

S. S. SCHWARZ, A. V. POKROVSKI, V. G. ISTCHENKO,
V. G. OLENJEV, N. A. OVTSCHINNIKOVA & O. A. PJASTOLOVA

Biological Peculiarities of Seasonal Generations of Rodents, with Special Reference to the Problem of Senescence in Mammals

Biologiczne właściwości sezonowych generacji gryzoni,
ze specjalnym uwzględnieniem problemu starzenia się ssaków

[With 10 Figs. & 11 Tables]

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I. INTRODUCTION

Since the beginning of the thirties of our century many investigations, carried out on different species, have provided evidence of significant biological differences between seasonal generations of rodents and certain other mammals. All these data, however, were mostly fragmentary or even incidental and therefore they could not seriously affect work on general problems of taxonomy, ecology and the science of the dynamics of animal populations.

This state of affairs altered markedly with the publishing of a series of papers by Prof. A. Dehnel and his numerous disciples. A great part of their papers were devoted to a many-sided analysis of seasonal variations in the morphological and physiological characters of a large number of species of mammals.

In his first great work (1949) Dehnel had already discovered the striking fact of seasonal variability of the main craniological features of *Soricidae*. This discovery was later corroborated by the detailed investigations made by Pucek (1955, 1957) — who continued the research instituted by Dehnel. This discovery is of prime importance. It shows that a correct grasp of the specific peculiarities of a given species can be obtained only when the seasonal variations of the main characters of the animals are duly taken into consideration. The investigation of less stable characters (in comparison with craniological ones) without the investigation of their seasonal variations is practically impossible. This was shown by a series of papers, prepared in Dehnel's laboratory, devoted to the investigation of different morphological systems of animals.

These investigations clearly demonstrated that animals born in different seasons differ by a whole complex of different peculiarities: growth rate, development rate, activity of certain endocrine glands, fecundity and rate of sexual maturation, weight of certain internal organs etc. (Dehnel, 1949; 1952; Adamczewska, 1959; Bazan, 1952; 1955; Bielaak & Pucek, 1960; Tarkowski, 1955; Wasilewski, 1955 and many others).

As a result of these findings the investigation of seasonal variation reached a new higher stage of development and stimulated work on this interesting problem in different countries.

In our laboratory the investigations of the biological peculiarities of seasonal generations of rodents began in 1949 and the results were first published in 1955 (Schwarz, Pavlinin & Susjumova, 1955). In this paper we have tried to summarize various data concerning the biology of reproduction and nutrition of *Arvicola terrestris* (Linnaeus, 1758) and some species of mice, belonging to different generations. Later on these investigations were broadened and extended. Special attention was paid to analysis of the seasonal reproductive cycle of the animals, their growth rate, development rate and rate of sexual maturation, the weight of certain internal organs (heart, liver, kidney, intestines, adrenals, thymus), haematological indices, oxygen consumption, the content of vitamins A and C in various organs and tissues and so on. The results of these investigations have been published in a series of notes and generalized papers (Schwarz, 1954; 1956; 1958; 1959; 1959; 1960; 1961, 1963; Schwarz & Smirnov, 1957; 1959; Livtschak, 1959; 1960; Kopein, 1960; and oth.) and lead us to the conclusion that the biological specificity of seasonal generations of mammals can be manifested by all the species observed in every geographical environment (the work was carried out in areas varying from semidesert regions to tundra). This specificity is very pronounced. On these grounds we are enabled to speak of a distinctive interchange of generations in mammals.

It is the aim of this paper to focus attention on this regularity and to examine the possibility of using it in the analysis of some fundamental problems of general biology. One of these problems is the senescence of animals.

The process of senescence is one of the most interesting and significant problems of general biology but it has hitherto been investigated only by physiological and biochemical methods. Zoological data are seldom used in the discussion of general problems of the ageing process and then only in the form of interspecies comparisons. The differences in the life span of different species served as a foundation for many hypotheses attempting to establish a correlation between the rate of senescence and the particular biological features of different organic forms. The best known of these hypotheses are as follows: a) The life span of larger animals is greater than that of

small ones. b) The life span is in inverse proportion to the growth rate of the animals compared. c) The life span is in inverse proportion to the rate of sexual maturation and fecundity.

Each of these hypotheses is based on numerous data (its analysis is facilitated by the appearance of special monographs published in recent years — Comfort, 1959; Wolstenholme & O'Connor, 1959, where numerous data concerning the life span of different species are summarized), but none of these can serve as a sufficient basis for a general theory of comparative gerontology. There is, however, a definite correlation between all the hypotheses mentioned above. Large body size, slow growth rate and slow sexual maturation, and decreased fecundity — all these and analogous characters are peculiar to animals with a decreased metabolic level. Therefore it is quite natural that a synthetic theory was soon created which connected the life span with the metabolic level of the animals. This regularity has already been pointed out by Rubner and is nowadays used as a basis for modern theories (Brody, 1945; Bourliere, 1960).

This theory is substantiated by a great number of facts, i.e. that species with relatively decreased metabolic level are characterized by a long life span; that in numerous species of poikilothermic animals (lizards *Sceloporus*; pilchards, sticklebacks, some American graylings, etc.) the life of northern populations with a slow growth rate is longer than that of southern ones (Brown, 1943; Miller, 1946); that experimentally induced increase of the metabolic level in different *Arthropoda* is accompanied by a significant decrease in life span (Pearle, 1928; McArthur & Baillie, 1929). Groups of rats were reared on a diet sufficient in all other constituents but deficient in calories, and their longevity increased (McCay, 1952; Nikitin, 1961).

All these and similar data show that a hypothesis which connects the life span of the animals with their metabolic level can serve as a starting point for a general theory of aging. An analysis of certain concepts of this theory can easily be made by a comparison of biological peculiarities and the life span of seasonal generations of small mammals of different metabolic levels. Such an approach to the problem retains all the advantages of the comparative observations mentioned above, but is free from possible mistakes connected with genetic differences between different forms, (and even more so species) of the specific influence of experimental conditions.

The second and related purpose of this paper is to explain some aspects of this major problem.

II. BIOLOGICAL PECULIARITIES OF SEASONAL GENERATIONS OF RODENTS

1. Growth rate

One of the more important peculiarities of seasonal generations of rodents is their growth rate. Animals born in the spring (let us call them "spring animals" or "spring rodents") have a great growth rate and reach their maximum weight at the age of 3—4 months. Subsequent alterations in their weight are governed primarily by seasonal regularities (Pokrovsky, 1960). The animals born in the fall (let us call them "fall animals" or "fall generations") do not reach the maximum weight in the

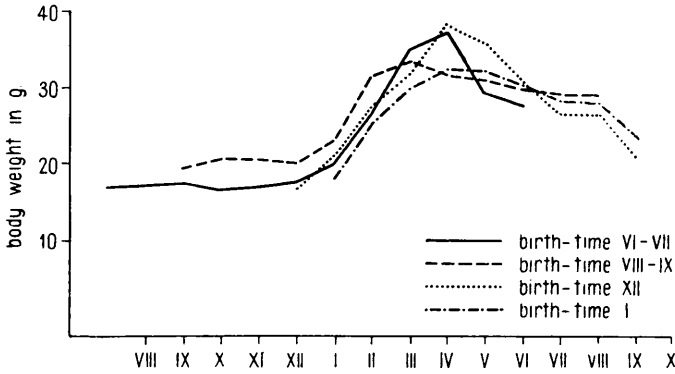


Fig. 1. Seasonal variations in body weight of *L. lagurus* (♂♂) with different birth-times.

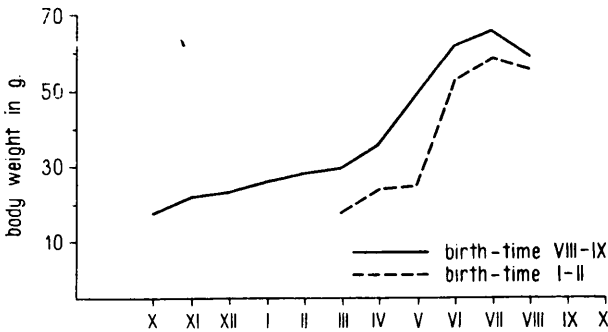


Fig. 2. Seasonal variations in body weight of *M. gregalis major* with different birth-times.

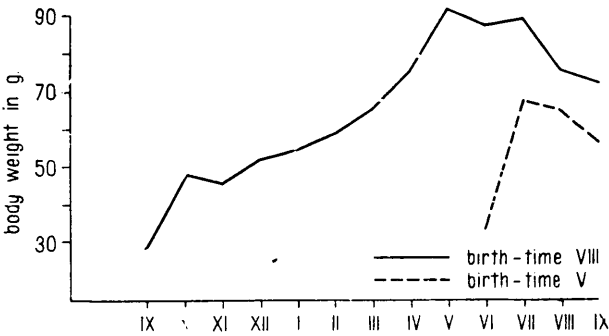


Fig. 3. Seasonal variations in body weight of ♂♂ *M. oeconomus* with different birth-times.

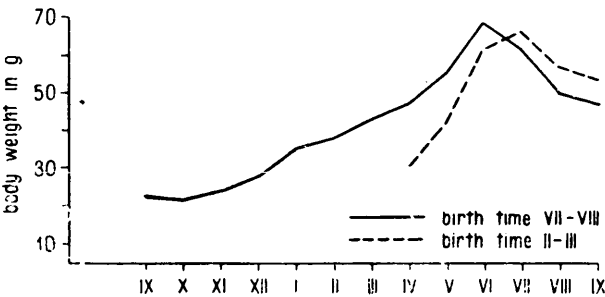


Fig. 4. Growth rate and seasonal variations in body weight of *M. mid-dendorffi* with different birth-times.

first period of their life and at the age of 1.5—2 months a cessation of their growth is observed. They began to grow again in the early spring. The maximum size of animals of different generations practically coincides in time (in different species the period of maximum weight is slightly different), but in spring animals it is established at the age of 2 months, and in the fall generations — not until the age of 10 months.

