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**Intensity of reproduction
of the *Apodemus flavicollis* (Melchior 1834)
during the period 1954–1959**

**Intensywność rozmnażania myszy wielkookiej leśnej,
Apodemus flavicollis (Melchior 1834) w latach 1954–1959**

[With 1 Fig. and 4 tables]

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I. INTRODUCTION

The yellow-necked field mouse, *Apodemus flavicollis* (Melchior 1834) is one of the most abundant mammals in the Białowieża National Park. The degree of its fecundity, like that of the bank vole, *Clethrionomys glareolus* (Schreber 1870) depends chiefly on the fruiting of deciduous trees, the seeds of which form their basic food. From the observations made by Sviridenko (1951) it appears that the fluctuations in numbers of the yellow-necked field mouse are governed almost entirely by intensity of reproduction, which in turn depends on the amount of food available. According to this author, meteorological factors, ecto- and endoparasites, and predators are of practically no significance. My own observations, however, led me to conclude that in addition to the dominant role played by food, the climatic conditions prevailing during the winter

and spring are of some significance. Endoparasites may also exert a certain influence in reducing numbers.

As the breeding season is dependent on external conditions and in particular on the fruiting of deciduous trees, there is no fixed breeding period occurring at the same time each year, even in the same area, and it is for this reason that certain authors give different dates for the breeding season. Löhrl (1938) encountered the first pregnant females in March, and caught young animals in June and September. Serzhanin (1949) states that this species produces three litters per year: at the end of March, or the beginning, of April, in June and in August, the middle litter being the largest. Vinogradov & Gromov (1952) are of the opinion that the first birth takes place between the 80th and 90th day of life of the female. The number of litters per year according to them varies from two to four, and interval between them from 40 to 60 days. Smirnov (1956) found, on the basis of material obtained by breeding in captivity, that one female gave birth to its first young at 143 days of age and a second female considerably later. Only one female had three litters during the course of one year — in April, in May and in August, and others at most two litters, e.g. in May and in June, or in January and in September. Sablina (1953) noted the highest percentage (45%) of pregnant females in May, and also found that 33% of the females bear young twice per year, while only 14.1% give birth three times. The authoress emphasises the effect of food on reproduction in this species. Sviridenko (1951) on the basis of a very large collection obtained over a period of many years from climatically different areas, proves that numbers and intensity of breeding differ and fluctuate within very wide limits for each type of feeding and climatic conditions, and even between different populations under apparently similar conditions. My own observations on the great variation of the timing and intensity of reproduction of this species confirm to a great extent the results obtained by Sviridenko. Because of this variability, this data for the yellow-necked field mouse from the Białowieża National Park may not be in complete accordance with data from other years and from other geographical regions.

II. MATERIAL AND METHODS

The material analysed in the present work consists of 2151 specimens (1052 ♀♀ and 1099 ♂♂) caught in the Białowieża National Park during the years 1954—1959. Captures were made on two permanent capture areas (50 traps were set in a grid 5 × 10 m on 250 m² area), chiefly by spring snap traps and cylinders. During 1955 special ecological investigations were carried out and additional material was collected from six further areas.

Data on the fruiting of deciduous trees for the period were obtained from the Forest Administration in Białowieża. These data did not come from the area formed by the National Park itself, but from the four forest districts surrounding it.

Temperature and depth of snow were measured in the National Park within a permanent meteorological area in the 340th section, at height of 5 cm above ground level, the depth of snow being measured on 10 positions.

Measurements were made from 1955 onwards by the same member of the staff of the Bioclimatological Laboratory of the Mammals Research Institute.

The material was preserved in 80% methyl alcohol, each individual being weighed and measured before being fixed. Two measurements — length and thickness — were also made of the testes. The areas of the maximum crosssection of the testes were calculated (according to the formula for area of ellipse $ab\pi$). Pregnancy was noted only in the later post-implantation stages and thus the number of embryos was not always determined. On this account these data were not taken into consideration.

Histological examination was made of a total of 329 gonads (221 ♂♂ and 108 ♀♀). The gonads were taken from specimens previously fixed whole in alcohol and therefore slides were not suitable for detailed histological interpretation. Sections were cut at 5 μ and stained with Mayer's hematoxylin and eosin.

Sexual maturity was determined on the basis of the presence of spermatozoa in the testis (Brambell & Hall, 1939), or of corpora lutea in the ovary. It proved difficult to find females with a completely mature Graafian follicle in this material, which was probably the result of the very short duration of the final preovulation stage. The full sexual cycle lasts six days with *Apodemus sylvaticus*. In the case of the domestic mouse the rapid growth of the Graafian follicle does not take place until two days before the beginning of the oestrus, during which time its size increases from 0.4 mm. to 0.7 mm. (Asdell, 1946).

