Conservation of energetic balance as the strategic way for adaptation to cold climate in homothermal animals

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Russian ecologist professor Nickolai Kalabukhov (1946, 1950) developed the study on conservation of energetic balance as the base of adaptation. He showed that “all adaptations appears just in fact that they, regulating of energy coming or loss, ensure the energetic balance of organisms or a total population at the changing environmental conditions».
During the last 50 years we studied the ways of warm-blooded animals adaptations to conditions of extremely severe cold climate of Yakutia – all recognized Cold Pole of men-inhabited part of the Earth. It is established that all birds and mammals, from small rodents and passerine to large ungulates and the most large gallinaceous, watery and predatory birds living here, have a behavioral, ecology-physiological and morphologic mechanisms of energetic resources economy in cold time of a year and insurance of good warm-cycling in hot summer days.
At this report, except of our own data, we used the other researchers results of homoithermic animals study on the North.
In Yakutia, the most important meaning belongs to economization of an organism energetic resources. Even academic A.F. Middendorff paid his attention to some adaptive features of Siberian animals as thick and rich fur, ability to accumulate large fat resources to winter time and life style features in his wonderful book «Traveling to North and East of Siberia» (1869) . From that time, the science collected many new facts confirming these watching of this Russian Science’s classic.

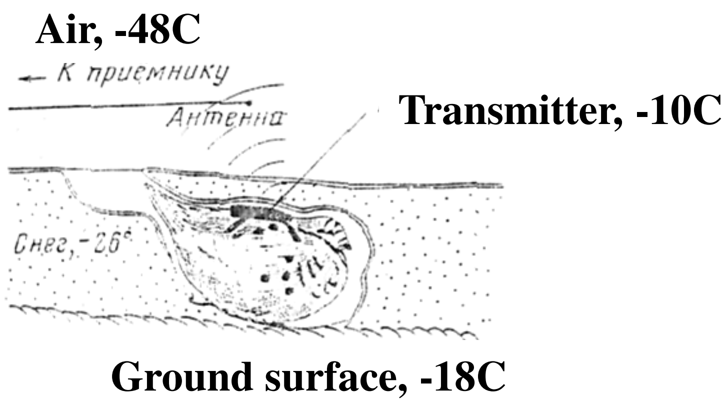
Adaptations of warm-blooded small and large animals to cold climate appear differently. However, in all cases, these are different forms of adaptive behavior, changes of some ecologic parameters such as shifting of life activities seasonal cycles, feeding character and features of population's reproduction. Morphological changes of breathing, digestion and movement have the most important significance. It is well-known that animal distribution in new severe regions accompanies with changes on their behavior types (Elton, 1930; Kambukov, 1940, 1950; Shwarts, 1963, etc.). Adaptive behavior appears, by Elton, in animal's selection of a suitable environment.

Let see this on the concrete examples. On the North, where microclimate differences in separate biotopes are so great even in the limits of one geographic point (Tab.1), the particularly significance is the animals ability to find the most optimal conditions for their wintering refuges and holes. The table shows that frost-free period varies in different biotopes of interfluves from 55 to 97 days and in Lena River valley – from 46 to 81 days. Soil temperature varies significantly. According to M.K. Gavrilova (1969), the average annual temperature of the soil at a depth of 50 cm in the open wide valley is - 6°C, in a narrow valley icing – 1.0 ° C, in a dense spruce forest with crown density 0.7 - 0.8 - 3.5 ° C. Depth of seasonal permafrost thawing in the Lena valley, according to our data, ranges from 0.6 m to 2.5 m. There is a rapid freezing of the soil cover in autumn. By December, all active soil layer freezes entirely and is connected to the ground permafrost. `

