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An Attempt at Assessing the Duration of Residence
of Small Rodents in a Defined Forest Area and the Rate of
Interchange Between Individuals

Próba oceny stopnia osiadłości i tempa wymiany osobników
drobnych gryzoni na określonej powierzchni leśnej

[With 1 fig. and 5 tables]

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I. INTRODUCTION

The paper deals with an attempt at assessing the duration of residence, the tendency to migration and the rate of interchange between individuals in small rodents living in a defined section of forest.

Material for this work was collected between 1955—1958 in the Kampinos Forest near the Field Station of the Ecological Institute of the Polish Academy of Sciences, at Dziekanów Leśny near Warsaw. The forest area in which the investigations were carried out was rectangular (ratio of sides 1 : 1.5), 2.5 ha in area and not isolated from the surrounding parts by either habitat or artificial boundaries. The size of the study area was chosen so that a sufficient number of separate sectors of the individual species of rodents examined were contained therein, and also so that the transfer of single individuals from one sector to another within this area happened very seldom.

The forest covering the study area was about forty years old, and comprised the *Pineto-Quercetum* association, changing gradually on two of its fringes into *Cariceto elongate-Alnetum*.

This area was inhabited by three species of rodents: *Clethrionomys glareolus* (Schreber, 1780), *Apodemus agrarius* (Pallas, 1771) and *Apodemus (Sylvaemus) flavicollis* (Melchior, 1834), but from 1956 onwards the number of specimens of *Apodemus (Sylvaemus) flavicollis* was so small that material of this species collected in 1957—1958 was not taken for statistical analysis.

The method used for the investigations (Andrzejewski & Pielowski, 1956) consisted in the capture of rodents by live-traps placed within the study area to form a network with permanent stations at intervals of 13 m. Capture of the animals took place once a week on each of these stations, one day on stations with odd numbers, and the next day on stations with even numbers. In order to accustom the mice living in the area to visiting the points of capture, bait in the form of approximately 10 grains of oats was left on all the points on the remaining days of the week.

The animals captured were marked with individual numbers, toe clipping (Naumov N. P., 1951) released on the place of capture, both when captured for the first time and after every repeat capture.

Captures of the mice were carried out for 168 weeks. Only those individuals were used for analysis, the residence of which in the study area fell completely within this period of 168 weeks. It became clear that all the individuals caught in the first 148 weeks disappeared from the study area during the following 20 weeks (up to the 168th week of observation). Those individuals were therefore analysed which were caught during the first 148 weeks, and re-caught up to the end of the 168th week of observation. During the whole of this period 1328 individuals were caught, and over 5000 captures made.

II. ANALYSIS OF MATERIAL

From analysis of recaptures (Andrzejewski & Wierzbowska, in litt.), for each particular individual the duration of its residence in the area surveyed was determined. On compiling these data made it possible to state how many individuals captured on the study area during the given time section (for basic analysis we took time sections of one year) for the first time, lived in it one, two, three etc. weeks (generally t weeks). A graph drawn up according to the system thus obtained gives the curve of the number of animals which survive after the expiry of a defined number of weeks from the moment of entry to the study area. To simplify matters we shall call this curve the survival curve of rodents. The systems of numbers of animals which survived t weeks

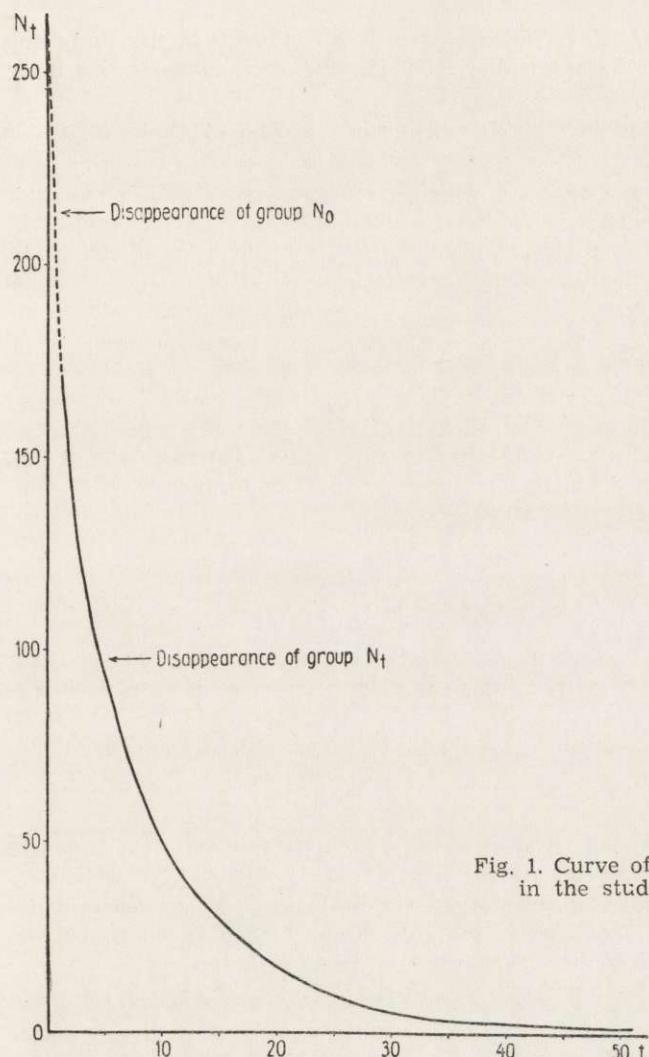


Fig. 1. Curve of stay of *C. glareolus* in the study area (1955/56).

is given for the different years of observations and species in Table I, and one system represented in the form of a survival curve is given as an example (Fig. 1).

1. Rate of disappearance.

Examination was made of the constancy of the disappearance rate of rodents from the study area and in particular, whether the index of the disappearance rate of mice caught for the first time (group N_0 , i.e. N_t for

$t = 0$) is the same for mice staying longer than one week in the study area (N_t for $t \geq 1$). For this purpose the following statistical analysis was made.

The following symbols were chosen:

N_t — the number of individuals which spent at least t weeks ($t \geq 0$) in the study area.

\bar{N}_t — the number of individuals which spent exactly t weeks in the study area and did not appear again.