The material was divided into four age groups according to the extent of wear of the molars (Adamczewska, 1959). This method has recently been checked. During the summer of 1959 young individuals were caught in live traps, marked and released in the same area. At the end of March and beginning of May 1960 ten specimens were caught which had been marked in July of the previous year. Wear of the molars was similar to that of the IV age group of individuals marked the previous year, that is, it was in complete agreement with the assumptions previously accepted. I am, however, of the opinion that wear of the teeth does not take place uniformly in different habitats. It is, therefore, probable that the standards worked out apply only to the Białowieża National Park, or to the same biotope — *Querceto-carpinetum* — from which both the study material and also the control specimens were taken.

III. BREEDING SEASONS

The material as a whole is shown in Table 1, arranged according to the month of capture and the age class as shown by tooth wear.

In the first half of 1954 there were few captures, and it therefore proved impossible to determine when the first young specimens began to appear in the spring. The few young animals caught had

Table 1.
Quantitative composition of the *Apodemus flavicollis*.

Year	Age	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	No.
1954	I							1		6	1	1		9
	II							2	3	3	5	4	6	23
	III	1	1								1	3	14	20
	IV	2				2								4
1955	I					17	36	43						96
	II	13			3	23	33	155	22	2				251
	III	3	10	3	3	15	74	228	168	506	48	134		1198
	IV		2	7	6	2	9	35	9	74	28	41		213
1956	I						1			1				2
	II												1	1
	III	3			2					3		3	6	17
1957	I													13
	II				1	1	5	5	3	16	2			27
	III	11	5	6	1			4	3	18	4	1	44	100
	IV	1	1	2	1								1	6
1958	II													5
	III	5	1		1		1	1			1	2	7	19
	IV	4	2		1		1							8
1959	I					1	12	1						18
	II	3			4	7	7	4						29
	III	2	3	6	3	5	15	16	11	8	8	1		78
	IV			3	3		3	1	2	1	1			14
Total		48	25	33	33	70	198	502	231	638	99	194	80	2151

already reached the III or IV age group. Specimens from the I age group did not begin to be captured until July, and the last young animal was caught in November. In January 1955, however, animals were caught belonging to age group II. Individuals belonging to age group III did not appear until October 1954, while representatives of age group IV were not found at all. It is therefore clear that the breeding season of the yellow-necked field mouse lasted uninterruptedly from summer to late autumn.

Winter began fairly late that year, the whole of December being relatively warm, with a minimum night temperature of -5°C .

Table 2.

Fruiting of deciduous trees from 1954—1959 in the Białowieża Forest area. Amount of given in kg., fruit of the spruce in kg. of cones.

Year	<i>Quercus robur</i> L.	<i>Carpinus betulus</i> L.	<i>Acer platanoides</i> L.	<i>Tilia cordata</i> Mill.	<i>Fraxinus excelsior</i> L.	<i>Picea excelsa</i> Lam.
1954	184082	19.20	5	20.40	41.50	3668
1955	-	48.30	14.05	2.40	19.90	1620
1956	-	53.8	19	1.4	68.65	-
1957	21013.5	148.7	30.2	-	63	3673
1958	3557	5	227	0.20	2985	1087
1959	597919	111.5	121.5	4.95	57	5842

In 1954 deciduous trees were very fruitful, especially the oak (Table 2). It is therefore clear that conditions in the autumn and winter of 1954/55 were particularly favourable for the yellow-necked field mouse, and the intensive autumn breeding season was undoubtedly closely connected with this (Sviridenko, 1951; Sablina, 1953).

In January 1955 a group of young specimens born in the autumn of 1954 was obtained. They reached maturity in February and March. The mass appearance of young individuals in age group I begins in May, and ends in July. From August onwards, on the other hand, right through the autumn, not one such young specimen

was caught. In September 1955 the last individuals belonging to age group II were caught.

The crop of seeds was exceptionally poor that year. The oak bore no fruit at all, and other trees produced a relatively small amount of seeds (Table 2). Midway through December there were frosts as severe as -20°C . for several days, then snow fell and the temperature at the end of December rose to 0°C . After light frosts a thaw took place midway through January 1956, followed at the end of the month by extremely hard frosts which lasted until the end of February. Temperatures fell to -23°C ., and on the warmest day did not rise above -5°C . Under such conditions a covering of ice formed on the surface of the snow at the end of January, and halfway through February there were fresh falls of snow. Frost continued throughout the whole of March, a complete thaw not taking place until after the middle of April.

Contrary to the preceding year, the winter of 1955/56 was a very difficult one for mammals to survive. These conditions affected not only small mammals, but larger animals also. For instance, great numbers of the wild pigs in the Białowieża Forest died of hunger in the spring of 1956 (C a b o Ń, 1958). The yellow-necked field mouse was in even more difficult circumstances, as it had had no opportunity of collecting stores of food for the winter as in „normal” years. The ice covering made it impossible for it to seek food under the snow, and as a result the majority of the population of yellow-necked field mice in the Białowieża National Park died.