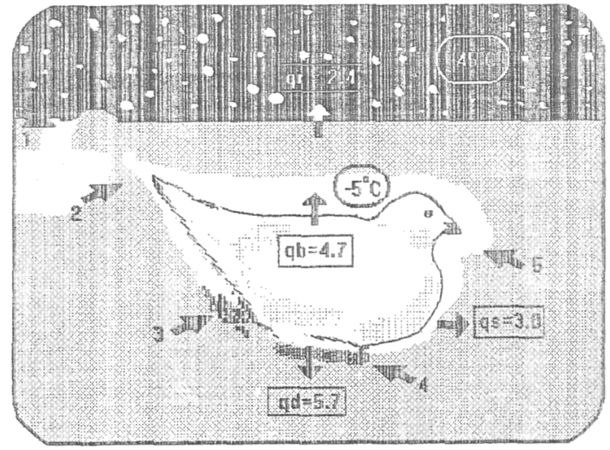
In connection with such features of soils, burrowing rodents of Central Yakutia have a number of well-defined adaptations. First of all, it is the significant sizes of wintering holes in a raw of species. According to our data, the total length of the water vole burrows can reach 100 m. The nesting chamber is usually at a depth of 40-50 cm. According to M.M. Davydov (1953), the length of the passages in muskrat burrows is 15 m. Large sizes of holes have value in soil freezing, for example, for water vole as this animal can still fed only within its burrow.

Tab. 1. The frost-free period in days according to observations at a height of 2 m (compiled based on D.I. Shashko, 1961)

Location	Dare of the frost		Duration of the frost-free period
	Last	First	
Lena-Amga interfluve			
Farm of «Path of socialism» in Megino-Khangalasski district. Open rye field on the second terrace of the Lena	May, 28	September, 3	97
Field on the southern slope of Chagada lake (width 200 m, length 1500 m)	June, 5	August, 24	79
Field among the dense forest, 3 ha	June, 12	August, 16	64
Vegetable garden in alas Queleriki over the water, forestless bank over the settlement	June, 6	22 августа	76
Alasc Second Queleriki, 35 m of depth, meadow surrounded with dense mossy large forest	June, 16	11 августа	55
Valleys of taiga rivers	June, 9-12	August, 16-19	64-70
Larch forest	June, 9-11	August, 16-19	64-70
Middle Lena Valley			
Pokrovsk station, 1951. Potato field on the third terrace a) southeastern slope	July, 7	August. 28	81
б) northwestern slope	June, 9	August, 26	77
Field surrounded with forest, second terrace	June, 15	August, 19	64
River Pokrovka valley, its expanded part, forested banks	June, 18	August, 16	58
Rver Pokrovka valley, its more narrow part, forestless banks, air flow is difficult	June, 23	August, 9	46



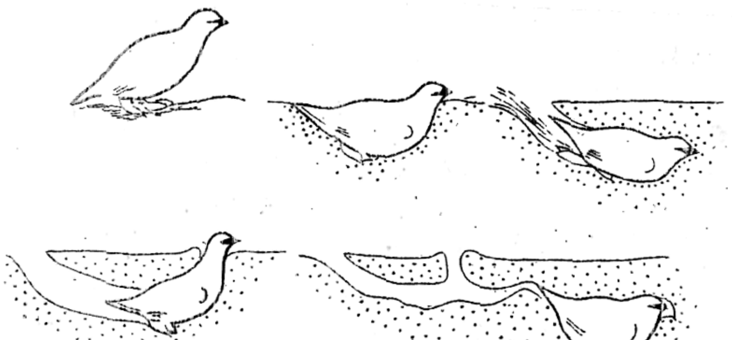
1. Hazel Grouse



2. Temperature conditions in the snow chamber of Willow ptarmigan.

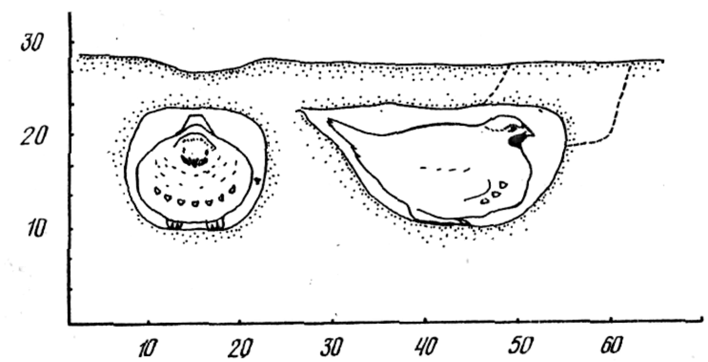
qr, qb, qd, qs – the densities of the heat flow at various points of the chamber, mW / cm ³.

Arrows indicate the character features of the chamber: 1 - hole to look around before burying; 2 - snow tube, closing access to cold air; 3 - excrement; 4 - zone of partial snow thawing amplifying the heat loss; 5 - snowy ledge where the bird pecks snow.



