cages.

No. — population's number; t — time of living of population (in months); \bar{Y} — average number of individuals (females or males); $TD_{\frac{1}{2}}$ — period of time of numerical predominance of females; A — amplitude; St — duration of numerical stabilization; D — mortality.

No	t	\bar{Y}_{σ}	\bar{Y}_{\varnothing}	P	$TD_{\frac{1}{2}}$	A_{σ}	A_{\varnothing}	St_{σ}	St_{\varnothing}	D_{σ}	D_{\varnothing}
	1	2	3	4	5	6	7	8	9	10	11
Z ₁	42.0	6	10	.000	69	20	16	9.3	8.7	100	80
Z ₂	58.0	10	14	.000	81	39	26	6.8	6.0	150	93
Z ₃	30.5	16	31	.000	100	40	32	6.1	5.8	125	87
Z ₄	13.0	11	19	.000	100	54	54	5.0	5.0	236	152
Z ₅	29.0	9	18	.000	93	36	35	6.1	5.5	100	67
Z ₆	34.5	10	18	.000	93	37	28	7.6	5.2	150	83
Z ₇	15.0	18	26	.000	68	24	7	8.3	8.5	139	38
Z ₈	17.0	8	23	.000	100	21	26	6.3	6.0	150	65
Z ₁₂	14.0	17	30	.000	100	30	11	4.0	6.0	188	63
Z ₁₃	15.0	9	16	.000	41	42	16	6.4	6.4	130	59
Z ₁₄	18.0	6	12	.000	50	34	26	4.8	3.8	306	153
Z ₁₈	19.0	13	24	.000	100	37	40	6.0	6.2	154	78
Z ₁₉	19.5	16	26	.000	100	40	35	5.2	5.2	121	56
Z ₂₀	18.0	20	21	.001	84	51	32	4.4	5.6	112	57
Z ₂₁	17.5	19	18	.195	35	38	32	7.5	7.0	93	62
Z ₂₂	18.0	18	24	.000	100	43	37	5.3	4.5	122	67
Z ₂₃	17.0	19	18	.229	25	72	47	2.4	3.2	160	107
Z ₂₄	17.0	19	19	.381	44	53	46	4.8	4.0	135	97
Z ₂₅	17.0	11	20	.000	100	33	34	10.0	8.0	153	68
Z ₂₆	18.0	22	28	.000	94	42	34	7.2	8.4	73	34
Z ₂₇	17.0	18	22	.000	81	58	50	6.8	2.8	133	102
Z ₂₈	17.0	15	24	.000	93	38	50	5.0	3.0	106	80
Z ₂₉	16.5	10	19	.000	74	27	25	6.0	7.2	144	25
Z ₃₀	12.5	12	18	.000	100	28	25	3.3	4.0	108	39
Z ₃₁	12.5	14	20	.000	100	44	29	1.9	2.6	136	45
Z ₃₂	12.0	13	14	.295	50	37	31	6.0	5.4	54	62
Z ₃₃	12.0	27	21	.000	18	51	30	4.5	5.0	67	38
P ₁	77.0	11	12	.036	77	47	32	5.8	5.3	223	146
P ₂	20.0	10	23	.000	100	34	43	8.0	5.0	170	87
P ₃	47.5	10	12	.071	70	23	20	8.5	6.5	136	113
P ₄	38.0	9	21	.000	100	25	38	6.1	3.6	155	119
P ₅	20.0	8	7	.322	30	14	17	10.2	7.8	88	143
P ₆	28.5	8	11	.000	70	24	9	8.8	7.5	125	64
P ₇	16.0	12	25	.000	100	21	18	8.2	8.1	158	36
P ₈	18.5	13	28	.000	100	56	56	5.2	5.2	169	67
P ₉	16.0	15	21	.000	100	48	33	7.5	6.5	160	57
P ₁₀	16.0	20	32	.000	100	55	68	5.3	2.3	73	58
Zm ₁	37.5	10	16	.000	82	36	26	6.0	7.0	170	94
Zm ₂	43.0	7	19	.000	100	25	27	8.0	5.5	204	69
Zm ₃	55.5	11	15	.000	82	36	32	7.3	5.6	172	108
Zm ₄	27.0	8	12	.000	100	22	20	9.0	7.0	100	75

Table 1 (continued).

	1	2	3	4	5	6	7	8	9	10	11
L ₁	26.5	8	14	.000	96	50	32	7.0	7.0	200	100
L ₂	26.0	7	15	.000	100	30	35	6.0	6.0	143	93
L ₃	23.0	6	9	.000	91	25	18	7.0	6.5	150	111
L ₄	15.0	11	14	.000	72	33	27	9.0	8.4	127	71
L ₅	36.0	8	6	.322	43	22	18	7.3	7.0	159	186
L ₆	14.0	8	4	.000	11	24	15	7.2	6.5	100	250
D ₁	48.5	10	15	.000	88	39	37	6.3	4.9	203	133
D ₂	52.0	12	14	.011	69	40	27	6.6	6.0	164	88
V ₁	48.0	5	9	.000	81	30	24	7.8	6.4	304	148
V ₂	13.0	17	13	.000	20	45	26	6.5	6.0	178	107
A ₂	20.5	8	14	.000	100	35	29	8.0	7.2	225	100
A ₃	58.0	7	13	.000	86	26	20	7.2	6.1	194	80
A ₅	21.5	9	11	.000	83	19	17	6.9	5.9	150	92
A ₆	24.0	11	20	.000	100	24	23	9.0	7.8	136	55
A ₉	18.0	16	19	.000	50	30	24	8.3	7.0	68	71
A ₁₀	16.0	18	17	.229	38	37	22	7.1	7.6	95	53
A ₁₁	15.5	14	13	.172	47	32	24	8.6	7.4	69	57
A ₁₇	14.0	11	18	.000	100	30	32	8.0	6.4	45	50
A ₁₈	12.0	9	19	.000	100	29	28	9.5	9.0	167	63
Avg.	25.1	12.6	17.9		72.9	35.6	29.5	6.7	6.0	143	8.9

The statistical significance of the difference in the number of cases as between $TD\varphi > TD\sigma$ and $TD\varphi \leq TD\sigma$ was checked with the aid of the criterion: the difference between P_1 and P_2 is statistically significant when $|P_1 - P_2| : \sigma \geq 3^4$.

The difference proved statistically significant since $|P_1 - P_2| : \sigma = 6.91 > 3$.

Further (Fig. 2), the number of populations has been found to be:

23 cases (38%) when $TD\varphi = 100\%$

0 cases (0%) when $TD\varphi = 0\%$, and

38 cases (63% = P_3) when $TD\varphi > 80\%$.

The number of populations where females outnumbered males over 80% of the time, or longer (P_3), differed significantly from the number of populations where $TD\varphi \leq TD\sigma$ (P_1), since $|P_1 - P_3| : \sigma = 3.03 > 3$.

⁴) P_1 — percentage of populations where $TD\varphi > TD\sigma$; P_2 — number of populations where $TD\varphi \leq TD\sigma$; and σ is the standard deviation of the variable expressed as:

$$\sigma = \sqrt{\frac{P_1(100-P_1)}{n_1} + \frac{P_2(100-P_2)}{n_2}}$$

Table 2.

Numerical data relating to populations bred in size A, B and H cages.

No	t	\bar{Y}_\varnothing	\bar{Y}_σ	TD \varnothing	A σ	A \varnothing	D σ	D \varnothing
A ₁	24.0	11	7	100	8	7	99	58
A ₂	9.0	17	13	100	17	10	67	30
A ₃	7.0	19	7	100	12	3	171	15
A ₄	22.0	14	7	100	8	11	104	70
A ₅	7.0	16	7	100	24	12	43	56
A ₇	26.5	10	6	100	10	11	140	139
A ₈	18.0	7	7	47	8	18	69	228
A ₉	7.5	12	11	59	6	12	52	98
A ₁₀	9.0	13	8	92	35	13	185	46
A ₁₁	13.5	12	11	60	23	20	38	83
A ₁₂	12.5	8	5	100	6	11	175	26
A ₁₃	11.5	4	14	14	17	11	34	210
A ₁₄	8.0	8	12	4	24	13	31	67
A ₁₇	7.0	17	10	100	11	5	54	10
A ₁₈	9.0	13	7	100	17	13	97	58
Average	12.8	12	9	78	15	11	91	80
B ₁	51.5	19	15	69	47	32	127	101
B ₂	25.5	25	13	100	32	34	115	48
B ₃	19.5	23	10	100	28	27	220	70
B ₅	21.0	27	15	100	59	63	133	67
B ₆	31.5	18	18	36	23	19	104	79
B ₇	31.5	19	19	68	32	23	147	91
B ₈	24.0	12	6	95	71	57	294	147
Average	29.2	20	14	81	42	36	163	86
H ₁	32.2	27	22	72	81	82	189	153
H ₂	32.2	39	30	88	96	88	151	108
H ₃	32.2	58	53	65	144	135	142	123
H ₄	32.2	74	67	82	158	166	111	101
Average	32.2	49	43	77	120	118	148	121

Characteristic is the distribution of the magnitude $TD\varnothing - TD\sigma$, namely:

the value $TD\varnothing - TD\sigma$: $< -50\%$, $-50\% - 0\%$, $1\% - 50\%$, $51\% - 100\%$

Number of cases: 3 9 9 39

percentage of cases: 5% 15% 15% 65%

Calculations have also been made for all populations jointly of the average time over which females outnumbered the males ($\overline{TD\varnothing}$) and when $Y\varnothing \leq Y\sigma$ ($\overline{TD\sigma}$). It has been found (Table 3) that $\overline{TD\varnothing} > \overline{TD\sigma}$ in all types of populations.

