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Population dynamics of rodents from northern and mountainous geographical zones

The dynamics of rodent populations in northern and mountainous geographical zones has been investigated. It has been shown that an increase in the numbers of a population can be determined by a general period of reproduction, rate of sexual development of different generations, their life length and fertility. These indices are different not only for rodents in different geographical conditions, but also for different species within the same zones.

1. INTRODUCTION

A considerable number of facts has been collected by now which show quite clearly that there are specific peculiarities in the biology of reproduction and population dynamics in rodents from different geographical zones. These peculiarities can be treated as a complex of adaptations to the specific conditions of existence. The purpose of the present paper is to show the specific character of the dynamics of rodent populations in northern geographical zones and analogous mountainous belts.

2. MATERIALS AND METHOD

The material presented was collected in 1956–1967 in various geographical zones and mountainous territories of the USSR: the tundra zone (the Yamal peninsula), the forest tundra and southern tundra (the lower reaches of the rivers Khadyta, Sob, Ob, Poluy), the mountains of Subarctic zone (the lower reaches of the Lena river — the Kharaulakhskiy range and Yakutia), the forest zone (the Middle Urals,

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the vicinity of Sverdlovsk), the forest-mountainous belt and the dwarf mountain pine zone (the Northern Urals — the Kasvinskiy Kamen and Denezhkin Kamen mountains; altitude 600–1200 m above the sea level), the high mountain region (the mountains of Middle Asia: the Pamirs — 2,500–3,500 m above the sea level and Tian Shan — Kirghizskiy range — 2,500–3,000 m above the sea level).

In order to determine the age of rodents and subdivisions of populations into generations we have applied a complex of age indicators (weight and size of body and skull, the degree of wear of the teeth in a number of species, the growth of tooth-roots, number of spots on uterine horns in females). We also frequently took into account dimensions of the thymus which form one of the reliable age indicators. In a number of cases we used vivarium materials. All these indicators taken together made it possible to refer rodents to one of the generations with almost complete accuracy.

A detailed analysis of the population dynamics of rodents has been given in the works of our laboratory[1] for the following species: *Lemmus sibiricus* Kerr. Vinogr., *Microtus gregalis* Pall., *M. oeconomus* Pall., *M. middendorfii* Poljakov, *Lagurus lagurus* Pall., *Arvicola terrestris* Linn., *Ondatra zibethica* L., *Clethrionomys rutilus* Pall., *C. glareolus* Schreb., *C. rufocanus* Sundev., *Apodemus agrarius* (Pall.), *A. sylvaticus* L., *Alticola lemminus* Miller.

3. POPULATION DYNAMICS OF RODENTS FROM DIFFERENT GEOGRAPHICAL ZONES

Specific populational dynamics of typical subarctic species, inhabiting in the tundra, is analyzed here on the basis of the following three species: *Microtus middendorfii*, *M. gregalis major* Ogn. and *Lemmus sibiricus*.

Our data on the population dynamics of the *Microtus middendorfii* can be presented as follows. Their reproduction starts at the end of April — beginning of May. The first generation, from those which had hibernated, appears at the end of May — beginning of June. In July a young individual from the first generation reaches the weight of 25 g and takes part in reproduction. Young *M. middendorfii* weighing 14–16 g were found to be pregnant. Some cases were observed when females weighing 5–8 g had an enlerged uterus. Females which had hibernated give birth to their second generation. The weight of such animals then reaches 60 g. Some females bear a third generation, which appears in August. In July individuals which had hibernated make up more than 35% of all the animals. The mortality of the older animal is, however, very high, and in August those animals which had hibernated are not recorded, and even individuals from the first generation are then quite

[1] Švarc and Pavlinin (1957, 1960), Švarc (1959a, b, c, d, 1960a, b, 1962, 1963), Livčak (1960), Bol'šakov and Švarc (1962a, b), Bol'šakov (1965), Švarc and Bol'šakov (1965), Švarc, Smirnov and Dobrinskij (1968).

rare (Tab. I). At the end of August–September populations of *Microtus middendorfii* are made up basically of the second and third generation animals produced by animals which had hibernated and the first litters of the rodents from the first generation. At that time some of them take part in reproduction. No pregnant females were recorded in October. Thus in autumn populations of *Microtus middendorfii* are made up of animals from the second and third generations, and more than 80% of the animals weigh less than 25 g. It should be particularly pointed out that some individuals of *M. middendorfii*, even those from late-summer generations, reach sexual maturity in the year of their birth.