3. Behavior of Rock ptarmigan at instillation in the snow

A – choice of the place, B – start of instillation, C – the digging of the tunnel, D – the bird is looking out, E – the most possible position of Ptarmigan under (by: Andreev, 1975).



4. Position of Spruce grouse during night in the thick snow. Restored to fathom holes in nature and photographs of birds on the trees in ball pose. In ordinate and axis - length, cm (by: Andreev, 1975).

Fig.1. Features of under-snow hole- chamber for grouse overnight

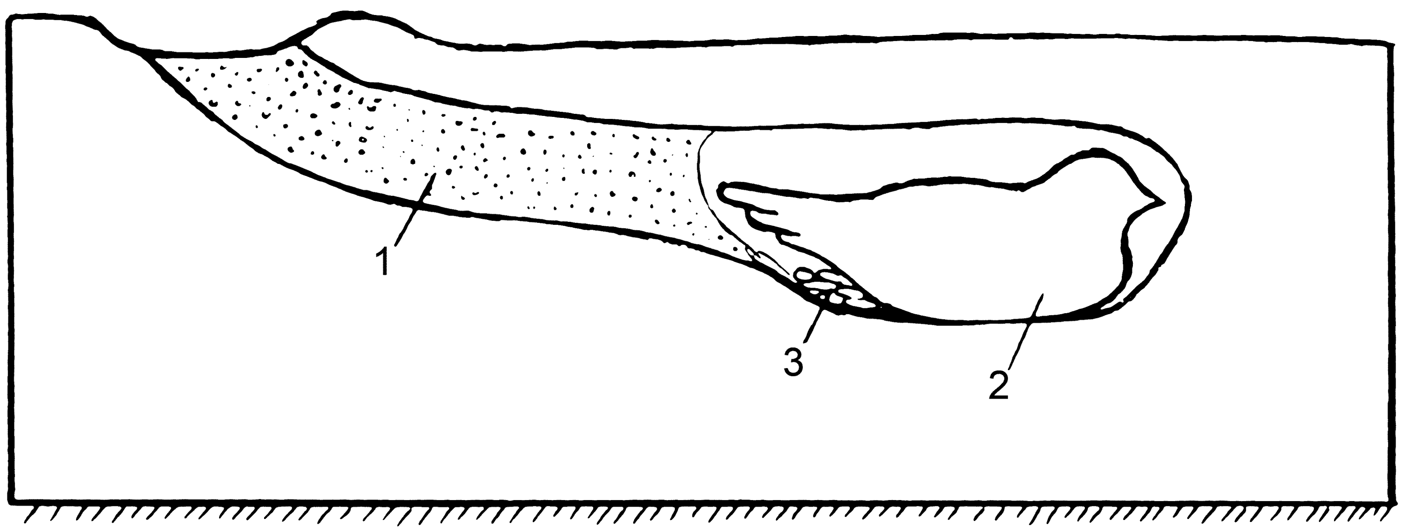


Fig.2. Features of under-snow hole- chamber for grouse and capercaillie overnight in Yakutia 1- tightly packed with snow tunnel, 2-position of bird in cave, 3- solid excrements (by Arkady P. Isaev)

