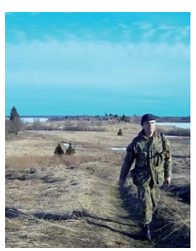
Nature-lovers know that the common adder (Vipera berus L., 1758) has spread over the vast area stretching far to the North. However, only few of them imagine all the variety of the adaptive mechanisms providing existence of this species in various conditions including polar areas. The list of such unique properties includes both the ability of an organism of the adder (toxicity, nonspecific diet, tissues resistance to cold, effective thermoregulation), and the features of population structure (two- and even a multi-year reproductive cycle, multiple copulation, ovoviviparity, long lifetime). On the basis of our 18 years investigations, we have a possibility to carry out a system research on biology of the adder. We are going to display in detail the integrity of these various biological properties of the adder in relationship providing its existence in the North.

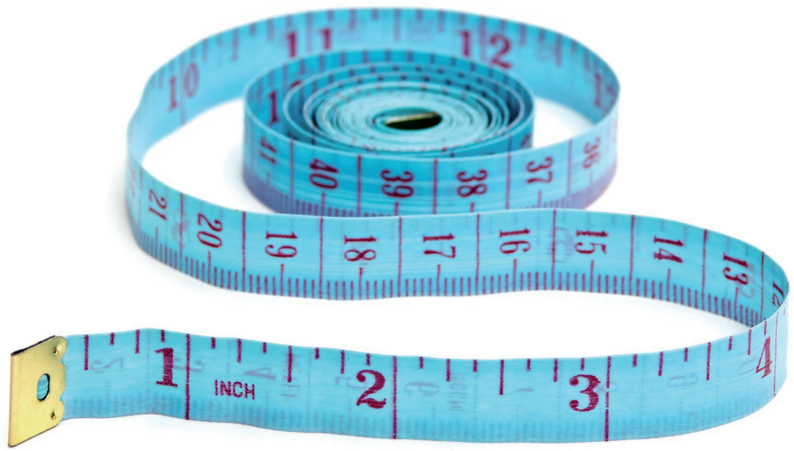


Korosov Andrei Viktorovich. Doctor of Biological Sciences, Professor of Petrozavodsk State University, Petrozavodsk, RF. Field of Interest: animal ecology (theiology, herpetology), methodology of science (system approach), methods of quantitative processing of biological data (biometrics, simulation, GIS).

978-620-2-06315-9

System ecology of the common adder

Korosov



Andrei Korosov

System ecology of the common adder

Facts and models

LAP LAMBERT Academic Publishing

Andrei Korosov

System ecology of the common adder

Andrei Korosov

System ecology of the common adder

Facts and models

LAP LAMBERT Academic Publishing RU

Imprint
Any brand names and product names mentioned in this book are subject to trademark, brand or patent protection and are trademarks or registered trademarks of their respective holders. The use of brand names, product names, common names, trade names, product descriptions etc. even without a particular marking in this work is in no way to be construed to mean that such names may be regarded as unrestricted in respect of trademark and brand protection legislation and could thus be used by anyone.

Cover image: www.ingimage.com

Publisher:
LAP LAMBERT Academic Publishing
is a trademark of
International Book Market Service Ltd., member of OmniScriptum Publishing Group
17 Meldrum Street, Beau Bassin 71504, Mauritius

Printed at: see last page
ISBN: 978-620-2-06315-9

Copyright © Andrei Korosov
Copyright © 2017 International Book Market Service Ltd., member of OmniScriptum Publishing Group
All rights reserved. Beau Bassin 2017

Reviewers - ***Dr.Sc. V.A. Ilyukha, PhD V.N. Kuranova***

Translation from Russian - ***Dr.Sc. V.A. Cherlin, N.D. Chernysheva***

Contents.

Introduction……..... 3

Chapter 1. The habitat of the adder 7
Chapter 2. Reptiles of Karelia 15
2.1. Herpetofauna 16
2.2. Annual life cycle of adder 34
2.3. Population status of the adder on Kizhi island 42
Chapter 3. Thermoregulation 47
3.1. Material and methods 48
3.2. The body temperature 53
3.3. Heating 68
3.4. Cooling 86
3.5. The model of thermoregulatory behavior 106
Chapter 4. Breeding 133
4.1. Chronology of mating 134
4.2. Wintering with embryos 144
4.3. Fertility 148
Chapter 5. The growth 151
5.1. Molting 152
5.2. Linear growth 156
5.3. Weight gain 170
5.4. Interior characteristics 186
Chapter 6. Metabolism 208
6.1. Basal metabolism 212
6.2. Cost of individual's life 226
6.3. The energetic requirements of a population 228
Chapter 7. Survival 232
7.1. Materials and methods 232
7.2. Calculation of survival on marking data 238
7.3. Mortality factors in adders on the Kizhi island 247
7.4. Sexual structure of population 253
7.5. Life span 256

Chapter 8. Reproduction 273
8.1. Materials and methods 274
8.2. Assessment of relative number 275
8.3. Assessment of absolute number by analytical methods 277
8.4. Assessment of absolute number in modeling 283
8.5. Age structure of island population 304
Chapter 9. Feeding..... 325
Chapter 10. Place of the adder in zoocenosis 337
10.1. Material and methods 337
10.2. Number of amphibians 340
10.3. Number of birds 347
10.4. Number of small mammals 350
10.5. Total volume of food resources 361
Chapter 11. Spatial movement 364
11.1. Total characteristics of movement 365
11.2. Individual mobility 379
11.3. Death on the roads 385
Chapter 12. Distribution 388
12.1. Adders' habitats on Kizhi 389
12.2. Allocation of adders on the island of Kizhi 393
12.3. Distribution of adders over the islands 406
Chapter 13. Keeping adders in captivity 413
Chapter 14. Technology of simulating 419
14.1. Development of dependence (descriptive model) 419
14.2. Reconstruction of the process (dynamical model) 425
14.3. Parameters of macro "Solver" 430

Conclusion 436

Bibliography 443

Introduction

Nature-lovers know that the adder (*Vipera berus* L., 1758) has spread over the vast area stretching far to the North. However, only few of them imagine all the variety of the adaptive mechanisms providing existence of this species in various conditions including polar areas. The list of such unique properties includes both the ability of an organism of the adder (toxicity, nonspecific diet, tissues resistance to cold, effective thermoregulation), and the features of population structure (two- and even a multi-year reproductive cycle, multiple copulation, ovoviviparity, long lifetime).

Specific biology of the adder in the North can be adequately presented by means of the hierarchy of the adaptive features, each of them is supported by the characteristics at the underlying level of the biological organization and at the same time it provides the manifestation of the biosystems properties at the higher level. So, a short and cool summer (ecosystem level) determines the low speed of fat reserves accumulation (tissue level), which does not allow females (organismic level) to have offspring more often than once per two years, therefore the proportion of females able to breeding (population level) becomes lower than males, and the rate of reproduction slows down. We are going to display in detail the integrity of these various biological properties of the adder in relationship providing its existence in the North. Biology of the adder is well described in articles of different authors, but the complete picture of its life is lacking today. On the basis of our 18 years investigations, we have a possibility to carry out a broad systemic research on biology of the adder. (Though, we did not set the goal to conduct a comprehensive review of all materials published on this subject.)

The systemic approach to research means (Korosov, 2000):

- the set of clear (ecology-zoological) goals of the research,
- hierarchical structuring of information in accordance with the goal,
- construction of quantitative descriptions of studied properties in the form of models,

- summarizing, synthesis of quantitative descriptions of different levels of hierarchy,
- the estimate of the role of discovered adaptations in advancing to the North.

There is an important positive precedent of such type of investigation (Zamolodchikov, 1993). However, this experience cannot be considered as optimal, because:

- cited paper is based entirely on literary data (therefore different organization levels are objectively disproportional; for example, the population analysis is practically missing),

- proposed models are not well understandable and interpretable, and they do not correspond completely to the study subject.

The goal of our work is to explain quantitatively why the adder lives in the studied area, to give quantitative estimates of the adaptive traits of the adder, allowing it to exist in the harsh environment of the North-West of Russia (on the example of its island population). It is necessary to explain the ***functioning*** of the boreal population of this species, examine it from an environmental point of view.

It is important to divide the tasks into available and unavailable ones. Generally, on the basis of animal ecology we can answer two questions:

1. Why can the species live and actually lives in this area?

2. Why does exactly the number of individuals of this species live there, not more or less?

In future, we will consider to a greater extend the second question that lies in the field of demecology (reproduction, chrono- and chorologic population structure, population dynamics), as well as synecology (trophic and cenotic relationships), that is less studied and is in the area of our interests. So, the object of our study – functional zoology of the adder at three levels of organization: organism, population and ecosystem (cenotic) (Fig., Table).

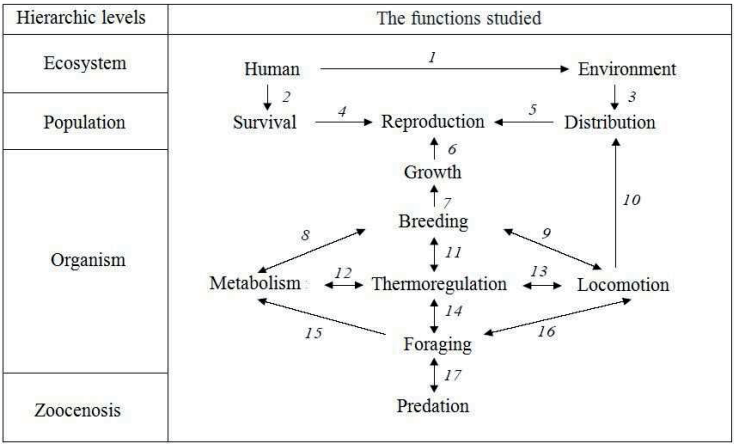


Fig. The hierarchy of the studied objects. *1–17* – see Table

Table. Relationship (connection and dependence) between the objects.

No	The description of relationship
1	Transformation of habitats, degradation of farmlands
2	Strict elimination of animals
3	Compliance of habitats' ecotop to the needs of the adder Influence of unfavorable and pernicious factors
4	Participation of survived individuals only in restoration of population
5	Casual association of couples – a consequence of multidirectional migrations (realization of panmixia)
6	Puberty and the recovery of individuals after reproduction
7	Age-related increase in individuals' size
8	Propagation requires large energy inputs Only individuals with large fat reserves can participate in reproduction
9	Migrations and mating behavior
10	Distribution is connected with the variety of snakes' displacement
11	Thermoregulatory behavior depends on animal status Temperature determines the possibility and rate of development and growth
12	Metabolism rate depends on body temperature Thermoregulation needs large energy expenses
13	The adder is characterized by complicated thermoregulatory behavior
14	Digestion rate is determined by body temperature Behavior of replete and hungry snakes differs

15	Production is manly determined by the feeding characters
16	The adder is an active predator Availability of food objects is defined by a habitat of an individual Forage reserve (quantity of prey) limits the level of predator population.
17	Size of predator population determines the strength of its effects on island populations of victims.

ACKNOWLEDGMENTS

The author is deeply grateful to all leaders of the host organizations, friends, colleagues and students who provided their own information on biology and habitats of some species and rendered all possible assistance in the research work; among them: A. V. Artem'ev, A. V. Bogdanova, S. V. Bugrymin, E. V. Gerasimova, S. A. Gil'bo, V. V. Gorbach, M. M. Gudkov, P. I. Danilov, O. A. Ermolenko, Ya. S. Zaharova, I. V. Zenkova, V. B. Zimin, S. R. Znamenckij, A. A. Zorina, V. A. Il'in, V. A. Iljuha, N. M. Kalinkina, N. T. Kishchenko, A. A. Korosov, V. I. Korosov, S. A. Korosov, A. P. Kudarenko, O. I. Kukkarina, A. P. Kutenkov, Yu. I. Lazarev, N. V. Lapshin, M. V. Lopatkin, D. D. Lugovoj, V. V. Lukanin, M. M. Kalinkin, A. M. Makarov, Yu. V. Maklakova, N. V. Medvedev, A. V. Myurulainen, A. E. Panarin, S. A. Pozdnyakov, T. A. Prohorova, S. A. Ryabov, Yu. A. Safronov, A. R. Tyulin, N. N. Tyutyunnik, R. I. Fillipova, T. Yu. Hohlova, S. I. Chernyh, M. A. Shreders, V. I. Shubin, E. Yu. Schelupanova, M. V. Yakovleva. The study became possible due to the favorable acceptance of the work of the administration of the museum-reserve "Kizhi" (director M.V.Lopatkin, D.D.Lugovoy, E.V.Aver'yanov) and permanent organizational help of its employees Yu. G. Protasov, R. S. Mart'yanov, A. R. Buyalo, A. A. Korosov, N. A. Korshunova, and others. The author is grateful to an inventive post-graduate student T. N. Khilkov for his difficult and important work with the adder in the laboratory. With appreciation it should be noted a very large contribution, made in the implementation of this work by S. N. Fomichev, professional herpetologist, a member of numerous zoological expeditions. I would like to express my gratitude to the head of the department of zoology and ecology of Petrozavodsk state university E. V. Ivanter, who during the years in every possible way helped in the organization of the author's scientific work. It is especially pleasant to thank my life companion – Yu. M. Korosova (Matrosova) for a big role in implementation of numerous expeditions.

This book is a translation into English of a Russian-language monograph (Korosov, 2010).

Chapter 1.

The habitat of the adder

The adder occupies a vast area, i.e. it is not very demanding to habitat conditions. However, it is possible to compose the list of its obligatory requirements to the habitat. As it is most effective to conduct research on mass material, the islands of the Kizhi archipelago were selected, there the abundance of adders (common name – "gady") is reflected in the local toponymy: Gazheostrov, Gazhij Navolok, Gazh'ya guba...

Climate of the region is characterized as transitional from marine to continental with considerable overcast and excess moistening; the long, quite soft winter is replaced by the short cool summer (Climate of Petrozavodsk, 1982). The Republic of Karelia is located in the Northwest of Russia and stretches from 60° 40' to 69° 54' NL. One of the leading weather factors – periodic transfer of warm and damp air masses from the northern Atlantic. In winter they cause thaws, but in summer they reduce temperature and bring precipitation. The anti-cyclones have the opposite effect. They come from the North and the Northeast, lower the air temperature, and cause frosts. In general, in Karelia climate is distinctly warmer and wetter than at the same latitudes in eastern parts of Russia, but cooler, than in the neighboring Finland. On the Kizhi archipelago located in the central part of Lake Onega (Kizhi has coordinates 35° 22'EL and 62°08'NL), weather conditions are slightly softer, with milder winters and later incoming of cold weather (The medico-biological reference book, 1990). In this regard the studied territory of southern Zaonezh'ye is close to the northern Priladozh'ye, which is 150 km southwest. It is important to note that extreme weather instability during different seasons is characteristic for Karelia. It affects the variability of the period favorable for reproduction and feeding of our species, which in different years lasts from 2.5 to 4.5 months.

In the southern Karelia spring (when the mean daily air temperature became over 0°C) begins in the second decade of April. In the second half of May (when the bird cherry tree begins blossoming) cold weather returns. It

is connected with the change of the type of atmosphere circulation from winter to summer. In southern Karelia (northern Priladozh'ye) a warm period (>10°C) lasts 120 days. Only two reptile species – a sand lizard and grass snake – can hatch and develop in this minimal period. Further to the North the warm period is reduced (up to 110 days in the project area on the Kizhi archipelago) and only viviparous species have the possibility to reproduce. Early fall (temperature below 10 °C) is observed in the third decade of September. At that time amphibians and reptiles pass into winter shelters and later they almost never appear on the ground surface. In southern Karelia snow cover is usually set in at the end of November, but in recent years this date shifted to December. Here the reptiles' hibernation lasts about 210 days, or 7 months.

The ***landscape*** of the Kizhi archipelago is formed under the influence of strong geological forces and is unique in many ways (Golubev, 1999; Demidov, 1999; Lukashov, 1999; Lukashov, Demidov, 2001; Zhilina, Solomatova, 1999). The whole territory of Karelia is located in the eastern part of the crystalline Baltic shield, composed of ancient granites more than 3 billion years ago. However, in the territory of Zaonezh'ye there are three types of Proterozoic rocks (2.2 billion years old)over the granite basis – carbonate (limestone, dolomite, and fossil plants), schungites, hardened lava (volcanic rocks: basalts and gabbros), which is covered by young Quaternary sediments formed as a result of glacier activity.

For the past 1.5 billion years, this territory had been either a sea accumulating precipitation or dry land; the mountains were occasionally disintegrating, the relief was flattering (denudation). The most destructive process began 100 thousand years ago, when advancing glaciers periodically stripped all strata of the last 1.5 billion years from the territory of Zaonezh'ye and scattered them over the European part of Russia from the shores of Lake Onega to the Dnieper rapids. Under the giant body of the glacier, that was a 1.5 kilometer thick and moved from the North-West, the earth's crust flexure, subjacent underlying rocks, particularly the least firm, rubbed into the sand. The most solid monolithic igneous lava rocks smoothed by the glacier formed numerous rounded rocks (common name

"sel'gi", "shchelgi", or "the sheep's foreheads") that stretched from the North-West to the South-East. Crushed rocks and their fragments were saved in declivities between shchelgi. From the rubbed shungite layers the shungite soil was formed, containing a rich mineral composition, and further from it very fertile soil was formed – "the Karelian chernozem" (Kizhi island and other islands of the archipelago). Abrasion of limestone, dolomites and stromatolites also led to the formation of fertile carbonate soils of Volk-island (limestone neutralize acidic volcanic rocks).

The last glacier began its retreat about 15 thousand years ago. Snow-melt carried scuff debris and sand accumulated earlier. Their beds carved out inside the glacier accumulated these residues (fluvio-glacial deposits) and kept them in the form of long ranges with steep ridges ("ozy"). The most part of the island of Kizhi (east coast) is a fragment of such an “oz” that is noted on the islands and the mainland over a length of 80 km. Snowmelt flooded the vast area of the formed Onega basin, the lake was much larger than the modern one,; whole area of Zaonezh’ye, except the highest places, was under water. When the heavy body of the glacier disappeared, the earth's crust started to straighten up, and the water of the lake flew into the White sea, then into the Baltic sea. Surfs gradually washed out the fine soil fraction of appearing land and water retreat left lake terraces covered with boulders – stones of different sizes. Washed out soft soils settled on the bottom and formed the plain areas. Shallow lakes remaining inside the land were gradually overgrown by aquatic vegetation and become swamps. All areas more or less dry were overgrown with pine forests. Currently the level of the Onega is influenced by marked intra-annual fluctuations related to the snowmelt flow. Its maximum occurs at the end of the snow melting period (beginning of June). At that time water filled most of the coastal wetlands. Before the human settlement all the islands of the Kizhi archipelago were covered with forests, except exposed rocks and swamps occupying vast area. After the retreating of glacier and climate warming about 10 thousand years ago the spread of forests began. At first tundra dwarf birch-willow communities (with dwarf birch) were supplanted by pine-birch forests and in wet places – by black alder forests. Then (8 thousand years ago) the spruce came, fol-

lowed by broad-leaved species – oak, maple, elm, linden. The relatively warm climate of that time was favorable for men. The cooling after 4500 years ago forced out the most thermophilic tree species from Zaonezh'ye, but some of them (rough elm, cordiform tillet) survive to the present day on the Kizhi archipelago. Before the human settlement indigenous spruce and spruce-pine forests dominated on the rich soils in depressions between "sel'gi" and on former lake terraces, pine forests – on the ridges, birch and black alder forests – in a shallow and well flowing depressions; swamps were vast. The bottoms of depressions between "sel'gi" were usually swamped.

With the advent of man (about 1600 years ago), who had used the slash-and-burn method of land management by the XIX century, the role of spruce forests reduced and the low forest spread. At that, the cut wood was burnt, and the burnt areas were sown with different crops (mostly turnip). After gathering the crop these lands were left to rest for a few years, because the processing of the soil with many boulders was very difficult. Arable farming began to develop with the arrival of settlers from Novgorod (1000 years ago). When people reclaiming this land found the fertile properties of shungite and carbonate soils, they began grubbing up these soils of boulders, putting them on the shores of bogs and lakes in circular piles ("rovnitsy") or long ridges ("zaborya"). The soil rid from boulders was treated with a plow. In these places people sowed grain, made hay and pastured cattle. Up to 90% of crops were cereals (oats, rye, barley), as well as turnips, peas, buckwheat, flax, hemp, since 1838 – potato. Of all the land used by people the amount of an arable land composed 8%, a slash-allotment – 17%, hay – 24%, the pasture for cattle – 22%, a forest plot – 21%, an inarable land – 8%. Even "sel'gi"s were used, where trees were cut down and pastures were made, and marshes were used for haymaking and pastures. By the end of the XIX century the indigenous forests were cut in the ¾ of the area of the Kizhi archipelago (up to 15% of the land was occupied by stone ridges and roves). The photographs of the northern part of Klimetsky island dated by this time shows the vast hilly plain without trees, and Kizhi island had the same landscape up to the 60-ies.

Each event of the turbulent XX century (the First Japanese War, the Stolypin's reforms, the first World War, the intervention and British occupation, revolution, civil war, collectivization, the Finnish War, the second World War, the Finnish occupation, Khrushchev's reforms of consolidation and destruction of small farms, reformation and transition to market economy) led to a reduction of the peasant population and Zaonezh'ye desolation. At present, a tiny part of previously agricultural lands is occupied by vegetable gardens, haymaking grounds and pastures, and the number of peasants is close to zero. For the last hundred years more and more new lands have been involved in the process of natural succession. Arable lands have quickly turned into meadows or homogeneous forests (birches, lindens, pines, spruces). Meadows have overgrown with low forests (alders, bird cherries, rowans, birches, aspens).

The adder (as well as the second local reptile species – viviparous lizard) has very favorable conditions here. Large areas of the natural (sel'gas, wetlands, shore) and anthropogenic (meadows) open tracts provide the direct access to the sunlight. Extensive swamps are densely populated by frogs, the main food of adult and young snakes. Prior to human advent these animals could find the suitable summer and winter shelters only in the cracks of the rocks, but at present the best shelters are in numerous stone ridges, gathered by peasants as if it is special for adders. On the islands, where this combination of factors is found (meadows, marshes, roves), the number of snakes is a hundred times more than in other suitable areas of Karelia – up to 20 animals /ha of adult snakes (up to 50 specimens of all ages).

Biotopes are closely connected with the history of mastering these lands by men. The studied area is located in the middle taiga subzone (Ivanter, 2001). It is characterized by the dominance of green moss pine and spruce forests as well as high diversity of plant communities. Due to the intensive exploitation for more than three centuries, the appearance of taiga has changed significantly. On the islands of the Kizhi archipelago upland meadows, secondary deciduous and coniferous-deciduous forests (birches, alders, aspens, lindens) dominate. All meadows in the island – the secondary, formed in place of cropland and pastures (at sel'gas). In the absence of

regular mowing (on the island of Kizhi it actually stopped in 1994) meadows start overgrowing with the wood, first of all with low forest. Pure upland meadows can remain for a long time because annually dying plants create a powerful pillow of dry stalks, which prevents the penetration of trees' seeds to the earth and their germination (Znamenskij, 1999). At first meadows overgrow with rhizome plants (gray alders, aspens), which take root and move from the periphery of a meadow to its center. Stone ridges become other centers of overgrowing. Everything begins from the fieldfares, carrying mountain ash berries with their dung over roves and relief protrusion. Expanding, mountain ashes shade and oppress herbs under crown, thereby create favorable conditions for germination of seeds of bird cherries, birches, alders, pines, aspens, lindens. As a result in 20–50 years the young upland motley grass deciduous woods are formed: low forest with shamrocks, May lilies, ferns and grasses, birch wood with May lilies and brackens, grey alder wood with May lilies, birch wood with grasses, May lilies and roebuck berries with single pines and spruces, aspen wood with grasses and aise-weeds. For the driest rocky meadows (on the basic rocks) typical rock species are characteristic – fragrant European mint, German catchfly, rib grass, St. John's wort, Prickly Sedge (*Carex muricata*) (registered in the Red Book of Karelia). On the crest of the rocky outcrops a mixture of forest species is often found (May lily, red bilberry, common Melick) serving as indicators that earlier there was a pine forest. On sel'ga slopes backfilled by moraine, one can find cereal – motley grass upland meadows with predominance of grasses from the St. John's wort and bluebell to trefoil and cornflower, there are areas with Golden Hairgrass (characteristic of acid soils) and meadow fescue (it was sown at the beginning of the XX century). On rocks and roves there are a lot of epilithic licens. For the last hundred years many new lands have been involved in the process of natural succession. The earlier the territories were brought out of land use, the older are the wood and the more coniferous woods are there. Modern landscape is absolutely different than it was 100 years ago: the agricultural lands have been replaced by all-aged woods mostly small-leaved. Coniferous woods are gradually forcing out deciduous ones (more than 70 years). Sometimes, missing a small forest stage,

on rich soils of meadows pine forests can be restored very quickly (Bukol'nikov island) and fir groves (southern part of Klimetsky island.) having a gain of annual rings up to 1 cm.

Prey and predators. Five species of Karelian amphibians live there (Korosov, 2005b). Common and banded newts, toads are extremely rare (only on the Klimetsky island), but frogs are numerous. The number of grass frogs is defined by the amount of caviar which they shed into the pools, after they got free from ice on the edges of bogs (a natural biotope), into ditches, sand-pits, karst funnels (an antropogenic biotope) in the early spring. The moor frog mastered natural low-lying and coastal bogs almost not depending on man (but depending on the water level in the Onega regulated by man). This species has especially favorable conditions on the archipelago and its number is 5 times greater, than in other parts of Karelia at the same latitude. Frogs serve as a forage resource for a large number of different animals, including adders, minks, buzzards and seagulls. The number of adders is high only due to big resources of frogs.

The modern antropogenic landscape (a significant factor of biodiversity) combines some elements of the former taiga, secondary uneven-aged woods, meadows, and bogs (Khokhlova, Semina, 1988; Yelina, Filimonova, 1999). This small-size landscape mosaic satisfies the needs of the most different birds – both inhabitants of open spaces and forest dendrophilous species. There the population density of background species (willow warbler, chaffinch) reaches very large sizes – 2 couples/ha, and all species together – up to 8 couples/ha. Except the willow warbler, chaffinch, redwing and robin, rosefinch, Old World warbler, a garden warbler, a greyish-brown Old World warbler can be attributed to the background species (Khokhlova, 1999). The number of the birds, nesting low over the earth and can be potential food objects for the adder (small seagulls, wryneck, lark, yellow-hammer, chiffchaffs, white-throats, redbreast, thrushes), is rather small in meadows. The central part of Klimetsky is quite uninhabited and there it is possible to meet rare birds of prey – golden eagle, white-tailed sea eagle; here the fish-hawk nests regularly and its foraging migrations is possible to observe every day on the east coast of the island. Other predatory birds are ordinary here – the

buzzard, honey-buzzard, hobby, a kestrel. Except the birds of prey, a certain danger for the adder come from small weasels, badgers, and also pets – cats and dogs. However their number is very low. For 15 years of our work on islands of the archipelago (except Klimetsky and Big Lelikovsky) only one hole of a badger, which existed one season, has been found.

On numerous islands of the Kizhi archipelago quite favorable conditions for the adder are formed: vast meadows open access to insolation, numerous stone heaps and ridges put by peasants serve as winter and summer shelters, and extensive lakeside bogs are rich with food objects – brown frogs (Korosov, 1996b).

Chapter 2.

Reptiles of Karelia

In the Northwest of Russia there are a few reptiles. Although the studies of the herpetofauna began long ago (Kessler, 1868), they were not intense (Ivanter, Marvin, 1968; Ivanter, 1975; Kataev, Makarova, 1984). Only recently specific data on phenology, distribution and abundance of reptiles' populations have been collected (Kutenkov, 1988; Korosov, 1988, 1995a, 1995б, 2000a, 2000b, 2003, 2005, 2008; Korosov, Fomichev, 2000, 2003). Among them a special attention is paid to the adder. In the first part the distribution of all Karelian reptile species is considered, in the second part – phenological life cycle of the adder is described.

Materials and methods

The data were collected in Karelia in 1975–2007 both by the author and employees of the "Kivach" reserve (Chronicle of nature reserve "Kivach", 1980–1997), "Kostomukshsky" nature reserve, Kandalaksha reserve, the zoological laboratory of Karelian Scientific Centre (KSC) of Russian Academy of Science (RAS) as well as the students of the biological faculty in expeditions organized by the author. This data also include the findings of a survey among the employees of the KSC RAS (Institutes of biology, forest, geology) about their encounters with snakes and slow worms (210 locations). In addition, during this period regular short expeditionary trips were performed to the various parts of Karelia for reptiles' route census. This work was performed according to standard methods (Darevskij, 1987; Korosov, 1994). At that, transect was 2 m wide in biotopes with high grass stand and shrubs and 4 m in more open habitats. The variable Karelian weather does not allow selecting the most favorable time for reptiles, so the counts were conducted during the period of their activity at different time of day – from 6 to 22 o'clock. In this chapter the total numbers of two species according to their repeated capturing were calcu-

lated by the Schumacher method (Koli, 1977). In such cases, combination of colored dots placed on the dorsal side by a nail polish served as markers for lizards.

2.1. Herpetofauna

Species. Five reptile species inhabit the region: slow worms, viviparous and sand lizards, European grass snakes and adders (table 2.1.1). The fact that of three species (slow worm, sand lizard and European grass snake) inhabit the limited area is the reason for them to be included into the Karelian Red Book (Korosov, 1995a, 2007), and the sand lizard – into the Red Book of Finnoscandia (Terhivuo, Korosov, 1998).

Table 2.1.1. Species composition and the number of reptile encounters in Karelia

	Species		Number of individual animals found		
			literature data	survey data	own data
Slowworm	*Anguis fragilis*	Af	>15	5	9
Sand lizard	*Lacerta agilis*	La	8	4	–
Viviparous lizard	*Zootoca vivipara*	Zv	>50	>350	>400
European grass snake	*Natrix natrix*	Nn	10	8	109
Adder	*Vipera berus*	Vb	>50	>300	>5000

Distribution. The Northern part of the republic is inhabited only by viviparous species, and oviparous are found only in the South (Korosov, 1995b).

The viviparous lizards occur in Karelia and Kol'sky region almost everywhere, even on the islands of the Solovetsky archipelago (Table 2.1.2).

The most northern location where one sand lizard was found in 1967 is the outskirts of the village Karku in Pitkyaranta region (61° 20' NL) (Ivanter, 1988). Southward of that place this species was found in the middle reaches of the river Olonka (61° 10' NL) (Kaisila, 1949) in the outskirts

of Olonets (61° NL) (Marvin, 1948; Ivanter, 1975), on the shore of lake Ladoga near the village Ustye Obozhanki (60° 50' NL) (Zimin, Kuz'min, 1980).

The distribution of slow worm was tracked in the southern part of the republic: earlier – at the western shore of Lake Onega and in Zaonezh'ye (Kessler, 1868), later – in Priladozh'ye (Marvin, 1948) and in other parts of the region (Ivanter, 1975). Northernmost locations were found by E.V.Ivanter (personal information) in 1958–1959 in the outskirts of the village Rebola (63° 50' NL) and Rugozero (63° 5' NL).

The distribution of the European grass snake was studied in detail in a number of expeditions. We can add some new locations of this species (table 2.1.2) to the known ones near the northern border of its area in Karelia (Bannikov et al., 1977; Korosov, 1995b; Orlov, Anan'yeva, 1995; Anan'yeva et al., 1998; Korosov, 2000b; Mil'to, 2003). The northernmost location was found by A.R.Tyulin on the bridge in the village. Lojmola (31° 45' EL, 61° 59' NL). Numerous grass snakes found to the South and West of this location show, that this species has though patchy, but quite continuous area. Apparently, in other places of Karelia except Priladozhye there are no sustainable habitats of these snakes. The border of this species area, mapped by K.D.Mil'to (2003) (fig. 2.1.1, 5), may correspond to the first third of the previous century, when natural peasant farms still existed and there were numerous places for reproduction in manure heaps near stockyards. Such situation retains in Finland where anthropogenic factors allow the grass snakes to spread 150 km further north (up to 63° 20' NL) (Terhivuo, 1993) than in Karelia (fig. 2.1.1).

Due to collectivization, war and restructuring of agricultural production the conditions for grass snakes' reproduction were abolished, and now the border of the species area has shifted to the South. We can assert that at the points 1, 2, 3, 19, 20, 21, 22 of the map made by K.D.Milto (2003) snakes are absent for more than half a century.

The northernmost populations of this species in Karelia are also associated with human activities, occasionally organizing favorable habitats for them – south-exposed slopes not overgrown by grass (fig. 2.1.2), that

are well warmed and provide the normal development of eggs (probably, not every year).

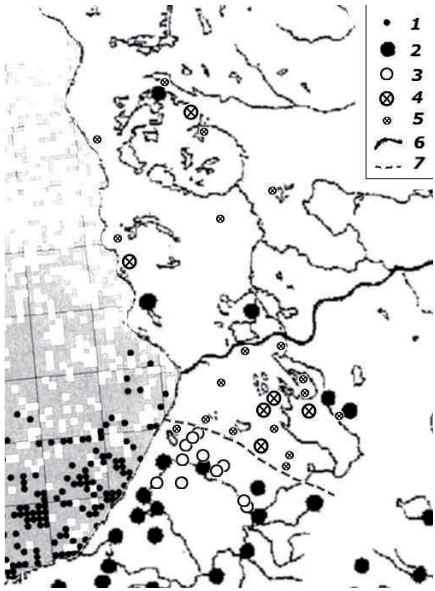


Fig. 2.1.1. Distribution of adder in the region: *1* — points of finding in Finland (Terhivuo, 1993), *2* – points of finding in Russia (Milto, 2003), *3* – our findings of adder, *4* – Locations of research stations where adder have not been registered for many years of observations (reserves «Kandalakshskiy», «Kostomukshskiy», «Kivach, Kizhi, biological research stations «Gomselga»,» Kaskesnavolok «,» Konchezero «), *5* – places with two and more case of reptilesregistration, *6* – border of the areal (Milto, 2003), *7* – border of the areal constructed by us with the latest data on the distribution of the species in Karelia

Approaching the creation of objective area boundaries of any species, it is necessary, firstly, to follow the methodology of cartography, secondly, to explain "dropped out" points. "Area is the region of distribution of the phenomenon at some level of manifestation of its essence... Part of the earth's surface, within which the given species is found" (Popov, 2008).

By the definition, the main characteristic of population is that it steadily exists in given territory, i.e. reproduce itself for a long time. To the North of the line marked by us the sustainable settlements of grass snake were not found, therefore, these areas may not be included in the distribution area of this species. The appearance of the points of snake location mentioned by K.D.Mil'to out of these boundaries is due to four reasons. In Zaonezh'ye, Pudozh region, and possibly in Kondopoga district snakes lived earlier, but not now. In the vicinity of the border with Finland (Muezersky district), snakes could pass from its territory. In Kandalaksha and Segezha regions snakes brought by people either as pets, or by accident (for example, with agricultural products – hay, grain) most likely were registered. Some evidence is clearly based on ambiguity. For example, in Pudozh region locals name adders as grass snakes, and these survey data get into scientific literature. On the basis of these facts, the modern northern border of the distribution of the grass snake in Karelia should be shifted farther southward (Fig. 2.1.1, 7).