TABLE I

Dynamics of the age structure of the Microtus middendorfii population

Months	Age groups (amount of the material investigated)							
	up to 15 g		15–25 g		25–35 g		more than 35 g	
	number	per cent	number	per cent	number	per cent	number	per cent
April	—	—	21	77.7	5	18.6	1	3.7
May	—	—	2	28.6	4	57.2	1	14.2
June	1	16.7	—	—	1	16.7	4	66.6
July	11	7.9	34	24.5	40	28.8	54	38.8
August	—	—	9	64.3	5	35.7	—	—
September	30	33.3	41	45.5	19	21.2	—	—
October	8	6.8	94	80.3	10	8.6	5	4.3

On the basis of an analysis of the entire material Figures 1 and 2 were drawn up — they show structural changes in populations of *Microtus gregalis major* Ogn. and *Lemmus sibiricus*. Figure 1 shows that the July population of *M. gregalis major* is represented by three generations. In August the bulk of the population is made up of animals from the first and second summer generations (90%) although there are also individuals from earlier litters. In September and particularly in October the population which is going to hibernate is made up of animals from summer litters of the given year, with predominance of the last generation. In May populations of *M. gregalis major* are made up of individuals which had hibernated and those which were born in winter. In June the number of animals which had hibernated drops sharply. Their percentage decrease is caused not only by an increase in the number of young animals, but basically by a high degree of mortality. In May the ratio of animals which had hibernated to those born in winter is 1:2, while in June it changes to 1 : 9. The most mixed age composition is characteristic of the June population, in which all the generations born in the given year are represented, although to different degrees, as well as a considerable number of animals which had hibernated. More than 50% of the population is made up of young summer litters displaying a maximal rate of growth. Dynamics of changes in the age structure of populations of *Lemmus sibiricus* is basically similar to the one shown by populations of *Microtus gregalis major.* Thus the populations of *M. gregalis major* and *Lemmus sibiricus* just starting to hibernate are made up of young animals from summer litters, with predominance of the last one which, together with animals from the winter generation, contribute most to the increase in the numbers of *M. gregalis major* in the spring of the next years.

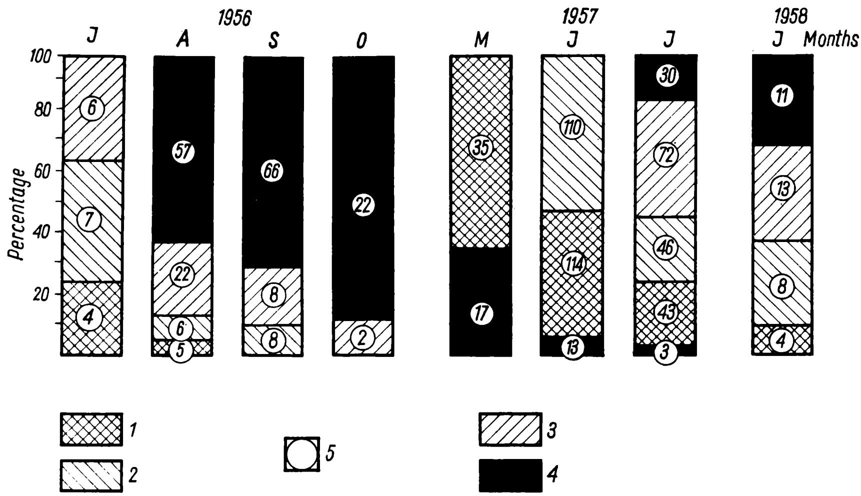

FIG. 1. Age structure of the population of *Microtus gregalis major* (after KOPEIN 1958)
1 — winter generation, *2* — spring generation, *3* — first summer generation, *4* — second summer generation, *5* — animals examined

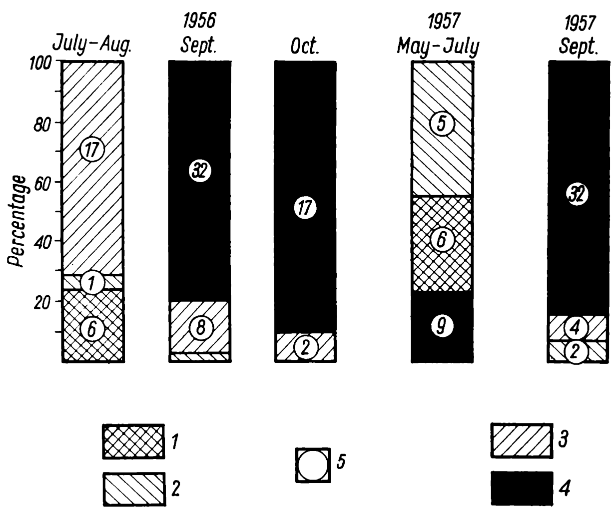

FIG. 2. Age structure of the population of *Lemmus sibiricus*
1 — winter generation, *2* — spring generation, *3* — first summer generation, *4* — second summer generation, *5* — animals examined

Generations born in spring and at the beginning of summer contribute most to the increase in the numbers of the population which hibernates. Both species are characterized by a quick succession of generations.

A completely different picture was recorded when investigating subarctic populations of species inhabiting large areas in the southern tundra and forest tundra — *Microtus oeconomus*, *M. agrestis* L., and *Arvicola terrestris*. Let us consider the specific character of the population dynamics of animals from this group, taking *Microtus oeconomus* as an example.