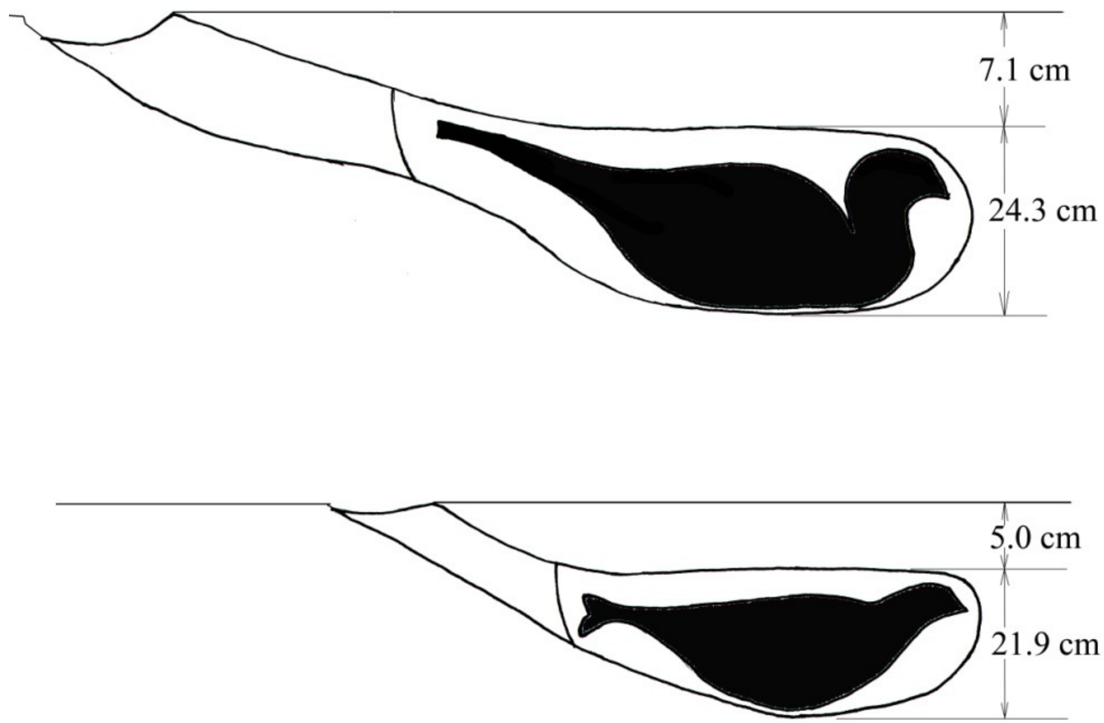


Fig.3. Features of under-snow hole- chambers for Capercaillie and Northern Black Grouse overnighting in Yakutia (by Arkady P. Isaev)

- Remarkable adaptation to winter conditions with limited access to the surface of the soil is strongly developed instinct of storing in large number individuals of the species. According to our data, up to 30 kg of stored food may be found in some wintering Yakutian water vole burrows (Solomonov, 1960).
- The great importance for water vole is use of the snow cover insulating properties. It usually build up its wintering holes in areas that are convenient for the snowbound (Table 2)

Table 2. Depth of snow cover over burrows of wintering water vole *Arvicola terrestris* (cm).

Place of measurement	Months							
	November		December		January		March	
	n	M±m	n	M±m	n	M±m	n	M±m
Depth of snow in open areas	10	18±2,6	5	28	5	30	5	31
Snow depth over wintering burrows	6	34±2,9	4	46	4	48	4	55

Apparently, snow cover has even more importance for lives of small voles (narrow-headed *Microtus gregalis* , tundra vole *Microtus oeconomus*, northern red-backed vole *Gleyhryonomus rutilos*). We conducted a survey of the narrow-headed vole wintering areas in the valley of the middle Lena (Table 3).

Table 3. Distribution of narrow-headed vole wintering colonies.

№	Stations	Number of sightings	Depth of snow cover (March), cm
1	Open steppe areas including: a) level areas c) areas with cup-shaped depressions and other irregularities	8 2 6	28 70±11,2
2	Edge of pine forest	7	36±3,4
3	Willow groves and their edges	8	33±2,8
4	Birch groves and their edges	2	32
5	Field edges	6	35±2,4
6	Hummocky sites with free-standing shrubs	5	40±4,8

It is seen that the largest number of wintering burrows were located on the edges of shrubs and pine forests, and in the open steppe - in areas with irregularities and depressions convenient for snow covering. These recesses are cup-shaped formation with depth to 60 cm and diameter of 3.5 m. In fall, rodent burrows arranged at the bottom and the inner wall of the “cup”. When snowfall they are under a thick layer of snow.

Voles are active under the snow. Under-snow ways go in different directions from the colony. Some of them reach the nearest shrubs of willows bark of which to spring time is partially picked.

In hummocky places, wintering dwellings of narrow-headed voles as well as tundra voles are usually located on no-mowed parts. Vole nests are arranged inside of gnaw-out by them cavities in hummocks, or on a tussock, or even between the tussoks. The no-mowed grass may ducks at snowfall and voids appear under this. These voids are used for voles movement. Such extensive voids appear to have a value for the aeration. Often these homes are combined with under-ground burrows which are usually arranged under the roots of a willow standing alone. Tundra vole and especially narrow-headed vole often make significant stocks of winter food.

There is no doubt that under-snow dwelling of voles trapped under a thick layer of snow are lesser affected with frost. This relates to all small mammals - shrews, rodents, pikas, small predators: weasel and stoat.

