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

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Reproduction, Mortality and Longevity of the Bank Vole under Laboratory Conditions

[With 7 Figs and 11 Tables]

Under the laboratory conditions a total of 782 litters (2862 young) were obtained from 264 female bank voles, *Clethrionomys glareolus* (Schreber, 1780). The bank voles breed throughout the whole year but the maximum number of litters and young per female were obtained in April and May. Females mature sexually at the age of 1—1.5 months; males at the age of about 2 months. Ability to breed in both sexes is maintaned up to the age of over two years. The average number of litters per female is 3.09. The number of young in a litter is 1—10 (average = 3.6). In 83.7% of the litters the number of young was 2—5. Females aged 6—14 months have the largest litters and from the 15th month of life the average litter size gradually decreases. Intervals between successive litters was 16—35 days in 45.6% of the litters. Mortality among young from birth to the age of 15th days was 15%. The losses of the complete litters were observed in 9.8% of the cases. On an average a female produced — 11.1 young, and reared up to the 21st day of life — 9.4 young. Sex ratio is 1:1. Bank voles live for over 4 years in captivity. Individuals from breeding pairs live longest, and those in communal cages the shortest time. Males always live longer than females.

I. INTRODUCTION

Breeding of the bank vole — *Clethrionomys glareolus* (S c h r e b e r, 1780) under laboratory conditions is connected with the constantly increasing requirements for laboratory animals. Newly-introduced species may possess properties which the laboratory animals used up to the present do not exhibit and may thus form more valuable material than that hitherto used in research work.

The bank vole has been used for a long time now for assessing acquired resistance induced by the BCG vaccine. It has been found to be »extremely sensitive to infection with virulent bovine tubercle bacilli« whereas white mice are »very resistant to both human and bovine tubercle bacilli« (J e s p e r s e n & B e n t z o n, 1963). This therefore enables more accurate experiments to be carried out on bank voles.

The breeding colony of these animals was started in 1956 in the Mammals Research Institute, Polish Academy of Sciences at Białowieża, for the purpose of obtaining material for morphological and physiological studies and to adapt the species to life under laboratory conditions. The present study forms a summing-up of the results of the first stage of this work (1956—1966), based mainly on outbreeding.

II. MATERIAL AND MANAGEMENT

1. Material

The initial group of animals was obtained from the Białowieża National Park. One female from the Lublin voivodship area and several animals caught in 1960 and 1961 in the Tatra Mountains (Table 1), were included in the breeding stock. Animals introduced into the stock later on were combined with each other, but sometimes also with the offspring of females breeding from the start of the colony.

A total of 264 females were chosen for the studies, from which 2862 young were obtained in 782 litters.

2. Housing

The animals were kept in a basement (3 × 4 m) with a large window, heated by a radiator installed under the ceiling. The room was ventilated by a normal grating in the wall of the building and the window was kept open in winter for ½—1 hour, and in summer even for the whole of the twenty-four hours.

The cages were placed on metal racks, the shelves of which sloped slightly forwards, which ensured that any liquid in the cage ran out in the direction of the run. The space between the shelves is large enough to permit of removing the cages without difficulty. Light reached the running compartment of each row of cages (Fig. 1).

The cages, which measured 40 × 25 × 15 cm, are made of metal sheet and 0.5 cm diameter mesh wire netting. The netting covers the top and front of the cages.

A metal partition with two holes in the lower corners divides the cage into the nesting part (10 × 25 × 15 cm) and run. The nesting part is opened from the top, and the running compartment from the front (Fig. 2). Activity wheels were installed in the run of a large number of cages and the bank voles readily made use of them. The wooden cages at first used proved unsuitable for keeping bank voles in as the animals nibbled through them.

The nesting part of the cages is cleaned once weekly, and the run every 1—2 days. Peat is used as litter, and hay for bedding material. When the cages are inspected the quickly decaying remains of food were removed from the nests. The cages were inspected every 1—2 days.

3. Lighting, Temperature and Humidity

In addition to daylight, four 40 W fluorescent lamps provided additional ligth, prolonging the light phase of the day to about 18 hours. The lamps are arranged above the upper row of cages.

Table 1.

Initial material used for breeding at Białowieża.

First line for each locality gives the numbers of voles caught (1) and the second line — numbers of voles which gave birth (2).

Locality		Years										Total
		1956		1957		1958		1960		1961		
		♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	
Białowieża	(1)	1	2	17	24	1	3			8		56
	(2)	1	2	16	19		1			5		44
Werbkowice	(1)					1						1
	(2)					1						1
Tatras	(1)							3	7		5	15
	(2)							2	6		3	11

Variations in temperature and humidity were recorded on a weekly thermo-hygrograph. Temperature and humidity were not constant in the room, but changes depending on the time of the year and of the day. Periodical, short but considerable fluctuations were observed, especially in winter when the room was aired. The temperature usually fluctuated within limits of 15—18°C, but never fell below 10—11°C. Relative humidity varied from about 60 to over 80%, increasing when the animals were fed large amounts of fresh green plants to as much as 100%. In summer when the window was kept open all day the amplitude of temperature was similar to that out of doors.

Insufficient humidity in the room was remedied by placing a dish with water on the radiator or putting damped mats on the floor and sponges on the cages.

4. Diet

Food was provided *ad libitum* once daily, in the morning. It consisted of oat grains, red beet, green feed and acorns. The oats were soaked in water for 24 hours

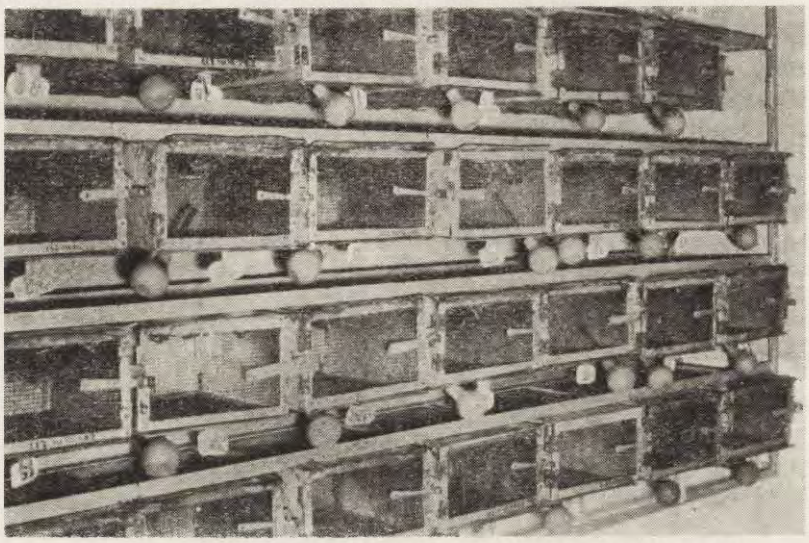

Fig. 1. View of breeding room.

