A C T A T H E R I O L O G I C A

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Productivity Investigation of an Island Population of *Clethrionomys glareolus* (Schreber, 1780). I. Dynamics of Cohorts*)

[With 2 Figs. & 6 Tables]

An isolated population of *Clethrionomys glareolus* (Schreber, 1780) was investigated over the course of one year. Marking of all trappable individuals and knowledge of the time in which the various individuals were born made it possible to distinguish 5 age groups (cohorts). The maximum participation in the current year's population mass, expressed by the number of individual-days, was that of the early summer cohort (56%), the maximum participation in natality — (53.6%) — was that of the early spring cohort. It was also found that individuals from the early summer cohort were the most numerous survivors to the following year (they formed 75% of the population in the spring). The disappearance rate of the young animals is far higher than that of trappable individuals in the summer. Disappearance of the young of spring and early summer cohorts is lower than that of the late summer and autumn cohorts. Disappearance of the trappable part of the population is lower in the winter than during reproduction.

The aim of this study is to define the participation in natality and maintenance of the reproductive stock for the next year of different »cohorts« (individuals born within a relatively short time), the way in which the role of these cohorts changes in time, their mortality and length of life, and the participation of different cohorts in the mass of the population.

The greatest emphasis was laid on questions of method, particularly the way in which material was elaborated, as field observations did not permit of establishing whether the phenomena observed recur, *i. e.* whether they are regular.

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1. AREA, MATERIAL, STUDY METHODS

The object of the studies was formed by a population of *Clethrionomys glareolus* (S c h r e b e r, 1780), inhabiting a 4 ha island in Lake Bełdany (Mazurian lake district). As the minimum distance of the island from the shore was 120 m it may be assumed that, practically speaking, there was no interchange of small rodents between the island and land. We were therefore concerned with an isolated population of animals living within a small area and without exchange of individuals (emigration and immigration), which greatly facilitated the work of tracing its dynamic of numbers, natality, mortality and other parameters.

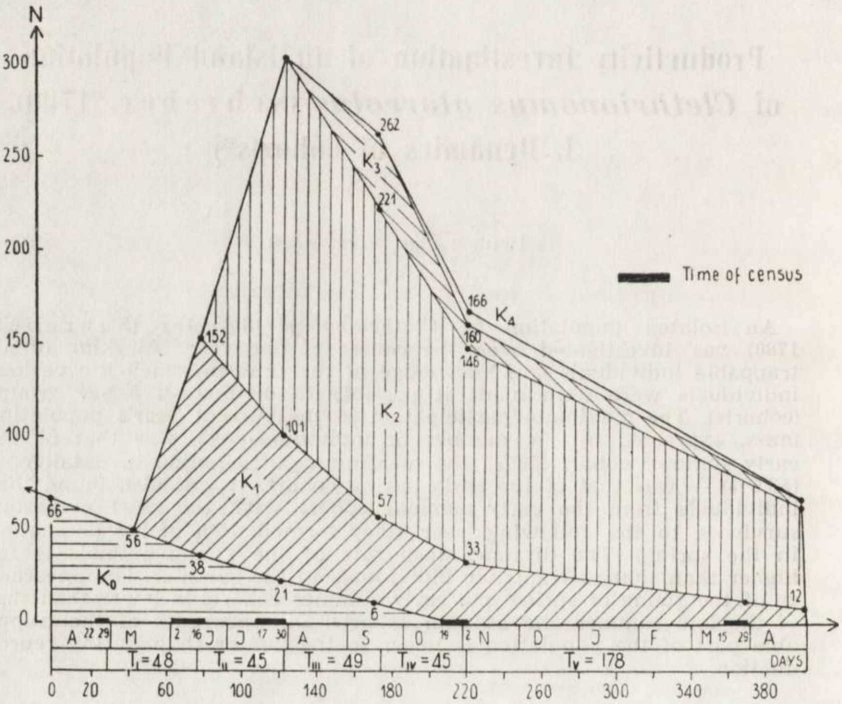

Fig. 1. Population dynamics.
$K_0 - K_4$ — cohorts; Solid points — empirical data; Circles — calculated data; Figures on graph — numbers; Figures in rectangle of month — date of observations.