The magnitude of difference between \overline{TD}^{\ominus} and \overline{TD}^{σ} , analyzed by Student's test for populations Z and A, was statistically significant (for Z-populations at the level of 0.0000, and for A-populations — 0.01). The difference has not been checked statistically for populations B and H owing to scarcity of replications. However, the long period of observation (128 months for H and 204 for B), and the fact that all results point in one direction, allow these results to be trusted.

Table 3.
TD-score in populations of varying types.

Cage	No. of population	Percentage of cases when:					Average	
		$TD_{\ominus} > TD_{\sigma}$	$TD_{\ominus} < TD_{\sigma}$	$TD_{\ominus} > 80\%$	$TD_{\ominus}=100\%$	$TD_{\sigma}=100\%$	\overline{TD}_{\ominus}	\overline{TD}_{σ}
Z	60	80	20	63	38	0	78	22
A	15	80	20	67	60	0	78	22
B	7	86	14	100	43	0	81	19
H	4	100	0	50	0	0	77	23

Table 4.
Statistical analysis of differences between average numbers of sexes ($P < .01$).

Statistical	Number of cases when :		Total
	$\overline{Y}_{\ominus} > \overline{Y}_{\sigma}$	$\overline{Y}_{\ominus} < \overline{Y}_{\sigma}$	
significant	47	3	50
non significant	3	7	10
Total	50	10	60

Hence, the numerical predominance of females in confined mice populations over most of the time may be supposed to be a generally regular phenomenon ⁵⁾.

* * *

The numbers of males and females (Y_k^{σ} and Y_k^{\ominus}) have been analyzed for 60 populations bred in type Z cages. With this in view,

⁵⁾ It will be remembered that the expression TD_{σ} also covers the period of numerical equilibrium between the sexes within a population.

the mean numbers of males and females (\bar{Y}^σ and \bar{Y}^φ) have been calculated separately for each population of type Z (Table 1, columns 2 and 3). This mean has been computed from the half-monthly counts recorded in the graph, for the period between the end of the first peak and the end of the experiment (death of the population or termination of observations) or, alternatively, January 1, 1960. By ignoring the period before the first peak, the pre-existing numerical disproportion between the sexes, due to the starting of the population with different numbers of males and females, has been discounted (in the cages of types Z, A and B, the populations were usually started with three males and five to eight females)⁶⁾.

Subsequently, the statistical significance of the differences between mean number of females (\bar{Y}^φ) and males (\bar{Y}^σ) in each population was checked with the aid of Student's test and by analyzing the series $Z^k = Y^\varphi_k - Y^\sigma_k$ where Y_k is the number of the animals of the given sex at the time k. The differences proved statistically significant at the levels of 0.01 in 50 (83%) and at 0.001 in 49 (82%) cases (Table 1, column 4 and Table 4). There were only 3 cases (5%) where the differences was statistically significant and $Y^\varphi \leq Y^\sigma$.

A check-up has been made to see whether the differences between the percentages of all these cases were statistically significant:

	Number of cases	
$\bar{Y}^\varphi > \bar{Y}^\sigma$	50	$P_1 = 83\%$
$\bar{Y}^\varphi \leq \bar{Y}^\sigma$	10	$P_2 = 17\%$
$\bar{Y}^\varphi > \bar{Y}^\sigma$ and this difference is significant	47	$P_3 = 78\%$
all the remaining cases (100% — P_3)	13	$P_4 = 22\%$
$\bar{Y}^\varphi \leq \bar{Y}^\sigma$ and significant	3	$P_5 = 5\%$

The computations gave:

$$|P_1 - P_2| : \sigma = 8.69 > 3$$

$$|P_3 - P_4| : \sigma = 8.11 > 3$$

⁶⁾ To see whether the starting numerical differences between the sexes affect mean numbers, Y^σ and \bar{Y}^φ have been calculated for three populations ignoring altogether the periods till the death of starting animals. The differences between the means calculated with and without the starting animals were expressed in centesimal fractions and not above 0.1, while \bar{Y}^σ and \bar{Y}^φ were used in round figures.

Hence, the difference may be said to have been statistically significant in all comparisons. And even the percentage of the cases where the females significantly outnumber the males is significantly larger than the percentage of the remaining cases, that is, of those where the numerical difference between the sexes is statistically nonsignificant or the females are less numerous than males. And the criterion used in this case is rather severe. For, among the ten populations where the differences between the sexes were not statistically significant, there doubtless are such where this was due to small n (brief observation period).

Table 5.

Frequency of the values of differences and quotients of females and males numbers (expressed in percentage of the number of cases).

Quotient		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 <	Avg.	
$Y_{\text{f}} : Y_{\text{m}}$		2	16	35	34	10	3	0	5.3	
$Y_{\text{f}} : Y_{\text{m}}$	at peaks	4	27	37	19	7	4	2	4.2	
	at min.	3	11	17	16	7	7	40	6.4	
Difference	< 8	-7 - 4	- 3.0	1 - 4	5 - 8	9 - 12	13 - 16	17 <		
$Y_{\text{f}} - Y_{\text{m}}$		0	5	13	28	25	19	10	0	1.42
$Y_{\text{f}} - Y_{\text{m}}$	at peaks	6	10	15	21	24	13	6	5	1.45
	at min.	2	3	9	24	30	16	10	6	2.00

To have a more comprehensive numerical comparison of males and females within the populations concerned, an analysis was made of the frequencies of: the mean numbers of females (\bar{Y}_{f}) and males (\bar{Y}_{m}) and the differences and quotients of the mean numbers of females and males ($\bar{Y}_{\text{f}} - \bar{Y}_{\text{m}}$ and $\bar{Y}_{\text{f}} : \bar{Y}_{\text{m}}$) in Z-type populations (Table 5, and fig. 3).

The average number of males (\bar{Y}_{m}) varies between the populations from 5 to 27, and for almost half of the cases (26 cases, i.e., 43%) from 8 to 11 (Fig. 3a). The usual range is 8—19 males per population (in 49 populations, i. e., 82% of cases).

Females averaged from 4—32 per population, with peak more extending than for males and distinctly shifted towards higher values (Fig. 3a).

An analysis of the ratio between female and male averages ($\bar{Y}_{\text{f}} : \bar{Y}_{\text{m}}$) shows (Table 5) those from 1.1 to 1.5 and from 1.6 to 2.0

to be the most frequent since these apply to 41 populations, which makes 69% of all the populations investigated. It will be noted that in a fair number of populations the average sex ratio ($\bar{Y}^{\varphi} : \bar{Y}^{\sigma}$) was distinctly larger than a unit (in 47 populations $\bar{Y}^{\varphi} : \bar{Y}^{\sigma} \geq 1.6$). In only 11 populations (18%) the females averaged less than the males. An analysis of the frequency of the differences $\bar{Y}^{\varphi} - \bar{Y}^{\sigma}$ (Table 5) shows that in 54% of the populations (32 in 60) females outnumbered males more than 5.

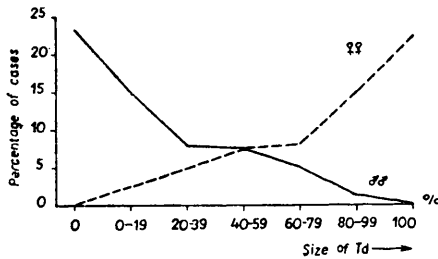
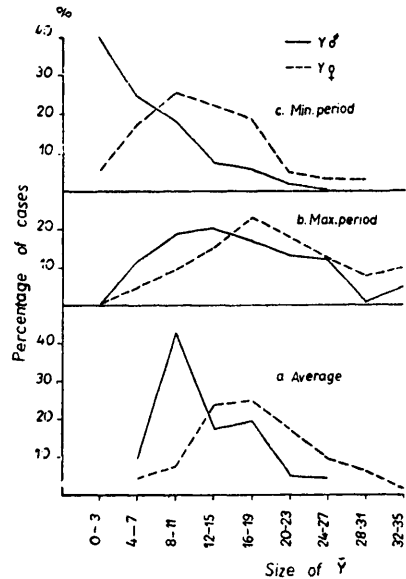


Fig. 2. Td score distribution.

Fig. 3. Frequency of male and female numbers; a — over-all mean; b — at peak periods; c — at minimum periods.



The mean from all Z-type populations (grand mean) was for males 12.6 and for females 17.9; hence, an over-all average female-to-male ratio of 1.42 is obtained.