This regularity was traced under experimental conditions in our laboratory on 4 species (*Lagurus lagurus* (Pallas, 1773), *Microtus gregalis*

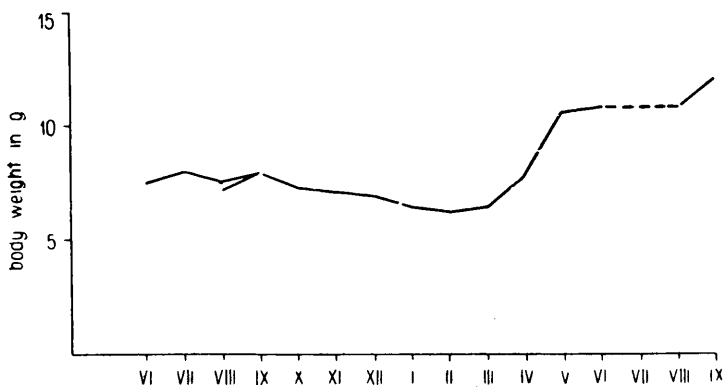


Fig. 5. Growth rate of *A. agrarius* under natural conditions.

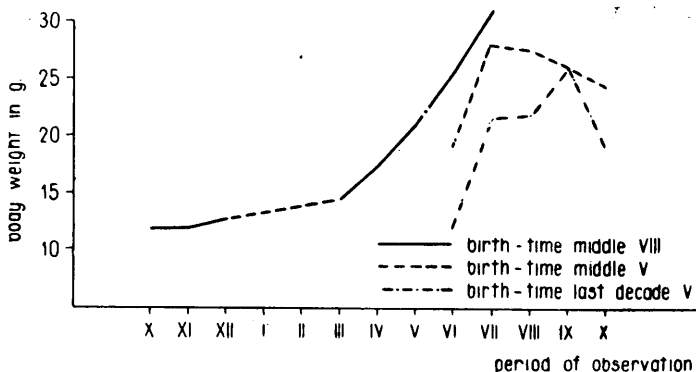


Fig. 6. Seasonal variations in body weight of *S. araneus* (♂♂).

(Pallas, 1779), *M. middendorffi* (Poliakov, 1881), *M. oeconomus* (Pallas, 1776), and under natural conditions on *Apodemus agrarius* (Pallas, 1771), *A. sylvaticus* (Linnaeus, 1758), *Clethrionomys glareolus* (Schreber, 1780), *C. rutilus* (Pallas, 1779) and some other species. The following figures give a good idea of this phenomenon as manifested by different species (Figs. 1—4). Special attention must be drawn to the fact that early in the spring the rodents of fall generations

grow almost as fast as the young animals born in the spring. The same regularity can be easily observed in investigation of the populations under natural conditions (Figs. 5, 6).

2. Sexual maturation

Field observations of many zoologists (Brambell & Rowlands, 1936; Pavlinin & Schwarz, 1953; 1955; Pavlinin, Schwarz & Susjumova, 1957; Kubik, 1957; Kryltzov, 1957; Karaseva, Nerskaja & Bernstein, 1957, and others) clearly demonstrated that the age of sexual maturation of voles correlates well with their birthtime. This phenomenon can be described as follows. The animals from spring and early summer litters reach sexual maturity very fast and begin to reproduce early in the summer. The animals born in the second half of the summer do not become sexually mature until the following spring and do not reproduce in the year of their birth. In other words the spring generations have a very short vegetative phase of development, the fall generations — a prolonged one.

Almost all the investigators try to explain the delay in sexual maturation by the direct influence of unfavourable conditions. Examples of relative rapid sexual development of the animals of some fall generations are adduced in corroboration of these views, but this is not the only possible explanation of the phenomenon described.

Stieve (1923) long since put forward a theory that the fall generations represent a "special physiological group" of animals which can attain sexual maturity only in the spring. A correct analysis of this phenomenon cannot, however, be based on field observations only, because it is difficult or even impossible to establish whether the cessation of growth and sexual maturation in late summer and in the fall are connected with unfavourable living conditions (low temperature, scarcity of food) or whether it is a manifestations of the physiological peculiarities of the fall generations of rodents.

We investigated this problem experimentally, which makes it possible to exclude the influence of different life conditions (except the alteration in the length of day) on the development of the animals. The main results of this work have been published (Pokrovsky, 1952), and we have therefore permitted ourselves to cite here only a table supplemented with new data and to say a few words in explanation (Table 1).

The experiment was carried out on *L. lagurus*. A strict correlation between the mean age of sexual maturation and the birthtime was established. For certain reasons it was impossible to make analogous observations of other species of rodents but fragmentary data obtained from the observations of two subspecies of *M. gregalis* (*M. g. gregalis* and

Table 1.

Age of sexual maturation of different generations of rodents under experimental conditions.

(M — mean age of maturation, in days, n — number of animals investigated).

Birth time Species		January	February	March	April	May	June	July	August	September	October	November	December
		<i>Lagurus lagurus</i>	n M	23 84.5	12 56.3	12 43.2	9 28.9	17 21.6	17 29.8	12 55.9	5 126.8	4 127.0	11 140.9
<i>M. gregalis gregalis</i>	n M	4 91.5	2 59.5	7 55.9	5 35.8	5 35.2	— —	— —	7 122.6	7 136.9	— —	— —	— —
<i>M. gregalis major</i>	n M	4 58.2	— —	6 58.0	3 58.0	6 52.0	3 51.7	4 39.5	3 62.0	7 132.6	— —	— —	3 101.7

Table 2.

Age of sexual maturation of different generations of *M. g. major*.

Generation	Birth-time	The period of sexual maturation	Age of sexual maturation and minimal body weight of mature animals (in g.)	
			♂♂	♀♀
Winter	February-March	April-May	2.0—2.5 months (20—30)	2.0—2.5 months (20—30)
Spring	April-May	June	1.0—1.5 months (25—30)	1.0—1.5 months (25—30)
Summer	June	End June-beginning July	1.5—2.0 months or 3.0—9.0 months (24.0—26.0)	10—15 days (10.0—12.0)
Fall	July	February-March	8.0—9.0 months (30.0—35.0)	8.0—9.0 months (25.0—30.0)

M. g. major) provide good evidence (especially if compared with the results of the experiment with *L. lagurus* and field observations) that the seasonal variation in the age of sexual maturation is not a special feature of *L. lagurus* but is a phenomenon widely distributed among rodents.

It must be especially emphasised that this regularity is well pronounced under the extreme living conditions in the Far North also, which can be demonstrated on *M. g. major* from the tundra regions of Jamal (Table 2). The very short reproduction period means that the age of maturation in



the polar forms takes place very early in life (Table 2, for reviews see Kopein, 1960).

We therefore reach the conclusion that not only the fall generations, but all the seasonal generations are "special physiological groups". One of their major particularities is the specific age of sexual maturation. Some other peculiarities of these groups will be cited later in this paper, some others were described earlier (Schwarz, Pavlinin & Susjumova, 1957).

As to the facts of winter reproduction of fall-born animals — they are a simple result of the great variation in the age of sexual maturation, which is common to each physiological group of animals. We cannot here go into details of this problem because it was thoroughly discussed in our paper cited above.

It is difficult to doubt that the difference in the age of sexual maturation and in the growth rate are determined by a complex of differences in more particular physiological patterns of the animals of different generations. Attention was drawn to some of them in our previous papers (Schwarz, 1959; Schwarz & Smirnov, 1959; Schwarz, Kopein & Pokrovsky, 1960), others, bearing particularly on the special aim of this article, will be discussed below.

3. Alterations in metabolic level and the weight of organs

In the animals from spring litters the metabolic level is markedly increased when compared with animals of fall litters of the same age. In addition to strict observations, this can be established by numerous indirect indices, such as enlargement of some internal organs (Schwarz, 1959; Schwarz & Smirnov, 1959; Kopein, 1960). The use of these indirect indices enables us to reveal some significant details concerning the physiological peculiarities of rodents born in different seasons.

A. Weight of adrenals

The adrenal weight may be regarded as one of the best indices of the physiological state of an organism. An enormous amount of literature exists (for reviews see Christian, 1950; Selye, 1950; Frank, 1953), which indicates that every condition which evokes a mobilization of internal forces of an organism as a reaction to stress causes hyperfunction of the adrenals, which is reflected in their histological structure¹⁾ and weight. Therefore it is especially interesting to investigate the weight of the adrenals in animals of different generations.

¹⁾ Special investigation, carried out on *Arvicola terrestris* (Krotova, 1962) in our laboratory, was devoted to this problem. •

Let us begin with the animals of the last generation, born in late summer or in the fall. Our data concerning 2 species of mice and one species of voles are given in Table 3.

Table 3.

Seasonal alterations in relative adrenal weight in animals of fall generations.

Month	<i>A. agrarius</i>		<i>A. sylvaticus</i>		<i>C. glareolus</i>	
	B o d y w e i g h t					
	10.1—15.0	15.1—20.0	15.1—20.0	20.1—25.0	15.1—20.0	20.1—25.0
IX	0.170±0.002 n = 184					
X	0.160±0.0040 n = 115	0.175±0.007 n = 20	0.310±0.017 n = 16		0.180±0.005 n = 43	
XI	0.147±0.008 n = 14	0.155 (0.095—0.228) n = 4	0.276±0.014 n = 11		0.137±0.010 n = 18	0.179±0.007 n = 7
XII	0.116 (0.080—0.173) n = 4		0.263 n = 1		0.212±0.013 n = 39	
I						
II					0.151±0.014 n = 17	0.152 (0.120—0.195) n = 4
III	0.113 (0.73—0.154) n = 2	0.170 n = 1	0.255 (0.240—0.270) n = 2		0.127±0.08 n = 17	0.094 (0.093—0.095) n = 2
IV	0.158±0.005 n = 15	0.166±0.009 n = 19	0.309±0.018 n = 12	0.201±0.012 n = 23	0.206±0.012 n = 17	0.282±0.063 n = 7
V		0.153 (0.100—0.194) n = 3		0.245±0.022 n = 8		
VI	0.154±0.011 n = 15		0.183±0.014 n = 9			

As long as the rodents of the last generation begin their independent life when the weather is really cold with heavy rains their relative adrenal weight is high (the concrete indices differ significantly with different species, but in comparison with the animals which developed under more favourable conditions, the increase in adrenal weight is quite obvious in all the species examined).

During the process of adaptation of animals to winter life conditions the adrenal weight decreases markedly and reaches a minimum value in mice as early as December, and in *C. glareolus* not until the end of the winter. It should be mentioned that with animals of different weight an

analogical alteration in the adrenal weight is observed, but the larger animals possess larger adrenals.