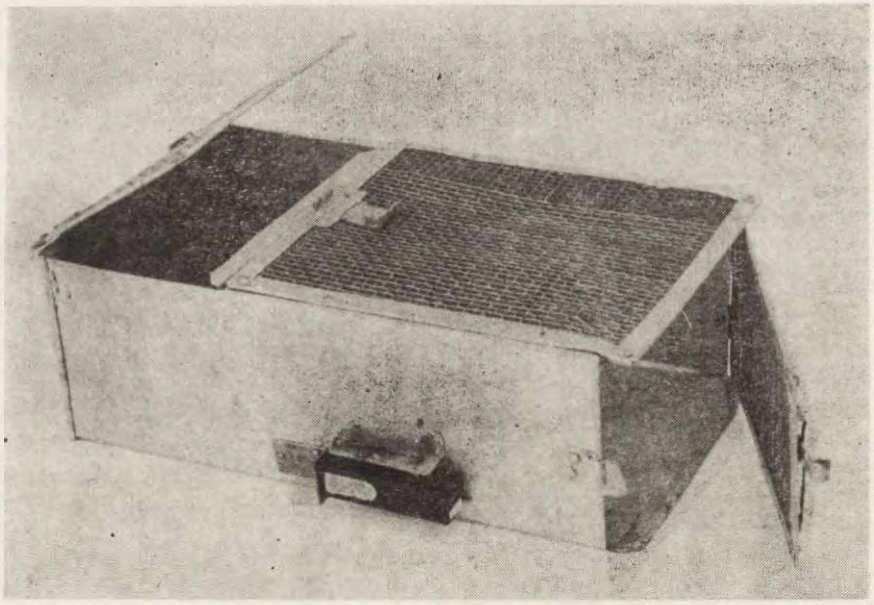

Fig. 2. Cage for keeping captive voles.

before feeding the animals. Fodder beet was sometimes given instead of red beet. The green feed consisted of meadow grass with some species of herbs during the summer and autumn. It was changed by wheat germinated or sprouted up to 7—8 cm and fed whole. Small branches of deciduous trees were added as a suplementary food in autumn and winter. From time to time the animals were given

carrot and in addition to acorns other seeds of trees and also berries. Very young animals left motherless were given rolled oats. Drinking water was always kept in the cage and changed daily, being supplied in rubber bulbs ending in a glass pipe with a smooth end.

5. Care of Animals

The bank voles were usually kept in monogamous mating pairs or in group of 6—8 animals of one sex. Healthy, mild and well-grown individuals were chosen for breeding. Any animals exhibiting repeated attemps at biting, escape when picked up or during other manipulations, jumping out of the cage as soon as it was opened were eliminated from further breeding. Animals exhibiting progressive loss of weight or any symptoms of disease, or failing to breed despite a change in partners, were also eliminated.

Efforts were made to select for further breeding relatively numerous and successfully fed offspring of females which were never observed to eat their young. Bank voles from different mothers, but approximately corresponding in respect of number of generations in the colony, counting from the initial female taken from field conditions, were combined in pairs. During the first few years of the breeding work litter mates were also combined, but as this was less effective than outbreeding this was not the usual procedure. If no offspring were obtained for a period of 3—4 months, and the animals were in good condition, the female or male in the pair was changed. This often gave good results. Some of the females exhibited low fecundity and produced too small a number of offspring to continue their reproduction. This brought about reduction in the initial stock.

The young animals were taken from their mothers on the 15th day of life at the earliest. The author's own observations show that when young are separated from their mothers a little later on they stand up to the separation better. S t e v e n (1957a) »has found it preferable to leave them with the mother until the 17th to 18th day«. The separated individuals were kept in group of one sex, as far as possible of similar age. The separated individuals were given their own number and card on which a record of its life history was kept. Remarks were made on females' card referring to offspring up to the time of separation and of the numbers given to the young animals.

The animals were marked by notches on the ears or by toe-clipping. The first method prove impractical, since when the voles were kept in communal cages for some time the mark might be lost during fighting.

The bank voles were combined in pairs after distinct signs of sexual maturity were observed (in females open vagina, in males — protuberance of the testes in the inguinal region). In the case of some of the females vaginal smears were taken in order to determine the oestrus cycle and duration of pregnancy.

III. BREEDING

1. Intensity of Reproduction during the Yearly Cycle

The number of litters and number of young born each month were divided by number of females reproducing in a given month. The number of litters obtained from an average female in different months of

the year varied from 1.0—1.14, and the number of young obtained within limits of 3.4—4.6.

The maximum average number of young per female is observed in January, and again in April and May, and the minimum in July and November. After a decrease in June — July the number of young again increases in August and is maintained until October on an almost unchanging level, to drop again in November. The number of litters per female varies similarly, maximum value being observed in August. In January (with maximum average number of young per female) the number of litters is lower then in April and May (Fig. 3).