The island is covered by a forest belonging to 4 phytosociological associations. The wet coastal belt is covered by the *Salici-Franguletum* M a l c., 1929 association, the central areas, the highest and dryest part of the island, are covered by the *Tilio-Carpinetum typicum* T r a c z y k, 1962 association, while in the remaining parts this association changes into sub-association *Tilio Carpinetum stachyetosum silvaticae* and in the wet depressions in the area, into *Circeo-Alnetum* O b e r d o r f e r, 1953.

In 1963 and 1964 a population of the bank vole, numbering about 300 individuals, was found on the island, which justifies the assumption that the island habitat is suitable for this species. The investigations carried out on this island in 1965 for other purposes ended in total removal of the small rodents and for a few months the island remained uninhabited by these animals. In July 1965 200 individuals of *C. glareolus* caught in the population in the Białowieża National Park were introduced on to the island. These individuals were given consecutive numbers (by toe-clipping) and formed the beginning of the study population.

Collection of the material contained in this study was begun in April 1966, carrying out 5 censuses during the season from spring to autumn 1966, and in April 1967 (Fig. 1, Table 1).

The field method of investigations was based on the Catch-Mark-Release principle (*CMR*). Each census lasted 2 weeks, apart from April 1966, when captures were made for one week only. Intervals between censuses lasted about one month.

During the censuses the island was covered with a network of points with live traps. arranged chequerwise at intervals of 15 m. On each of 159 points there was either one, two or three traps, their number being changed on each point

Table 1.

Numbers of various cohorts.

Date	29th April 66		16th June		31st July		18th Sept.		2nd Nov.		29th April 67	
Sex	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂
K_0	24	32	16	22	7	14	3	3	1	0	0	0
K_1	—	—	57	57	41	39	24	27	14	18	3	9
K_2	—	—	—	—	105	98	79	85	58	53	29	22
K_3	—	—	—	—	—	—	18	23	11	5	5	0
K_4	—	—	—	—	—	—	—	—	2	4	0	0
	24	32	73	79	153	151	124	138	86	80	37	31
Total	56		152		304		262		166		68	

every day, placing two traps in place of one, three in place of two and one in place of three. There were thus on an average two traps on each point. This arrangement of traps was dictated by studies on population structure, the results of which will be published separately.

The traps were examined twice daily: at 7,00 and 19,00. A record was kept of the capture point and the number, weight and sex of the animal; a vaginal smear was taken from sexually mature females, then the individuals were released on the place of capture.

During all the censuses (from April 1966 to April 1967) a total number of over 7.000 captures were made (424 in April, 1252 in June, 2.369 in July, 2.412 in September 1966 and 793 in April 1967) of 420 individuals (214 ♂♂ and 206 ♀♀).

2. PARTICIPATION OF VARIOUS COHORTS IN »DYNAMICS« OF NUMBERS

2.1. Differentiated Cohorts

The numbers of *C. glareolus* on the island were ascertained six times (Fig. 1, Table 1). Estimates of the numbers of »trappable« individuals were made by means of the general census method of all individuals during the study period [1]). The number of individuals calculated from the general census was conventionally accepted as the state of population numbers on the final day of the general census.

It may be assumed that numbers obtained in this way (*N*) faithfully reflect the number of individuals actually present at the given moment. The following premises argue in favour of this assumption.

1. In earlier studies (Andrzejewski, Petrusewicz & Waszkiewicz - Gliwicz, 1967) it was found that a two-week period of captures makes it possible to register all the individuals present on the island.

Table 2.
Rapidity of registering individuals already marked.

