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Productivity Investigation of an Island Population of *Clethrionomys glareolus* (S c h r e b e r, 1780). IV. Production*)

[With 2 Figs. & 3 Tables]

Calculation was made, on the basis of individual growth and empirical survivorship curves, of the productivity achieved by a population of *C. glareolus* during the course of one year ($P = 11,429$ g live weight/ /year/population). Production achieved during the reproduction season was $P = 10.263$ g and during the winter $P = 1166$ g. During the reproduction period the value was determined of the production of young achieved at the mother's expense (up to the 21st day of life) — $P_r = 5848$ g and value of production due to growth — $P_g = 5581$ g.

1. INTRODUCTION

The subject of the present study is an attempt at estimating the production of a population of *Clethrionomys glareolus* (S c h r e b e r, 1780), with particular emphasis on the ratio of production due to reproduction (P_r) and production due to growth (P_g), and the productivity of the generations (cohorts) distinguished in different phenological periods.

Calculation of production was carried out for a free-living population of *C. glareolus* inhabiting an island in Lake Bełdany in northern Poland (Mazurian lake district). This island, 4 ha in area, covered by mixed forest, was a natural habitat of *C. glareolus* (for detailed description of the habitat see T r a c z y k, 1965, and G l i w i c z *et al.*, 1968).

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2. MATERIAL

Investigation of settlement of the island was carried out seven times by means of the method giving a general census of the whole trappable part of the population, recording: date, sex and weight, and marking each individual with a separate number. Vaginal smears were taken from adult females. These censuses made it possible to mark the whole trappable part of the population in November 1965 and April 1966. The newly-registered individuals (not marked) could be considered as having been born after the last census and thus it was possible to define the period in which they had been born. This permitted of distinguishing 5 cohorts: K_0 — overwintered animals of unknown age, K_1 — early spring cohort with mean date of birth May 5th (from April 1st to May 26th), K_2 — early summer cohort with mean date of birth June 19th (from May 27th to July 10th), K_3 — summer cohort, mean date of birth August 2nd (from July 11th to August 28th), K_4 — autumn cohort, mean date of birth Sept. 10th (from August 29th to October 1st 1966). An individual growth curve (B u j a l s k a & G l i - w i c z, 1968) was drawn for each of these cohorts, and also survivorship curve (G l i w i c z, 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).

The survivorship curve for trappable part of the population was drawn on the basis of empirical data-numbers of the given cohort at the time of the census (see Fig. 1 presenting the survivorship curve of cohort K_1). We assume that this part of the survivorship curve gives a very accurate representation of the real situation (G l i w i c z *et al.*, 1968). The survivorship curve for untrapped individuals (up to approx. 43 days) was based on: (1) calculated number of animals born established by means of the formula $v_r = (\overline{N}_p \cdot T \cdot L) : t_p$, where $\overline{N}_p$ — mean numbers of pregnant females in this period T, L — size of litter, t_p — duration of pregnancy (22 days); (2) empirically defined numbers of registered individuals during the first census from the number born during the reproduction period preceding this census (B u j a l s k a, A n d r z e j e w s k i & P e t r u s e w i c z, 1968); (3) calculation of the mean balanced date of birth (day which divided the number born into two equal halves), and (4) the assumption that from the mean date of birth, when there were v_r of them, disappearance up to the time of registration took the form of an exponential curve [1].

Individual growth curve was drawn for the trappable part of the population from empirical field data (weights of individuals of known mean age). The shape of the curve from the individual growth was accepted for the untrapped part of the population, for *C. glareolus* in captivity (D r o ż d ż, 1965), extrapolating (lowering) the weight in proportion to the mean weight on the day of capture and weight on the same day in captivity (B u j a l s k a & G l i w i c z, 1968).