The reproduction of *Microtus oeconomus* in the subarctic region starts at the end of April and beginning of May. Hence it follows that the mass occurrence of the first litter falls in June. They are animals from the first generation. At the end of June animals which had hibernated give birth to the second litter which is recorded in the July collections. Consequently, the second generation is made up of animals born in June, while the third one, the July generation, is much more complex in its constitution. It is made up of the first litter of animals from the first generation and the third litter of those which had hibernated. The fourth generation is born in August — this is the second litter of animals from the first generation. A few individuals were found to be pregnant in September. Consequently, there is a fifth generation in the population, much less numerous than the previous ones. Thus, the age composition of the population varies in different periods of the year. In May animals which had hibernated and individuals of the first generation can be recorded. In June — animals which had hibernated, and those of the first and second generations. A more complex structure of the population can be recorded in July and August. In July there are still individuals which had hibernated in the population. In different years the percentage of *Microtus oeconomus* individuals which had hibernated may be as great as 35.4% in this period.

In August animals which had hibernated occur relatively rarely. Beside the first, second, and third generations of animals which had hibernated, as well as the first litter of the first generation, it was possible to record animals of the fourth generation produced by those females which had hibernated and by the first litter of the first generation.

In September the population is mainly made up of individuals from the second, third, and fourth generations. Animals of the first generation are not numerous and form only an insignificant percentage. Table II illustrates the dynamics of the age structure of *Microtus oeconomus* populations. The analysis of the data leads to a conclusion that animals of the youngest age groups dominate in autumn.

One of the characteristic peculiarities of *Microtus oeconomus* is formed by the small numbers of the first generation. As we were not able to determine sterility among females in the period of reproduction, it seems to be certain that the smal number of the first generation is determined not by the fact that only some of the females take part in reproduction, but by an exceptionally high mortality of young animals from the first generation during the period of the spring thaw. The

TABLE II

Dynamics of the age structure of the Microtus oeconomus population

Genarations	Venue and time of collection																	
	Khadyta river, 1958		Khadyta river, 1959		Polar Urals, 1960		Polar Urals, 1961		lower reaches of the Sob river, 1960		Lake Severniy, 1962		Lake Yuzhniy, 1962		lower reaches of Poluy, 1962		Sasykul, 1963	
	July 15–Aug. 12		July 10–Aug. 12		Aug. 14–Aug. 26		July 23–Sept. 2		July 21–Aug. 29		Sept. 16–17		Sept. 12–16		Sept. 7		May 16–June 27	
	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%
Animals which hibernated	45	35.4	9	26.5	2	7.0	4	6.4	13	28.8	1	1.9	0	0	0	0.0	63	52.5
1st generation	19	14.9	7	20.6	5	18.0	8	12.8	8	17.8	16	30.8	20	34.5	2	6.0	33	27.5
2nd generation	27	21.3	9	26.5	6	21.4	22	35.6	19	42.3					7	21.2	24	20.0
3rd generation	36	28.4	7	20.6	8	23.6	14	22.6	5	11.1					7	21.2	—	—
											35	67.3	38	65.5				
4th generation	—	—	2	5.8	7	25.0	14	22.6	—	—								
Total	127		34		29		62		45		52		58		33		120	

second generation has better conditions in their early stages; their mortality is not so high and consequently it dominates throughout the whole summer. Unusually high mortality of animals of the first generation sharply distinguishes northern populations of *Microtus oeconomus* from southern ones as well as from subarctic populations of rodents better adapted to the conditions of the Far North. In spite of the high mortality of animals of the first generation they can play a significant part in the dynamics of numbers. Under normal conditions they only increase the numbers of the third generation, but in years with an exceptionally early spring the mortality of animals of the first generation decreases and this leads to a sharp increase in the number of animals of the third generation, which, in turn, may lead to an eruption in population numbers. It follows from this that the leading factor determining the numerical dynamics of *Microtus oeconomus* is favourable weather in spring and early summer. A mild spring without a sudden thaw contributes to an increase of their numbers.

The population dynamics of rodents from the forest zone (plains) is analyzed here on the basis of the *Apodemus agrarius*. Analogous regularities were found out when investigating *Apodemus sylvaticus*, and *Clethrionomys glareolus*. The well known exception is the *Microtus arvalis* Pall. which, as a result of reproduction under the snow cover, not recorded in the case of other rodent species in the Urals, displays certain peculiarities in its population structure.

The structure of *Apodemus agrarius* populations over the course of the annual cycle is represented by five successive generations. In separate periods of the year the population can be represented by various generations, and their numerical relations vary considerably according to the season.

At the beginning of the spring reproduction the population is made up of rodents which had hibernated. The first generation appears in the period from the 10th of May until the first days of June (Fig. 3). The second generation appears during June. Like the first one, the second generation is produced by individuals which had hibernated and are their first litters. The third generation appears between the end of June and the end of July. The bulk of the individuals of the third generation is produced by females of the first generation and males which had hibernated (males of the first generation attain sexual maturity later). A small part of the generation is produced by males which had hibernated and females of the early litters of the second generation. Thus, the third generation is mixed in its origin and it cannot be referred to either the first or the second generation, but rather occupies an intermediate position.