Census \ Day of census	1	2	3	4	5	6	7	8	9	10	11	12	13	14	N
April 1966	65.5	81.0	89.6	96.5	100	100	100								56
June 1966	92.1	100	100	100	100	100	100	100	100	100	100	100	100	100	38
July 1966	76.5	92.2	96.0	96.0	98.0	98.0	99.0	99.0	99.0	100	100	100	100	100	101
Sept. 1966	67.4	85.1	90.1	92.4	94.7	96.5	97.9	97.9	97.9	98.7	98.7	98.7	100	100	221
Nov. 1966	75.4	90.5	96.8	98.2	98.2	98.8	98.8	98.8	98.8	98.8	100	100	100	100	160
April 1967	70.2	91.2	95.6	95.6	98.6	98.6	98.6	100	100	100	100	100	100	100	68
Average	74.5	90.0	94.7	96 5	98.2	98.4	98.8	99.1	99.1	99.5	99.7	99.7	100	100	

2. During 14 measurements of numbers on the island (counting those which were taken into account in the previous studies and the measurements made in 1967, which have not yet been included in the present studies) a situation in which an individual registered in one census failed to appear in the next, but appeared again in the third census, never once occurred.

3. The presence of an individual marked on the neighbouring land was never found.

4. Capture of individuals already marked took place very rapidly. 75% of the individuals marked in the preceding censuses were found in traps during the first day of the given census, and 95% after three days (Table 2).

[1]) In using the term »trappable« both here and later on we are guilty of a certain degree of simplification, as the censuses took place over the course of approximately one month, hence during the first registration for each of the cohorts, the rodents were already more than 21 days old, which is the dividing line between the »trappable« and »nest« ages. It would be more accurate to speak of »captured« individuals.

5. All the individuals registered for the first time weighed so little that it could be safely assumed that they had reached trappable age after the previous census (that during the previous census they had been less than 21 days or had even been born after the census was made).

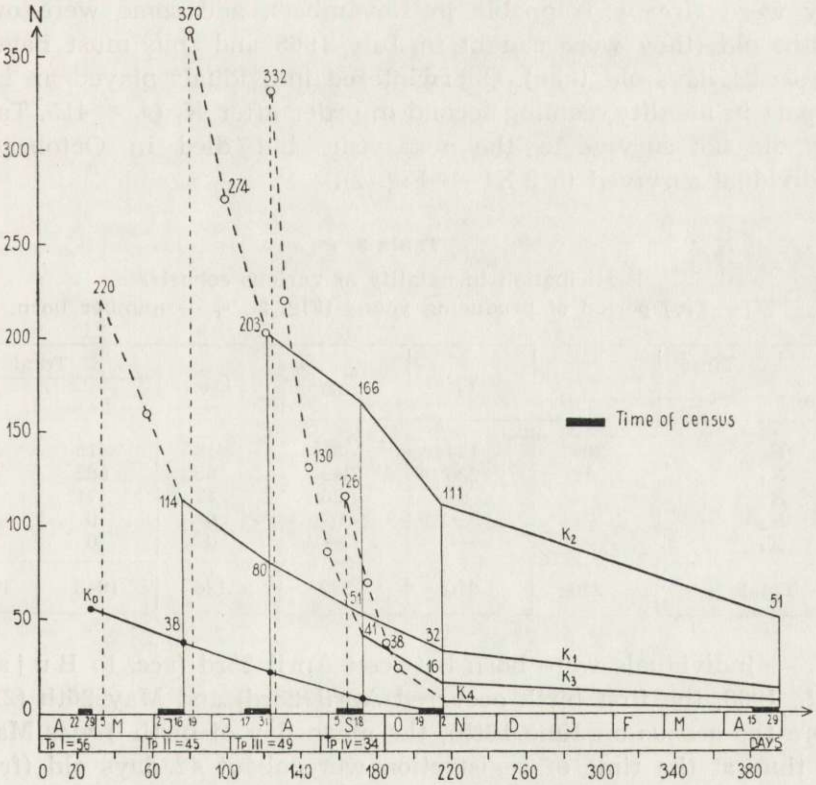

Fig. 2. Dynamics of different cohorts.
$K_1 - K_4$ — cohorts, $T_{PI} - T_{PIV}$ — time in which the young animals of a given cohort were born; Solid points — empirical data; Circles — calculated data; Solid lines — numbers of trapped part of population; Thick dotted line — numbers of nest part of population; Thin line — numbers of part of the trappable population (older than 21 days) but not registered. Numbers of unregistered animals recording to exponential curve.