In 1956 only single specimens were caught. The young individuals of age group I indicate that the breeding season began late in the summer, and despite difficult food conditions lasted until the autumn. In 1956, like the preceding year, the crop produced by deciduous trees was very poor. The hornbeam and ash bore slightly more seed than the previous autumn, but the oak produced no fruit at all.

The winter of 1956/57 was a very light one. The first frosts occurred in December but did not fall below -14°C (one night only), and similarly in January and February the temperature was almost constantly above 0°C . No frosty nights occurred until the first half of March, and even then the minimum temperature did not fall below -15°C . Climatic conditions made it possible, therefore, to obtain a sufficient quantity of the very scanty food avai-

lable that winter, and this was probably the reason why a relatively intensive breeding season began in the spring of 1957.

Specimens from age group I were caught in 1957 from June to August, but as individuals belonging to age group II were obtained in April, and May, it must be assumed that breeding began in February and March. The last specimens from age group II were caught in October. The absence of older specimens of age group IV from May to November is interesting, and conveys the impression that animals born in 1956 were in very poor condition and died soon after the birth and rearing of the spring litters.

Only a very few yellow-necked field mice were caught in 1958, not a single individual of age group I being found in the entire material. Five specimens of age group II were caught in November and December, and three in January 1959. This would indicate breeding in the autumn and winter, and a complete lack of spring breeding season. This is the more surprising since fruiting in the autumn of 1957 was relatively good, and the animals had considerable supplies for food for the winter available. It may, however, be explained to a certain extent by the climatic conditions prevailing in the winter of 1957/58. The average temperature was not, it is true, very low (minimum mean for the month was -6.7°C), but throughout the whole period jumps in temperature from 0° to -15° were noted. As the snow was deep (from 15—55 cm.) and lay from the beginning of February almost to the end of April, variations in temperature produced a hard icy surface on the snow which made access impossible both to their burrows and to those holes in trees, containing food supplies, which were situated near the ground. Also plants sprouted very late in the spring, thus making the question of obtaining food in the pre-spring period exceptionally difficult. Even if the animals matured and passed through the oestrus period, they were not probably able to feed their young, which therefore did not appear in the material.

The winter of 1958/59 was very mild. The minimum temperature reached -14°C , and occurred only during three successive nights in February. There was little snow, which melted completely in March, when the daytime temperature reached $+17^{\circ}\text{C}$. It is possible that both the mild winter and the ample amount of food caused the spring breeding season to begin early.

In 1959 specimens in age group I were caught from April to July, and the last individuals of age group II were obtained in

August. This again is unexpected, since in the autumn of 1959 all deciduous trees, especially the oak, fruited extraordinarily abundantly. Under such conditions breeding usually takes place in the autumn and winter, but that year breeding ended earlier than in any other of the years so far studied.

It may be presumed that the duration of the breeding season (taking the appearance of young as an index) of the yellow-necked field mouse is limited in some way, and does not exceed four months of the year. In none of the years studied was the spring-summer period of appearance of young animals extended into the autumn. Neither did I find the reverse situation, i. e. uninterrupted appearance from autumn through to the spring. Probably the duration of the breeding season depends on the geographical situation, i. e. in the vicinity of the Black Sea this species may breed uninterruptedly for nine months of the year, while further to the north this period is considerably shortened, (Sviridenko, 1951).

As will be seen from the above data, it is impossible to speak of a stable breeding season typical of *Apodemus flavicollis*. Generally speaking, two separate periods, not occurring during the same calendar year, may be distinguished. The first period varies in time between April and August, and the second, between August and December (i. e. the period in which young individuals become part of the population, and not merely the actual breeding period itself). I think that we can speak about two generations of *Apodemus flavicollis*, living in two, different periods — spring-summer and autumn-winter.

The breeding periods are basically dependent on the amount of food available, that is, chiefly on the degree of fruitfulness of deciduous trees. In a fruitful year an autumn breeding season takes place and a mass appearance of young animals follows in the spring of the following calendar year. If the year is a poor one, the spring-summer breeding season is checked. This cannot, of course, be taken as a hard and fast rule, as climatic conditions play a significant part here, for instance a very fruitful year may be followed by a hard winter, which restricts to a marked degree the appearance of young individuals (as in 1957/58), and conversely, even when food supply is poor, a mild and short winter is favourable to the revival of a population weakened by hunger (e. g. 1956/57) .

IV. MATURATION AND REGRESSION OF THE GONADS

Periods of sexual maturity may be determined either by finding young in the nest, embryos in the uterus or by histological analysis of the gonads. In the present work I have used the last of these criteria.