The fourth generation, which appears in the period between the end of July and the end of August, is completely represented by the progeny of individuals born in the given year (1st, 2nd, and 3rd generations). The fifth generation is also represented by the progeny of those young animals and appears in the period between the middle of August and the 20th of September, after which *Apodemus agrarius* individuals cease reproducing. The main bulk of the fifth generation individuals and the entire fourth generation make up the second litters — "grandsons" of those which had hibernated. Some of the individuals of the fifth generation, appearing in the first ten days of September and produced by individuals of the fourth generation, are already the third litters — "great-grandsons" of those which had hibernated.

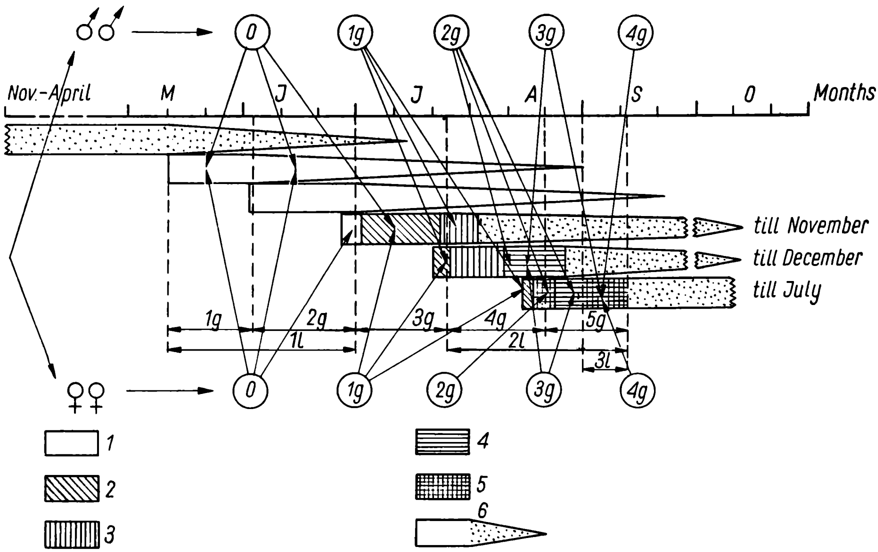

FIG. 3. Population structure and generations of *Apodemus agrarius*

1 — litters from old animals, *2* — litters from first generation, *3* — litters from second generation, *4* — litters from third generation, *5* — litters from fourth generation, *6* — life span of the generation, *O* — old animals, *1g, 2g*, ... — 1, 2 generations, *1l, 2l*, ... — 1, 2 litters

Each of the generations mentioned differs from the others not only by its origin and time of birth, but also by its specific features. Without going into a detailed analysis of peculiarities displayed by each of the generations, we should point out here that the first four generations differ considerably from the fifth (autumn) one. Summer generations are characterized by high mortality: in the period of postembryonal life, until they are a month old, only 10–20% of them survive. They are all characterized by early sexual development of females (they attain sexual maturity when they are a month old, and the males two weeks later), and by rapid growth — they reach adult size by the third month of their life. Their life-span, even of the most vital individuals of summer generations surviving their critical postembryonal period, is very short. Only 1–6% of the total number of mice born survive their 4th month. By December representatives of summer generations, with the exception of separate individuals, are extinct.

Due to the early maturation of the majority of surviving females from summer generations, they manage, in spite of their short life-span, to have 2–3 litters (females of the fourth generation, and even not all — 1 litter). Thus their progeny make up about 70% of the total number of the animals born in this summer: those which had hibernated (approximately) about 30%, females of the 1st generation — 15%, 2nd — 13%, 3rd — 28%, 4th — 13%. (These figures were obtained by indirect calculations of the relations of fertility and per cent of trappability of representatives from different generations.)

Young individuals of the fifth (autumn) generation, appearing at the end of August — beginning of September, have other peculiarities. More than 70% of them survive their first month of life. They differ also from the summer generations in later periods by lower mortality — by April of the next year about 35% of the total number of animals born manage to survive, and about 30% of them survive their 9th–10th month. In addition, representatives of the autumn generation are characterized by delay in sexual development in the year of their birth and cessation of their growth quite early on. In September their average weight (according to average data for a number of years) turned out to be 12.6 g (8.1–14.9), in October — 12.3 g (7.3–14.9), in November — 12.2 g (8.6–14.1), in December — 13.7 g (10.5–15.6). According to these data, until the beginning of the period of spring growth and sexual maturation (March–April), individuals of the autumn generation, in spite of their considerable age by the spring, can be characterized as subadults. After the start of reproduction the mortality of individuals of early generations increases, and by July only some of the individuals manage to survive. Consequently, if we exclude autumn and winter from their life-span, as they do not reproduce then, they live 3–4 months. Hence it is possible to conclude that the life-span of rodents is determined not only and not so much by the time of their birth, as first of all by the period of their life-activity: period of intensive growth and reproduction requiring the mobilization of their entire vitality.