3. PRINCIPLES FOR CALCULATING PRODUCTION (P)

Calculation of production was based on data obtained from the survivorship curve and individual growth curve (Fig. 1). Production was estimated separately for each cohort. Calculation was made for each section of time of the production of those animals which were eliminated, multiplying the number of eliminated animals ($\Delta N_T, = = N_o - N_T$) by weight increase to the middle of time T': (silent ass-

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[1] Individuals from cohort K_4 only up to the 21st day of life.

umption: an average individual survived to half the time T'; after this we add the production of those animals which survived: the product of the number at the end of the section (N_T) times weight increase for time T ($\Delta W = W_T - W_o$). As a result we obtain production for time T':

$$P_{T'} = \Delta N_{T'} \cdot \Delta W_{T'/2} + N_T \cdot \Delta W$$

Next, totalling the production of all K sections, we obtain realized body growth (P_g) for time T:

$$P_T = \sum_{i=1}^{i=K} (\Delta N_{T'} \cdot \Delta W_{T'/2} + N_T \cdot \Delta W)_i$$

In order to obtain complete production for the period from birth to the above sum it is necessary to add the biomass of newborn animals.
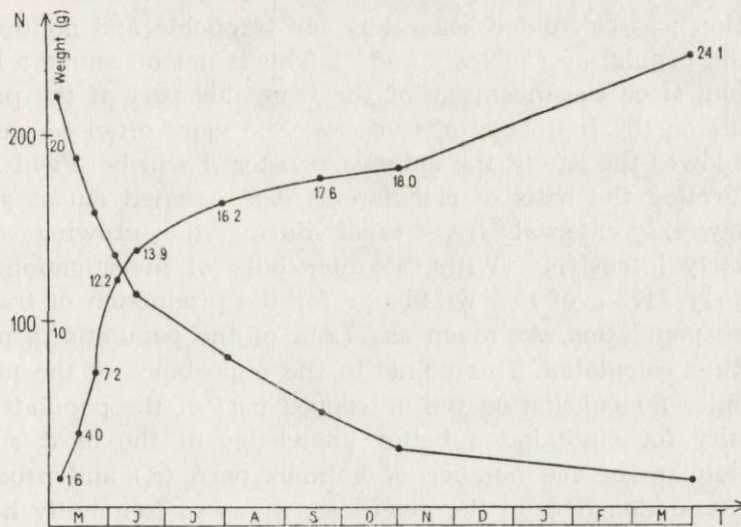

Fig. 1. Growth curve and survivorship curve of K_1 cohort of a population of *Clethrionomys glareolus* from birth up to 12 months of life.

R e m a r k 1. Weight increase to half period T' is not always equal to half the increase for the whole period T', since the individual growth curve is not a straight line. It is only in the later periods when weight increase was very slight that there were cases when $\Delta W_{T'2} = \frac{1}{2} \Delta W_T$.

R e m a r k 2. For the trappable part of the population the loss of the number of individuals in the cohort was taken as forming a straight line (since no information was available on what had happened in the meantime). For the untrapped part of the population calculation was made of how many individuals there would be on a given day T,

according to formula $N_T = N_r \cdot e^{-\mu T}$, μ being obtained having the number born, number registered from among those born and the time from mean day of birth to the census. Calculation was made for the trappable part of the population for the sections described by days of censuses as April 29th, June 16th, July 31st, September 18th, November 2nd or dates describing phenological periods: reproduction began April 1st, the census was April 29th, and therefore the curve of elimination of overwintered animals (K_0) was extrapolated up to April 1st; in the same way we defined the numbers of the cohorts on October 1st, which was accepted as the end of the reproduction period.

4. DISCUSSION OF RESULTS

Production was calculated separately for trappable and nontrappable parts of the population (Tables 1 and 2). This is not of course a biological division, since the mean age of the trappable part of the population depends on the frequency of censuses. The more often censuses are made, the lower the age of the animals registered will be. Field investigations forming the basis of calculations were carried out at approximately 6 weekly intervals (five times during the growing season), that is, fairly intensively. With the intensivity of investigations there were scarcely 2302 g of live wt/4 ha/yr for the production of trappable part of the population. As much as 77.6% of the population's production was thus calculated. This points to the importance of the methods and principles for calculating the untrapped part of the population and the necessity for obtaining a better knowledge of the most accurate possible estimate of the number of animals born (ν_r) and production due to reproduction (P_r). In the given case — as so frequently happens in ecology — we can foresee the direction of the error in our estimation of the number born (ν_r) but we do not yet know how to assess the extent of the error. We realize that the number born (ν_r) assessed by the formula:

$$\nu_r = \frac{\overline{N}p \cdot T \cdot L}{t_p} = \frac{\overline{N} \cdot s \cdot f \cdot T \cdot L}{t_p}$$

overestimates the number born since it does not completely take into account the mortality of pregnant females (partially taken into account by taking $\overline{N}_p$ — mean numbers of pregnant females as a basis). We do not, however, yet know how to estimate the extent of this observation.