Even better the snow role is described for grouses (Semenov-Tyan-Shanski, Potapov, Andreev, and others). In recent years, Arkady Petrovich Isaev presenting here conduct a special study of these birds under-snow lives in Yakutia.

Characteristic of thermal and physical features of under-snow grouse cameras is given below (Figure 1).

Thermic conditions of under-snow hole-cameras for the night are particularly well shown by A.V. Andreev for Willow Ptarmigan and A.V. * Andreev and A.V. Kretzschmar for Hazel grouse.

In the first case, at the outside air temperature -45°C, in the air space between the chamber ceiling and the bird body was -5°C retained. At the second case, at the outside air temperature -48°C, the air temperature of radio-transmitter attached to the back of the bird was -10 ° C. There is no doubt that such a temperature in the chamber was provided by a heatproof role of snow cover and heat release of the bird itself.

The great role of snow as a heat shield can be learned from our measurements of the temperature under the rotten stump in the middle Lena valley in 30 km to north from Pokrovsk town where was wintering Siberian Salamander (Fig. 4).

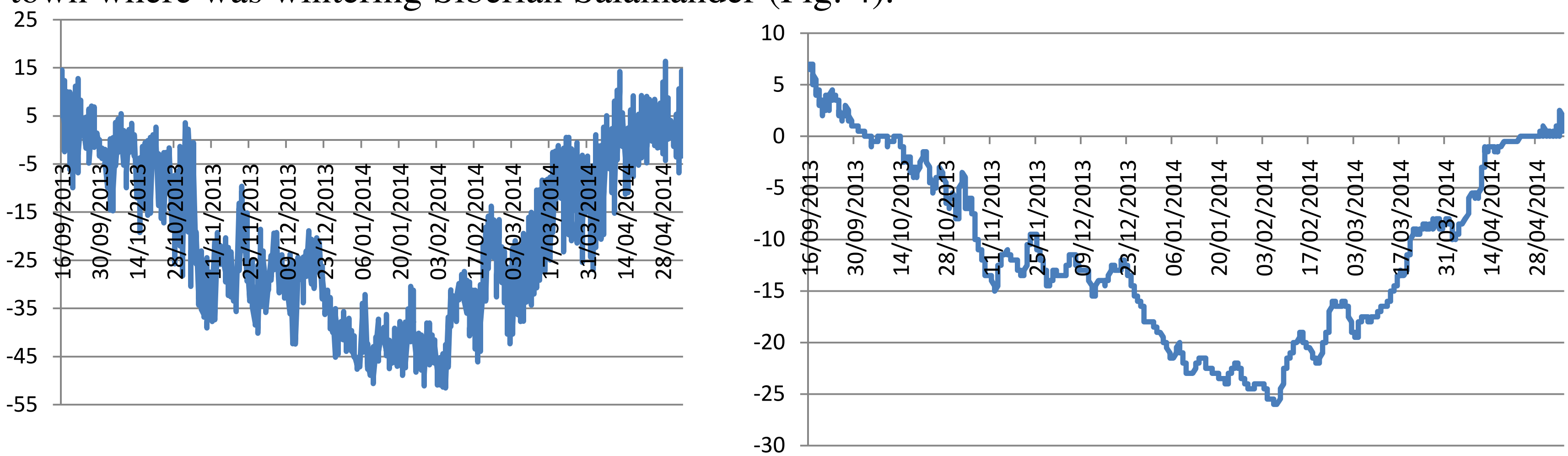


Figure 4. Air temperature and temperature under stump where Salamanders wintered.

* In the temperate climate of the Leningrad region all grouses spend nights in under- snow cameras while Willow Ptarmigan shows the lowest propensity to this (Potapov, 1985). Even at frost to -25°C it spends the night in the surface holes and only occasionally inexplicably digs into the snow.

In the near-polar regions of the North-East Asia where its wintering ground for many weeks has ambient temperature below -50°C, the same Willow ptarmigan overnights constantly under the snow in the chambers (Andreev, 1999). This allows it to stay at relatively comfortable conditions during about 18-hours.

Serious threat to North animals is the deterioration of their food base: the disappearance of many attractive for them plant species, the diet of some animals becomes everyphagic while others shift to mass but nutrient-poor food in winter. The last is characteristic of Arctic Hare from mammals and of grouses from birds. During the summer, these species have no shortage in food. In winter, for 7-8 months, Arctic Hare feeds exclusively with wooden-shrub vegetation in Central Yakutia and in Upper Yana district.