In our further consideration of this question, for the sake of simplification, we shall call the group of mice which stayed in the study area at least t weeks ($t \geq 0$) group N_t .

The sequence of observations N_t was divided into two sequences:

- 1) covers all values N_t ($t \geq 0$)
- 2) omits group N_0 ($t \geq 1$)

Let T be the length of stay of an individual in the study area.

Let us assume that this variable has an exponential distribution, and therefore its given density function is expressed by the formula:

- a) taking into consideration all N_t values

$$f(t) = \begin{cases} 0 & \text{for } t < 0 \\ P \cdot e^{-Pt} & \text{for } t \geq 0 \end{cases} \quad (1)$$

- b) omitting group N_0

$$\frac{f(t)}{\int_t^\infty f(x) dx} = \begin{cases} 0 & \text{for } t < 1 \\ \frac{f(t)}{\int_t^\infty f(x) dx} = P \cdot e^{-P(t-1)} & \text{for } t \geq 1 \end{cases} \quad (2)$$

P occurring in formulae (1) and (2) is positive ($P > 0$). It is the index of the disappearance of the population from the study area. The probability that the individual will disappear in the time section $(t, t+a)$ does not depend on how long it had been in the area (does not depend on t), but on the length of the time section. We therefore denote this by:

$$P(t \leq T < t+a | T \geq t) = 1 - e^{-Pa} \quad \text{for } t \geq 0 \text{ and for } t \geq 1$$

Continuing, to make the line of reasoning clear, indices of disappearance of the population for the sequence including all N_t ($t \geq 0$), and omitting group N_0 ($t \geq 1$) was correspondingly marked by P_0 and P_1

$$P_0 = f(t | T \geq t); \quad P_1 = f(t | T \geq t).$$

If, therefore, the length of stay of an individual in the study area has an exponential distribution defined by the formulae (1) and (2), and if the lengths of stay of individual mice are independent of each other, then the number of individuals which remained in the study area at least t weeks is expressed by the equations:

$$\begin{aligned} N'_t &= N_0 \cdot e^{-P_0 \cdot t} && \text{for } t \geq 0 \\ N''_t &= N_1 \cdot e^{-P_1 \cdot (t-1)} && \text{for } t \geq 1 \end{aligned} \quad (3)$$

Table 1.

System of duration of stay of animals in the study area, and statistical analysis of disappearance rate of animals from it.

Explanation of symbols: t — duration of stay in the study area, counted in weeks from moment of first capture, N_t — number of individuals which survived in the study area for at last t weeks, \bar{N}_t — number of individuals (empirical) which remained in the study area exactly t weeks, and did not appear again, \bar{N}'_t — for sequence embracing all N_t ($t \geq 0$) and \bar{N}''_t — for sequence omitting group N_0 , — number of individuals (theoretical) which remaind in the study area exactly t weeks and did not appear again.

t	N_t	\bar{N}_t	\bar{N}'_t	$\frac{(\bar{N}_t - \bar{N}'_t)^2}{\bar{N}'_t}$	\bar{N}''_t	$\frac{(\bar{N}_t - \bar{N}''_t)^2}{\bar{N}''_t}$
1	2	3	4	5	6	7
<i>Clethrionomys glareolus 1955/56</i>						
0	261	87	39.92	55.5242		
1	174	24	33.63	2.7576	20.91	0.4566
2	150	30	28.52	0.0768	18.39	7.3296
3	120	13	24.31	5.2619	16.18	0.6250
4	107	12	20.48	3.5113	14.03	0.2937
5	95	10	17.46	3.1874	12.74	0.5893
6	85	9	14.71	2.2165	10.94	0.3440
7	76	8] 14	12.00] 23.10	9.71] 18.25		
8	68	6] 14	11.10] 23.10	8.54] 18.25		
9	62	9] 15	8.96] 16.59	7.52] 14.13		
10	53	6] 15	7.63] 16.59	0.1524	6.61	0.0536
11	47	6] 11	6.43] 11.91	0.06953	5.82] 10.94	0.0003
12	41	5] 11	5.48] 11.91		5.12] 10.94	
13	36	3] 10	4.62] 14.71		4.51] 15.00	
14	33	4] 10	3.94] 14.71		3.96] 15.00	
15	29	1] 10	3.32] 14.71		3.46] 15.00	
16	28	2] 10	2.83] 14.71		3.07] 15.00	
17	26	2] 10	2.38] 14.71		2.70] 15.00	
18	24	5] 10	2.03] 14.71		2.38] 15.00	
19	19	3] 10	1.71] 14.71		2.09] 15.00	
20	16	0] 10	1.45] 14.71		1.84] 15.00	
21	16	1] 10	1.24] 14.71		1.62] 15.00	
22	15	2] 10	1.04] 14.71		1.43] 15.00	
23	13	2] 10	0.89] 14.71		1.25] 15.00	
24	11	1] 10	0.75] 14.71		1.10] 15.00	
25	10	1] 10	0.64] 14.71		0.98] 15.00	
26	9	1] 10	0.54] 14.71		0.85] 15.00	
27	8	1] 10	0.46] 14.71		0.75] 15.00	
28	7	1] 10	0.39] 14.71		0.66] 15.00	
29	6	0] 10	0.33] 14.71		0.58] 15.00	
30	6	0] 10	0.28] 14.71		0.51] 15.00	
31	6	2] 10	0.24] 14.71		0.45] 15.00	
32	4	0] 10	0.20] 14.71		0.40] 15.00	
33	4	0] 10	0.17] 14.71		0.35] 15.00	
34	4	1] 10	0.14] 14.71		0.31] 15.00	
35	3	0] 16	0.12] 9.49	4.4658	0.27] 15.08	0.05613] 15.08
36	3	0] 16	0.10] 9.49		0.24] 15.08	
37	3	0] 16	0.09] 9.49		0.21] 15.08	
38	3	0] 16	0.08] 9.49		0.18] 15.08	
39	3	0] 16	0.06] 9.49		0.16] 15.08	
40	3	0] 16	0.05] 9.49		0.14] 15.08	
41	3	0] 16	0.04] 9.49		0.13] 15.08	
42	3	0] 16	0.04] 9.49		0.11] 15.08	
43	3	0] 16	0.03] 9.49		0.10] 15.08	
44	3	1] 16	0.03] 9.49		0.09] 15.08	
45	2	0] 16	0.02] 9.49		0.08] 15.08	
46	2	1] 16	0.02] 9.49		0.07] 15.08	
47	1	0] 16	0.02] 9.49		0.05] 15.08	
48	1	0] 16	0.01] 9.49		0.05] 15.08	
49	1	0] 16	0.01] 9.49		0.05] 15.08	
50	1	0] 16	0.01] 9.49		0.04] 15.08	
51	1	1] 16	0.00] 9.49		0.03] 15.08	
Total	261	260.95		84.7762	173.76	13.5216