Table 2.1.2. The list of animals' detection places in Karelia and on the Kola Peninsula

Species	Locations (highlighted in bold are the points which are not presented in article: Корсов, 2000)
Slowworm	1.Village Kurkiyoki, 3. Sortavala, 4. Village Impilahti, 6. Village Karku, 9. S. Moyachino, 10. Vil. Gumbaritsy, **17.** Middle current of river Uksunyoki (2006), 20. Village Reboly, 21. Village Rugozero, 22. Village Tivdia, 23. Entry of Ileksa river, Kolatsel'ga, 25. "Kivach" reserve, 26. Koncheosero, 28. Village Krivonogovo, 29. Shun'ga, 30. South bank of Sbyatuha bay, 31. Petrozavodsk, 31a. Mashezero lake, 32. Outskirts of Pudozh, 33. Pedasel'ga, 34. Shoksha, 35. Village Ihala, 36. West bank of Yanis'yarvi lake, 37. Village Koyrinoya (Kessler, 1868; Marvin, 1948; Ivanter, 1975; Borkin, Klever, 1987; author's and survey data)
Viviparous lizard	Everywhere, including 49, Solovetsky island (Yurkanskyj, 1927; Marvin, 1976).
Sand lizard	6. Village Karku, 7. Olonka river, 8. Near Olonets, 9. Moyachino, 11. Near Pedasel'ga, 10. Village Gumbaritsy, (Kaisila,1949; Marvin, 1948; Ivanter, 1975; Zimin, Kuz'min, 1980; Darevskij,1983; survey

Species	Locations (highlighted in bold are the points which are not presented in article: Коросов, 2000)
	data)
European grass snake	1. Village Kurkieki (1951, 1985), 2. Village Tervus (1987), 3. Honkosaari lake, near Sortavala (1948), 4. Near village Impilahti (1948), 5. Valaam island (1988, 2003), 9. On the bank of Ladoga lake, Moyachino (2006) (32°48' EL, 60°44' NL, 5 snakes.), 10. Vilage Gumbaritsy (1987), 11. Kil'pola island (1969), 12. Putsari island (1974), 13. Near Suystamo (1972), 14. Near Salmi (1991) (31°58' EL, 61°22' NL, 1 snake), 15. Near Raykankoski (1996, 2007)(31°33' EL, 61°56' NL; 64 snakes.), 16. 6 km south of Raykankoski (1996), 17. Middle course of Uksunyoki river (1997, 2006, 2007) (31°51' EL, 61°35' NL, 40 snakes); 17a. Rift Yukkokoski on Uksunyoki river (2006) (31°42' EL, 61°34' NL; 1 snake), 18. On the road near Uksunyoki river in Loymola (1998)(31°45' EL, 61°59' NL, 1 snake), 19. Lelikovsky island, Zaonezhye (1940); 17b. 17. Meadow near Cyuksyuyarvi lake (2007) (31°32' EL, 61°45' NL, 1 snake) (Marvin, 1948, 1951; Ivanter, 1975; Valaam…, 1988; Mil'to, 2003; author's and survey data)
Adder	5. Valaam island, 25. Durak island (Koncheozero lake), 27. Kizhi island and others, 38. South-West bank of Kamennoye lake, 39. Alakurti, 40. Village Nyamozero, 40a. 50 km west of Kandalaksha, 41. Kandalaksha, 42. Lodochnaya river (10 km from Varzuga river), 43. South bank of Kolvitskoye lake, 44. 15 km south of Apatity, 45. 10 km south of Monchegorsk, 46. Laplandsky reserve, **128.** Middle reach of Lotta river (1967) (28° 38.85' EL, 68° 28.98' NL), **196.** Bank of Girvas lake (30°16.83' EL, 67° 46.97' NL), **202.** Pados hill, upper course of Nota river (1995) (29°35.85' EL, 68°5.32' NL), 48. Upper course of Nyuhcha river, 48a. Shore of White sea near Nyukhcha, 50. Golyj island, 51. Suysar island, 52. Lychnyj island (Sandal lake), 53. Sidorov island, 54. Velikij island and others, 54a. Near Kartezh, throat of Chupinskaya bay (2002) (Marvin, 1948, 1976; Pashchenko, 1953; Ivanter, Danilov, 1966; Ivanter, 1975; Kataev, Makarova, 1984; Borkin, Krever, 1987; author's and survey data)

In the region the adder has nearly continuous area. However, there is an ample evidence of geologists working in the North that in the large areas (the basins of the lakes Pyaozero, Topozero, V. Kuito, Kamennoye, Ohta

river, the swamps near the river Ileksa), as well as to the East from the Umba river (except the Tersky coast), adders are absent. The northernmost finding (reported by K.M.Kalinkin) was the middle reach of the river Lutta (28°39' EL, 68°29' NL).

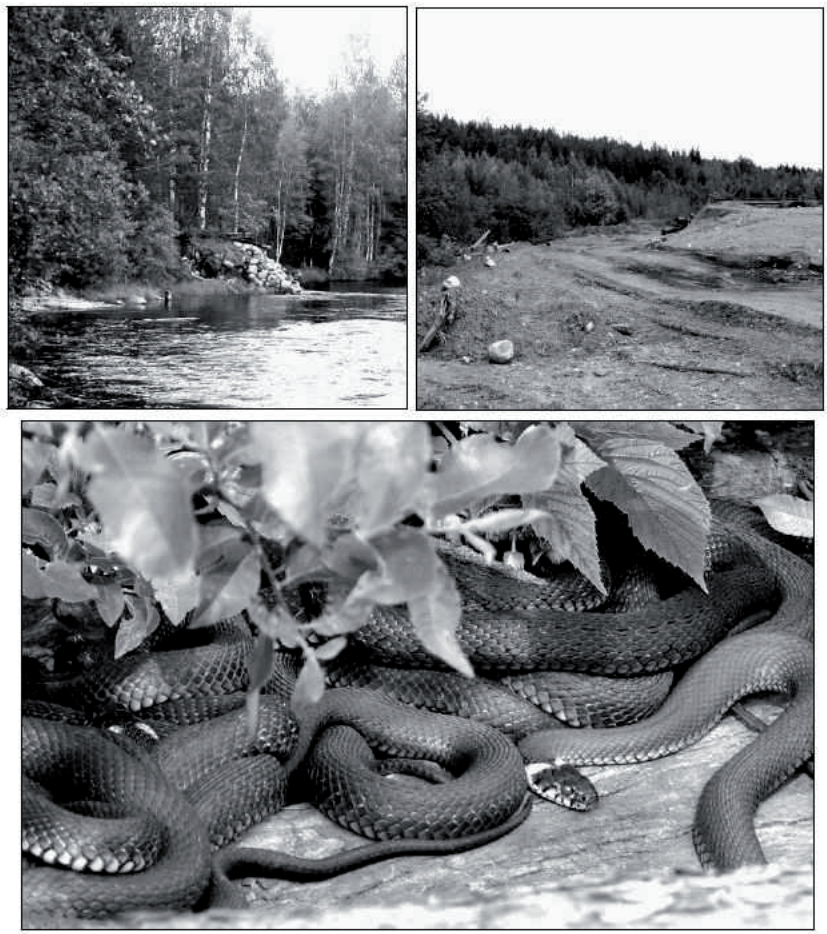


Fig. 2.1.2. Sandy embankment of the old bridge and a timber yard – an grass-snake habitat

Causality of the area borders. Severe climate mainly determines the northern boundary of reptiles' spreading (Korosov, 1995b). New data (Korosov, 2000b, 2003) and modern GIS-technologies (Korosov A.V., Korosov A.A., 2006) allow to make and clear our preliminary conclusions. Using some sources (Atlas..., 1934; Atlas..., 1989; Medico-biological reference book, 1990), 11 vector maps of the distribution of climatic, phenological and landscape characteristics of Karelian nature were constructed (Fig. 2.1.3, 1–11; Tables 2.1.3, 1–11).

Table 2.1.3. Environmental factors taken into account and their connection with the number of reptile species in Karelia and with each other (Atlas..., 1934; Atlas..., 1989; Medico-biological reference book, 1990)

No	Parameter	Range of variability	Correlation with number of species	Factor loading PC_1	Factor loading PC_2
1	Period without frost	75–135 days	0.66	–0.84	0.17
2	Frost period, temperature lower than –5°C	100–135 days	–0.74	–0.97	0.05
3	Sum of temperatures higher than 10°C	1000–1600°	0.69	1.00	–0/06
4	Average January temperature	–8... –12°C	0.79	–0.93	0.00
5	Return of starlings (snowmelt)	34–56*	–0.70	0.96	0.09
6	Fluffing of alder (spring)	55–71*	–0.63	0.93	0.07
7	Ripening of cowberry	163–184*	–0.68	0.93	0.08
8	Yellowing of birch (autumn)	199–209*	0.70	–0.85	0.03
9	Bogginess of the territory	3 zones: 15–25, 3–50, 40–80	–0.04	–0.04	1.00
10	Share of farmlands by 1985	1, 2, 5%	0.70	–0.90	0.00
11	Density of rural population	1, 2, 3, 4 man/km^2	0.56	–0.81	0.25
12	Reptile species number	1–5	1.00	–0.86	–0.09

All the territory of the republic was divided into 290 squares 25x25 km (Fig. 2.1.3, 12; tables 2.1.3, 12). This network was the basis for comprising database. The number of reptile species found in Karelia was taken as the 12th feature. As the studies of the reptiles' fauna were not conducted throughout the whole republic, it was found that our materials cover only 99 square compartments (Fig. 2.1.3, 12). Thus, the database of all environmental characteristics and reptiles' fauna was formed within these 99 cells: 99 records were composed of 12 environmental characteristics, corresponding to the territory of a given cell. From the environment of MapInfo the table of size 12x99 numbers was transferred to Excel environment and there the component analysis was performed using of the author's package (Korosov, 1996, 2007).

Almost all the factors (except bogginess) appeared to correlate significantly with each other and with the reptile species number – the values of factor loading are high, ranging from 0.8 to 1.0. The first conclusion: in the territory of Karelia agricultural development and phenological processes are closely associated with heat supply. This trend is well reflected by the generalizing feature, the first main component, ГК1, which considered 69% of the data variability. It may be called "temperature-habitat quality of the conditions in Karelia favorable for reptiles". The second component (9% of the total variance) takes into account almost solely the bogginess of the territory, which is not associated with reptiles; the other components are insignificant.

Using the values of the first main component in 99 points, the landscape of this index was calculated for the whole territory of Karelia by means of the program Serfer by the method of krigging, and then it was presented as a contour map (Fig. 2.1.3, 13). As is seen, with constant general latitudinal trend – the decrease in total heat and the proportion of farmlands towards the north – local regional peculiarities of climate and landscape are reflected: more and better-warmed habitats in the vicinity of large lakes and along the White Sea coastline.

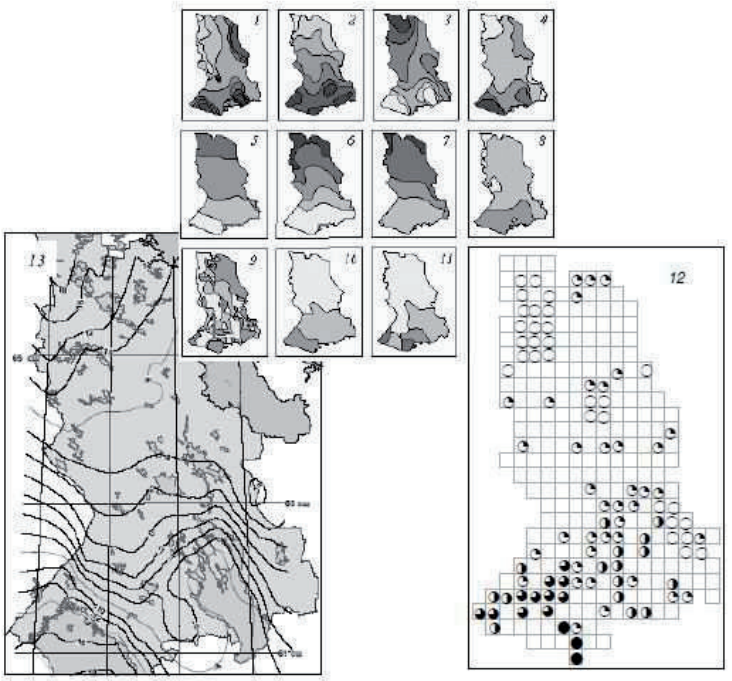


Fig. 2.1.3. Schemes of spread of environmental factors on the territory of Karelia (*1–11*), the number of reptiles on the grid 25x25 km (*12*) (see the notation in Table 2.1.2) and the contours of the main component "habitat of reptiles (*13*)

The number of reptiles' species increases together with the values of the component "quality of conditions" in the direction North – South and West-East (minimum dimensionless values of the first component correspond to the best conditions). Similar trends – the growth of reptiles' density in the coastal areas – were noted in the West and South of Finland (Terhivuo, 1989).

In Karelia the worst conditions for reptiles have developed on the southern shore of Lake Pyaozero (PC_1 = 18), the best ones – in Lahdenpoh'ya and Olonets districts (–14). Isolines of some components

replicate the boundaries of species areas. The value less than –8 covers all known habitats of the grass snake including the island of Valaam, and the north-western and north-eastern Priladozh'ye, forming the border of its area (Fig. 2.1.1, *7*). It is interesting, that the value of the first component "allows" the existence of the grass snake in Zaonezh'ye (where this species did live before the war). The climate of the Kizhi archipelago, which is located almost in the center of Lake Onega, has a soft, "seaside" character with relatively mild winters and late onsets of cold (Medical biological reference book, 1990). In this regard, the southern Zaonezh'ye is almost similar to the northern Priladozh'ye that is 150 km South-West. The isoline –14 of the component outlines the places where the sand lizard was observed and the line ГК1 = 6 is a presumed northern border of the slowworm's area.

Habitats. Reptiles remain heat-loving animals in the North. The severe conditions affect a lot of their biological features, including their habitat distribution. In all shaded habitats of the region, in summer daytime temperatures are too low to provide reptiles a sufficient level of metabolism (Korosov et al., 1999). For this reason, all the reptile species inhabit the open stations that are available for a direct insolation close to necessary shelters and food (Table 2.1.4). Their reproduction, digestion and warming (basking) occur required for normal growth processes. During hunting and seasonal migrations these animals can be found in the most unexpected places. For example, 23.04.1984 fishermen found a live adder on the ice of Lake Ukshozero at 300 m from the shore.

Relative numbers. The problem of determining reptiles' numbers is rather complicated, because the activity of these secretive animals is highly dependent on changeable weather. The classical approach taking into account the frequency of animals in transects gives but a rough idea of the relative number of reptiles, particularly adders. Only a very long and mass census estimates precisely a population density (Korosov, 2008). In other cases, these estimates give only the order of the value. Table 2.1.5 shows the data of the route census of reptiles in the territory of Karelia only for open habitats (meadows, the coast, more rarely – openings, roadsides), as

in the rest landscape facies the reptiles' occurrence is low (adders –0.01, lizards –0.1 ind. / km).

The data of the Tables 2.1.5–2.1.6 allow tracking three distinct phenomena. Firstly, only two reptile species (viviparous lizard and adder) are quite common in the region.

Table 2.1.4. The preferred habitats of reptiles in the North

	The summer habitats	The places of coupling and development
A. fragilis (Af)	The lighted outskirts of pine forests on well-drained soils bordering to deciduous woods, clearings, marshes, roads; meadows, rivers shores	Coupling was noted in the new clearing (survey of A. P. Kutenkov)
*L. agilis (*La)	The stony shores of Lake Ladoga, meadows	?
Z. vivipara (Zv)	Any surface plots with the direct access to the sunlight and shelter: sparse pine forests, edges of swamps, forest edges, rocky outcrops, meadows with stone ridges, roadsides, clearings, piles of debris, the shores of lakes, rivers	The same
N. natrix (Nn)	In the North – the micro relief in the form of bare slopes of running banks near rivers (log yard in Raikankoski – piles of logs, mixed with sand and sawdust), to the South: (Ukunyoki, the shore of Lake Ladoga, Valaam) – a river's uremia, flood lands, vicinity of farmyards, drainage ditches, filling bridges of ground roads, rocky and grassy shores of rivers, lakes.	Egg clutches were observed in rot dung remainders from farmyards, heap of sawdust, in the sandy banks of bridges on ground roads
V.berus (Vb)	Surface areas with the direct access to the sunlight, the shelter and food source: meadows periphery with stone ridges, rocky sites in the woods and swamps, and open rocky banks of rivers, lakes, marshes, filled flood lands in the White sea coastal swamps, roadsides	Coupling at direct insolation or in light shelters in any habitats in the vicinity of the wintering places

Table 2.1.5. Relative numbers of the adder (Vb), viviparous lizard (Zv), slowworm (Af) and European grass snake (Nn) in different regions of Karelia according to the data of the route census (the transect width is 4 m) (1978–2007)

Region	The route length	Number of animals without one-year-olds			Occurrence, ind. / km			Density, ind. / ha		
		Vb	Zv	Af(Nn)	Vb	Zv	Af(Nn)	Vb	Zv	Af(Nn)
Louhsky	30	5	6	0	0.17	0.20	0	0.42	0.51	0
Medvezhyegorsky	130	31	93	0	0.24	0.72	0	0.60	1.8	0
Kondopozhsky (outskirts of Konchezero lake)	140	46	123	6	0.33	0.08	0.04	0.82	2.2	0.11
Kondopozhsky ("Kivach" reserve)	29	104	61	0	3.5	2.1	0	8.8	5.2	0
Prionezhsky: a) Kizhi archipelago	267	592	28	0	2.2	0.10	0	5.5	0.26	0
b) Kizhi island	679	3741	15	0	6	0.02	0	15	0.05	0
Pryazhinsky	18	1	16	0	0.06	0.90	0	0.14	2.2	0
Pitkyarantsky	37	11	23	0	0.30	0.62	0	0.75	1.6	0
Suoyarvsky	18	8	17	0	0.45	0.96	0	1.1	2.4	0
Lahdenpohsky	61	3	6	0	0.05	0.10	0	0.12	0.25	0
Sortaval'sky (Valaam island)	117	22	27	0(49)	0.19	0.23	0 (0.42)	0.5	0.57	0 (1.0)
Total in Karelia without Kizhi isl.	729	801	373	6	1.1	0.51	0.01	1.28	1.28	0.02
Lapland reserve (Kataev, Makarova, 1984)	357	6	23	0	0.02	0.04	0	0.1	0.1	0

Secondly, the reptiles' numbers are higher in the areas with long-term observation. ("Kivach", village Konchezero, Kizhi). The reason is clear: with the uneven distribution of reptiles, the thorough study of a territory allows to discover their rare pockets. Thirdly, in the reserve on Kizhi the habitat conditions are almost optimal for the adder (Korosov, 1996b).

As to the rest, in the region rather low number of reptiles can be stated. So, for adders the calculation of trade density over the entire area of the region (in all habitats) gives 3.6 individuals / km^2, because the average density of the species in inhabited open sites is 275 ind. / km^2, and the proportion of these habitats (farmlands) is near 1.3% of the total area of the regions (Atlas..., 1989). This value lies below the threshold of justified cropping (4 ind. / km^2) and is in stark contrast to plenty of adders in the Central regions of Russia – 60–80 ind. / km^2 (Bozhansky, 1997).

Table 2.1.6. Numbers of the viviparous lizard in different biotopes of Kondopoga region (*outskirts of Konchezero lake and "Kivach" reserve) according to data of route census (the transect width is 2 and 4 m)

Biotope	Length of the route, km	Numbers of lizards	Occurrence, ind. / km	Transect width, m	Density, ind. / ha
Sides of ground roads	42	38	0.9	2	4.3
Upland meadows with stones	29	98	3.2	2	16
*Overgrown floodplain of the Suna river	51	133	2.6	2	14
*Pine forest	12	1	0.1	4	0.2
*Outskirts of high bogs	23	25	1.1	2	5.2
*Humid shore of a lake	27	62	2.3	4	5.8
Total in region	194	369	1.9	2.7	7.6

Reptiles depend closely on direct insolation, it affects their number and transform their habitats. Thus, on the dried up bank of the Suna river (after the river runoff control in the 70th) the lizards settlement had been existing for many years when osier-beds with alders thrived on the damp sludgy coast and darkened completely the sunlight (Table 2.1.7).

One can present the similar examples for other reptile species. Over the last 50 years the main trend of the change in herpetofauna is connected with the elimination of the age-old practice of land use: the typical upland meadows are disappearing (they are overgrowing with woods, or, on the

contrary, they are being cleared of stone ridges), followed by decreasing numbers of all reptile species and declining the area of their distribution.

The data on the occurrence of the grass snake are worth mentioning. Practically all individuals of the species occurred out of registration routes, except Valaam. There were two numerous colonies: in the point 17 in the area of 10x10 m 40 snakes were captured, in the point 15 in the area of 20x100 m – 64 snakes. For this reason it is impossible to calculate the grass snake density using extrapolation to the neighboring territories where snakes did not occur. To determine the characteristics of such localized and self-replicating population groups (the clutches and individuals of all ages were found) presents a separate scientific problem.

Table 2.1.7. The population dynamics of the viviparous lizard in the flood-plain of the Suna river, overgrown with small-leaved saplings (reserve "Kivach") (data by A.P.Kutenkov)

Year	1976	1980	1981	1982	1983	1984	1985	1986	1987	1988	1989
Length of the route, km	2	2	2	1	1	12	7	10	5	1	1
Lizards numbers	27	17	10	50	0	16	29	25	11	0	0
Occurence, ind. / km	14	9	5	50	0	1	4	3	2	0	0
Density, ind. / ha	35	22	12	125	0	2	10	8	5	0	0

Number of reptiles on the Kizhi archipelago. In addition to common adders and viviparous lizards, the natives say that 30–50 years ago the grass snake dwelled on these islands, some of them say they saw "medyanka" (the slowworm), others – "the large gray lizard" that may be the sand lizard. However, for 17 years of our work on the islands of the Kizhi archipelago we found only two first kinds of reptile species. Adders occur on islands of very different size in rather large quantities, lizards are less common. (Table 2.1.8).

Table 2.1.8. Occurrence of reptiles in meadow biotopes on islands of the Kizhi archipelago

Island	The route length, km	Adder			Viviparous lizard		
		Snakes	ind. / km	ind. / ha	Lizards	ind. / km	ind. / ha
Klimenetsky	139	375	2.7	6.7	34	0.2	0.6
Kizhi	679	3748	5.5	13.8	15	0.02	0.06
Other islands	195	403	2.1	5.2	6	0.03	0.08
In whole	1013	4526	4.5	11.2	55	0.05	0.14

The viviparous lizard as a forest species is widely distributed over Eurasia.

The closer to the North, the more it prefers open stations to warm up in weak sun rays. On the archipelago they spread everywhere. The estimates of the occurrence of this long-living species are rather stable and equals to about 0.1–0.6 ind./ ha, maximum values obtained on the old shore road on the island of Klimenetsky. (1.5 ind./ ha). On the islands covered with woods (Karelsky island), and also on the islands with high density of adders (Eglov, Volkostrov, Kizhi, Olen'yi, Bukol'nikov, Vojnovalok), lizards occur much more rarely. On the islands the estimates are the most representative due to the regular census: 0.08 ind. / ha on the Kizhi island and 0.01 ind. / ha on Wolkostrov island vs. estimates for Klimenetsky island – 0.3 ind./ha (southern part), 0.8 (center), 1.25 (northern part). Such fluctuations of numbers in abundance of food resources make it possible to say that the adder as an active predator plays the role of a limiting factor for the population of viviparous lizards. Considering the trends of changes in the species number, it can be stated that it constantly declines following the overgrowing of meadows.

The adder has rather low density (0.04 ind. / ha) even in favorable habitats of Karelia (Korosov, 2001). It is confined to open biotopes even more than the viviparous lizard, but because of a large size it is demanding to food and shelter. On the islands of the Kizhi archipelago (Eglov, Volkostrov, Kizhi, Olen'yi, Bukol'nikov, the northern part and Cape

Voynavolok of Klimenetskiy island) the adder finds the necessary trio (insolation, wintering, food) – lots of good summer and winter shelters (roves), the abundance of food sources (2 species of frogs, densely inhabiting the lakeside swamps) and the vast open spaces of meadows (Korosov, 1996b). There the number of adders is two orders greater than the average value for the southern Karelia (5–14 ind. / ha); it became a dominant species in a lot of island zoocenoses controlling the number of its co-members (see section 10).

The absolute number. Unlike warm-blooded animals, reptiles are not active every day of the week. For example, lizards come out on the ground surface only for 4–6 days of 10 on an average (Zamolodchikov, Kolosova, 1995). For this reason, during the census the observer does not see most animals; therefore, it leads to the significant underestimation of population number. The same effect is caused by the permanent variation in weather conditions affecting the activity of reptiles: the multiple census in the same habitats around Konchezerskaya biological station in July gave adder density estimates different by an order of value – from 1.3 to 15 ind./ ha. Year-to-year variability is even higher. According to our observations, in the "snake years" when villagers and field workers see large adult animals more often, it does not mean the irruption (as in rodents), but the increased activity of snakes due to the alternation of contrast weather conditions during the summer season. On warm days the activity of adders increases because they seek to compensate the heat deficiency of cold days, therefore, they can be seen. The minimal number of meetings was in the hot summer (1988), when snakes' requirement of warmth was satisfied early in the morning and during daytime – in shelters.

Capture-mark-recapture method combined with the calculation of the saturation of population with marked specimens and the abundance of animals allows determining the number of animals of given species more accurately (Coley, 1979). For this purpose viviparous lizards were captured and marked in a meadow near the border of the forest (area of 0.6 ha in the reserve "Kivach") from 17.7 to 26.7.1997 and from 15.6 to 28.7.2003) in the morning and in the evening. Adders were captured and marked on the

island of Kizhi (204 ha) from 1991 to 2007 in spring and autumn (see section 8). The calculation results are presented in Table 2.1.9 (number of met animals is larger than the number of marked ones because some of them were caught more than once).

Table 2.1.9. Absolute number of reptiles in meadows of Kizhy[1] (our data) and in "Kivach"[2] reserve (data by Gerasimova E.V., Zaharova)

Species	Number of marked / repeatedly captured animals	Number of met / repeatedly met animals	Quantity, individuals	The extrapolation area, ha	Density, ind./ha
Z. vivpara[2], ad+sad, 1997	57 / 8	76 / 16	36–176	0.6–2.5	40–70
Z. vivpara[2], ad+sad, 2003	31	56 / 25	12–40	1.2	10–30
V. berus[1], ad, 1994–2007	1901 / 365	2353 / 452	1500–2800	200	8–12

The estimation of the absolute number is purely technical task, while determining the area for extrapolation presents a problem. It is easy in the case of island population of adders – this is the territory of the island (Kizhi). The habitat area of the studied group of lizards can be identified using the data of animals' migration away from the marking site. So, in 1997, 8 days after the beginning of marking a few animals were caught at 50 and 70 m away from that site. So, the area size was approximately 2.5 ha. The interpolation of the area size to all days of the experiment allows to calculate the density variation of adult (ad) and young (sad) animals (excluding current-year young); the interval was from 40 to 70 ind./ha (Table 2.1.9). To get more detailed information on capturing in 2003, a diagram of the number of repeatedly captured lizards depending on the distance from the first capture point was plotted. Then the distance at which 95% of the

marked lizards moved was determined. 95% of lizards appeared to move not more than 16–22 m from the marking place on an average for 10 days after capture, i.e. the area of extrapolation should be equal to the marking square (0.5 ha) plus 20 m band along its perimeter, i.e. in total 1.2 hectares.

Calculations of the adder number in favorable habitats on the island of Kizhi (inclusive of mortality) give steady annual estimates of about 8–12 ind./ha of animals (Korosov, 2008) or up to 37 ind./ha of all ages except yearlings (Korosov, Prokhorova, 1999).

Activity and reproduction. The well-known data on the active period and the number of reptiles in the southern part of Karelia are summarized in Table 2.1.10. The reduction of warm period inevitably results in shortening of the activity period in reptiles from 120 days in the South (Korosov,1995б) to 80–100 days in the North of the region (Kataev, Makarova, 1984), that was repeatedly noted in literature (Viitanen, 1967). Oviparous species, the embryos of which develop in eggs passively (only due to the inflow of heat from a substrate), react to this factor in a similar way – they do not live in the area where summer lasts less than 110 days. Females of ovoviviparous species (slowworm, viviparous lizard and adder) actively seek out the sources of heat (especially direct insolation) necessary for the development of embryos in the oviducts. At the latitude of Kondopoga, the fertility of the viviparous lizard amounted to 5.3±0.28 (4–7) ind. (n = 12), in adder – 7.6±0.17 (2–14) ind.(n = 128).

It is interesting that adders can hibernate with embryos. In the spring of 1998 in the oviducts of females from Zaonezh'ye (62°5′ S. sh.) in addition to 8 eggs we found 6 embryos ready to be born (see section 4.2). On the island Veliky in the White Sea on 27.7.1986 A. E. Panarin found young adders most likely born in spring. These specific adaptations allow three species of viviparous reptiles to move far to the North (Ivanter, Korosov, 2002; Korosov, Ivanter, 2003).

Table 2.1.10. Usual period of fattening (ending of wintering – beginning of wintering) and development of young reptiles (mating- oviposition- breeding) at different latitudes of the region according to the literature data

(Darevsky, 1983[1]; Marvin, 1948[2]; Kataev, Makarova, 1984[3]), A.P.Kutenkov[4], A.E.Panarina[5] and own[6] (extreme values are given in brackets)

Species, see table 2.1.4		Priladozh'e 62˚30′±10′	Kondopoga[4] –Kizhi isl.[6] 62˚15′±10′	Belomorsk [2,6] 64˚50′±10′	Chupa[6]– Kovdor[5] 66˚30′±10′	Monchegorsk [3] 67˚ 40′±10′
Af	fattening	?	18.5–9.9	?	–	–
	develop-ment	?–20.8	21.5–15.8	?	–	–
La	fattening	1.5–15.9	–	–	–	–
	develop-ment	5.5–5.6–15.8	–	–	–	–
Zv	fattening	?	26.4(11.4)–13.9(6,10)	–	15.5–?	24.5–30.8
	develop-ment	?	1.5–27.7(13.7)	?–20.7(8.8)	?–5.7–(10.8)	?
Nn	fattening	20.4–15.9	–	–	–	–
	develop-ment	5.5–5.7–5.9	–	–	–	–
Vb	fattening	30.4–?	28.4–(15.4)–26.9(9.11)	?	17.5(4.6)–?	31.5–30.8
	develop-ment	?	20.5(11.5)–6.8(15.9)	20.5–?	?–20.8(27.7)	?

2.2. Annual life cycle of adder

Despite the attempts of standardization of the most important phases in the reptiles' life (Garanin, 1983; Bozhansky, 1997), every herpetologist has his own view on their value. From our (systemic) point of view, it is important to represent each phase as a link in the chain of cause-effect connections caused by one factor and invoking the next vital manifestations. The second consideration concerns the possibility to model the situation quantitatively. Even if we do not have enough quantitative data, a description of a seasonal activity of an animal should be structured, to serve as a

basis for a future model. Anticipating the model of the vital manifestations description, this section provides a general picture of seasonal phenomena in the life of adders that dwell in Karelia (mainly on the island of Kizhi).

Wintering. On Kizhi adders spend winter in the stone ridges (see Fig. 12.2.2). Wind constantly blows and creates rather large snow drifts on all sides of the ridges. As a result, to the end of winter, the coldest period a large snowdrift is formed around each ridge. Such snowdrifts are 10–30 cm higher than the ridge and compose 40–300 cm, depending on the size of the ridge. The snakes' shelters inside the ridge are well thermally insulated, and the inside temperature is always positive, as in the South Karelia in winter the isotherm of 0°C never drops below 1.6 m (Climate handbook of the USSR, 1975). These conditions provide a successful wintering in any part of the island for most adders, because the ridges are everywhere on Kizhi. An additional positive aspect of the shelter structure is a long history of their formation. The stones, which were thrown on the edges of the fields along marshes and lakes, have formed steep rocky shores of 2–3 m high due to annual plowing and "smoothing" of an arable land. Such shelters are covered with a rather thick layer of soil. In winter this layer serves as an additional buffer between the wintering place of adders and outside air.

However not all the ridges are large enough to prevent adders' freezing. How do adders choose the "reliable" wintering shelter? We have no data on this subject. It is assumed that adders move to the wintering place, where they were born (Völkl, Biella, 1988). It is possible that on Kizhi they realize their choice in the late autumn days, finding those ridges which preserve the heat accumulated during the day longer than others and, therefore, are larger and potentially more effective as winter shelters.

Leaving winter shelters. The first appearance of adders on the surface was observed at the end of April, 24.4.1997/98, and the first mass crop up – in May 1–2 (Table 2.2.1). There is a distinct asymmetry in the time of appearance of adders and their leaving for wintering: the level of solar radiation in early May is the same as in mid-August, one and a half month before the beginning of wintering. Why do not adders appear on the surface

earlier, although the stones in the ridges are out of snow in early April? In other words, what determines the spring phenology of adders?

Observations in nature, both direct (Kaletskaya, 1956; Viitanen, 1967; Larionov, 1977), and using radio telemetry (Sexton, Hunt, 1980), show that snakes maintain mobility throughout all winter period and move deeper into the shelters, or closer to the surface depending on the distribution of temperature. The reason of these movements is the desire of adders to get into the place, where the temperature is 3–6° higher than in the former one (Korosov, 2008б). For thermoregulation not only a temperature gradient is important, but also sensitivity of a snake: only significant differences in temperature could cause the appropriate reactions. As for the spring activity, it means that adders will appear on the surface after the temperature of outer stones is 3–6° higher than that of inner ones. To this moment the sun can heat the outer surface of the stones to a high temperature, but a layer of cold rocks still remains between the warm surface of ridges and their relatively warm deep layer and isolates adders from the surface. The relationship between isotherms at different depths (Handbook..., 1975) shows exactly the desired moment of temperature equality between a surface and the inside of a stone ridge – the end of April (Fig. 2.2.1, 2.2.2). At that time adders crop up to the surface. The sequence of adders' leaving wintering shelters is the same as in other parts of the area (Bannikov et al., 1979; Biella, 1979; Yakovlev, 1985): males – end of April, beginning of May, females – beginning, middle of May, young – middle, late May (Table 2.2.1).

Migration. On Kizhi we did not note exactly directed seasonal migrations, because a lot of convenient shelters (roves) provide effective wintering in almost any part of the island (see section 11). After snow melting the same snakes stay on the wintering ridges for a long time. Males complete molting, and then begin to move actively around the island searching for females, and after mating season – for food. Mature females leave their wintering places in search of food before males (it need not to creep far, because at that time lots of frogs migrate from Lake Onega towards swamps for reproduction). According to our data, no directed migration to-

wards wintering places takes place. More precisely, adders don't seek for the place of last year's wintering; however, they form small (up to 60 snakes) wintering aggregations. In our opinion, these aggregations are formed in autumn on the ridges with the most favorable temperature conditions.

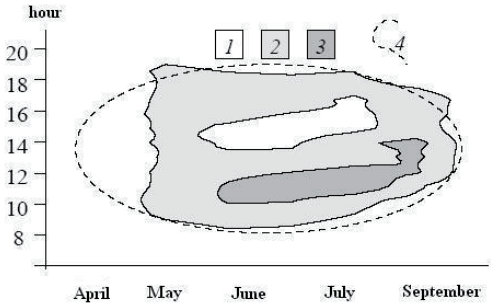


Fig. 2.2.1. Proportion of vipers (%) encountered in different times of day: *1* – 0–6%, *2* – 6–13%, *3* – 13–21%, *4* – contour of the ellipse (nmay = 1580, niyul = 216, nsent. = 576 ind.)

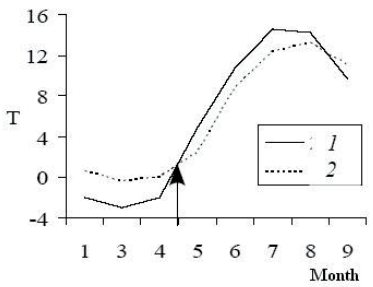


Fig. 2.2.2. Annual variations of soil temperature at various depths (*1* – 20 cm, *2* – 80 cm), arrows indicate the time of temperature equalization of surface and deep soil layers

The first hunting. In spring the animals with undigested food are rarely found (Table 2.2.1). The fact of recent feeding can be registered more often, when in capturing an adder "shoots" the content of the cloaca for the purpose of self-defense.

Table 2.2.1. The dates of phenological processes in the adder population on Kizhi

Phenomenon		Extreme dates of observations	Usual dates
Exit of males from hibernation		24.4.97, 24.4.98	1.5
Exit of females from hibernation		8.5.97; 2.5.2009	5.5
Exit of young from hibernation		25.5.92, 22.5.95	23.5
LT<30mm			
30<LT<45mm		8.5.97	23.5
First hunting (with pray)	males	12,27.5.97; 23,24,25,26.5.99; 26.5.97; 5.5.2009	20.5
	females	8.5.98; 14,19,25.5.97; 21,30.5.99; 3.5.2009	4.5
Molting of males	stage 1, 2	9,11,14.5.97; 19.5.98; 1.5.2009	5.5
	shade snake-skin	14.5.97; 18,24,25.5.94; 10.5.2009	10.5
Molting of females	stage 1, 2	30.5.91; 24,25.5.2009	20.5
Mating		31.5.1979; 18.5.94; 14,18,15.5.97; 14.5.2009; 19,24.5.98	12.5
Birth of yearling		9.11.92; 11.9.95; 14.9.96	11.9
Exit for hibernation		26.9.97	25.9

Dark, brown, black excretions with dense consistency confirm that a prey animal was recently digested (about 10 days after hunting – according to the observations in captivity); if the excretions are yellow, it means that the snake has not eaten for a long time (2 weeks or more). In capturing males after May, 5th and females after May, 25th one can make sure that almost all of them have already eaten this spring. Thus, many fertile females hunt before mating: in 2009 up to May, 15th (before the beginning of reproduction) from 26 females with eggs 12 had food in their stomach (46 %); from 23 females without eggs only 2 specimens contained food (9 %). Thus, there was only one of 150 males with black excrement (<1 %). From our numerous observations it can be concluded that some of the males feed immediate-

ly after the exit from hibernation, but most of them – after mating; many fertile females often eat after hibernation before mating.

First molting. Growth of reptiles is associated with periodic shedding of horny integuments that in snakes get off as a "stocking" (see section 5). Molting is rather long and energy consuming process, closely coupled with other physiological performances – feeding, reproduction, thermal regime, etc.

In the spring the process of mass molting of adders takes place in rather clearly defined timescales, when the majority of snakes we met are at the 1–3-th stage of molting, and several days later the same snakes shine with bright and vibrant patterns of their new skin. This process was monitored the most carefully in the spring of 1997–1998 (Fig. 2.2.3; Table 2.2.1).