It will be interesting to compare the figures now obtained with those reported in the preliminary communication (Petrusewicz, 1958). The latter have been derived from a scantier material (47 v. 60 populations) and shorter observation, and yet — as regards the differences and averages — agreement is striking:

	\bar{Y}^{φ}	\bar{Y}^{σ}	$\bar{Y}^{\varphi} - \bar{Y}^{\sigma}$	$\bar{Y}^{\varphi} : \bar{Y}^{\sigma}$
Petrusewicz (1959)	15,9	10,9	5,0	1,49
present paper	17,9	12,6	5,3	1,42

It has been demonstrated that the number of cases where $Y^{\varphi} > Y^{\sigma}$ was significantly larger than where $Y^{\varphi} \leq Y^{\sigma}$. To check

whether the magnitudes of this difference is also statistically significant, Student's test was used. The analyses concerned the difference ($\bar{Y}_\varphi - \bar{Y}_\sigma$) as well as quotients ($\bar{Y}_\varphi : \bar{Y}_\sigma$); the computations gave for $t=7.20$ and 24.83 respectively. This means that in either case the analysis has shown the likelihood of $\bar{Y}_\varphi = \bar{Y}_\sigma$ to be $P(|t| \geq t_\alpha) = 0.0000$.

Since in 49 of the 60 populations $\bar{Y}_\varphi > \bar{Y}_\sigma$ and the grand average for any one Z-type population $\bar{Y}_\varphi = 17.9 > \bar{Y}_\sigma = 12.6$, the average number of females (\bar{Y}_φ) may be said to exceed in confined populations the average number of males (\bar{Y}_σ) in a statistically significant way.

For the sake comparison, computations were made of average male and female numbers, differences and quotients of these numbers, as well as the number of cases where $\bar{Y}_\varphi > \bar{Y}_\sigma$, for populations bred in cages of sizes A, B and H. In all these populations the females proved to outnumber males (Table 6).

Table 6.

Numbers of females and males in population bred in varying types of cages.

Cage	Number of population	\bar{Y}_φ	\bar{Y}_σ	$\bar{Y}_\varphi - \bar{Y}_\sigma$	$\frac{\bar{Y}_\varphi}{\bar{Y}_\sigma}$	Number of cases when:	
						$\bar{Y}_\varphi > \bar{Y}_\sigma$	$\bar{Y}_\varphi < \bar{Y}_\sigma$
Z	60	17.9	12.6	5.3	1.42	50	10
A	15	12	9	3	1.3	12	3
B	7	20	14	6	1.4	5	2
H	4	49	43	6	1.1	4	0

* * *

It has, consequently, been demonstrated that on the whole females are more numerous in confined populations than males. A survey, though, of the basic data (Fig. 1) shows these numerical differences between the sexes to be inconstant — as could be expected after all. At times males outnumber females, for instance, in population L₁ in November 1954 (Fig. 1), while at other times, the females outnumber males even some dozens of times. Hence, it has been investigated whether variations in the sex ratio are in some regular relation to phases in the population's dynamic. With this in view,

for populations, bred in Z-type cages the numbers of males and females (Y^{σ} and Y^{φ}) were computed separately for the periods of population highs (peaks) and lows⁷⁾. The numerical differences between the sexes proved to be smaller in the peak periods, what was proved with both the differences and the quotients of average numbers as well as the number of cases when $Y^{\varphi} > Y^{\sigma}$ (see table 7). The distribution of the magnitudes Y^{φ} and Y^{σ} (Figs. 3b and c) also shows in the peak periods smaller dissimilarities between the curves as for males and females.

Table 7.

Numbers of females and males in type Z population at peaks and minimum periods.

Period	No. of observation	\bar{Y}^{φ}	\bar{Y}^{σ}	$\bar{Y}^{\varphi} - \bar{Y}^{\sigma}$	$\frac{\bar{Y}^{\varphi}}{\bar{Y}^{\sigma}}$	P		Percentage of cases when:				$\frac{P_1 - P_2}{d}$
						$\bar{Y}^{\varphi} - \bar{Y}^{\sigma}$	$\bar{Y}^{\varphi} : \bar{Y}^{\sigma}$	$Y^{\varphi} > Y^{\sigma}$ P ₁	$Y^{\varphi} \leq Y^{\sigma}$ P ₂	$\frac{Y^{\varphi}}{Y^{\sigma}} > 2$	$\frac{Y^{\varphi}}{Y^{\sigma}} > 3$	
Min.	208	12.5	6.1	6.4	2.05	.0000	.0000	86%	14%	54%	40%	21.43
Max.	213	20.3	16.1	4.2	1.45	.0000	.0000	69%	31%	13%	2%	8.76

It has further been shown that at both highs and lows of a population the difference between the percentages as of cases where $Y^{\varphi} > Y^{\sigma}$ (P₁) and $Y^{\varphi} \leq Y^{\sigma}$ (P₂) was statistically significant since $t = |P_1 - P_2| : \sigma > 3$ (at peaks $t = 8.76$; at lows $t = 21.43$ — see table 7).

Therefore, highs and lows were compared as to the percentage of cases where $Y^{\varphi} > Y^{\sigma}$, which was found to be 86 and 69 respectively. The difference proved statistically significant, since $|P_1 - P_2| : \sigma = 4.19 > 3$.

The cases where females (Y^{φ}) outnumber males (Y^{σ}) twice or thrice are conspicuously fewer at peaks (Table 7).

Next, population highs and lows have been compared as to the value of the differences between Y^{φ} and Y^{σ} . This has been done with the Student's test, analyzing the series of both the differences

⁷⁾ The calculations have been made for the same periods as the means for the population's entire life-time (cf. p. 112). As points of peaks have been taken the points of an increase by 5 or more individuals after which there was a fall. The numbers for the period of population low were calculated for the last point before a rise by not less than five individuals,

$(Y_k^{\text{♀}} - Y_k^{\text{♂}})$ and quotients $(Y_k^{\text{♀}} : Y_k^{\text{♂}})$. The calculations have shown the differences between $Y^{\text{♀}}$ and $Y^{\text{♂}}$ to be statistically significant at either, population highs and lows (cf. table 7).

The numerical superiority of females as at highs and lows was compared with the aid of Student's test.

Calculations showed that at lows the numerical superiority of females was statistically significantly larger than at peaks ($P < 0.001$).

The analysis bears out that:

1. the numerical differences as between populations where $Y^{\text{♀}} > Y^{\text{♂}}$ and such where $Y^{\text{♀}} \leq Y^{\text{♂}}$ are statistically significant;
2. the mean average number of females within a population is above that of males (the difference being statistically significant) for the population's entire life-time as well as for its highs and lows;
3. the sex ratios — defined by either $Y^{\text{♂}} - Y^{\text{♀}}$ or $Y^{\text{♀}} : Y^{\text{♂}}$ — are variable, depending on the phase in the population's cycle. The numerical superiority of females is greatest at population lows, and least at population highs.

III. THE RATE AND AMPLITUDE OF NUMERICAL CHANGES

In order to investigate the numerical dynamics for either sex, the respective absolute increments and decrements as revealed by consecutive counts, i. e., on the 1st and 15th of each month, have been summed up for each population separately ($\sum |Z_k - Y_{k-1}|$ ⁸). This sum gives the amplitude of the numerical changes for the given sex. Since the particular populations were bred and observed over different periods of time, the values have been prorated on a one-year basis to have comparable magnitudes and

$A = \frac{\sum |Y_k - Y_{k-1}| \cdot 12}{2n}$ has been obtained, where Y_{k-1} and Y_k the totals for the given sex at two consecutive half-monthly counts (cf. Fig. 1), and n the number of such counts ($2n =$ number of months).

⁸ The values of numerical changes have been computed for the period ending January 1, 1960 for populations still alive, and for the entire life-time for populations liquidated earlier.

Thus calculated, the amplitude of numerical changes (A) corresponds roughly to the sum of the animals born and surviving at least three weeks and of the deaths of animals more than three weeks old. In some cases, the numerical data taken from the graph are by a few units lower than the real natality plus mortality. This is so because the census was taken half-monthly (1st and 15th of each month). Within that half-month of the count there may have been deaths as well as maturations. The differences were slight. For the sake of control, the differences between the real annual amplitudes and those calculated from the graphs have been computed for two populations. The differences were -0.3 and $+1.4$ for P_5 and P_4 respectively. The unreliability, in some cases, of daily death recordings prompted the use of accurate half-monthly counts — from which the basic graphs have been plotted (Fig. 1) — as the basis calculating the amplitude difference for the sexes.

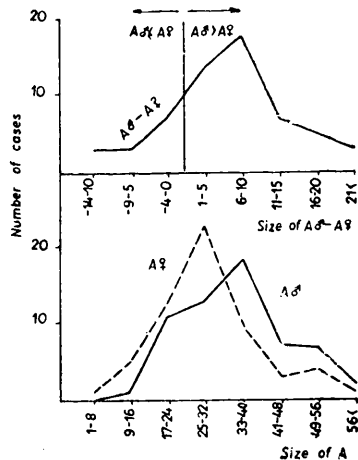


Fig. 4. Distribution of male and female amplitudes and their differences ($A^{\sigma} - A^{\text{♀}}$).