1	2	3	4	5	6	7
<i>Clethrionomys glareolus</i> 1956/57						
0	203	97	55.57	30.8881		
1	106	17	41.43	14.4056	21.19	0.8278
2	89	15	29.02	6.7732	16.95	0.2249
3	74	14	21.08	2.3779	13.56	0.0140
4	60	11	15.30	1.2085	10.85	0.0020
5	49	14	11.11	0.7517	8.68	3.2563
6	35	10	8.28	0.3573	6.97	1.3121
7	25	7	5.80		5.55	
8	18	2	4.21		4.44	13.54
9	16	1	3.22		3.55	
10	15	3	2.06		2.84	
11	12	5	1.61		2.28	
12	7	2	1.17		1.83	
13	5	0	0.87		1.46	
14	5	2	0.61		1.16	
15	3	0	0.44	7.72	0.93	13.02
16	3	0	0.32		0.75	
17	3	2	0.27		0.60	
18	1	0	0.16		0.48	
19	1	0	0.12		0.38	
20	1	1	0.09		0.31	
Total		203	202.74	64.4160	104.76	6.8637
<i>Clethrionomys glareolus</i> 1957/58						
0	138	66	37.89	20.8650		
1	72	11	27.56	9.9504	14.22	0.7291
2	61	12	19.97	3.1800	11.41	0.0305
3	49	10	14.44	1.3620	9.53	0.0232
4	39	7	10.50		7.28	
5	32	2	7.61	4.5827	5.84	13.12
6	30	8	5.31		4.69	
7	22	5	3.99	1.2895	3.91	2.2512
8	17	3	2.91		2.99	
9	14	3	2.10		2.40	
10	11	5	1.52		1.92	
11	6	3	1.10		1.54	
12	3	1	0.80	5.4320	1.29	1.5863
13	2	1	0.58		1.98	
14	1	0	0.42		0.79	
15	1	1	0.30		0.63	
Total		138	137.20	46.6616	69.42	5.9140
<i>Clethrionomys glareolus</i> , Autumn /X-XI-XII/ 1955						
0	74	13	5.96		4.80	
1	61	0	5.61	0.1923	4.42	
2	61	19	4.81		4.08	17.06
3	61	6	4.63		3.76	
4	55	13	4.26	9.5100	3.46	
5	42	4	3.92		3.19	9.59
6	38	13	3.60		2.94	
7	34	5	3.31	0.4224	2.71	
8	29	3	3.04		2.49	
9	26	2	2.80		2.30	
10	24	2	2.57		2.11	
11	22	1	2.37		1.95	
12	21	0	2.18		1.80	2.6903
13	21	0	2.00	4.7984	1.65	
14	21	10	1.84		1.52	
15	20	1	1.68		1.40	
16	19	2	1.55		1.29	
17	17	0	1.43		1.19	
18	17	1	1.31		1.10	
19	16	0	1.21		1.01	
20	16	3	1.11		0.93	
21	13	3	1.02		0.86	
22	10	0	0.94		0.79	
23	10	1	0.86		0.73	
24	9	2	0.79		0.67	
25	7	1	0.73		0.62	
26	6	1	0.67		0.57	
27	5	0	0.62		0.52	
28	5	0	0.57		0.48	
29.	5	0	0.53		0.45	
30	5	1	0.47			

1	2	3	4	5	6	7
31	4	0	0.44		0.41	
32	4	0	0.41		0.38	
33	4	1	0.37		0.35	
34	3	0	0.34		0.32	
35	3	0	0.32		0.30	
36	3	1	0.29		0.27	
37	2	0	0.26		0.25	
38	2	0	0.25		0.23	
39	2	0	0.23		0.21	
40	2	0	0.21	13.8	0.3507	0.20
41	2	0	0.19		12.75	0.18
42	2	0	0.18			0.17
43	2	0	0.16			0.15
44	2	0	0.05			0.14
45	2	0	0.14			0.13
46	2	1	0.12			0.12
47	1	0	0.11			0.11
48	1	1	0.11			0.10
Total		74	72.67	15.2738	59.81	4.9518

Clethrionomys glareolus, Spring /V-VI-VII/ 1956

0	64	30	12.64		4.44	
1	34	0	10.14	37.45	3.86	
2	34	15	8.14		3.36	14.58
3	34	4	6.53		2.92	
4	30	11	5.24	9.45	2.54	
5	19	5	4.21		2.21	6.67
6	14	3	3.38		1.92	
7	11	1	2.71		1.67	
8	10	2	2.17		1.45	
9	8	0	1.75		1.26	
10	8	1	1.40		1.10	
11	7	3	1.12		0.95	
12	4	0	0.90		0.83	
13	4	0	0.72		0.80	
14	4	1	0.58		0.63	
15	3	0	0.47		0.54	
16	3	1	0.37		0.41	0.3152
17	2	10	0.30	16.91	0.47	11.94
18	2	0	0.24		0.36	
19	2	0	0.19		0.31	
20	2	0	0.16		0.27	
21	2	0	0.12		0.23	
22	2	0	0.10		0.20	
23	2	0	0.08		0.18	
24	2	1	0.06		0.15	
25	1	0	0.05		0.13	
26	1	1	0.04			
Total		64	63.81	5.3585	33.19	1.1412