We assume that the standing crops shown are accurate and reliable.

Starting from this point we were able to accept, with a considerable degree of probability, that individuals registered for the first time were born earlier than 21 days before the given census [2]) and later than 20 days before the previous census. This enabled us to distinguish

[2]) It was accepted (Bujalska, Andrzejewski & Petrusewicz, 1968) that by the age of 21 days *Clethrionomys glareolus* can begin to be caught, since this is the mean day that nursing of these young individuals ceases, and in consequence the day on which they leave the nest (Kowalski, 1964).

several groups of individuals born at a definite time, termed by us cohorts (K), the fate, participation in natality and mortality of which could be traced in time.

K_0 — overwintered individuals (Fig. 2, Table 1), the age of which was not exactly defined, were not less than 6 months old in April 1966 (they were already trappable in November), and some were over 11 months old (they were caught in July 1965 and thus must have been at least 21 days old then). Overwintered individuals played an important part in natality, coming second in order after K_1 ($\nu_r = 415$, Table 3). They did not survive to the next year, but died in October (only 1 individual survived to 2.XI — Fig. 2).

Table 3.

Participation in natality of various cohorts.
($T_I - T_{IV}$) period of producing young (Fig. 2), ν_r — number born.

Cohort \ Time	T_I	T_{II}	T_{III}	T_{IV}	Total	
					ν_r	% ν_r
K_0	208	134	55	18	415	39.6
K_1	12	236	249	65	562	53.6
K_2	—	0	28	43	71	6.8
K_3	—	—	0	0	0	0.0
K_4	—	—	—	0	0	0.0
Total	220	370	332	126	1048	100.0

K_1 — individuals were born between April 23rd (acc. to B u j a l s k a *et al.*, 1968, the first birth occurred April 23rd) and May 26th (21 days before the census on June 16th), the mean day of birth [3]) was May 5th, and thus at the time of registration were about 42 days old (from 21 to 54 days). These were individuals born from overwintered animals only. This statement is based on the calculation of the time, after April 1st (beginning of pregnancy), required by the progeny of the young animals of that year to attain trappable age: 22 days pregnancy + 35 days maturescence + 22 days pregnancy of that year's animals + 21 days from birth to reach trappable age makes 100 days. Even if maturescence was shorter than 35 days (23—28 days — B u j a l s k a *et al.*, 1968 in accordance with observations S c h w a r z *et*

[3]) The mean day of birth accepted after A n d r z e j e w s k i, B u j a l s k a & P e t r u s e w i c z (1968) as the mean weighed day of birth (the number born before and after this date is uniform). The time from the mean day of birth to the census (42 days for K_1) is approximately the age of the cohort at the time of the census; in reality, however it is slightly over-estimated, as the individuals born earlier were more likely to die, and there is therefore less of them during the time the census is taken.

al., 1964, regarding earlier maturescence of the spring generation and the time of pregnancy was shorter than 22 days), then the progeny of that year's young voles could not attain trappable age before June 16th [4]).

K_1 played the most important part in reproduction in the current year, as 53.6% of all the young animals were born from these parents (Table 3).

K_2 — are individuals born between May 27th and July 10th, average June 19th (Bujalska, *et al.*, 1968), and thus at the time of making the census (July 31st) they were from 21—66 days old, with a mean of aprroximately 42 days. In the current year's natality their participation was slight: 71 born, 6.8% of the total number born in the current year (Table 3); they formed the main mass of the population in the spring of the next years (75% of the standing crop in April 1967 — Table 1, Fig. 2). The vast majority were the progeny of K_1, and partly of K_0.

K_3 — individuals born between July 11th — August 28th, mean day August 2nd (Bujalska, *et al.*, 1968) registered on Sept. 18th at the age of 21—68 days old, mean value 47 days. The greater part were progeny of K_1, while K_0 and K_2 participated to a slight degree in the number produced. They were not included in reproduction in the current year.