Firstly the male gonads were studied, since with them it is easier to define the distinct limits between different stages of maturation than is the case with the female gonad.

From the material set out in table 3 it is clear that the males in age group I are in the full process of spermatogenesis. The age of the maturing animals and rapidity of maturation are the same both in the spring and autumn periods. As a rule first order spermatocytes occur in the testes of specimens from this age group, also often those of second order, (only one individual of the total number of specimens was found to have no spermatocytes at all).

Males from age group II exhibit great heterogeneity in the state of the gonads, that is, there are specimens, in the testes of which there is no spermatogenesis process at all, and only spermatogonia and Sertolian cells are visible. Of a total number of 28 specimens of age group II, 17.8% are in this phase. Specimens with developing or regressing spermatogenesis form the most numerous group here — 64.3%, finally 17.8% of the individuals were completely mature with spermatozoa in the testes.

The state of the gonads of males in age group III is similar to the relations in age group II (over 2 months of life outside the nest). Here there are both fully mature specimens in a state of advanced spermatogenesis, and also specimens in the phase of complete regression. The only difference is in the ratio of animals in the various stages as compared with that in age group II, i. e. of 132 individuals the largest group is formed by mature and active individuals (52.0%), then males having spermatozoa in their seminal canals, but without spermatozoa (30.3%), the least numerous group being formed by specimens in a state of regression (17.4%).

This relation is different again in the case of the oldest individuals (age group IV — specimens having spent over 5 months out of the nest). It is true that we have here the most mature males capable of reproduction (50.0% of a total number of 28 specimens) but the second most numerous group of specimens is that composed by animals having complete regression of the gonads

(28.5%), individuals with spermatocytes (exclusively of I order) in their testes coming third (21.4%). Here, therefore, extremes are chiefly represented, and judging by the periods during which the old specimens with spermatocytes only were caught, this is the state of seasonal regression of the gonads, and not a secondary attainment of sexual maturity. This process in the IV age group is not, however, one of senile regression. Only in one case did I find a complete absence of the sexual membrane (only Sertoli cells); with all the remaining specimens in this age group spermatogonia occurred exactly as in the case of inactive specimens from the younger age groups. The disappearance of spermatozoa is connected here with the season during which the yellow-necked field mouse does not breed, and not with senile degeneration.

As will be seen from the data given above, in all age groups the state of the testes is completely dependent on the stage of sexual activity or pause in activity reached by the animal at the time of capture.

Young specimens which begin to appear in the traps at the time they enter a free-living population have already started the spermatogenesis process. If they are born at the beginning of the breeding season spermatogenesis takes place normally, and continues on to spermiogenesis, but if they are born at the end phase of the breeding season, the animals do not mature, spermatogenesis is completely arrested and a regression to the state of spermatogonia only follows. Such specimens finally mature during the next breeding season. This same phenomenon was observed by Brambell & Hall (1939) in the case of *Microtus agrestis hirtus* (Bellamy 1839).

During a period of inactivity, the testes decrease considerably in size. This is followed by marked narrowing of the seminal canals, in which there is practically no lumen. In connection with this process it is relatively easy to determine a definite size of the testis, above which spermatozoa as a rule occur. Many authors have used this criterion in determining the maturity of males.

Popov & Mironov (1949) consider that in mature males the testes have a minimum length of from 10 to 13 mm. Sviridenko (1951) established the limit for maturity of testes at 10 mm. Naumov (1940) states that 7 mm. is a sufficient length. Brambell & Hall (1939) determine sexual maturity on the basis of the testes.

Table 3.

States of sexual maturity of males of *A. flovicollis*, taking into consideration age of specimen.

	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	I-XII			N	
													▲	●	■		
1954	I								●	●				-	2	-	2
	II								●	●●	●●	●●		-	7	-	7
	III									●	●		●●●●	-	4	5	9
1955	I				●●●●●●●●●●	●●●●●●●●●●	●●●●●●●●●●							-	18	-	18
	II	▲●		●	■	●	●●	●						1	6	2	9
	III	■	■	■	■	■	■	■	●●●●●●●●●●	●●●●●●●●●●	▲●●●●	▲▲▲	▲▲▲▲	11	11	20	42
	IV		■	■	■						▲▲▲▲●	▲●		4	4	6	14
1956	I					●								-	1	-	1
	II													-	-	-	-
	III	●			■				■		●	▲●●●●		1	5	3	9
1957	I			●			●	●						-	3	-	3
	II						●	●	▲▲					2	2	1	5
	III	■	■	■	■	●	■	●●●●	▲●●●			▲▲▲▲		6	8	11	25
	IV		■	■								▲		1	-	3	4
1958	II										●			-	1	-	1
	III	●	■			■	■				■	●●●●		-	2	7	9
	IV	▲	▲		●		■							2	1	1	4
1959	I			▲●●●		●●●●●●								1	9	-	10
	II	■				■	▲▲	●●						2	2	2	6
	III	■	■	■	■	■	■	■	●●●●	▲▲●●	▲●●●	▲●	●	5	10	22	37
	IV			■	■		▲	■						1	1	4	6
	16	11	16	18	15	31	28	17	15	15	16	23	37	97	87	221	

▲ — inactive, spermatogenesis absent. ● — in proces of maturation, spermatogenesis present.