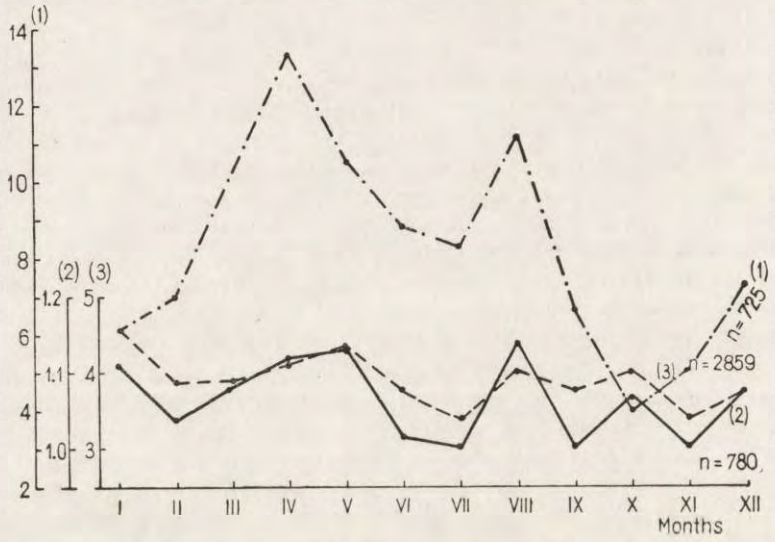

Fig. 3. Percentage of females breeding (1), average number of litters (2) and average number of young (3) per average female over the yearly cycle. Data for period 1957—1966.

Differences were found in intensity of reproduction between females taken from natural conditions and transferred to the laboratory (group I), and females derived from parents kept in captivity for several years (group II) (Fig. 4).

In females from natural conditions the highest numbers of litters and young born occur in March and June, with a subsequent considerable decrease in July. The number of litters decreases by 83% in July in relation to June, and the number of young in litters by 84%. In autumn the number of litters and young again increases gradually.

In captive females (group II) after a high level is attained in March — May, reproduction continues for the following two months with

a decrease in the number of litters of 36% and 49%, and in the number of young by 38% and 56%, in relation to May. The second peak of reproduction is observed in August.

Differences between the two groups can also be seen in the percentage distribution of the number of reproducing females. Females derived from captive parents do not exhibit the same abrupt fluctuations in the percentage of individuals taking part in reproduction during the period from March to September as the females brought to the laboratory from natural conditions (Fig. 4).

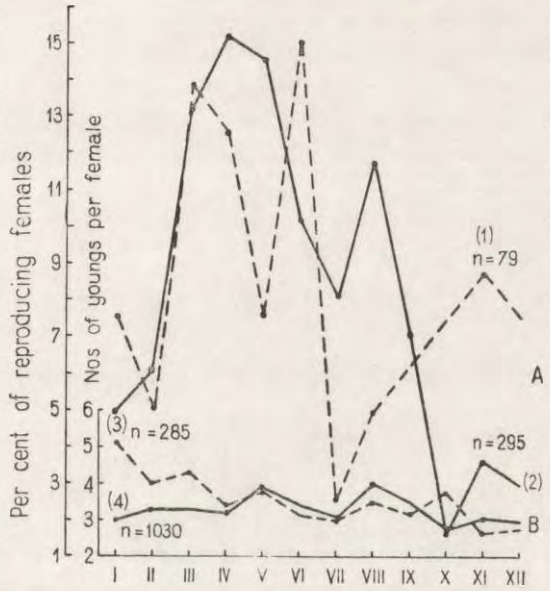

Fig. 4. Percentage of females participating in breeding (A) and number of young per average female (B), in females brought from natural conditions to the laboratory (1, 3 — respectively) and deriving from voles kept in captivity for several years (2, 4 — respectively).

Females from group I show a higher intensity of reproduction from January to April than females in group II. This is expressed by higher average number of young per female and during the period from January to March also by the higher number of litters. During this period the average number of young per litter is also greater in females from group I than from group II. This could be explained by much better conditions during these winter months in the laboratory as compared with those in the forest.

In the remaining months of the year the differences between the two groups of females are slight but the number of young per female is

higher in group II (Fig. 4). The reverse situation is observed only in October. Long-term observations show, however, that in October there is a decrease both in the number of litters and young, which may be connected with the effect of the fixed seasonal rhythm. The fact that the number of young per female may be lower during certain periods in group II than in group I would seem to indicate that the laboratory conditions are not as yet fully optimal. The noticeable change in the seasonal rhythm of reproduction with the tendency to reproduction all the year round is clearly observed as the number of generations produced in the laboratory increases (Fig. 4).

2. Sexual Maturity

The majority of the females become sexually mature at the age of 1—1.5 months. For instance, when a female mated with a male on the 60th day of its life the litter was born on the 84th day, in a female mated at the age of 67 days — on the 87th day *etc.* The earliest litter was obtained from a 42-day old female.

Table 2.

Duration and effectiveness of reproduction in bank voles over 20 months old.

Life span, months	Females		Males	
	20—24	Over 24	20—24	Over 24
Per cent of the reproducing individuals *)	12.0	2.6	20.0	6.1
Litters produced (%) **)	12.4	1.0	6.5	2.0

*) births, effective mating, **) in relation to all litters obtained.

Young males can mate successfully at the age of about 2 months. The first effective mating was observed at the age of 67 days.

Bank voles continued reproducing up to the age of over two years (Table 2). The three oldest females had offspring in the 30th, 30.5 and 33 months of their lives, the two latter successfully nursing their young. The last effective mating was observed in males aged 31, 31.5 and 33 months.

3. Number of Litters and Litter Size

Breeding of bank voles in the Białowieża laboratory was unfavourably affected by the fact that a large number of animals were used for various

experiments. Not all the sexually mature voles were combined in pairs, or were so combined at an advanced age. Taking young animals for investigations at different ages could also cause disturbances in reproduction of females. Seventy five per cent of the 352 females combined produced young. From this number 184 females were chosen, which were not used for experiments. They produced 570 litters.

During the whole reproduction period there were from 1—11 litters per female (average 3.09) (Table 3). A considerable percentage (46%)

Table 3.

Numbers of litters per female during breeding period in captivity (females taken for experiments were not included in calculations).

Number of litters		1	2	3	4	5	6	7	8	9	10	11	Total	Avg.
Females	*N*	46	39	41	20	14	10	7	2	3	1	1	184	3.09
	%	25.0	21.2	22.3	10.9	7.6	5.4	3.8	1.1	1.6	0.5	0.5	100	

consisted of females which produced only one or two litters. The cause of so high a percentage of small number of litters might have been that the animals were permitted to breed too late. Nearly 70% of the females were not combined until more than 100 days old.

The number of young in a litter varied from 1 to 10 (average 3.6 ± 1.46). 83.7% of these litters consisted of 2—5 young. Larger litters (7—10 young) formed only 3.3% of the whole number (Table 4).

Table 4.

