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). II. Natality*)

[With 2 Figs. & 3 Tables]

In a free-living isolated population of *Clethrionomys glareolus*, in relation to which a very accurate knowledge was obtained of the numbers of the whole population, pregnant females (N_p) and thus also $f = N_p : N_{♀}$, and the reproduction period (T), while the size of the litter (L) and length of pregnancy (t_p) were taken from literature, the number of young born were defined by formula:

$$\nu = \frac{\ln\left(\frac{L}{2}+1\right) \cdot f \cdot \bar{N} \cdot T}{t_p}$$

and the formula proposed by the authors:

$$\nu_r = \frac{L \cdot \bar{N}_p \cdot T}{t_p}$$

The result which was obtained by the first formula was about twice lower than that obtained by the second. In two cases the first formula gives unreliable results. The number born calculated from two censuses per year (»Standard-Minimum« method) gives results 3% lower than those based on full information.

1. INTRODUCTION

The number of individuals born during a given period often forms an essential parameter in studies on the biological productivity of rodents. It is generally impossible to obtain this figure empirically. It is therefore necessary to resort to calculations, for which the starting data is formed by the size of the litter, duration of pregnancy and standing crop of pregnant females (or numbers of females and percentage of pregnant females). With different principles of the means for arriving at these calculations it is necessary to make several premises. It would

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therefore appear useful to compare different methods of estimating the number of animals born for the area in respect of which reliable empirical data are available.

2. METHOD

The investigations were concerned with an isolated population of the bank vole living on the Crabapple Island situated in Lake Bełdany (Mazurian lake district). The botanical description of this natural habitat of the vole is to be found in the study by Traczyk (1965). The study methods have been described in detail in the paper by Gliwicz *et al.* (1968).

From April to November five consecutive two-week censuses were made at monthly intervals (Fig. 1, Table 1), thus obtaining empirical information on the level of numbers of animals including numbers of pregnant females over the whole reproductive season. This period, under the conditions prevailing on the island, is sufficiently long to permit of counting all the individuals currently living in this area (Andrzejewski, Petrusewicz & Waszkiewicz-Gliwicz, 1967).

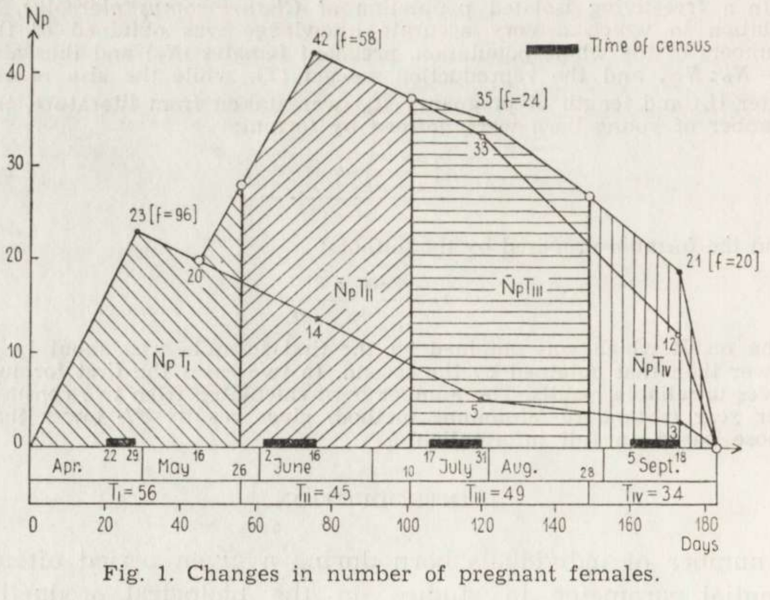

Fig. 1. Changes in number of pregnant females.

In order to simplify calculations parameters relating to level of natality obtained from successive study periods were referred to one day — the final one — of each of these periods. Pregnant females were distinguished on the basis of a microscopic analysis of a series of vaginal smears (stained with methylene blue) obtained from each adult female each time it was captured.

If, when the female was caught, the vaginal plug or bloodstained discharge from the placents was found, or birth took place in the trap, it was possible to define pregnancy unequivocally even on the basis of one observation. Such cases were, however, fairly rare and thus diagnosis of pregnancy was of necessity based on the changes taking place in the vagina, established by means of taking vaginal smears at each consecutive capture. The main criterion was the presence of nucleoid or corneous cells pointing to the occurrence of the oestral cycle (*i.e.* absence of pregnancy Bujalska & Ryszkowski, 1967). As there is a possibility of mistaking the microscopic picture of pregnancy (particularly its early stage) for the picture of the dioestrus phase, analysis was made only of these cases for which the oestral cycle was not found to occur for at least 8 days (that is, a period equal to the average length of the oestral cycle — Larina & Golikova. 1960).