Table 4. Geographic features of Arctic Hare winter nutrition (frequency of eating,%) in S.P. Naumov, 1967.

Kinds	Regions		
	Vologodskaya district	Central Yakutia	Upper Yana district
Deciduous	86	59	34
Coniferous	5	27	21
Berry semi-shrubs and herbaceous plants	9	14	45

Mountain Hare has behavioral and physiological adaptations in connection with such feeding character. First of them boil down to the low mobility of the hare in winter (Popov, 1960, Naumov, 1967).

In 1973, we suggested that the evolution of Mountain Hare in strong frosts and an abundance of low-value feed aims to maximize the use of these resources and to less mobility, reducing the size of the body and increase the species number (Solomonov, 1973).

According to Bergman rule, one would expect that Mountain Hare inhabiting Central Yakutia and Upper Yana/ Verkhoyansk could be large because they live in the coldest region. In fact, hares of these populations the smallest and most numerous in the world. Because of nutrient-poor although plentiful food the animals can not be large. With periodic population outbursts, when it near of its peak, the animals enhance their mobility and more or less noticeable migration occurs what is associated with both a decrease in food availability and increase in predators.

This distracts the energy balance: the animal adapted to a relatively sedentary lifestyle, dramatically increases its activity. Increase in the metabolism level quickly leads to a rapid loss of reserves, weakens the body, lowers resistance to disease and eventually lead to "the collapse of the population“.

Important implications for energy economization by grouses are features of climatic conditions and morphological adaptations to rapid and economical eating of twig food. N.I. Volkov (1970) found that the birch and willow shoots become brittle and more accessible for Ptarmigans and other grouses just in cold times: in Silver and Pubescens birches - at -12℃, Swamp birch - -3.3℃, Gray willow - -9.5℃, Goat willow – -18.3℃, Willow triandra - -4.2℃. At such temperatures, Willow ptarmigan quickly and effortlessly peck shoots but at higher temperatures they have to spend a lot of effort. A Capercaillie’s beak is adapted to quickly and effortless pecking of larch shoots. This beak has a well-developed bone-horn comb through which this bird easily breaks off two pieces of twigs with just one movement.

Another physiological feature distinguishes birds and mammals the basis of nutrition of which constitute twig food. It is an exclusive development of blind intestine. R.L. Potapov , A.V. Andreev and their students are showed in their works that actively processing of food mass is in the colon of animals. The contents of the blind intestine and its excrement have much higher calorie than eaten sprouts and earrings (Potapov, Andreev, 1973). In the case of Willow Ptarmigan, it is noted that it allocates less than 2.3 times the excrement from the colon than Rock Ptarmigan does. It is assumed that the efficiency of nutrients absorption in the colon of Willow Ptarmigan is significantly higher.

Our Laboratory's collaborators A.E. Pshennikov, Z.Z. Borisov and I.S. Vasiliev (1988) conducted a special study of the so-called koprophagy in Mountain Hare and showed that when this animal eats soft faeces produced in its colon and then re-eats these it gets high-quality product that contains a lot more protein than eaten willow shoots (Table 5).

Table 5. Content of crude protein and fiber in the diet, food mass and excrements* of Mountain Hare in Central Yakutia

Material	**Protein**	**Fiber**
Willow shoots	6.11 (3.2-9.7)	(29.2-34.1)
Content of pyloric stomach	13.2 (8.33-14.58)	30.0 (23.0-35.5)
Content of the colon	32.1 (19.8-51.5)	20.3 (11.0-21.0)
Soft faeces	39.4 (28.1-44.7)	17.2 (12.5-24.1)
Solid excrements	8.7 (5.2-11.7)	29.7 (23.1-34.5)

*The results of faeces investigation collected in Arctic Hare habitats in winter or received at the opening of hunted animals, are shown (data on the number of air-dry substance, %)

It should be noted that in the case of Grouses, there are normal digestive processes occur in colon, and in case of Mountain Hare, the microorganisms take undoubtedly part in fiber refining in the colon. This is evidenced by the fact that increasing of the protein content in food mass and excrement of Hare is accompanied with simultaneous decrease in the fiber content of the colon and soft faeces.

Thus, behavioral, morphological and physiological

adaptations of homeothermic animals

in the North aimed to preserve

their energy balance in severe conditions.

THANK YOU FOR YOUR ATTENTION!