The total value of yearly production $P = 11\,429$ g live wt/4 ha/yr. Its energy value was calculated accepting after G ó r e c k i (1967) the

mean annual energy equivalent of 1 g of biomass of adult *C. glareolus* as 1454 and 1030 cal/g for newborn animals. We obtained $P = 0.4$ kcal/m²/yr. This value can be compared with selected values of production taken from W i e g e r t & E v a n s (1967) which, in kcal//m²/yr are:

Old field mouse	0.12	Old field, South Caroline, USA
Deer mice	0.01	Old field, South Michigan, USA
Elephant population	0.34	Uganda
Orthoptera	4.00	Old field, South Caroline, USA
Grasshoppers	11.00	Coastal Salt Marsh, Georgia, USA.

It can only be said that the results we obtained are high, but are distributed in an order of already known values. We fully realize the hitherto limited possibilities of such comparison on account of the considerable difference in accuracy of empirical data and differences in methods of calculating production.

Production is realized by reproduction (P_r) and growth of individuals (P_g). These values, interesting from the point of view of ecology and evolution, and in particular their proportions, have not often formed the object of investigations. From the literature available (cf. P e t r u-s e w i c z & W a l k o w a, 1968) we know that these values were defined for an individual of *Oniscus asellus* (P h i l i p s o n, 1967) and for *Tribolium castaneum* (K l e k o w s k i, P r u s & Ż y r o m s k a--R u d z k a, 1967) and for a population of white laboratory mice (W a l-k o w a, 1967; P e t r u s e w i c z & W a l k o w a, 1968).

With mammals a difficulty arises as to what to consider as production due to reproduction: whether the weight at the time of birth, or, as P e t r u s e w i c z (1967) and P e t r u s e w i c z & W a l k o w a (1968) suggest, the whole production from birth to the end of nursing. It seems to us that this latter value should be treated in the case of mammals as production due to reproduction (P_r) since this is production realized at the mother's expense. A further question then arises: to what day should the production of suckling animals be treated as production due to reproduction (P_r): to the end of the nursing period, until the beginning of independent feeding, or for some intermediate date expressing how much has been produced at the mother's expense. Our material did not make it possible to define either the start of independent feeding or the end of nursing. We therefore accepted the age of 21 days given as the end of nursing by K o w a l s k i (1964) and confirmed by our observations (the youngest animals caught were, judged by weight and growth curve, about 21 days old). Production up to the 21st day of life was therefore considered as production due to reproduction (P_r).

Table 1.

Estimation of production of nontrappable part of population
(for each cohort the top line in number, weight and production of newborn).

Cohort	T'	$\Delta NT'$	$W_{T'/2}$	$N_{T'} \times W_{T'/2}$	N_T	$\Delta W_{T'}$	$N_T \times \Delta W_{T'}$	$P(g)$	
K_1 (1 April — 26 May)	0				220.0	1.6	352	352	
	10	33.0	0.8	26	187.0	2.4	449	475	$Pr = 1382$
	21	28.8	1.7	49	158.2	3.2	506	555	
	31	23.0	3.3	76	135.2	5.0	676	752	to Pg 959
	42	21.2	0.6	13	114.0	1.7	194	207	
K_2 (27 May — 10 July)	0				370.0	1.6	592	592	
	10	49.1	0.7	34	319.9	2.2	704	738	$Pr = 2257$
	21	46.4	1.7	79	273.5	3.1	848	927	
	31	36.4	3.2	116	237.1	4.7	1 114	1 230	to Pg 1595
	42	34.1	0.6	20	203.0	1.7	345	365	
K_3 (11 July — 28 Aug.)	0				332.0	1.6	531	531	
	10	119.7	0.8	96	211.3	2.4	507	603	$Pr = 1688$
	21	81.6	1.7	139	129.7	3.2	415	554	
	34	56.8	3.8	216	72.9	5.3	386	602	to Pg 725
	47	31.9	0.9	29	41.0	2.3	94	123	
K_4 (29 Aug. — 1 Octob.)	0				126.0	1.6	202	202	
	10	55.7	0.5	28	71.3	1.9	135	163	$Pr = 521$
	21	33.5	1.5	50	37.8	2.8	106	156	

Table 2.

Estimation of production of trappable part of population.