As has already been said cessation of growth occurs during the winter and animals of most species do not begin to grow again until April. During this period a rapid increase of the adrenals can be observed in all the animals examined. Some time afterwards a new decrease of the adrenals is observed.

These data indicate clearly that there are 2 periods of increased adrenal weight: in spring (in connection with reproduction) and in the fall (in connection with unfavourable conditions). The same phenomena can be observed in other seasonal generations of rodents, but in this case the picture is more complex, because the relative reaction of different species to cold stress and to reproduction is different. This depends not only on

Table 4.

Seasonal alterations in mean adrenal weight in *M. g. major*.

	Winter generation	Spring generation	Summer generation	Fall generation
n	111	63	32	16
$M \pm m$	0.119 ± 0.028	0.119 ± 0.021	0.186 ± 0.015	0.196 ± 0.021
lim.	0.052—0.233	0.052—0.294	0.069—0.432	0.085—0.392

the differences in living conditions but also on the physiological specificity of the animals.

In the case of the muskrat it was shown (Schwarz & Smirnov, 1960) that the spring generations are characterised by significantly larger adrenals when compared with the animals of the second generation at the same age. In females born in spring the adrenal weight is almost three times as great as in animals of the same age but born in summer. It was shown that this difference is due to the beginning of sexual maturation and the hyperfunction of the hypophysis in spring animals.

In some other species a reverse phenomenon is observed: the animals of those generations which begin their independent life later in the summer are characterized by more pronounced enlargement of the adrenals.

An especially interesting picture of the alteration of the weight of the adrenals may be observed in *M. g. major* — a typical representative of tundra fauna. In this species (Table 4) a regular increase of the adrenals can be observed in the subsequent generations. Animals born in winter have a minimum adrenal weight — it reflects the relative good and stable living conditions under the snow. Reproduction under the snow is charac-

teristic of this form — as it is of the lemmings. The summer and fall generations which develop under the extremely severe conditions of the Far North have large adrenals.

These data, like many others published earlier — as we may recall — demonstrated that the adrenal weight reflects the alterations in life conditions and the physiological differences between seasonal generations of rodents.

Additional data may be obtained by analysis of the same phenomenon under experimental conditions. Table 5 indicates that the differences between the seasonal generations of rodents in respect of their adrenal

Table 5.

Seasonal alterations in adrenal weight in *M. o. chahlovi* under experimental conditions. All the animals compared at the age of 3 months.

Birth time	n	Body weight	Relative adrenal weigh
I	24	60.3±3.4	0.125±0.009
III	15	67.5±3.5	0.108±0.012
IV	6	62.1±3.9	0.122±0.023
V	12	54.8±2.4	0.163±0.013
VII	13	29.4±2.2	0.154±0.016
IX	16	29.5±1.9	0.140±0.012

weight can also be observed in animals in captivity, due to stable living conditions. All the animals investigated are of the same age (3 months). It is therefore evident that the differences observed cannot be attributed to age differences in the animals. An obvious but important conclusion derived from this table is the statistically significant decrease in the adrenals in the late summer and fall generations. This shows that an increase in the weight of the adrenals of the fall generations is, under natural conditions, a direct reaction to cold-stress. Starting with animals born in July a clear decrease in adrenal weight takes place in the subsequent generations. The minimum adrenal weight is established in the animals born in March. A rapid increase in the weight of the adrenals then occurs and the voles born in May have the largest adrenals (0.163 mg/kg). This means that the spring enlargement of the adrenals is manifested in captivity as well as in nature. It is worth mentioning that the enlargement of the adrenals fully coincides with the time of the animals' most rapid growth but does not coincide with the beginning of sexual maturation and sexual activity. It is obvious from the same table

that the enlargement of testes (a sign of sexual development) is evident in the generations born in January, and that the enlargement of the adrenals takes place parallel to the decrease in the weight of the testes. This phenomenon deserves special analysis.

It was previously shown that in nature sexual development is accompanied by an increase in the adrenals. It is more pronounced in females, but can be observed in males as well. As this is not the case in captivity (in our experiments each pair of voles was kept in a separate cage) we came to the conclusion that the real reason for the spring enlargement of the adrenals in males is not sexual maturation and reproduction *per se* but is connected with the phenomena which accompany reproduction: search for females, fights between males, migrations, all of which takes place under relatively unfavourable spring living conditions. All these phenomena are excluded if each pair of animals is kept in a separate cage and the enlargement of the adrenals does not take place at the time of sexual maturation.

A rapid increase in the adrenals is observed only in the animals born in May and examined in August. In the animals of this generation the absolute and relative weight of the testes decreases (compared with the animals born earlier). In itself this phenomenon, which indicates a decrease in sexual activity, is quite understandable, because the maturation of the animals occurs in the second half of the summer, but the parallel increase in the adrenals is very interesting. It indicates that reproduction during a period of decrease in sexual activity is accompanied by a greater strain on the organism than in spring months. Here we can perceive an analogy with the hyperfunction of the endocrine glands in the reproducing animals of considerable age, when the reaction of the sexual glands on endocrine influences has decreased. From this point of view the animals born in May are already old at the age of 3 months²⁾. This conclusion is very important to the special aim of this paper and can be supported by analogous observations of the same subspecies in nature³⁾.

It is well known that rapid increase of the adrenals takes place during pregnancy. The older the female the more distinct is the enlargement. This regularity was demonstrated by comparison of the adrenals of females of *M. oeconomus* caught in Jamal tundra in July 1958. At that time the weight of the adrenals of the male voles was $= 259 \pm 23.0$ mg/kg (in the older males 233 ± 11.4). All the females were pregnant and accordingly their adrenal weight was significantly higher: in old fe-

²⁾ Hyperfunction of the adrenals is regarded as a compensatory mechanism connected with physiological stress induced by reproduction.

³⁾ The breeding stock was formed from the animals of a tundra subspecies — *M. oeconomus chahlovi*.

males = 477.0 ± 26.1 , in the young ones = 330.0 ± 36.4 mg/kg. The results of these observations agree with the theoretical expectation: the older the female the better expressed is the increase in the adrenals during pregnancy. The most interesting fact, however, is that an enormous increase in adrenal weight was observed not only in really old animals (born the previous year) but also in females 3 months old. Their adrenal weight was even greater in comparison with really old females — 488 ± 48.4 mg/kg. It would seem that the spring generations of rodents in some respects become physiologically old at a very young calendar age.

These data may serve as an indirect but significant demonstration of the senescence rate of the spring generations, because the decrease in the capacity of the animals to maintain normal existence under increased physiological stress without compensatory endocrine mechanism is rightly considered one of the main indications of senescence (C o m f o r t, 1959).

To sum up. All the data mentioned above demonstrate that seasonal generations of rodents differ significantly as to the weight of their adrenals. Concrete manifestation of this phenomenon is different in the species compared but as a general rule the spring generations, other things being equal, are characterized by large adrenals. This corresponds with their growth rate, development rate and certain other biological peculiarities.

B. Thymus weight

The weight of the thymus is one of the most important indications of the development of the young animals. A well developed thymus gives evidence of a high degree of vitality in young animals and is connected with their rapid growth and development. This observation was substantiated by many different species and its biological significance is nowadays sufficiently clear. An involution of the thymus takes place in adult animals (in humans approximately at the age of 15 years).

Investigation of the alterations in the thymus weight is a suitable method for the analysis of the differences in development of different seasonal generations.

In the spring generations the thymus reaches its maximum weight very rapidly (in *A. agrarius* for instance as much as 2000 mg/kg body weight) and decreases to 100 mg/kg in the early fall. In the spring generations a practically full involution of the thymus takes place by the age of 4 months. Development of the thymus in rodents born in late summer is quite different. In these generations the decrease in the thymus weight in the fall is also well pronounced but in the spring a corresponding increase of the thymus weight takes place parallel to the renewal of growth of the animals.

Curves (Figs. 7, 8) give a good picture of the main point of this process, which was observed in our laboratory on *A. sylvaticus*, *A. agrarius*, *M. oeconomus*, *C. rutilus* and some other species of rodents. The animals from fall litters are at approximately the same stage of development at the age of 10 months as the spring animals at the age of 2—3 months. It

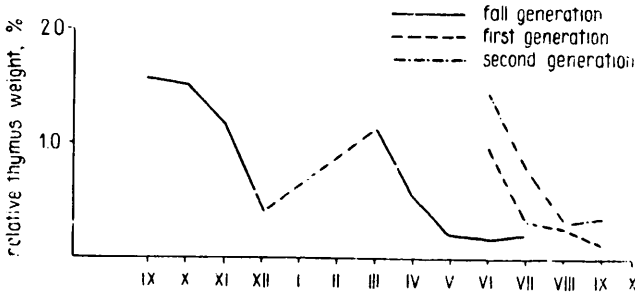


Fig. 7. Seasonal variations in thymus weight of *A. agrarius* under natural conditions.

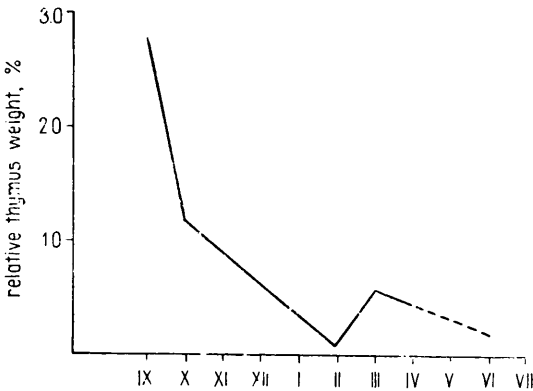


Fig. 8. Seasonal variations of the thymus weight of *C. glareolus* in the fall generation.

must be mentioned that this phenomenon was observed in different geographical environments (from the steppe regions to the tundra) and must therefore be regarded as a common feature peculiar to the age physiology of mouse-like rodents.

C. Heart and kidneys

In our previous papers we have already had the opportunity of demonstrating that seasonal generations of rodents differ significantly as to the weight of heart and kidneys. Thus, for instance, the first generations of *Ondatra zibethica* have (in comparison with the animals of spring generations of the same age) lesser relative weight of the heart, liver and intestines (Schwarz & Smirnov, 1959). Analogical data were ob-

Table 6.