Clethrionomys glareolus, Autumn /X-XI/ 1956

0	43	18	0.98		3.24	
1	25	6	0.96	2.87	2.82	6.06
2	23	2	0.93		2.46	0.0006
3	19	3	0.91	1.80	2.14	0.0348
4	16	2	0.89		1.86	
5	14	4	0.87		1.62	
6	10	1	0.85		1.44	
7	9	7	0.83	4.94	1.23	0.0050
8	8	1	0.81		1.07	
9	7	0	0.80		0.93	
10	7	0	0.78		0.81	
11	7	3	0.76		0.70	
12	4	1	0.74		0.61	
13	3	0	0.72		0.53	
14	3	0	0.71		0.46	
15	3	7	0.69	6.86	0.40	0.3500
16	3	2	0.68		0.35	
17	1	0	0.66		0.31	
18	1	0	0.65		0.27	
19	1	0	0.63		0.23	
20	1	1	0.62			
Total		43	16.37	162.1062	23.45	0.3904

1	2	3	4	5	6	7
Apodemus agrarius, 1955/56						
0	230	133	75.21	44.4048		
1	97	21	50.62	17.3320	20.08	0.1836
2	76	21	34.07	5.0139	15.99	1.5700
3	55	14	27.88	6.9101	12.62	0.1509
4	41	7	10.45	2.2450	10.00	
5	34	14	10.39	20.84	7.96	0.8731
6	27	2	7.00		6.28	
7	25	6	4.71	14.88	4.98	15.23
8	19	3	3.17		3.97	
9	16	0	2.13		3.13	
10	16	2	1.44		2.48	
11	14	3	0.96		1.98	
12	11	3	0.65		1.56	
13	8	2	0.44		1.24	
14	6	2	0.30		0.98	
15	4	0	0.20		0.78	
16	4	16	0.13	6.50	0.62	0.1466
17	3	1	0.09		0.49	
18	2	0	0.06		0.39	
19	2	0	0.04		0.31	
20	2	0	0.03		0.24	
21	2	0	0.02		0.19	
22	2	2	0.01		0.15	
Total		230	230.00	90.7921	96.42	4.0991
Apodemus agrarius, 1956/57						
0	323	196	128.47	35.4970		
1	130	37	77.84	21.4274	34.37	0.2012
2	93	34	47.09	3.6387	25.35	2.9516
3	59	19	28.51	3.2280	18.58	0.0094
4	40	10	17.33	3.1003	13.67	0.9853
5	30	3	10.50	10.08		
6	27	5	6.35	20.71	7.39	22.91
7	22	5	3.86		5.44	
8	17	5	2.34		4.01	
9	12	3	1.42		2.94	
10	9	1	0.86		2.16	
11	8	2	0.52		1.59	
12	6	0	0.32		1.17	
13	6	1	0.19		0.86	
14	5	1	0.12		0.63	
15	4	1	0.07		0.47	
16	3	0	0.04	5.95	0.24	14.93
17	3	1	0.03		0.25	0.2870
18	2	0	0.02		0.19	
19	2	0	0.01		0.14	
20	2	0	0.01		0.10	
21	2	0	0		0.07	
22	2	0	0		0.05	
23	2	0	0		0.04	
24	2	2	0		0.02	
Total		326	326.00	90.2631	129.71	8.7212
Apodemus agrarius, 1957/58						
0	63	35	21.65	8.2320		
1	28	9	14.24	1.9282	6.60	
2	19	2	9.32		5.05	0.8727
3	17	3	6.13		3.87	
4	14	2	4.01	22.09	2.96	1.1955
5	12	3	2.63		2.25	
6	9	3	1.73		1.72	
7	6	1	1.13		1.32	
8	5	2	0.75		1.00	
9	3	2	0.49		0.77	
10	1	0	0.32	4.88	0.59	0.8305
11	1	0	0.21		0.45	
12	1	0	0.14		0.34	
13	1	0	0.09		0.26	
14	1	1	0.02		0.20	
Total		63	62.86	20.2555	27.38	2.8987

1	2	3	4	5	6	7
Apodemus flavicollis, 1955/56						
0	117	60	30.58	28.3040		
1	57	11	22.53	5.9006	9.86	0.1318
2	46	10	16.70	2.6880	8.20	0.3951
3	26	5] 10	12.34] 9.11] 21.45	6.1120	6.74] 5.57] 12.31	0.4335
4	31				4.63]	
5	26	6	6.71			
6	20	3] 11	4.98] 15.37	1.2425	3.81] 11.59	0.0300
7	17	2	3.68		3.15]	
8	15	4	2.71		2.62]	
9	11	3	2.01		2.15]	
10	8	1	1.48		1.78]	
11	7	1	1.10		1.47]	
12	6	2	0.81		1.22]	
13	4	0	0.60		1.01]	
14	4	0	0.44		0.83]	
15	4	1	0.33		0.69]	
16	3	0	0.24		0.57]	
17	3	0	0.18		0.47]	
18	3	0	0.13		0.39]	
19	3	0] 15	0.10] 10.39	2.0454	14.86]	0.0013]
20	3	0	0.06		0.27]	
21	3	0	0.05		0.22]	
22	3	0	0.04		0.18]	
23	3	0	0.03		0.15]	
24	3	0	0.02		0.12]	
25	3	1	0.02		0.10]	
26	2	1	0.01		0.08]	
27	1	0	0.01		0.07]	
28	1	0	0.01		0.06]	
29	1	0	0.01		0.05]	
30	1	1	0		0.04]	
Total	117	117.02		46.2925	56.82	0.9917

The number of individuals which remained in the study area exactly t weeks and did not appear again is given by the formulae:

$$\begin{aligned} \bar{N}'_t &= N_o \cdot (e^{-P_o t} - e^{-P_o (t+1)}) && \text{for } t \geq 0 \\ \bar{N}''_t &= N_i \cdot (e^{-P_i (t-1)} - e^{-P_i \cdot t}) && \text{for } t \geq 1 \end{aligned} \quad (4)$$

The agreement of empirical results with the exponential distribution was checked by means of Pearson's χ^2 agreement test*). The values of parameters P_o and P_i occurring in the above formulae were obtained by the method of maximum likelihood. P_o and P_i were obtained by solving the equations:

$$\frac{\partial \ln \bar{L}}{\partial P_o} = 0, \quad \text{and} \quad \frac{\partial \ln \bar{L}}{\partial P_i} = 0$$

where:

$$\begin{aligned} L &= f(t_1 + P_o) \dots f(t_{N_o} + P_o) = P_o^{N_o} \cdot e^{-P_o} \cdot \sum_{i=1}^{N_o} t_i = \\ &= P_o^{N_o} \cdot e^{-P_o} \cdot \sum_{t=0}^m (t+0.5) \cdot \bar{N}_t \end{aligned}$$