Thus, we can say to recapitulate that, starting from December until the appearance of the first generation in May, the population structure of *Apodemus agrarius* is quite simple — it is mainly represented by individuals of the fifth generation and a small number of animals of the fourth generation which did not reproduce in autumn. Starting from May the structure becomes more complex. By July the population is made up of animals which had hibernated and two litters of the first generation. From July the population is almost entirely made up of rodents born in the given year, and its structure becomes more complex with the appearance of successive generations. The bulk of the population in the summer period is made up of rodents up to two months old, because when they reach this age they die off in large numbers. Therefore as early as August the percentage of representatives of the first cohort, particularly of the first generation, is negligible. After the termination of the reproductive period, from the middle of September, all the individuals which took part in reproduction gradually disappear, males in particular, and the fifth generation becomes more and more dominating, and from December the population is mainly made up of them.

Analysis of the reproductive abilities of summer and autumn generations of

Apodemus agrarius indicates the part which they play in the population. Summer generations ensure increase in population numbers during the most favourable period of the year, and the autumn generation forms the bulk of the population which survives till the next year. In view of this, representatives of summer generations are characterized by rapid sexual development and considerable rate of growth, and rodents which were born in autumn by the fact that they do not reproduce in the year of their birth and that their development is delayed until the next spring. The significance of these peculiarities of summer and autumn generations to the population is beyond any doubt.

Characteristic features of the dynamics of rodent populations from the forest-mountainous belt and subalpine zone in the Ural mountains differ from those displayed by rodents inhabiting plains. One of the most characteristic rodent species from the Ural mountains, inhabiting stone querries in mountain ridges, is the *Clethrionomys rufocanus*. Its fertility is relatively low: features characterizing this species are the short period of reproduction, the small number of litters produced by females which had hibernated, and particularly in the case of animals born in the given year, the small number of young in the litter.

The first pregnant *Clethrionomys rufocanus* females in the Ural range were captured in the first half of May. In May the population is entirely made up of individuals which had hibernated. In the middle of May practically all the females captured had embryos. During the reproduction period females of *Clethrionomys rufocanus* which had hibernated reached the weight of 36.5–42.4 g, and males — 35.9–43 g. Isolated young individuals of *Clethrionomys rufocanus* weighing 12–14 g started being trapped in the last days of May and beginning of June. In the middle of June the second pregnancy was recorded in the case of females which had hibernated. On the whole, the per cent of females taking part for the second time in reproduction in the Urals was fairly large: out of 8 females captured on 16–17 June 6 females (75%) were pregnant for the second time. No differences in the number of embryos in females pregnant for the second time were recorded as compared with their first pregnancy. Females which had hibernated weighed 36.4–43.6 g at that time, the males — 34.8–50.8 g. By the end of June young *Clethrionomys rufocanus* individuals of the first litter reach the weight of 22.6–33.7 g. No young individuals of this species taking part in reproduction were captured in the entire period of observations. The age composition of the population in this period can be easily determined by means of the teeth-roots of specimens which hibernated (and by their lack in young individuals), as well as by their body weight.

Apparently, only some of the females which had hibernated produce a third litter in the mountainous regions of the Urals: at the beginning of August we were able to record one such female out of the five females captured (20%). Young females of the first litter start reproducing in July. Pregnant young females are captured over the course of a long period: the period of reproduction and the appearance of the first litter is much more prolonged than in the case of animals which had hibernated. The weight of *Clethrionomys rufocanus* individuals, born in May and in beginning of June, reaches 24.0–36.2 g at the end of August, and in many cases they do not differ, as far as their weight is concerned, from old individuals. Some individuals born in May and in beginning of June may have their second litter in August: out of the six such females investigated in the period 18–23 August 1960, one female (16%) was found to be pregnant for the second time. By the end of August the reproduction of *Clethrionomys rufocanus* ceases entirely. The age composition of the population at that time is very much diversified. The population is made up, in the first place, of a relatively small number of individuals born in the previous year and easily distinguished by the development of roots, in the second, also of a small number of animals born in the given year at the end of May and beginning of June in the first litter and reaching by the end of reproduction the weight and size of hibernating animals, and lastly, of a large number of animals of the second and third litters borne by old females, and the first and partly second litters borne by the first females of those which had hibernated. The latter group differs in this period according to weight and size from the first two groups, but it is impossible to discern separate generations inside it. At the end of August, 1960, the relations between the groups mentioned were as follows (20 animals were investigated): old individuals — 12.5%, first animals of the given year — about 16.5%, young animals of later litters — 71%. Apparently, it is this last group which plays a basic role in maintaining the numbers of the population in the next year.