Comparison of the frequencies of the amplitude values (Fig. 4) shows that the curve for A^{σ} is distinctly shifted to the right (towards higher values). The mean annual amplitude for all populations also is higher for males than for females, since $\bar{A}^{\sigma} = 35.6$ versus $\bar{A}^{\text{♀}} = 29.5$. Hence, the mean difference between the annual amplitudes as for males and females ($\bar{A}^{\sigma} - \bar{A}^{\text{♀}}$) is 6.1. An analysis of the frequencies of the differences between male and fe-

male amplitudes ($A^\sigma - A^\varphi$) in particular populatinos shows 1—i0 to be the usual range (32 cases, i. e., 53%) and $A^\varphi \geq A^\sigma$ in only 13 cases (22%), but $A^\sigma > A^\varphi$ in 47 (78%) populations. The numerical difference between the cases where $A^\sigma > A^\varphi$ (78%) and $A^\varphi \geq A^\sigma$ (22%) is statistically significant since $|P_1 - P_2| : \sigma = 7.93 > 3$.

To see whether the value of difference between male and female amplitudes is statistically significant, use was made of Student's test. The test has proved it is, since the likelihood that \bar{A}^σ and \bar{A}^φ are not different was $\alpha = 0.000$. Since $\bar{A}^\sigma > \bar{A}^\varphi$, the amplitude of numerical changes in confined Z-type populations may be said to be for males higher.

Table 8.

The annual amplitude of changes in the numbers of males and females.

Cage	Number	\bar{A}^σ	\bar{A}^φ	$\bar{A}^\sigma - \bar{A}^\varphi$	Number of cases when	
					$A^\sigma > A^\varphi$	$A^\sigma < A^\varphi$
Z	60	35.6	29.5	6.1	47	13
A	15	15.1	11.3	3.8	10	5
B	5	41.8	36.4	5.4	5	2
H	4	120.1	117.8	2.3	3	1

In order to check whether this applies generally, annual amplitudes of numerical changes in A, B, and H type cages have been computed for males and females. The data obtained (Table 8) show that the amplitudes were in all the types of populations higher for males.

* * *

As the score the rate of numerical changes (rate of growth) has been taken the difference between the numbers of males (or females) at two consecutive moments expressed as per cent (δ) of the first:

$$\delta\sigma_k = \frac{|Y\sigma_k - Y\sigma_{k-1}| \cdot 100}{Y\sigma_{k-1}}$$

where δ_k — the score of the rate of growth, and $Y\sigma_k$ the number of males at the moment k and $Y\sigma_{k-1}$ that a half-month earlier (and analogically for females).

The rate of growth scores (δ_k) have been calculated for the period till July 1, 1957, for the 41 Z-type populations then observed (Table 9). On analysis, the mean rate of growth score for a given

population (δ) proved (Fig. 5) to be distinctly higher for males (δ^σ) than for females (δ^φ). The curve for δ^σ is distinctly shifted towards higher values (Fig. 5) and notably extended. In most cases δ^φ is 5%—12.5%, the maximum being 21.6%. With males the maximum is 68% and in as many as 14 (34%) population δ^σ is above 25%, a value never attained by δ^φ .

The number of population in which $\bar{\delta}^\sigma > \bar{\delta}^\varphi$ was 37, as against only four in which $\bar{\delta}^\sigma \leq \bar{\delta}^\varphi$. Obviously, this difference is statistically significant since $|P_1 - P_2| : \sigma = 12.2 > 3$.

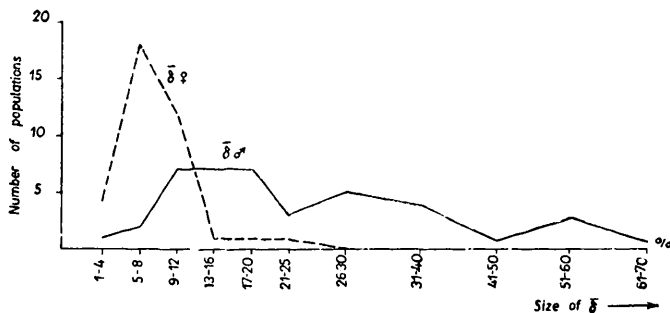


Fig. 5. Frequency of the growth rate score.

Student's test was used to see whether in general the difference between the rate of growth indices as for males and females ($\bar{\delta}^\sigma - \bar{\delta}^\varphi$) was for all populations statistically significant. It proved to be so ($\delta^\sigma \neq \delta^\varphi$), since $t_\alpha = 5.265 > t_{0.0001} = 3.551$.

Since $\bar{\delta}^\sigma > \bar{\delta}^\varphi$ in 37 of the 41 populations investigated, and $\bar{\delta}^\sigma = 25.82 > \bar{\delta}^\varphi = 8.74$, the rate of growth score may be said to have been higher for males than for females in a statistically significant manner for the entire material.

To compare in character the rate of growth indexes as for females and males the differences in their variations have been investigated for each population (Table 9, columns 3—5).

Differences in variation between male and female rates of growth will be considered statistically significant within a population when $|S^\sigma - S^\varphi| \geq 3\sigma$, or which amounts to the same, when

$$\Theta = \frac{S^\sigma - S^\varphi}{\sigma} \geq 3.$$

In 33 of the 41 populations statistically analysed was $\Theta > 3$ (cf. Table 8, col. 5), and, consequently, the difference in the variation of the rate of growth index as between males (S^σ) and females (S^φ) — statistically significant. In 36 cases was $S^\sigma > S^\varphi$, and $S^\sigma \leq S^\varphi$ in only five. Hence in 31 (76%) of 41 populations,

Table 9.

Index of the rate of numerical changes (δ) and its dispersion (S)⁹⁾.

$$\bar{\delta} = \sum \frac{Y_k - Y_{k-1}}{Y_{k-1}} \cdot \frac{100}{n}; S = \sqrt{\frac{1}{n-1} \cdot \sum_{k=1}^n (\delta_k - \bar{\delta})^2}; \Theta = \frac{S^\sigma - S^\varphi}{\sigma};$$

	$\bar{\delta}^\varphi$	$\bar{\delta}^\sigma$	S^φ	S^σ	Θ		$\bar{\delta}^\varphi$	$\bar{\delta}^\sigma$	S^φ	S^σ	Θ
	1	2	3	4	5		1	2	3	4	5
Z ₁	7.8	17.5	12.9	11.2	8.37	Zm ₃	8.0	27.5	15.6	85.1	8.17
Z ₂	8.1	33.1	11.7	79.4	11.92	Zm ₄	6.9	17.2	12.2	63.7	8.04
Z ₃	11.7	29.7	36.0	76.7	5.42	P ₁	9.5	25.4	15.3	34.4	8.59
Z ₄	17.2	55.3	48.1	153.9	4.44	P ₂	13.8	51.4	44.0	221.6	6.47
Z ₅	7.5	17.9	12.5	44.4	7.41	P ₃	8.7	22.3	13.8	76.2	9.30
Z ₆	7.2	37.4	14.3	165.8	10.17	P ₄	10.7	21.5	17.4	50.2	6.80
Z ₇	1.7	10.9	2.8	15.1	5.30	P ₅	11.0	10.6	21.4	18.9	0.78
Z ₈	7.7	68.8	12.0	328.0	7.21	P ₆	6.5	8.8	12.5	13.9	0.70
Z ₁₂	2.5	13.4	2.4	16.3	5.47	P ₇	5.5	16.7	11.0	29.3	4.06
Z ₁₃	3.6	11.1	4.8	17.3	5.11	L ₁	12.2	58.4	18.0	236.3	9.08
Z ₁₄	5.5	9.9	5.4	20.7	4.74	L ₂	12.1	16.7	25.5	22.9	0.68
A ₂	6.7	12.7	10.7	34.2	7.14	L ₃	11.6	23.9	29.3	51.9	3.18
A ₃	6.5	14.0	14.6	29.5	6.22	L ₄	9.6	12.6	24.1	28.0	6.15
A ₅	6.7	13.5	13.0	42.7	6.90	L ₅	10.8	36.8	24.3	145.5	7.25
A ₆	5.6	10.4	13.9	22.1	3.31	L ₆	21.6	35.2	37.0	122.0	5.00
A ₉	7.0	5.1	22.6	12.9	3.29	D ₁	7.7	11.6	14.4	18.2	1.31
A ₁₀	13.8	7.8	24.5	12.8	3.80	D ₂	7.8	16.8	16.2	23.6	1.94
A ₁₁	8.4	13.3	23.9	30.4	1.41	V ₁	12.5	43.2	13.3	70.1	5.73
A ₁₇	12.0	15.6	31.9	38.7	1.03	V ₂	7.9	27.3	8.9	38.8	5.24
A ₁₈	2.0	0.5	14.6	26.0	2.75						
Zm ₁	7.6	26.7	18.8	60.3	18.80						
Zm ₂	8.9	17.7	12.3	41.9	7.11						
						AVG.	8.78	22.59	18.0	64.15	

⁹⁾ S^σ and S^φ stand for the variation of δ^σ and δ^φ resp., and are defined as $S^\sigma = \sqrt{\frac{1}{n-1} \cdot \sum_{k=1}^n (\sigma^\sigma_k - \sigma^\sigma)^2}$ (S^φ analogically), and σ is the

standard error of the difference $S^\sigma - S^\varphi$ and is $\sigma_s = \sqrt{\frac{1}{2n}(S^{\sigma^2} - S^{\varphi^2})}$, while n indicates the number of observations — in our case twice the number of the months over which the populations had been surveyed.

the difference $S^\sigma - S^\varphi$ was statistically significant and $S^\sigma > S^\varphi$.