*) This agreement was examined by means of Kolmogorov's test in the work by Andrzejewski, R. & Wierzbowska, T., 1960.

and analogically:

$$\begin{aligned} L &= \overline{f(t_{N_0+1}, P_1)} \cdot \dots \cdot \overline{f(t_{N_0}, P_1)} = P_1^{(N_0 - \bar{N}_0)} \cdot e^{-P_1 \left[\sum_{t=N_0+1}^{N_0} t_i - (N_0 - \bar{N}_0) \right]} = \\ &= P_1^{N_1} \cdot e^{-P_1 \left(\sum_{t=N_0+1}^{N_0} t_i - N_1 \right)} = P_1^{N_1} \cdot e^{-P_1 \left[\sum_{t=1}^m (t+0.5) \cdot \bar{N}_t - N_1 \right]}. \end{aligned}$$

Corresponding estimations P_0 and P_1 are defined by the formulae:

$$\begin{aligned} P_0^* &= \frac{1}{\bar{t}_0}, \text{ where } \bar{t}_0 = \frac{\sum_{t=0}^m \bar{N}_t (t+0.5)}{N_0} \\ P_1^* &= \frac{1}{(\bar{t}_1 - 1)}, \text{ where } \bar{t}_1 = \frac{\sum_{t=1}^m \bar{N}_t (t+0.5)}{N_1} \end{aligned} \quad (10)$$

Values P_0^* and P_1^* are given in table 2.

K. Pearson's statistics serving as a measure of the deviation of two distributions, given using the formula:

$$\chi^2 = \sum_{t=0}^m \frac{(\bar{N}_t - \bar{N}'_t)^2}{\bar{N}'_t} \text{ for the sequence embracing all } N_t (t \geq 0) \quad (5)$$

$$\chi^2 = \sum_{t=1}^m \frac{(\bar{N}_t - \bar{N}''_t)^2}{\bar{N}''_t} \text{ for the sequence omitting group } N_0 \text{ has the distribution}$$

χ^2 of $(m - 1)$ or $(m - 2)$ degrees of freedom.

In the case of numbers in the different age groups being too small, observations of the random variable T were combined in larger groups (about 10 observations).

We verify our hypothesis on the level of significance $\alpha = 0.05$. If the value χ^2 calculated from the sample is greater than the value $\chi^2_{0.05}$ taken from the tables of χ^2 distribution for $r = 0.05$ and degrees of freedom $(r - 2)$ or $(s - 2)$ (r and s is the number of the groups into which observations of the random variable T were divided), then we admit that the empirical distribution differs significantly from the exponential, if, on the other hand, $\chi^2 \leq \chi^2_{0.05}$, then we have no grounds for rejecting the hypothesis as to the agreement of the given empirical system with the hypothetical one. Values χ^2 and $\chi^2_{0.05}$ calculated using formula (5) are given in table 2.

Analysis of the data showed that:

- 1) the distribution of duration of residence of mice in the study area is exponential only where the group of individuals caught for

Table 2.

Results of investigation of disappearance rate of individuals from the capture area, and average duration of stay for three species of rodents and three years of experiment.

Explanation of symbols used in tables 2—5:

- P^* — Coefficient of disappearance rate from study area for sequence omitting group No_o.
 P_0^* — Coefficient of disappearance rate from study area for sequence embracing group No_o.
 χ_0^2 — Values χ^2 for sequence omitting group No_o.
 χ^2 — Values χ^2 for sequence embracing group No_o.
 \bar{t} — Average length of stay in study area.
 $S(\bar{t})$ — Estimate of standard deviation of variable \bar{t} .
 N_0 — Number of individuals caught for first time.
 N_0'' — Number of freshly-resident individuals.
 N^* — Number of migrating individuals.

Species	<i>A. flavi-collis</i>	<i>Apodemus agrarius</i>			<i>Clethrionomys glareolus</i>		
		1955/56	1955/56	1956/57	1957/58	1955/56	1956/57
P_1^*	0.19032	0.23235	0.30732	0.26923	0.1279	0.22315	0.22222
P_0^*	0.30270	0.39587	0.50076	0.42140	0.16545	0.32248	0.32168
χ_0^2	0.9917	4.0991	8.7212	2.8987	13.5216	6.8637	5.9140
$\chi_{0.05}^2$	7.815	9.4888	9.4888	3.841	18.307	12.592	9.488
χ^2	46.2925	90.7921	90.2831	20.2555	84.7762	64.4160	46.6616
$\chi_{0.05}^2$	9.488	11.070	11.070	5.991	19.675	14.067	11.070
\bar{t}	5.25	4.30	3.25	3.71	7.82	4.48	4.50
$S(\bar{t})$	0.633	0.389	0.245	0.614	0.556	0.389	0.475

the first time is omitted (N_0). This rule applies to all the years of observation and in all three species of rodent discussed in this work.

2) the index of disappearance in the group of individuals captured for the first time is greater than in the remaining weeks (i. e. for $t \geq 1$) of stay in the study area.

2. Composition of the group of individuals caught for the first time.

Let us now in turn estimate the value N_0'' expressing the number of individuals which group N_0 should possess, if disappearance from it remained at the same rate as in later weeks ($t \geq 1$).

For the sequence omitting group N_o , the number of individuals staying in the study area at least one week was defined by means of the formula:

$$N''_t = N_1 \cdot e^{-P_1(t-1)} \quad \text{for } t \geq 1 \quad (6)$$

Let us extend the function given by the formula (6) as follows:

$$N'_t = N_1 \cdot e^{-P_1(t-1)} \quad \text{for } t \geq 0 \quad (7)$$

The function defined by formula (7) differs from the function defined by the equation (6) in that it is defined for $0 \leq t < 1$ also. At point $t = 0$ it accepts the value $N''_0 = N_1 \cdot e^{P_1}$.

Table 3.

Composition of groups of animals trapped for the first time.