Comparing the timescales of mass inclusion of adders in molting in 1997–1998, it can be stated that in males the appearance of sloughs was observed in 10–11 days (24.5) after the first stage (13.5). The females start the first stage 1–2 days later (25.5) and complete molting in late May – early June.

These timescales vary individually depending on the adders' habitat (different parts of Kizhi, slopes with different exposure, islands of different size).

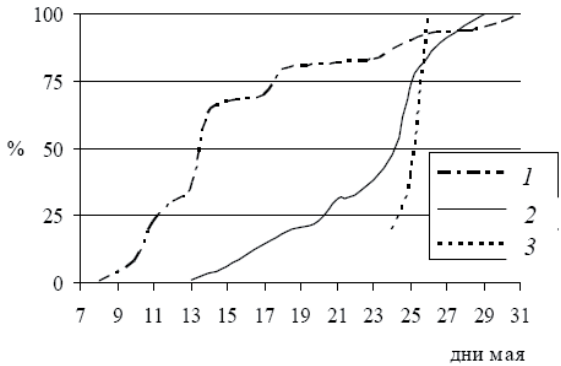


Fig. 2.2.3. Increase in the number of males (*1, 2*) and females (*3*) initiating (*1, 3*) and completed (*2*) molting in 1997–1998

Mating. The researchers' interest to molting is due to the fact that it serves as a good indicator of the beginning of the process of reproduction. Males begin reproduction immediately after molting, when the bright patterns and strong smell excites both their partners and competing males.

Females do not begin to molt at that time. On the basis of the dynamics of molting, it can be supposed when the copulation took place in any spring, even not watching it. However, occasionally we observed the reproductive behavior such as fighting, and attempts to copulate in males that had not melt.

Mating is preceded by fierce battles of males (see section 4). The period of mating in one place (on one ridge or a few adjacent ridges) is short – 2–3 hot days. However, due to the specific nature of different habitats, on Kizhi as a whole mating lasts up to 10 days. Modal dates are the 20–23th of May with overall amplitude the 16–31th of May. It must be noted that on Kizhi phenological processes are 7–10 days delayed in comparison with the mainland. And mating here takes place later than, for example, in the reserve "Kivach" (see Table 2.1.10).

Molting in summer. The annual dynamics of the investment change (timescales of stage 1–2 in 367 individuals of 1971 captured were taken) shows three clear peaks (fig. 2.2.4): in May – June (60–100 days), July – August (120–160 days) and in September (200–210 days) or, more roughly, in the mid – late May, in July, in mid – late September, as in other points of the area (Sokolov, 1989). Their periodicity is valid ($p < 0.01$), and the period is close to 90–60 days (Fig. 2.2.5). At that, the coincidence of the periods of molting with the periodicity of field work seems only external, but mainly the periods of mass molts do not coincide with the timing of regular agricultural field works. It is important to note that there is an important apparent bimodality in the distribution of the number of molting snakes in May, as it reflects the molting periods firstly of males, and then females. Later the process becomes less strict and covers the most of July and early August. In autumn not all the animals molt, many of them go into hibernation with old skin. It is especially noticeable in spring when a part of the population even

before spring molting has a fairly bright cover, and the other part is dull and brownish. To the early summer the majority of adders become uniformly bright.

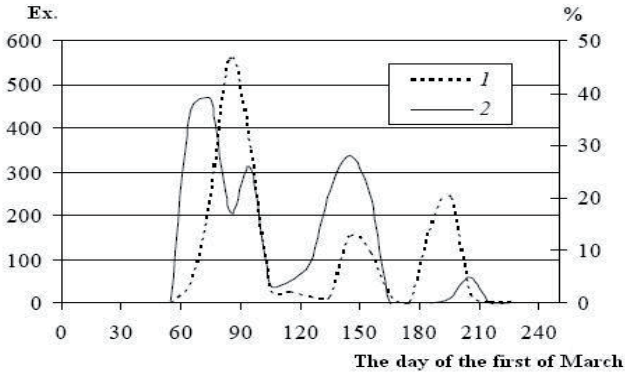


Fig. 2.2.4. Proportion of individuals (*2*, %), initiating molting (stage 1–2), among trapped in a decade (*1*, ind.)

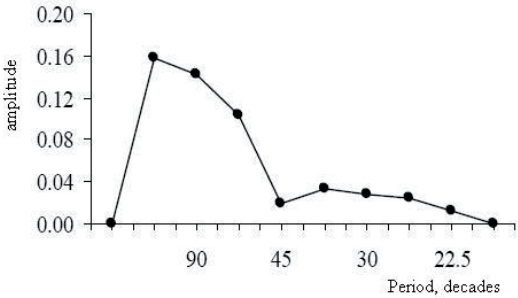


Fig. 2.2.5. Periodogram of the dynamics of molts in the decades

Birth of young. On Kizhi young adders appear in the beginning of September (Table 2.2.1; see section 4). The life of newborn adders in captivity showed that they remained inactive for a few days. In wild nature we saw dozens of young adders, basking in groups in the sunshine, not very hot in September among the dry, lying down grass. After the second molt (in a week) the young snakes start looking for food. Their food is the yearlings of frogs and newts (which young adders burp after capturing). As the number of young frogs on Kizhi is immense, there is no need of feeding migrations.

Apparently, therefore, in September the aggregations of young snakes contain a lot of older adders, dwelling in the place of their birth for several years.

Leaving for wintering. Distinct migrations to wintering places or from them were not noted. Our latest finding of snake on Kizhi was on the 26.9.1997. It is obvious that this date is close to the timing of the final departure of the adders from the surface. Nevertheless, a temporary warming may allow some adders to leave their shelters. For example, adders were seen near Petrozavodsk during the thaw on the 6.11.1974.

2.3. Population status of the adder on Kizhi island

The peculiarity of every species-specific population is determined by panmixia within its range (Mair, 1974; Timofeev-Resovsky et al., 1977), genetic and morphological features (Yablokov, 1987; Rozhkov, Pronev, 1994), the uniformity of the structure dynamics (quality) and the number of a population (Shvarts, 1980). The development of universal criteria for distinguishing individual populations is complicated by the difference in the content of the term "population" of various researchers (dem, people, culture...), the difference in the context of the solved problems (evolutionary, ecological, taxonomic, applied...), using multi-level characteristics (genetic, genotypic, phenetical, morphological ...), and many other circumstances (representativeness of methods, specialization of researchers, financing...). At the same time, there are a number of proven methods based on the studying of spatial distribution of separate groups of individuals and the degree of their similarity in genetic composition (Rozanov, 1983), phenetic structure (Baranov, 1986) or magnitude dynamics (Mikheeva et al., 1979). The similarity of these groups allows to join them in one population, and a sharp variation and long maintenance of difference between them allows to present them as independent populations (Yablokov, Larina, 1985; Dubinin, 1986), as relatively mutual independence and sustainability of two genetic systems (Altukhov, 1983).

Dwelling on islands often leads to a significant isolation, if "throughout one generation less than one migrant from the outside breeds … " (Giplin, 1989). This affects greatly the genetic and ecological uniqueness of an island population and may cause inbreeding effects, if the island area is small, and the population number is small (Sulej, 1983).

From the point of view of proposed criteria (a massive studies of geno – and phenogeography of species), we do not have enough information to determine the adders' island population status, since we do not possess neither wide geographical, nor deep historical materials about the adder on Kizhi. However, our data on migration (see part 12), genetic polymorphism of the venom (Table 2.3.1) (Korosov et al., 1995), the structure of the head and body scalation in snakes (Table 2.3.2) allow us to make some fundamental conclusions.

Obviously, the population of adders on Kizhi is significantly isolated from the populations of other islands and the mainland. In a functional ecological sense the immigration and emigration do not affect clearly the abundance and reproduction of this group. Territorial isolation allows assessing rather precisely the number and age structure of the adders' population, to study its trophic relationship with other members of the island zoocenosis. From this point of view, the adders dwelling on Kizhi present a self-sufficient group, and can be considered as a population.

Table 2.3.1. Test characteristics of adders' poison from different points of Karelia

Location	All tests	Components in the tests, %			
		protein	LDH	esterase	
				overall	of them homozygote, %
Kizhi Isl.	59	47	18	18	100
"Kivach" reserve	15	13	7	8	0
Konchezero	12	9	2	3	0
Altogether tests	76	69	27	29	29

Table 2.3.2. The scale number on different parts of the adder's body on Kizhi and in continental regions of Karelia

Phenocomlex	Kizhi island		Continental part	
	min	max	min	max
Lower labial	6	9	8	9
Chin scales	4	5	4	4
Ventral	133	156	144	157
n	22		55	
Dorsal	17	23	17	21
Upper labial	7	10	8	9
Subcaudal	30	44	29	45
n	105		55	
Internasal	1	4	2	2
Prefrontal	2	20	7	14
Supraocular	1	7	2	6
n	1500		55	

On the other hand, in an evolutionary ecological sense there are no substantial differences in genetic and phenetical signs between adders' population on Kizhi, that on the neighboring islands and the other parts of Karelia. It is possible that homozygosity of all individuals on Kizhi and that of all continental ones in the venom esterase, could evidence the specificity of island population, but the sample sizes are not large enough for this purpose (Table 2.3.1). In our case we ought not to say about the inbreeding effects, because they are typical only for reptiles' populations less than 2000 individuals (Sulej, 1983).

As for phens, well studied variability of pileus of the adder on Kizhi (Table 2.3.2) comprises almost all the variations of other regions in Karelia, turning some differences of extreme values to a random result caused by small sample sizes on the mainland. Essentially, the only difference of the adders of Kizhi from others concerns the chin scales: only on Kizhi there are forms with elongated unpaired fifth chin scale ($p \approx 4$ %) (Fig. 2.3.1). As for the sample size it should be mentioned, that they are not so significant only for the assessment of the phenetic structure peculiarities, while they are quite

sufficient for the sought frequency fluctuation of phenes. Another thing is that this fluctuation failed to be found. As a result, from this point of view, the adders' population of Kizhi cannot claim the status of independent population, and acts as one of many numerous more or less independent subpopulations of a vast local area of the adder.

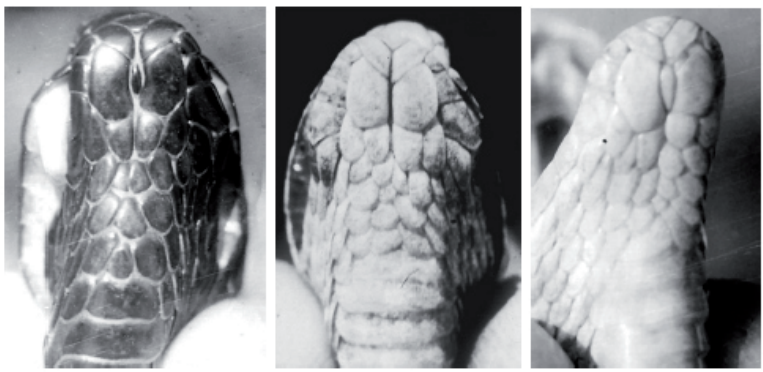


Fig. 2.3.1. The degree of manifestation of gypsy premaxillary scale

In addition, there is another factor that impedes the discussion of the status. According to local residents, in the 70s a "Moscow snake catcher" A.V.Ryumin "brought suitcases with snakes and released them on the islands" (now it is impossible to contact him, for he died in 2006). These events do not seem true. On the contrary, he is known to store up adders for the Moscow serpentarium. However, this version still has a small chance to be true, and it would be awkward for us to confirm the population status of adders from Kizhi by the phen, typical for Moscow region.

One way or another, but the population of adders on Kizhi is considered by us to be as such only in relation to the process of self-reproduction, but not in respect of the uniqueness of evolutionary destiny.

The distinctness of the reptiles' fauna in the Republic of Karelia is connected with the activity of man who transformed the taiga landscapes, and thus made it possible for many reptile species to inhabit this region or

widen significantly their habitats in this northern territory. The destruction of age-old peasant manner of life leads to a gradual reduction in the number of convenient habitats and abundance of most reptile species in Karelia.

Chapter 3.

Thermoregulation

The current body temperature of poikilothermic animals determines the whole process of their vital activity (maturation of sexual products, initiation of reproductive behavior, the rate of the development of embryos and growth processes, the intensity of metabolism and the requirement for food) (Kashkarov, 1938; Shmidt-Niel'sen, 1982). In turn, body temperature depends on both the intensity of the flow of external heat and specific thermoregulatory (thermoregulating) behavior that changes the availability of these flows to an animal (Shilov, 1985). In the conditions of excessive heat, an animal tends to avoid overheating, and at the shortage of it demonstrates the behavior that is directed to its enhanced assimilation.

Phenomenology of reptiles' thermoregulation has been well studied (Bartholomew, 1982; Pough, Gans, 1982; Cherlin, 1983, 1984, 1991; Cossins, 1987). The traditional study of reptiles' thermoregulation is to determine the body and environmental temperature in order to identify certain critical values associated with the changes in thermoregulatory behavior of animals. Such temperatures include minimum and maximum voluntary, preferred, optimal, upper and lower critical temperatures, etc. Such behavioral acts include heating, basking, thermoneutral behavior, cooling, etc. Despite the large amount of accumulated data, for example, on thermal biology of the adder (Chan-K'yen, 1967; Saint-Girons, 1975; Schiemenz, 1978; Drobenkov, 1990; Spaendonk et al., 1990; Litvinov, Ganshchuk, 2003a, 2003б, 2009), a lot of the mechanisms of heat exchange processes and active (physiological and behavioral) thermoregulation, especially quantitative estimation of the key parameters, remain poorly understood. The problems of species-specific thermoregulatory activity, peculiarities of its manifestation in different geographical areas and the relationship with basic life functions can be called the most relevant.

In the frame of our research there is a problem to what extent the northern climate and weather conditions of Karelia affect the biology of the

adder that dwells here, on its nutrition, growth, reproduction, and phenology. The quantitative basis of this concept should be a thermoregulation model of an animal in different temperature conditions (Korosov, 2001). The purpose of the study was to determine the details of the thermoregulation processes and quantifying basic equations. However, thermal biology of reptiles is so interesting that we have devoted it several sections of this Chapter, slightly distant from the main course of the work.

3.1. Material and methods

The studying of adders' thermal biology was conducted in 1978–1981, in 1989–2002, and in 2006–2007, both in the field and in the laboratory. Adders capturing was performed using the "herpetological tweezers" and a canvas bag with the mouth drop outspread on a branch-fork. "Tweezers" represents two battens (2 cm wide and 0.9 m in length), tailed to each other (it plays the role of handle). At the other end, the battens were pulled apart at 3–5 cm. Here, one of the battens had a hole at 5 cm from its end. A thick line was thread through this hole. One end of this line was fixed to the other lath, and other end – to a lever, attached to the handle. The pressure on the lever stretches the line that slips into the hole and pushes both ends of laths together. The adder captured between the ends of the battens is well fixed and not damaged.

Capturing is carried out in two stages. Snatching the snake with pulled apart ends of tweezers and pressing it slightly, we put adders into the bag; two twists of the tweezers screw the bag's mouth, and reliably block the exit. The difference of our capturing method from using of herpetological hooks is, mainly, in effectiveness: if we see 2–4 adders together, by the hook we can catch only one, and other will escape. The combination of our simple methods allows us to catch quickly almost all snakes that were seen (up to 8 snakes) in one bag. After that it is possible to describe each individual without hurrying. Temperature characteristics were determined only at the sole or the first of several caught adders.

After capturing a number of characteristics (Cherlin, 1991) was identified: 1) the temperature of the dorsal surface of the body was measured with a distant thermometer (DT) "Thermopoint", precision 1 °C, 2) rectal and oral (internal) body temperatures were measured with a mercury contact thermometer (CT), precision 0.2 °C 3) the substrate surface temperature near the place of a capture was measured by both devices. In the text rectal temperature is used more often, except for specially stipulated cases. Remote thermometer "Thermopoint" is a compact, portable device with autonomous power supply recording thermal radiation from the local area where it is directed. At the distance of 1 m. its detected area is approximately 0.5 sm2. Depending on the operation mode it can show either current, maximum, minimum temperature at a given point with the precision 1 °C or an average temperature during the observation time (while you press the power button) with the precision 0.2 °C.

Taking a substrate temperature was carried out immediately after the shading of a measured plot to prevent the contact thermometer of sunlight as well as the object-glass of the remote thermometer of sunlight reflected from the surface. Thus the emitting capability of the objects was studied. Comparing the readings of the contact and remote thermometers when measuring sun lighted snakes, it was found that the reflected light adds to the readings of DT approximately 1 °C, and it was subtracted from readings obtained from the observation of "free" heating snake. A mercury thermometer was placed on the soil surface or in the shelter. Readings were estimated in 1 min. exposure, and by the remote thermometer – in 5 s. Initial temperature of the shelters, the soil and radiation flows was measured in the field or taken from the literature (Reference book on the climate in the USSR, 1966, 1974, 1975; Climate in Petrozavodsk, 1981).

The reactions to a heat source were studied in nature and in laboratory conditions (in the vivarium of PetrSU) in 1996–2002, 2009. The animals (12 specimens) were of different sex, similar age (Lt = 53–62 cm), at different body temperatures (from 14 to 35 °C), fed long ago (2–3 weeks earlier). In the experiments the body temperature was not measured, it was assumed to be equal to the air and substrate temperature. As a heat radiator a black tin

was used, where the incandescent lamp connected to the rheostat was placed. The experiments took place in a large terrarium an hour later when adders were placed there (adaptive period). The reactions of snakes, their heads were located at 16–35 cm from the heat radiator, were recorded (usually snakes took a pose of loose knot). During the experiment: the temperature of the black thermal radiator was gradually increased, and at the beginning of the displacement of an adder towards the radiator from the cooler part of the terrarium, the temperature of the radiator and environment, the snake body temperature and the distance of the animal from the radiator were recorded.

Daily activity was assessed both in units of number (fraction) of specimens that were present at a given hour in an observations area and by determining the type of the shelter, where a snake was housed.

Movement of snakes during the day was recorded both visually and with the original actograph (Khilkov, Korosov, 1997; Korosov, Khilkov, 2008) that have been designed by us on the basis of known constructions (Kalabukhov, 1951). The device (300 x 20 x 20 cm) has four cameras connected by passages; each of the cameras corresponds to one of four types of adders' nature shelters (n) by their temperature and light conditions (Table 3.1.1). Each camera has the movable floor that is able to swing on transverse axis. These movements are mechanically or electrically transmitted to the pen arm that records all the movements of an animal during the day on the paper tape-actinogram (fig. 3.1.1, 3.1.2).

The experiments were carried out with each animal for five days. One day was aimed for adaptation of the animal to the device, others – to record activity. Using different modifications of actographs, we had the ability to change modes and the gradients of temperature and illumination on cameras.

Digitized actograph tape represents a table (see Table 3.3.1), that shows the number of shelter types, where adders were every five minutes during the day. A similar table was formed for visual observations of the movements of adders in nature. The statistical treatment consisted of the calculation of " average hourly shelter" for each hour within 24 hours and the arithmetic mean for 12 five-minutes observations of each hour (Mn) and "mobility" – a characteristic of the shelters change within each hour, the

standard deviation (Sn), and also the sum of minutes when an animal stays in a given shelter for each hour of the day.

To observe ***forced heating and cooling*** of an adder, the animal was attached to a smooth dry batten by means of narrow sticky tape in several places. Here the mercury thermometer introduced into the cloaca was fixed (rectal temperature was measured). Personal experience of adders' captivity shows that the adders are patient creatures. Assure itself in failure of escape the adders calmed down after some time (10–20 min.), and then observations were conducted.

In the study of heating and cooling of the animals bodies, several experiments were carried out. The cooled adders were exposed to the sun or, on the contrary, warmed adders were shaded (analyzed on 8 series of observations).

Table 3.1.1. Types of adders' shelters

n	Shelters in nature	Camera of actograph	Radiation flow
1	no; direct sunlight	open	full
2	dry grass; weak shade	semi-open	weakened
3	lively grass; shade	closed	diffuse
4	hole; darkness	closed	no

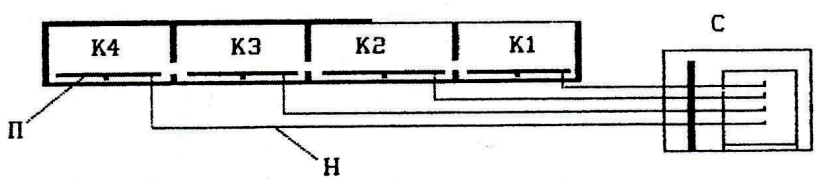


Fig. 3.1.1. Scheme the actograf (in section): С – recorder, К – Camera, П – moving floor, Н – threads transmission

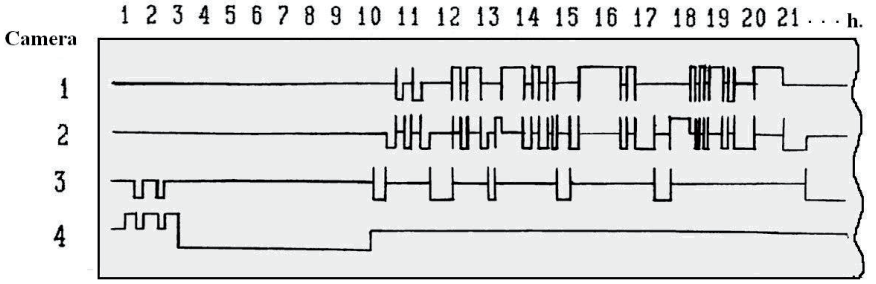


Fig. 3.1.2. Fragment of daily viper actogram (the temperature is fixed, natural photoperiod)

In natural conditions we observed the cooling of the snakes' body by shading basking adders with our own shadow (50 cm wide). Such situation is common in variable cloud or due to the daily movements of plants shadows. Observations of cooling and heating dynamics in freely basking animals (obtained on 12 series of observations) were performed using a remote thermometer; the temperature of the skin (TS) was measured (the main difficulty was not to scare the snake). In different experiments the body temperature was recorded in 1 min. or 15 s. The monitoring lasted up to 50 min. All the measurements were taken from large species with the body length more than 40 cm.

Thermopreferent behavior was studied in the laboratory (see section 13) using thermogradient-device (Khilkov, Korosov, 1996), in which the construction principles of N.I.Kalabukhov were realized (Kalabukhov, 1951). It represents a flat, smooth cement plot 200 x 20 cm. Inside there are tubes with circulating water heated at one edge and cooled at the other edge of the plot. The device forms a linear temperature gradient from 22 to 40 °C. From outside this plot was covered by the net (200 x 20 x 20 cm). On one side of the plot the thermometer scale was indented to register the snake location (at a chosen temperature). Animals one by one were let into the device and after 30 min. the place of its location was noted. Young animals quickly choose the suitable substrate temperature zone and then calmed down. Adult individuals crawled into the device slower – for 0.5–2 h while

finding the exit, until they calmed down. The round thermogradient device recommended by V.A.Cherlin (1991), is quite different from the terrariums, where snakes dwelled, and therefore are not more "familiar" to them, than those we used; in experiments the devotion of snakes to the corners of the cage was not observed.

As for the quantitative descriptions the dynamic simulation models were taken as a basis. But they sometimes have too complex structure (Beckman et al., 1971; Splotila et al., 1973), to use regression analysis. The models were constructed in the Microsoft Excel environment (see section 14). The general idea of modeling (as also the construction of regression equations) was to find the coefficients in the equation describing the proportions between some studied variables. The parameters of the dynamic models were chosen using the program "Decision making" built in Excel. The program is able to choose such parameters, in which the difference between calculated (yi) and the empirical Эyi values of the studied variables is reduced almost to zero:

$$\Phi = \Sigma\phi i = (yi - Эyi)2 \rightarrow 0,$$

i.e., the predictions of the model do not differ significantly from the dynamics of characteristics observed in nature. To assess the adequacy of the obtained descriptions dispersion analysis was conducted: by means of Fisher's criterion F we assessed the test significance (p) of the difference between model and residual dispersion (Korosov, 2002б).

3.2. The body temperature

Our observations in South Karelia in the warm period (May – September) shows that the adder occurs on the soil surface at the air temperature from 3 to 25 °C and at the substrate temperature from 8 to 33 °C (Fig. 3.2.1, 3.2.2). The body temperature varies widely (from 9 to 34 °C), but does not exceed $T_T \approx 34$ °C. It is known that by means of the heat influx from outside reptiles tend to raise their body temperature to some preferential level for optimal physiological processes (Slonim, 1986). The number of behavioral acts for thermoregulation includes seeking favorable thermal environment and

posture changes. As in Karelia variable daily cloud prevails in the warm period (Reference book on the climate in the USSR, 1974), snakes actively change locations all day, moving between open sites and different kinds of shelters, heating in the sun, or cooling in the clouds shadows. On clear hot days they are forced to hide in shelters. In other words, adders rarely have the possibility to maintain the maximum desirable body temperature all day. For this reason, it is impossible to obtain smooth curves of diurnal variation in body temperature, which is given in the work of V. A. Cherlin (1983).

The dependence of the body temperature of adders on the temperature of the environment is not linearly proportional, it is more complex. Firstly, the daytime body temperature is almost always higher than that of air and substrate (Fig. 3.2.3, 3.2.4), it is characteristic of all reptiles of temperate latitudes (Vitt, 1974); the range of difference is 0–19 °C (average 6.8 °C).

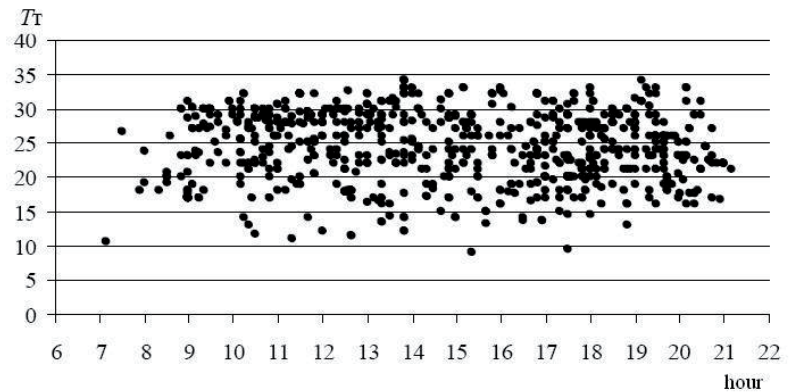


Fig. 3.2.1.Viper body temperature in southern Karelia (800 measurements 1990–1999)

Sparse points below the isotherm Tbody = Tenvironment correspond to the animals that just crawled out of shelters on a warmer soil surface. This means that in determining the large adders' body temperature in Karelia the leading role belongs to the heat flow of the sun; the environmental temperatures (substrate, shelter) mainly determine the minimum temperature T_T.

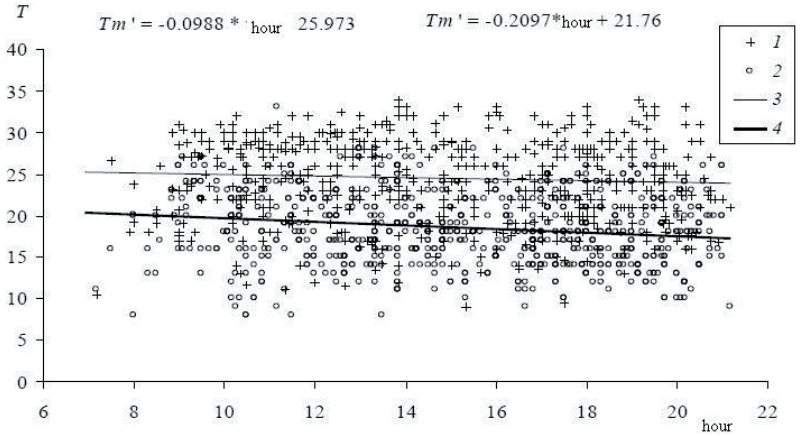


Fig. 3.2.2. Variability in viper body temperature (T_T, *1*), substrate temperature (T_C, *2*) and their average trend (Tm ', *3*, *4*) in the summer in the south of Karelia

Requirements of small juveniles are less understood. A few data on young adders show that the nature of their average body temperature T_T = 22.4 (±1.2) not significantly differs from the body temperature of adults T_T = 24.5 (± 0.2) °C, whereas the maximum is 4 °C lower (30.5 vs. 34.5).

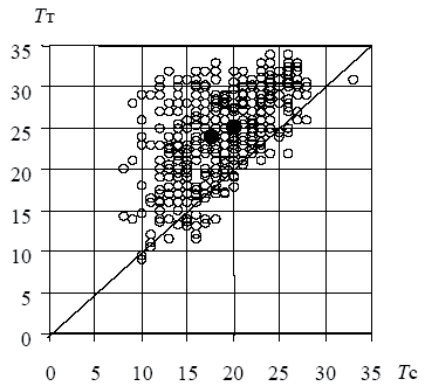


Fig. 3.2.3. The relation between substrate temperature (Tc) and viper body temperature (TT). The line indicate relation $T_T = T_C$.

In adult snakes, the body temperature may exceed the temperature of the substrate by 19 °C, on an average by 6.8 °C. Saint-Girons (1975) gives similar figures. Using regression (Fig. 3.9.2), we can calculate this difference for any time of a day, for example for 8 o'clock a.m. – 5.1 °C for 8 o'clock p.m. – 6.4 °C.

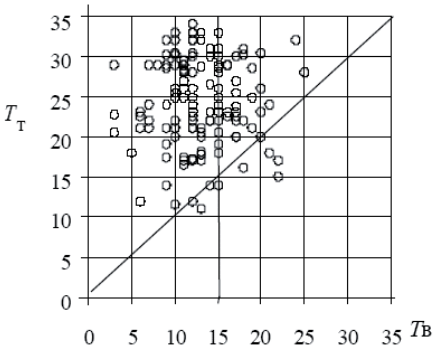


Fig. 3.2.4. The relation between air temperature (Tв) and body temperature viper (Tт). The line indicate relation Tт = Tв

Under any circumstances the body temperature of an adder does not exceed 35 °C. At any environmental temperature their body temperature can take values in the range from the minimum T_T = Tshelter (or T_T = Tsubstrate) up to this maximum. According to various sources, the value 34–34.5 °C is specific for our species (Saint-Giron, 1975, 1978; Spaendonk et al., 1990; Drobenkov, 1990), this value is taken as the maximum voluntary temperature.

The presented materials allow to make an important, although quite trivial, first conclusion: in southern Karelia in establishing the body temperature of adders the leading role plays the heat flow of the sun; environmental temperature defines only the minimum value of a possible variation range. In other words, the adder behaves as an active heliothermal organism.

Manifestations of thermoregulation can be considered in more details using the diagram showing the difference between the body and substrate temperature dT = T_T – Tc (Fig. 3.2.5).

A lot of observations form a right-angled triangle. Four diagram sections (the area inside the triangle and outside regions) correspond to the different thermoregulation mechanisms of the adder. The hypotenuse given in dotted line corresponds to a situation when the adders' body temperature is $T_T \approx 34–35$ °C. This is indicated by the sum of any values on the axes (arrows show the sum of 15 + 19 and 35 + 0 °C).

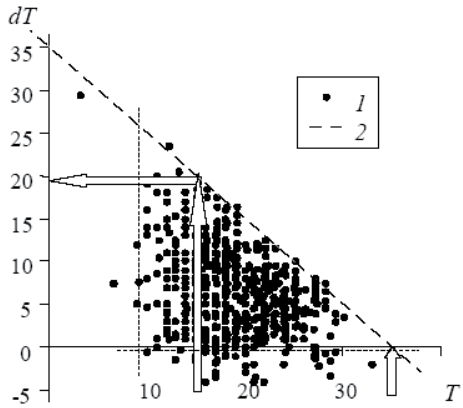


Fig. 3.2.5. The relation between the difference (dT = Tт – Tc, *1*) and substrate temperature (Tc). The dotted line (*2*) shows the isotherm of Tт = 35 °C

To the right and above the hypotenuse lies the area where the adders' body temperature would be out of the upper limit of species tolerance (voluntary maximum temperature), so here there are no data. The clear boundary of this region is associated with the realization of a specific thermoregulatory behavior directed to the avoidance of overheating. The most important reactions are changing a shelter, moving to a more favorable place for basking.

To the left and below the hypotenuse is the area of body temperatures acceptable for adders. Reptiles differ from a simple physical object by active, regulated heat transfer inside the body. The blood passing through the skin brings warmth to other parts of the body. Therefore, the adders' body

temperature is usually higher than the temperature of surrounding objects, and significantly: in the morning – by 20–25 °C and during the day – by 10 °C (on an average). The variations of Tт within the distinguished triangle are determined by heat inflow to the adders' body and its ability to perceive it (usually in summer). The main heat source is the solar radiation. In different weather conditions, seasons and day time as well as in different shelters heat flow varies, causing changes in the body temperature of snakes. Within this indicated area the whole complex of thermoregulatory reactions occurs – both physiological (change in the heart rate, vasomotor reaction) and behavioral (changing the body shape, posture, moving to a shelter).

To the left of the triangle lies an area for those rare cases, when the substrate temperature is low, but the solar activity is sufficiently high to allow adders heating. Such situation is possible in early spring and early autumn in clear mornings after frost, when the snake chooses a dry area in the midst of covered with frosty fields and heats up quickly in the sun. The upper left point draws attention. It represents the case when the snake crawl to the edge of frosty meadows with the substrate temperature of the 2 °, but its body temperature is above 28 °C!

The bottom leg of the triangle (dT = 0) separates the observation area, when the snake body temperature is below the substrate surface temperature and averages out the soil temperature; clearly, these individuals have just came out of shelters.

Vasomotor regulation due to subcutaneous shunts of peripheral blood vessels is expressed in the changes of the blood flow velocity in upper layers of the skin. As a result the temperature difference of the external and deep tissues of an animal was observed (Schmidt-Nielsen, 1982). This effect is found in adders both in heating and in cooling. So, the captures of adders at daily cloud showed that the difference between the internal temperature (rectal, measured by KT), and the external temperature (investment, measured by DT) changes from positive to negative, from –2 to +4 °C.

In adder cooling in a cloud shadow, its investment is cooler than internal organs, in heating in the sun the investment becomes warmer (on an average by 1.6 ° C) (Table 3.2.1). By placing an animal in a thermo-

insulated "place" (a textile bag), one can observe the leveling of the temperature of different layers lasting for 0.2–0.5 min. Body investment of adders coming out from the shadow heats up step-wise, but those warmed in a blaze of the sun – cool down, then their temperature declines more gradually. Similar temperature jumps occur when a cooling adder changes its posture and squirms when attached to a batten with a sticky tape.

Table 3.2.1. Distribution (%) of difference between the internal temperature (T_T) and that of dorsal investment (Tp) of adder in different weather conditions

Weather	The temperature difference between T_T and Tп							n
	–2	–1	0	1	2	3	4	
Clear	6.3	31	50	6.3	6.3	0	0	16
Haze	2.2	6.5	70	11	4.3	2.2	4.3	46
Cloudy	14	8	54	20	4	0	0	50
Over-cast	0	0	57	0	43	0	0	7
Total	7.6	10	60	13	6.7	0.8	1.7	119

The temperature difference in different parts of the body is a consequence of the redistribution of heat due to physiological and physical mechanisms (Schmidt-Niel'sen, 1982). As it was shown by external measurements using DT, the highest body temperature is noted in the central part of the body and reduces towards the neck, the head and tail (Fig. 3.2.6 A, B). At the same time, the measurements by a contact thermometer revealed that the oral temperature is 1–3 °C (on an average 1.6 in 15 measurements) higher than rectal.

The temperature distribution within adders' body in a specific posture, for example, squatted into a "ball", is rather complex. In this posture the "outer-inner" and "central-regional" temperature gradients are synthesized. In the center of this "ball", the temperature of all tissues is equally high; the skin periphery is significantly colder, the difference can reach 4 °C (Fig. 3.2.6, D, E). The adder is able to organize a buffer zone between the internal parts of the body and environment that provides a significant inertia in

changing internal temperature and gives smoothness to its dynamics in contrast to the more sharp jumps of the skin temperature.

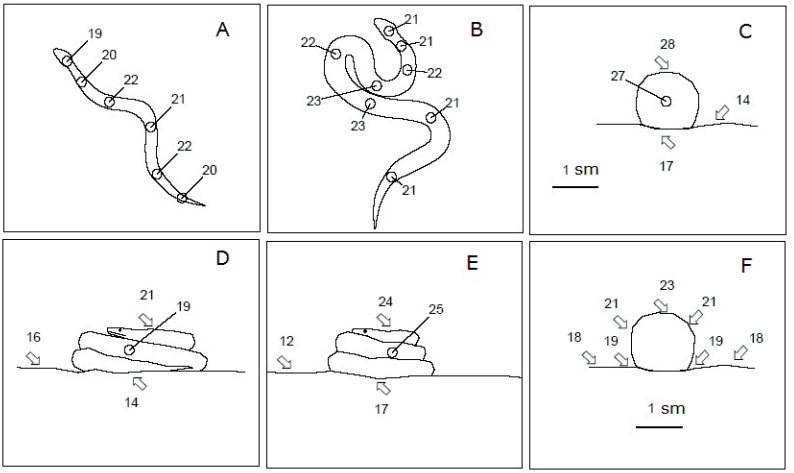


Fig. 3.2.6. The temperature of the substrate and the different parts of the vipers body in a free position (A), curled in “semi spiral” (B), on a «cut» during heating (C), while basking (F), when heated in position of "semi tangle" (D), while cooling in the position of «tangle» (E)

The role of environmental factors

Season has a leading role in setting the body temperature in poikilothermic animals. In winter the body temperature of adders is equal to the temperature of wintering shelter (+0.5–4.5 °C) (Drobenkov, 2001). It is shown that adders can withstand a short-term temperature decline to –7 °C and for a relatively long time (up to 16 hours) they can survive at –1.5 °C (Bakiev et al., 2008) and even –2.5 °C (Viitanen, 1967). Freezing point lies between –3.8 to –2.1 °C (Andersson, Johansson, 1994; Andersson, 1995).