K_4 — born between August 29th — October 1st, mean day September 10th (Bujalska *et al.*, 1968) registered on November 2nd at the age of 31—61 days, mean value 53 days. They were not included in reproduction the current year, and none of them survived to the next year.

2.2. The Role of Different Cohorts in Natality

During the current reproductive season the number of young produced by different cohorts may be arranged in the following order: K_1 (53.6%), K_0 (39.6%), K_2 (6.8%), K_3 (0%) and K_4 (0%) (Table 3).

It must, however, be emphasised that K_2, which played a completely negligible part in natality during the current season, form 75% of the

[4]) This calculation induces us to propose a change of dates for capture by means of the standard minimum method. Grodziński, Pucek & Ryszkowski (1966) suggested the beginning of April, September and April. We are now of the opinion that the most suitable dates would be: beginning of June, September, beginning of June. In June old adults can easily be distinguished from animals born the same year, and it is thus possible to define the numbers of overwintered old adults. Knowing their numbers in September of the previous year it is possible to define with a fairly great degree of accuracy the numbers in April (beginning of reproduction). Animals born up to June form a large part of those born (40%) in a given season (Table 3).

total number of next year's survivors. Participation in the reproductive stock of the following years was: 17.7% for K_1, K_3 — 7.3%, K_4 and K_0 did not survive until the following year [5]).

To recapitulate: under the ecological conditions of the island overwintered K_0 began reproduction, produced the early spring generation (K_1) and play a fairly important part in later natality. The early spring generation (K_1) formed the main reproductive mass of the population. The summer generation (K_2), the progeny of K_1 and K_0, produced the basic part of the trappable population of the current season, participated only to a small extent in the natality of the current year but formed the majority of the next year's stock.

2.3. The Role of Cohorts in Variations in Numbers of the Trappable Part of the Population

Interpolating 6 levels of numbers (Table 1) defined in 6 points of time (final day of each census) by straight lines, a graph was obtained illustrating the variations in population numbers of the whole year (Fig. 1). This permits of defining approximately the numbers of individuals and participation of different cohorts in an optional point of time. On account of the relatively short intervals of time between consecutive estimates of levels of numbers, connecting the points on the diagram with a straight line only slightly distorts the picture of the course taken by variations in numbers over the year. Only points indicating numbers in April and June were left unconnected directly by a straight line since, as mentioned above, we had only overwintered animals in the April record. The data contained in the study by B u j a l s k a *et al.* (1968) on natality on the island during this period show that the first attained the age of 21 days (*i.e.* trappable age) about May 14th. It was therefore assumed that up to May 14th the numbers of the whole population are equal to the numbers of overwintered animals (K_0), but as from May 14th the number of individuals in the population of trappable age began to increase.

In the first part the picture of variations in numbers of *C. glareolus* on the island agreed with data in literature. The lowest level of numbers was in May (Fig. 1), when the population consisted entirely of adult overwintered animals (K_0) and then began to increase as far more young made their appearance (cohort K_1) than old animals died. The peak numbers occurred on the island in July, whereas in Central

[5]) We have no material elaborated for 1967 as yet, so we cannot state how many young the current year's cohorts will produce as overwintered animals — this will form the subject of a future elaboration — we can only give the percentage of the initial stock.

Poland this usually occurs at the turning point between September and October (A n d r z e j e w s k i, 1963). This difference may result from the specific character of the years (a favourable spring for rodents, high degree of survival of the early born animals) or the specific nature of the ecological conditions on the island. As from July a continuous decrease in numbers of individuals was observed, as more individuals died than were born (cohorts K_3 and K_4 of trappable age were by this time far from numerous). Numbers in November could be considered as the state of the population on entry into winter reduction, since reproduction ended on the island on October 1st (B u j a l s k a *et al.*, 1968) and all the young animals had attained trappable age.