Species	A. flavi-collis	Apodemus agrarius			Clethrionomys glareolus		
Year	1955/56	1955/56	1956/57	1957/58	1955/56	1956/57	1957/58
N_o	117	230	326	63	261	203	138
N''_o	68.9	122.33	176.71	36.6	197.76	132.48	89.9
\bar{N}^*	48.1	107.67	149.28	26.4	63.24	70.52	48.1
Participation of migrants in group caught for the first time	0.41	0.47	0.65	0.42	0.24	0.35	0.35
Participation of freshly-resident rodents in group caught for the first time	0.59	0.53	0.35	0.58	0.76	0.65	0.65

In connection with this, the density function of the random variable T for resident mice is expressed by the formula:

$$\overline{f(t)} = \begin{cases} 0 & \text{for } t < 0 \\ \frac{N_1 \cdot e^{-P_1(t-1)}}{N''_o} \cdot P_1 = P_1 \cdot e^{-P_1 t} & \text{for } t \geq 0 \end{cases} \quad (8)$$

Values N_o (number of individuals caught for the first time), N''_o (assessment of the group of individuals freshly resident), \bar{N}^* (group of migrating individuals) and the participation of the two latter groups in the group of individuals caught for the first time, are given in table 3.

3. Length of residency of the rodents in the study area.

The next aim of the reasoning is to find the average length of stay of the mice in the study area. In calculating this average, the distribution of stay of resident mice in the study area was taken into consideration, and thus is given by formula (8).

Table 4.

Results of investigation of disappearance rate of individuals from capture area, and average duration of stay.

Month,year	X-XI-XII.1955	V-VI-VII.1956	X-XI.1956
P_1^*	0.082	0.140	0.139
P_0^*	0.084	0.220	0.023
χ^2_0	4.9518	1.1412	0.3904
$\chi^2_{0.05}$	5.991	3.841	
χ^2	15.2738	5.3585	162.1062
$\chi^2_{0.05}$	7.815	3.841	
$E(\chi^2_0)$			3.0
$D^2(\chi^2_0)$	*		5.8202
$E(x^2)$			3.0
$D(x^2)$			6.3396
\bar{t}	12.2	7.1	7.1
$s(\bar{t})$	1.4	0.89	1.32

Table 5.

Results of investigation of composition od group No (individuals caught for first time).

Month,year	X-XI 1955	V-VI 1956	X-XI 1956
N_0	74	64	43
N''_0	66.2	39.1	28.73
\bar{N}^*	7.8	24.9	14.27
Participation of freshly resident mice in group caught for the first time	0.89	0.61	0.66
Participation of migrants in group caught for the first time	0.11	0.39	0.34

Estimation of the average length of time spent by the resident mice in the study area is the arithmetical average $\bar{t} = \frac{1}{P_1^*}$; estimation of standard deviation of the arithmetical average \bar{T} is the expression:

$$S_{(t)} = \frac{1}{\sqrt{N_o'' \cdot P_1^*}}$$

Table 2 gives the values t and $S(t)$ for resident mice. The calculations given above were made for the various species and for one-year periods of observation.

4. Comparison of specimens of *C. glareolus* caught for the first time.

Identical calculations were made for specimens of *Clethriomys glareolus* caught in the autumn period (X—XII) of 1955, the spring (IV—VI) of 1956 and the autumn (X—XI) of 1956, the limit distribution not being made use of for the autumn of 1956 (the numbers according to the division of observations during this period are too small), but the value χ^2 observed was compared with the average $E(\chi^2) = r - 1$, and with the standard deviation:

$$D^2(\chi^2) = 2(r-1) + \frac{1}{N_0} \cdot \left(\sum_{i=1}^r \frac{1}{P_i} - r^2 - 2r + 2 \right) \text{ of variable } \chi^2 \text{ and analogically:}$$

the value χ^2_0 observed was compared with the values: $E(\chi^2_0) = s - 1$

$$\text{and } D^2(\chi^2_0) = 2(s-1) + \frac{1}{N_1} \cdot \left(\sum_{i=1}^s \frac{1}{P'_i} - s^2 - 2s + 2 \right)$$

r, s — number of groups into which the observations were divided, P_i, P'_i — the probability that the random variable T takes on the value belonging to the i group.

An analysis of the spring period of 1955 and the spring and autumn periods of 1956 reveals results analogical with those obtained when considering periods of a whole year. Detailed results of the analysis are given in tables 4 and 5.

III. DISCUSSION OF RESULTS

1. Analysis of the disappearance rate of rodents from the study area made it possible to show that the disappearance of the group of mice living in the study area fulfills the exponential system, i.e. the number of mice which survived in the study area for one, two, three etc. weeks, decreases with each week on an average by a constant percentage, calculated in relation to the number which had survived up to that week. This process of disappearance of the mice in the various species and in consecutive years of observation revealed a decrease in the number of mice in consecutive weeks from the moment when they were first caught (Table 1). As an example one such series was plotted in the form of curve of disappearance of the mice from the study area (Fig. 1). Indices of the disappearance rate (percentages of disappearance) for these species and for consecutive years are given in table 2.

Therefore the disappearance rate (% of disappearance) of the group of rodents which entered the study area in a given year and survived in it for at least a week was constant. When considering periods of a whole years, it was further shown that the disappearance rate of mice caught for the first time is greater than the disappearance rate of rodents in the remaining further weeks of their stay in the study area.

This phenomenon would appear to be justified in the light of opinions as to existence of populations of resident and migrant individuals (Borowski & Dehnel, 1952; Kaleda, 1954; Náumov, 1956, and others).

As the study area was very small in relation to the possibilities of migration by individuals of the species examined, (both on account of the size of the area and also of the ratio of size of the study area to the habitat area of the populations of the species examined) the individuals not settling within the study area (migrating) quickly disappear from it.

Therefore, among the animals caught for the first time, there are migrants which disappear from the study area very quickly (during the first week after capture), and freshly-resident mice, which have chances of remaining in the area for a longer time. The group of animals caught for the first time is there, on account of the possibilities of their remaining in the study area, not homogeneous, and on account of the fact that part of the group is composed by disappearing migrants, has as a rule a higher disappearance index.