The relative weight of heart and kidneys in *A. agrarius*, *A. sylvaticus* and *C. glareolus* of different generations.

(Age — 3 months, body weight — 15-20 g.).

Month	<i>A. agrarius</i>		<i>A. sylvaticus</i>		<i>C. glareolus</i>	
	heart	kidney	heart	kidney	heart	kidney
VIII	7.2 ± 0.16 n = 21	8.0 ± 0.27 n = 21	8.3 ± 0.18 n = 7	8.6 ± 0.29 n = 7	6.1 ± 0.15 n = 18	8.0 ± 0.23 n = 17
IX	8.7 ± 0.15 n = 40	7.8 ± 0.21 n = 39	8.5 ± 0.23 n = 14	7.5 ± 0.31 n = 13	6.9 ± 0.14 n = 17	7.9 ± 0.21 n = 17
X	9.1 ± 0.24 n = 21	7.7 ± 0.4 n = 20	8.9 ± 0.22 n = 16	7.8 ± 0.26 n = 15	7.2 ± 0.13 n = 46	7.7 ± 0.12 n = 44

Table 7.

Seasonal changes in heart weight and kidneys weight of the rodents of the last fall generations.

(Birth-time of all animals examined — August—November, body-weight — 15-20 g.).

Month of observation	<i>A. agrarius</i>		<i>A. sylvaticus</i>		<i>C. glareolus</i>	
	heart	kidney	heart	kidney	heart	kidney
IX	9.6 ± 0.09 n = 184	8.5 ± 0.08 n = 184	8.5 ± 0.23 n = 14	7.5 ± 0.31 n = 13		
X	9.8 ± 0.1 n = 121	8.5 ± 0.11 n = 120	8.9 ± 0.22 n = 16	7.8 ± 0.26 n = 15	7.2 ± 0.13 n = 46	7.7 ± 0.12 n = 44
XI	10.5 ± 0.31 n = 14	7.6 ± 0.15 n = 14	9.1 ± 0.22 n = 10	7.7 ± 0.37 n = 11	7.0 ± 0.19 n = 18	6.8 ± 0.17 n = 18
XII					6.9 ± 0.12 n = 40	6.7 ± 0.16 n = 39

tained on some other species of rodents (Schwarz, Kopein & Pokrovsky, 1960).

Some additional details of this interesting question are discussed in the present paper.

In the south regions of the forest zone reproduction of *A. agrarius* and *A. sylvaticus* takes place during the whole of the warm period of the year, their populations being therefore replenished by new generations of mice

every month. It is therefore possible to analyse the differences between litters born 20—30 days apart. Table 6 illustrates the differences between mice of summer, late-summer and fall litters.

If the animals of the same age and equal size are compared it is evident that every subsequent litter differs from the previous one by increased weight of the heart and decreased weight of the kidney. Below we shall try to outline the concrete biological sense of these differences, but it must

Table 8.

Seasonal changes in relative heart weight and kidneys weight of *M. g. major* of different generations.

Weight group		20.0—30.0 g.					30.1—40.0 g.				
Period of observation		15. IV.—20. V.	1. VI.—20. VII.	1. VII.—15. VII.	1. VIII.—30. VIII.	10. IX.—15. X.	15. IV.—20. V.	1. VI.—20. VI.	1. VII.—15. VII.	1. VIII.—30. VIII.	10. IX.—15. X.
kidney	n	12	35	26	10	13	11	57	20	12	8
	lim.	4.1—7.2	4.6—8.3	6.0—11.3	5.9—8.1	4.3—7.0	4.5—7.0	4.5—7.8	5.7—9.9	5.9—9.9	6.1—8.1
	M± m	5.7 ±0.25	6.7 ±0.15	8.3 ±0.23	6.8 ±0.17	5.9 ±0.47	5.2 ±0.19	6.0 ±0.10	7.8 ±0.22	7.7 ±0.32	7.0 ±0.23
heart	n	12	35	26	14	23	11	46	22	16	10
	lim.	4.5—7.6	4.3—7.9	5.5—7.9	5.1—8.6	5.5—7.4	5.0—6.6	4.9—8.7	5.6—7.8	5.1—7.9	5.8—7.5
	M± m	6.2 ±0.23	6.2 ±0.14	6.8 ±0.11	6.1 ±0.11	6.4 ±0.11	5.7 ±0.44	5.7 ±0.14	6.3 ±0.13	6.4 ±0.24	6.6 ±0.16

also be remembered that significant differences are exhibited in the relative growth rate of several organs. This is especially apparent if the animals from the last litter (born in August—September) are examined (Table 7). Animals from these generations cease their growth as soon as they reach a weight of 10—20 g (at the age of one month or even younger). Nevertheless the relative weight of the heart continues to increase from September till November, while that of the kidney decreases. The general peculiarities of these alterations coincide well in the species examined. Thus very significant morpho-physiological differences can be observed even between subsequent litters. It is quite natural that when spring and fall litters are compared these differences may be much more pronounced. Since examples of such differences have been given in previous papers

we shall confine ourselves to data on the northern subspecies of *M. gregalis* (Table 8). We must also add that in some cases the differences between seasonal generations can lead to a disturbance of well-known morpho-physiological dependences.

In the vast majority of animals the relative kidney weight is inversely proportional to the size of the body. But in a field mouse weighing 20—25 g, born in July and examined in August, the kidney index = 8.0 ± 0.23 and in mice weighing 10—15 g, born in September and examined in November, this value is only 7.6 ± 0.15 . We could give many examples of this sort.

Let us now refer to the analysis of data obtained under laboratory conditions. Six generations of *M. oeconomus chahlovi* are represented in

Table 9.

Relative heart and kidney weight of *M. oeconomus chahlovi* of different birth-times at the age of 3 months.
(Experimental colony).

Birth time	n	Heart	Kidney	Body weight
I	24	3.27 ± 0.093	3.65 ± 0.085	60.3 ± 3.4
III	15	3.51 ± 0.14	3.79 ± 0.12	67.5 ± 3.5
IV	6	3.45 ± 0.13	4.26 ± 0.17	62.1 ± 8.9
V	12	3.61 ± 0.08	4.45 ± 0.17	54.8 ± 2.4
VII	13	4.23 ± 0.15	4.32 ± 0.12	29.4 ± 2.2
IX	16	4.41 ± 0.4	4.30 ± 0.10	29.5 ± 1.9

Table 9. From this table it is apparent that the general direction in the alteration of the relative heart weight is inversely proportional to the alterations in body weight (growth rate); the greater the body weight the smaller the relative heart weight. Careful analysis of the data, however, enables us to detect some deviation from this regularity. The growth rate of voles born in the late summer remains practically unaltered. Therefore voles 3 months old born during the period from June to September attain on an average the same weight. Nevertheless the voles born in September have a significantly higher heart index (the differences are statistically significant).

Even more interesting is the seasonal alteration of the kidney index. The growth rate of the first 3 generations is nearly equal, but in each subsequent generation a regular increase in the kidney index can be observed

and reaches a maximum in the animals born in May. After this time, despite a decrease in body size, the kidney index decreases. The alteration in relative growth rate of different organs in the animals of different generations can be detected under experimental conditions.

In accordance with the special aim of this paper we have paid more attention to the differences between the fall and the spring generations. All the data mentioned above, as well as some others published earlier, show that the fall generations are characterized by a decreased kidney index and an increased heart index.

It is known that the relative kidney weight is a fairly reliable index of general intensivity of the metabolic rate (S c h w a r z, 1960). This does not of course mean that the metabolic rate of an animal can be measured by

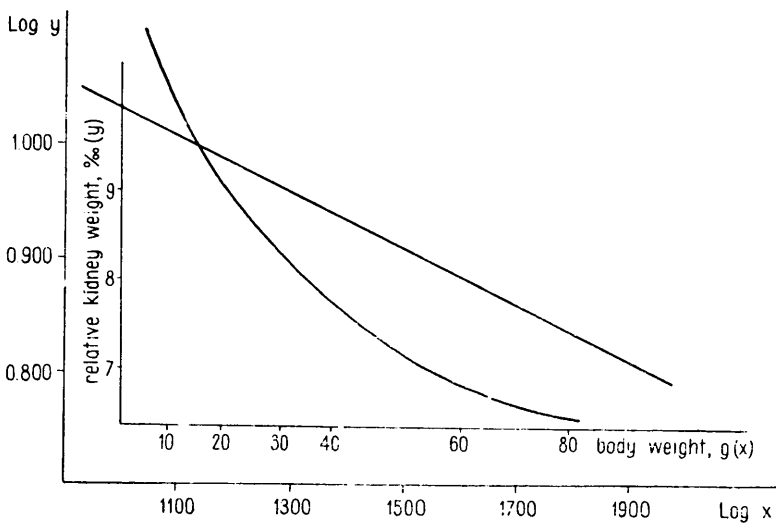


Fig. 9. The relation between body weight and relative kidney weight of *M. oeconomus*, Polar Ural, August, 1961.

weighing the kidney; the relation here is more complex. In the vast majority of cases, however, all the conditions which favour intensification of metabolism are accompanied by an enlargement of the relative kidney weight. A decrease in metabolic level is connected with a relative decrease of the kidney index.

On the basis of this regularity the small kidney weight of the fall rodents can be explained by their low metabolic level. This explanation is in agreement with observations which show that in the autumn and winter the metabolic level of various animals decreases and therefore, taking into consideration the biological peculiarities of the fall generations

(cessation of reproduction, their way of life under snow, etc.), is not likely to give rise to objections.

The relative heart weight is also generally connected with body size by inverse correlation. In some cases, however, a decrease in kidney weight is accompanied by an increase in the heart index. This contradiction is easily explained by means of an ecological analysis of some particular observations. It was found that in all such cases a general decrease in metabolic rate was accompanied by an increase in the physical activity of the animals (an intensification in heart activity) at least in some particular periods of the life cycle (Schwarz, 1960; 1962). We come across a similar situation in investigating the biological specificity of seasonal generations of rodents. The cessation of reproduction, the decrease in the growth rate and a way of life under snow lead to a general decrease in the metabolic level. The decrease in the metabolic level is of greatest importance to the animals since it creates conditions for the formation of reserves of energy (in the form of fat or glycogen) in the organism. It is at this very time, however, that a fall redistribution of rodents takes place; changes of habitat sometimes become real migrations. An increase of movement, of physical activity of the animals is therefore inevitable. In accordance with the alterations in the life history of the animals their heart index increases and that of the kidney decreases.