The maximum numbers were attained by K_2 (203 individuals in July), but the participation in the mass of population is better illustrated by the number of individuals per day (*NT*) for each cohort, since that is the mass which consumed, assimilated *etc.* in the study period. Table 4 shows that the main mass of the population, both during the summer season (43%), and even more so during the winter period, was formed by K_2 — the early summer generation (56% of the whole trappable population — Table 4). The late summer generation K_3 formed a small (6%), and the autumn generation a negligible (1%) part of the population (Table 4, Fig. 1).

2.4. Mortality Among Different Cohorts and its Variations in Time

Knowing the numbers of different cohorts at the time of each census and (from the study by B u j a l s k a *et al.*, 1968) the number and average of the animals born, it was possible to make a graph of the survival of these cohorts (Fig. 2).

The curve of survival presented in this way requires explanation. The curve of overwintered animals (K_0) does not represent absolute age. It was drawn up for introduced individuals of unknown age, released in July 1965 when of trappable age, and young born after July 1965. In April 1966 some of them were not less than 6 months (those born on the island) and some more than 11 months old (introduced animals), and thus had survived (to October 1966) to an age of not less than 12 or 17 months.

The dynamics of cohorts K_1, K_2, K_3 and K_4 represent the absolute age of cohorts in days calculated from the mean day of birth.

It must also be pointed out that data illustrating the number of trappable individuals (continuous line on Fig. 2) of the cohorts form the empirically defined standing crop. The moment of appearance of each cohort, on the other hand (circle — Fig. 2) is conventionally

Table 4.

Participation of various cohorts in formation of trappable part of the population. N_T — number of individuals; $\overline{NT}$ — number of individuals per day.

Cohort	Time of reproduction			Winter period			All the year		
	1 Apr. — 1 Oct. 66		$T=183$ days	1 Oct. 66 — 1 Apr. 67		$T=182$ days	1 Apr. 66 — 1 Apr. 67		$T=365$ days
	N_T	$\overline{NT}$	$T\%$	N_T	$\overline{NT}$	$NT\%$	N_T	$\overline{NT}$	$NT\%$
K_0	66	6 156	23.8	5	96	0.4	66	6 252	12.3
K_1	114	8 205	31.7	46	4 773	19.1	114	12 978	25.5
K_2	203	11 020	42.6	148	17 194	68.8	203	28 214	55.5
K_3	41	487	1.9	34	2 375	9.5	41	2 862	5.6
K_4	0	0	0	6	546	2.2	6	546	1.1
Trappable population	424	25 868	100.0	230	24 984	100.0	430	50 852	100.0

Table 5.

Mortality of different cohorts in time.
Mortality expressed by disappearance per day per 1 average individual. Means weighed in respect of time and mean numbers.

Cohort	T_I	T_{II}	T_{III}	T_{IV}	Mean for period of:		
					Reproduction		Winter
					Young	Trappable	
K_0	0.008	0.014	0.022	0.022	—	0.010	—
K_1	0.015	0.008	0.009	0.009	0.015	0.008	0.004
K_2		0.014	0.004	0.009	0.014	0.006	0.004
K_3			0.033	0.017	0.033	0.017	0.006
K_4				0.035	0.035	—	0.010
Mean*	0.008	0.009	0 006	0.010	0.024	0.008	0.005

* Mean for trappables only.

situated in time. Thus there were never these particular numbers in the population at any one given moment; it is the number of individuals born in the preceding period (B u j a l s k a *et al.*, 1968, see also section 2.1). Having the total number born (νr) and number which was registered from among those born (N) after a known time T (time from mean day of birth to time of census) it is possible to calculate from formula $N_T = \nu r \cdot e—\mu T$ mortality (μ) of young individuals up to the time of the first capture. Up to their first registration (about 43rd day of life) it was assumed that young animals constantly disappeared, *i. e.* the exponential curve of survival. For periods after the first registration, however, the curve of numbers (*i. e.* the curve of survival) took a course very similar to a straight line (Fig. 2). In this case it appeared to us that acceptance of constant losses would differ very greatly from actual conditions. In order to be able to compare mortality of non-

Table 6.
Mortality with acceptance of exponential curve versus disappearance per day per individual.