If an individual remains in the study area for a week or longer it indicates that this is a resident animal, and thus the constancy of disappearance rate is typical of the group of animals staying in the study area longer than one week, that is, resident rodents.

2. The number of resident and migrant animals among the total number of specimens caught for the first time was next assessed. The assumption was taken as a basis here, that if the disappearance rate is constant among resident animals, beginning from one week of their stay in the study area, then we may expect that it is the same among freshly resident animals, the more so as resident mice, caught for the first time, stay in the study area for a certain period of time from the actual moment of settling in (this time is determined by the frequency of repeat captures of individuals (Andrzejewski & Wierzbowska, in litt.).

On the strength of the above we carried out the extrapolation of the function (by a curve) of residence of rodents in the study area, calculated for mice living there more than a week, up to the moment of capture of the given group of animals. The value obtained gives us the approximate number of resident animals among the specimens caught for the first time. The difference in the number of animals caught for the first time and the numbers of resident animals gives us the approximate number of migrants which we obtained from captures. Table 3 shows, according to species and year of observation, the number of animals which were caught for the first time, how many of them settled in, how many were migrant and what the percentage was of these animals in the group of mice caught for the first time.

The number of animals settling in the study area, estimated in this way, should be close to the real number of resident mice. The number of migrant animals is, however, in proportion not only to the number of animals which did in fact pass through the study area, but also to the number of traps and the time at which they were set; in general therefore to the chance of catching a migrant individual.

With the given method, the ratio of numbers of migrant animals caught to the numbers of resident mice is a good relative measurement for describing the degree of the migrational tendency of the population. The variations in this index in the species we examined and in different years is given in table 3.

3. Finally the average lengths of stay of resident animals in the study area were calculated for the different species of rodent in the consecutive years of observation, and the standard errors of these averages (Table 2). The data obtained indicate that the average length of stay of rodents in the study area is relatively short, and the populations in the area are characterised by a high interchange rate between individuals.

4. The calculations give above were made for periods of one year. In many cases, however, it is interesting to find what is the degree of settlement and interchange rate between individuals during a short period of time. The possibility of carrying out an analogical analysis to the one given above depends on sufficiently numerous material being available during a short observation period.

As an example we analysed, by means of the method given above, the constancy of disappearance rate of the group of resident

animals, the number of migrating and resident specimens in a group of mice caught for first time, and the average duration of their stay, for a population of *Clethrionomys glareolus* in this area, for the following three periods: 1. autumn (X—XII) 1955, during which period this species appeared in the study area (in the summer of 1955 this species was not found in the study area), 2. spring (IV—VI) 1956 — it was characterised by the high numerical level of the population, which was maintained throughout the whole of the summer of 1956, and 3. autumn (X—XI) 1956 — the population in the study area was stable, and numerical level ligh.

Statistical analysis showed (see table 4) that the rate of disappearance is constant for resident mice (for autumn 1956 $\chi^2 = 0.3904$ differs from the average by 45% of the standard deviation, and therefore for the sequence omitting group N_0 , agreement with the exponential system must be considered as good). For the sequence embracing all N_t ($t \geq 0$) we must reject the hypothesis put forward.

IV. CONCLUSIONS

1. The process of disappearance of a given group of resident individuals from the study area under the conditions examined is characterised by a constant disappearance rate.
2. The greater disappearance rate of animals from the study area during the first week following their capture, in relation to successive weeks of their stay in this area, is caused by the capture, in this group, of migrating individuals, which merely pass through the study area.
3. Owing to the constancy of the disappearance process, it proved possible to determine the number of resident and migrating animals in the specimens caught for the first time. These data lead to the conclusion that the number of migrant animals is very large in relation to the number of resident animals.
4. The area in which the investigations were carried out is characterised by the high rate of interchange between individuals and the short period in it spent by the animals.

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STRESZCZENIE

Materiały do niniejszej pracy zbierano w latach 1955—1958 w Puszczy Kampinoskiej w pobliżu Stacji Terenowej Zakładu Ekologii Polskiej Akademii Nauk w Dziekanowie Leśnym. Powierzchnia leśna na której prowadzono badania posiadała kształt prostokąta (o stosunku boków 1:1,5) o obszarze 2,5 ha i nie była izolowana od okalających ją terenów granicami środowiskowymi czy sztucznymi. Porastający ją las przedstawiał zespół *Pineto-Quercetum*, przechodząc z dwóch brzegów w *Cariceto elongate-Alnetum*.

Powierzchnię tę zamieszkivały trzy gatunki gryzoni: *Clethrionomys glareolus* (Schreber, 1780), *Apodemus agrarius* (Pallas, 1771) i *Apodemus (Sylvaemus) flavicollis* (Melchior, 1834).

Metoda badań (Andrzejewski & Pielowski, 1956) polegała na połowach gryzoni pułapkami żywołownymi, ustawionymi na badanej powierzchni w kratę co 13 m w stałych punktach. Połów zwierząt odbywał się raz w tygodniu na każdym punkcie, z tym, że jednego dnia w punktach o numeracji nieparzystej a następnego w punktach o numeracji parzystej. W pozostałe dni tygodnia w miejscach połówu wykładana była przynęta w postaci kilku do kilkunastu ziaren owsa, dla przyzwyczajenia myszy zamieszkujących badany teren do odwiedzania miejsc połówu. Łapane zwierzęta znakowane były indywidualnie i wypuszczane w miejscu złapania, zarówno przy pierwszym jak i przy powtórnych złapaniach danego osobnika.

Odlów myszy prowadzono przez 168 tygodni, z pierwszych 148 tygodni wzięto do opracowania wszystkie odławiane osobniki, z pozostałych 20 tygodni (to jest aż do zniknięcia z powierzchni badań osobników znakowanych w wyżej omówionym okresie pierwszym) tylko osobniki znakowane w ciągu pierwszych 148 tygodni. W całym okresie obserwacji złowiono 1328 osobników drobnych gryzoni i osiągnięto dla nich przeszło 5 000 złapań.