■ — mature, spermatozoa present in testes.

My observations are in general agreement with those of Popov & Mironov, and Sviridenko, i. e. that spermatozoa occur in testes 10 mm. long. Another factor must be considered, however, namely that the shape of the testes undergoes certain changes in the successive phases of the sexual cycle. During the period of active spermatogenesis the testes are round in shape, during the regression period they decrease in size, particularly in thickness, and as a result become elongate in shape. I therefore consider that it is better to take both length and thickness of the testes into consideration, or like Brambell & Hall, the weight of this gland.

When comparing the size of the testes with their histological picture I found that sexual maturity in males occurs when the maximum cross-section of the testis has an area of 45 mm². Fluctuations are very slight and do not exceed 5 mm² either way. In all the study years, both in the spring and in the autumn breeding seasons, this size is the limit for this species.

It can be seen from the material obtained that the females mature slightly earlier than the males, and this confirms the fact previously described, that the growing period of the females lasts for a shorter time than that of the males (Adamczewska, 1959).

Corpora lutea are encountered in females of the II age group, and there was even one instance of a female from I age group with completely mature corpora lutea. Females without corpora lutea from the II age group were caught towards the end of the breeding season. This is evidence of arrested process of maturation in the females after the breeding season, to the same degree as in the males¹).

¹) The fact is worthy of special notice that corpora lutea occur in females of the II and III age groups in periods in which the breeding season, and even nursing of the young, has long since passed. For instance, in October and November 1955, despite the fact that no young individuals had appeared since August, I found normal corpora lutea present in the ovaries of 6 females. The corpora lutea had exactly the same structure as in the ovaries of pregnant females. The most likely assumption here would appear to be that these are ovulating bodies, and possibly pseudo-pregnancy takes place here. Thus, during a period in which the males are incapable of breeding, the females may be completely capable being fertilised. I have not dealt more fully with this problem in the present work, but it is worthy of further investigation.

The period during which mature males are capable of breeding may be considerably longer than that during which reproduction occurs judging by the appearance of young. In the autumn it lasts in general about six months, and the spring-summer season is from four-five month. This period may be shortened or extended in certain individuals.

Thus, for example, animals (males and females) born during the autumn breeding season of 1954 attain sexual maturity in December. Up to June 1955 inclusively we encounter adult males fully capable of breeding. These are probably the final months of life of the generation which produced young entering the population in May 1955. If some of the individuals survived to August and September, they would undoubtedly enter the stage of regression of the testes. The material, however, indicates that the older generations die out during this very period. It would appear from this that the specimens born in the autumn are sexually active throughout the whole period of their lives, and do not undergo regression of the gonads at all („generative” generation). The same conclusions may be reached on the basis of the generation born in the autumn of 1958, some of which were probably capable of reproduction until it disappeared in June—July 1959.

The situation is different in the generation born in the spring. The first litters mature and are capable of reproduction, but regression ensues very soon afterwards. The following litters born during the summer breeding period do not attain full maturity and in the autumn the gonads both of the former and the latter are in a stage of complete regression („vegetative” generation). They may mature in the spring of the following year, but produce a far from numerous young generation (Table 3).

From the above data it is quite clear that the generation affecting population numbers and mass appearance is the autumn generation. The generation born in the spring and summer as it were maintains the population, is itself usually numerous, but produces few young. While the specimens born in the autumn are sexually active throughout almost the whole of their lives, the spring generation is capable of reproduction only for short periods of time.

It must be assumed that the fundamental factor affecting the uneven reproduction potency of two generations of yellow-necked field mouse is the nutritive value of the food available, especially

during the period after leaving the nest. As is well known, this species is a typical seed-eater, and therefore starting from the second half of summer when the fruits of deciduous trees begin to fall, the yellow-necked mouse has food of the maximum nutritive value. The spring generation is forced to feed mainly on green foods in the first period of their live.

The fruit produced by trees in a given year plays a significant role here. After a fruitful years a mass appearance of this species is usual, and therefore it can be assumed food exerts a basic influence on the intensity of reproduction.

Schwarz & Smirnoff (1959) have stated some morphological differences between the generations of *Ondatra zibeticus* (Linnaeus 1766) born in Spring and Autumn. These differences were caused by non-uniform conditions of development in these periods. This phenomenon has important consequence for the ability to keeping a winter period by autumnal generation.