	Period of reproduction		Winter
	Non-trappable	Trappable	
μ	0.035	0.014	0.007
m	0.024	0.008	0.005

-trappable and trappable animals we accepted as a measure the mortality measured by loss per time, per individual, *i. e.* by the formula:

$$\frac{N_0 — N_1}{T \cdot (N_0 + N_1) : 2}$$

where N_0 — numbers at the beginning and N_1 at the end of the study period, T — period for which mortality was measured (Tables 5 and 6). For purposes of comparison calculation was made of μ for the trappable part of the population.

The comparison given (Fig. 2, Tables 5 and 6) makes it possible to draw the following conclusions: (1) decrease in numbers within the cohort (Table 5, Fig. 2) was far greater for young individuals (not trappable) than for trappable individuals; (2) losses for the trappable part of cohorts K_0, K_1, K_2 and K_3 during the growing season (from April to November) were similar to a straight line; (3) losses in the trappable part of the cohorts whose fate can be traced during the year of birth (K_1, K_2 and K_3) were far greater during the growing season (up to November) than during the winter (from November to April), and finally (4) losses of young animals (up to the first registration) of the early spring cohort (K_1) and early summer cohort (K_2) are very similar to each other and far smaller than the losses in cohorts K_3 and K_4.

The fact is remarkable that the survival curve of the trappable part of the population was similar to a straight line during the growing season. This would mean that a constant number, and not a constant percentage, disappeared from the population per unit of time, which is contrary to the view generally held in ecology. The shortness of the study period did not permit of drawing conclusions of a more general nature.

The apparently long life of the trappable part of the population is worthy of emphasis (Table 6). The picture presented here is not of course complete, as observations have not yet ended.

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BADANIA NAD PRODUKTYWNOŚCIĄ WYSPOWEJ POPULACJI
CLETHRIONOMYS GLAREOLUS (SCHREBER, 1780). I. DYNAMIKA KOHORT

Streszczenie

Materiały zawarte w niniejszej pracy pochodzą z badań nad izolowaną populacją *Clethrionomys glareolus* (Schreber, 1780), żyjącą na 4 ha wyspie na jez. Bełdany. W ciągu roku (IV. 1966 — IV. 1967) przeprowadzono 6-krotną ocenę liczebności gryzoni metodą CMR (Tabela 1, Ryc. 1). Wykazano, że każdorazowa ocena wiernie oddaje liczbę osobników obecnych na powierzchni (Tabela 2). Z młodych osobników, które zarejestrowano po raz pierwszy w czasie kolejnych ocen liczebności (czyli osobniki urodzone w określonych odcinkach czasu przed połowem) utworzono grupy zwane kohortami (Ryc. 2). Wyróżniono kohortę wczesnowiosenną (K_1), wczesnoletnią (K_2), późnoletnią (K_3) oraz późnojesienną (K_4). Osobniki stare — przezimki, które stanowiły populację na wiosnę (IV. 1966) połączono w kohortę K_0 o nieznanym dokładnie wieku.

Prześledzono losy poszczególnych kohort i ich rolę w populacji.

Stwierdzono, że największą masę populacji (56%) wyrażoną jako $\overline{N}T$ (Tabela 3 i 4) stanowiły osobniki z kohorty K_2 zarówno w okresie rozrodu, jak i w okresie redukcji zimowej. One też miały największy udział w populacji (75%) wczesną wiosną następnego roku (IV. 1967).

Największy udział w rozrodzie miała kohorta K_1 (54%) i K_0 (40%). Kohorta K_2 rodziła zaledwie 7% (Tabela 3).

Kohorty jesienne K_3 i K_4 miały najmniejszy udział w dynamice liczebności, jak i w rozrodzie w badanym roku udziału nie brały.

Smiertelność młodych jest dużo większa niż osobników łownych (Ryc. 2, Tabela 5 i 6). Śmiertelność osobników łownych w sezonie rozrodczym wzrasta z czasem (od wiosny do jesieni) i wyraźnie maleje w okresie zimowym.