Na podstawie analizy powtórnych złapań poszczególnych zwierząt wyznaczono dla każdego konkretnego osobnika odcinek czasu w jakim przebywał on na badanej powierzchni. Zestawienie tych danych pozwala ustalić liczbę zwierząt jaka pozostała na powierzchni badań po upływie określonej ilości tygodni od momentu pierwszego ich złapania. Przedstawienie tych danych w postaci wykresu daje nam krzywą przebywania gryzoni na powierzchni badań (Rys. 1).

Przeprowadzono analizę tempa ubywania gryzoni z powierzchni badań oraz sprawdzono czy tempo ubywania grupy osobników łapiących się po raz pierwszy, jest większe niż osobników łapiących się wielokrotnie. Konieczność sprawdzenia tego łączy się z obecnymi poglądami na zróżnicowanie osobników wewnątrz populacji, w której powinny znajdować się w pewnym udziale osobniki migrujące, a więc przechodzące tylko przez powierzchnię badań (Kalela, 1954; Naumov, 1956 i in.).

Analizę wykonano następująco:

Oznaczamy N_t — ilość osobników, która przebywała na powierzchni badań conajmniej t tygodni, \bar{N}_t — ilość osobników, która przebywała na powierzchni badań dokładnie t tygodni i więcej się nie pojawiła.

Zgodnie z przypuszczeniem, że tempo ubywania z powierzchni badań jest w grupie myszy łapiących się po raz pierwszy większe niż dla myszy przebywających na powierzchni badań dłużej niż tydzień ($t \geq 1$), rozbito ciąg wartości N_t ($t \geq 0$) na dwa ciągi: 1. uwzględnia wszystkie wartości N_t ($t \geq 0$), 2. pomija osobniki złapane po raz pierwszy (grupa N_0).

Stosując tekst zgodności χ^2 Pearsona wykazano, że rozkład długości czasów przebywania osobników na powierzchni badań jest wykładniczy tylko dla ciągu pomijającego osobniki złapane po raz pierwszy (grupa N_0), a więc, że tempo ubywania osobników z powierzchni badań jest stałe tylko dla osobników przebywających dłużej niż jeden tydzień na tej powierzchni.

Ponieważ mały obszar powierzchni badań (2,5 ha) stwarza bardzo małe szanse na pozostawienie na niej migranta w ciągu tygodnia, należy wnioskować, że stałość tempa ubywania charakteryzuje daną grupę osobników osiadłych, to znaczy, że procent osobników ubywających w danej jednostce czasu jest stały i proporcjonalny do ilości osobników jako do tego momentu przetrwała na badanej powierzchni. Procent ten jest współczynnikiem tempa ubywania (P_1 w tablicy 2).

Dalej analiza pozwala stwierdzić, że tempo ubywania gryzoni z powierzchni badań jest istotnie większe niż w pozostałych tygodniach przebywania myszy na tej powierzchni.

Stwierdzenie stałości tempa ubywania zwierząt osiadłych w całym okresie ich osiedlenia na powierzchni badań z wyjątkiem pierwszego tygodnia (dla zwierząt tych zachodzi równanie: $N''_t = N_1 \cdot e^{-P_1(t-1)}$, pozwala na przyjęcie założenia, że myszy osiadłe również w pierwszym tygodniu po osiedleniu giną z powierzchni badań w tym samym tempie. Zatem, wzrost wskaźnika ubywania w pierwszym tygodniu po pojawienniu się danej grupy zwierząt, spowodowany jest udziałem w tej grupie zwierząt migrujących.

Dokonano oceny ilości zwierząt migrujących, odejmując od ilości zwierząt złapanych po raz pierwszy (N_0) ilość osobników osiadłych (N''_0) w grupie N_0 .

Oceny ilości osobników osiadłych dokonano opierając się na wyżej omówionej stałości procesu ubywania i przedłużając funkcję $N''_t = N_1 e^{-P_1(t-1)}$ dla $t \geq 1$ w następujący sposób: $N''_t = N_1 e^{-P_1(t-1)}$ dla $t \geq 0$, a więc ilość osobników świeżo osiadłych u grupy łapiących się po raz pierwszy wynosi $N''_0 = N_1 e^{-P_1}$.

Tablica 3 przedstawia nam ilość zwierząt jakie u poszczególnych gatunków i w poszczególnych latach obserwacji złapały się po raz pierwszy (N_0) ile z tego się osiedliło (N''_0), ile było migrujących (\tilde{N}^*) i jaki był ich udział.

Oceniona w ten sposób ilość zwierząt osiedlających się na powierzchni badań powinna być bliska rzeczywistej ilości osiedlających się zwierząt. Ilość zwierząt migrujących będzie proporcjonalna do ilości pułapek i czasu w jakim były one nastawione, oraz do ilości zwierząt jakie faktycznie przeszły przez powierzchnię badań; ogólnie zatem do szans złapania się osobnika migrującego. W związku z tym że ekspozycja pułapek wynosiła dwa dni w tygodniu, można powiedzieć, iż w ciągu danego okresu obserwacji przez badaną powierzchnię przechodzi conajmniej trzy i pół raza więcej osobników migrujących niż ilość migrantów przedstawiona w tablicy 3. Dane te zatem pozwalają sądzić, że ilość migrantów w populacji jest bardzo duża w stosunku do ilości osobników osiadłych.

Przy danej stałej metodzie połówu stosunek ilości zwierząt migrujących do osiadłych będzie dobrą względną miarą do scharakteryzowania stopnia migracyjności populacji (tablica 3).

Obliczono wreszcie średnie czasy przebywania gryzoni na powierzchni badań oraz błędy standartowe tych średnich w poszczególnych latach obserwacji. Wielkości te wyliczono z równań: $\bar{t} = \frac{1}{P_1}$, $S_{(t)} = \frac{1}{N''_0 \cdot P_1}$. Otrzymane dane wskazują, że średni czas przebywania gryzoni na powierzchni badań jest stosunkowo krótki i populacje na tym terenie charakteryzują się zatem dużym tempem wymiany osobników (tab. 2).

Powyzsza charakterystyka tempa ubywania przeprowadzona była dla trzech rocznych okresów obserwacji omawianych gatunków. Dla porównania przeprowadzono również identyczne obliczenia dla jesieni 1955 oraz wiosny i jesieni 1956 u *C. glareolus*. Wyniki tych przeliczeń zawierają odpowiednia część tablicy 1 oraz tablice 4 i 5.

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