In more widely-distributed in the highest regions of the Urals the *Clethrionomys rutilus* and the *Microtus agrestis* the dynamics of populations and peculiarities of reproduction are similar to those displayed by the species described above. Females of these two species have more or less the same fertility as these inhabiting plains, but their period of reproduction is shorter. Females which had hibernated usually give birth to three litters. Young animals of the first spring generation start reproducing in the year of their birth and usually have one, but only rarely two, litters. Animals of later generations take part in reproduction only in a few cases and not every year. The basic difference from *Clethrionomys rufocanus* lies in the fact that individuals of the first spring litters have lower mortality. The analysis has shown that in autumn the bulk of the *Clethrionomys rutilus* population is made up of young animals born in that year — on an average about 95%. Among them animals of the first spring litters can be distinguished by the development of their teeth-roots. The per cent of such *Clethrionomys rutilus* individuals in the captures is considerable — on average 23%. Besides it should be added that the remaining group can include animals of several generations, and therefore their significance to the population is not smaller than in the case of animals of spring litters. In mountainous populations of *Clethrionomys rutilus* and *Microtus agrestis* individuals born in spring survive till autumn and play a significant part in the reproduction of the population. It should be pointed out that the available materials indicate the long life-span of separate individuals in the mountains: *C. rutilus* individuals with their molars completely worn make up, in separate years, up to 5–14% of adult rodents captured.

A simple age structure is characteristic of *Alticola lemminus* — a species which has adopted itself to living in the specific conditions of the mountainous tundra in the Far North and in the north-eastern parts of the Soviet Union. The following are the characteristic features of the reproduction of *Alticola lemminus* in the Kharaulakhskikh mountains (the lower reaches of the Lena river, Yakutya): only one litter borne by females which had hibernated, very slow sexual development of young animals and their participation in reproduction only in the next year at the age of 10–11 months. In spring and at the beginning of summer the population is exclusively made up of animals born in the previous year, and, apparently, of a very small number of animals more than a year old. The mating period of *Alticola lemminus* commences at the beginning of May and the young are born in the second half of June. From the middle of July young individuals start their adult life and are trapped. In the second half of July — beginning of August it is easy to distinguish animals which had hibernated from those born in the given year, by reason of their body weight and size (Tab. III). At the end of July and beginning of August

TABLE III

Weight and size composition of Alticola lemminus populations

Year	Young animals				Adult animals			
	body weight (g)		size (mm)		body weight (g)		size (mm)	
	from–to	average	from–to	average	from–to	average	from–to	average
1963	13.2-20.6	16.9	79–97	86	23.3–40.0	33.6	105–118	112
1964	12.3–19.0	15.9	74–92	84	22.0–39.0	31.5	103–116	110

the population consists of two age groups: adult individuals which hibernated and those born in the given year. By the onset of winter individuals which hibernated at the age of 12–13 months form only an insignificant part of the population — about 20%, the bulk of the population is made up of young animals. Hence it is possible to conclude that the deciding role in the maintenance and dynamics of the population numbers in the spring–summer period should be given to this last age group. For *Alticola lemminus* inhabiting the Kharaulakhskikh mountains a considerable number of young in the litter is quite characteristic; the stability of the annual index — on average 7.7–7.4 embryos per female — is significant in itself. It has been determined, when analyzing the age structure of the population in an isolated plot with complete capture of *Alticola lemminus* individuals, that there are approximately 7 young per female at the end of summer. The very similar figures of the number of embryos and young animals per one female indicate low mortality of young individuals. Peculiarities in the biology of reproduction and the age structure determine, on the whole, the numerical stability of *Alticola lemminus* in separate years.