Number of young in a litter (all young born, whether live or dead, were included).

Number of young in litter		1	2	3	4	5	6	7	8	9	10	Total	Avg.
Litters	*N*	48	126	183	229	117	53	17	7	1	1	782	3.6
	%	6.1	16.1	23.4	29.3	14.9	6.8	2.2	0.9	0.1	0.1	100	

In the average female gestation and lactation occupied 47.4% of the time it spent in the laboratory after combining with a male (one or several in turn). The length of interval between consecutive litters, which varied within limits of 20 to over 100 days, directly affected this percentage. In 7.5% of the females the duration of the reproducing period in relation to the time spent in the laboratory after combining was 80—100% (Table 5).

4. Gestation Period

In view of the fact that post-partum oestrus occurs and that mating can take place during this time (Steven, 1957a; Sviridenko, 1967), duration of successive pregnancy may be considered as approximately equal to the length of the interval between the births of successive litters (Steven, 1957b).

Table 5.

Average time taken to produce a given number of litters and numbers of young obtained, also duration of period during which females bred expressed in percentages of the time spent in captivity after being combined with a male (either one male or several successively).

Number of:		Period of reproduction, days	Intervals between consecutive litters, days	Numbers of young:			Breeding period of females in captivity (%)
Litters	Females			Born	Weaned		
					N	%**)	
11	1	341	31	44	33	75	57.1
10	1	320	32	37	17	46	*)
9		283—596	31.4—66.2	31—37	9—27		58.3—87.8
	3	447	49.7	33.3	17.7	53	69.3
8	2	215—502	26.9—62.7	28—46	15—42	50—91	59.5—100
7		172—717	24.6—102.4	16—32	14—19		57.8—98.9
	7	401.4	57.3	24.1	16.1	67	74.7
6		188—594	31.3—99.0	12—33	5—27		31.3—100
	14	382.5	63.7	21.2	14.8	70	67.5
5		132—438	26.4—87.6	11—29	0—21		36.0—97.1
	17	263.2	52.6	18.6	14.2	72	60.0
4		108—512	27.0—128.0	9—21	0—21		28.2—100
	26	229.3	57.3	14.5	9.4	60	61.1
3		56—449	18.6—149.7	5—21	0—14		12.5—100
	53	154.2	51.4	11.1	6.6	59	44.1
2		40—286	20.0—143.0	2—18	0—10		9.8—100
	49	96.9	48.4	7.0	4.7	58	32.6
1		26—910		1—7	0—6		4.1—100
	51	212.1	37	3.6	2.9	61	17.4
Total	224	96—910	18.6—149.7	1—46	0—42		4.1—100
Avg.		161.3	52.0	11.3	7.9	63	47.4

*) female transferred from natural conditions to laboratory, **) young taken from mother before weaning (at different ages) and used for experiments were also included.

Length of the interval between successive litters under the breeding conditions at Białowieża was observed in 212 litters which were born at intervals of 16—35 days, and 253 litters born at intervals longer than 35 days.

Duration of pregnancy calculated on the basis of an analysis of 212 litters was in 80.7% of the cases from 16—25 days (average 20.16

days) — Fig. 5. Length of the interval between successive litters was counted from the day of the birth of the previous litter to the day preceding the birth of the subsequent litter. According to Drożdż (1963) bank voles most often give birth to the subsequent litters between the 18th and 25th day of pregnancy. Average duration of pregnancy calculated in this way for the Białowieża material was correspondingly 20.67 days.

The results of vaginal smears (number of females = 14) showed that duration of pregnancy is 19—20 days. 29.2% of the total number of 212 litters were born within this interval.

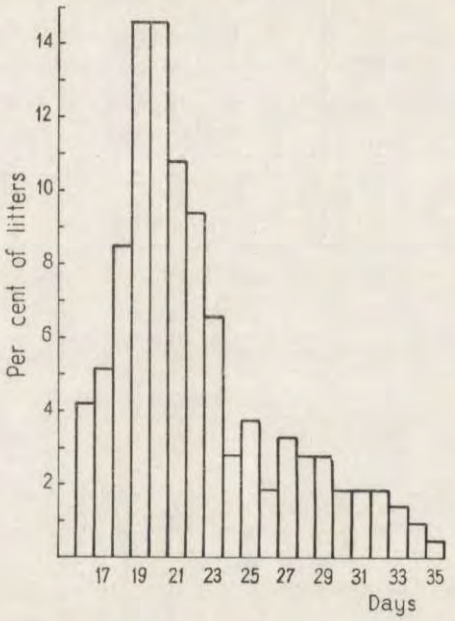

Fig. 5. Length of interval between successive litters ($n = 212$).

The nine cases found of 16-day pregnancy (4.2% of litters) and 11 cases of 17-day pregnancy (5.2% of litters) are remarkable as being some of the shortest of those so far observed. The slightly greater number of litters in the 25-day interval could be explained by the fact observed by Steven (1957b), who found that when mating was ineffective during the post-partum oestrus, the next oestrus may appear 4—5 days later.

The data in Table 6 show that about 63% of the litters in the Białowieża laboratory were born at intervals not exceeding 2 months. Two hundred twelve litters (45.6%) originated from matings taking place immediately after the birth of young or after lactation, that is, with length of interval between consecutive litters of 16—35 days. The interval of about 2 months between consecutive births might have been

due to the females not mating until after prolonged lactation, to resorbed embryos or to the whole of the newborn litter being eaten, which is less likely. Intervals of 4—9 months in about 54% of the cases usually occurred during the autumn and winter months.

The series of vaginal smears made showed that a four-day oestrus cycle occurs in bank voles. It may possibly be repeated until effective

Table 6.

Number (*N*) and frequency (%) of occurrence of intervals between successive litters produced by voles in captivity.