A question still remains to be explained. Are the morphophysiological peculiarities of the fall generations a direct reaction to their mode of life and external conditions or should they be regarded as being to some degree a manifestation of a genetically fixed rhythm of rodent physiology.

An analysis of experimental data gives us an answer to this question. In captivity under almost stable life conditions the same alterations in morpho-physiology of the fall generations were observed as in nature. This means that the seasonal alterations of the light factor act like a signal, which induces a decrease in growth rate, accompanied by an increase in the heart index and a decrease in the kidney index.

During the winter the relative weight of the kidney remains at a comparatively low level and begins to increase only with the beginning of the spring. At this time, however, a rapid increase in growth rate occurs. A simple confrontation of the kidney weight of animals in different spring months cannot therefore explain the real regularities which govern the relative growth rate of different organs, and for this reason we used an examination of allometric dependences for this analysis.

Correlation between the body weight of separate organs is expressed by an allometric equation $y = bx^a$ (x — body weight, y — organ weight, a — allometric exponent which reflects the correlation between body weight

and organ weight, b — a coefficient which reflects the alterations in weight under the influence of all the other factors except the body weight). In most cases $a \neq 1$, organ growth is not isometric, but allometric growth.

In the case of the kidneys a is always less than 1; with the increase in body weight a decrease in relative kidney weight occurs. Comparison of animals with different birth-dates shows that this correlation is expressed in a specific way. To illustrate this we shall use an experimental colony of *L. lagurus*.

The correlation between the kidney index and the body weight in animals born in the spring and killed when 120 days old can be described by the equation $y = 107x^{-0.893}$. In voles of the same age, but born in winter,

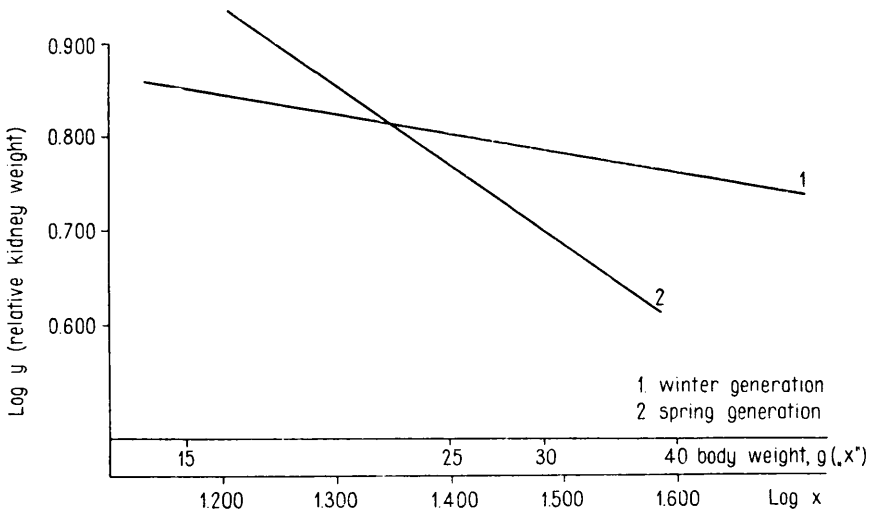


Fig. 10. The relation between body weight and relative kidney weight in *L. lagurus* of different generations.

$y = 14.62x^{-0.254}$. Comparison of these equations shows that the correlation between the body weight and kidney weight in these two groups of animals from one colony is different. First of all the equations demonstrate that when all the other conditions are equal, the kidney weight of spring voles is essentially greater than that of animals born in winter (factor b is 8 times as great). This result is of some interest but could be foreseen, as it reflects an increase in the metabolic rate of the animals in spring. Another phenomenon is more interesting. The allometric curves show that the increase in body size in the spring voles is connected with a much greater decrease in relative kidney weight when compared with the animals born in winter. The following explanation of this unexpected fact can be given.

The whole life of the animals born in spring — from birth to death — is a period of rapid growth. Under these conditions the relation between body weight and kidney weight is manifested very clearly. The position with the animals born in winter differs completely. The first stages of their development coincide with the period of retarded growth. As spring begins some of the animals enter the phase of fast growth. The larger animals are those which react earlier to the seasonal alterations in life conditions and begin to grow faster, and their metabolic rate and kidney increase accordingly. A decrease in the relative kidney weight with increasing body weight becomes less pronounced.

Analogical investigation was made of *M. oeconomus*. The data obtained are shown on Fig. 11. In winter voles the relation between the body weight and kidney index is expressed as $y = 11.25x^{-0.268}$, in spring voles as $y = 57.46x^{-0.64}$. This result concurs with the result of the observations of *L. lagurus* even as to details.

All the data represented above demonstrate that significant morpho-physiological differences are evident between seasonal generations of rodents. These differences are manifested in the regularities of relative growth of the internal organs and are based on differences in metabolic level.

The range of problems discussed provides an analysis of one question more. It is well known that in many if not all species (including man) sexual maturation is accompanied by an increased growth rate (for review see Schwarz, 1962). This regularity is especially well expressed in shrews. Individual animals from this group, which attain sexual maturity in the first year of their life, greatly exceed the unmaturing animals of the same age in size. It would seem that sexual maturation stimulates rapid growth. New data enable us to go into some details of this interesting problem.

The weight of the testes is positively correlated with the body weight in all the species investigated (in *M. oeconomus* the coefficient between these indices $r = + 0.814 \pm 0.091$). If the transition of an animal from the vegetative to the generative phase of development is initiated by sexual maturation the relationship described must be especially well expressed early in the spring, because the larger animals are those which enter the generative phase earlier. In reality a reverse phenomenon is observed. In 3-months old *M. oeconomus* born in January the correlation coefficient between body weight and testes weight is only $r = + 0.354 \pm 0.178$. This means that the spring acceleration of the growth rate and the corresponding increase in kidney weight occurs earlier than the beginning of the enlargement of the testes. On this basis it is of course difficult to state that the spring increase in the secretion of gonadotropic hormones of the

hypophysis begins later than that of the somatotropic ones, because the possibility cannot be excluded that the initial phases of the activation of sexual glands do not induce enlargement of the testes. These data, however, undoubtedly indicate that the transition of animals from the vegetative phase of development to a generative one is a complex physiological process integrating the increase in growth rate, sexual maturation and metabolic rate of the animals.

D. The lens weight

Of recent years the dry weight of the lens of the eye has been used as an indicator of the age of different animals (for reviews see Lord, 1959), and in all probability this method will become widely used in the near future. It was tested in our laboratory in connection with other problems, on *O. zibethica*, *A. terrestris* and some other species of voles, *Alopex lagopus*, *Mustela erminea* and by L. Toporkova (in litt.) on frogs. In all the experiments the results were the same: the senescence of animals is accompanied by a regular increase in the weight of the lens.

W. Popov & A. Al-Sakini (1962), in summing up modern views on the peculiarities of the growth of lens write: "The eye lens of the *Vertebrata* are subject to regular histological alterations throughout almost the whole of their life. These alterations consist in permanent formation of lens fibres owing to reproduction of the cells of the anterior epithelium and the degeneration of old centrally situated fibres, which leads to a formation of a compact homogenous nucleus of fibrous mass". As mentioned above the dry lens weight increases during the whole of the life of the animal; the lens growth curve takes on the character of a hyperbole. It indicates a gradual decrease in the reproduction rate of the epithelium cells, that is, the tempo of the aging process on cell level. It is therefore especially interesting to investigate the development of this process in animals of different generations. Our investigations were carried out on two species, and the following results were obtained:

M. gregalis, animals 110—149 days old, born in January, the dry lens weight was $=2.16 \pm 0.07$ mg, in animals of the same age but born in May $=2.72 \pm 0.06$ mg.

M. oeconomus, animals 90—100 days old, from spring (March) and late summer (July) litter were compared. In the first group the lens weight was $=2.54 \pm 0.147$, in the second 1.94 ± 0.08 mg. In both cases the differences between the seasonal generations in respect to lens weight are statistically significant. These differences are pronounced if not absolute but the relative lens weight (in relation to body weight) is compared.

From these data it appears that the vegetative phase in the development of rodents is characterized by a decreased rate of cell reproduction. An

obvious conclusion derived from this study is that the slowly growing generations of rodents are physiologically younger than the animals of the same age from the faster growing generations; they retain their capacity for fast growth with the alteration of life conditions in the spring.

4. The life span of different generations in nature

The age of the animals from natural populations was estimated by means of several methods (general look of the skull, the degree of wear of teeth, adrenal weight, thymus weight, development of gonads, lens weight etc.). It is therefore possible to estimate the age of the animals with sufficient accuracy. Errors are possible but if the data are biometrically treated they are negligible. If we subdivide the animals in age groups (first generation, second generation... fall generation and so on) these errors are eliminated.

It then becomes possible to estimate the life span of animals of different generations in nature. The relevant data are summarized in table 10.

Table 10.

The life span of different seasonal generations of rodents under natural conditions.

Species	Fall generation			Spring generation			Maximum life span during the snowless period (in months)	
	Birth-time	Time of disappearance from the population	Maximum life span (in months)	Birth-time	Time of disappearance from the population	Maximum life span (in months)	Fall generation	Spring generation
<i>A. agrarius</i> (Sverdlovsk region)	Aug.-Sept.	July	11—12	May-July	Sept.	6	6	6
<i>C. rutilus</i> and <i>C. glareolus</i> (Udmurt ASSR)	Aug.	Oct.	14	May	May	12	9	7
<i>M. middendorffi</i> (Jamal)	July-Aug.	Sept.	14	May-June	Oct.	5	6—7	5
<i>M. gregalis</i> (Jamal)	June-July	July	12—13	Apr.-May	Sept.	5	5	5
<i>M. oeconomus</i> (Jamal)	Aug.	Aug.	12	May	Oct.	5	5	5

From these data it appears that rodents born in late summer live essentially longer as compared with the animals of spring generations. This conclusion agrees with some data in literature on this subject, but the reason for this phenomenon is not clear.

First of all we have to disprove one of the possible and often used explanations. The major part of the life of the fall generations of rodents is lived during the winter period. In winter shelter conditions are more favourable, the rodents suffer less from predators and therefore their mean life span increases. This assumption is based on real facts: in winter time the rate of mortality due to predators decreases sharply. Examination

Table 11.