Table 1.
Dynamic of number and number born, determined oby Golley's (1961) formula and by the formula proposed.

Period of time	L	K	$\overline{N}$	$\overline{N}_{♀}$	$T \cdot N_p$	$v_r = \frac{\ln\left(\frac{L}{2}+1\right) f \overline{N} \cdot T}{t_p}$	$v_r = \frac{\overline{N}_p \cdot T \cdot L}{t_p}$
T_I = 56 days 1 April — 26 May	5.15	K_0	56	26	890	112	208
		K_1	27	13	50	6	12
T_{II} = 45 days 27 May — 10 July	4.83	K_0	37	15	610	82	134
		K_1	94	47	1 073	120	236
		K_2	54	28	0	0	0
T_{III} = 49 days 11 July — 28 Aug.	4.49	K_0	20	7	269	41	55
		K_1	78	40	1 218	129	249
		K_2	178	91	135	14	28
		K_3	12	5	0	0	0
T_{IV} = 34 days 19 Aug. — 1 Oct.	4.43	K_0	8	3	90	11	18
		K_1	52	25	324	37	65
		K_2	166	80	216	24	43
		K_3	35	15	0	0	0
		K_4	<1	<1	0	0	0
T_{I-IV} = 184 days 1 April — 1 Oct.	4.9	K_0	121	51	1 859	246	415
		K_1	251	125	2 665	292	562
		K_2	398	199	341	38	71
		K_3	47	20	0	0	0
		K_4	<1	<1	0	0	0
Total			818	396	4 865	576	1 048

In the case of the above series an additional pointer was formed by the results of palpating embryos through the abdominal wall and the rate of increase in body weight. As females were repeatedly caught it would appear that the number of pregnant females was defined with a considerable degree of accuracy.

Six values were obtained for the standing crop of pregnant females (two for the beginning and end of the reproduction period, when this value is 0, and four from consecutive investigation periods).

3. BEST ESTIMATION OF NUMBER OF ANIMALS BORN (ν_r)

3.1. Principles For Calculating ν_r

The number of individuals born in a population can be defined by means of different formulae. In the present study two formulae have been used as a basis: one of them was proposed for calculation of small rodent natality by Golley (1961), the second is the modification, proposed by the authors, of Edmondson's (1960) and Winberg's, Pečen's & Šuškina's (1965) formula for defining the natality of plankton.

The following parameters were identified:

N — population numbers at a given moment,
$N♀$ — numbers of females,
N_p — numbers of pregnant females,
f — pregnancy ratio ($f = N_p : N♀$)
s — sex ratio ($s = N♀ : N$)
t_p — duration of pregnancy
L — size of litter
T — observation time (time during which young were born)
ν_r — number of individuals born in T time

The mean values were indicated by a dash above the symbol (*e. g.* $\overline{N}$ = mean numbers).

The formula proposed by Golley (1961) accepts the sex ratio as 1:1 and takes the following form:

$$\nu_r = \frac{\ln\left(\frac{L}{2}+1\right)\cdot f \cdot \overline{N} \cdot T}{t_p}$$

The modification of Edmondson's and Winberg's formula is based on the following reasoning: if L — size of litter, then $\frac{L}{t_p}$ — mean number born during one day by a pregnant female. If on an average there were $\overline{N}_p$ pregnant females in the population, then the mean number of individuals born during one day by those females will be $\frac{L\cdot\overline{N}_p}{t_p}$; hence the number born in T days will be:

$$\nu_r = \frac{L\cdot\overline{N}_p\cdot T}{t_p}$$

If it is difficult to obtain empirical data on the numbers of pregnant females ($\overline{N}_p$) but the pregnancy ratio (f) and sex ratio (s) are known, then our formula will have the following form:

$$\nu_r = \frac{L\cdot\overline{N}\cdot T\cdot f\cdot s}{t_p} \approx \frac{L\cdot\overline{N}\cdot T\cdot f}{2t_p}$$

As our data directly gave the numbers of pregnant females (N_p) the first version of our formula was used.