Duration of interval	*N*	%
16—35 days	212	45.6
up to 2 months	82	17.6
up to 3 „	65	13.8
4—5 „	72	15.3
6—9 „	33	7.0
longer	1	0.2
Total	465	100

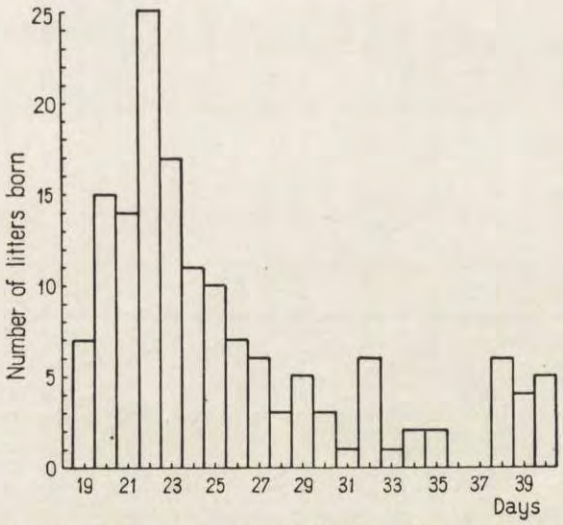

Fig. 6. Length of interval between mating female and male and birth of first litter.

mating takes place. A similar fact can be observed when we consider the number of days elapsing between combining and the birth of the female's first litter. This is shown by data from Fig. 6 referring to the number of birth on the 22nd, 29th, 32nd and 38th day after combining females and males.

No relation was found between the number of young being nursed and the length of simultaneous pregnancy. The correlation coefficient between them was not statistically significant ($r = 0.17$). It would seem that further investigation of this problem is required on the basis of vaginal smears accurately defining length of pregnancy.

5. Litter Size and Age of Females

On an average females aged from 6 to 14 months have the most numerous litters. The size of the litter in females over 15 months gradually decreases (Fig. 7).

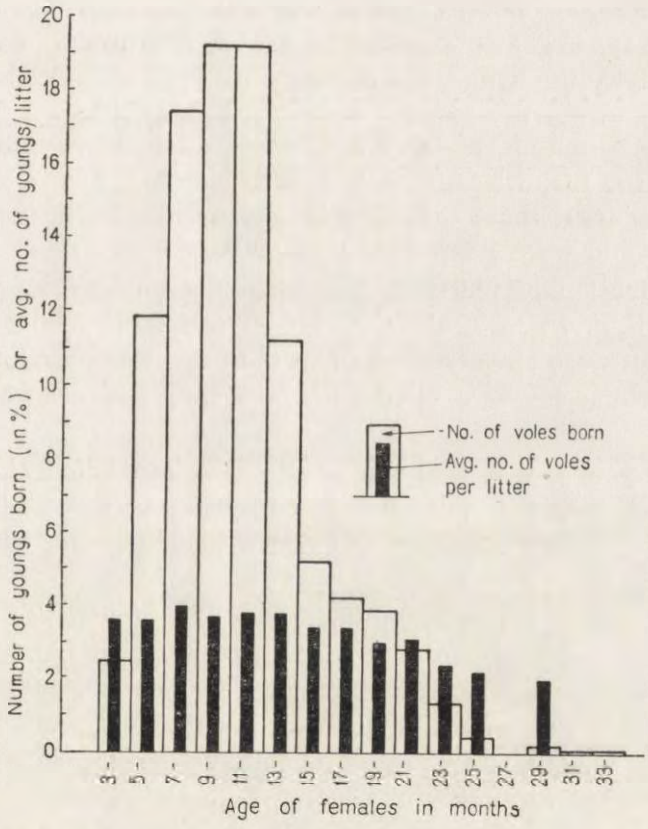

Fig. 7. Distribution of number of voles born and average number of young per litter, depending on age of females.

Statistically significant differences were found between the average size of litter in females from 7—8 and 13—14 months old, and those from 19—20 months old (Student test, $P < 0.05$). The differences

were not statistically significant between the average litter size of females aged 3—4 and 19—20 months or between 13—14 and 15—16 and 17—18 and 19—20 months ($P > 0.05$).

IV. MORTALITY OF YOUNG ANIMALS

Mortality among young animals is formed by: (a) individuals born dead (or dying during birth — impossible to check without observing each birth), (b) dying after birth and (c) so-called »missing individuals«, which means that on the given day when the cages were inspected these animals were not found in them. In such cases remains of fur *etc.* were often found, which would seem to indicate that cannibalism takes place, this being observed more often in the bank vole than in other voles (Barrett-Hamilton, after Steven, 1957a). In some strains kept in captivity the bank voles not only ate dead individuals, but killed each other and ate the victims even when the animals were supplied with food ad libitum (Steven, 1957a). Cases of cannibalism were observed in the Białowieża laboratory, although fights were not observed in family cages. It must therefore be presumed that the weaker individuals died and were eaten by the others.

The distribution of mortality among young animals up to the 21st day of life is given in Table 7. Day 0 in this table includes the individuals which were already dead when the litter was found. Since, however, their stomachs were filled with milk they had probably not died at birth.

Forty six young, that is, 1.6% of all those born, died at birth. The young animals included in day 0 form 1.1% of all born. These two figures point to the relatively low mortality rate among young bank voles at birth.

Mortality among the young animals during postnatal life is unevenly distributed. In addition to the high mortality on days 0—8 (64.5%), a considerable number of young animals died on the 15th day of life (5.9%) (Table 7). This may be connected with their postnatal development. At the age of about 7 days the young voles begin actively to crawl after the mother within the nest, and their incisors erupt during this time. At the age of about 15 days they are weaned and independently leave the nest (data after Sviridenko, 1959; and Petrov & Ajrapetjanc, 1961). These are most certainly critical periods of development. In relation to the number of young born — 13.6% of individuals are lost during the period from birth to transition to independent life (up to 15th day), and 15.7% up to expected time of parturition of

Table 7.

Mortality among young voles on different days of life and percentage dying, in litters of a given size.

Litter size	Consecutive day of life in the nest																						No. born	Total dying	
	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21		*N*	%
1	1	1		1		1										1			1		1		48	7	14.6
2		12		5	2	1	4			1	3		2	4	2	1	1		2		2		252	42	16.7
3		22	5	4	2	5	3	1	5	2	2			3	3	4	1	3	1	3	2	3	549	74	13.5
4	11	31	5	19	3	9		3		1	4	4	1	2	8	1	3	6		1	1	2	916	115	12.5
5	1	8	19	6	7	8		10	8			1	3			12	6			1	6	2	585	98	16.7
6	12	6	6				3	5			6	3	6	6	1	7					2		318	63	19.8
7	7	1		7	7	2			7					1					1				119	33	27.7
8																		8					56	8	14.3
9										3													9	3	33.3
10																							10	—	—
N	32	81	35	42	21	26	10	19	20	7	15	8	12	16	14	26	11	17	5	5	14	7	2862	443	
%	7.2	18.3	7.9	9 5	4.7	5.9	2.2	4.3	4.5	1.6	3.4	1.8	2.7	3.6	3.2	5.9	2.5	3.8	1.1	1.1	3.2	1.6		100	

Table 8.