Period of time (T)	Cohort	$N_{T'}$	$W_{T'/2}$	$N_{T'} \times W_E$	N_T	$W_{T'}$	$N_T \times W_{T'}$	P	P_T
1 April 66 — 16 June	K_0	28	0.75	21	38	1.5	57	78	78
16 June — 31 July	K_0	17	0.3	5	21	0.5	11	16	248
	K_1	34	1.4	48	80	2.3	184	232	
31 July — 18 Sept.	K_0	15	0.0	0	6	0.0	0	0	701
	K_1	29	0.8	23	51	1.4	71	94	
	K_2	39	2.1	82	164	3.2	525	607	
18 Sept. — 1 Oct.	K_0	2	0.0	0	4	0.0	0	0	109
	K_1	5	0.1	0.5	46	0.2	9	10	
	K_2	16	0.2	3	148	0.4	59	62	
	K_3	8	0.5	4	33	1.0	33	37	
Total for reproduction period 1st April — 1 October									$\Sigma = 1\,136$
1 Oct. — 2 Nov.	K_0	3	0.0	0	1	0.0	0	0	366
	K_1	14	0.1	1.5	32	0.2	6.5	8	
	K_2	37	0.5	19	111	0.8	89	103	
	K_3	17	1.2	20	16	1.8	29	49	
	K_4	32	4.9	157	6	7.4	44	201	
2 Nov. — 1 April 67	all cohorts	82	3.2	262	84	6.4	538	800	800
Total for winter period: 1 October — 1 April									$\Sigma = 1\,166$

Table 3 shows that for the population over half (51.2%) of yearly production (57% of production during the reproduction season) is formed by production due to reproduction (P_r). The high percentage (14.7% of annual production, and 16.3% during the reproduction season) for the biomass of newborn animals (P_b) is also worthy of emphasis.

The reproductive season and winter season were distinguished as follows: the beginning of the reproduction season was accepted after B u j a l s k a *et al.* (1968) as April 1st. We accepted 1st October after A s d e l l (1946) as the end of reproduction. This is confirmed by our data for 1966, since by October 19th all the females had closed vaginas (B u j a l s k a *et al.*, 1968). The late autumn cohort (K_4) had a mean date of birth as September 10th (B u j a l s k a *et al.*, 1968), that is, on October 1st (to be exact October 2nd) its individuals had already left the nest and become independent components of the population. We

Table 3.

Per cent of production.

Period of time	Cohort	Production in:			Per cent of P		
		g	Per cent of P		P_b	Pr	Pg
			Summer	All year			
Reproductive period	K_0	94	1	1	—	—	100
	K_1	2 677	26	23	13	52	48
	K_2	4 521	44	40	13	50	50
	K_3	2 450	24	21	22	69	31
	K_4	521	5	5	39	100	—
	Mean or Σ	10 263	100	90	16	57	43
Winter	All cohorts	1 166	—	10	—	—	100
All year	All cohorts	11 429	—	100	15	51	49

therefore accepted October 1st as the end of the reproduction season. If therefore we accept that the reproduction season lasted from April 1st to October 1st (183 days) and the winter reduction season from October 1st to April 1st of the next year (182 days) then the production of the reproduction season ($P = P_r + P_g$) is as much as 90% and winter production which took place at the expense of growth only ($P = P_g$) is only 10%.

During the reproduction period production, which is high as it forms 10 263 g live weight, as much as 7759 g (77%) form elimination (failure to survive to the winter), and only 2504 g live wt (23%) form increase