To see whether the higher variation of the δ^σ index, i. e., S^σ , is not generally (for all populations) due to chance, use was made of the criterion $|P_1 - P_2| \geq 3\sigma$, where P_1 is the cases where $\theta \geq 3$ and at the same time $S^\sigma > S^\varphi \cdot (P_1 = \frac{31 \cdot 100}{41})$; P_2 stands for the number of cases where the difference $S^\sigma - S^\varphi$ is statistically nonsignificant ($\theta < 3$), or alternatively $S^\sigma \leq S^\varphi$. Consequently, the difference in question proved significant, since $|P_1 - P_2| = 0.447$, and $\sigma = 0.092$, i. e., $|P_1 - P_2| = 0.447 > 3\sigma = 0.276$.

Hence, in general term, considering all populations jointly, the variation of the rate of growth index, may be said to be higher for males.

IV. DURATION OF THE PERIODS OF NUMERICAL STABILIZATION FOR MALES AND FEMALES

With a view to exploring more fully sex differences in numerical dynamics within a population, the sum has been calculated for each population of the periods over which the given sex remained on a constant numerical level. As such periods have been assumed those where not more than one animal of the given sex died between four consecutive counts (i. e. during 3 halfmonths periods). The absolute length of the constancy periods obviously depended on the period of observation. Since this period was not alike for all the populations, the results have been prorated on a one-year basis in order to obtain comparable values as between individual populations; thus has been obtained the average number of months in a year over which the number of animals of the given sex remained constant within a population (Table 1, col. 8 and 9). These magnitudes are here referred to as stabilization indexes for males or females (St^φ or St^σ).

The frequency of these indexes (Fig. 6) shows that those for males are usually of a higher order of magnitude. The maximal indexes also are those for males. The average value of the index for all the populations is for males higher since $\overline{St}^\sigma = 7.24$, and $\overline{St}^\varphi = 6.48$ ($\overline{St}^\sigma - \overline{St}^\varphi = 0.76$). The cases where the difference in stabilization indexes as between males and females is 0.6—1.0 are the most frequent (Fig. 6).

$St_{\text{♀}} \geq St_{\text{♂}}$ was in 18 populations (including seven where $St_{\text{♀}} = St_{\text{♂}}$) and $St_{\text{♂}} > St_{\text{♀}}$, in 42 populations. The difference between the two groups of cases is significant since $|P_1 - P_2| : \hat{\sigma} = 4.78 > 3$.

The difference between the mean stabilization indexes as for male and females ($\overline{St}_{\text{♂}} - \overline{St}_{\text{♀}}$), calculated for all Z-type populations, also is statistically significant, as has been shown by Student's test at the significance level $\alpha = 0.001$ ¹⁰). This gave $t = 5.93$,

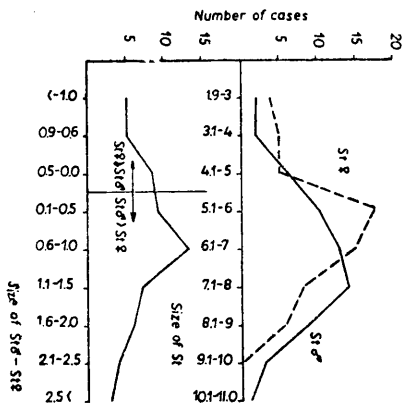


Fig. 6. Distribution of the index of numerical stabilization periods.

and $t_{0.001} = 3.551$, which means that the value $St_{\text{♂}}$ is significantly different from $St_{\text{♀}}$. And since $\overline{St}_{\text{♂}} > \overline{St}_{\text{♀}}$, and the number of cases where $St_{\text{♂}} > St_{\text{♀}}$ is 70%, we may say that the stabilization index has been proved to be for males higher.

V. MORTALITY AND NATALITY RATIO ACCORDING TO SEX

Youngs were sexed when 18—21 days. The number of young ones which survive three weeks is obviously much smaller than the number of births. In 47 Z and B-type populations, with an over-all life-time of 1107 months, there were 13121 youngs born, which gave only 2801 animals that survived three weeks. There

¹⁰) The series $St_{\text{♂}} - St_{\text{♀}}$ had to be transformed into one having normal distribution ($St' = St + a$, where $a = 134$, and $V = \log St'$).

is much likelihood that mortality among the newborns, mostly due to devouring and killing, is in absolutely no relation to sex. In a dozen or so cases the animals were sexed at an age of 6—8 days, and up to the age of 21 days no differences in mortality were noted between the sexes¹¹⁾. Hence, it is safe to assume that the sex ratio among three-week olds is roughly the same as among newborns.

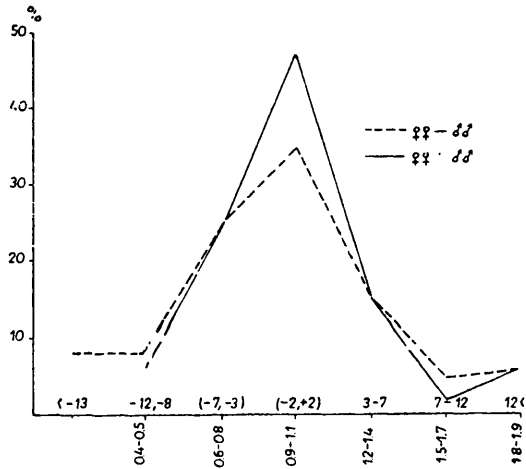


Fig. 7. Distribution of the numbers of young animals which have survived 3 weeks.

Now, among the 2801 animals which survived the first three weeks there were 1415 females and 1386 males, which makes 50.51% and 49.49% respectively. In 22 (47%) of the populations analyzed, the male/female ratio was among the animals which survived the first three weeks 0.9—1.1, and in most (40 in 47) of the populations the ratio was : 0.6—1.4 (Fig. 7). This shows that males and females are born and added to the populations in virtually equal numbers.

To calculate mortality, the number of deaths of males (or females) aged three weeks or more (i. e. marked and reckoned among adults) recorded for a population was divided by the number of years of observation. From the annual average of deaths thus obta-

¹¹⁾ Altogether sexed — 123 youngs; including 60 males and 63 females; left after three weeks: 16 (26.7%) males and 16 (25.4%) females.

ned was computed the percentage it constituted of the average number of males or females, and this has been termed the mortality index

$$D^{\sigma} = \frac{\text{Number of males died} \times 100}{\text{Number of years} \times Y^{\sigma}} \quad (D^{\text{♀}} \text{ analogically --- see table 1, column 10 and 11, and table 10).}$$

Table 10.

Annual mortality (as percentage of mean numbers).

Cage	Number	\bar{D}^{σ}	$\bar{D}^{\text{♀}}$	$\bar{D}^{\sigma} - \bar{D}^{\text{♀}}$	Number of cases when:	
					$\bar{D}^{\sigma} > \bar{D}^{\text{♀}}$	$\bar{D}^{\sigma} < \bar{D}^{\text{♀}}$
A	15	91	80	11	9	6
Z	60	143	85	58	24	6
B	7	163	86	77	7	0
H	4	148	121	27	4	0

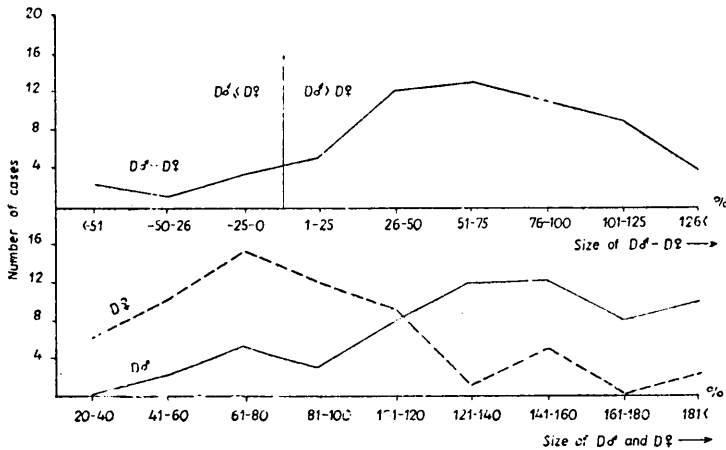


Fig. 8. Distribution of males and females mortality.

An analysis of D magnitude shows mortality to have been very high under the experimental conditions. Among the 60 populations there were for females 16 and for males 49 where $D > 100\%$, and, consequently, annual deaths above the average number of females or males in a given population (Fig. 8). In extreme cases, the index was higher than 300% (Table 1, col. 10 and 11). The frequency of the values $D^{\text{♀}}$ and D^{σ} (Fig. 8) indicates major differences between

the sexes. $D^{\text{♀}}$ was commonly 41—81%, namely in 37 (62%) of the populations. $D^{\text{♂}}$ was on average much higher, usually 121—160%. In only six (10%) populations was $D^{\text{♀}} \geq D^{\text{♂}}$. The difference $D^{\text{♀}} - D^{\text{♂}}$ is large, for it was in a vast majority, 45 cases, within the range of 26—125% (Fig. 7). These differences are so conspicuous that no statistical analysis is needed to say that mortality is higher among males.