Number of complete litters lost on consecutive days of development in the nest (percentage of complete litters lost was calculated in relation to total number of litters obtained with a given number of young per litter).

Number of: young in litter	litters	Number of litters lost on consecutive days of development in the nest																						Litters lost	
		Days																							
		0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	*N*	%
1	48	1	1		1		1										1			1		1		7	14.6
2	126		5		2	1		2				1		1	2	1				1				16	12.7
3	183		6	1	1		1	1		1					1	1	1				1		1	16	8.7
4	229	2	4	1	4		1					1	1			1			1					16	6.9
5	117			2	1	1	1	2	1								2							10	8.5
6	53	2	1	1								1		1	1									7	13.2
7	17	1			1	1				1														4	23.5
8	7																		1					1	14.3
Total		51 (66.2%)								15 (19.5%)							11 (14.3%)							77	100

the next litter, *i.e.* up to 21st day. Hence the number of young born per litter is on an average 3.6, but those surviving up to the 21st day of life only 3.04.

Mortality distinctly increases if the young remain longer with the parents. Thus a further 16% of the young died in litters which for various reasons were not taken from the parents' cages after the 21st day of life. In addition, while the percentage of »missing individuals« was 18.0% in our material up to the 21st day of life, over 21 days this figure was as high as 52.8%. After taking into consideration the mortality of young animals up to the time they are taken from the parents' cages, the number of surviving young per litter is further reduced to 2.4.

In our material the females successively reared 8 and 10 young. There were, however, general difficulties in bringing up litters numbering more than 6 young. For instance in litters consisting of 7—9 young, mortality was 23.9% as compared with 12.5% — 19.8% mortality in litters of 1—6 young (Table 7). The average number of reared young is 63%. Only one female, which produced 10 litters, and 3 females which produced 9 litters, reared only about half of the young born (Table 5).

The percentage of dead young increases with increasing age of the females. 15.2% of young die in litters from mothers 1—12 months old; 17.2% of young from litters of females from one year to two years old and almost twice as many, *i.e.* 28.5% from litters of females over two years old.

Cases in which the complete litters were lost forms 9.8% of all the litters produced. Of these the small and large litters which lost more often than litters of medium size (3—5 young per litter) (Table 8). During the period of development in the nest a peak in the mortality of complete litters was observed during the first seven days of life (about 66%). This shows that particular attention must be paid to the nursing females during this period.

Increased mortality in the last litters of multiparous females was not observed, neither was the size of these litters lower than the average.

V. PRODUCTIVITY OF FEMALES

Production of young per average female was approximately as follows:

young born: $3.09 \times 3.6 = 11.1$ (100%);

young reared to the 21st day of life: $3.09 \times 3.04 = 9.4$ (84.7%);

young reared up to the time they were taken from the parents' cages, after allowing for high mortality among young animals after the 21st day of life: $3.09 \times 2.4 = 7.4$ (66.7%).

In order to obtain a fuller picture of productivity 27 females were chosen which during their breeding life had no long intervals between successive litters, and in which the time taken for production of one litter was from 18.6 to 37.8 days. An average number was obtained of 16.7 young born and 11.8 reared (70.6%) up to the time the young were taken from the parents' cages.

Comparison was also made of the productivity of two groups of females, some of which were mated at ages up to 3 months (group A) and the remainder at the age of over 7 months (group B).

In group A ($n = 36$) 12.5 young born and 10.2 (81.5%) reared up to the 21st day of their life was obtained per female. In group B ($n = 50$) average figures per female were 9.7 and 8.3 (85.2%), the production time of one litter being on an average 53.7 days in group A and 61.0 days in group B. The average breeding time of females in relation to the period spent in the cage after combining them with males was respectively 46.7 and 53.1%. After allowing for mortality of young up to the time they were taken from the parents' cages, their production per female was on an average 8.3 in group A and 6.1 in group B. Losses in relation to the numbers of young produced by an average female were respectively 33.5% and 37.6%. These results demonstrate the adventages of using animals combined early for the production of young.

Table 9.

Sex ratio of adult voles depending on age.

Age, years	$< 1/2$	$1/2$	1	$1\,1/2$	2	$2\,1/2$	3	$3\,1/2$	4
Number of individuals	475	373	234	149	92	51	19	6	1
Males (%)	49.7	50.9	51.7	60.4	60.9	68.6	63.1	83.3	

VI. SEX RATIO

Sex ratio was determined at the time of taking the reared young from the mothers. 636 females and 656 males were obtained. 184 females and 195 males were obtained in the litters in which some of the young died. In neither case was the slight predominance of males statistically significant (Chi-square test, $P > 0.05$).

Let us consider the sex ratio in the litters in which all the young were reared. Predominance of males was found in January and during the

period from March to July, and of females from August to December and in February. Neither of these differences appear to be statistically significant when chi-square test was used ($P > 0.05$).

In the case of adult bank voles up to the age of one year, the population consisted of practically equal numbers of individuals of the two sexes. As from the age of 18 months of the animals' life the females begin to die far more rapidly than males, particularly those more than three years old (Table 9).

VII. LONGEVITY OF THE BANK VOLE IN CAPTIVITY

Bank voles survived for over four years in captivity. It was found that longevity is affected by the sex of the individuals, sexual activity and their captivity conditions. The mean life span of reproducing females is about 17.5 months, and of males about 23 months. Individuals forming breeding pairs live longest (males longer than females), and life span is shortest in communal cages in which individuals of one sex and similar

Table 10.

Life span of the bank vole under laboratory conditions (in days).

Group	Females		Males	
	N	Avg.	*N*	Avg.
Reproducing	146	525.0	116	683.2
Not reproducing	32	309.8	46	417.2
Not combined, from the communal cages	61	162.0	74	208.5

age were kept for long periods, with from 6—8 animals in a cage. The differences in life span of females and males are statistically significant (Student test, $P < 0.05$) (Table 10).