Differential mortality of different generations.
(Explanation in the text).

W/I — the relation (in %) of the number of animals of fall generations to the number of spring generation (W/I + W).

I/II — the relation of the number of animals of the first generation to number of second generation.

Period of observation	Species							
	<i>A. agrarius</i> (Sverdlovsk region)		<i>M. oeconomus</i> (Jamal)		<i>M. gregalis</i> (Jamal)			
	W I	I II	w I	I II	W/I	I II	II III	III/IV
V	—	—	—	—	33±6.5	—	—	—
VI	48±9.0	89±7.4	92±5.4	—	10±2.6	49±3.3	82±3.6	—
VII	27±13.4	44±11.7	60±2.6	81±9.0	6±3.2	46±4.7	40±3.9	69±4.0
VIII	20±17.5	40±15.5	37±11.0	52±12.5	—	46±15.0	22±7.8	28±5.1
IX	22±13.8	29±9.3	—	38±8.8	—	—	—	11±3.6

of table 10 shows that the life span of fall generations, even during the snowless period, exceeds the whole life span of the spring generations.

On the other hand, if we compare the mortality rate (removal from the population) of rodents of different generations during a period when the compared groups do not differ in respect of behaviour, reproduction and the degree of general activity (under these conditions the differences in mortality rates caused by predators are not significant), it will be seen that the mortality rate of "old" animals is higher than that of the "young" ones. In the animals of fall generations, however, the increase in mortality rate can be observed at the age of 10 months, and in spring generations as early as at the age of 3 months. This is illustrated by Table 11.

It is clear that data on the mortality rate of different generations agree with their morpho-physiological peculiarities.

III. DISCUSSION

An obvious conclusion suggested by the data given is that significant ecological and morphological differences exist between different generations of rodents. These differences are based on the peculiarities of seasonal generations in respect of development rate, growth rate and metabolic level.

As has already been said, a considerable amount of various and well co-ordinated data indicate that a decrease in metabolic rate leads to an increase in the life span, and thus there are grounds for expecting to discover signs of "physiological youth" in old animals from fall generations. This supposition was corroborated by the results of the present study.

At the present time there are no universally recognized criteria of senescence. Investigation of the aging process on a molecular level (Medvedev, 1961; Oeriu, 1962 etc.) justify optimistic conclusions, but the problem is far from solution. Suffice it to say that the author of one of the most valuable recent summaries of the problem — Comfort (1959) adheres to the opinion that it is useless even to search for some universal character of senescence.

Senescence is a complex biological process, which starts as early as in the embryonic period of life and can be characterized by a permanently increasing differentiation of an organism and by alterations of main physiological features. The most significant manifestation of this process takes place more slowly in fall generations than in spring generation owing to the prolongation of the vegetative phase of development. The following phenomena must be especially emphasised:

1. A complex of biological peculiarities reflects the decrease in metabolic level of fall generations.

2. The rodents of fall generations which survive the winter period possess energy of growth comparable to that of spring rodents 3—4 times younger. The physiological mechanisms of this phenomenon are apparently connected with the anabolic effect of the androgens and estrogens stimulating protein synthesis. It is most significant that the organisms of old animals from the fall generations maintain their capacity for rapid growth, as rapid as in very young animals. The intensification of protein synthesis still inhibits the phenomena of skin degeneration and external signs of senescence. The fall rodents at the age of 10 months are in the true sense of the word young animals, as soon as the assimilative processes in them predominate over the dissimilative ones.

3. In the spring a remarkable increase in thymus weight of fall rodents can be observed; in spring animals of the same age the thymus is comple-

tely involuted. In order to draw correct conclusions from these observations the well known role of this gland in the process of growth and development of young animals, its role in protein metabolism and the classical experiments of P a r h o n (1959), which demonstrated that signs of rejuvenation can be observed even by very old animals under the influence of thymus extracts, must be borne in mind. The injection of thymus extracts evokes activation of tissue metabolism.

4. The experiments with the lens weight clearly demonstrate that during the vegetative phase of development the tempo of cell reproduction decreases markedly. It may therefore be assumed that the process of tissue differentiation is inhibited, which in the end leads to a prolonged maintenance of physiological youth.

All these data as a whole indicate that the vegetative phase in development of rodents is not only a period of inhibited growth rate and sexual maturation but also a period of inhibited senescence. This conclusion is in agreement with experimental data (M c C a y, 1952; D i c k e r s o n & W i d d o w s o n, 1960; N i k i t i n, 1961) and modern conceptions of the relation between the life span of animals and their metabolic rate. This paper indicates that alteration in the rate of senescence can be observed during the normal course of the life cycle of animals under natural conditions. Great differences in calendar age are not therefore always accompanied by corresponding differences in the physiology of the animals compared. This means that the rate of senescence is not strictly fixed genetically but may vary to a great degree.

In fact fall rodents spend more than half of their life in a state of inhibited senescence. Under experimental conditions the temperature and nutrition regime remain unaltered during the whole year and the sole cause of the transition of the animals from the vegetative to the generative phase of development may be the alteration of light conditions. The shortening of the day light in the fall leads to a hypofunction of the hypophysis and inhibits sexual maturation with all the accompanying phenomena (decrease in metabolic rate and growth rate, hypofunction of other endocrine glands etc.) which together result in inhibition of senescence.

The results of these investigations show that it is in principle possible to regulate the process of senescence by the influence of external conditions without such violent influences as chronic starvation (compare M c C a y, 1952). It becomes evident that prolongation of the life span can take place not only at the expense of the prolongation of the later stages of development ("active old age"), but at the expense of youth. In natural conditions it can be observed in a great number of species. This is quite understandable. If the fall rodents grew old at the same rate as the spring

animals they would become decrepit senile animals before the season of reproduction occurs and could not maintain the reproduction of the population. Therefore the prolonged life span of fall rodents is biologically fully understandable.

Are the phenomena described typical of rodents only? We have no completely analogical data on other groups of animals, but some fragmentary data on *Soricidae* and *Lagomorpha (Ochotona)* indicate that similar phenomena are observed in other orders. Further development of our investigations tends in this direction, and will be accompanied by attempts at working out methods of influencing the process of senescence in mammals of different groups.

IV. SUMMARY

Many observations in comparative gerontology, carried out on different animals (insects, fish, mammals) by different biologists demonstrated that one of the possible cause of the tempo of the ageing process may be the relative intensity of the metabolism. The investigations of the authors of this paper show that this point of view find substantiation by the analysis of the chronographic variability of different species of mammals. One of the main ways of the investigation of this problem is the analysis of the biological peculiarities of seasonal generations of animals which was initiated by the famous investigations of prof. August Dehnel and his laboratory on the variability of *Soricidae*.

In the present paper a summary of the works of the Laboratory of Zoology of the Biological Institute (Ural Branch of the Academy of Sciences, USSR) on the biological peculiarities of rodents is given. The analysis of the data is directed on a better understanding of the general laws, which govern the ageing process in mammals. The investigations were carried out from 1951 in experimental conditions and in nature in different climatic zones (from the steppe-zone till tundra) on different species: *Lagurus lagurus*, *Microtus gregalis*, *Microtus middendorffi*, *Microtus oeconomus*, *Lemmus obensis*, *Arvicola terrestris*, *Ondatra zibethica*, *Clethrionomys rutilus*, *Clethrionomys glareolus*, *Apodemus agrarius*, *Apodemus sylvaticus* and some others.

1. The specific growth rate is one of the main peculiarities of seasonal generations of rodents. The animals from spring litters reach their maximum weight at the age of 3—4 months. By the animals from fall generations at the age of 1.5—2 months a cessation of growth is observed and they began to grow anew only in the spring of the next year. The maximum weight of the animals of different generations practically coincides in time, but take place at different age. In spring the rodents of fall generations grow almost as fast as the young animals. It demonstrated that the fall generations maintain their possibility for fast growth till a comparatively very high age.

2. Field observations of many zoologists demonstrated that the age of sexual maturation of voles and other rodents correlates well with their birth-time. The animals from spring litters reach sexual maturation very fast and begin to reproduce early in the summer; the animals from fall generations do not reproduce in their birth-year, they become sexually mature only in the following spring. The investigation of this regularity in experimental conditions demonstrated that the seasonal generations of rodents must be regarded as physiologically different groups of

animals. Especially significant differences are observed by comparison of the animals from spring and fall litters, but they can be detected as well if the animals from subsequent litters are compared.

3. In accordance with the differences in growth rate and rate of sexual maturation seasonal generations differ greatly in the development of some organs. Especially significant differences between generations are observed by the investigation of the thymus weight. By the spring generations a practically full involution of the thymus take place at the age of 4 months. In the animals from fall litters the decrease of the thymus weight coincides in with the cessation of growth and is well pronounced, but in the spring, parallel to the renewal of growth of the animals, a correspondingly increase of the thymus weight take places. In respect of thymus weight the animals from fall litters at the age of 10 months are approximately in the same stage of development as the spring animals 2—3 months old.

4. It is demonstrated that the alterations in adrenal weight reflect the alterations in life conditions of the animals. During the life history of the population there are two periods of increased adrenal weight, in spring (in connection with the reproduction) and in the fall (in connection with the beginning of the cold time). But in comparable life conditions the rodents from spring generations are characterized by greater adrenal weight, what indicates on the intensification of their metabolism. New data are represented which demonstrate that the hyperfunction of the adrenals (which is manifested by their enlargement), must be regarded as an adaptive reaction to different external stress-factors. The older the animal — the stronger is the expression of this reaction. It was manifested that in comparable age the rodents from spring generations react on different stress-factors by a greater enlargement of the adrenals if compared with the animals born in the fall. It is a significant indication of more rapid senescence of the animals from spring generations.

5. In equal life conditions the rodents from spring generations are characterized by relative greater heart and kidney. The fall generations are always characterized by a decrease of the kidney weight, but by some species an enlargement of the heart may be observed. Special analysis demonstrates that this phenomenon can be explained by an increase in activity (fall migrations), accompanied by a decrease in metabolic level. It is especially significant that seasonal generations of rodents differ not only in respect of their organ weight, but also in respect of their relative growth rate. These differences indicate on deep physiological differences between the animals compared.