After the end of the frosty weather, the average body temperature is maintained at a high level, increasing somewhat in mid-summer and decreasing by September (Fig. 3.2.7).

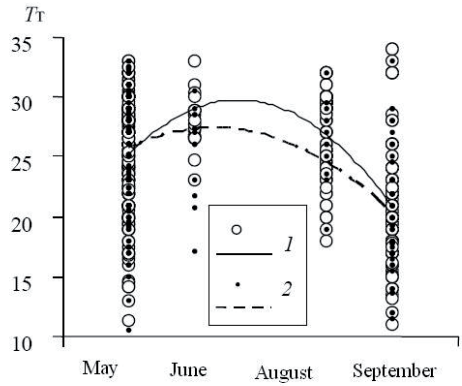


Fig. 3.2.7. Body temperature in different seasons and polynomial regression curves for females (*1*) and males (*2*) viper

The diagram shows that the range of variability of T_T remains. At the same time the time duration, when adders are able to get out to the surface and maintain body temperature at a high level, is significantly reduced by the fall (Fig. 3.2.8).

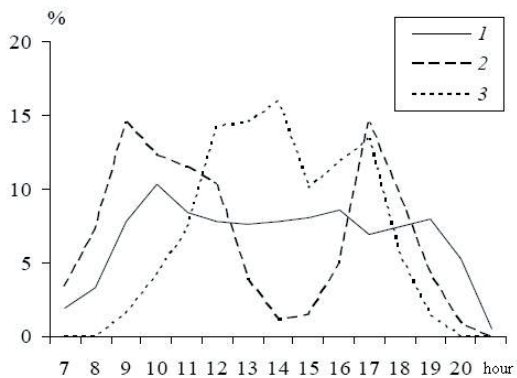


Fig. 3.2.8. Proportion of vipers (%) encountered in different times of day in May (1, 1580 ind.), June – July (*2*, 216 ind.) and September (*3*, 575 ind.)

Weather conditions are also responsible for wide variations in the body temperature of the adder. At that, choosing a suitable shelter is of great importance; this specific behavior allows an adder to control the body temperature during the day trying to keep it at a desirable level. In fine weather the heat flux from the sun increases smoothly reaching a maximum at the astronomic noon (13 hours), then it gradually decreases (Fig. 3.2.9). While heating a snake changes their shelters (see section 3.3) and maintain rather high and stable body temperature 28–30 °C (Fig. 3.2.10).

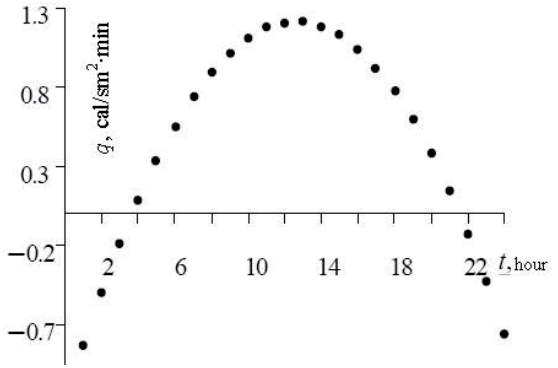


Fig. 3.2.9. The intensity of the heat flux (q), coming to the ground during the day (an astronomical noon – 13 pm 05/20/1996)

In contrast, in cloudy weather the sun shines for a limited number of hours a day, but not the whole day. In variable cloud temperature variability of a substrate and an animal body increases (Fig. 3.2.11). In rough weather changes, when the sun is overclouded, the temperature of environment and the adder's body also decreases (Fig. 3.2.12).

Our materials allow us to determine the body temperature of an animal under different weather conditions (Table 3.1.2, Fig. 3.1.13). In any weather, the body temperature can be both lower (by 3 °C) and higher (up to 28 °C) than the substrate temperature. In fine weather a deficiency was ob-

served in the morning when the snakes come out of cold night shelters. Throughout the day the body temperature is higher than the ambient one by 6–10°C on an average.

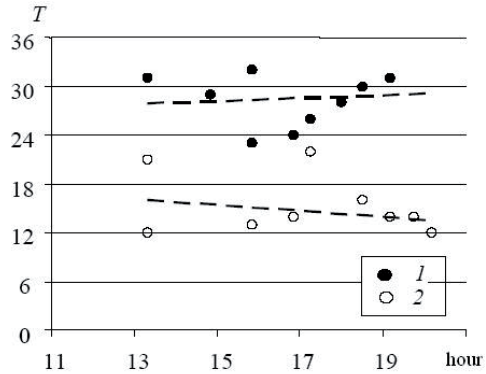


Fig. 3.2.10. Variation of viper body temperature (Тт, *1*) substrate (Тт, *2*) in clear weather, on 10/05/1998

In variable cloud the difference between the temperature of the body and a substrate is less. In cloudy weather the body temperature of snakes is also higher than the ambient temperature (by 2–9 °C) because at low density of the clouds snakes catch the infrared radiation (data were considered only for those cloudy days, when snakes were found on the surface and there was a faint heat flow from the sun). When the sun does not penetrate through the dense clouds at all, snakes remain in underground shelters.

The choice of one or another type of shelter substantially determines the body temperature (Table 3.2.2). In natural conditions five types of shelters are clearly recognized (Table 3.1.1): open surface (1), light shade from dry grass or high shrubs (2), the dense half-shade from fresh grass or trees (3), the dense shadow from rocks or a tree trunk (4), underground shelter (5). In our opinion, the conditions in these shelters are contrasting, but not absolute. This is expressed in that the passage of adders from one shelter to another is associated with significant change in heat flow (see sections 3.3, 3.4).

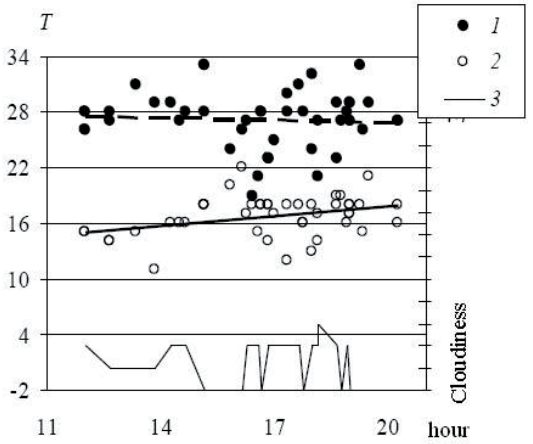


Fig. 3.2.11. Variation of viper body temperature (Тт, *1*) substrate (Тс, *2*) with variable density (*3*) of the clouds, on 17.05.1998

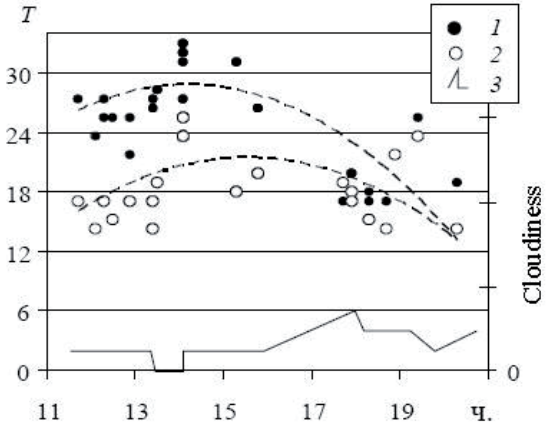


Fig. 3.2.12. Change of the substrate and viper body temperature with weather change on 09/07/1998

In underground shelters the body temperature of adders is equal to the ambient temperature. Under the direct sunrays and in variable cloud adders heat up quickly (see section 3.3) and move to a shelter, where the reduced

solar radiation heats them up to the highest temperature (Table 3.2.2). Both in females and in males the body temperature in light shelters was higher than in the open air (Fig. 3.2.13). At that, average values of the body temperature of females and males do not differ significantly. Wind (forced convection) plays a certain role too. On the unprotected Kizhi it blows almost always, cooling the open surfaces without affecting the light shelters. In addition, in clear weather the time of maximum body temperature is difficult to register.

Table 3.2.2. The relationship between the body temperature of adders (T_T) and substrate temperature in different shelters (Tc) under various weather conditions

Parameters		Clear			Cloudy		Overcast		
		open	penumbra	shadow	open	penumbra	open	penumbra	shadow
T_T	M	26.2	29.8	25.4	24.3	25.8	23.4	24.6	22.0
	S	3.7	3.4	3.7	3.3	3.1	4.2	3.4	0.0
	Me	27	30.5	25.25	23.5	26	25	22.75	22
	Min	16	13	21	18	19	14.6	21	22
	Max	33	33	30	32	31	29.2	30.5	22
Tc	M	18.1	19.1	26.0	15.9	16.3	14.3	18.5	20.0
	S	3.6	5.1	2.2	3.6	1.9	3.7	5.3	0.0
	Me	18.0	18.0	26.5	16.0	17.0	14.0	19.5	20.0
	Min	11	2	23	9	12	10	11	20
	Max	27	28	28	25	18	24	24	20
T_T–Tc	M	8.1	10.6	–0.6	8.4	9.5	9.2	6.1	2.0
	S	4.8	6.1	2.4	4.5	4.0	4.0	6.0	0.0
	Me	9.0	10.0	–1.8	8.0	10.0	8.6	6.8	2.0
	Min	–1	–3	–2	–2	1	3	–0.5	2
	Max	20	28	3	19	19	17	14	2
n		83	53	4	64	17	31	8	4

One of the purposes of our analysis is to find the formal rules for calculating the body temperature of the adder, based on the surrounding thermal environment. A version of such formula was proposed for the monitor lizard (Tsellarius, Tsellarius, 1997): $TT = 0.5 \cdot Tc + 0.5 \cdot Tв$. For the adder the fol-

lowing ratio can be proposed: the body temperature is higher than the substrate temperature by some value: $T_T = T_C + dT$ (°C). In different weather and in different shelters the extra term dT will vary. In spite of the fact that the environmental (substrate) temperature is included into the formula, it does not affect directly the body temperature of snakes, but plays the role of an indicator of thermal environment surrounding the snake, including radiation from the sun and from surrounding objects – the higher is the substrate temperature, the higher must be the body temperature of the adder (but mainly due to insolation). On the basis of the data in Table 3.2.3, it can be accepted that $dT_1 = 8$ for the soil surface, $dT_2 = 10$ °C for the half-shade and $dT_3 = 6$ °C for the shade.

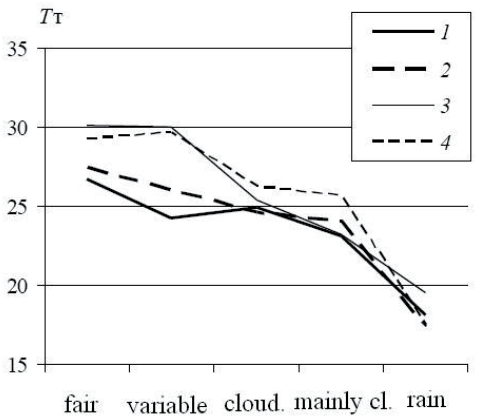


Fig. 3.2.13. The average level of body temperature in females (*1, 3*) and males (*2, 4*) adder at different weather conditions on the open surface (*1, 2*) and in the penumbra (*3, 4*)

The data obtained during the observation of adders under different conditions help to present a complete picture. In the diagram (fig. 3.2.14) the empirical values of the difference between the adders' body temperature and the temperature on the surface and in the light shelters (May) are shown. Apparently, within the same equal breadth of dT, its linear trend on the open surface is somewhat lower than the trend for the half-shade data.

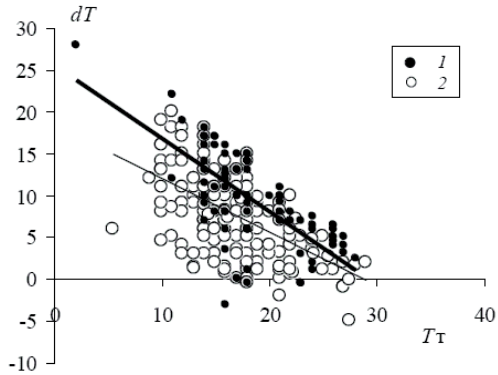


Fig. 3.2.14. Dependence of the difference (dT = Tт –T_C) from the substrate temperature (T) at various shelters: *1* – open, *2* – penumbra

The reason is that in backing adders prefer to stay in light shelters, where the influence of wind is weakened; there is no negative radiation and the influence of solar radiation is not so hard. At the same time, considering all peculiarities is not consistent with the purpose of modeling – it is important for us to reflect the dynamics of the body temperature of snakes in general, and such nuances as the exposition of a mount, on which a snake lies, or the strength of the wind blowing around it, should be left beyond our consideration.

The dependence of the snake's body temperature on its size, according to our data, is not observed (fig. 3.2.15, 3.2.16). Despite the fact that captured males are smaller than females, their ranges of temperature variability are similar and their regression lines of the body temperature along the body coincide and run parallel to the OX axis (average values are equal, correlation is absent).

When the situation is stabile, the average body temperature of both sexes in May (25 °C, fig. 3.2.15) is 5 °C higher than in September (20 °C, fig. 3.2.16). It is important to note that young snakes (the minimum size) have not so high maximum voluntary temperatures than larger and older ones.

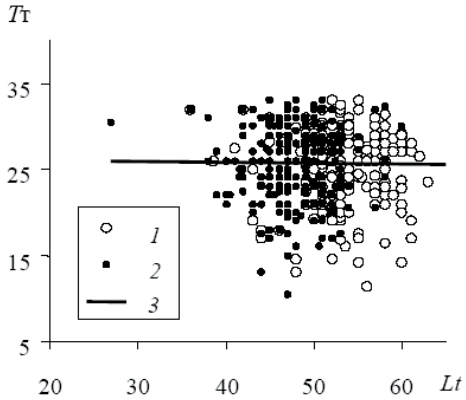


Fig. 3.2.15. The body temperature of viper females (*1*) and males (*2*) with different body length (Lt) May; *3* – the matching regression line

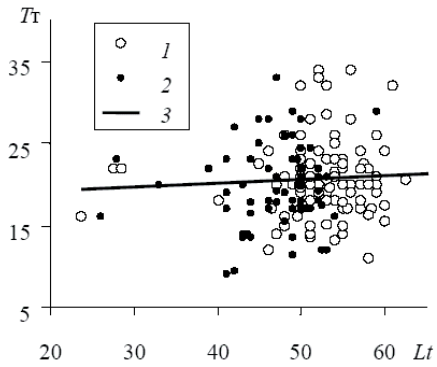


Fig. 3.2.16. The body temperature of viper females (*1*) and males (*2*) with different body length (Lt) September; *3* – the matching regression line

3.3. Heating

The body temperature of many reptiles does not follow the temperature of environment, and simple extrapolations between providing the environment (e.g., soil) and animals' body by warmth, as a rule, are unfounded

(Vitt, 1974). Day body temperature of adders (as heliotherms) is almost always higher than a substrate temperature. So, the leading role in its maintenance belongs to insolation unlike, for example, the body temperature in Turkestan plate-tailed geckos (and other geotherms), which is to a greater extent dependent on a substrate and air temperatures (Cherlin et al., 1983). The adaptive behavior aimed at maintaining a high temperature enough to survive in our high latitudes, is of crucial importance. A series of behavioral acts allows maintaining the body temperature that corresponds to the current physiological condition of an animal; primarily basking, i.e. heating in the sun (Kalabukhov, 1951; Cherlin, 1983). It is considered, that poikilothermic animals coming out to the surface for heating use solar thermal energy to bring their body temperature up to some preferred level that plays the role of internal criterion for encouraging actions to ensure normal physiological processes (Slonim, 1986). Not only the temperature but also the illumination of the substrate outside the shelter serves as a signal for basking (Tlenbergenova, Isabekova, 1991; Khilkov, Korosov, 1997; Khilkov, 1998; Korosov et al., 1999, 2008a). It is possible to understand and quantitatively describe a heating process only if it is known the preferred temperature, for achieving it adders choose one or another behavior pattern.

Reaction to light. The daily activity of the adder, including the reaction to light and heat, was studied in laboratory conditions by means of actograph designed by the authors (Korosov, Khilkov, 2008a) (see section 3.1). The animal's activity was recorded on a paper tape.

Primary processing of daily actogram consist of determining the chamber where adders stay for each 5 min within 24 hours (Table 3.3.1), because the time interval less than 5 min. is impossible to distinguish on the actograph paper tape of 30 cm long. Total 24 h x 60 min / 5 min= 288 acts of adders' activity was recorded.

The data from the Table 3.3.1 was summarized as follows. Firstly, the "time budget" was calculated – the number of minutes spent by an adder in a given shelter within each hour (Table 3.3.2, t_i), and the average time of snake's staying in different chambers within 24 hours (Table 3.3.2, M_T).

Table 3.3.1. Digitized daily actogram: the number of the chamber where a snake mainly stay for each 5 min. within 24 hours

Мин.	Время суток, ч.																							
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
1–5	4	3	4	4	4	4	4	4	3	1	3	1	1	2	2	1	2	2	1	2	1	3	2	4
5–10	4	3	4	4	4	4	4	4	3	1	2	1	1	2	1	1	2	2	1	2	1	4	2	3
10–15	4	4	4	4	4	4	4	4	2	1	1	2	2	1	1	1	2	2	1	2	1	4	2	3
15–20	4	4	4	4	4	4	4	4	2	2	1	2	2	1	1	2	2	2	1	2	2	4	3	3
20–25	3	4	4	4	4	4	4	4	2	2	1	3	2	1	1	2	3	2	1	1	2	3	3	3
25–30	3	3	4	4	4	4	4	4	1	2	2	3	2	1	1	1	3	2	1	1	2	3	4	3
30–35	3	3	4	4	4	4	4	4	1	2	2	2	1	2	1	1	3	2	2	1	2	3	4	3
35–40	4	3	4	4	4	4	4	4	1	2	2	2	1	2	1	2	3	1	2	1	2	2	4	3
40–45	4	4	4	4	4	4	4	4	2	3	1	2	1	3	1	2	3	2	2	1	3	2	4	2
45–50	4	4	4	4	4	4	4	4	2	3	1	1	1	3	1	2	3	1	1	1	3	1	4	2
50–55	4	4	4	4	4	4	4	3	1	3	1	1	1	3	1	2	2	2	1	1	3	1	4	3
55–60	3	4	4	4	4	4	4	3	1	3	1	1	2	2	1	2	2	2	2	1	3	1	4	4

Table 3.3.2. Average length of time in minutes (t_{ij}) of a female adder staying in different natural shelters (K1–K4) each hour within 24 hours (time budget from 11.8.1994 to 11.8.1994)

	Time of day, hours																							
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	M_T
K1	0	0	0	0	0	0	0	0	25	15	35	25	35	20	55	25	0	10	40	40	15	15	0	0	14.8
K2	0	0	0	0	0	0	0	0	25	25	20	25	25	25	5	35	30	50	20	20	25	10	15	10	15.2
K3	20	25	0	0	0	0	0	10	10	20	5	10	0	15	0	0	30	0	0	0	20	20	10	40	9.79
K4	40	35	60	60	60	60	60	50	0	0	0	0	0	0	0	0	0	0	0	0	0	15	35	10	20.2

Secondly, the "average hourly shelter" – the average number of the chamber where an adder stays within each hour (M_K) (the character of the adder's location with the values of the most necessary factors) and "hourly mobility" – the standard deviation of the chamber number where adders stay within each hour (S_K) (reflects the process of seeking optimal conditions by a snake) were defined. The key characteristics of daily activity are the time when an adder comes out of a shelter, the duration of its active period and the time when it finally leaves for a shelter.

Table 3.3.3. Average hourly shelter (M_K) and hourly mobility (S_K) of an adder

	Time of day, hours																							
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	M_T
M_K	3.7	3.6	4	4	4	4	4	3.8	1.8	2.1	1.5	1.8	1.4	1.9	1.1	1.6	2.5	1.8	1.3	1.3	2.1	2.6	3.3	3	2.59
S_K	0.5	0.5	0	0	0	0	0	0.4	0.8	0.8	0.7	0.8	0.5	0.8	0.3	0.5	0.5	0.4	0.5	0.5	0.8	1.2	0.9	0.6	1.19

Under the term "activity" we mean any form of behavior that allows the adder to maintain the most comfortable body temperature, to avoid adverse environmental influences and to choose optimal conditions.

In natural conditions (July) the behavior of an adult female adder (Fig. 3.3.1) expressed in accepted characteristics of activity is as follows.

Snakes come out of their deep shelters on heated sunlit areas in 6–8 o'clock. With the rise of the body temperature and its approaching to critical value (it differs in animals of a different sex, age and state) adders begin seeking shelters with a thermal flux of smaller intensity. From 9 to 10 o'clock snakes are in the shadow of the second chamber ("grass"), from 11 to 17 o'clock – in the solid shadow of the third chamber. From17 to18 o'clock the re-emergence of animals on the open sites warmed throughout the day is observed. With the rise of negative radiation, from 19 to 20 o'clock adders moved into deep ("underground") shelters where they stay all night long. The share of time spent in different chambers is 12, 6, 15 and 28% – even in summer snakes stay in shelters most of the time.

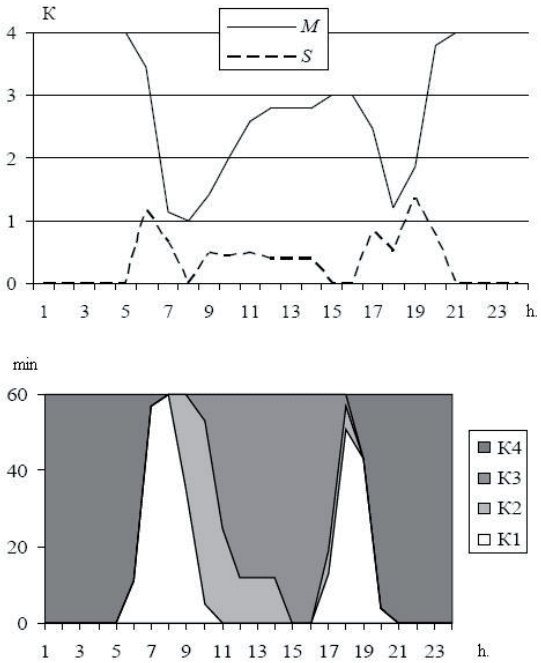


Fig. 3.3.1. Mean cover number (M), mobility (S) and the daily time budget (T) of a viper with the natural dynamics of temperature and light

The second experiment was carried out in the summer indoors with the natural change of lighting and constant temperature (18–21 °C) (Fig. 3.3.2). Changes of shelters throughout the day are similar: in daytime snakes are in open chambers and by night they pass into closed chambers and do not move ($S = 0$). The distinctive peculiarities of their behavior are that in daytime adders do not leave the outdoor chambers because they do not feel overheating. The ratio of the time spent in different chambers (15, 15, 10, 20%) was almost equivalent to natural conditions – snakes spend in the night shelters the most time. Thus in daytime they permanently move ($S \approx 0.8$), trying to find the best conditions for heating, as the temperature in the open chamber is substantially lower than the optimum. These materials

clearly show that light is an important factor in the regulation of circadian rhythm of adders' activity.

In the third experiment the constant air temperature of 20 °C and illumination were maintained (Fig. 3.3.3). All day and night adders showed increased spontaneous activity (S ≈ 1), moving within a closed actograph, apparently, in searching a higher temperature environment. Staying in chambers 1–4 during the day was 12, 20, 19, 9%, respectively. Obviously, for a single casual any side chambers going the snake need to pass twice through an adjacent central chamber – it produces the effect of the equal two-fold reduction in side chambers going as compared with the central one.

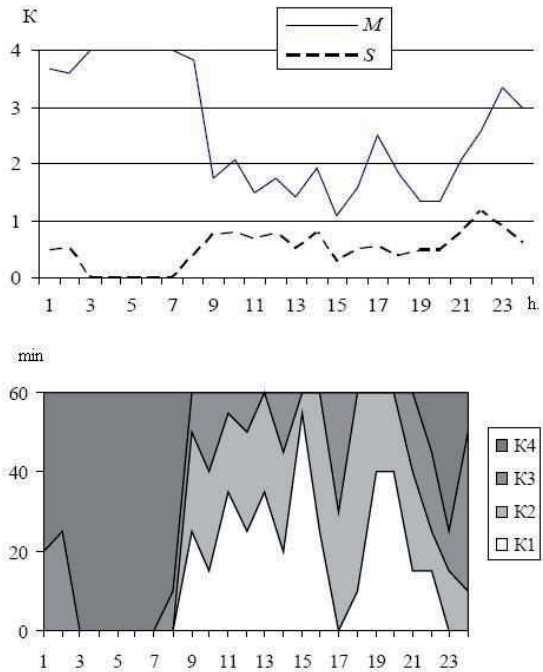


Fig. 3.3.2. Mean cover number (M), mobility (S) and the daily time budget (T) of a viper under the natural photoperiod and constant temperature in all cells

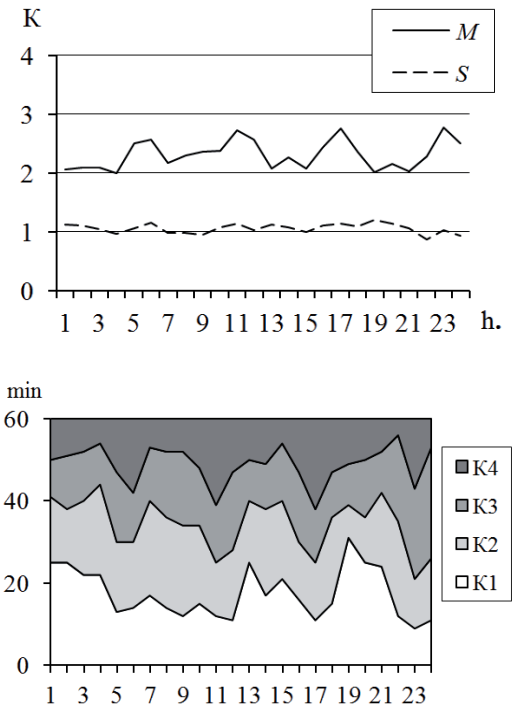


Fig. 3.3.3. Mean cover number (M), mobility (S) and the daily time budget (T) of a viper at constant light and constant temperature in all cells

Our experiments clearly show that the light factor is an important signal for the beginning of thermoregulatory activity of the adder, but only at a sufficiently high temperature of environment. In general, the adder shows a very simple ("automatic") response to the considered environmental factors and it allows approaching the study of its behavior in detail using the automaton model (see section 3.5).

Reaction to heat. It is believed that two reactions lie in the basis of the behavioral thermoregulation – leaving an overheating zone and striving to a warmer area. From this point of view the actual motive, that makes reptiles move from one area to another, warmer one, including coming out

on the soil surface to bask in the morning, or in the case of shading (e.g. from trees) to move into warmer sunlit areas, is missed. To react in such a way, to move solely to warm places of the surface the adder should have “a heat vision". Observations show that when the set of heat preserving postures of cooling adders is exhausted (see section 3.4), the snake starts to look around and rushes in the direction of warm objects (stones, hummocks...). This indicates good heat sensitivity of the snake's skin (in the first place, the head surface). Unlike boas and rattlesnakes which distinguish temperature difference up to 0.2 °C – (Terashima, Goris, 1974), adders, however, is confidently oriented in the heat conditions.

Our observations in nature gave such figures. At the body temperature 22–25 °C and from the distance of 20–30 cm an adder definitely feels the surface heated up to 25–30 °C. The same figures were received from five observations of the first adders emerging from 7.15 to 7.45 a.m.: from night shelters with a temperature of 10–13 °C snakes come out on the surface when environmental temperature is 15–17 °C. The close range of differences 1–5 °C between rectal and substrate temperatures was given by I.Y.Yumashev (1995). On an average, it turns out that snakes react to nearby (20–40 cm) objects that are 3–6 °C warmer than its body investments. Laboratory experiments (5 snakes, 14 experiments) confirmed the field observations (Fig. 3.3.4).

Adders begin to react upon the black heat emitter if the temperature (Ти) essentially exceeds body temperature of the snake: the higher the body temperature, the greater must be the excess to cause positive taxis in the adder. In the diagram the arrow shows that when T_T = 13–15 °C (night shelters in summer) the temperature excess causing the reaction is dT = Ти–Тт = 5 °C, at T_T = 20 °C it is dT = 9–10 °C. This dependence is described by power-law regression $dT = 0.0065 \cdot Tт^{2.4}$.

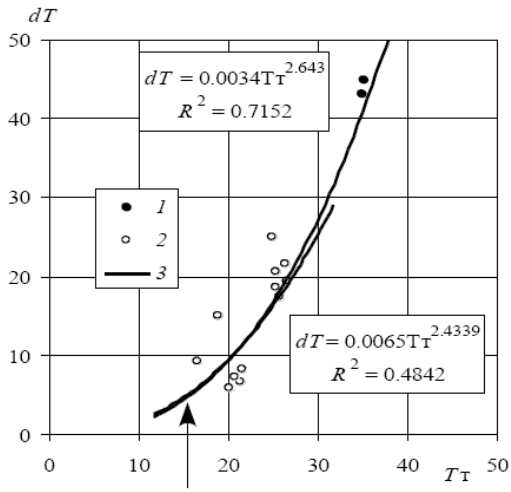


Fig. 3.3.4. . Relationship between the increase of temperature going from the radiator (dT = Ти–Тт, °C), and viper body temperature (Тт, ° C): *1* – data for the extreme conditions of the experiment, *2* – data for normal conditions of nature, *3* – the degree of approximation the arrows marked the situation in the morning

The white circles in the diagram correspond to the usual natural temperature range when the temperature of the objects surrounding the adder cannot exceed 50 °C (dT + T_T = 25 + 25). The black dots show that even at the body temperature close to critical (34 °C) adders can react to heat and go to a warmer region.

The obtained values do not have high precision (depending also on the exact distance of a snake from a radiation source) and require a further research. However, these dependences allow determining the order of values and can be the basis for the imitation model.

It is important to note that the solar radiation flux, which provides heating a substrate by 6 °C above air temperature, is enough to provide heating a snake's body. Thus this range can serve as a criterion of adder's

leaving the shelter in a thermoregulation model, it can be called the "threshold of thermal reaction" – the intensity of the heat flow from surrounding objects that motivate an animal to move from colder areas to warmer ones.

Thermopreferendum. A characteristic feature of the behavior in poikilothermic animals is striving to the area with a certain temperature, called preferred, "preferential" temperature (Kaufman, 1989). The content of the terms varies, but they reflect a striving of animals for the particular preferred temperature. Maintaining of this temperature generally provides the most effective, optimum functioning of the body (Dawson, 1975), for example, the maximum affinity of trypsins to the substrate during the digestion (Hofer et al., 1975). This assumes that the temperature selected by an animal corresponds to the optimal body temperature, but this may not be true. The thing is that the standard thermogradient devices monitor the temperature of a substrate, but not the entire thermal environment. Therefore, in general the choice of a given temperature by an animal can only mean that there is some compromise between the sensitivity of the internal and external abdominal thermal receptors (not very cool body and not very hot floor), while the current body temperature is far from a certain "preferred". Due to the radiation from the dorsal side, even choosing an obviously hotter area, the animal will have a lower body temperature than the optimum. Exact correspondence of the selected temperature to the optimum level can be achieved when heat fluxes in all sides of an animal are the same.

Such conclusions are made on the basis of the above observations on basking adder in nature showing that a skin temperature is higher than a body temperature (up to 2 °C, Table 3.2.1). The same was shown by our experiments on the assessment of preferred temperatures (Khilkov, Korosov, 1996, 1997). So, for the adult snakes captured in nature (n = 11) at the air temperature $T_в$ = 14–18 °C the average preferred substrate temperature – $T_п$ = 38.4 ± 0.39 °C, although in nature the body temperature never exceeds 34–35 °C. Almost the same maximal values of the substrate temperature were obtained by other authors – 34.88 °C (Spaendonk et al.,

1990, 1991). In our case the excess of a substrate temperature over "the voluntary maximum body temperature" was 4 °C. It is obvious, that at a higher air temperature this difference will be smaller.

The observation of the animals raised in captivity, allowed to study another important aspect – the dependence of thermopreference on living conditions, physiological state and the age of an animal. After eating adders like other reptiles (Naulleau, Marques, 1973; Lysenko, Gill, 1980; Slip, Shine, 1988; Gibson et al., 1989) choose high temperatures (Тп = 30–34 °C), and over time – lower and lower, to 20–25 °C by the end of the week (Table 3.3.4). The curve of the reptiles' body temperature received by a long-term observation resembles a sinusoid (Berk, Heath, 1975). Periodic variations of preferred temperatures result in changes in duration of animals' staying on the soil surface. Thus, the older the animal, the lower the temperature it chooses.

Table 3.3.4. Mean* (n=8) soil surface temperature, chosen by adders after feeding

Adders age		Days after feeding						
months	conditional years**	1	2	3	4	5	6	7
7	3	34.0	32.1	34.1	29.1	28.8	27.8	26.0
8	3.5	33.8	32.6	28.9	27.4	24.3	22.4	21.4
9	3.9	33.6	29.8	28.4	27.6	24.8	22.8	22.1
10	4.3	30.0	28.3	25.8	24.9	24.5	21.9	20.6
11	4.8	28.1	25.4	24.9	24.4	23.0	22.1	20.4
On an average		31.9	29.6	28.4	26.7	24.3	23.4	22.1

* The errors of average values vary from 0.2 to 0.4 °C, **See section 5.

Two-week staying of adders in different environmental temperatures also influences significantly the preferred substrate temperatures (Table 3.3.5). The adder compensates low air temperatures (TV = 16 °C) at the first opportunity by choosing a high substrate temperature (35.4 °C). Long stay in the too warm atmosphere (30 °C) forced her looking for coolness (20.8 °C).

In one of our experiments a relay was accidentally broken and an adder was for some time (15–30 min.) in the chamber with the floor temperature clearly above 40 °C. After rescue it hid in the coldest corner of a terrarium (TC ≈ 18 °C) and spent 3 days there.

So, the "preferred" temperature in adders of different status varies widely.

For this reason, the search for common preferred (and voluntary maximum temperature) is meaningless. The point must be searching some range, specific for adders of a given age and conditions. Results in Table 3.3.5 contain such ranges for adult males and females.

Forced heating. The dynamics of the forced heating in the sun was investigated in the experiments with immobilized adder previously cooled to 15–18 °C (Fig 3.3.5). The body temperature of the snake raised by 11–16 °C (up to 34°) for 18 – 20 min., i.e. with the average speed of 0.5–1 °C per minute (depending on the presence of haze in the sky). At that any clear polypnea reaction was not observed. When body temperature (T_T) approached 35 °C, the snake attempted actively to escape. This reaction shows once more that the upper voluntary threshold of the body temperature in adders is 35 °C.

Table 3.3.5. Substrate temperature, chosen by adders (Tc), acclimated (for 10 days) to different conditions

Parameters	Temperature of acclimation, °C			
	16	24.5	25.3	30
M	35.4	34	33.3	20.8
S	0.99	0.84	0.80	1.33
n	21	21	21	21
m	0.21	0.18	0.17	0.29

While studying the abilities of adders to heating, it is reasonable to describe quantitatively only the most intense processes. The power regression $T_T = 16.4 \cdot t^{0.25}$ (t is the observation time) ($R^2 = 0.97$, $p = 0.005$) describes heating rather well.

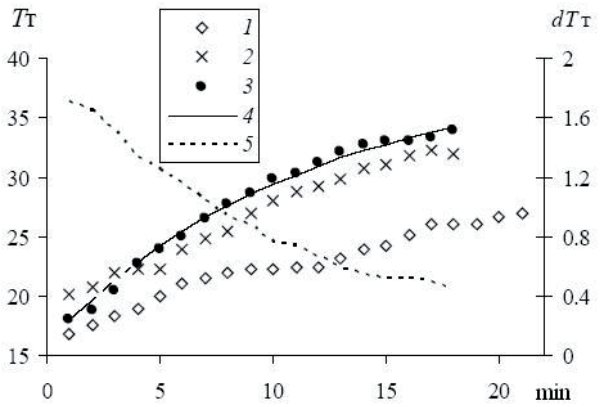


Fig. 3.3.5. Dynamics of «forced» heating of the body of different vipers (*1, 2, 3*), model description of the most rapid process (*4*, *T*т) and its real speed (5, *dT*т)

The details of the process are clarified only by a simulation model ($p = 0.00001$), calculated for the time step of 1 minute (Fig. 3.3.6). The model consists of two equations: one calculates the increment values of the studied variable (dT_{Ti}) during one time step (i) depending on having already achieved body temperature T_{Ti}, i.e. it expresses the process speed.