It may be assumed that females from non-breeding pairs were physiologically weaker individuals than females from the breeding pairs. The former did not breed and lived for shorter periods.

Maximal longevity of bank voles in the Białowieża laboratory was for females: about 45, 41 and 39 months, and for males: about 50, 47 and 44 months. It can be taken that animals which survived for about 40 months in captivity died of old age. This is borne out by their external appearance: they were emaciated and their fur was ruffled, their movemens uncertain and activity low, with simultaneous absence of symptoms of disease.

The following instances are given of other causes of death among reproducing females — 1.5% of pregnant females died; 0.7% died during birth; 4.9% died during the period from the second to the seventeenth day post-partum, usually together with the young.

VIII. DISCUSSION

Under laboratory conditions the bank voles continued reproduction throughout the whole year. The maximum number of litters calculated per female were born in August, than in May, the minimum in June — July and September and November. The maximum numbers of young, also calculated per breeding female — were found in January, then in April and May (Fig. 3). Steven (1957a) states that the litters were also obtained in all months in an outdoor colony the whole year round. The largest number of litters was obtained in April and May, the smallest number in December and after reaching a peak level in May breeding was maintained on a high level to August. The breeding observations made by Petrov & Ajrapetjanc (1961) also show that sexual activity continued all year round in this species. Drożdż (1963) also found that bank voles kept in a laboratory bred throughout the year.

In the Białowieża colony the females mated effectively at the age of 1—1.5 months, and males at the age of about 2 months. Sviridenko (1959) states that bank voles one month old differ very little from adults and some of them already begin to participate in reproduction. The earliest litter in his animals was produced by a 49-day old female (mating had taken place at the age of 31 days) (Sviridenko, 1967). Similarly Petrov & Ajrapetjanc (1961) found that bank voles from 1—1.5 months old take part in breeding. According to Drożdż (1965) mature spermatozoa appear in the testes of males about the 30th day of life and full spermatogenesis occurs at the age of 50 days. Although he obtained 5 litters from voles about 50 days old first litters were most often obtained from animals 3—5 months old.

As was the case with the Białowieża animals, Petrov & Ajrapetjanc (1961) observed a 4—5 day oestrus cycle in females transferred from field conditions to the laboratory.

The data obtained on duration of pregnancy (19—20 days), and length of interval between successive litters which could be taken as gestation period (average 20.7 days), come within the range of results obtained in other breeding colonies of bank voles (Table 11). Cases of 16- and 17-day pregnancy were also observed by Drożdż (1963).

»Prolongation« of pregnancy with the first litter of females which occurred in our material (Fig. 7) can be explained by the occurrence at the beginning of the breeding period of several cycles before conception

took place. A s d e l l (1964) states that at the beginning of the breeding season many females exhibit a varying number of cycles, usually three, before becoming pregnant.

The Białowieża material did not provide unequivocal proofs of the occurrence of the phenomenon of prolonged pregnancy when nursing a large number of young in the previously born litter. W r a n g e l (1940) states that a female which was simultaneously nursing young had a longer pregnancy ($21^1/_2$ days) and that the interval between litters, including both pregnancy and lactation, may be 38—39 days. M a z á k (1962) gives 21—$21^1/_2$ days in such cases. D r o ż d ż (1963) states that the length of consecutive pregnancy »depends ... on the size of the previous litter causing longer lactation«.

Table 11.

Some data on the breeding biology of the bank vole under laboratory conditions.

Gestation, days	No. of litters Min. – Max. (Avg.)	No. of young in litter Min. – Max.	Avg.	No. of young weaned per litter	Duration of the interval between consecutive litters, days	Authors
			4			
17.5—18						Wrangel (1940)
20.6±0.17		1 — 7	4	3.44±.04		Steven (1957 a, b)
17.5			3.61			Mazák (1962)
17.5	15—16	1 — 8	4.05		18—25 (most often)	Drożdż (1963)
18	4—7 (13) (5.5/female/yr)	1 — 7	4.4*) 3.7*)		18—134	Sviridenko (1966; 1967)
19—20	1—11 (3.09)**)	1 —10	3.6	3.04	16—268 (366)	Buchalczyk (1959) this study

*) refers to single females, **) per female, during the breeding period in captivity.

The length of the interval between successive litters exerts an important influence on effectiveness of reproduction, directly affecting the number of litters obtained. S v i r i d e n k o (1966) reports that longer intervals occur and states that they took place during both winter and summer months. In our material there are 6—9 months intervals (7.0% cases) but in about 54% they occurred only, or mainly in the autumn-winter months. Shorter intervals, up to 2 months (17.6% of all intervals) occurred in every season of the year. Generally speaking — 63% of the litters were born at times which could be considered as normal. This figure include longer intervals between successive litters, *i.e.* cases when a female did not conceive in the post-partum oestrus.

D r o ż d ż (1963) and S v i r i d e n k o (1967) obtained the maximum number of litters per one captive female, *i.e.* 13 or 16 (Table 11). At least two facts exerted a reducing influence on our lower numbers:

(1) not all the females observed were combined with males from the time they attained sexual maturity, (2) interference in reproduction was very considerable — before weaning the young were often taken for different investigations. However, the maximum number of young per litter — 10, were obtained in the Białowieża colony (Buchalczyk, 1959).

The productivity of female bank voles in the Białowieża laboratory is not yet high, since we obtained 11.1 born and 9.4 young reared up to the 21st day of life per average female. Losses up to 15th day of life of the young animals amounted to 13.6% and up to the expected time of the successive parturition, *i.e.* 21 days, — 15.7%. After adding young born dead — 17% loss is obtained. Drożdż (1963) observed an average mortality as 32%, and human interference as one of the important contributory factor to this. It is, however, the time the young are weaned and separated from the mother that would appear to be particularly important. This should take place before the parturition of the successive litter. In one of the cases the female of the Białowieża colony was observed to retain the young from the preceding litter in the nest, after producing a later litter. This make it impossible for the animals in the first litter to obtain food, and they died.