6. The senescence of animals is accompanied by a regular increase in the eye lens weight. In comparable age the lens weight of the animals from spring generation is much greater in comparison with the rodents or fall generation. From these data it appears that in the fall rodents the tempo of cell reproduction is decreased; it indicates on a decrease of the tempo of the ageing process on cell level.

7. The sum of the data represented in this paper demonstrates clearly that seasonal generations of rodents have well expressed biological peculiarities. The vast majority of these data show that the rodents from fall generations are characterized by a comparatively decreased metabolic level. Some theoretical considerations (for review see § 1) allow us to suppose that the increase in metabolic level is accompanied with an acceleration of the ageing process. Field observations substantiate this supposition: the life span of fall generation is greater in comparison with spring generations.

8. The alteration in the tempo of senescence can be observed during the normal course of the life cycle of the animals in natural conditions. The tempo of senescence

is not strict fixed genetically and can vary in a great degree. Therefore it is in principle possible to regulate the ageing process and to prolongate the life span of the animal not only by a prolongation of the later stages of development ("active old age"), but by the expense of the physiological youth.

REFERENCES

1. Adamczewska, K. A., 1960: Intensity of reproduction of the *Apodemus flavicollis* (Melchior, 1834) during the period 1954—1959. Acta theriol., 5, 1: 1—21. Białowieża.
2. Bazań, I., 1952: Morphohistologische Veränderungen des Thymus im Lebenszyklus von *Sorex araneus* L. Ann. Univ. M. Curie-Skłodowska, C 7, 5: 253—304. Lublin.
3. Bazań, I., 1956: Untersuchungen über die Veränderlichkeit des Geschlechtsapparates und des Thymus der Wasserspitzmaus (*Neomys fodiens fodiens* Schreb.). Ann. Univ. M. Curie-Skłodowska, C 9, 5: 213—259. Lublin.
4. Bielański, T. & Pucek, Z., 1960: Seasonal changes in the brain weight of the Common shrew (*Sorex araneus araneus* Linnaeus, 1758). Acta theriol., 5, 13: 297—300. Białowieża.
5. Borowski, S. & Dehnel, A., 1952: Angaben zur Biologie der *Soricidae*. Ann. Univ. M. Curie-Skłodowska, C 7, 6: 305—448. Lublin [In Polish with German and Russian summ.].
6. Bourliet, F., 1960: Species differences in potential longevity of vertebrates and their physiological implications. Biol. of Ageing. Washington.
7. Brambell, F. W. R. & Rowlands, I. W., 1936: Reproduction in the Bank Vole (*Evotomys glareolus* Schreber). I. The oestrous cycle of the female. Philos. Trans., B 226: 71—97. London.
8. Brody, S., 1945: Bioenergetics and growth. New York.
9. Brown, C. J., 1943: Age and growth of Montana grayling. J. Wild. Mgt., 7.
10. Christian, I. I., 1950: The adreno-pituitary system and population cycles in mammals. J. Mammal., 31, 3.
11. Comfort, A., 1959: The biology of senescence. London.
12. Dehnel, A., 1949: Studies on the genus *Sorex* L. Ann. Univ. M. Curie-Skłodowska, C 4, 2: 17—97. Lublin [In Polish with English summ.].
13. Dickerson, J. W. T. & Widdowson, E. M., 1960: Some effects of accelerating growth. Proc. Roy. Soc., B 152, 947.
14. Frank, F., 1953: Untersuchungen über den Zusammenbruch von Feldmausplagen (*M. arvalis*). Zool. Jb., 82, 1—2.
15. Karaseva, E. V., Narskaja, E. V. & Bernstein, A. D., 1957: Polevka ekonomka, obitajuščaja v okrestnostjach ozera Nero, Jaroslavskoj oblasti. Bjull. MOIP., biol., 62, 3: 5—18.
16. Kopein, K. I., 1959: Inter'ernye osobennosti obskogo lemminga i bol'šoj uzkočerepnoj polevki. Bjull. Ur. Otd. MOIP, 2: 69—74, Sverdlovsk.
17. Krotova, L. G., 1962: Izmenenie nadpočecnikov i uglevodnogo obmena u vodjanoj polevki (*Arvicola terrestris*) v vesenne-letnij period. AN SSR, Ur. filial. Tr. In-ta biol., 29: 129—140, Sverdlovsk.
18. Kryltzov, A. I., 1957: Izmenenie vesa stepnych pestrušek (*Lagurus lagurus* Pall.) v zavisimosti ot ich pola i vozrasta. Zool. žurn., 36, 8: 1239—1250.
19. Kubik, J., 1957: Vorläufige Untersuchungen über die Gattung *Arvicola* L a cépede. Ann. Univ. M. Curie-Skłodowska, C 10, 9: 245—268. Lublin [In Polish with German summ.].

20. Livtšhak, G. B., 1959: Materialy k èkologo-fiziologičeskoj charakteristike mlekopitajuščich Zapoljar'ja. Sb. "Mat. po faune Priobskogo Severa i ee ispol'zovaniju". Tr. Salehard. st., 1: 280—292. Tjumen.
21. Livtšhak, G. B., 1958: Soderžanie askorbinovoj kisloty v počkach poljarnych polevok i nekotorye zakonomernosti ego izmenenija. Bjuil. Ur. otd. MOIP, 1: 103—108.
22. Livtšhak, G. B., 1960: Termotaktičeskij optimum, chimičeskaja termoreguljacija i soderžanie glikogena v pečeni poljarnych polevok. AN SSSR, Ur. filial, Tr. In-ta biol., 14: 179—191. Sverdlovsk.
23. Lord, R. D., 1959: The lens as an indicator of age in cottontail rabbits. J. Wildl. Mgt., 23, 3: 358—360.
24. Mc Arthur, J. W. & Baillie, W. H., 1929: Metabolic activity and duration of life. J. Exp. Zool., 53.
25. McCay, C. M., 1952: [In Cowdryss "Problems of ageing"]. 1—139. Baltimore.
26. Medvedjev, G. A., 1961: Starenie organizma na molekularnom urovne. Usp. sovr. biol., 51, 3: 299—316.
27. Miller, R. B., 1946: Notes on the Arctic grayling, *Thymallus signifer* Richardson, from Great Bear Lake. Copeia, 3.
28. Nikitin, V. N., 1961: Dlitel'noe sderživajuščee rost pitanie i processy ontogeneza. 5 Meždunar. biochim. Kongress, vol. 1:504. Moskva.
29. Oeriu, S., 1962: Dannye k poznaniju biohimičeskogo mehanizma processa starenija i k dejstvuju nekotorych svojstvennyh organizmu veščestv na vosstanovlenie narušenogo biohimičeskogo ravnovesija u starogo životnogo. Usp. sovr. biol., 54, 2: 248—264.
30. Parchon, K., 1959: Vozrastnaja biologija. Bucharest.
31. Pavlinin, V. N. & Schwarz, S. S., 1953: Myševidnye gryzuny Urala. Sverdlovsk.
32. Pavlinin, V. N. & Schwarz, S. S., 1955: Podderžanie žiznennosti u mlekopitajuščich v prirodnyh uslovijach. Zurn. obšč. biol., 16, 4: 306—315.
33. Pearl, R., 1928: The rate of living. New York.
34. Pokrovsky, A. V., 1962: Individual'naja izmenčivost' skorosti polovogo sozrevanija samok stepnoj pestruški (*Lagurus lagurus* Pall.). AN SSSR, Ur. filial, Tr. In-ta biol., 29: 121—123. Sverdlovsk.
35. Pokrovsky, A. V., 1960: O plodovitosti samok stepnoj pestruški v zavisimosti ot vozrasta i sezona razmnoženija. Tr. Ur. otd. MOIP, 2: 75—88.
36. Popov, V. V. & A. K. Al'Sakin, A. V., 1962. Vnutrennyie sloi setčatki i razvitie chrustalika. Zurn. obšč. biol., 23, 5: 350.
37. Pucek, Z., 1955: Untersuchungen über die Veränderlichkeit des Schädels im Lebenszyklus von *Sorex araneus araneus* L. Ann. Univ. M. Curie-Skłodowska, C 9, 4: 163—211. Lublin.
38. Pucek, Z., 1957: Histomorphologische Untersuchungen über die Winterdepression des Schädels bei *Sorex* L. und *Neomys* Kaup. Ann. Univ. M. Curie-Skłodowska, C 10, 15: 299—428. Lublin.
39. Schwarz, S. S., 1956: K voprosu o razvitii inter'nyh priznakov u pozvonočnyh životnyh. Zool. žurn., 35, 6: 804—819.
40. Schwarz, S. S., 1954: K voprosu o specifikje vida u nazemnyh pozvonočnyh životnyh. Zool. žurn., 33, 3: 507—524.
41. Schwarz, S. S., 1958: Metod morfofiziologičeskich indikatorov v èkologii životnyh. Zool. žurn., 37, 2: 161—173.
42. Schwarz, S. S., 1959: Nekotorye voprosy problemy vida u nazemnyh pozvonočnyh životnyh. AN SSSR. Ur. filial, Tr. In-ta biol., 11, 1—132. Sverdlovsk.