The mechanism „informing” the animals of approaching fruitfulness or of impending catastrophe is unknown. It is possible that the factor heralding these conditions is constituted by the unripe seeds falling from the trees during fruitful years. They would form an early, highly nutritive food, which would be a stimulus to a long period of sexual activity.

The material also reveals a certain cyclic character of the period of intense and weak reproduction, that is, the autumn breeding season is followed by mass appearance in the summer, which ends in catastrophe. The scanty population then has an autumn breeding season, and the specimens from these litters, similarly to those in previous years, produce numerous young in the spring and summer, after which catastrophe again occurs. In the material obtained during the period 1954—1959 this cycle was repeated three times. In 1954, 1956 and 1958 mature individuals were caught in the autumn, which produced numerous young in the spring of the following respective years, i. e. 1955, 1957 and 1959. In these latter years the young animals were born in the spring and summer only, after which regression of the gonads took place in all the individuals.

It may be presumed that this regularity is a coincidence only, nevertheless the fact of occurrence of two different biophysiological states in the yellow-necked field mouse during the winter period, i. e. sexual activity or regression, is beyond dispute in the case of this species.

V. BODY WEIGHT AND MATURITY

Many authors consider that body weight may be taken as a basis for determining whether the given specimen is or is not sexually mature.

Naumov (1940) considers that the females of *Apodemus flavicollis* mature when they attain at least 22 g. of body weight. Popov & Mironov (1949) state that maturation occurs in females when they weigh 28—30 g., and in males when body weight is 30—34 g. Sviridenko (1941) investigated the maturation of the yellow-necked field mouse in various parts of the Soviet Union and found that in the most southerly populations (near the Black Sea) the females may mature when their weight is 16.5—17 g., while in the Tartar Republic their weight on maturing is 28 g. Sablina (1953) established the body weight limit as 26 g. Turček (1952) considers that body weight regulates reproduction through the hormonal system. Before attaining the weight of 31—35 g., the yellow-necked field mouse, or bank vole, cannot be sexually active.

As will be seen from the data cited, the views of authors on this subject differ, each of them giving a different body weight as an indicator of the attainment of sexual maturity.

On the basis of material collected during the years 1954—1959 I found that the females maturing the earliest (*corpora lutea* present) in the Białowieża National Park weighed over 10 g., and males with spermatozoa 20 g., only exceptionally 15 g. These weights can, however, only be considered as the lower limit at which animals of this species can attain sexual maturity. This does not mean that all males weighing more than 20 g. must necessarily be mature. Evidence of this is given by Table 4, in which a comparison is made of average body weights of males in successive months with the percentage of mature males in the same months. From this it is clear that beginning in June, the percentage of mature males falls sharply, reaching zero in October. Average weights are diametrically opposite to this, as they gradually rise through the entire summer, to reach their maximum in October. However the period of capture is not the only factor of significance in the formation of these relations, since there may be heavy individuals without spermatozoa and relatively light ones with spermatozoa in their testes at the same time. For instance, in July

1957, on the same day, two males were caught belonging to the II age group, one of which weighed 18 g. and has mature spermatozoa, and the second weighed 27.8 g., having only order I spermatozoa. This is not the only example of this kind. All are evidence of the fact that the body weight is not a reliable criterion for determining the sexual maturity of an individual. The non-uniform conditions of development, which are individual for each litter, such as malnutrition of the mother (low percentage of casein in milk (Leatham, 1959) may play an important part here.

A fact worthy of special notice is that the rate of maturation of young specimens born during one breeding season is not uniform in successive months of the spring and summer.

Table 4.

Comparison of percentage of mature males with monthly average body-weights in 1955.

Months	June	July	August	September	October
No. of individuals	74	235	101	300	40
Percentage of adult males	58.1	14.0	11.8	1.5	-
Average body weight	24.98	25.98	28.68	29.85	30.80

When examining young specimens belonging to the I and II age groups, caught between May and August 1955, I found that there was a fairly close correlation between body weight and size of the testes. The correlation coefficient (r) for successive months is as follows: May — 0.6001, June — 0.7988, July — 0.5843, August — 0.5513. No statistically significant differences can be found between these coefficients²⁾.

Consideration of the averages of body weights and size of testes for May — August for the same individuals from the I and II age groups revealed their conversely proportional growth tendencies. (Weight: May — 13.92 g., June — 16.02 g., July — 20.24 g., August — 24.0 g.). The significance of this growth is confirmed by von Neumann's test³⁾. This test does not permit of establishing

²⁾ Fisher's test on the equality of correlation coefficients gives a value $\chi^2 = 2.689$; critical value χ^2 with tolerance of 3° equals 7.81.

³⁾ The established value of von Neumann's test is 0.799. Critical value for 5% risk of error is 1.041.

significant differences for averages of size of testes in these months. Despite this, the differences between averages are fairly large in pairs of successive months. Test *t* (Student's) was therefore applied, which showed that the difference observed is statistically significant ($t = 27.66$; $t_{0.05} = 4.303$).