The second equation serves for consecutive summation of all the effects, received during every time step, and also expresses the studied variable T_{Ti+1} reached by a current (i + 1) step:

$$T_{Ti+1} = T_{Ti} + dT_{Ti},$$

$$dT_{Ti} = 3.138 – 0.083 \cdot T_{Ti},$$

where T_{Ti+1} – current body temperature of an adder, T_{Ti} – body temperature a minute ago, dT_{Ti} –body temperature increase per 1 min., 3.138 and – 0.083 – coefficients of the linear equation for heating speed.

The model shows that for the first minutes heating goes very quickly (nearly 2 °C in a minute), but as approaching maximum voluntary temperature the heating speed decreases to 0.4 °C / min. The body temperature reaches high values rather quickly, though distinct polypnea reaction was

not observed. With approach to the temperature T_T = 35 °C snakes undertake active attempts to release (at this moment the experiment was finished, no snake perished). For 18 min. heating (from 18 to 34 °C) the adder's temperature increased by 16 °C, the average speed was 0.92 °C / 1 min.

This figure seems faceless if not to compare it with a solar radiation flow, only due to which heating happens in general.

In a clear sunny summer at noon the thermal flow from the sun is F_S = 1.2 cal/cm^2 · min., at haze – about 1 (Climate of Petrozavodsk, 1982). The heat of sunlight falls on the top surface of the adder's body (its area is S ≈ 50 cm^2 (see Table 3.4.2). The part of heat is reflected, the coefficient of heat absorption by the skin (or radiating ability) in reptiles is e ≈ 0.7 (Comparative physiology of animals, 1977). The volume of energy which falls on 1 cm² of snake's body per minute is:

$Q = e \cdot S \cdot F_S = 0.7 \cdot 50 \cdot 1.2 = 42$ cal/cm^2 · min.

It is enough to warm a body of the mass W = 100 g with the thermal capacity c ≈ 0.8 cal/g in a minute only by 0.5 °C (Shmidt-Nielsen, 1982):

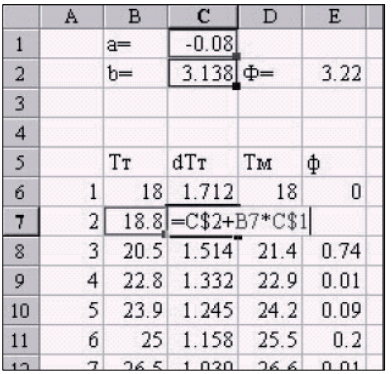
$dT = dQ / c \cdot W = 42 / (0.8 \cdot 100) = 0.5$ °C.

Actually a snake heats up with the average speed of 1 °C / min. Where the additional 0.5 °C (or 42 cal/cm^2 · min., or 0.21 J/cm^2 in a second) comes from?

Here it is worth to remember a characteristic pose of extraordinary heating: as other snakes, the adder sometimes "spreads" on the ground, exposing significantly larger part of a body surface to sun light that is 30% larger than in a normal state (see Table 3.4.2). It causes an increase of parameter S in the equation. Thus the reference angle of sun rays to the flattened body sides also changes. At that, the albedo decreases and the perceived heat flow increases. Besides, the radiation from the subjects surrounding an adder can also play a big part (we exclude endogenous thermogenesis as in the most part of our experiment an adder does not strain its muscles).

Using a well-known formula for radiation (Belanovsky, 1984, p. 75) $dQ/dt = q \cdot e \cdot S \cdot T_c^4$ ($q = 5.669 \cdot 10^{-8}$ J/sec.·m^2·K^4 – Stephane–Boltzmann constant), modified as $S = dQ/dt \cdot \sigma \cdot e \cdot S \cdot T_c^4$, it is possible to calculate the surface

area with the temperature of 20 °C (293 °K), radiating sought 42 cal/min.: $S = 0.21 / (1 \cdot 0.0000000566 \cdot 0.8 \cdot 293^4) = 0.0064$ m^2.



	A	B	C	D	E
1		a=	-0.08		
2		b=	3.138	Φ=	3.22
3					
4					
5		Tт	dTт	Tм	ϕ
6	1	18	1.712	18	0
7	2	18.8	=C$2+B7*C$1		
8	3	20.5	1.514	21.4	0.74
9	4	22.8	1.332	22.9	0.01
10	5	23.9	1.245	24.2	0.09
11	6	25	1.158	25.5	0.2
12	7	26.5	1.039	26.6	0.01

Fig. 3.3.6. Fragment of an Excel worksheet with a customized model of the dynamics of viper heating (Tт – raw data, Tм – simulated temperature of the body and its growth (dT_T),ϕ – differences of pair of values Tт and Tм, Φ – the sum of differences, a, b – model parameters)

So, the adder can receive additional 42 cal only from the area $S \approx 60$ cm^2, i.e. from the plots of a surface directly adjacent to a snake's body. It is clear that the intensity of a thermal flow will depend on the character of a surrounding micro-relief. Observations show the same – the adder warms up most often in the midst of some objects, such as dry grass, logs, stones, in relief breaks. Our illustration shows that the only way for giving a larger commonness to the considered model – is to include the temperature of relief imperfections surrounding an adder and its characteristics as well as the insolation conditions as additional variables. But to do that we have not got any data yet.

Free heating. We have very fragmentary observations on free heating of live adders in nature (Fig. 3.3.7) as it is very difficult to catch the moment when a snake comes out from its shelter. Besides, at that time it is very suspicious and does not allow using the remote thermometer. As it can be noticed on the diagram, the first 6 points correspond to a heating pro-

cess; exactly these points were used to assess the regression parameters. The power coefficient remained almost the same, as in the equation for the "forced" heating ($R^2 = 0.76$, $p = 0.053$), but the proportionality coefficient ($b = 26$) turned out significantly higher, than in the first equation ($b = 16.4$) that corresponds (perhaps, unrealistic) to a high speed of body heating – 4.5 °C/min. Such dynamics contradicts slightly with the data of forced heating, but in principle it reflects a fast growth of a snake's body temperature. These materials differ from the literary data obtained in controllable conditions (Saint-Girons, 1975).

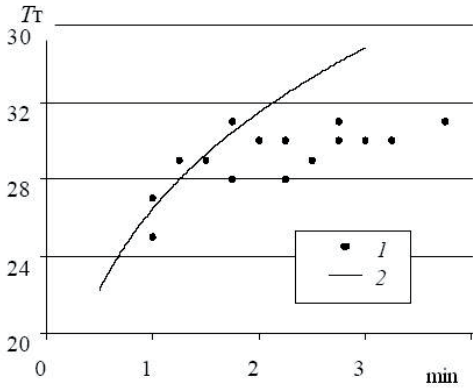


Fig. 3.3.7. Heating of a common viper body (W ≈ 100 grams) during a day in the sun after the departure of the clouds: *1* – Data *2* – power regression line, constructed on the first six points

According to the graph of daily temperature dynamics provided by the author (Fig.1, B) for the period from 8.30 to 9. 10 a.m. the equation of regression $T_T = 24.3t^{0.086}$ was calculated, where the power coefficient was very small ($a = 0.086$). The speed of body heating in an adder was less (about 0.4 °C/min.), than we observed (Fig. 3.3.8).

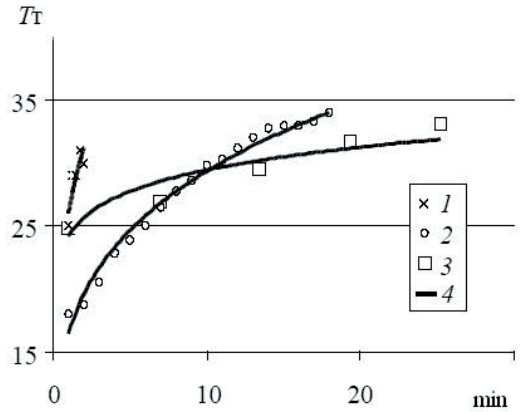


Fig. 3.3.8. The dynamics of the common viper body heating ($W \approx 100$ *g*): *1* – heating during a day in direct sunlight, *2* – immobilized specimen, *3* – heating in the morning (data from: Saint-Girons, 1975), *4* – power trend

The cause of the difference is in following: in the latter case a snake gradually heated up during morning sunrise, but it was not under direct sun rays in the afternoon as in our experiments. A low heating speed is also noticed in other snake species in the morning (Gibson, Fall, 1979). But in the summer afternoon when the sun breaks through the clouds a snake can reach the highest body temperature ("a voluntary maximum") in a few minutes.

For a heating period the change of postures is characteristic. Like other snakes, the adder sometimes "spreads" on the ground, exposing significantly larger than in a normal state part of its body surface to the sun, (a posture of extreme heating, Fig. 3.3.9; see Table 3.4.2). At the same time the temperature of external body layers exceeds the temperature of internal ones by 1–2 °C (on average 1.5°C) (Table 3.3.4). Such posture is observed rather seldom, generally early in the morning or in the afternoon after a long nasty weather, i.e. when the sun has just started heating, but not strongly heat. Having heated up for several minutes, the adder "rounds" its body, and at strong insolation – passes into one or another shelter.

Fig.3.3.9. Heating of the viper in the early morning on lichens and dry grass (position: flat)

Passage into shelter. This specific form of reptiles' behavior allows animals to avoid an overheating under direct sun rays at an excess heat flow. The occurrence of animals on a soil surface at different day time (Table 3.3.6, see Fig. 3.2.8) serves as a widespread form of studying snakes "activity" (Bozhansky, Semenov, 1978; Kosov, 1983; Ushakov, Pestov, 1983). The passage between shelters repeated in nature by some snakes many times turns into histograms by summation (in the morning there are many snakes, at noon there are only few, by the evening they appear again) (Korosov, 1988; Zuff, 1995) (see fig. 2.2.1, 3.5.14).

Timing gives more detailed picture of the course of basking (see Table 3.3.2). Before noon an adder being unable to withstand overheating crawls into a light ground-level shelter at first, and then – into an underground shelter. The snake rarely stays lying to midday. Free heating of the

adder lasts until body temperature exceeds a certain threshold level, "the maximum voluntary temperature", Tm (Cherlin, 1983). At that, the time of leaving for shelter is defined by the referent temperature depending on the status and condition of an animal. It is considered that changes of shelters allow an adder to maintain its body temperature at the highest (desirable) level during the day and at the same time to avoid overheating (Cherlin, 1984). The investigations of thermoregulatory behavior, first of all, are connected with studying these critical temperatures. To express the behavioral reaction of the adder to a thermal stimulus two characteristics are quite enough – the current body temperature of an adder T_T and the characteristic of its sensitivity to overheating – the maximum voluntary temperature Tm.

Table 3.3.6. Occurrence of adders (snakes/ha) on Kizhi at a constant route in a clear weather (June, 10 days, 220 snakes)

Parameter	Time of day, hours		
	8–9	14–15	19–20
M	15.9	1.1	3.5
S	1.7	1.1	2.9

In the environment of Excel the condition of adder's passage into a new shelter is expressed by the if/then statement IF:

IF (T_T> Tm, then ni+1 = ni + 1, otherwise ni+1 = ni):

IF body temperature becomes higher than the maximum voluntary temperature Tm,

THEN it is necessary to pass to a new cooler shelter (ni+1),

OTHERWISE it is necessary to remain (to continue basking) in old shelter (ni).

3.4. Cooling

In a shadow the heat stored up by an adder is gradually lost due to the radiation from a body surface, a heat transfer (to a substrate and air),

convection (including wind), evaporation (from mucous surfaces and from excrements) (Shmidt-Niel'sen, 1982). In this transient process studied by us neither excrements nor evaporation plays any significant part. Cooling due to a substrate is also insignificant, because for basking the adder chooses a thermoinsulating substrate (Fig. 3.4.1) – lichen, dry moss, dry grass stalks, boards, logs, but not sand, soil or open stones. For this reason the difference between the temperature of the belly and the back is usually less than 1 °C (Ganshchuk, 2000; Litvinov, Ganshchuk, 2009). Besides, the adder avoids the influence of wind, settling down in the depth shapes or plant environment. It is only occasionally possible to meet snakes that keep a thin balance on the sharp brink of overheating and overcooling, lying on the raised places blown by a wind and heated under the scorching rays of midday sun.

The main factor of adders cooling is the heat radiation from their body surface. It is due to it that 50–60% of the general heat emission occurs in warm-blooded animals, despite their thermoinsulating integuments (Белановский, 1984). In reptiles this is 80–90% (Comparative physiology, 1977).

Forced cooling. The process of cooling was studied in the experiments with immobilized previously heated live animals (W ≈ 100 g) placed in a shadow (air temperature T_V = 11 °C, the initial substrate temperature was Ts = 19 °C). During the observations snakes periodically tried to release, performing some movements characteristic for crawling. Initially the rectal temperature (T_T) coincided with temperature of integuments (Tp).

Characteristic and the quickest dynamics of a male weighing 100 g was as follows (Fig. 3.4.2). Since 34 °C the body temperature gradually decreased and reached the substrate temperature in 19 min. (the loss was 13.5 °C). Every minute heat losses varied from 2 to 0.2 °C, on average 0.72°C/min. The energetic "cost" of radiating heat losses e = 0.7 at the temperature T_T = (305K) from 1 cm² (0.0001 m²) of a body surface per minute will be 32 °C (Belanovsky, 1984): $dT = dQ/dt = e \cdot S \cdot \sigma \cdot Tc^4 = 0.7 \cdot 0.0001 \cdot 5.669 \cdot 10^{-8} \cdot 305^4 = 0.034$ J/cm^2·sec. = 0.49 cal/cm^2 · min.

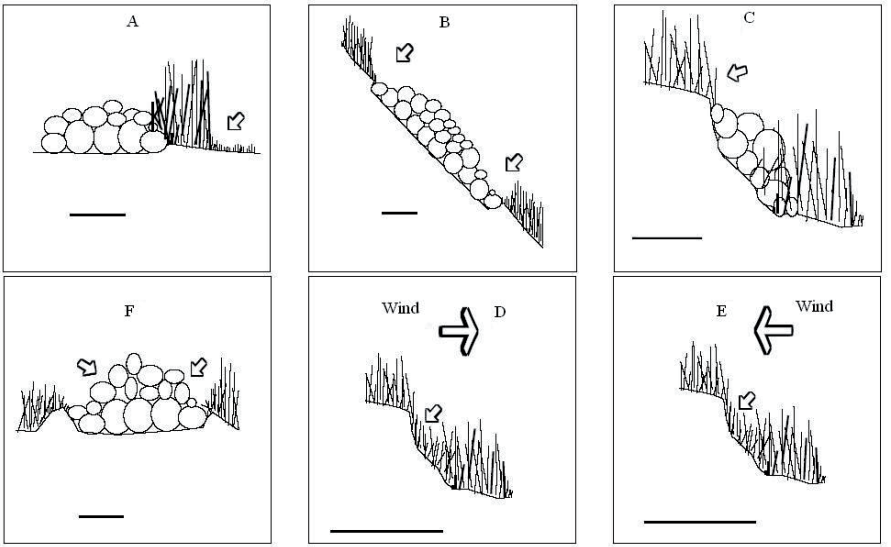


Fig. 3.4.1. Viper basking places: A – on the edge of the mowing, B – Grass slopes, C – in the shade of scattered dry grass on a clear day, F – among hot stones in the rain, D – in wind shadow, E – in the windward wind shadow

From the area of 100 cm^2 the adder will lose, respectively, 49 cal/min. At the body temperature T_T = 20 °C it would be 40 cal/min. Since the snake heating from 18 to 34 °C (by 16 °) for 18 min gained a large speed on average 0.92 °C /1 min, it is possible to conclude that the temperature hysteresis, characteristic for reptiles (Ekkert et al., 1992), is also inherent to the adder. The adequate (p = 0.0001) model description of cooling process is given by a simple imitating model (tab. 3.4.1) using the following linear equation:

$Tm_{i+1} = Tm_i - dT_i$,

$dT_i = 0.0918 \cdot Tm_i - 1.66$ (°C / 1 min.).

For example, after 4 min. of experiment the calculated body temperature is equal to Tm_4 = 29.88 °C, losses in a minute are $dT_4 = 0.0918 \cdot 31 - 1.66 = 1.16$ °C, and in 5 min. the body temperature becomes Tm_4 = 28.72 °C. It is important that the model is based on the calculation of heat loss (in

degrees) per 1 min. (dT_T) for any body temperature, i.e. in principle it expresses the law of heat losses.

Table 3.4.1. The fragment of simulation system on the sheet of Excel after adjustment of model parameters (1 min interval.)
(T_T – observed and T_m – model body temperature)

		b = 0.09184		Disparity
		a = –1.6604	$T_i = T_{i-1} - dT_{i-1}$	$\Phi = 3.78$
t, min.	T_T	dT	T_M	$(T_T - T_M)^2$
1	34	1.46	34	
2	33	1.38	32.54	0.4235
3	32	1.28	31.16	0.9581
4	31	1.16	29.88	0.9331
...	...	...	...	...
19	21	0.27	20.84	0.0654
20	21	0.22	20.57	0.0117
21	20	0.19	20.35	0.0013

It would seem that there are all reasons to apply this model for the whole temperature range of adder's dwelling. However, the linear equation turned out to be physically invalid beginning with 18 °C, because the forecast of heat loss becomes negative (fig. 3.4.3). For this reason we calculated a more complex, *power* dependence of heat losses per minute on a current body temperature:

$T_{M_{i+1}} = T_M - dT_i$,

$dT_i = 0.000039 \cdot T_{M_i}^3$ (°C / 1 min.).

The equation well describes the process of animal's cooling both in the studied thermal conditions (Fig. 3.4.4) and throughout the range of possible body temperatures of the adder (0–35 °C) without crossing the x-axis (see fig. 3.4.3). This model can serve as a baseline for the characteristic of cooling.

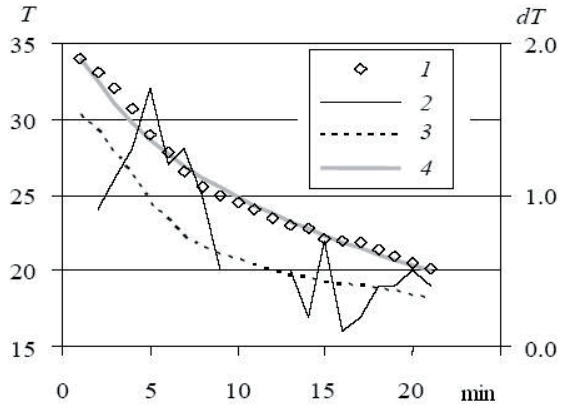


Fig. 3.4.2. Dynamics of immobilized vipers cooling: the real values of body temperature (*1*, T_T), minute losses (*2*, dT_T), heat loss, calculated by the linear model (*3*, *dT*), and the estimated body temperature (*4*, T_M)

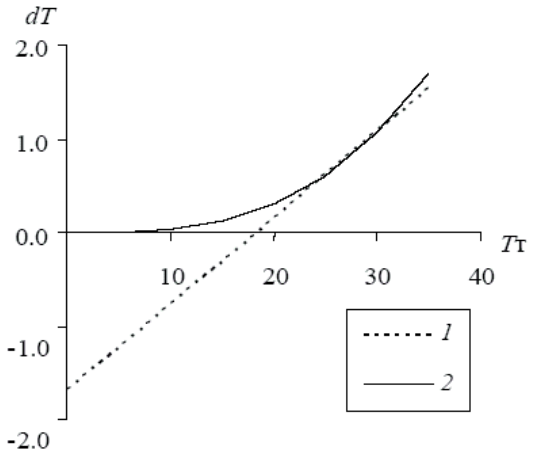


Fig. 3.4.3. Models of viper body temperature loss per 1 min. cooling: *1* – linear, *2* – power law

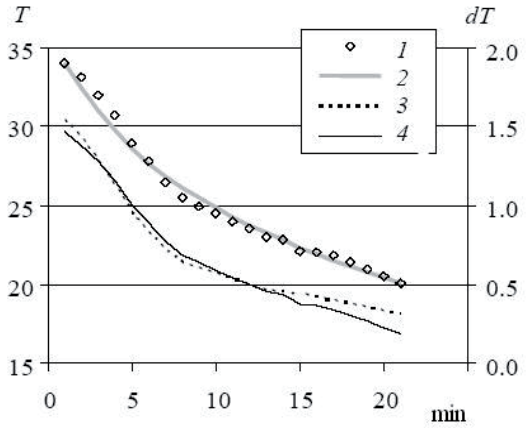


Fig. 3.4.4. Dynamics of immobilized viper cooling: real (*1*, Тт) and calculated by the model (*2*, Тм), body temperature, heat loss per minute, calculated by the linear model (*3*, dT) and by model (*4*, dT)

Free cooling. We investigated cooling of the adder's body when basking in natural conditions setting the snake in our shadow (50 cm wide). Similarly, the shadow of clouds or plants from time to time covers the snakes at daytime because of a variable cloud and movement of the sun. In cooling the adder periodically changes the posture from "arbitrarily stretched" to more compact (ring, spiral). The number of postures change could be rather high, more than 10 per hour. By the end of the observation all adders compresses in a dense tangle. If the snake felt more warmed plots nearby (20–30 cm), it passed to them. If not, the snake located in the midst of the grass went to a shelter. Observations lasted up to 50 minutes and were interrupted by the disappearance of adders. Experiments were conducted with several animals in different environmental conditions (measuring the skin temperature T_A) and on the basis of their results, an adequate dynamic simulation models were calculated. These models used different types of the dependence of heat loss per minute on the snake's body temperature (with a step of 1 min). All these descriptions relate only to the specific conditions of the experiments (given snake, environmental temperature near 11 °C) and can have another form in the other scenario. To simu-

late this process the simple linear model was calculated that evaluates the heat loss of the adder with a step of 15 s:

$T_{M_{i+1}} = T_{M_i} - dTi$,

$dTi = 0.0261 T_{Mi} - 0.486$ (°C / 15 s).

The preference was given to a linear model, because unlike the power model, in this model the equation's coefficients have a simpler interpretation.

A change of posture. In contrast to forced cooling, in these variants of natural experiment graph of the dynamics of the decrease in body temperature was flatter and saw-tooth, but not smooth. Every time when a snake changed its body posture, its skin temperature rose by 1–2 °C (Fig. 3.4.6). Apparently, at this moment partial or complete leveling of the temperature of the skin and internal parts of the adder's body $T_A \approx T_T$ took place. In other words, the role of posture changes is twofold. On one hand, a compact allocation of the body parts is believed to be aimed at the preservation of internal heat (Brodsky, 1978; Drobenkov, 1990). Diverse reptile species use different postures as a thermoregulation method: crocodiles change the tilt angle of the body position to the sun's rays in water (0–44 °C) (Fish, Cosqrove, 1987), lizards increase or decrease contact area with a heated substrate (4 to 24 variants) (Losos, 1987; Wirminghaus, 1990), snakes not only change their posture and position of the body, but also aggregate, helping to retain heat (Schiemenz, 1978; Graves, Duvall, 1987). On the other hand, as it turned out, the work of the muscles during this act leads to the distribution of heat in the body and promotes the release of a certain portion of heat into space.

The main difference in the dynamics of the body temperature in free (T_{TS}) and forced (T_{TP}) cooling in animals of similar habitus (P = 100 g) under the same environmental conditions (T_V = 11, T_C = 19 °C) can be expressed by means of linear regression analysis. For a single snake these equations were: $T_{TP} = 33.403 - 0.828 \cdot t$ and $T_{TS} = 30.673 - 0.563 \cdot t$ (Fig. 3.4.6), for the other one: $T_{TP} = 32.253 - 0.643 \cdot t$ and $T_{TS} = 33.597 - 0.174 \cdot t$.

In both cases, the regression coefficients differed reliably ($p = 0.001$), and in the second snake they were lower. Cooling of adders

changing their posture occurs really slower than those motionless. Total benefit of posture change can be estimated by the sum of temperatures accumulated during the observations and calculated in the model. In four experiments this value was surprisingly small – an average about 7 %. (4–21 %)

Observations of animals' cooling raise a number of ecological and physiological questions: what is the specific reason (starting stimulus) of posture changing; why does the adder change the position many times, but not coil up into a knot at once; what is the mechanism (starting stimulus) of moving from the shadows into the warm areas; why do adders sometimes move not to a warm place, but into a night shelter having certainly lower temperature than the adder's body?

Let us consider a single behavioral act, for example, the first coiling up the body into a ring from a free position on the litter. There are no obvious motives for this act, because it happens 1–2 min. after shading. It is possible, of course, to assume the presence of a signals normal for regulatory processes – lowering of controlled characteristic (body temperature) below a certain critical level. The feedback of thermoregulation in endothermic animals is organized in such a way (Shmidt-Niel'sen, 1982).

However, to accept this hypothesis of the one and only criteria is impossible, since similar postures are taken by adders at different body temperatures, and cooling can begin at different body temperatures (Table 3.4.2). In addition, the adder consequently changes its posture several times (more than 10), and the assumption of the existence of separate criteria for each posture seems absurd. It is thought about another signal parameter (T_K) that controls the difference between the temperature of the skin and inner body layers in the adder (T_T–T_P). (We consider only the behavioral thermal regulation, at that the problems connected with providing tissues with thermoreceptors are beyond our competence. See: Cherlin, 1989).

In cooling the adder's skin, this difference may soon exceed critical value of $T_T - \boldsymbol{T_A} > \boldsymbol{T_k}$, which starts the behavioral act. The simulation model of free cooling allows investigating this process in detail. This involves combining the previously discussed model of forced cooling and the model

of posture changes that reduce the area of the outer body surface from which the heat is radiated into space. The model of heat loss must take into account the change of posture, to adjust the radiation area, the heat loss from given area per unit time, the resulting body temperature.

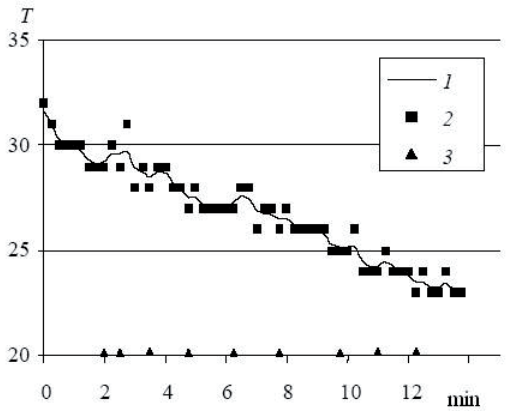


Fig. 3.4.5. The dynamics of body temperature during free cooling of the viper (*1*, Тп), moving average (*2*, Тп'), the moments of posture change (*3*, П)

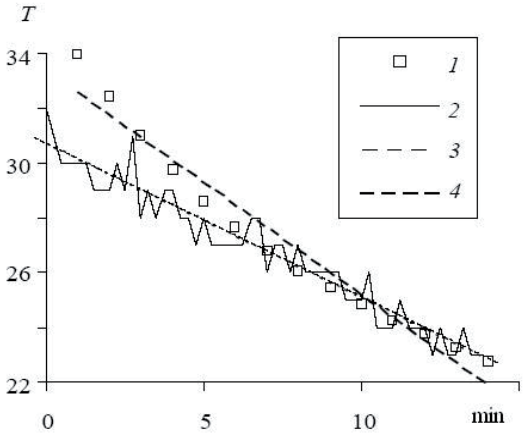


Fig. 3.4.6. Comparison of «free» (*1*, Тт)) and «forced» (*2*, Тп) cooling of viper: *3, 4* – linear trends

The model of cooling with the change of posture. To test quantitatively this idea and to study the details of the process, a simulation model of cooling was built. Let us assume that in the shade the temperature of the upper body layers in the adder (T_P) reduced in accordance with the model of free cooling in proportion to the surface area (S). A large snake can be presented as a cylinder 40 cm. long with a diameter of 1.2 cm. having a surface area equal to $S = 1.2 \cdot 3.14 \cdot 40 \approx 150$ cm^2. About a third of this area (50 cm^2) lies on the belly, which almost do not lose heat. Different postures of a snake consisting of pressing by sides and overlying of body parts on each other reduces the outer surface. Surfaces, pressed to each other inside the snake's rings as well as the belly in contact with a good heat insulator share heat to each other but do not lose it. The most compact two- and a three-storey body arrangement (tangle, knot) leaves outside less than 50% of the original body surface (Table 3.4.2).

The new values of the radiation surface were calculated at each change of posture according to the equation $S_{n+1} = k \cdot S_n$ where S_0 is the maximum possible radiation surface (100 cm^2) at a position number n = 0, S_n, S_{n+1} – body surface at the next change of posture, k – is the speed of the surface area reduction in posture changing (the proportion of the area remaining after the next posture change). The outer surface cannot be reduced less than 50 cm^2, this condition was taken into account in setting up the model.

Table 3.4.2. The outer surface of different parts of adder's body in different postures

n	Pose	The surface area, cm^2			
		lower	inner	external, S_i	body in whole
	Flat	70	0	80	150
0	Normal	50	0	100	150
1	Ring	50	25	75	150
4	Spiral	50	35	65	150
7	Tangle	30	70	50	150

In cooling the surface layers of the body (T_P) inner layers temporarily retains the original temperature (T_T). When the gap between the outer and inner temperatures reaches a critical value T_C ($T_T - T_P > T_C$), the adder changes its posture.

The change of posture was calculated as the change in its number: n = n + 1. After the posture change the temperature between the outer and inner layers levels in proportion to the ratio of the mass of the skin to that of the internal tissues. According to our data, the skin, the skeleton and somatic musculature form 50 % of body weight, all internal organs and fat – 50% (see section 5). So, we can assume that after the posture change the temperature of the skin and viscera becomes equal to the average temperature of the whole body of the adder:

$$\mathbf{T_{T+1} = T_{Pi}+1 = (T_{Ti} + T_{Pi})} / 2$$

As a result of posture change, the external body surface reduces; the temperature drop in the external layer slows down.

The total heat loss from the body surface at each time step (15 s) was estimated using the equation derived earlier: $dT_i = 0.0261T_{Mi} - 0.486$ (°C/15 s) related to the current radiation surface and to the mass of the surface layer. As its mass is two times less than the mass of the body, cooling will occur approximately two times faster: $\mathbf{dT_i = 2 \cdot S_i \cdot (0.0261 \cdot T_{Pi} - 0.486)}$ (°C / 15 s).

Since the moments of posture changes (changes of the radiation area) are discrete, it presents a known difficulty for modeling Building the model in Excel environment, we used a logical operator (= IF) both to determine the moments of the posture changes specified given by the criterion $\mathbf{T_k}$, and to start the regulation of heat exchange. The full architecture of the model based on the considered ratios and focused on a single time step 15 s, is as follows:

$n_{i+1} = n_i$

(we suppose that the posture remains the same as in the previous step),

$T_{Ti} - T_{Pi}$

(we determine the difference of temperatures between body layers),

IF ($T_{Ti} - T_{Pi} < T_k$, then $n_{i+1} = n_i + 1$, otherwise $n_{i+1} = n_i$),

(if the difference between the layers has reached a critical threshold, then the posture changes, otherwise the posture remains the same),

IF ($n_{i+1} = n_i$, then $S_{i+1} = S_i$, otherwise $S_{n+1} = k\ S_n$

(in maintaining the posture the skin surface area do not change, in changing the posture this area decreases).

IF ($n_{i+1} = n_i$, then $T_{Pi+1} = T_{Pi} - 2 \cdot S_i \cdot (0.0261 \cdot T_{Pi} - 0.486)$,

otherwise, $T_{Pi+1} = TP_{i+1} = (T + TP_i) / 2$)

(in maintaining the posture the heat loss from the outer layers is calculated, in changing the posture the temperature of the layers levels),

IF ($n_{i+1} = n_i$, then $T_{Ti+1} = T_{Ti}$, otherwise $T_{Ti+1} = T_{Pi+1} = (T_{Ti} + T_{Pi}) / 2$)

(in maintaining the posture the body temperature remains unchanged, in changing the posture, the temperature of the layers levels).

In the model (Table 3.4.3), the following starting values are set: the number of the first posture $n_0 = 0$, the initial peripheral area $S_0 = 1$, the starting body temperature ($T_T = T_P = 32$ °C), the equal masses of the outer and inner body layers. The number of a posture, the surface of radiation area (S_i), heat loss per each time step (dT_{pi}) and the temperature of body layers (T_{Ti}, T_{Pi}) are calculated. The maximum temperature deviation of adder's internal tissues from the surface body temperature (T_k) and the rate of surface area change (k) are used as parameters.

Unfortunately, for those cases when the adjusted parameter (in our case it is T_k) is included in the condition structure of the logical operator IF, the optimization program "Finding solutions" cannot change it. Therefore, to determine it 30 models with different values of T_k in the range 0.4 to 2.2 °C were built. The value of the second parameter k was chosen by the procedure "Finding solutions", which tried to nullify the difference between the calculated (T_{Pi}) and observed in nature ($^{э}T_{Pi}$) skin temperature:

$$\Phi = \Sigma\phi = \Sigma = (T_{Pi} - {}^{э}T_{Pi})^2 \rightarrow 0.$$

As additional criteria of adequacy we considered a number of posture changes during cooling (actually we watched 9 changes), as well as the final external surface area of adders (in observations – about 50–60 %).

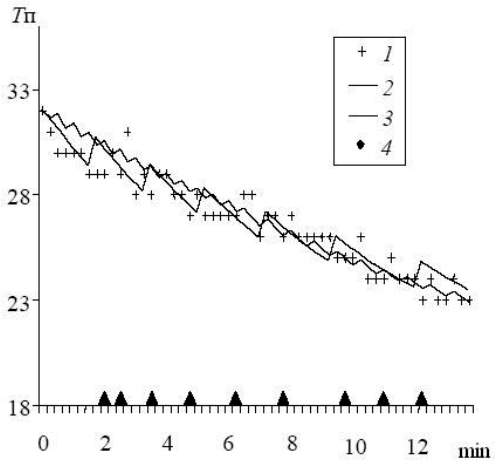
Table 3.4.3. The fragment of Excel sheet showing calculations on the model of free cooling with posture change

Observations			Simulation						
t, мин.	$^{э}T_{П}$	^{э}n	n	S_i	$T_{Т}$	$T_{К}$	$dT_{П}$	$T_{П}$	Φ
0	32	0	0	1	32	0	0.35	32	
0.3	31	0	0	1	32	0.35	0.68	31.7	0.424
0.5	30	0	0	1	32	1.03	0.64	31	0.944
0.8	30	0	0	1	32	1.67	0.61	30.3	0.107
1	30	0	1	0.96	31.2	0	0.63	31.2	1.354
1.3	30	0	1	0.96	31.2	0.63	0.6	30.5	0.285
1.5	29	0	1	0.96	31.2	1.23	0.57	29.9	0.874
1.8	29	0	1	0.96	31.2	1.8	0.54	29.4	0.134
2	29	1	2	0.93	30.3	0	0.56	30.3	1.6
…	…	…	…	…	…	…	…	…	…
12.5	24	8	9	0.72	24.9	0.67	0.21	24.2	0.036
12.8	23	9	9	0.72	24.9	0.88	0.2	24	0.965
13	24	9	9	0.72	24.9	1.08	0.19	23.8	0.048
13.3	23	9	9	0.72	24.9	1.28	0.19	23.6	0.347
13.5	23	9	9	0.72	24.9	1.46	0.18	23.4	0.163
13.8	24	9	10	0.69	24.1	0	0.2	24.1	0.018

In each of 30 cases the adequate ($p < 0.01$) simulation descriptions were received, which in general reflected body temperature falling. Despite a good degree of adequacy of the models (Fig. 3.4.7), none of them copies the initial data, the reasons are both a stochastic noise of initial observations and certain rough assumptions underlying the model descriptions (snake like a "cylinder", the equal "layers" volumes).

If "the temperature sensitivity threshold" was set low, then posture changes happened too often, if it was set high, then posture changes were less frequent than in reality (Fig. 3.4.7, 3.4.9). In addition, in the vicinity of these values (1.42–1.53 °C) the model selects such a proportion of the radiation area reduction ($k = 0.93–0.96$), at which at the end of cooling the remaining area was close to really observed ($S \approx 50–70$ %). In this case, however, the total differences in temperatures (Φ) between the model and

reality were not minimal, but other local minima (e.g., at T_k = 0.6 and T_k = 2.0) does not correspond to the value of n (the number of posture changes).



Fig, 3.4.7. Monitoring of the cooling viper temperature (*1*, $T_П$) and its simulation with the following values of the criteria of posture change: T_K = 0.4 (*2*, $T_П$) и T_K = 2.2 °C (*3*, $T_П$); *4* – moments of change in posture in reality

However, the models reproduce well the dynamics of delayed cooling and provide an opportunity to discuss the value of a regulatory parameter – the "temperature sensitivity" of adders. The differences between the models concerned the number of cycles in posture changes and the remaining outer surface area (Fig. 3.4.8). The coincidence of the number of postures with reality (9 times) was in the models with the criterion values in the range of T_k = 1.42–1.53 °C.