3.2. Calculation of Essential Parameters

T — time in which young were born. The whole reproductive season was divided into sections of time so that the group of young born in the various sections could leave the nest (and in consequence so that these young animals could be caught in traps) before the end of the nearest census (*i. e.* not later than the last day in the given census). Division into sections was thus made subtracting from the last day of the census 21 days (21 days is the mean time of termination of nursing, and in consequence of leaving the nest, cf. Kowalski, 1965). The latest day of birth of those young animals which could be caught in the nearest census was defined in this way: young born one day later could not be caught until the next census — this day is therefore the earliest day of birth of the next group of young.

Four periods of reproduction: T_{I}, T_{II}, T_{III} and T_{IV}, in which young were born were distinguished in this way (Fig. 1). This made it possible to distinquish and analyse the following »cohorts«:

K_0 — overwintered animals,

K_1 — individuals registered for the first time on June 16th. These are young produced by the overwintered animals; the period during which they are born is from 1.IV — 26.V (T_{I} — 56 days),

K_2 — individuals registered for the first time on July 31st, born during the period from May 27th to July 10th (T_{II} — 45 days),

K_3 — individuals registered for the first time on Sept. 18th, born during the period from July 11th to August 28th (T_{III} — 49 days),

K_4 — individuals registered for the first time on Nov. 2nd, born during the period from August 29th to October 1st (T_{IV} — 34 days).

All the calculations were made separately for the different cohorts in the reproduction periods T_{I} to T_{IV} distinguished [1]).

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[1]) It is worth while drawing attention to the different participation of different cohorts in reproduction. K_1 form the productive mass of the population under the conditions of this study (Fig. 1). They participate in the reproduction very early on, at age of about 26 days (attention was drawn to the earlier maturescence of individuals born in the spring by Schwartz *et al.*, 1964). We can conclude this from the following facts: the first birth in the spring among K_0 was observed on April 23rd; it is not likely that K_0 could have young before April 23rd. Evidence of this is formed by the absence of nursing females, and also the high percentage of females in advanced pregnancy during the April census (23 pregnant out of the 24 present). An actual birth by a female of the K_1 cohort was, however, observed as early as June 7th, that is, there was a period of 45 days from the birth of a young female to her giving birth to young; if pregnancy lasts 22 days then the females must have become pregnant at the age of 23 days. It is however known (Drożdż 1963) that with *Clethrionomys* duration of pregnancy may fluctuate within limits of 14—30 days. Under the conditions examined K_1 females might therefore have become pregnant at the age of 23—31 days. K_2 participate in reproduction to a very small extent: during period T_{III} only 2% of the females among them are pregnant, and in T_{IV} — 12%. K_3 and K_4 do not participate in reproduction during the current reproductive season.

Establishment of the start of reproduction in the spring for overwintered females was based on information of the earliest birth (April 23rd), then calculation of the earliest day of start of pregnancy (assuming t_p — 22 days).

October 1st was taken as the end of reproduction (Asdell, 1946).

N_p — number of pregnant females. During the first census T_I — 24 females, T_{II} — 72, T_{III} — 153 and T_{IV} — 120 females were investigated, with a sum total of over 4.000 captures. In this way, as mentioned above, the standing crop of pregnant females was defined empirically for five moments (Fig. 1): April 1st ($N_p = 0$), April 29th, June 16th, July 31st and Sept. 18th (Fig. 1). The sixth standing crop $N_p = 0$ was accepted from literature as October 1st. In addition, on the basis of information of the earliest birth by a female of cohort K_1 (June 7th), the earliest date of start of pregnancy for K_1 was defined as May 16th. The start of pregnancy for females of cohort K_2 was defined analogically as July 11th.

Thus altogether the standing crop for 8 moments was obtained.

Assuming that variations in the number of pregnant females take place straightforwardly the values of the standing crop in successive days permitted of charting the dynamics of numbers of pregnant females. The straight line connecting the point in which N_p of the given cohort is 0 with the point in which N_p was defined on the basis of empirical observations gives an approximate illustration of the rate at which the females examined become pregnant.

As the value $\bar{N}_p.T$ (number of individual — days of pregnant females) enters into the formula defining ν_r (number of animals born), this value was calculated by integrating numerically the curve formed by connecting the successive values of the standing crop of pregnant females (*i.e.* calculation was made of the area defined by the curve of dynamic of numbers of pregnant females during the given period T_I, T_{II} *etc.* (Table 1).