TABLE IV

Population dynamics of rodents in different geographical zones

Zones	Species	Period of reproduction	Number of generations	Characteristic features of generations: first	second	third	fourth	fifth	Peculiarities of reproduction
Tundra	*Lemmus sibiricus*	Winter (November–December, end of March–April) until October inclusive	5–6	Winter generation. Animals start reproducing in the year of their birth. They manage to have 4 litters	Spring generation. Animals start reproducing in the year of their birth. They have 2–3 litters	1st summer generation They make up the bulk of the population hibernating in winter (80% — 2nd summer generation, 20% — 1st summer generation)	2nd summer generation	3rd summer generation	Winter reproduction, high fertility, although lower than in subarctic species (about 8 embryos per female)
Tundra	*Microtus gregalis major*	March–September	4	Winter generation. Animals start reproducing in the year of their birth. They have 2, only rarely 3 litters. In the litter, on average, 6.6 embryos per female	Spring generation. Animals start reproducing in the year of their birth. They have 1 or 2 litters. In the litter, 8.7 embryos per female	1 st summer generation They make up the bulk of the population hibernating in winter (90% — 2nd summer generation, 10% — 1st summer generation). In the litter, 9.9 embryos per female	2nd summer generation		Exceptionally high fertility, early sexual development, early start of reproduction
Forest tundra and southern tundra	*Microtus oeconomus chahlovi* Scalon	Beginning of May—beginning of October	4–5	Animals start reproducing in the year of their birth. They manage to have 2 litters. They die off in the second half of summer	Animals start reproducing in the year of their birth. They have 1 litter. Some individuals hibernate	Animals do not reproduce in the year of their birth. They make up the bulk of the population hibernating in winter		The generation appears in September — beginning of October	Exceptionally high fertility, early sexual development
Mountains of subarctic regions (lower reaches of the Lena river, Yakutia)	*Alticola lemminus*	Beginning of May – middle of June	1	Animals do not reproduce in the year of their birth. By winter they form 80% of the population	None	None	None	None	Animals have a characteristic number of young in the litter (7.4–7.7 per female), numbers permanent in separate years
Southern taiga	*Apodemus agrarius, Apodemus sylvaticus, Clethrionomys glareolus*	End of April – first half of September	5	Animals start reproducing in the second half of June. They have 2–3 litters. Their life-span — May–September (only separate individuals survive by September)	Animals start reproducing in July and have 2 litters. Their life-span — June–September	Animals start reproducing at the end of July — in August. They have 1 litter, rarely 2 litters. Their life-span — June, July–October	Animals start reproducing in August, and have 1 litter. Their life-span — July–October (individuals born in the second half of August do not take part in reproduction)	Animals do not reproduce in the year of their birth	Fertility: in spring — 5, in summer — 6.3, at the end of summer — 8.3, in autumn — 6.2 embryos per female
Mountainous taiga (Northern Urals)	*Clethrionomys rufocanus, Clethrionomys rutilus, Microtus agrestis*	Second half of May–August	3	Animals start reproducing in the year of their birth and manage to have 1 litter, only rarely 2 litters. Not fewer than 25% of individuals survive until winter	Animals do not reproduce in the year of their birth with the exception of some individuals By winter individuals from the 2nd and 3rd generations make up about 70% of the population	Animals do not reproduce in the year of their birth	None	None	As regards the number of young in the litter there are no differences as compared with populations inhabiting plains
Highlands of Middle Asia (the Pamirs — 2,500–3,000 and Tian Shan — 2,500–3,000 m above sea level)	Highland specialized species: *Microtus juldaschi, Alticola roylei*	May–August, in a number of cases — September	2–3	Animals start reproducing in the year of their birth, and, as a rule, they have 1 litter. *A. roylei* sometimes has 2 litters. By winter they make up about 30–40% of the population	Animals do not take part in reproduction in the year of their birth. In winter they make up only 50–60% of the population		None	None	Number of young in the litter is small: *M. juldaschi* (on average) — 3.5–3.9, *A. roylei* — 4.8
	Mountainous populations of widely distributed rodent species: *Apodemus sylvaticus, Cricetulus migratorius*	March–October; some cases of winter reproduction were recorded	3–4, sometimes 5	Animals start reproducing in the year of their birth, and they have not fewer than 2–3 litters. Most probably they die off completely in winter	In the year of their birth the animals have up to 3 litters	Animals start reproducing in the year of their birth, and they have 1 litter Apparently they make up the bulk of the population in winter	Animals do not reproduce in the year of their birth with the exception of the most favourable years	None	Characteristic of them is a large number of young in the litter: in the case of *C. migratorius* — 8.2

A more complex age composition was recorded for populations of mountain rodent species inhabiting the subalpine and alpine belts of mountain ridges. Let us consider their dynamics on the basis of specialized mountain species inhabiting the high regions of the Middle Asia — the *Microtus juldaschi* Severtzov and the *Alticola roylei* Gray. Characteristic of the majority of mountainous rodent species is the shorter, as compared with species living in plains, period of reproduction (in *Microtus juldaschii* — three months, in *Alticola roylei* — 3.5 months), an insignificant number of generations (usually 2, rarely 3), a small number of young individuals in the litter (on average, 3.5–3.9 in *Microtus juldaschi,* 4.8 in *Alticola roylei*), later sexual development of the young (individuals of the first litter, which start participating in reproduction and manage to have, as a rule, only one litter). The analysis of the populational age structure of *Microtus juldaschi* indicates that by autumn, when their reproduction is terminated, the population mainly consists of young animals, but the mortality of the first generation individuals is relatively low, and therefore they make up not less than 30–40% of the population. Animals of later generations make up only 50–60% of the population, which proves their relatively considerable mortality. Old animals which hibernated survive till autumn — up to 10% of the population. Thus, the dynamics of the population structure of mountainous rodent species is characterized, on the whole, by an insignificant intensity of reproduction, and, apparently, by the lower mortality of their individuals.

A completely different type of dynamics is displayed by mountainous populations of widely-distributed rodent species. As an example we can take two species with a wide range, living at similar altitudes to *Microtus juldaschi* and *Alticola roylei* — *Apodemus sylvaticus* and *Cricetulus migratorius* Pall. Their characteristic feature in the high mountains is the intensification of reproduction: an increase in the number of litters in females which had hibernated, early sexual maturation of young individuals and their active participation in reproduction in the year of their birth, an increase in the number of young individuals in the litter as compared with the lower lying regions of their area. The age structure of the population is very complex. It is characterizing by the dying off of young animals of the first generations by autumn, and owing to that, by the onset of winter, the bulk of the population is made up of young individuals of the last litters. On the whole, their population dynamics resembles the one displayed by animals inhabiting plains: summer generations contribute to the increase in the species numbers in the most favourable period of the year, while the autumn generations prepare grounds for the maintenance of the necessary density of the population in the next year.