In general, the simulations showed that the adder changes its posture in the moment, when the outer part of the body will have the temperature 1.46 °C lower than the inner one. It is important to note that this model threshold (1.4 °C) is almost equal to the real average difference between the outer and inner temperature of adders found in nature (1.6 °C, Table 3.1.3). In other words, the adder can control its internal temperature only to

the extent to which it is able to distinguish it from the external temperature. This ability, as if it were unformed, to recognize only rather strong heat loss has, in our opinion, a clear biological meaning. Repeatedly mentioned "laziness" and inactivity of adders "in backing" is connected with a fairly wide range of temperatures, where the adder apparently did not respond to the temperature changes and tolerate their spikes regardless of changing weather conditions.

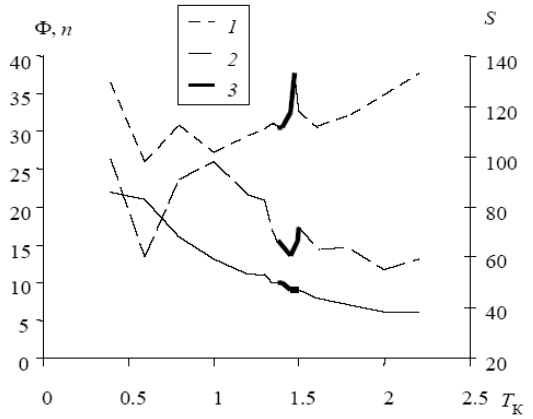


Fig. 3.4.8. . Comparison of 30 viper cooling models. The dependence of the total difference of models on reality (*1*, Φ), on the residual area of radiation after 13 min. of cooling (*2*, S) and on number of acts of changing posture (*3*, п) for different values of the shift postures criterion (horizontal axis, T_K). Thick line shows area of most probable values of T_K

If the sensitivity threshold were higher (for example, in endotherms it is about 0.4–0.8 °C (Pokrovsky et al.,1997) a snake would have to carry out thermoregulatory motions stretching on the substrate or coiling into the ring. A large temperature spread determined by the parameter T_k, evidently saves for the snake's muscular energy and makes it less noticed. Similar inertia of adder's behavior is also typical in heating (see section 3.3).

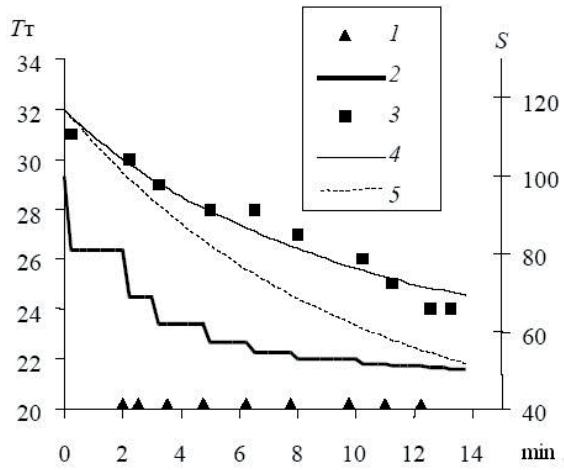


Fig. 3.4.9. Change in posture (*1*), surface area (*2*) of the body and the real (*3*) and smoothed (*4*) body temperature during free cooling of the viper and forced cooling (*5*)

Cooling under different conditions. The dynamics of adder's cooling under various temperature conditions differ significantly. Under the term "thermal conditions" (thermal environment) we mean the total heat flow from the objects surrounding snakes: clouds, air, grass, stones, litter, soil; the sun is not on this list as the animals are in the shade. We carried out 24 observations of the adders' cooling in the shade and it allowed us to define the main characteristics of the process, including calculations of the parameters of the linear (1) and power (2) cooling models (Table 3.4.4).

The calculated models not only smooth "wavy" lines of integument temperature decreasing (similar to the lines in Fig. 3.9.9), but approximate the internal body temperature decrease in adders, which is defined, as in model (3), by "splashes" of the skin temperature after posture change. To describe this dynamics both linear and power models were used:

$T_{Ti+1} = T_{Ti} - dT_{Ti}$,

$dT_{Ti} = b + a \cdot T_{Ti}$ или $dT_{Ti} = b \cdot T_{Ti}^{a}$.

In the models the coefficient **a** is the cooling rate of a body (the line slope), the coefficient **b** – the temperature with zero radiation. The accepted time step of the model is 15 s. The change in the area of the external surface is not taken into account. The parameters (a, b) of these models are calculated by optimization. All models are adequate at p = 0.01.

Table 3.4.4. Characteristics adder's cooling under different temperature conditions

Parameter		Observations on several snakes and on average on 24 ind.							
No of ind.		4	23	17	5	9	M	Min	Max
T °C soil (5 cm)		6	6	6	6	6	7	6	8
T °C air		14	8	8	9	7	9.3	7	14
T °C substrate		23	13	19	20	17	18.9	15	24
T_T °C before shading		28	29	31	33	33	31.6	28	34
T_T °C before leaving		22	21	21	28	25	25	18	29
Time of cooling, min.		13	31	16	7	8	9.7	3	44
Passing to a shelter (L) or to blazing sun (C)		C	У	У	C	C			
Linear model	a	0.045	0.013	0.047	0.113	0.057	0.027	–0.24	0.186
	b	–0.96	–0.24	–0.99	–3.12	–1.34	–0.39	–3.99	6.87
Power model	a	3.25	2.9	3.21	3.34	2.82	3.25	–7.2	3.73
	b	4E-06	7E-06	6E-06	3E-06	2E-05	4E-06	3E-06	2E+09

A family of curves that describe the model dynamics of cooling in several snakes, beginning with the same starting body temperature (Fig. 3.9.10, $T_T = 33$) is illustrative of the distinction in the speed of adders' cooling at different temperatures. The power model of heat loss was selected. As it can be seen in the diagram, the speed of free cooling varies widely depending on the temperature (T_C) of surrounding objects (rocks, logs, surface litter) and even exceeds the rate of forced cooling in spite of a posture change. The lower the background temperature, the higher is the cooling rate.

According to these data the correlation between the values T_T and T_C is $R_{TC} = 0.67$.

In fact, here we can see the combination of two processes – cooling due to the heat radiation from the skin surface and heating adders' body due to radiation gain from surrounding objects.

In that context it is important to support quantitatively the known fact: the body temperature of reptiles depends on the location of snakes among surrounding objects. One portion of heat is obtained by a snake located on the hillock; the other portion is obtained by an adder in grass thickets, on the boards, between rocks or logs (Fig. 3.4.11). While snakes bask in the sun, their body temperatures are almost the same, but as soon as the sun goes behind a cloud, the dynamics of temperature decline and the body temperatures of these snakes differ. In this regard, our descriptions (Table 3.4.4) were specially selected: only the animals that chose a similar environment – the outskirts of stone ridges – were observed. Therefore, the character of calculated curves was also similar – it was a gradual reducing the body temperature (in contrast to the stabilization of the body temperature in animals basking between protruding objects).

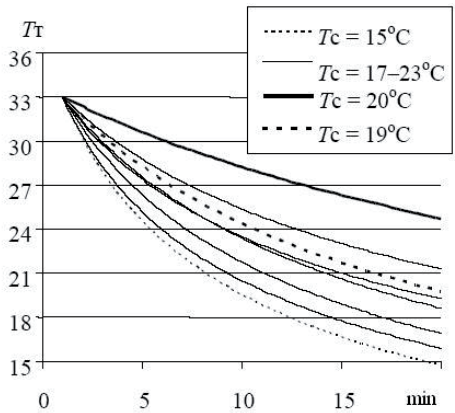


Fig. 3.4.10. Estimated decrease in body temperature during free and forced (19 ° C) cooling of vipers in the shadow of the substrate at different temperatures (Tc = 15–23 °C) (power law model)

However, in this case the body temperature of adders cannot be defined for a long time, since, experiencing severe discomfort from the declining temperatures, snakes in a few minutes pass to a lighted and heated place, or into an underground shelter; in both cases, the heat loss is lower than in the shade under the open sky. So, when occurring in the intermittent shadow of trees, they move into sun lighted areas, occasional rain in summer day make them move from the surface of the ridge and hide among the external dry and hot stones. In turn, leaving for a "hole" is associated, apparently, with the fact that a cooled snake does not "see" around itself warmer places for basking being, for example, in a trampled patch among fresh grass. For this reason, it waits warming for a long time and leaves surface at the lowest body temperature (21 °C, Table 3.4.4).

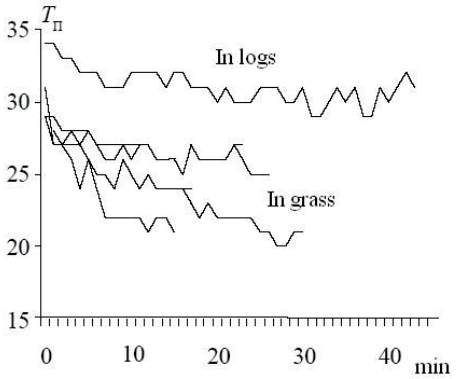


Fig. 3.4.11. The temperature of the vipers body surface ($T_П$) with the free cooling in different environments and frequent change of posture

Sometimes the behavior of snakes is beyond the scope of the proposed explanations. These are the cases, for example, when snakes stay for a long time (over 2 hours) in the open place at overcast. It may happen in the daytime "sleep", a state when snakes lapse at a comfortable diffuse insolation and hardly react to the movement of the approaching observer.

It is important to note that at the moment, when an adder leaves a shadow there is no correlation between the body temperature T_T and the tempera-

ture of soil (T_C) and air (T_V): $R_{TC} = 0.16$, $R_{TV} = –0.13$ (n = 20). In our view, it indicates the existence of individual sensitivity thresholds to ambient temperature (minimum voluntary temperature was 18, 21, 21, 28 °C), according to status (gender, age) and state (pregnancy, disease, hunger) (see section 3.4).

Generalized model of cooling. As the most general model of the ratio of individual's and environmental heat, a formula for physical heat exchange was proposed considering only a temperature difference of these objects (Shmidt-Niel'sen, 1982):

$$dQ = C \cdot (T_{body} – T_{environment}).$$

Here, the constant of heat exchange C integrates all the physiological and ethological mechanisms of thermoregulation of an individual. This version of the model consists of two equations:

$$Tri_{+1} = Tri – dTri ,$$

$$dTri = b + a \cdot (Tri – Tc) \text{ (linear)}$$

or $$dTri = b \cdot (Tri– Tc)^a \text{ (power)}.$$

Using our data, by optimization we found the common parameters of new general models for all the curves of dynamics in adder' body temperature (°C / 15 s) in different thermal environment (p = 0.0001).

The linear model has the following form:

$$dTri = –0.1973 – 0.0567 \cdot (Tri – Tc),$$

powe model:

$$dTri = 0.001786 \cdot (Tri – Tc)^{2.2765}.$$

The correlation between the real body temperature at the end of cooling and temperatures predicted by a general model was $R_{MT} = 0.60$ for linear forms, for power ones $R_{MT} = 0.64$. Quite good correspondence to the real data allows representing the theoretical curves of adders' free cooling with a different thermal background (Fig. 3.9.12) and using these equations to calculate the annual adders' thermal regime.

In general, because of the close functional relationship between all characteristics of thermal environment of ground vegetation, a more accurate model would be possible to construct.

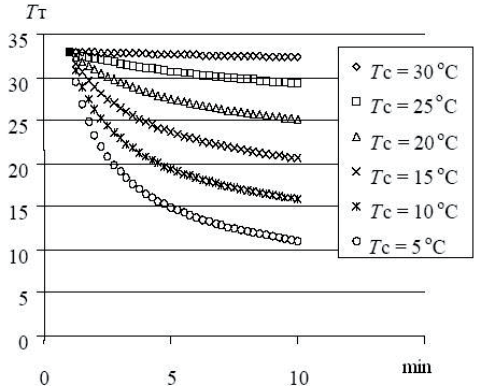


Fig. 3.4.12. Free cooling of the viper at different temperature conditions, calculated from the single model (power law option)

In any thermal environment it two processes should be included: adder's body cooling due to the heat emission from the skin surface and heating due to the radiation from surrounding objects.

There are two well-known equations, the third one is added:

$Tт_{i+1} = Tт_i - dTт_i + qTт_i$,

$dTт_i = b + a \cdot Tт_i$ or $dTт_i = b \cdot Tт_i^a$,

$qTт_i = d + c \cdot Tc_i$ or $qTт_i = d \cdot Tc_i^c$,

where $qTт_i$ – heat gain from surrounding objects, Tc_i – temperature of surrounding objects (substrate), d , c – coefficient determining the intensity of heat gain.

However, in the frame of our investigation there is no serious necessity in it, because the body temperature is determined not so much by the possibilities of the environment, but by the needs of snakes. Therefore, the presented semi-empirical calculation of the heat balance of individuals is sufficient to estimate the degree of meeting adders' needs in warmth in the environmental conditions of Karelia.

3.5. The model of thermoregulatory behavior

In the context of a goal (building a thermoregulation model), it is important to consider the entire process that can be observed in nature.

Sunrise causes heating of a substrate and soon the appearance of adders. When a snake warms up enough in the sun it "looks around" and creeps slowly from hot stones to a shade, dry grass, and other light shelters. "Looking around" plays the role of thermolocation and serves for determining the direction where there is no strong heat radiation. When appearing in a new place, the adder stays motionless for some time, analyzing its sensations. To cool down in those few seconds is impossible for the snake. But the snake finds out at once that radiation here is not as hard as in the previous location. Apparently, in this situation it also uses the skin thermoreceptors, urgently assessing the environmental comfort (Cherlin, 1989). In conditions of the hardest insolation (noon), snakes usually hide in underground night shelters. Getting in the shadow of trees, the adder after some time crawls straight to a warmer place (if it "sees" them by heat vision) or strikes heat-saving postures, and then rushes to the underground shelter (when it feels more comfortable conditions around itself or on its way no more). The shade may be associated with trees and clouds shading the sun as well as with the sunset. In the shelters (on Kizhi they are stone ridges) snakes are located near the exit, having the ability to compare the temperature conditions inside and outside the ridge. When heat abates and clouds disappear the snakes return to the warm ground surface, but nightfall makes them pass deeper into shelters.

Our description of the thermoregulatory behavior of the adder in a clear day can be represented as a series of individual passages from one shelter to another: leaving the night shelter at the time when the sun heat becomes rather intense, periodical changes of shelters with more favorable temperature conditions at the surface, leaving for the night shelter. In addition, the snake periodically changes its posture and body shape, performs vasomotor reactions that provide heat redistribution inside the body. The motivation for one or another behavior pattern depends on several key parameters. Among them: the reaction threshold (the ability to thermolocation) T_L, the parameters of the heating and cooling dT_i, maximum voluntary temperature T_M, the preferred substrate temperature T_S, the criterion of posture change T_K, the minimum voluntary temperature T_{min}.

The model structure. The purpose of modeling is to achieve maximum similarity of calculated dynamics of body temperature in adders with observations in nature, using minimum computational tricks. The body temperature in a snake can be calculated based on the heat balance equation. However, it is a difficult way. Besides, it is possible to consider the simplified calculations of a snake's body temperature in a shelter in a clear day.

On the whole, the simulation model contains the following five blocks (Fig. 3.5.1):

– field data of the temperature in different shelters (T_{C1}–T_{C5});

– calculated possible temperatures (T_{Tci}) of snakes' body in each of five shelters.

Body temperature (T_{Tc}) can be calculated by adding some mean value (dT_i), to the known temperature in different shelters (T_{Ci}). The snake's temperature can be increased by this additional value in given shelter if the sun shines. This value depends on the type of shelter and weather: $T_{Tci} = T_{Ci} + dT_i$ (Fig. 3.5.1). According to our data (see Table 3.2.2), it can be accepted that on average on the open surface $dT_1 = 8$, in the half-shade $dT_2 = 9$, in the shade $dT_3 = 6$, in underground shelters the temperature of the body is equal to that of the soil $T_{T4} = T_{C4}$, $T_{T5} = T_{C5}$;

–formulas for adder's choice of a definite type of shelter depending on the environmental conditions and temperature sensitivity of an individual. The exit from underground shelters (in the morning or after nasty weather) is defined by using a critical temperature of thermolocation T_L (Fig. 3.5.2, see section 3.3). The passage from a hot shelter (1, 2 or 3) in a more comfortable one (2, 3, or 4) is defined as the moment when in this shelter the body temperature exceeds the maximum voluntary body temperature T_M (Fig. 3.5.3, see section 3.3). Passage from external shelters into underground ones occurs when the body temperature decreases below the voluntary minimum T_{min} (fig. 3.5.4, see section 3.3);

–formulas for determining a current snake's body temperature (T_T) in the shelter chosen by it (1, 2, 3 or 4): it helps to determine possible adder's

body temperature (T_{Tci}) which was calculated for the chosen type of shelter (fig. 3.5.5), is determined.

	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T	U	V	W	X	Y
1								dT1	dT2	dT3				Тл	Тм			Тмин.						Ф	
2								8	9	6				5	30			18						1846	
3	t	Tc1	Tc2	Tc3	Tc4	Tc5		Ттс1	Ттс2	Ттс3	Ттс4	Ттс5		1 \ 4	2 \ 1	3 \ 2	4 \ 3	4 \ 123		Тт	замер Тт		Ts	ф	
4	1	10	12	10	14	11		10	12	10	14	11		4	4	4	4	4		14					
5	2	9	12	10	12	11		9	12	10	12	11		4	4	4	4	4		12					
6	3	9	11	10	12	11		=ЕСЛИ(B5<B6,(B6+H$2),B6)						4	4	4	4	4		12					
7	4	9	11	10	11	11		9	11	10	11	11		4	4	4	4	4		11					
8	5	10	11	10	11	11		18	11	10	11	11		4	4	4	4	4		11					
9	6	12	13	13	12	11		20	22	19	12	11		4	4	4	4	4		12					
10	7	16	16	16	12	11		24	25	22	12	11		4	4	4	4	4		12					
11	8	20	19	18	13	11		28	28	24	13	11		1	1	1	1	1		28	28		20		
12	9	23	21	20	13	11		31	30	26	13	11		1	2	3	3	3		26	26		34	62.2	
13	10	25	23	22	14	11		33	32	28	14	11		1	2	3	3	3		28	28		33	22.6	
14	11	29	25	24	14	11		37	34	30	14	11		1	2	3	3	3		30	30		34	14.1	
15	12	35	26	25	15	11		43	35	31	15	11		1	2	3	4	4		15			33	341	
16	13	42	27	25	15	11		50	36	31	15	11		1	2	3	4	4		15			35	383	
17	14	44	28	26	16	11		52	37	32	16	11		1	2	3	4	4		16			31	237	
18	15	43	28	26	16	11		51	37	32	16	11		1	2	3	4	4		16			34	300	
19	16	40	28	25	17	11		48	37	31	17	11		1	2	3	4	4		17			33	266	
20	17	38	27	24	17	11		=ЕСЛИ(B$24<B20,(B20+H$2),B20)						2	3	4	4			17			32	217	
21	18	33	26	23	18	11		41	35	29	18	11		1	2	3	3	3		29	29		31	2.45	
22	19	27	25	21	18	11		35	34	27	18	11		1	2	3	3	3		27	27				
23	20	24	23	19	17	11		32	32	25	17	11		1	2	3	3	3		25	25				
24	21	19	20	17	16	11		19	20	17	16	11		1	1	1	1	1		19	19				
25	22	13	18	14	15	11		13	18	14	15	11		1	1	1	1	4		15					
26	23	12	14	11	14	11		12	14	11	14	11		1	1	1	1	4		14					
27	24	11	13	11	14	12		11	13	11	14	12		1	1	1	1	4		14					
28																									

Fig. 3.5.1. Simulating of thermoregulatory behavior of viper in May in clear weather (defined criteria values Тл = 5, Тм = 30, Tmin = 18 °C) on an Excel worksheet. Selected are the formulas for calculation of the possible viper body temperature on the soil surface. They include the condition that the sun heats the surface, i.e. before 2pm the substrate temperature rises (for example, B5<B6), after 2pm does not fall lower than that at the moment of sunset at 9pm (e.g., B$24<B20). Two screenshots of Excel worksheet are combined

All the parameters of the presented model were defined beforehand; it only synthesizes this information. Model shows in detail how the adders' daily thermoregulation activity directed on the maintenance of as possible as the highest desired body temperature, is performed and it allows evaluat-

ing the daily heat equilibrium. Different components of this model can be modified by monitoring the activity of a virtual adder.

Replacing the data of the substrate temperature in different seasons, it is possible to evaluate seasonal variations of the adders' activity. Changing dT in different shelters, one can select more appropriate curves of the diurnal dynamics of body temperature. Varying the parameters T_L = 5, T_M = 30 or T_{min} = 18 °C, one can imitate the behavior of individuals with different needs in the thermal environment. As parameters monitoring the work of the model, the average body temperature of snakes obtained in nature as well as literature data on telemetry, can be used (Saint-Girons, 1975).

	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T
1								dT1	dT2	dT3				Тл	Тм			Тмин.		
2								8	9	6				5	30			18		
3	t	Tc1	Tc2	Tc3	Tc4	Tc5		Ттс1	Ттс2	Ттс3	Ттс4	Ттс5		1 \ 4	2 \ 1	3 \ 2	4 \ 3	4 \ 123		Тт
4	1	10	12	10	14	11		10	12	10	14	11		4	4	4	4	4		14
5	2	9	12	10	12	11		9	12	10	12	11		=ЕСЛИ((B5-N$2)>K5,1,N4)						12
6	3	9	11	10	12	11		9	11	10	12	11		4	4	4	4	4		12

Fig. 3.5.2.The formula for the transition of the viper from an underground shelter 4 onto the soil surface (1 \ 4), when the surface temperature exceeds the temperature of the shelter by the value of the threshold temperature sensitivity of Тл = 5 ° C

	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T
1								dT1	dT2	dT3				Тл	Тм			Тмин.		
2								8	9	6				5	30			18		
3	t	Tc1	Tc2	Tc3	Tc4	Tc5		Ттс1	Ттс2	Ттс3	Ттс4	Ттс5		1 \ 4	2 \ 1	3 \ 2	4 \ 3	4 \ 123		Тт
4	1	10	12	10	14	11		10	12	10	14	11		4	4	4	4	4		1
5	2	9	12	10	12	11		9	12	10	12	11		4	=ЕСЛИ(H5>O$2,2,N5)					1
6	3	9	11	10	12	11		9	11	10	12	11		4	4	4	4	4		1
7	4	9	11	10	11	11		9	11	10	11	11		4	4	4	4	4		1

Fig. 3.5.3. . Formulas that determine the move of the viper from the open surface (1) into the penumbra (2 \ 1) and from the penumbra (2) – into the shadow (3 \ 2), when body temperature exceeds the maximum voluntary temperature (Тм = 30 ° C)

Simulation of thermoregulation. The results of the work of simulation model with the initially accepted parameters are presented in Fig. 3.5.6. Daily dynamics of body temperature shows two peaks – at 8–11 a.m. and at 6–7 p.m.

In the clear morning first of all the soil surface (T_{C1}) is quickly heated in direct sun rays and then the snake (T_T) leaving the night shelter attracted by warmth.

Heated up to the maximum voluntary temperature (T_M =30 °C), an adder leaves the soil surface (Y_1) and passes first to a light shelter (Y_2), then into a deeper shadow (Y_3) and even into an underground (stony) shelter (Y_4). On coming out of the shelter when the day heat abated (5–6 p.m.), the adder once again shows a significant increase in body temperature, and then slowly cools down to a minimum voluntary temperature and returns into its night shelter (Y_4).

The essential point of the described dynamics is the midday "failure" of thetemperature curve associated with passing into shelters, more isolated from the sun. Not only for adders, but also for other reptile species it is shown that passing into any shelter is always associated with decreasing the body temperature below the maximum voluntary one (Morev, 1980, et al.).

The reality of this phenomenon is indicated by the fact that the average body temperature observed in reptiles in the daytime (at clear weather), is always below the maximum voluntary temperature determined in the laboratory. It had long been repeated following L.M.Kaletskaya (1953) and Chan K'yen (1967), that the adder's optimal body temperature is 25°C in males and 28°C in females (Bannikov et al., 1977) or higher – from 27 to 30 °C (Yumashev, 1995; Litvinov, 2004).

However, the laboratory and some field observations show that the maximum voluntary temperature is much higher – T_T = 34–34.5 °C (Saint-Girons, 1975, 1978; Spaendonk et al., 1990; Drobenkov, 1990; Korosov et al., 1999) (see section 3.2).

The CHOOSE function allow to select the value from a specified list of cells whose number is given by the first reference. In the example the first is the cell with reference to Q5, containing the number 4, so the

CHOOSE function returns the fourth value from the list of H5, I5, J5, K5, L5, ie, K5 = 12. This number is used by the IF function: since K5 <R $ 2 (12 <18) then value 4 is stored in the cell R5

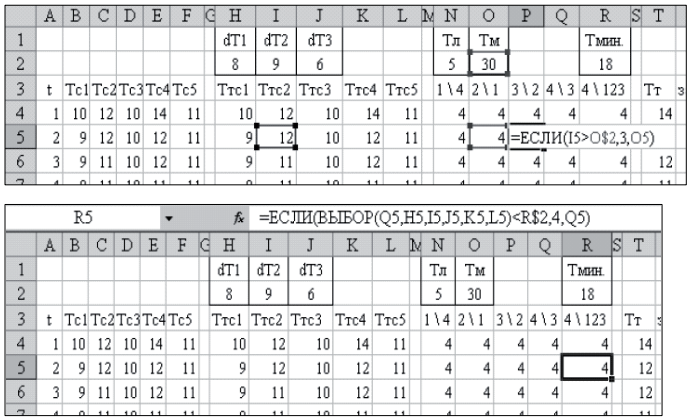


Fig. 3.5.4. The formula for the move of the viper into the underground shelter (4 / 123), if the body temperature in any outdoor shelter (1, 2, 3) falls below the minimum voluntary temperature (Tmin. = 18 ° C).

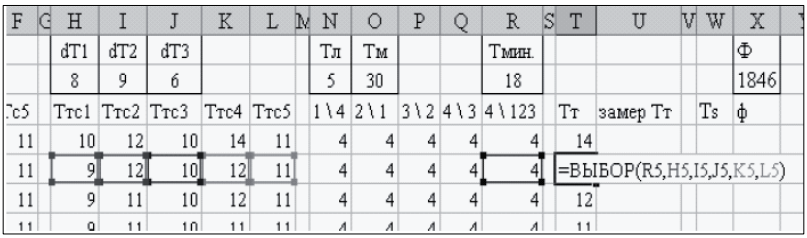


Fig. 3.5.5. Formula for determining the body temperature of a viper in the selected shelter (see comments on Fig. 3.5.4)

The paradoxical situation evolved: in light shelters adders are overheated quickly and forced to seek more shaded shelters, where there is no warmth to heat up to the "best" body temperature. An adder try to reach the maximum voluntary temperature, but almost never reaches it as it has to

wait out the period of hard insolation in shelters that cannot provide the maximum temperature. Avoiding overheating in one shelter, an adder passes into another one, where it will have the level obviously lower than maximum voluntary temperature.

It means that so-called “optimal” body temperature is a statistical phenomenon (ecological characteristic): it depends on heat condition of the shelter where the snake was captured. However, this value is lower than maximum temperature – the temperature that snakes prefer (physiological characteristic).

Such significant discrepancy (5–7 °C) between the physiological indicator and environmental one at first characterizes the thermoregulatory ability of the adder as rather undeveloped. In fact, there is a physiological requirement of an organism to be heated up to 34 °C, but it is satisfied at best only up to (100 · 28 / 35) 80 %!

No organism can withstand the constant shortage of 20% of needed resource. The theory makes search for other explanation without deficiency. Our model gives the key to this explanation. Maximum voluntary temperature (T_M), a physiological thermoregulation constant, plays the role of the target parameter to which the system strives, but almost never can reach it. According to our data, the body temperature above 30 °C is presented in less than 10% of observations (Fig. 3.5.7). Usually, a lower temperature 28–30 °C is achieved. But it is just the right "optimal" (from a physiological point of view) temperature for the adder (T_o), at which the processes of metabolism, development, growth, digestion, etc., are performed properly.

The subtlety lies in the fact that if an adder strived for the optimum body temperature 30 °C, it could reach only the average level of 22–25 °C! The simulation model clearly shows that an "attractive" temperature for the adder should be about 5 °C higher than physiologically optimal. The optimum body temperature is not the parameter determining snake’s thermoregulatory behavior; this parameter is the maximum voluntary temperature. Striving to it, in our environmental conditions the snake "automatically" reaches the optimal body temperature.

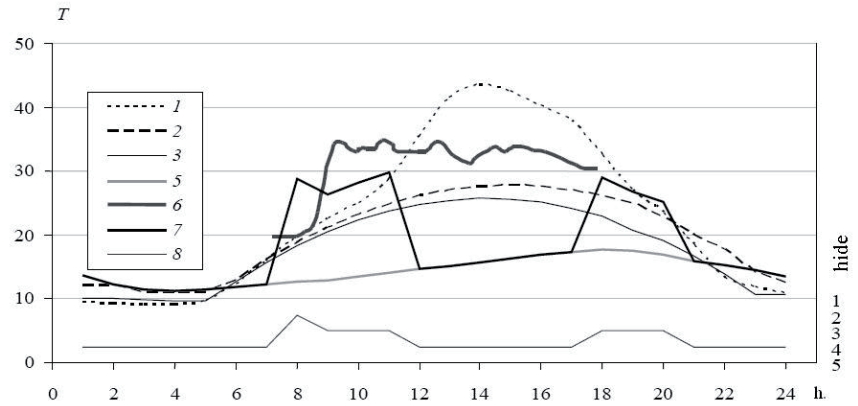


Fig. 3.5.6. . Modeling the thermoregulatory behavior of common viper (for Karelia in May): Change in shelters (bottom line, 8) with different levels of temperature (Tc_1–Tc_5, 1–5), diurnal variation of the estimated body temperature viper (Тт, 7) and observed with telemetry (Ts, 6) (Saint-Giron, 1975). The following parameters are used: $dT_1 = 8$, $dT_2 = 9$, $dT_3 = 6$, Тл = 5, Тм = 30, Tmin = 18 ° C (see Fig. 3.5.1)

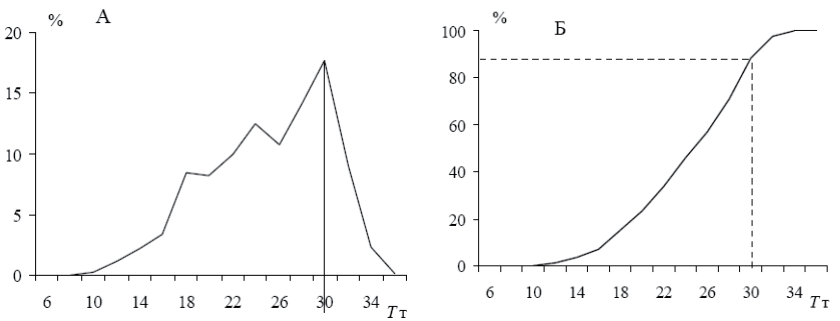


Fig. 3.5.7. Distribution (А) and cumulative (Б) of rectal body temperature of viper (n = 998) in natural conditions

Here T_M is the pseudo-aim, striving to which provides true aim – physiologically optimal body temperature. This situation is quite common

in physiology. For example, ingestion stops at "saturation", when the walls of the stomach are sufficiently strained for mechanoreceptors to inform the brain about the achievement of pseudo-aim – "the stomach is filled." The true aim (the entry of nutrients into the organism) is achieved only several hours later (Pokrovsky et al., 1997). In the case of the adder, the situation is complicated by the fact that in the attainment of real aim (optimum 30 °C) not only the organism of a snake, but also the environmental factors are involved.

However, there are no fundamental differences from the "purely physiological" processes. Similar regulation mechanisms can be expressed using double-circuit feedback scheme (Korosov, 2008).

Verification. Comparing the graphs (Fig. 3.5.6) showing the dynamics of the temperature (T_T) received in accordance with the model with the data on telemetry presented in literature (T_S, Saint-Girons, 1975), it is easy to notice their significant discrepancy. In quantitative way it can be expressed for each hour of observation as the squared difference $(T_T - T_S)^2$ (column Φ in Fig. 3.5.8, database X3:X21), and for the entire period of observations – as the sum of squares (cell X2) equal to Φ=1846.

The noticed difference between the model and reality is, probably, due to the fact, that the key parameters of thermoregulatory behavior in a living adder differ from those accepted in this version of the model. Unfortunately, when using logical operators IF in Excel environment, one cannot use the program of optimization models "Finding solutions" (see section 14), therefore the setting was carried out by sequential manual sorting out. With the selected parameters the model and empirical curves almost coincided (total deficiency decreased by two orders and was equal to Φ = 10.5) (Fig. 3.5.8, 3.5.9).

After setting the values of the "addition" dT in different shelters became slightly higher than the average, but they remained within the natural range (Table 3.2.2.). The formula for calculating the differences between the model and reality is selected. For 8am the difference between the values of body temperature was not calculated because at this time it depends not

on the thermoregulatory behavior of the viper, but on the temperature of shelters, which was higher in France than in Karelia

	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T	U	V	W	X	Y	Z
1								dT1	dT2	dT3				Тл	Тм			Тмин.						Ф		
2								12	10	8				8	35			18						10.4		
3	t	Tc1	Tc2	Tc3	Tc4	Tc5		Trc1	Trc2	Trc3	Trc4	Trc5		1 \ 4	2 \ 1	3 \ 2	4 \ 3	4 \ 123		Tт	замер Тт		Ts	ϕ		
4	1	10	12	10	14	11		10	12	10	14	11		4	4	4	4	4		14						
5	2	9	12	10	12	11		9	12	10	12	11		4	4	4	4	4		12						
6	3	9	11	10	12	11		9	11	10	12	11		4	4	4	4	4		12						
7	4	9	11	10	11	11		9	11	10	11	11		4	4	4	4	4		11						
8	5	10	11	10	11	11		22	11	10	11	11		4	4	4	4	4		11						
9	6	12	13	13	12	11		24	23	21	12	11		4	4	4	4	4		12						
10	7	16	16	16	12	11		28	26	24	12	11		4	4	4	4	4		12						
11	8	20	19	18	13	11		32	29	26	13	11		4	4	4	4	4		13			20			
12	9	23	21	20	13	11		35	31	28	13	11		1	1	1	1	1		35	35		34	0.04		
13	10	25	23	22	14	11		37	33	30	14	11		1	2	2	2	2		33	33		33	0.02		
14	11	29	25	24	14	11		41	35	32	14	11		1	2	2	2	2		35	35		34	=(T14-W14)^2		
15	12	35	26	25	15	11		47	36	33	15	11		1	2	3	3	3		33	33		33	0.12		
16	13	42	27	25	15	11		54	37	33	15	11		1	2	3	3	3		33	33		35	1.49		
17	14	44	28	26	16	11		56	38	34	16	11		1	2	3	3	3		34	34		31	6.67		
18	15	43	28	26	16	11		55	38	34	16	11		1	2	3	3	3		34	34		34	0		
19	16	40	28	25	17	11		52	38	33	17	11		1	2	3	3	3		33	33		33	0.03		
20	17	38	27	24	17	11		50	37	32	17	11		1	2	3	3	3		32	32		32	0.06		
21	18	33	26	23	18	11		45	36	31	18	11		1	2	3	3	3		31	31		31	0.19		
22	19	27	25	21	18	11		39	35	29	18	11		1	2	2	2	2		35	35					
23	20	24	23	19	17	11		36	33	27	17	11		1	2	2	2	2		33	33					
24	21	19	20	17	16	11		19	20	17	16	11		1	1	1	1	1		19	19					
25	22	13	18	14	15	11		13	18	14	15	11		1	1	1	1	4		15						
26	23	12	14	11	14	11		12	14	11	14	11		1	1	1	1	4		14						
27	24	11	13	11	14	12		11	13	11	14	12		1	1	1	1	4		14						

Fig. 3.5.8. Simulation of thermoregulatory behavior of viper in May in clear weather (defined criterial values Тл = 8, Тм = 35, Tmin = 18 °C) on an Excel worksheet .

The parameter of temperature sensitivity T_L increased up to 8 °C (against a specified range 3–6), and the maximum voluntary temperature coincided with the species limit of T_M = 35 °C. Thus, the model clearly shows how the adder manages to maintain a relatively constant body temperature – still due to the changes of shelters and passage into a deeper shadow in daytime.

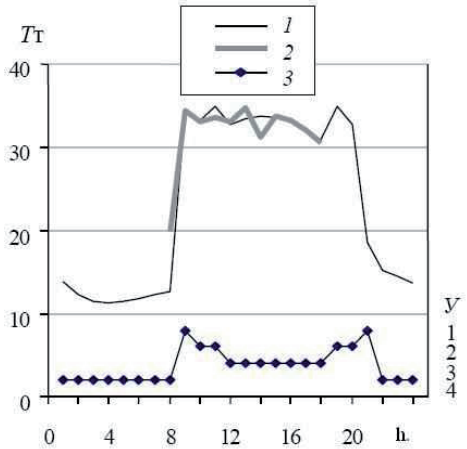


Fig. 3.5.9. Simulation of the thermoregulatory behavior of common vipers in May: a change of shelters (У, *3*) with different levels of temperature (Tc1–Tc5), diurnal variation of the estimated body temperature of a viper (Тт, *1*) and observed with telemetry (Ts, *2*) (Saint-Giron, 1975). The following parameters are used: $dT_1 = 12$, $dT_2 = 10$, $dT_3 = 8$, Тл = 8, Тм = 35, Тмин. = 18 °C (see Fig. 3.5.7)

Despite rather primitive construction, the presented model agrees well with the real dynamics of the adder's body temperature. What is pointed out that even separate fragments of the curves T_T and T_S coincide: the rapid decline in the body temperature in the first shelter (from 9 to 10 a.m.) and gradual decline in a deeper shelter in the afternoon (3–6 p.m.). The advantage of simulation modeling (in contrast to the descriptive regression analysis) is the fact that it provides the explanation for the phenomenon by means of the limited number of key parameters.