Sviridenko (1967) finds in general that the average litter size among captive animals was lower than that observed under natural conditions. He anticipates that under optimum laboratory conditions the number of young voles per litter would increase and the intervals between litters would be shortened. Popov (1960) states that under field conditions postnatal mortality is 30% and greatly exceeds embryonic mortality. During the first 10 days of life 11.7% of the young animals die, and 15.1% during the next 5—8 days, and in some of the litters all the animals die. This author had only a small amount of material at his disposal.

Reproduction of the bank vole under natural conditions differs fairly considerably over the area of the range it occupies and depends, on weather conditions, biotope, season *etc.* The influence of food and climatic conditions is particularly emphasised (Koškina, 1957; Popov, 1960; Asdell, 1964; Terehovič, 1965). When the food supply is ample and temperature suitable bank voles can reproduce throughout the whole year (Zejda, 1962; Kubik, 1965; Sviridenko, 1966). Length of the breeding season also varies, as does the consequent number of litters obtained from one female. Zejda (1966) states that under natural conditions as the result of the high mortality rate and following lower average age of the females, it is seldom that the female is pregnant more than three to four times during its lifetime.

The number of young in a litter varies under natural conditions depending on the year, biotope, season and population, and also the generation (Popov, 1960; Sviridenko, 1966, 1967; Kubik, 1965). It is usually higher under natural conditions than in captivity. Zejda (1966) gives an average number of embryos in a pregnant female as 4.9 in Moravia, which is a value close to the average number of young obtained per litter in captivity.

Duration of pregnancy of bank voles under natural conditions is, according to Popov (1960), 17—18 days; Bujalska & Ryszkowski (1966) give an average of 22 ± 2 days. Similar values were obtained for captive animals. Higher values are, howeer, also given for voles under natural conditions — *e.g.* Naumov (1948) — 20—30 days (average 25). According to the data given by Larina & Golikova (1960) length of the oestrus cycle in bank voles was 7—8 days and was thus longer than was observed in the Białowieża laboratory.

Under the Białowieża laboratory conditions bank voles survived for over four years (a record male lived 4 years and 2 months) (Table 10). Drożdż (1963) had four individuals in his material which survived 29—32 months and seven alive at the time the study was completed were over two years old. Mohr (1950) gives the life span of bank voles as 2—3 years (probably under laboratory conditions); Sviridenko (1966, 1967) as 1.5—3 years (513—1164 days). Our records are thus the highest.

Bank voles relatively easily accustom themselves to captivity conditions. The observations already made show that the prospects for breeding this species in captivity are good. The fecundity of the animals shows a tendency to increase. This is shown by: distribution of the number of litters and number of young in litters in seasons of the year, not excessive mortality of young animals, fairly rapid sexual maturity and fairly long period of fertility.

Improvement of existing breeding conditions and careful selection of animals intended for reproduction, early mating and punctual separation of weaned young from the mothers should yield better breeding results in the future.

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ROZRÓD, ŚMIERTELNOŚĆ I DŁUGOŚĆ ŻYCIA NORNICY RUDEJ W WARUNKACH LABORATORYJNYCH

Streszczenie

Celem hodowli prowadzonej od 1956 roku było przystosowanie nornicy rudej, *Clethrionomys glareolus* (Schreber, 1780), do warunków laboratoryjnych oraz uzyskanie materiału doświadczalnego. Nornice pochodziły przede wszystkim z terenu Białowieskiego Parku Narodowego (Tabela 1).

Rozmnażały się one przez cały rok, przy czym największą ilość miotów i młodych na samicę uzyskano w kwietniu — maju (Ryc. 3). W miarę wzrastania ilości pokoleń w laboratorium — nornice wykazywały tendencje do całorocznego intensywnego rozrodu (Ryc. 4).

Samice dojrzewały płciowo najwcześniej w wieku 1—1,5 miesiąca; samce około 2 miesięcy. Zdolność do rozrodu zachowywały do wieku ponad dwa lata (Tabela 2). Ilość miotów na samicę wynosiła 1—11 (średnio 3,09); ilość urodzonych młodych na miot 1—10 (średnio 3,6) (Tabela 3 i 4). Przeciętna samica, po połączeniu z samcem, rozradzała się w ciągu 47,4% czasu swego przebywania w hodowli (Tabela 5). Na taką samicę przypadało 11,1 — młodych urodzonych oraz 9,4 — odchowanych do 21 dnia życia.

Długość ciąży, oznaczona za pomocą rozmazów pochwowych, wynosiła 19—20 dni. Długość przerwy między kolejnymi miotami w 45,6% miotów — 16—35 dni. U 80,7% tych miotów wynosiła 16—25 (średnio 20,16) dni. Przerwy dłuższe, 4—5-miesięczne obserwowano w 15,3% a 6—9-miesięczne w 7,0% miotów (Tabela 6).

Nie stwierdzono wyraźnie powiązania pomiędzy długością przerwy między kolejnymi miotami a ilością młodych karmionych w urodzonym miocie. Największe mioty miały samice w wieku 6—14 miesięcy życia a u samic starszych niż 15 miesięcy wielkość miotu stopniowo maleje (Ryc. 7).

Młode urodzone martwo lub padłe przy porodzie stanowiły 1,6%. Śmiertelność od urodzenia do okresu przechodzenia na samodzielny tryb życia (tj. 15 dni) wynosiła 15%; do czasu pojawienia się oczekiwanego następnego miotu (21 dni) — 17%. Natomiast przy dłuższym przetrzymywaniu młodych po wykarmieniu, z rodzicami, wzrastała o dalsze 16% (Tabela 7). Padanie całych miotów stwierdzono w 9,8% przypadków a 66% tych miotów padło w czasie pierwszych siedmiu dni życia (Tabela 8).

Stosunek płci, określany w momencie odłączania młodych, wynosił 1:1. U dorosłych nornic stosunek płci począwszy od półtora roku życia zwierząt zmienia się stopniowo na korzyść samców (Tabela 9). Samce nornicy przeżywają w hodowli do 4 lat i 2 miesięcy, samice do 3 lat i 9 miesięcy. Różnice w przeżywalności samic i samców z par rozmnażających się, par nie rozradzających się i klatek zbiorczych są statystycznie istotne (test Studenta, $P < 0{,}05$). Najdłużej żyją nornice z par rozmnażających się (Tabela 10).