N and $N_♀$ — numbers of the whole population and numbers of females. The mean numbers, which had been calculated (integrating numerically the corresponding fields and then dividing the values obtained by the number of days composing the periods distinguished) were defined for the whole population and separately for $N_♀$. By dividing the mean numbers of pregnant females in the reproduction period distinguished by the mean numbers of females, the mean pregnancy ratio (f) was obtained for the reproduction periods distinguished ratio (T_I — T_{IV}).

L — size of litter. The data possessed did not permit of empirically defining the size of the litter. This value was therefore accepted after Z e j d a (1966). As this author gives values L for calendar months which did not coincide with our periods $T_{I} - T_{IV}$), the weighed mean was calculated for successive periods (Table 1).

The mean duration of pregnancy (t_p) was accepted for the whole reproductive season after B u j a l s k a & R y s z k o w s k i (1966) as 22 days.

3.3. Number of Animals Born (ν_r)

The parameters calculated above made it possible to define the number of animals born in each of the periods $T_{I} - T_{IV}$ distinguished, and their sum total for the whole reproduction season, both by the method proposed by the authors and that used by G o l l e y (1961). The results point to the considerable difference in findings obtained by means of the above mentioned formulae. ν_r calculated by means of our formula is almost twice higher than that calculated by G o l l e y's formula (Table 1).

Table 2.

Comparison of number of voles born (ν_r), calculated by proposed and G o l l e y's (1961) formulas and number of voles trapped (N), during the consecutive periods of time.

Period of time	$\nu_r = \frac{\overline{N}_p \cdot T \cdot L}{t_p}$	N trapped	$\nu_r = \frac{\ln\left(\frac{L}{2}+1\right) \cdot f \cdot \overline{N} \cdot T}{t_p}$
T_{I}	220	114	118
T_{II}	370	203	202
T_{III}	332	41	184
T_{IV}	126	6	72
T_{I-IV}	1 048	364	576

Both formulae should produce results overhigh in relation to the real number born, as the multiplier is $\overline{N}_p$ or $\overline{N} \cdot f$. This assumes that each pregnant female gives birth to a definite part of the litter daily, whereas it may happen that the pregnant female is killed before producing the young.

The fact itself that the formula now proposed gives results twice as high as those obtained by G o l l e y's formula does not indicate which of them is better (assesses the number born more correctly). Comparison of the number born and the number among them registered during the approximate census (Table 2) indicates, however, that the results obtained by Golley's formula are unreliable in two cases. It is not possible that a larger number would be caught than were born in the reproduction period preceding the census — cf. Table 2 estimate for period T_{II}, or that the number born only slightly exceeds the number caught, as is the case in period T_I. We must point out here that the factual number present may be greater than the number registered, but most certainly cannot be smaller.

4. NUMBER BORN (ν_r) CALCULATED ON THE BASIS OF TWO MEASUREMENT OF THE STANDING CROP

It is often impossible to carry out several censuses during the reproductive season. An expression of this is formed by the proposed method of »Standard-Minimum« (Grodziński, Pucek & Ryszkowski, 1966) in its modified form (Gliwicz *et al.*, 1968). This method involves

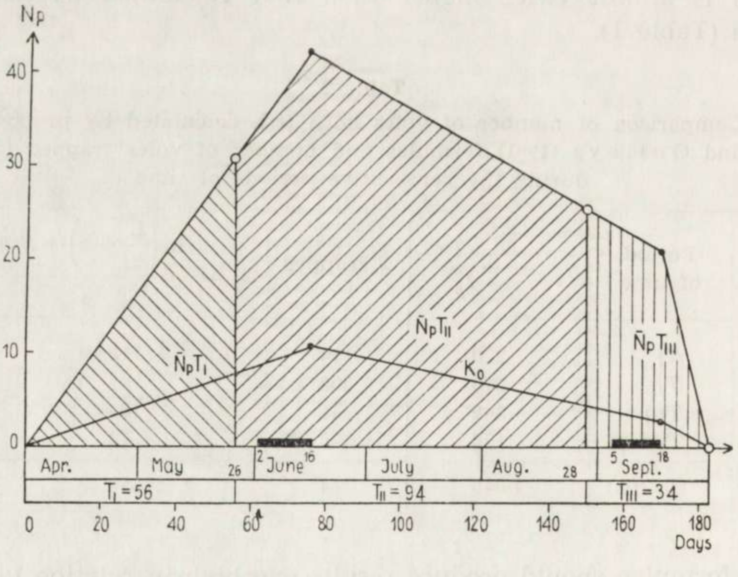

Fig. 2. Changes in number of pregnant females calculated from Standard-Minimum census.