43. Schwarz, S. S., 1959: Nekotorye voprosy teorii akklimatizacii. AN SSSR, Ur. filial., Tr. In-ta biol., 18: 3—22. Sverdlovsk.
44. Schwarz, S. S., 1960: Nekotorye zakonomernosti èkologièeskoj obuslovlennosti inter'ernych pokazatelej pozvonoènyh. AN SSSR, Ur. fil., Tr. In-ta biol., 14: 113—178.
45. Schwarz, S. S., 1961: O putjach prisposoblenia nazemnyh pozvonoènyh (preimuščestvenno mlekopitajuščich) k uslovijam Subarktiki. "Problemy Severa", 4: 75—94.
46. Schwarz, S. S., 1960: Principy i metody sovremennoj èkologii životnyh. AN SSSR, Ur. filial., Tr. In-ta biol., 21: 1—50. Sverdlovsk.
47. Schwarz, S. S., 1963: Puti prisposoblenia nazemnyh pozvonoènyh k uslovijam suščestvovanija v Subarktike. AN SSSR, Ur. filial., Tr. In-ta biol., 33: 1—132.
48. Schwarz, S. S., 1960: Rol' želez vnutrennej sekrecii v prisposoblenii mlekopitajuščich k sezonnoj smene uslovij suščestvovanija. Tr. Ural. otd. MOIP, 2: 137—146.
49. Schwarz, S. S., 1960: Vozrastnaja struktura populacij mlekopitajuščich i ee dinamika. Tr. Ural. otd. MOIP, 2: 3—22.
50. Schwarz, S. S., Kopein, K. I. & Pokrovskij, A. V., 1960: Sravnitel'noe izučenie nekotoryh biologièeskich osobennostej *Microtus g. gregalis*, *Microtus g. major* i ich pomesej. Zool. žurn., 39, 6: 912—926.
51. Schwarz, S. S., Pavlinin, V. N. & Susjumova, L. M., 1957: Teoretièskie osnovy postroenija prognozov čislennosti myševidnyh gryzunov v lesostepnom Zaural'e. AN SSSR. Ur. filial., Tr. In-ta biol., 8: 3—59. Sverdlovsk.
52. Schwarz, S. S. & Smirnov V. S., 1959: Zur Physiologie und Populationsdynamik der Bisamratte in der Wald-Steppe und in Hohem Norden. Zool. Jb. (Syst.), 87, 4—5: 363—386.
53. Selye, H., 1950: The physiology and pathology of exposure to stress. Montreal.
54. Smirnov, V. S. & Schwarz, S. S., 1957: Sezonnnye izmenenija odnositel'nogo vesa nadpočečnikov v prirodnyh uslovijach. Doklady AN SSSR, 115, 6: 1193—6.
55. Stieve, H., 1923: Untersuchungen über die Wechselbeziehungen zwischen Gesamtkörper und Keimdrusen. Mitt. II. Arch. mikr. Anat. Entw. mech., 99, 2.
56. Tarkowski, A. K., 1955: Studies on reproduction and prenatal mortality of the Common shrew (*Sorex araneus* L.). Part II. Reproduction under natural conditions. Ann. Univ. M. Curie-Skłodowska, C 10, 8: 177—244. Lublin.
57. Wasilewski, W., 1955: Untersuchungen über die morphologische Veränderlichkeit *Microtus oeconomus* in Białowieża-Nationalpark. Ann. Univ. M. Curie-Skłodowska, C 9, 8: 354—386. Lublin.
58. Wolstenholme, G. E. & O'Connor, M. [eds.], 1959: The lifespan of animals. CIBA foundation Colloquia on Ageing, 5: 1—324 + XII.

Academy of Sciences of USSR,
Ural Branche,
Biological Institute,
Laboratory of Zoology,
Sverdlovsk.

STRESZCZENIE

Badania z zakresu gerontologii porównawczej przeprowadzone przez wielu autorów na różnych obiektach wykazały, że jedną z możliwych przyczyn określających szybkość procesu starzenia się jest intensywność przemiany materii zwierząt. Badania autorów wykazały, że ten punkt widzenia znajduje potwierdzenie i w chronograficznej zmienności poszczególnych gatunków ssaków (Schwarz, 1963). Jednym z ważnych sposobów analizy tego problemu są badania biologicznej specyfiki sezonowych generacji zwierząt, które zapoczątkował prof. dr A. Dehnel i kierowany przez niego Zakład, znakomitymi pracami nad zmiennością ryjówek.

W niniejszej pracy zebrano wyniki badań Zakładu Zoologii Instytutu Biologii Uralskiej Filii Akademii Nauk ZSRR dotyczących biologicznej specyfiki szeregu gatunków gryzoni. Przy analizie otrzymanych wyników zwrócono uwagę na poznanie ogólnych praw rządzących procesem starzenia się u ssaków. Badania prowadzono od 1951 roku, zarówno w warunkach eksperymentalnych, jak i w terenie, w różnych strefach krajobrazowych (od stepów do tundry). Podstawowymi obiektami badań były: *Lagurus lagurus* (Pallas, 1773), *Microtus gregalis* (Pallas, 1779), *Microtus middendorffi* (Poliakov, 1881), *Microtus oeconomus* (Pallas, 1776), *Lemmus obensis* Brants, 1827; *Arvicola terrestris* (Linnaeus, 1758), *Ondatra zibethica* (Linnaeus, 1758), *Clethrionomys glareolus* (Schreber, 1780), *Clethrionomys rutilus* (Pallas, 1779), *Apodemus agrarius* (Pallas, 1771), *Apodemus sylvaticus* (Linnaeus, 1758).

1. Szybkość wzrostu jest jedną z ważniejszych cech, odróżniających generacje. Gryzonie należące do generacji wiosennej osiągają maksymalny ciężar ciała w wieku 3—4 miesięcy. U zwierząt z generacji jesiennej, wzrost zatrzymuje się w wieku 1,5—2 miesięcy i wznowia się dopiero na wiosnę następnego roku. Zwierzęta z różnych generacji osiągają maksymalny ciężar praktycznie biorąc w tym samym okresie. Na wiosnę wzrost generacji jesiennych odbywa się tak samo intensywnie, jak i zwierząt urodzonych w tym sezonie. Wskazuje to na fakt, że zwierzęta urodzone jesienią zachowują zdolność do energicznego wzrostu i rozwoju.

2. Dojrzewanie płciowe. Badania terenowe wielu autorów mówią o tym, że wiek dojrzewania płciowego norników zależy od okresu ich urodzenia. Mioty wiosenne dojrzewają szybko i wchodzą do rozrodu jeszcze w tym samym roku, jesienne zaś wykazują przerwę w aktywności płciowej i zaczynają rozmnażać się dopiero wiosną następnego roku. Badanie tej prawidłowości w warunkach eksperymentalnych (na *L. lagurus*) wykazało, że sezonowe generacje powinny być rozpatrywane jako fizjologicznie odmienne grupy zwierząt. Szczególnie wyraźne różnice zachodzą przy porównaniu generacji wiosennych i jesiennych, ale mogą się one uwidaczniać i u zwierząt następujących po sobie pokoleń.

3. Odpowiednio do różnic w szybkości wzrostu i dojrzewania płciowego, generacje sezonowe różnią się rozwojem szeregu organów i czynności fizjologicznych. Szczególnie istotne różnice pomiędzy generacjami stwierdzono przy badaniu wiekowej zmienności ciężaru grasicy. U generacji wiosennych grasicca szybko osiąga maksymalny ciężar, w wieku około 4 miesięcy następuje prawie całkowita inwolucja tego organu. U miotów późnych obserwuje się jesienią zmniejszenie wymiarów grasicy. Jednakże na wiosnę, równoległe ze wznowieniem wzrostu, grasicca powiększa się. W ten sposób gryzonie generacji wiosennych w wieku 10 miesięcy znajdują się na tym samym etapie rozwoju, jak wiosenne w wieku 2—3 miesięcy.

4. Wykazano, że ciężar nadnerczy zmienia się zależnie od warunków bytowania zwierząt. Stwierdzono istnienie różnic pomiędzy sezonowymi generacjami gryzoni. W życiu populacji obserwuje się dwa okresy szybkiego podwyższenia ciężaru nad-

nercza: wiosenny (w związku z dojrzewaniem płciowym i rozmnażaniem) i jesienny (w związku z nastaniem chłódów). W jednakowych warunkach środowiskowych, gryzonie należące do generacji wiosennej posiadają wyższy wskaźnik nadnercza. Wskazuje to na intensyfikację ich przemiany materii. Przedstawione nowe dane, pokazujące, że hyperfunkcja nadnerczy, przejawiająca się zwiększeniem ich wymiarów, jest przystosowawczą reakcją zwierzęcia na dowolne bodźce zewnętrzne, wymagające mobilizacji wewnętrznych sił organizmu. Należy zauważyć, że im zwierzę jest starsze tym reakcja ta jest wyrażona silniej. Ustalono, że w równym wieku gryzonie pokoleń wiosennych reagują na działanie czynników stressowych silniejszym powiększeniem nadnerczy niż zwierzęta urodzone na jesieni. Fakt ten może świadczyć o szybszym starzeniu się gryzoni z pokoleń wiosennych.

5. W jednakowych warunkach bytowania gryzonie generacji wiosennych charakteryzują się stosunkowo dużym rozwojem nerek i serca. Pokolenia jesienne zawsze charakteryzują się obniżeniem wskaźnika nerek. U niektórych gatunków jesienią obserwuje się zwiększenie wymiarów serca. Wykazano, że jest to związane z podwyższeniem aktywności ruchowej zwierząt w okresie jesiennych migracji. Generacje gryzoni różnią się nie tylko absolutnymi wymiarami organów, ale i zmianą tempa wzrostu. Różnice te są szczególnie istotne i wskazują na głębokie fizjologiczne różnicowanie porównywanych grup zwierząt.

6. W procesie starzenia się zwierząt ma miejsce wzrost ciężaru suchej masy soczewki oka. Ustalono, że gryzonie urodzone wiosną, charakteryzują się większym ciężarem soczewki niż zwierzęta tego samego wieku z późniejszych miotów. Różnice te wskazują na zwolnienie tempa podziałów komórkowych u gryzoni pokoleń jesiennych, a tym samym świadczą też o różnicach w szybkości procesu starzenia się zwierząt urodzonych w różnym czasie.

7. Całościowo otrzymanych wyników wskazuje, że sezonowe biologiczne generacje gryzoni różnią się między sobą w sposób istotny. Zwierzęta z pokoleń wiosennych posiadają wyższy poziom metabolizmu. Teoretyczne założenia pozwalają sądzić, że równocześnie fizjologiczny proces starzenia się przebiega u nich stosunkowo szybciej niż u pokoleń jesiennych. Założenia te potwierdza analiza materiału zdobytego w terenie. Długość życia pokoleń jesiennych jest większa niż wiosennych.

8. Zmiany szybkości procesu starzenia się obserwowane są w przebiegu cyklu życiowego naturalnych populacji zwierząt. Dochodzimy więc do wniosku, że nawet 4—5-krotne różnice w wieku zwierząt nie odbijają się na ich fizjologicznym stanie. Szybkość procesu starzenia się nie utrwała się dziedzicznie, może się ona zmieniać w szerokim zakresie. Możliwe jest zatem znaczne przedłużenie życia zwierząt przez wydłużenie ich okresu młodości, lecz nie przez przedłużenie końcowych etapów ich cyklu życiowego.