We used 6 parameters: $dT_1 = 12$, $dT_2 = 10$, $dT_3 = 8$, $T_L = 8$, Тм = 35, Tmin. = 18 °C, their values can differ depending on the status and state of the adder. The aim of the further description is to show the individual and seasonal variations of snakes' behavior that is connected with changing key thermoregulation parameters.

Thermophily. In the course of a whole life and even one season, the heat demand in adders change, Table 3.5.1. In spring during the breeding season males are more thermophilic: on the ground surface on clear days there were 72 % of males among all met adders; their average body temperature is slightly higher than in females (27.4 vs 26.7 °C). In summer, when pregnant females do not eat (from the middle of July to early September), they seem the most thermophilic. Of all the snakes met out of shelters on a clear day in August, 79 % were pregnant females (of 86 individuals). Their average body temperature is slightly higher than that of males – 27.1 vs 24.9 °C. They also have the highest recorded body temperature (Table 3.5.1). The snakes have the largest size, and therefore they are inert in heating and cooling. So, they can remain longer in the sun rays or in the shade not reaching the threshold temperatures, than individuals of other intrapopulation groups. In autumn the occurrence of females and males on the ground surface is the same (53% and 47% of encounters). Their average body temperature is not so high and the same both in cloudy and clear weather, the latter is rare and accompanied by frost, it is 19.1 (11–26) and 18.6 °C (11.5–25) (Table 3.5.1).

Table 3.5.1. The description of adder's body temperature (T_T) in different weather

Parameters	On the surface				In penumbra			
	May		September		May		September	
	females	males	females	males	females	males	females	males
M	25.2	25.4	21.1	18.2	27.3	28.5	21.3	21.9
S	4.2	3.7	4.1	4.6	3.9	4.0	5.2	4.7
Min	14.6	15	11	9	19	13	15	14
Max	34	33	34	28	33	33	34	33
n	72	184	63	35	45	62	35	29

In periodically eating animals (dry females and males) the preferred temperatures change (Table 3.2.1). Taking into account that one act "hunting – digestion" lasts 1–3 weeks (see section 9), it can be assumed that after changing an individual physiological state, the criterion maximum volun-

tary temperature changes from 34 to 21 °C, and after successful hunting – again to 34 °C (see Table 3.3.1, 3.3.2).

The change of the target parameter of physiological thermoregulation involves changes in ecological characteristics – the average daytime and average daily (24 hours) body temperature. The advantage of the presented model is that it allows calculating these values of average (and cumulated) body temperature for animals having different T_M (Fig. 3.5.10).

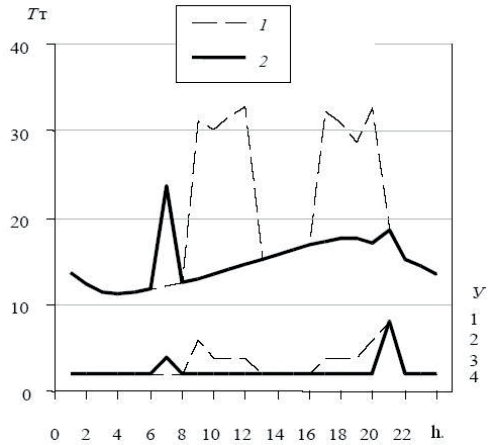


Fig. 3.5.10. Calculated dynamics of body temperature of snakes who have the maximum voluntary temperature Tм = 33 (*1*) and Tм = 25 (*2*) °C as a target criterion in May (dT_1 = 12, dT_2 = 10, dT_3 = 8, Tл = 8, Tм = 35, Tmin. = 18 °C, Fig. 3.5.8)

The application of the model with different values of T_M showed that the average body temperature in animals basking during the day on the ground surface or in light shelters is slightly less than the maximum voluntary – approximately by 2 °C (Table 3.5.2, Fig. 3.5.10). Thus, the average daily body temperature differs from voluntary maximal one by 6–13 °C (Table 3.5.1) and from the absolute maximum (35) – by 12–20 °C. It can be noted (Fig. 3.5.11), that while the attractive temperature T_M reduces a little, the average daily temperature decreases rather sharply, because, in general,

the length of snakes' staying on the ground surface is reduced, that is, in daytime they are forced to hide in underground shelters.

Seasonal dynamics. According to our data, the critical maximum voluntary temperature T_M depending on the condition of an individual as a whole does not change during the warm period (early May – early September). The similar maximum body temperature T_T = 34 °C was recorded by us in all summer months (see Fig. 3.2.7, 3.2.15, 3.2.16). At that, the average body temperature of snakes, found in nature, changes approximately from 25 to 20 °C following seasonal decline in solar energy flow and when the weather changes to cloudy (Table 3.5.1).

Table 3.5.2. The dependence of calculated average of daytime and daily (24 hours) body temperature on maximal voluntary temperature (T_M) in May (see Fig. 3.5.8)

T_M	Average T_T	
35	33	23
33	31.3	19.6
31	29.2	17.9
29	28.1	16.6
27	25.7	15.5
25	23.6	14.9
23	22	14.8
21	20.6	14.8

It is worth noting that even in late summer and autumn when the weather is clear the average daytime and daily (24 hours) adders' body temperatures are lower than in early summer, due to reduced time and intensity of sunshine. Our model gives the opportunity to investigate this problem (Fig. 3.5.12).

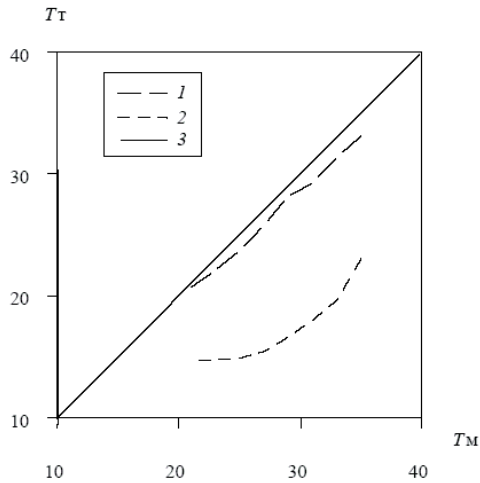


Fig. 3.5.11. The dependence of the calculated average body temperature during day (*1*, Тт) and during 24 hours (*2*, Тт) on the maximum voluntary temperature (Тм) in May, *3* – isotherm

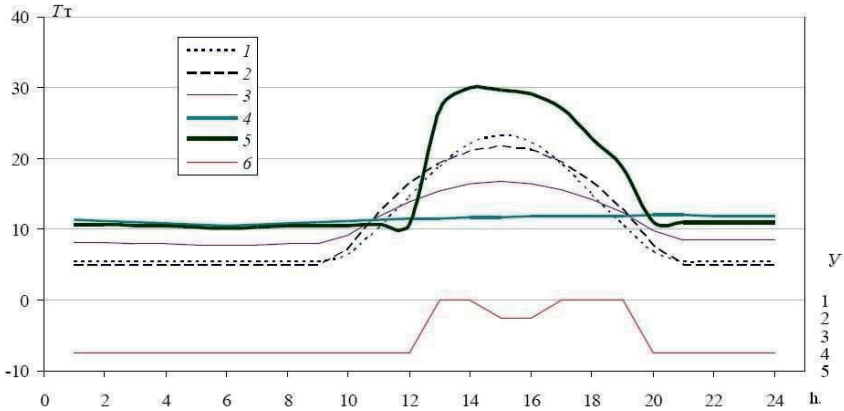


Fig 3.5.12. Simulation of the thermoregulatory behavior of common vipers: change of shelters (lower dashed line) with different levels of temperature (Tc_1–Tc_5) (in Karelia in September), the calculated diurnal variation of a viper body temperature(Тт): $dT_1 = 12$, $dT_2 = 10$, $dT_3 = 8$, Тл = 5, Тм = 33, Tmin. = 18 ° C (see Fig. 3.5.1)

For example, in clear weather in early September the night temperature falls to 0 – 5 °C (on the island frosts are rare) and the sun begins to warm the ground surface up to the acceptable temperatures for adders only at noon (Fig. 3.5.13).

At that time, individuals of all age groups – from newborns to adult males, appear on the surface. In one square meter we once counted 40 snakes. At 2–4 p.m. the bright sun makes the snakes pass into light shelters, but at 5 p.m. they appear on the surface again and can bask in the rays of the declining sun up to 10 p.m. (only on the slopes with western exposure). At that the average daytime body temperature (9–20 o'clock) with the same voluntary maximum one is always below it and depends on the season: in May – June – 25–28, in September – 18–22 °C. A similar body temperature dynamics, associated with seasonal insolation conditions, has been noted for other snake species (Fukada, 1985).

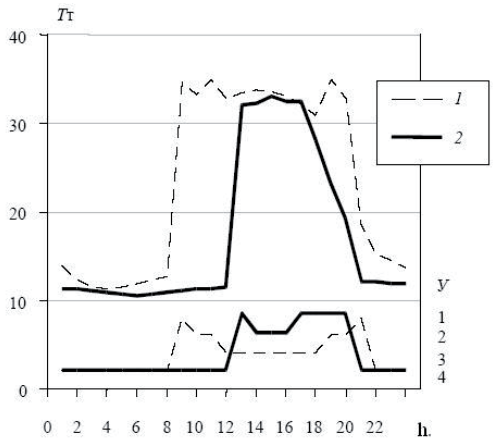


Fig. 3.5.13. Modeling the movements of the viper between shelters ($У_1$–$У_4$) while basking in May (1) and September (2) and the corresponding estimated daily dynamics of body temperature (Тт); $dT_1 = 12$, $dT_2 = 10$, $dT_3 = 8$, Тл = 8, Тм = 35, Тмин. = 18 °C

The behavior of adders described in the model is modified by specific habitat conditions, primarily by the slope exposure (Kizhi is the island elongated almost exactly from the North to the South). Different incidence angles of sun rays determine the difference in the heat providing of different habitats. In the morning the advantage in insolation have the snakes living on the eastern shore, and in the evening – on the western one. For this reason in nature active snakes are met before and after the indicated time limits (Fig. 3.5.14). Nevertheless, the presented model explains the factors of seasonal changes in adders' daily activity on the strict quantitative basis.

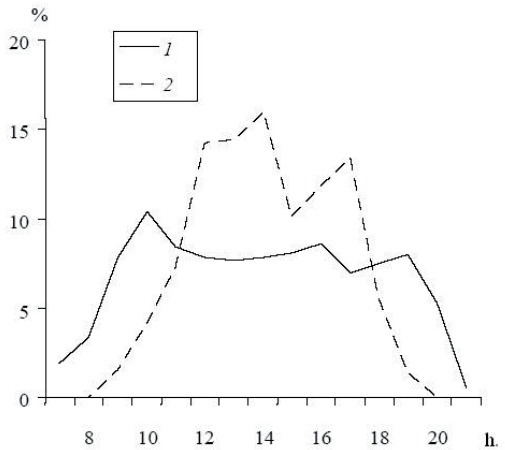


Fig. 3.5.14. Proportion of vipers (%) encountered in different times of day in May (1580 ind.) (*1*) and September (575 ind.) (*2*)

The model's stability. The study of the model's functioning depending on the variations of the key parameters is considered to be a necessary stage of modeling (Korosov, 2002). However, this is not a routine procedure. If the model's parameters have the clear biological meaning (as in our model), when the possible range of their variation is determined it is known how the mechanism of this biological phenomenon is realized. As an initial version let us take the model presented in Fig. 3.5.7 and 3.5.8 with the parameters $dT_1 = 12$, $dT_2 = 10$, $dT_3 = 8$, $T_L = 8$, $T_M = 35$, Tmin. = 18 °C. The

reaction to the change of the key parameter T_M is shown in Fig. 3.5.11 and Table 3.5.2. The studied range of preferred temperatures 21–34 °C corresponds to that actually observed (Table 3.2.2). As a whole the model is very sensitive to the changes in T_M.

According to the obtained lines, at the maximum preferred body temperature T_M = 35 °C the average daily temperature should be near 33 °C. In the conditions of Karelia this situation is extremely rare, but, according to the published data on telemetry in sunny France (Saint-Girons, 1975), the average daily temperature in adders on the ground surface is exactly equal just to this value, 33.2 °C.

The temperature sensitivity threshold T_L (the ability of thermolocation) influences insignificantly both the time when snakes appear on the ground surface and the body temperature dynamics as well as the average daily T_T.

Its minimum value cannot be lower than 2–3 °C, otherwise one would have to say about highly developed abilities of adders to thermolocation (which is not marked by anyone).

However, this threshold cannot be higher than 8 °C. Just this limit value was revealed in the experiment (see section 3.1). For normal snakes, apparently, the value T_L = 5–6 °C is typical. On a clear summer day, the morning hourly increase in the open substrate temperature is not less than 5 °C (Fig. 3.5.6) and it becomes higher than the temperature in the snakes' shelters very quickly, stimulating snake's activity. For this reason when the parameter T_L is varied, the appearance of snakes on the surface will be either one hour earlier (low T_L values) or one hour later (high T_L values). This slight difference in the model's dynamics at various T_L causes the difference between the mean estimates of daily temperature only in tenths of a degree that is irrelevant.

The variation of the minimum voluntary temperature T_{min} has a similar insignificant influence on the dynamics of the calculated body temperature of the adder. According to our observations, the body temperature range which the adder reaches in cooling is 18–21 °C (tab. 3.3.4), after that it passes into to an underground shelter. These values received by us in

field experiments concern large and healthy individuals having the maximum voluntary temperatures, probably, not less than $T_M = 30$ °C. In other intrapopulational groups these values can differ significantly. In particular, several times we found out snakes on the surface in a ball pose in the late evening after sunset and in cloudy weather with the body temperature up to 8 °C. All similar individuals seemed exhausted due to some internal disease, or strongly traumatized. Besides, we also have met some active healthy individuals at night (23, 24 and 3 o'clock) having the body temperature up to 12 °C, they, probably, went hunting.

Since our model considers only daytime conditions a range of minimum voluntary temperatures at basking was taken as 18–21 °C. The model responds to the substitution of the values of these parameters so that a model snake leaves for a model shelter either an hour earlier (at $T_{min.} = 21$ °C), or one hour later ($T_{min.} = 8$ °C). These variations have a negligible effect on the estimates of average daily body temperature.

The modification of "additions" dT, which the snake has got in different conditions, may change slightly the curve of the body temperature dynamics, but influences slightly the average T_T (Table 3.5.3, Fig. 3.5.15). If in the third type shelters (shadow) adders can heat up strongly ($dT_3 > 8$, variants 1–3), then in the daytime they have to move into underground shelters and their body temperature reduces significantly. The average daytime body temperature on the surface is 28–30 °C, and the average daily body temperature (24 hours) is less than 21 °C (Table 3.5.3). At other parameters (in moderate heating in the shade and half-shade, variants 4–9), the average daytime values vary within the range of 2.5 °C (27.8–30.3), and the average daily (24 hours) values are within the range of 1 °C (22–23).

These cases correspond to the situations observed in nature (Table 3.2.2), and the only difference was that in the natural habitats of the adder the set of shelters was more variable, and gradations of temperatures between them were smoother. However, as it was shown in sections 3.2 and 3.3, the adder is rather patient, and it withstands body temperature fluctuations of 10 °C without changing its location. When unfavorable situation

still forces the adder to change its shelter, its body temperature can jump (in 10–15 min., see graph of telemetry data, Fig. 3.5.6), i.e. here our model is quite adequate to reality.

Table 3.5.3. The average model daytime body temperature T_T in adder, calculated at different values of parameters dT_1, dT_2, dT_3 (T_L = 8, T_M = 33, $T_{min.}$ = 18 °C)

Variants	dT_1	dT_2	dT_3	Average	
				daytime	daily (24 hours)
1	16	10	12	28.8	17.2
2	14	12	10	29.3	18.5
3	12	10	8	30.1	20.5
4	12	6	4	29.1	22.3
5	10	8	6	30.3	23.0
6	8	6	4	29.3	22.4
7	8	10	4	27.8	21.5
8	8	6	2	28.6	22.0
9	6	4	2	29.2	22.4

In general it can be concluded that the variation of the parameter *dT* determining the level of adders' heating in different shelters has a negligible impact on the model functioning. The only key parameter determining the "behavior" of the model in nature is the maximum voluntary temperature T_M, which not only means the border between physiological potency (and demands) of the species, but also sets the ultimate aim of basking. The change in T_M leads to the change both in snake's behavior and in the dynamics of its body temperature. There is every reason to believe that individuals of different status and state can be distinguished from each other only at the levels of this threshold T_M. Other parameters play a clearly subordinate role. The voluntary minimum temperature T_{min}, obviously, also varies in different individuals, but it has little effect on the daily heat balance, since it is in the region of low temperatures. The thermolocation threshold T_L apparently is almost the same in all groups of animals, although this problem requires serious additional study. Of course, snakes of

different size differ significantly by heating rate – the smaller the snake, the faster it heats up (the less inertial is the body temperature dynamics). However, heating is a very rapid process and the indicated distinction is expressed only in the fact that smaller animals pass earlier into shelters from the burning sun. In our model, focused on 1–hour intervals, not these differences, but only a general reaction to overheating (the choice of different shelters) is reflected

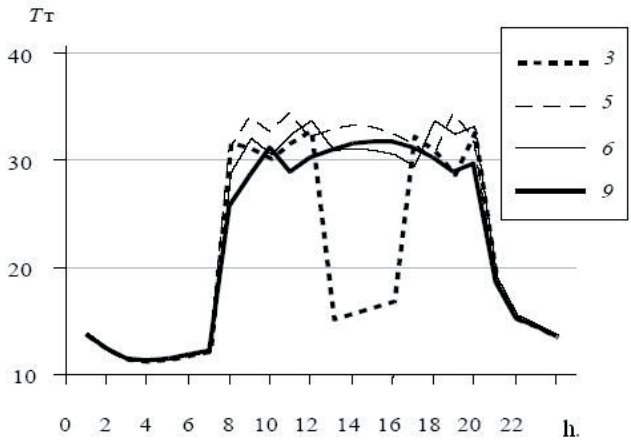


Fig. 3.5.15. Calculated dynamics of body temperature of snakes with the parameters Тл = 8, Тм = 33, Tmin. = 18 ° C and with different versions of "increment" dT (°C): *3* – $dT_1 = 12$, $dT_2 = 10$, $dT_3 = 8$; *5* – $dT_1 = 10$, $dT_2 = 8$, $dT_3 = 6$; *6* – $dT_1 = 8$, $dT_2 = 6$, $dT_3 = 4$; *9* – $dT_1 = 6$, $dT_2 = 4$, $dT_3 = 2$ (see Table 3.5.3)

Cloudy weather. It is more difficult to build the model of thermoregulatory behavior of the adder in variable and cloudy weather than in clear one. In the shadow of the dense and light clouds not only animals, but also the surrounding objects (stones, grass) cools down. The dynamics of this process is determined by air and soil temperature, forced convection, evaporation, clouds' size, wind speed, i.e. by the factors, which numerical characteristics are practically impossible to determine. An apparent decrease in temperature can be monitored only when the weather changes abruptly

(Fig. 3.2.12), in variable weather the adder's body temperature differs widely (Fig. 3.2.11).

The simulation model of this process would require the input of too many hidden variables, thus losing connection with reality. For this reason, we refused *to simulate* the dynamics of the adder's body temperature in variable weather, and favour the path of building reconstruction based on meteorological statistic data for Petrozavodsk, located at the same latitude as the island of Kizhi, but 60 km west (Table 3.5.4).

Table 3.5.4. Characteristics of duration and intensity of sunshine in Petrozavodsk (cal / $cm^2 \cdot$min.) (Reference book on climate in the USSR, 1981, p. 36, 39, 49, 75)

Parameter	Month					In average
	May	June	July	August	September	
Day duration	17.3	19.4	18.5	16.1	13.1	16.7
Sunshine (h./month)	249	300	294	219	128	238
Sunshine (h./day)	8.3	10	9.8	7.3	4.3	7.9
Periods of brightening, %	48	52	53	45	33	47
Clear weather (days/month)	5	4	4	4	2	4
Semi-clear weather (days/month)	8	7	5	6	6	6
Cloudy weather (days/month)	20	17	18	21	21	20
Direct radiation in fine weather on the 15th in 12.30	1.25	1.30	1.24	1.20	1.18	1.24
Radiation in medium clouds on the 15^{th} in 12.30	0.56	0.52	0.53	0.48	0.34	0.49

Clear weather differs from the cloudy one in that sun's rays fall on the earth surface for a limited number of hours per day, but not a whole day. Because most of the time the weather in Petrozavodsk is "cloudy with clearings", in May and September according to long-term observations, average sunshine duration is 7.9 hours, or 47 % of the total day length (Table 3.5.4).

It means that in medium variable clouds less than half of sunlight energy reaches the earth, or considering the incidence angle of sun rays – 39 % (0.49 against 1.24 cal / $cm^2 \cdot$min.).

The same figures have been obtained by satellite; for middle clouds the brightness of clouds was 30–50 % (group 3) and 50–90 % (group 4) (Reinol'ds, Khenderson-Sellers, 1984). In other words, in cloudy weather adders may bask on average only half a day, getting about 40 (10–70) % of a sunny day's energy. However, it is impossible to confine ourselves on one figure, because the summer weather in Karelia has very many gradations. Using the table of repeatability of continuous sunshine (Reference book on climate in the USSR, 1966, p. 75), we calculated the radiation loss for three grades of cloudiness (Table 3.5.5).

The obtained table generally corresponds to the data presented in Table 3.5.4, but the "overcast" category is divided into two groups. It is evident that in overcast weather about 12 % of the sunlight fall on the earth, in cloudy weather – 39, in semi-clear weather – 83, in clear weather – 88 %. The second feature of our generalized modeling is to refuse completely to calculate the adders' body temperature properly in basking, but to operate with the energy balance units of the individual, which differ under various weather conditions. In this approach, the energy characteristic of snakes it clear weather in June (when the sun allows them to maintain the maximum level of metabolism) is accepted as the "full" metabolism. In other months and weather conditions the extent of using the sun is calculated in proportion to the radiation losses presented in Table 3.5.4–3.5.5.

During a 24-hour period the adder is "guaranteed" the temperature equal to the soil temperature (in shelter), the rest it gets due to radiation from the sun and surrounding objects. Let us express the body temperature of a particular snake as the sum of soil temperature (T_S) and the temperature that the snake additionally get in specific weather conditions due to insolation ($dT_т = T_T - T_P$). Clouds reduce the intensity of solar radiation, and this addition becomes less (Table 3.5.5). Thus, in variable cloud the average losses are small, about 17 % (share of available radiation is pQ = 0.83),

but in cloudy weather 88% of the solar heat does not reach the earth surface, hence the snakes' body surface (pQ = 0.12).

To determine the temperature of the snake's body in any shelter in cloudy weather, a specified share of losses (pQ) should be subtracted from the temperature that a snake could get additionally due to the sunlight in clear weather ($dT_т$):

$dT_т = (T_T – T_A) \cdot pQ$.

For example, if the soil temperature is T_S = 10 °C in clear weather, a snake can heat up to 30 °C ($dT_т$ = 20), in cloudy weather the average increase is only 12 % ($dT_т = 20 \cdot 0.12 = 2$ °C) and adders' body temperature can be only $T_{T'} = 10 + 2 = 12$°C.

Based on the new calculations of the trajectories of the body temperature it is possible to determine the adders' metabolism rate under different weather conditions (Fig.5.16). For example, in the model the influence of cloudy weather is the reduction of the body temperature from the available temperature of 37 °C to 23 °C: $T_{тс1'} = {}_{TC4} + (T_{тс1} – T_{C4}) \cdot pQ = 4\ (37 – 14) \cdot 0.39 = 23$. The change of the "addition" affects the adder's behavior, the daily body temperature dynamics, and general metabolism (Fig. 3.5.17) (see section 6).

Table 3.5.5. Types of weather in Karelia in summer and radiation loss

Parameter		Overcast	Cloudy	Variable	Clear
Duration of sunshine, h/day	on average	2	6.5	14	17
	range	(0–4)	(5–11)	(12–15)	(16–19)
Radiation loss (cloudy), %		88	61	17	2
Duration (day/month)		10	13	4	3

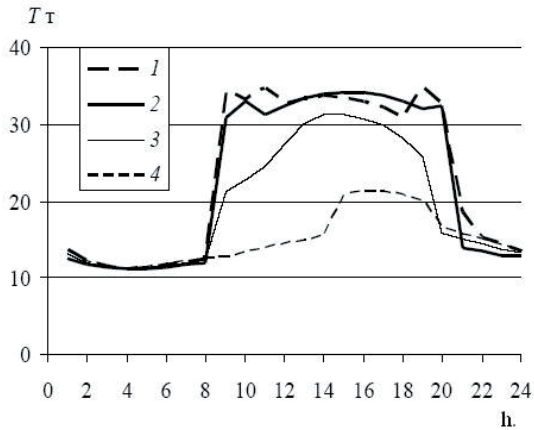


Fig. 3.5.16. Calculated dynamics of body temperature of a viper at different conditions: *1* – clear, *2* – partly cloudy, *3* – cloudy, *4* – overcast

The whole complex of thermoregulatory reactions of the adder can be explained by using a very limited number of physiological parameters estimated by us. The animal controls the heat flow from nearby objects (recognizing the temperature difference of 5–8 °C at the distance of 10–20 cm), the maximum temperature of its own body (after achieving this temperature it changes the shelter; the values differ in different animals from 28 to 35 °C), the difference between the temperature of inner parts of the body and integuments (threshold of 1.4 °C causes the change of posture to more energy-saving one), the minimum voluntary body temperature (leaving shelter is caused by the reduction to 12–18 °C). Another parameter remains out of our study (due to the complexity of registration of this flow) it is the heat flow falling on the animal's dorsal side from the sun or coming to the ventral side from the substrate, they both determine the adder's choosing another basking place. Based on the experiments on thermopreferendum, it can be assumed that the skin temperature may exceed the voluntary maximum by 3 °C. The variation of thermoregulation parameters is connected with season, sex, pregnancy, age, time of foraging, and the degree of animals' adaptation to the temperature conditions for the

previous 10 days. During the breeding season adders are more thermophilic, large and pregnant animals are more tolerant to high temperatures, during the process of digestion preferred temperatures decrease.

	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T	U	V	W	X	Y	Z	AA
1								dT1	dT2	dT3				dQ=	0.39					Tл	Tм			Tмин.			
2								12	10	8										8	35			18			
3	t	Tc1	Tc2	Tc3	Tc4	Tc5		Tтс1	Tтс2	Tтс3	Tтс4	Tтс5		Tтс1	Tтс2	Tтс3	Tтс4	Tтс5		1\4	2\1	3\2	4\3	4\123		T т	Дж/экз./ч.
4	1	10	12	10	14	11		10	12	10	14	11		**10**	**12**	**10**	**12**	**11**		4	4	4	4	4		12	77
5	2	9	12	10	12	11		9	12	10	12	11		**9**	**12**	**10**	**12**	**11**		4	4	4	4	4		12	73
6	3	9	11	10	12	11		9	11	10	12	11		**9**	**21**	**16**	**11**	**11**		4	4	4	4	4		11	71
7	4	9	11	10	11	11		9	11	10	11	11		**21**	**21**	**16**	**11**	**11**		4	4	4	4	4		11	70
8	5	10	11	10	11	11		22	11	10	11	11		**22**	**21**	**16**	**11**	**11**		4	4	4	4	4		11	70
9	6	12	13	13	12	11		24	23	21	12	11		**24**	**23**	**19**	**11**	**11**		4	4	4	4	4		11	71
10	7	16	16	16	12	11		28	26	24	12	11		**18**	**18**	**16**	**12**	**11**		4	4	4	4	4		12	75
11	8	20	19	18	13	11		32	29	26	13	11		**20**	**19**	**17**	**12**	**11**		4	4	4	4	4		12	76
12	9	23	21	20	13	11		35	31	28	13	11		**21**	**20**	**18**	**13**	**11**		1	1	1	1	1		21	149
13	10	25	23	22	14	11		**37**	33	30	14	11		**23**	**21**	**19**	**13**	**11**		1	1	1	1	1		23	166
14	11	29	25	24	14	11		41	35	32	14	11		**25**	**22**	**20**	**13**	**11**		1	1	1	1	1		25	189
15	12	35	26	25	15	11		47	36	33	15	11		**27**	**23**	**21**	**14**	**11**		1	1	1	1	1		27	235
16	13	42	27	25	15	11		54	37	33	15	11		**30**	**24**	**22**	**14**	**11**		1	1	1	1	1		30	288
17	14	44	28	26	16	11		56	38	34	16	11		**31**	**24**	**22**	**15**	**11**		1	1	1	1	1		31	313
18	15	43	28	26	16	11		55	38	34	16	11		**31**	**25**	**22**	**15**	**11**		1	1	1	1	1		31	313
19	16	40	28	25	17	11		52	38	33	17	11		**31**	**25**	**23**	**16**	**11**		1	1	1	1	1		31	302
20	17	38	27	24	17	11		50	37	32	17	11		**30**	**25**	**22**	**16**	**11**		1	1	1	1	1		30	285
21	18	33	26	23	18	11		45	36	31	18	11		**28**	**25**	**22**	**16**	**11**		1	1	1	1	1		28	249
22	19	27	25	21	18	11		39	35	29	18	11		**26**	**24**	**21**	**16**	**11**		1	1	1	1	1		26	210
23	20	24	23	19	17	11		36	33	27	17	11		**24**	**23**	**20**	**16**	**11**		4	4	4	4	4		16	99
24	21	19	20	17	16	11		19	20	17	16	11		**17**	**18**	**16**	**15**	**11**		4	4	4	4	4		15	93
25	22	13	18	14	15	11		13	18	14	15	11		**13**	**18**	**14**	**13**	**11**		4	4	4	4	4		13	81
26	23	12	14	11	14	11		12	14	11	14	11		**12**	**14**	**11**	**13**	**11**		4	4	4	4	4		13	79
27	24	11	13	11	14	12		11	13	11	14	12		**11**	**13**	**11**	**13**	**12**		4	4	4	4	4		13	79

Fig. 3.5.17. . The dynamics of body temperature of a common viper (W = 120 g) in cloudy weather (dQ = 0.39) in the simulation with the same parameters as in Table 3.5.7 (values of increment are indicated), and the values of total metabolic rate, calculated by the formula $0.663 \cdot (W_Г^{0.8}) \cdot e^{0.0744 \cdot Т_Т}$ °C (see Section 6.1)

At forced acclimation adders are disposed to alternative conditions: after hot weather they tend to hide in shadows, after a period of bad weather they prefer to creep out on the sunlight. Changeable summer weather stimulates active basking on rare fine days that causes talks about "snake" years. Adult adders in Karelia behave as active heliotherms, young individuals mainly using heat litter – as geotherm.

Chapter 4

Breeding

In the adder the ability to reproduction is formed up to 4–5 years (Chan-K'yen, 1967). The ripening of sexual products is linked to the attainment of a certain body mass and is provided by active hunting in the summer for one or two-three previous years (Viitanen, 1967; Biella, 1979; Edelstam, 1989). To initiate spermatogenesis wintering is necessary, i.e. a "cold pause" – the hibernation that in captivity may be short, 10–20 days (Igolkina, 1989). The final maturation of the males' sexual products (appearance of spermatozoa) is connected with the decline of the thyroid hormone level in the blood on shedding (Andren, 1975). Mating takes place in 1–2 weeks after emergence from hibernation (Bannikov et al., 1977). One female may be fertilized by several males (Still et al., 1986). The mating season is accompanied by the fights in which males spend a lot of energy and loose up to 8 % of body weight (Sokolov, 1989; Drobenkov; 2003). Ovulation and fertilization happens in about 3 months after coupling (Vainio, 1931; Nilson, 1981; Naulleau, 1986). Embryogenesis lasts about 3 months and ends with the birth of 2–8 live snakes with approximately equal proportion of males and females (Bannikov et al., 1977). Usually the larger the female, the more embryos it contains (Volsøe, 1944; Biella, 1979; Saint-Girons, Naulleaut, 1981; Iverson, 1987). After birth, females lose up to 50 % of body weight (Biella, 1979; Saint-Girons, Naulleau, 1981; Capula et al., 1992), because during the summer they almost do not eat (Schiemenz, 1978) and do not make up the loss, which have been used for the formation of eggs and embryos. In separate years a part of females leave for wintering with embryos for some reason, and the birth takes place in early summer of the following year (Madsen, 1989). Young females that have offspring are badly underweight in autumn, and they have not time compensate their weight loss for one next gain season and, apparently, they cannot breed every year, but only once in two-three years or more (Volsøe, 1944; Viitanen, 1967; Biella, 1979; Shane, Seigal, 1989). In this section in addition to the general descriptions of the

adders' reproduction process we present some quantitative indicators that are characteristic for the conditions of southern Karelia.

Materials and methods

The results of standard morphological and morpho-physiological study of 2489 animals were taken as a basis for investigation. Fertility was estimated by the number of embryos found by palpation of live females. Palpation is a rather rough procedure which can lead to injuries of embryos (Kudryavtsev, 1991). Therefore, on the island of Kizhi we used it not more than within two seasons (in July, August and September, 1998 252 snakes recorded, in May, 2007 – 71 due to the possibility to damage the reproduction dynamics in adders. Besides, the fertility was studied on the other islands of the Kizhi archipelago. Accuracy of a lifetime assessment of fertility was controlled by cadaveric material (34 snakes) (a food lump could not be accepted for embryos). The found corpses of adders and the destroyed by decapitation (32 snakes) were opened (Gurtovoy et al., 1978), their internal organs were weighed on pharmaceutical (accuracy within 0.1 g) or the torsion scales (accuracy within 0.002 g) depending on weight (Shvarts et al., 1968). The study of territorial distribution was carried out with the use of GIS-technology (see sections 7, 12).

4.1. Chronology of mating

The reproductive process of a sexually mature individual can be subdivided into the period of maturing of sexual products connected with fattening, and the period of reproductive activity, including mating dance, copulation, carrying pregnancy and the birth of offspring by females.

Puberty. In our database the females having mature eggs were ordered according to their body length of L.t. = 47, 47, 48, 48, 49, 50, 50, 50...cm. (In Fig. 4.1.10 one can see the cluster of points corresponding to the individuals with the increased weight and length beginning with 43 cm). A similar data row of the adult males shed in the first half of May be-

gins with L.t. = 38, 40, 40, 42, 42, 43, 43, 43... cm. Using the data on the dynamics of individual growth (Table. 5.2.2) obtained by us, it is easy to notice that the (minimum) puberty age of those females and males corresponds to 4 years.

Seasonal changes in body weight. The body weight of individuals of the same age changes during the season. A lot of females caught in the fall of the current year have the body weight 40–50 g less (Fig. 4.1.1) that is connected with pregnancy and giving birth. The effect of the birth is evident as for the distribution of females' weight in August and September – after birth a female having the average weight of 92 g lose about 42 g, or 46.6% (Fig. 4.1.3) that is close to estimates of other authors (52.3% – Biella, 1979). The same females are practically absent in captures in the spring of the next year. For some time, the females having given birth gradually gain normal weight and in September they make a group of the heaviest individuals who will breed the next year. Our data on marking snakes show that this process occurs slowly (Fig. 4.1.4, 4.1.5). In males the arithmetic mean increases by 26 g from May to September (Fig. 4.1.2; see section 5.3).

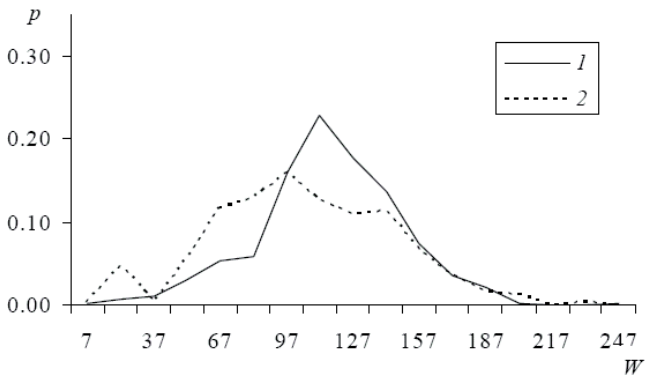


Fig. 4.1.1. Distribution of common viper females on body weight in May (*1*, 743 ind.) and September (*2*, 308 ind.)