in population biomass, ΔB (Fig. 2). During the winter period elimination is higher than the small amount of production (2977 *versus* 1166), that is, elimination, forming 256% of production, not only absorbs the whole production but part of the initial biomass as well. Increase in individual weight does not cover elimination and we have an negative biomass change ($\Delta B = -1811$) (Fig. 2).
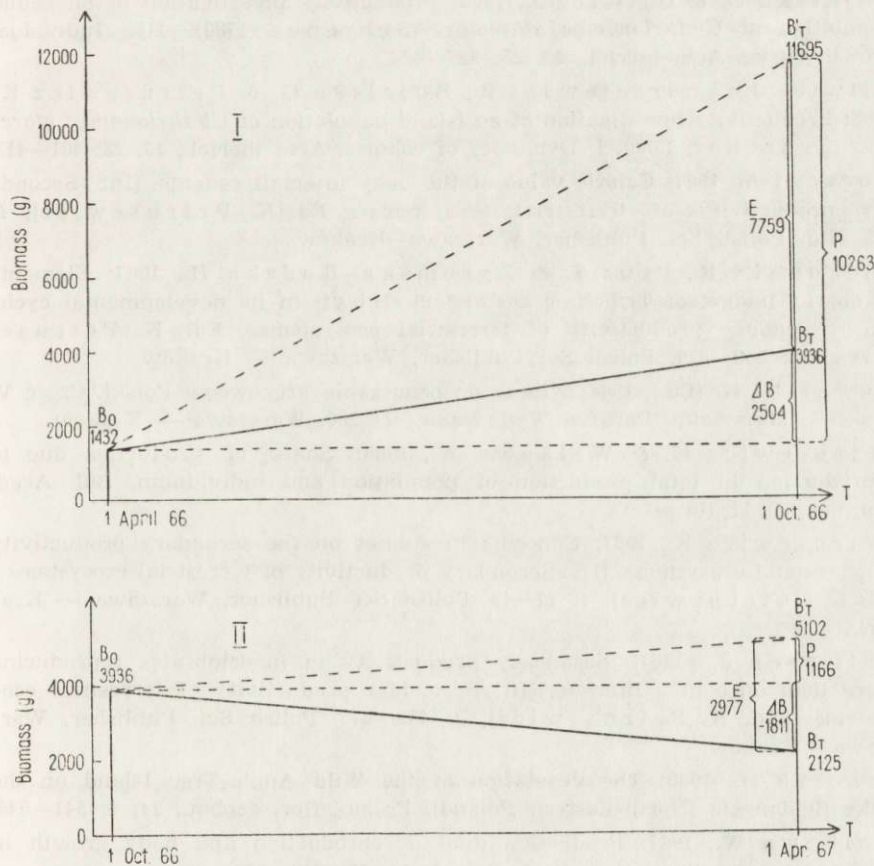

Fig. 2. Comparison of production (E — elimination and B — changes in biomass) for a population of *Clethrionomys glareolus* during the reproductive period (I) and during period of winter reduction (II).

As far as productivity of the cohorts is concerned K_2 takes the first place during the reproductive season (44% of the production of the reproduction season) and most certainly must also (judging by numbers) have played the greatest part in production during the winter period. Next in order was the early spring cohort K_1 and early autumn K_3.

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BADANIA NAD PRODUKTYWNOŚCIĄ WYSPOWEJ POPULACJI
CLETHRIONOMYS GLAREOLUS (SCHREBER, 1780).
IV. PRODUKCJA

Streszczenie

Przeprowadzono siedmiokrotną kontrolę stanu liczebności (i biomasy) populacji *C. glareolus* na wyspie na jez. Bełdany. Analizy zmian liczebności i ciężaru (Ryc. 1) dokonano dla 5 grup wiekowych — kohort $K_0 - K_4$ (G l i w i c z *et al.*, 1968).

Produkcję osobników od momentu urodzenia do pierwszego złowienia została oceniona w oparciu o znajomość liczby urodzonych (B u j a l s k a *et al.*, 1968) zakładając wykładniczy charakter krzywej przeżycia do momentu pierwszego złowienia (Tabela 1).

Produkcję osobników łowionych oparto o dane empiryczne (Tabela 2). Przyrost ciężaru osobników obliczono w oparciu o krzywe wzrostu zawarte w pracy B u j a l s k i e j i G l i w i c z (1968).

Produkcja całej populacji w okresie roku jest sumą produkcji kohort w kolejnych odcinkach czasu obliczoną wg wzoru:

$$P_T = \sum_{i=1}^{i=K} (\Delta N_{T'} \cdot \Delta W_{T'/2} + N_T \cdot \Delta W).$$

Wartość produkcji dla całego roku wynosiła 11 429 g/live wt/4 ha/yr. Produkcja w sezonie rozrodczym (1.IV.—1.X.) wynosiła 10 263 g i w okresie zimy (1.X.—1.IV.) 1166 g. Stosunek P_r — produkcji realizowanej kosztem matki (do 21 dnia życia) do P_g — zrealizowanej w okresie samodzielnego życia osobnika wynosił odpowiednio 51% i 49% (Ryc. 2, Tabela 3).