4. DISCUSSION OF MATERIALS

Specific data characterizing general regularities in the peculiarities of reproduction and the dynamics of the population structure concerned with the species investigated and discussed above are presented in the form of a Table (Tab. IV).

The increase in the population numbers is determined by the general period of the species reproduction, rate of sexual development displayed by separate generations, their life-span and fertility. These indices are not only different in the case of rodents living under different geographical conditions, but also in the case of different species within separate zones.

Analysis of Table IV reveals the basic differences in the type of population dynamics displayed by various species in ecological groups. The basic type of rodent population dynamics in the conditions of high mountains is as follows: short period of reproduction, small number of generations, their delayed development, their long life-span, and stable (in certain forms — low) fertility. Mountain populations of widely-distributed species already display a different type of numerical dynamics. Typical subarctic species are characterized by a prolonged period of reproduction, high fertility, early sexual development. The following is typical of the subarctic populations: a short period of reproduction, exceptionally early sexual maturation, highest fertility, very short life-span of separate generations (with the exception of the last one — hibernating). Table IV gives some idea of analogous regularities in other rodent groups. It should be pointed out that ecological group (in the meaning indicated) can include taxonomically distant species, or vice versa.

Continuous observations of separate populations make it possible to determine more precisely the life-span of separate generations, and consequently, to define their role in the dynamics of the species numbers. Thus, for example, in the conditions of the southern taiga 87.4% of the total number of the first generation individuals (*Apodemus agrarius*) die off by July, by August — 95.6, by September — 99.3. For the fourth generation the respective figures are as follows: by August — 86.9%, by September — 91.4, by October — 94.4; for the fifth generation: by September — 28.2%, by October — 40.8, by April of the next year — 65.1%.

The type of population dynamics also determines the character of numerical dynamics and the dynamics of rodent biomass. In the southern forest-steppe and in the southern taiga the deciding factors are spring weather conditions determining the possible number of generations reproducing in the year of their birth. In the mountains the intensity of rodent reproduction is relatively stable, and factors of mortality attain considerable significance. The numbers of subarctic populations of widely-distributed species are, to a considerable extent, determined by the number of animals surviving from the first generation (their participation in reproduction leads to a sharp increase in the number of reproducing animals), but a direct effect of deteriorating conditions becomes exceptionally significant (return of cold spells in spring and particularly in summer may lead to almost complete destruction of the species). Typical subarctic species are less affected by climate changes, and the role of intrapopulation processes in the dynamics of numbers is considerably increased.

The type of population dynamics determines in turn the dynamics of the species biomass. If we treat the number of young animals starting their hibernation in relation to each pair of reproducing animals in spring as characterizing population productivity in a general way, then in the case of equal productivity recorded for both mountainous and subarctic forms the dynamics of their biomass will differ considerably. In order to maintain stable numbers over the course of two years, it is sufficient for *Alticola lemminus* to realize its characteristic fertility in spring and to increase its numbers (as compared with the winter period) by approximately three times, which gradually decrease and by spring reach the initial level. The total biomass of the species does not vary significantly, and no special increase can be recorded when the numbers fluctuate (sharp changes in the numbers are not characteristic of this species). In order to maintain stable numbers over the course of two reproductive seasons of the subarctic *Microtus oeconomus* populations it is necessary to produce, in the course of the short summer period, not fewer than three generations whose numbers exceed many times (5–10 times) not only the initial (spring) numbers of the species, but also the final (autumn) numbers. Only when this condition is met can the autumn population of this species include a sufficient number of young animals able to survive the polar winter and start a new cycle of numerical dynamics from the initial level. Therefore, other things being equal, the type of dynamics of northern *Microtus oeconomus* populations can have a considerable effect on the life of the ecosystem ("pressure" on the vegetation, their contribution to the trophics of the higher links of the food chain, etc.). Analogous examples, concerned with other species, can be drawn from the Table IV. The study of the general theory of rodent biomass dynamics concerned with various ecological groups can be carried out on another basis.

It is natural that the type of population dynamics also determines the character of numerical changes. Direct observations have shown that *Microtus oeconomus* is able in the course of two incomplete seasons to reproduce in the conditions of the Far North and to raise its numbers from the minimum level (that is, almost complete disappearance of the species in the regions investigated) to the maximum one. In the period of the highest numbers the density of this form's populations reaches 160 individuals per ha. As the average biomass of the sedge (their basic food) amounts to 200 g/sq. m in those places where it is most abundant, populations of such density can cause considerable destruction of their food base in the course of one season. This, however, is not the case in nature as the intrapopulation mechanisms of numbers regulation then come to the fore.

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