From the data given it will be seen that when growth, that is, maturation of the testes takes place, the growth in body weight is relatively small, while in the final months (July, August) while maturation is very much slowed down, a rapid increase in weight takes place. This relation is illustrated in Fig. 1. Straight lines

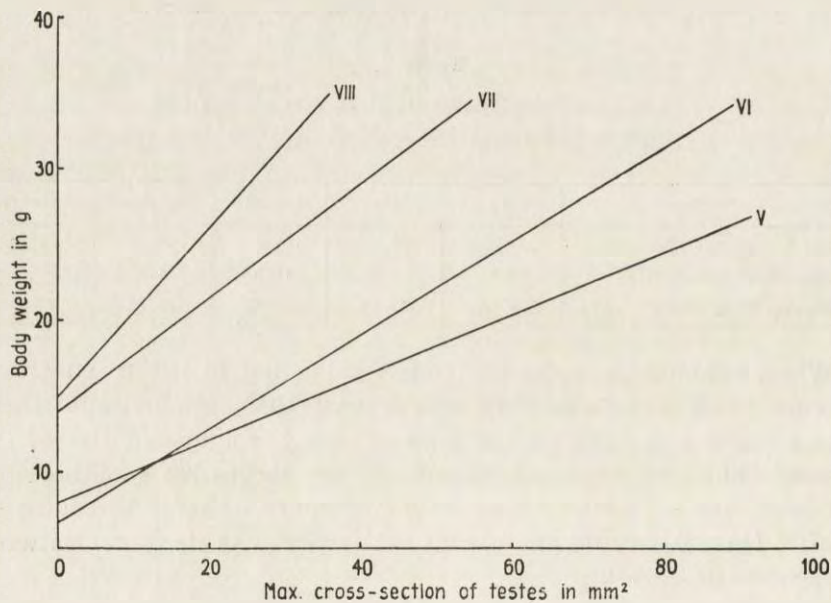


Fig. 1. Diagram of slope of straight lines fitted according to principle of least squares for: max. cross-section of testes and body weight in specimens from age groups I and II in May, June, July and August 1955.

were fitted to the data from material according to the principle of least squares. The regression coefficients for these straight lines had a systematic tendency to increase in successive months: May — 0.204, June — 0.309, July — 0.396, August — 0.541. This tendency is not a chance one (von Neumann's test based on successive differences gave a value of 0.867).

These data show that the process of maturation and growth of body of the males of the yellow-necked field mouse do not follow a uniform course in the case of all individuals. These processes depend on the period in which the given individual was born. My impression is that individuals born at the beginning of the spring-summer breeding season grow relatively slowly. Their entire development is directed at the maturation of the gonads, which as result develop very rapidly. On the other hand, the males which were born in the second half of the breeding period do not mature during the year of their birth, and as a consequence regression of the testes, in relation to the state of the gonads which are encountered in specimens caught very soon after leaving the nest, may even take place. These individuals, differently from the males born in the first months of the spring breeding phase, grow very rapidly and attain large body weights early on.

This is one more argument against making use of the body weight as a criterion in segregating animals into sexually mature and immature. Specimens caught at short intervals of time, and therefore practically speaking of the same age, may differ fundamentally as to body weight and sexual maturity. It may also happen that the heavier specimen is immature, while the lighter animal may be completely mature and sexually active.

VI. SUMMARY

1. The material analysed consists of 2151 specimens of the yellow-necked field mouse, *Apodemus flavicollis* (Melchior 1834) (1052 ♀♀ and 1099 ♂♂) caught in the Białowieża National Park between 1954—1959. Breeding periods were worked out on the basis of appearance of young specimens, and the periods of sexual activity on the basis of an analysis of 329 gonads (108 ♀♀ and 221 ♂♂).

2. The numbers of yellow-necked field mouse depends primarily on the amount of food available in a given year — the fruitfulness of deciduous trees, and on climatic conditions during the periods of late autumn, winter and early spring.

3. The period of entry of young individuals into the population does not in general exceed 4 months during the year. This applies to the geographical zone of the Białowieża National Park (latitude $\varphi = 52^{\circ}42'$, longitude $\lambda = 23^{\circ}51'$).



4. During the year there is, practically speaking, only one period of appearance of young, either in the spring-summer period, or in the autumn, the autumn generations giving a greater number of young than the generations born in the spring and summer.

5. The youngest males caught (age group I, i. e. less than one month of life outside the nest) are in the full process of spermatogenesis.