VI. DISCUSSION

The discussion is made necessary by the seeming contradiction between, on the one hand, the larger amplitude (A) and larger and more variable index of numerical changes (δ) for males, and, on the other, their longer periods of numerical stabilization. This means that numerical changes among males last shorter but are more pronounced. Since numerical differences between the sexes are among 3 weeks old animals virtually nil, mortality is the factor responsible for these changes. After reaching a certain numerical level, males begin to die rapidly, and this swift numerical decline is followed by a period in which there are no changes. This is not always plainly evident in the graphs showing numerical dynamics (Fig. 1) but can be demonstrated by statistical analysis. In some cases, though, this difference between males and females in the character of numerical dynamics may be noted even in the graphs, especially at periods of numerical decline, where for males there is a rapid fall with a subsequent period of relative stabilization, and for females, a prolonged but mild fall. This is the pattern, for instance, for population Zm_2 in February 1957 (cf. Fig. 1).

Many of the observations on confined populations of mice strongly suggest population numbers to be regulated by noncompetitive fights between males. This view may also be found in literature (Southwick, 1955b; Scott & Friederickson, 1951). However, in support of the view that fights are responsible for rapid numerical declines of males, one may quote only general quantitative observations. For, on examination of dead males, only a minimum percentage was found to have been outright killed. Killings occur only at population highs, and over a brief period of the beginning of numerical decline. In the usually long periods of numerical decline, continuing occasionally even over more than one

year, one finds dead mice with no signs of injury. Nor could any infection be revealed to explain mortality among males. Usually, neither injury nor disease could be demonstrated in the dead males. Though we cannot prove it, it seems reasonable to assume that the deaths involve males occupying a lower rank in the structure of dominance, which are continually harassed and, therefore, underfed and weakened. This appears to be confirmed by literature. Southwick (1955a) says that during overcrowding the per capita food intake was smaller irrespective of an actual excess of food.

The numerical superiority of females is more pronounced at population lows. This also can be explained by the higher male mortality caused by fights. Since mortality is higher among males, population lows are attributable primarily, though not exclusively of course, to a numerical decline of males. At population peaks there always are many young animals only just reaching adult stage; their sex ratio is more or less balanced. Hence, at peak periods, numerical differences between males and females are less, especially when only the difference ($Y^{\text{♀}} - Y^{\text{♂}}$) but the proportion ($Y^{\text{♀}} : Y^{\text{♂}}$) too is considered.

Similar, the larger amplitude of numerical changes among males also can be explained by higher mortality.

According to the above discussion, the mechanism responsible for many, or even most ecological phenomena in confined populations of mice may be perceived in noncompetitive fights between males. Southwick (1955b) gave an elegant analysis of intrapopulation processes which promote survival of the young and ultimately depend all on fights between the mice. Scott & Fredricson (1951) have demonstrated how noncompetitive fights between males intensify spontaneously as triggered reactions and involve eventually also females. Behaviour, reciprocal relations, the number of fights, pregnancy and numerous other phenomena determining in general living conditions, consequently also mortality among females, are thus secondary processes consequent upon noncompetitive fights between males, or are at least affected by these. The noncompetitive fights between males are in themselves the primary phenomenon. They are a population's permanent feature and primarily determine its structure (Petrušewicz, 1958). These noncompetitive fights between males are in their

turn intensified and aggravated in relation to the population's structure.

Hence, noncompetitive fights between males seem to be the main factor, regulating numbers as well as the character and rate of numerical changes in confined populations of mice.

The next point question: the regularities revealed in the numerical dynamics of sexes in mice, are they universal. As to the duration of the numerical domination of one sex, and amplitude and rate of numerical changes, no data have been found in the literature available to us. But the data characterizing numerically the sex ratio and mortality are confirmed by ecological literature.

Brown (1953) found mortality in confined populations of mice to be higher for males. The difference was distinct, since in his experiments the death roll was for males 50, versus 11 for females.

In a work essentially concerned with different aspects, Southwick gives graphs of the numbers of six populations (Southwick, 1955a, Figs. 5—10). Although no totals are given separately for the sexes, there are curves showing the numbers of „diseased or wounded” adult males and females. In five populations the corresponding figures were higher for females, and the difference was indistinct in only one population (population marked E), though even here the figure seems to have been higher for females¹²⁾. Although these figures illustrate the numerical proportions between „diseased and wounded” animals, the numbers of such males and females may safely be assumed as in some way related to the ratio within the given population. Hence, if wounded females are more numerous than wounded males, females may safely be assumed to be more numerous in general in the given population. This is all the more certain as in confined populations the percentage of wounded animals is in males always higher than in females. If this is so, males must have been in Southwick's material numerically even more inferior to females than would appear from the data for „diseased and wounded” animals.

The indirect data are further confirmed by the numerical status of the sexes in Southwick's populations on termination of the experiments, as males totalled 224 and females 270. And it should be noted that Southwick discontinued the experiments

¹²⁾ Owing to notable reduction, the figures cannot be read with adequate accuracy from Southwick's graphs.

at a time when all the populations were at a numerical high, that is, when — as has been demonstrated before — numerical differences between the sexes are usually less than at lows.

It is interesting to see whether the numerical dominance of females — which has been shown to be regular in confined populations — is confirmed by observations on free-living populations of house mice. Relevant data are not always unequivocal for, reports on natural populations frequently quote only numbers of trapped animals or only trapability (trappings per time unit, e. g., per trap-day, or per 100 trap-hours, etc.). And it is not always possible to derive from these data the actual numbers of males and females, and, consequently, the sex ratio. For, the number of captures may reflect the numbers of, and proportions between the elements trapped (sexes, age groups, etc.) only in the case of their random trapability. The number of trappings with any automatic devices is proportionate not only to the numerical status of the animals captured and trapping intensity (number and concentration of traps, and trapping time) but to the activity of the animals intensity of their cruising, extension of roving or home range etc.

In German literature on invertebrate ecology explicit distinction is made between trapability (number of individuals captured per time unit or encountered per area unit) and numerousness. The notion of trapability is rendered by the term „Aktivitätsdichte“ (Heydemann, 1953 — after Balogh, 1958; Tischler, 1955), „Aktivitätsdominanz“ (Balogh, 1958), and „dynamische Besiedlungsdichte“ (Heydemann, 1953). „Aktivitätsdominanz“ is defined by Balogh (1958, p. 154) as „die Anzahl der eine bestimmte Linie oder Fläche durch eigene Aktivität in einer bestimmten Zeiteinheit berührenden Individuen („Aktivitätsdichte“ oder „dynamische Besiedlungsdichte“ nach Heydemann)“ „Aktivitätsdichte“ is contrasted with „Individuendichte“ (or „Individuendominanz“), which indicates absolute numbers of the percentage they constitute.

Obviously, trapping results reflect the actual proportions within a population only when the elements trapped are equally liable to be captured. If any of these elements are more liable to be trapped than the others, the proportions in the catches will be distorted — in comparison to those actually existing — in favour of such elements as are more likely to enter the traps (i. e., those more active, having a larger roving area, less shy of, or more

attracted by the traps, etc.).

Reverting to our point numerical male/female proportions in mice, it will be seen that all the existing data indicate unequivocally a higher activity of males. Besides, this holds for domestic mice as well as for small mammals in general.

Brown (1953), who studied house mice populations in farm buildings (barn) says males are more active since points of their recaptures are farther between. Young, Strecker & Emlen (1950) conclude from studies on two populations in buildings that males have a wider roving range (140 feet v. 110) and average home range (13' v. 11' for females), the differences being statistically significant. The home range differed between the two buildings (i. e., depended on environmental conditions).

Strecker (1954) reports a slight predominance of males among migrants (47 : 44), and a distinct predominance of females (58% : 42%) among the nonmigrating part of the population.

Andrzejewski & Petrusewicz (in litt.) found — in a free-living but additionally fed population of house mice — habituation to a definite feeding site to be stronger among females. Andrzejewski, Petrusewicz & Walkowa (1959) show differences in trap success as between males and females, and differentiation in trappability between males according to the rank occupied in the structure of dominance. The greater activity of males has been inferred from the results of numerous field studies concerning various micromammalia species (Maksimov, 1948; Hayne, 1950; Lavrov, 1956; Hoffman, 1958; and Sakhno, 1959).

In view of such concordant results indicating a higher activity of males among mice and small mammals in general, we may say — wherever merely the number of trapped males and females is given, and not the real numbers of a population calculated from recaptures or intensive trapping that (1) if the numbers of trapped males are smaller, females may be concluded to be numerically superior, and (2) if the numbers of trapped animals are for males higher, no conclusions as to the actual sex ratio in the population may be drawn without additional information.