3 measurements: at the beginning of June, September and June of the next year (or previous year). An attempt was made at defining the number born on the island when possessing data for June (16th) and September (18th) only and at comparing results with the more accurate ones discussed in section 2.2.

April 1st was accepted, on the strength of observations, as the start of reproduction (in the event of lack of similar data it is possible to take data in literature as a basis), and October 1st (A s d e l l, 1946) as the end of reproduction.

Having the four values of the standing crop: April 1st — $N_p = 0$; June 16th — $N_p = 42$; Sept. 18th — $N_p = 21$; and Oct. 1st — $N_p = 0$ the simplified dynamics of numbers of pregnant females can be mapped on the basis of the empirically determined standing crop and data accepted from literature (beginning and end of reproduction) (Fig. 2).

Three periods of reproduction were distinguished over the whole reproductive season: T'_{I} — from the day on which reproduction starts until May 26th. This is a period in which the young born could leave the nest by June 16th at the latest, i.e. they were registered in mid--June. At this period they can easily be distinguished from overwintered animals. T'_{II} — from May 27th to August 29th (young born during this period may not be caught until the September census) and T'_{III} — from August 29th to October 1st — the young born during this period leave the nest after the end of observations, and cannot therefore be captured.

Table 3.

Number of voles born (ν_r) calculated from twc »Standard - Minimum« censuses.

Period of time (T) Date	Days	l	TN_p	ν_r
T'_{I} = 1 April — 26 May	96	5.15	888	208
T'_{II} = 27 May — 28 Aug.	94	4.66	3 249	688
T'_{III} = 29 Aug. — 1 Oct.	34	4.43	617	124
Total	184	4.9	4 754	1 020

The number of individual-days of pregnant females was calculated for successive periods in the way described in section 2.2.

The mean size of the litter for different periods was calculated on the basis of Z e j d a's data (1966). They are in order of periods T'_{I} — T'_{III}: 5.15; 4.66; 4.43.

The number born was calculated for each period, jointly for overwintered animals and those born during the current reproductive season (Table 3).

As can be seen the results obtained on the basis of data supplied by the »Standard Minimum« method give results 3% lower than the more accurate ones. This lowering of results is mainly due to under-estimation of the reproduction mass $(\overline{N}_p \cdot T)$ during the spring period (end of

April — beginning of May). A census not necessarily of the whole head, but only of pregnancy ratio (f) would enable the result of the »Standard-Minimum« method to get very near the best estimation of the number of animals born (ν_r) using the more exact method.

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BADANIA NAD PRODUKTYWNOŚCIĄ WYSPOWEJ POPULACJI *CLETHRIONOMYS GLAREOLUS* (SCHREBER, 1780). II. ROZRODCZOŚĆ

Streszczenie

W ramach kompleksowych badań nad wolnożyjącą izolowaną populacją *Clethrionomys glareolus* określono rozrodczość tej populacji w jednym sezonie rozrodczym. Oparto się głównie na danych empirycznych, jak N — liczebność populacji, $N_{♀}$ — liczebność samic, N_p — liczba samic ciężarnych (samice ciężarne wyróżniono analizując rozmazy pochwowe) oraz na informacjach z literatury, dotyczących t_p — czas trwania ciąży, L — liczby młodych w miocie.

Liczbę urodzonych w wyróżnionych okresach rozrodu T_{I}—T_{IV} oszacowano stosując zmodyfikowany wzór Edmondsona (1960): $\nu_r = \frac{L \cdot \bar{N}_p \cdot T}{t_p}$. Uzyskane wyniki porównano z wynikami otrzymanymi przy użyciu wzoru Golley'a (1961) — Tabela 1. Liczba urodzonych uzyskana przy użyciu wzoru Golley'a jest znacznie zaniżona w stosunku do stanu faktycznego o czym świadczy porównanie liczby urodzonych z liczbą tych, które przeżyły i zostały złowione (Tabela 2). Wyróżnione kohorty K_0 — K_4 różnią się udziałem w rozrodzie: główną bazę rozrodczą populacji stanowią K_1 i K_0. K_3 i K_4 nie włączają się do rozrodu w bieżącym sezonie (Tabela 1).

Liczbę urodzonych oceniono w oparciu o metodę »Standard-minimum« (Fig. 3). Jest o 3% niższa od liczby urodzonych oszacowanej przy kilku próbach (Tabela 3).