6. With mice older than 1 month (age groups II, III and IV) the actual state of the gonads depends primarily on the season of the year and the time of sexual activity in a given year, and not on the age of the animal. With mice born at the beginning of the spring breeding period (May, June) spermatogenesis continues to the formation of spermatozoa. With animals born at the end of the breeding period (July, August) spermatogenesis is arrested and regression of the gonads can be observed. Maturation of these specimens takes place at the end of the winter of the following calendar year.

7. Spermatozoa in the yellow-necked field mouse appear in the seminal canals when the cross-section of the maximum testis reaches 45 mm². This size may be accepted as the indicator of sexual maturity.

8. Sexual activity of the males lasts for 6 months in the autumn breeding period, and for 4—5 months in the spring-summer period.

9. Mass appearance of the yellow-necked field mouse is the result of an intensive autumn breeding season in a fruit ful year. The generation born in the late autumn produces an enormous number of young in the spring and summer of the following year.

10. Young females may attain sexual maturity after reaching a weight over 10 g., and males over 20 g. This cannot be taken as a rigid rule, since sexual maturation depends chiefly on the actual phase of the breeding season. Animals born at the beginning of the spring breeding period mature rapidly, but grow slowly. Conversely, in the second half of this period rapid growth and increase in body weight take place, while sexual maturation was not found. Therefore the development of the yellow-necked field mouse depends on the time of birth and may follow a different course in different individuals of the same age.

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STRESZCZENIE

1. Analizowany materiał składa się z 2151 okazów myszy wielkookiej leśnej, *Apodemus flavicollis* (Melchior 1834), (1052 ♀♀ i 1099 ♂♂) złowionych na terenie Białowieskiego Parku Narodowego w latach 1954—1959. Opracowano okresy rozrodu na podstawie pojawu młodych oraz okresy aktywności płciowej na podstawie analizy 329 gonad (108 ♀♀ i 221 ♂♂).
2. Ilość myszy wielkookich leśnych zależy przede wszystkim od ilości pożywienia w danym roku — urodzaju drzew liściastych, oraz od warunków klimatycznych w okresie późnej jesieni, zimy i przedwiośnia.
3. Okres napływania młodych osobników do wolno żyjącej populacji nie przekracza na ogół czterech miesięcy w ciągu roku. Odnosi się to do strefy geograficznej Białowieskiego Parku Narodowego ($\varphi = 52^{\circ}42'$, $\lambda = 23^{\circ}51'$).
4. W ciągu roku występuje praktycznie tylko jeden okres pojawu młodych. Ma on miejsce albo w okresie wiosenno-letnim, albo na jesieni, przy czym pokolenia jesiennie dają w sumie większą ilość potomstwa, niż pokolenia urodzone na wiosnę i w lecie.
5. Najmłodsze odławiane samce (I klasa wieku, tj. poniżej 1-go miesiąca życia pozagniazdowego) są w pełnym toku spermatogenezy.
6. U myszy starszych niż 1-n miesiąc (II, III i IV klasa wieku) aktualny stan gonad jest zależny przede wszystkim od pory roku i czasu aktywności płciowej w danym roku, a nie od wieku zwierzęcia. U myszy urodzonych na początku wiosennego okresu rozrodu (maj, czerwiec) spermatogeneza przechodzi w spermioogenezę i prowadzi do wytwarzania plemników. U zwierząt urodzonych pod koniec okresu rozmnażania (lipiec, sierpień) spermatogeneza zostaje zahamowana i obserwuje się regresję gonad. (Na skrawkach widoczne są tylko spermatogonie). Dojrzewanie tych okazów następuje w końcu zimy następnego roku kalendarzowego.
7. Plemniki u myszy wielkookiej leśnej zjawiają się w kanalikach nasiennych przy 45 mm² przekroju czołowego jądra. Wielkość tę można przyjąć jako granicę dojrzałości płciowej.
8. Aktywność płciowa samców trwa w jesiennym okresie rozrodu sześć miesięcy, w wiosenno-letnim od czterech do pięciu.

9. Masowy pojaw myszy wielkookiej leśnej jest wynikiem jej intensywnego jesiennego rozrodu w roku nasiennym. Pokolenie urodzone późną jesienią daje ogromną ilość młodych na wiosnę i w lecie roku następnego.

10. Dojrzałość płciową młode samice mogą osiągnąć po przekroczeniu 10 g wagi ciała, samce powyżej 20 g. Nie można tego przyjąć za regułę, ponieważ dojrzewanie płciowe zależy głównie od aktualnej fazy okresu rozrodu. Zwierzęta urodzone w początkach wiosennego okresu rozmnażania szybko dojrzewają płciowo, ale rosną wolno. Przeciwnie, u urodzonych w drugiej połowie tego okresu następuje szybki wzrost i zwiększenie wagi ciała, natomiast nie stwierdza się dojrzewania płciowego. A więc rozwój myszy wielkookiej jest uwarunkowany czasem urodzenia i u osobników w tym samym wieku może przebiegać w różny sposób.