Below we shall briefly discuss some specific results. Evans (1949) studied a free-living and initially very numerous population of mice in one of the laboratory rooms. With the aid of intensive recaptures he surveyed the entire population continually and was

able to give in each month the actual numbers of males and females. Males were less numerous and our calculations (Table 11) shows that difference in percentages was statistically significant in the four month when the population numbers were fairly high. Interesting to note, at the time of the population's numerical high (January and February), the predominance of females was less (the difference between the percentages as of males and females was nonsignificant). The female predominance increased, however, with the population's spontaneous numerical decline, so in March and April the figure for females was double, or better, that for males, and the difference in percentages was statistically significant. This fully confirms the observation, made on confined populations, that female numerical predominance depends on the phase in the cycle of population dynamics (cf. Fig. 3 and Tables 5 and 7).

Table 11.

Sex ratio in free-living population of mice (compiled from the Evans, 1949 data).

Month	Number of			Percentage of		$\frac{c}{b}$	$\frac{P_1 - P_2}{f}$
	Mice	♂♂	♀♀	♂♂	♀♀		
	a	b	c	P ₁	P ₂		
Januar	136	60	76	44.1	55.9	1.3	1.95
Februar	119	59	60	49.6	50.4	1.0	0.13
March	77	26	51	33.8	66.2	1.9	4.26
April	37	11	26	29.7	70.3	2.4	3.82
May	5	1	4	20.0	80.0	4.0	2.36

Young, Strecker & Emlen (1950) reported recaptures for males and females as 731 and 599 respectively. Males clearly predominante here, but — according to what has been said above — no conclusions as to the actual sex ratio in these populations may be drawn.

Strecker (1954) gives the figures for trappings in artificially created but free-living (migration possible) populations bred in the laboratory rooms. In two populations of 87 and 78 mice, males were 48 and 42 per cent, and females 52 and 58 per cent. Since figures are from intensive final trappings (liquidation of the populations), they may be regarded as a fair approximation of the

real numbers. In either population the females were more numerous.

It follows from as yet unpublished results of studies that females predominate in the free-living population of house mice in the building of the Field Station of the Institute of Ecology, P. A. Sc. and in the additionally fed but also free-living population of house mice in the attic of that building. In 15 months of intensive trapping with live traps 143 males and 111 females have been captured in the attic, and 115 males and 80 females in the lower floors.

A comparison of the results, as obtained from confined and free-living populations of mice in buildings, suggest certain conclusions. In either case males were less numerous. However, the mechanism responsible for this fact appears to have been different. In confined populations the factor responsible for this situation is probably noncompetitive fights between males. Their influence is occasionally direct (killings), and more frequently indirect through the establishment of a structure of domination in which the animals occupying the lower ranks are harassed, underfed and so forth, and therefore have a higher mortality. In free-living populations, the mechanism seems to be different. There is nothing to suggest direct consequences of fights, and it is rather reasonable to assume more intensive emigration to be responsible for the numerical reduction of males. Consequently, males decrease in numbers more rapidly and relatively more females remain in the population. Thus we have here an example of how the same ecological process (numerical decrease of males) is produced by different mechanisms (mortality or emigration). It remains an open question whether migration from the native site leads to greater mortality among the migrants, which are exposed to greater hazards during the migration or pushed into less congenial environments, or whether this is a loss merely affecting the local population. The ecological significance of this process also remains to be explored.

Finally, the following points should be called to attention. Data from field studies (woods, thickets, meadows and fields) on small mammals frequently indicate numerical superiority of males. This is reported by, for instance, Hoffman (1958) for two species on two sites, Sanderson (1950) for five species in a prairie grove, Burt (1940) for three species, Dunmire (1960) for one species at different elevations and age classes and Andrzejewski (unpublished) for three forest species, and so forth. Whether in these

field studies the larger numbers of males resulted from a trapability enhanced by the greater activity of the males, whether the rule of female numerical predominance — established for populations of house mice in buildings, i. e., their most natural environments — also holds for other small mammals, or whether sex ratios in micromammalian populations differ in relation to species and ecological conditions, these are questions that remain yet to be answered.

VII. SUMMARY

In confined populations of mice:

1. females predominate numerically over longer periods than males;

2. average numbers are higher for females, whose predominance varies according to the phase in the population's life; the numerical differences between males and females are larger at population lows, and smaller at peak periods;

3. the rate of numerical changes (in per cent of the number immediately before the change) is for males higher and more variable (has greater dispersion);

4. males have a larger amplitude of numerical changes, i. e., their numbers vary within a wider range;

5. the over-all time in which there are no numerical changes is longer for males;

6. the sex ratio is about balanced among newborns and three-week olds (i. e. those becoming selfsufficient member of the population);

7. mortality is higher among males.

The numerical superiority of females in populations is confirmed by studies on free-living populations of mice in buildings, but the process responsible for this essentially identical ecological effect (predominance of females) probably differs between free-living and confined populations: in free-living populations it is probably attributable to migrancy, more pronounced among males, while in confined ones it is due to noncompetitive fights.

REFERENCES

1. Andrzejewski, R., Petruszewicz, K. & Walkowa, W. — Preliminary report on results obtained with a living trap in a confined population of mice. Bull. Acad. Pol. Sc., Cl. II, Vol. 7, 9: 367—370. Warszawa, 1959.
2. Balogh, J. — Lebensgemeinschaften der Landtiere. Verl. Ung. Akad. Wiss.: 1—580. Budapest, 1958.
3. Brown, R. Z. — Social behaviour, reproduction, and population changes in the House mouse (*Mus musculus* L.). Ecol. Monogr., Vol. 23; 1—412, 1953.
4. Burt, W. H. — Territorial behavior and populations of some small mammals in Southern Michigan. Misc. Publ. Univ. Mich., No. 45: 1—58. Ann Arbor, 1940.
5. Calhoun, J. B. — A comparative study of the social behavior of two inbred strains of the House mice. Ecol. Monogr., Vol. 26, 1: 8—103. 1956.
6. Daumiere, W. W. — An altitudinal survey of reproduction in *Peromyscus maniculatus*. Ecology, Vol. 41, 1: 174—182. 1960.
7. Evans, F. C. — A population study of House mice following a period of local abundance. Jour. Mamm., Vol. 30: 351—363. 1949.
8. Hayne, Don W. — Apparent home range of *Microtus* in relation to distance between traps. Journ. Mamm., Vol. 31, 1: 26—39. 1950.
9. Heydemann, B. — Agrarökologische Problematik dargetan an Untersuchungen über die Tierwelt der Bodenoberfläche der Kulturfelder. Diss. Kiel, 1953.
10. Hoffmann, R. S. — The role of reproduction and mortality in population fluctuations of voles (*Microtus*). Ecol. Monogr., Vol. 28, 1: 79—109. 1958.
11. (Лавров, Л. С.) Лавров, Л. С. — К вопросу о характеристике популяции бобров Воронежского заповедника. Тр. Воронежск. гос. зап., Т.6: 5—11. 1956.
12. (Максимов, А. А.) Максимов, А. А. — О соотношении полов в популяции серой полевки, *Microtus arvalis* Pallas. Изв. Акад. Наук СССР, Сер. Биол. вып. 1: 67—72. Москва. 1948.
13. Petruszewicz, K. — Investigation of experimentally induced population growth. Ecol. Pol., Ser. A, Vol. 5, 9: 281—309. Warszawa, 1958.
14. (Сахно, И. И.) Сахно, И. И. — Влияние агротехнических мероприятий на соотношение полов и плодовитость некоторых мышевидных грызунов на полях луганской области. Зоол. журн., Т.38,12: 1856—1868. Москва, 1959.
15. Sanderson, G. C. — Small-mammal population of a Prairie Grove. Jour. Mamm., Vol. 31, 1: 17—25. 1950.
16. Scott, J. P. & Fredericson, E. — The cause of fighting in mice and rats. Phys. Zool., Vol. 24: 273—309. 1951.
17. Southwick, C. H. — The population dynamics of confined House mice supplied with unlimited food. Ecology, Vol. 36, 2: 212—224. 1955 a.
18. Southwick, C. H. — Regulatory mechanisms of House mouse populations: social behavior affecting litter survival. Ecology, Vol. 36: 1—788, 1955 b.

19. Strecker, R. L. — Regulatory mechanisms in House mouse populations: the effect of limited food supply on an unconfined population. *Ecology*, Vol. 35, 2: 249—253. 1954.
20. Tischler, W. — *Synökologie der Landtiere*. G. Fischer Verl. Stuttgart, 1955.
21. Young, H., Strecker, R. L. & J. T. Emlen — Localisation of activity in two indoor populations of House mice, *Mus musculus*. *Jour. Mamm.*, Vol. 31, 4: 403—410. 1950.

STRESZCZENIE

Dane uzyskano z obserwacji zamkniętych populacji myszy laboratoryjnych, hodowanych w klatkach: typu Z (P, Z, L, D, V) wielkości 80×80 cm (60 populacji, które żyły łącznie 1504 miesiące); typu A — 38×15 cm (15 hodowli, 191 miesiące); typu B — 160×80 cm (7 populacji, 204 miesiące) i typu H ok. 6 m^2 (4 hodowle, 128 miesiące). Po wpuszczeniu do klatki pewnej liczby myszy, jako bazy populacyjnej, pozwolono im mnożyć się swobodnie, nic nie dodając ani nie wyjmując. Jedzenie i woda były stale w nadmiarze. W analizie oparto się głównie na danych z populacji typu Z (najwięcej powtórzeń i najdłuższy czas obserwacji).

1. Obliczono procent czasu jaki przeciętnie (rocznie) jedna z płci jest liczniejsza niż inna

$$T_d\varphi = \frac{\text{czas w którym } Y\varphi > Y\sigma}{\text{czas życia populacji}} \cdot 100 \quad (\text{Tablice 1 i 3}).$$

Stwierdzono, że procent przypadków gdy $T_d\varphi > T_d\sigma$ (P_1), jak również gdy $T_d\varphi > 80\%$ (P_2), jest realnie większy od procentowego udziału przypadków gdy $T_d\varphi \leq T_d\sigma$ (P_3), gdyż $|P_1 - P_2| : \sigma = 6.91 > 3$ i $|P_1 - P_3| : \sigma = 3.03 > 3$. Również wielkość różnicy między $\bar{T}_d\varphi$ i $\bar{T}_d\sigma$ jest statystycznie istotną. Rozkład $T_d\varphi$ i $T_d\sigma$ oraz $T\varphi - T\sigma$ obrazuje fig. 2

2. Obliczono średnią liczebność (\bar{Y}) samców i samic oraz realność różnic między nimi w każdej populacji typu Z (Tabl. 1 i 4). Stwierdzono, że różnica ta jest realną na poziomie 0,01 w 50 przypadkach (Tab. 4); statystycznie realną i jednocześnie $\bar{Y}\varphi > \bar{Y}\sigma$ jest w 47 przypadkach (75%). Różnica między udziałem przypadków, gdy $\bar{Y}\varphi > \bar{Y}\sigma$ w sposób statystycznie realny (75%), i udziałem pozostałych przypadków (t. zn. łączny udział przypadków gdy $\bar{Y}\varphi \leq \bar{Y}\sigma$ oraz gdy różnica między płciami jest nieistotna) jest statystycznie realna, gdyż $|P_1 - P_2| : \sigma = 8.11 > 3$. Stwierdzono również przy pomocy statystyki Studenta, że wielkości różnicy między ogólną średnią dla wszystkich 60 populacji typu Z liczebnością samic ($\bar{Y}\varphi$) i samców ($\bar{Y}\sigma$) jest statystycznie realna (analizowane zarówno przy pomocy ciągu $\bar{Y}\varphi - \bar{Y}\sigma$ jak i ciągu $\bar{Y}\varphi : \bar{Y}\sigma$). Samice są liczniejsze niż samce również w innych typach populacji (Tab. 6).

Stwierdzono (Tab. 5 i fig. 3) że stosunki między liczebnościami samic i samców są zależne od fazy populacji. Największą przewagę ilościową mają samice w okresach ilościowej depresji populacji; najmniejsze zaś różnice między liczebnością obu płci są w szczytowych fazach populacji. Różnice między liczebnością samców i samic są realne, zarówno w okresach minimum

jak i maksimum (Tabela 7). Również realną jest różnica między stopniem przewagi ilościowej samic w okresach szczytów w porównaniu z taką przewagą w depresjach.

3. Obliczono dla populacji typu Z wskaźnik tempa zmian liczby obu płci:

$$\delta k_{\sigma}^{\sigma} = \frac{|Y_{\sigma}^{\sigma} k - Y_{\sigma}^{\sigma} k-1|}{Y_{\sigma}^{\sigma} k-1} \cdot 100 \quad (Y_k - \text{liczba płci w momencie } k, Y_{k-1} \text{ w momencie poprzednim tzn. o dwa tygodnie wcześniejszym}).$$

Stwierdzono (Tabela 9 i fig. 5), że średnie dla danej populacji δ_{σ}^{σ} jest większe niż δ_{σ}^{σ} w 90% populacji (P_1), podczas gdy $\delta_{\sigma}^{\sigma} \leq \delta_{\sigma}^{\sigma}$ tylko w 10% populacji (P_2). Różnica realna, gdyż $|P_1 - P_2| : \sigma = 12.2 > 3$. Wielkość różnicy średniej dla wszystkich populacji $\delta_{\sigma}^{\sigma} - \delta_{\sigma}^{\sigma}$ jest realna, gdyż $t = 5.265 > t_{0,001} > 3.551$. Ponieważ zaś $\delta_{\sigma}^{\sigma} = 22.59$ a $\delta_{\sigma}^{\sigma} = 8.78$ można stwierdzić, że dla całości materiału wskaźnik tempa zmian liczebności samców jest większy niż samic.

Obliczono i porównano rozproszenie (zmiennosc) wskaźnika tempa zmian samców i samic (S_{σ}^{σ} i S_{σ}^{σ} — patrz tabela 9). Dla 76% populacji rozproszenie wskaźnika tempa zmian samców (S_{σ}^{σ}) jest istotnie różna i większa niż S_{σ}^{σ} .

4. Za miarę amplitudy zmian liczebności przyjęto przeciętną roczną sumę przyrostów i ubytków ilości:

$$A = \frac{\sum |Y_k - Y_{k-1}| \cdot 12}{2n}, \quad \text{gdzie } Y_k \text{ liczebność w momencie } k, Y_{k-1} \text{ zaś liczebność w momencie poprzednim (pół miesiąca wcześniej, } n \text{ liczba pół miesięcy trwania populacji).}$$

We wszystkich typach hodowli liczba populacji gdy $A_{\sigma}^{\sigma} > A_{\sigma}^{\sigma}$ była większa niż liczba populacji w których $A_{\sigma}^{\sigma} \leq A_{\sigma}^{\sigma}$, jak również $\bar{A}_{\sigma}^{\sigma} > \bar{A}_{\sigma}^{\sigma}$ (Tabela 8 i fig. 4). Dla populacji typu Z różnica między udziałem przypadków gdy $A_{\sigma}^{\sigma} > A_{\sigma}^{\sigma}$ i $A_{\sigma}^{\sigma} \leq A_{\sigma}^{\sigma}$ jest istotna, gdyż $|P_1 - P_2| : \sigma = 7.93 > 3$. Również wielkość różnicy między A_{σ}^{σ} i A_{σ}^{σ} jest statystycznie istotna ($t > t_{0,000}$).

5. Przeciętny okres czasu, w którym rocznie dana pięć nie wykazywała zmian ilościowych, przyjęto za wskaźnik stabilizacji (St). Okazało się (fig. 6), że zarówno liczba populacji w których $St_{\sigma}^{\sigma} > St_{\sigma}^{\sigma}$ jest większa niż gdy $St_{\sigma}^{\sigma} \leq St_{\sigma}^{\sigma}$, jak $\bar{St}_{\sigma}^{\sigma} = 6.74 > \bar{St}_{\sigma}^{\sigma} = 6,00$ (różnice te są statystycznie realne gdyż $|P_1 - P_2| : \sigma = 4.78 > 3$ i $t = 5.99 > t_{0,000} = 3.551$).

6. U myszy określano pięć w wieku 18—21 dni. Obliczono, że w 47 populacjach, które żyły łącznie 1107 miesięcy, urodziło się 13121 młodych, z nich przeżyło do 3 tygodni (czas gdy określano pięć) 2801, w tym samic 1415 (50,51%) i samców 1386 (49,49%). Ponieważ należy przyjąć, że śmiertelność noworodków i młodzieży we wczesnym wieku (nie będącej jeszcze samodzielnym komponentem populacji) nie jest zależna od płci, można przypuszczać, że rodzi się jednakowa ilość samców i samic; napewno zaś jednakowe liczby obu płci wchodzi do populacji, jako samoistne jej elementy (fig. 7).

Śmiertelność samców (D_{σ}^{σ}) jest większa niż samic (D_{σ}^{σ}) (fig. 8). Dotyczy to zarówno liczby przypadków, gdy $D_{\sigma}^{\sigma} > D_{\sigma}^{\sigma}$ (90%), jak i średniej dla 60 populacji typu Z: $\bar{D}_{\sigma}^{\sigma} = 143\% > \bar{D}_{\sigma}^{\sigma} = 85\%$ (por. tab. 10). Śmiertelność w zamkniętych populacjach jest bardzo wysoka. U samic w 16-tu, a u sam-

ców w 49 przypadkach na 60 hodowli $D > 100\%$, tzn. liczba padłych rocznie, przewyższa średnią liczebność.

Przypuszcza się, że właśnie wybitnie większa śmiertelność samców niż samic, spowodowana głównie niekonkurencyjnymi walkami samców jest odpowiedzialna za: (1) większą liczebność samic (rodzi się obu płci tyle samo, samców więcej pada); (2) za większą różnicę w liczebności płci w okresach minimum (w okresach depresji więcej samców padło) niż w okresach szczytów (dochodzi młodzież w \pm równych ilościach płci), jak również (3) za różnice w tempie wzrostu liczebności samców i samic.

BIBLIOTEKA
Instytutu Biologii Ssaków
Polskiej Akademii Nauk

Nr Cz. 40.2

Wydawnictwo Instytutu Biologii Ssaków
Polskiej Akademii Nauk
Instytut Biologii Ssaków
ul. J. F. Głowackiego 17/19
60-348 Poznań, Polska
Tel. (061) 2673400
Fax (061) 2673401
E-mail: biologia@ibm.poznan.pl
Internet: <http://www.ibm.poznan.pl>