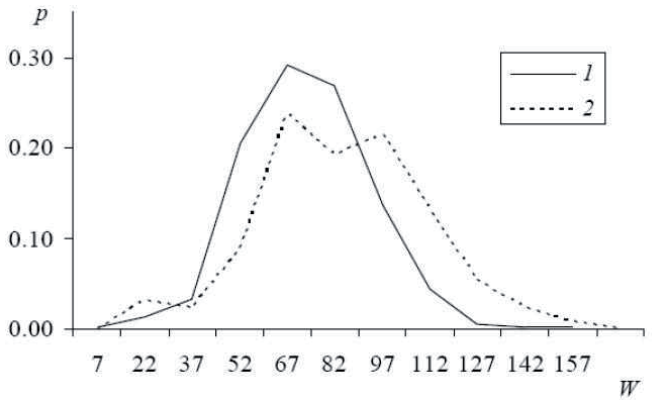


Fig. 4.1.2. Distribution of common viper males on body weight in May (*1*, 735 ind.) and September (*2*, 261 ind.).

Of the females caught in spring, 88% reduce their weight by the fall (86% of individuals – more than by 20%). Obviously, these are pregnant females losing weight after giving birth. Only 12% of them gain weight, but no more than by 20%; these are the snakes that were restored after giving birth. Indicated figures do not quite correspond to a true ratio between giving birth and restored females as in the fall pregnant females are caught first of all (they are less mobile and do not hide quickly in a high grass, as other females do).

Of the females caught in the spring, 73% lose weight by the spring of the next year (but only 15% of individuals – more than by 20%), 27% – increase their weight. This sampling is closer to a real ratio of the females of a different status as it includes the different individuals passing from wintering.

Of the females caught in the spring, 29% lose weight by the fall of the next year (but only 14% of individuals – more than 20%), 71% gain weight. This sampling mostly contains the females pregnant in the fall that had time to restore for one and a half previous years. The sample of the females marked in the fall and repeatedly caught in the fall in a year is presented only by the snakes (4 individuals) who gained weight (75% – more

than by 30 %). It is obvious that these are the females who could be restored for 1 year after giving birth. The average results on the body weight of females caught repeatedly in a year show that in 62% of cases there is a loss of weight (in 69% – more than by 20%), in 38% – increase of weight (in 31% – more than by 20%). In 2 years the similar values were received – 67% of females of adders lose weight, 33% – increase weight (Fig. 4.1.4).

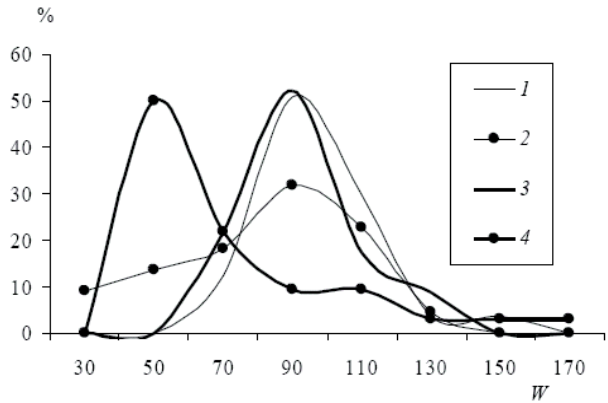


Fig. 4.1.3. Smoothed distribution of female vipers (134 ind.). For body weight (W, g) in August (*1, 2*) and September (*3, 4*) 1998: *1, 3* – pregnant women, *2* – barren and gave birth, *4* – only given birth

In our opinion, the observed ratio (1/3 of females gaining to 2/3 losing weight) corresponds to the situation that only a third of sexually mature females is capable to breed (to be pregnant) in the current year, and two thirds – are restored after the reproduction cycle.

These numbers approximately correspond to the idea of a three-year reproduction cycle of the adder – pregnancy lasts one year, restoration – two years. At the same time there are exceptions from this rule that will be considered below; for example, the individuals breeding every year were found.

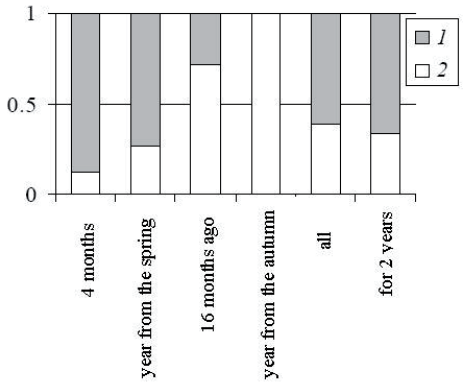


Fig. 4.1.4. Relation between tagged female vipers, who has reduced (*1*) or increased (*2*) body weight over time after the first catch: 4 months ago. – from May to September this year (16 ind.) one year from the spring – from May to May of next year (17 ind.), 16 months ago. – from May to September next year (7 ind.) one year from the autumn – from September to September of next year (6 ind.), all (all data, 44 ind.), For 2 years (23 ind.).

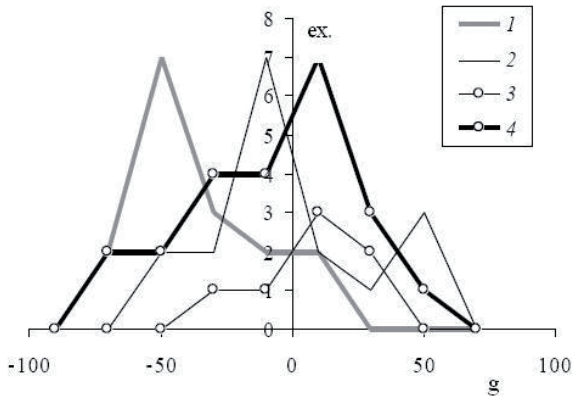


Fig. 4.1.5. Distribution of additional weights (*dW*, g) of tagged females recaptured after 4 months (*1*) 12 months (*2*) 16 months (*3*), 2 years (*4*)

Reproductive activity of males. After the end of shedding more and more males start searching for females. At that on a separate ridge it is possible to observe simultaneously both active movements of shedding males and passive basking of those have not shed. To monitor the males seeking for partners, their heads were marked by the nail varnish. In sunny weather each male continuously creeps round a stone ridge, on the ridge, near the ridge, quite for a long time, sometimes for all day long, but sometimes it darts off and creeps away. It seems that the snake keeps crawling around the ridge due to the heated stones (substratum temperature is T_c = 20–22 °C, body temperature – T_T = 32–34 °C).

Females also sometimes crawl somewhere, but the male crawling across her "hot" trace 3–5 min. later does not feel it and does not pursue. However, the movements round the given ridge are always caused by the presence of a female there. If it passes to the next ridge, a lot of males start to creep round a new ridge, probably, “bathing” in the atmosphere of the forthcoming reproduction, but having been unable to define quickly and precisely the location of subject of their desire.

Two males show a clear aggressive reaction when they meet. Recognition of sex (and sometimes – status) lasts 2–5 s., after that either fight, or flight with pursuit, or copulation attempt begins. The bright coloring obviously draws attention of snakes, but eventually the situation is defined by organoleptics (the vomero-nasal organ is used (Andren, 1982)) as the reaction to black males and black females is quite opposite. Adders can notice each other from the distance no more than 15 cm, but usually even less. If "fighting spirit" of males is strong enough (that is defined generally by the size), mating dances, "lekking", "fights" begin, though these words may be taken unquoted.

The aim of the fight is to press the opponent's head to the earth. For this purpose, one of males hooks a neck of the opponent by its own neck and pulls it to him and to the earth (for example, left-down).

Other male counteracting the first tries to do the right-up movement, and also, seeking to win, – to the right-down. Counteracting the enemy, the first individual pulls left-up and left-down. At these movements fighters

crawl a little in the rival's ring, so the place of contact of bodies displaces from the neck to the beginning of the trunk. Seeking to intercept an initiative, each of males rise above and again "seizes" the rival with its neck, doing thereby the second capture ring. Necks are pulled up and down, and capture follows capture with the speed of accelerated filming, about 3–5 hertz. They never "get up" highly vertical, using, unlike rattlesnakes, a half of the body, how it is frequently (and mistakenly) shown in popular publications. Sometimes they raise the head, but not vertically, and use no more than a quarter of a trunk length.

Males do not hiss, do not bite, but straining in ridiculous (because of the small sizes) efforts and rustling with a grass, creep as an intertwined wire, meter after meter, scaring away other males by the energy of the serious fight (Fig. 4.1.6, A). The fight can last up to 15 min. with "pauses", though usually tournaments come to an end earlier. Loser retires hastily, and winner tries to crawl on the running-away tail by its "chest". When small males meet larger ones, they take to heels, even without battle. The pursuit usually lasts 1–2 min., sometimes a little longer. In good weather and a large number of competitors fights begins and finishes with frequency of 5–10 min., strongly disturbing the normal copulation. The male which found a female the first, fights especially aggressively with competitors and pursues them for a long time. Most often it finishes by that it cannot find the road back and has to look for a female in the "Brownian" way again.

On the stone ridges of different size we observed "snake lekking" containing 2–36 males. The number of the females found on such lekking is always 2–4 times less, than males. At the same time, we have met a lot of copulating couples formed without any preliminary fights.

Coupling. At last, having run against the ball of a female, the mail distinguishes in 2–3 sec. that it is just a female. After that, the male moving with short jerks starts crawling over a female, trying to combine its body with her body: head – to head, tail – to tail. Using a long tail, it twists a female with one ring and "stretches" through it the back part of female's

trunk, trying to combine their cloacae. On achieving it the male turns outside one of its hemipenises into a cloacal cavity of the female (Fig. 4.1.7).

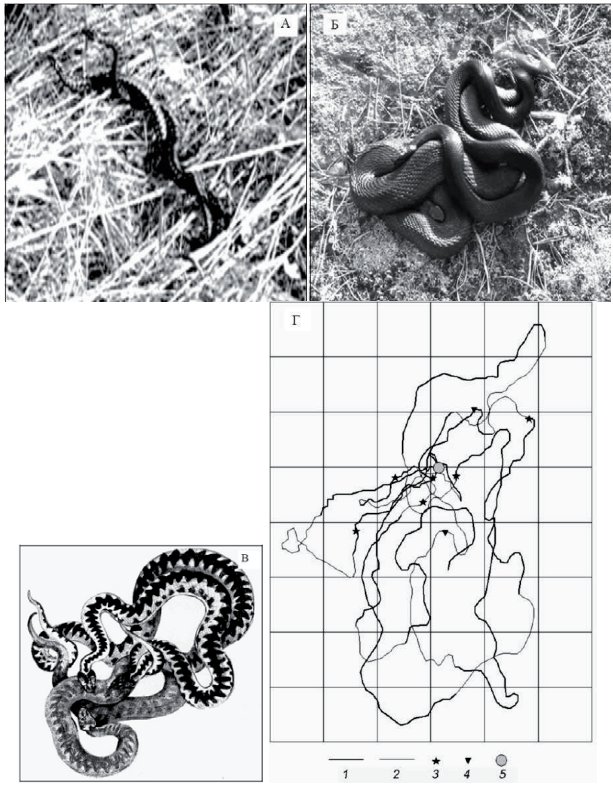


Fig. 4.1.6. Elements of reproductive behavior: males battle (А), an attempt copulation (Б), "false" copulation (В), displacement of the active male for 15 min. on 1 x 1 m grid (Г: *1, 2* – trajectory of the male during consecutive minutes, *3* – location of successful battles, *4* – places defeats in battle, *5* – position of females)

Such attempts have to meet understanding from the female, and then copulation can happen in only a few minutes (the fastest observable occurred in 1.5 min. after the beginning of attempts). Sometimes this process lasts long enough, especially if other males prevent copulation or a female

is already gravid. The copulation duration, according to our observations, varies from 20 min. to 1 h. 10 min. Having entered the copulation, the male absolutely loses aggression to the defeated competitors. Moreover, the recent opponent, when it find a female and the competitor linked to it, do not distinguish it as the other male, but more likely as a continuation of a female. It begins the copulation movements, which sometimes ends with a loop on the neck of a more successful competitor (Fig. 4.1.6, B).

Birth of juveniles. Young adders appear on Kizhi at the beginning of September (see Table 2.2.1). It is confirmed by the decreasing share of pregnant females (and growth of the share of those that have given birth) (Table 4.1.1), and by increasing number of newborns (Table 4.1.2). To distinguish a pregnant female from others in September is possible by dilated back part of its belly (embryos lie straightened and therefore almost cannot be palpated).

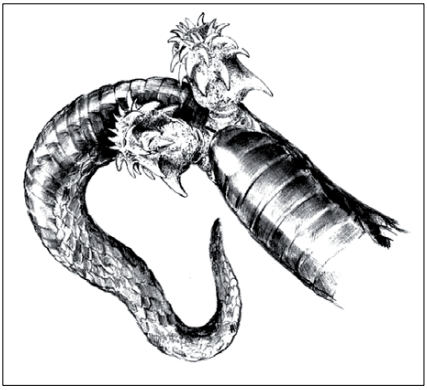


Fig. 4.1.7. Hemipenises of male viper

Table 4.1.1. The dynamics of juveniles' birth on the island of Kizhi in 1998

Share of females, % of sum	The day in September 1998						
(in all 58 snakes)	4	5	6	7	8	9	10
Giving birth (1)	0	66	38	71	100	–	87
Gravid (2)	100	33	63	29	0	–	13

To distinguish the female having given birth from barren ones in this year is rather simple by the relative body weight (fatness) – the majority of

them is obviously exhausted as in birth an adder loses 40–50 g of its weight, up to 50% of initial weight (see Fig. 4.1.3).

From our data, on the Kizhi island the birth happened by September, 15th, in the majority of adders. In captivity the young were born on September 9–14 (6 females). Some pregnant females, especially in cold years (1997), can occur until the end of September (26.09.1997) and even can hibernate with full blown embryos. The sex of newborns was defined by a ratio of the length of tail and body, which in females is less than 1.46 (Fig. 4.1.8), and in males – more. Among 92 newborns there were 52 (58%) females.

Table 4.1.2. The dynamics of appearance of current year's young on Kizhi in 1992–2008

Day in September	5	6	7	8	9	10	11	12	13	14	15	16
Number of current year's young	0	0	9	0	1	14	0	11	4	0	7	0
Share of current year's young	0	0	20	0	2	30	0	24	9	0	15	0
Cumulative percentage	0	0	20	20	22	52	52	76	85	85	100	100

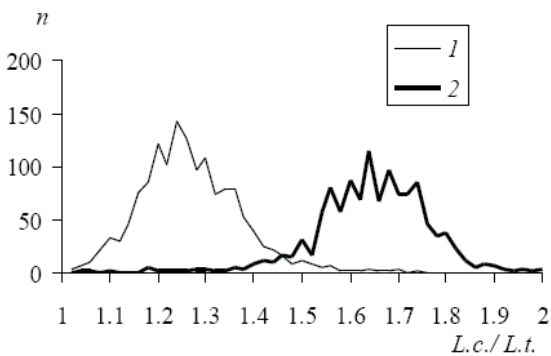


Fig. 4.1.8. Occurrence (n) of females and males of common viper on the Kizhi island with different ratios of tail length to body length (L. c. mm / L. t., cm)

4.2. Wintering with embryos

Viviparity is the most important survival strategy of reptiles in the North. The possibility of posterity carrying opens a way for the following adaptation – prolongation of pregnancy until the optimum development of young. At the end of the short (near 90 days) northern summer this moment may not come. As it is known now, in response to vagaries of weather, some snakes developed important adaptation – the pregnant females of the European asp (Vipera aspis) and common adder hibernate with embryos. This phenomenon is known in France, Kazakhstan, Sweden (Saint-Girons, Duguy, 1973; Berdybaeva, 1981; Madsen, 1989) and in Karelia (Korosov, 2000, 2012). The question is how wide this phenomenon is spread in population of adders in the south of Karelia?

The results of opening of 4 adult females of adders which finished the pairing period in spring of 1998 (on May 20) showed that in one female (the size: L.t. = 620 mm, L.c. = 85 mm, W = 165 g) there were five full blown embryos of females (2 specimens) and males (2 specimens) covered with thin transparent membrane, and also one male covered with dense thick hyperemic membrane. The size of embryos was close to the size of August newborns: females were L.t. = 152 mm, L.c. = 19.5 mm, W = 3.25 g, males – L.t. = 146.5 mm, L.c. = 25 mm, W = 3.4 g (on average). Bodies of the first four embryos were freely laid spirally (Fig. 4.2.1, A), and the last was densely packed (Fig. 4.2.1, B). (For this reason only this embryo could be palpated as a large dense lump.) Most likely, this embryo was at an early stage of a resorption, and 4 other embryos had to be born soon. Besides embryos, oviducts of this adder contained 8 large mature eggs (from 33 x 11 to 35 x 12 mm) (Fig. 4.2.1, V). So, this female not only was pregnant last year, but could breed even in a current year, i.e. it could become pregnant every year! In our opinion, good fatness of this not so young snake is the reason of such "anomaly". According to our data, losses associated with pregnancy and birth, compose from 20–40% (in large snakes) to 20–60% (in small snakes) for one season (Fig. 4.2.2, 1, 4). If we consider a longer period, and include a larger number of individuals in a

sample, it appears that the largest individuals (up to 5%) have slightly less weight loss than small (young) ones – up to 60%. Distinction between small (young) and large (older) snakes also is that young adders are capable to restore quickly the deficiency of weight to a lesser degree, than larger and older ones. On the basis of the found ratios (Fig. 4.2.2), it is possible to note that females weighing more than 160 g practically do not lose weight after giving birth. Probably, this category of females can breed every year and under adverse conditions they can leave for wintering with embryos. From their body size (see Fig. 5.2.2), the age of these animals has to be not less than 10 years. Within our population research it is interesting to estimate at least approximately the number of females wintering with embryos or breeding annually.

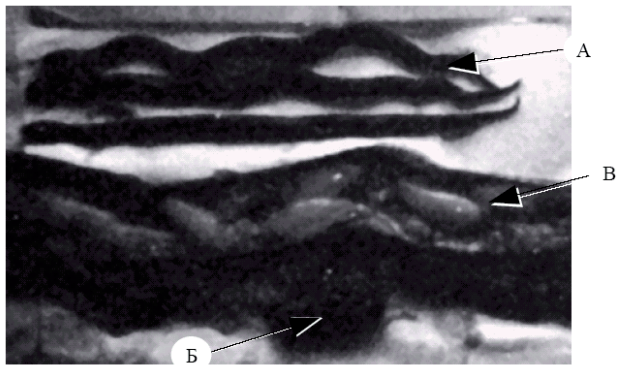


Fig. 4.2.1. Female common viper with embryos (А, Б) and mature eggs (В)

As the adder is a threaten species, it is impossible to get and open a large number of these snakes. In our opinion, the problem could be solved using the analysis of a female distribution of their body weight and regression of body weight according to their linear size. It is known that the weight of embryos and females increases by the end of pregnancy. It means that in the spring pregnant females will be the heaviest among hungry animals of the same size. Our data collected from 1991 to 2009 show that of the females caught in the spring there is a very small number of especially large individuals with body length more than 62 cm and weight – more

than 160 g. Among 1450 snakes there were only 18 such samples, or 1.2% (Fig. 4.2.3). Perhaps, individuals of a smaller size can also possess the ability to frequent reproduction, but their share cannot exceed 5% (the share of females heavier than 160 g is 3.7%, and longer than 62 cm – 1.9%). Based on the facts above, it is possible to claim that the share of the females breeding every year is no more than 3% ("old" females 10–15 years old), a share of the females breeding once in 2 years – 25% (it is the majority of middle-aged females), once in 3 years – 5% (evidently, it is just matured small females 4–5 years old).

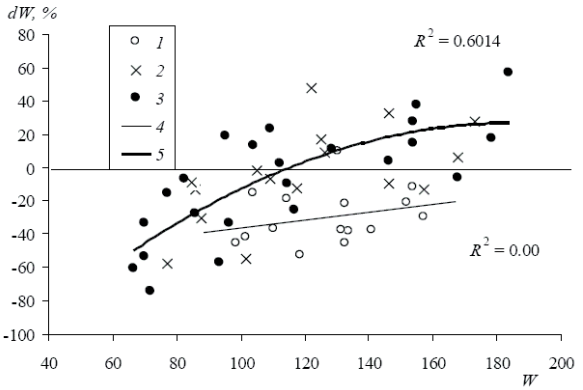


Fig. 4.2.2. The dependence of the " additional " weight of body (*dW*, *%*) of tagged females viper on the mass (*W*, g) of the body in the primary catching: *1* – growth at the end of the warm season, *2* – growth in 1 year, *3* – an increase in 2 years, *4* – trend for the 1, the trend for *2, 3*; R^2 – coefficients of determination of trends

One of the possible versions of data analysis is revealing individuals, abnormally heavy for their size. As weight anomalies are expected to be connected with reproduction, it is possible to build two regression lines of body weight according to body size and their confidence belt both for young, immature individuals and for all individuals, including breeding

ones (Fig. 4.2.4). As these animals are normal, though the heaviest ones, the level of confidential probability was accepted $P = 0.9$.

To reflect the allometric character of the ratio weight/length, the exponential equation of the type $y=ax^b$ was selected. It would seem reasonable that the confidential zone for still "slim" young would be narrower, than that for pregnant snakes, and that the weight anomalies connected with pregnancy would appear as "out-of-order options" from a confidential zone, characteristic for young adders. However, the constructed confidential zones almost do not differ from each other.

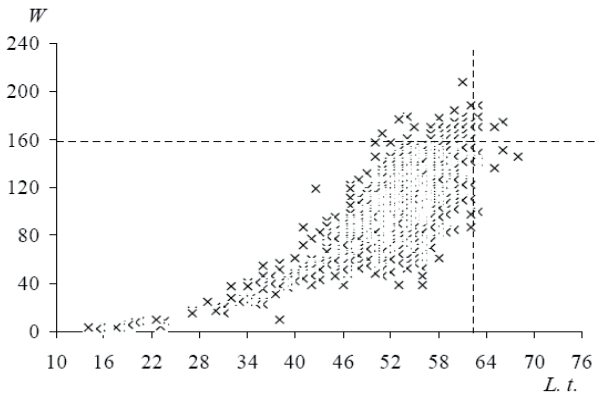


Fig. 4.2.3. The ratio between length (L. t. cm) and weight (W, g) of the of common viper females body

The upper bounds both for the young and for all individuals coincide completely, the group of 12 abnormally heavy individuals (0.8%) consists, probably, of the animals which have eaten recently and are not identified in sampling. In the area of a dimensional scale more than 60 cm the weight anomalies are not found. The lower confidential bound for all individuals is a little lower than for young; it shows that at birth there is a significant loss of weight, which is the most pronounced in animals having body length less than 58 cm. Thus, body proportions of adult individuals are founded during the juvenile period – there are fast and slowly growing snakes among both young and adults.

4.3. Fertility

The number of embryos was counted both by opening animals (26 samplings) and by palpation (128 samplings) in August – September, 1998. Accuracy of lifetime fertility was controlled by the subsequent opening of 22 individuals (July, 1998). The control showed that sometimes the palpation underestimate the number by 1 individual (on average 0.5–0.7 individuals), especially at the late stages of embryos development when thin and flexible embryos straightens and their bodies have only 2 bends.

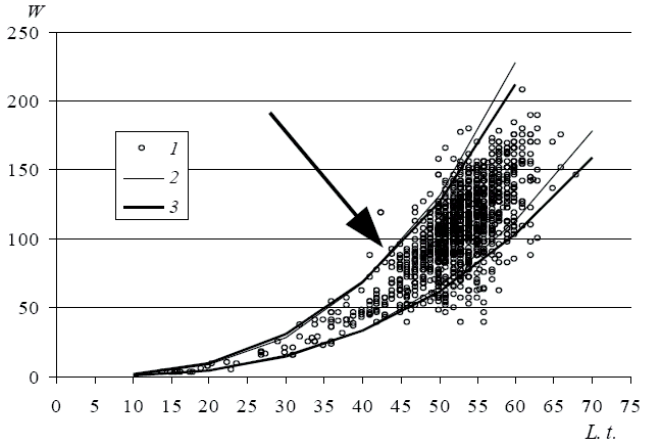


Fig. 4.2.4. Confidence zones for the variants, built around the regression lines of body weight (W, g) on body length (L. t., cm) of female vipers: *1* – initial data, *2* – extrapolation of the confidence zone regression, built for individuals with a body length less than 45 cm, and *3* – confidence zone regression for all individuals, the arrow indicates the concentration of points corresponding to the first pregnant females

Of the females opened in July pregnant snakes composed 52%. However, this number cannot serve as an indicator of a share of pregnant females in population, because some barren females restoring fat stocks after pregnancy and actively eating lead a secretive life. In general, the average fertility is 7.59 ± 0.15 per a female (Table 4.3.1). This value is lower,

than in other parts of adders' area, first of all due to the low maximum level – 12 embryos against 16–18 (up to 20) (Nikol'sky, 1903; Kaletskaya, 1953; Fromhold, 1969; Popoudina, 1976; Biella, 1979; Kuranova, Kolbintsev, 1981; Pikulik et al., 1988).

In opening one of females two encapsulated dead embryos were found, i.e. contrary to our assumption that $N_{embr.}=N_0$, the part of embryos will be lost.

Table 4.3.1. Fertility of adders on the Kizhi archipelago

Place	Month	M	Min	Max	S	m	n
Klimetsky isl.	07	8.1	5	11	1.9	0.28	44
Kizhi isl.	08	7.4	5	12	1.5	0.2	57
Kizhi isl.	09	7	4	10	1.4	0.3	23
On average		7.6	4	12	1.7	0.15	124

The correlation between the number of embryos and the female's size was significant, but not as high as it is given in literature (Iverson, 1987), r = 0.285, p <0.005. The correlation between the number of embryos and female's weight was greater and significant, r = 0.539, p <0.001. From above data the regression equation for the calculation of female fertility E with given weight W: $E=0.041 \cdot W+3.2$ can be proposed, however, its reliability is low (Fig. 4.3.1). The received fertility estimates (near 8 /female), sex ratio in a brood (53% of females), share of the females breeding every year (about 33%), and the average number of adult females on the Kizhi island from 2003 to 2007 (about 1000 specimens.) can be used for the calculation of an absolute number of newborns of both sexes: $N_0=1000 \cdot 0.33 \cdot 8=2640$, or 1531 females and 1109 males.

Dynamics of the processes of reproduction of adders in Karelia has no specifics. The lowered fertility is, most likely, a simple consequence of the smaller body size of the studied females.

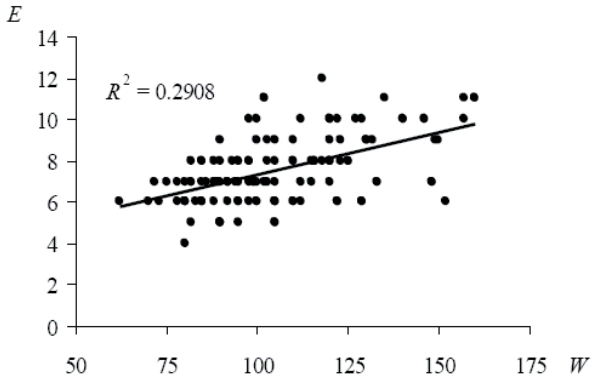


Fig. 4.3.1. Relationship between female weight and number of embryos (n = 154 ind.).

Chapter 5.

The growth

The size of animals as a general specific characteristic reflects not only the history of species formation (evolutionary aspect) (Shmal'gauzen, 1935), but also modern conditions of its existence (ecological aspect) (Shvarts et al., 1968). The most comprehension of the main natural factors can be received when studying the size changes of animals with age. It is important to distinguish ontogenetic and population statements of the question. In the first case the physiological (metabolic) conditionality of growth process influenced by internal (genetic) and external factors (food, temperature) is of importance. In the second case the dependence of the morphological aspect of a population on its structure, i.e. on the ratio of individuals of different age, sex, a maturity, is investigated. As the adder remains poorly known all fields of research are interesting. It is difficult to study this process in poikilothermic reptiles because the rate of their growth is extremely uneven as these animals grow only in a warm season that lasts 90–120 days in Karelia; in winter the growth process is weakly expressed. The pulsing nature of size changes is also connected with periodic changes of body covering (molt).

The main aim of the further exposition consists of designing a general model of age changes of the average size of animals living on the island of Kizhi. First, it will allow considering the influence of the main factors (temperature, food, mortality) on population morphology. Second, the model serves as a basis for synthesizing the data on a zoocenotic role of the adder.

Materials and methods

Some research information was received by monitoring the growth of animals in captivity at a definite temperature and feeding under control. The other data block was formed as a result of repeated measurements of

animals earlier caught on Kizhi. In addition, the individuals, which age was determined by the method of skeletochronology (see section 7.5), were measured. After capturing (see section 3) the length of the body (*L.t.*, mm) and the tail (*L.c.*, mm) was measured according to standard techniques (Bannikov, etc., 1977; Korosov 1994). As long-term practice shows, the accuracy of length measurements in live and actively resisting (not immobilized by an anesthesia) adders, unfortunately, is more than 2 cm (while the division value of a ruler is 1 mm). Snakes were weighed on spring balance (*P*, g) in a plastic bag. The division value of our scales was 5 g for the animals weighing more than 100 g, and 2 g. for those less than 100 g. At the beginning of researches (1991–1992) sex of animals was defined by the depth of hemipenis pits (Darevsky, 1987), and further by the existence of a constriction in the cloacal region and by postcloacal dilatation of the tail set (Terent'ev, 1961). The found fresh corpses (34 sampling) and 32 decapitated adders were opened and their internal organs (Gurtovoy et al., 1978) were weighed on pharmaceutical (accuracy within 0.1 g) or the torsion (accuracy within 0.002 g) scales, depending on their weight (Shvarts et al., 1968). All information was brought together into databases in Excel and Access environment.

5.1. Molting

The earliest sign of molt beginning is the change in coloration of the outer edges of belly shields (Környei, 1982) that can be seen only with a magnifying glass. In field conditions the first reliable sign of the beginning of molt (stage 1) is the change of usually black belly to light muddy-blue (1 day) (Fig. 5.1.1, A). Then (stage 2) the eyes (1–2 days) (Fig. 5.1.1, B) also become "turbid". After that the coloration disappears (stage 3): at first the coloration of belly is restored, then – of the eyes. For the next 3–4 days the horny epithelium exfoliates and, at last, peels up (stage 4) with the active efforts of a snake (Fig. 5.1.1, V, G). When molting in captivity, adders with visible pleasure dipped into a water tank; in nature we observed a dry molt. The total duration of the process from the moment of "a blue belly" to the

emergence of a slough is about 6 days in captivity and 10–12 days in nature (Frommhold, 1969; Korosov, 1988). In nature stages 1–2 can be registered most precisely. In males the bright coloration corresponding to stage 4 is well distinguishable within several weeks. It especially contrasts against the background of faded males and females, which have not molted yet (Fig. 5.1.1, V).

The first molting of newborns. We have observed the first molting of newborns in a few minutes after their birth, then – in a week. Further they molt every 2 weeks till the age of 4 months (about 3 years on "a natural calendar") and then this period gradually approaches species-specific norm – 25–35 days (Korosov, 1988). Similar figures have been given by other authors (Bakiev et al., 2008). Within a year the frequency of investment changes (stages 1–2 in 367 snakes of 1971 caught) has three obvious peaks (Fig. 5.1.2): in May – June (60–100 days, from March, 1st), July – August (120–160 days) and in September (200–210 days), or roughly – from the middle to the end of May, in July, from the middle to end of September, similar to the other points of an area (Sokolov, 1989). Their periodicity (Korosov, 2007б) is reliable ($p<0.01$), and the time period is about 60–90 days (Fig. 5.1.3). (At first sight the time of molts coincided with the time of field works, but statistically the time of mass molts did not depend on the time of our field works.) It is important to notice some peculiarity of molting – obvious bimodal distribution of the number of molting snakes in May as a reflection of the periods of molts first in males, then – in females (see section 2.2; Fig. 2.2.2). Further this process becomes less hard and covers the most part of July and the beginning of August.

Obviously, in the fall not all animals are bound to molt, a lot of them leave for wintering in an old skin. It is especially noticeable in spring when some animals are rather brightly colored even before a spring molt, and others remain dim and brownish. To the beginning of summer, the majority of adders become uniformly smart. Observations of snakes in captivity show that the most part of adult females and males has the autonomous period of molts equal 26 ± 3 days, but some healthy and normally eating individuals molt significantly less often – once in 60 days.

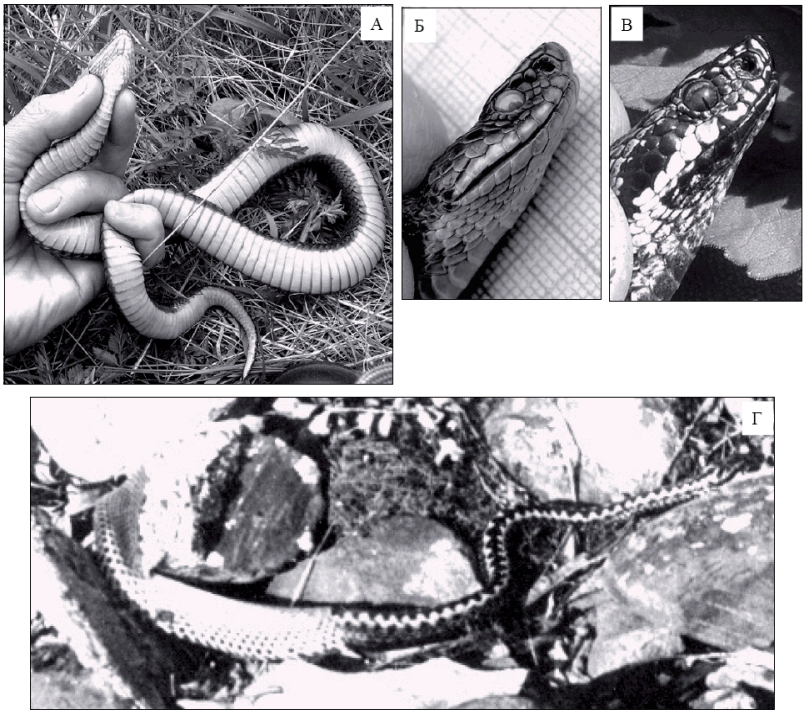


Fig. 5.1.1. Molting stages: Stage *1* – clouding of the abdominal flaps (А), stage *2* – clouding of the eyes, vertical pupils barely visible (Б), stage *4* – the dropping of the skin (Г) bright and fresh covers of male (В)

Our experience (and also other researchers – see: Bakiev et al., 2008) shows (Korosov, 1988) that the molt is a good indicator of snake's health. Its regularity is the evidence of well-being of an animal, but rhythm disturbance – of oppression and illness. Even the exfoliating covers may not descend from a snake's body up to the following molt (to remove them, warm baths have to be arranged for a snake).

There are some reasons why the analysis of change in size and body weight should be investigated separately. If the former directly depends on age and individual growth rates of an individual, the latter strongly changes depending also on season, satiety of an animal, its maturity, state of health, pregnancy stage and so forth. The second moment is connected with that

the main information on growth is received in nature on cadaveric material where weight characteristics are meaningless.

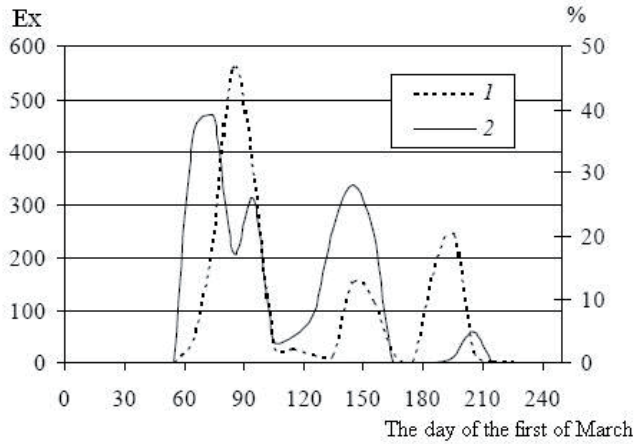


Fig. 5.1.2. . Proportion of individuals (2%), initiating molting (stage 1–2), among captured for each decade (1, ind.)

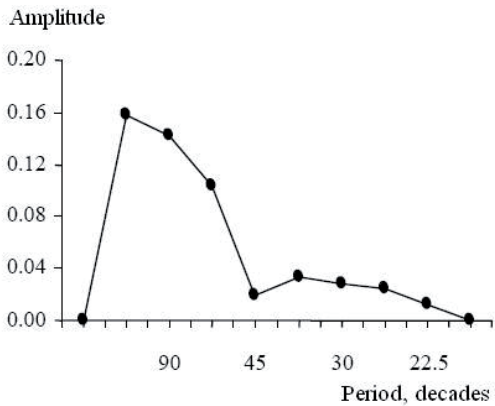


Fig. 5.1.3. Periodogram of molting dynamics in decades

5.2. Linear growth

The group growth. The general information on average growth rates of animals is often received when studying changes of the average body size in groups of even-aged animals. However, at that an average curve may not correspond to any of possible trajectories of individual growth (Mina, Klevezal', 1976). Therefore, first of all it is important to exactly determine the items of investigation. First of all, it is necessary to find out, what is the average body size of even-aged adders in the population on Kizhi, to study further animals growing and feeding. This problem was solved with the use of measurements of adders' corpses found on Kizhi and for which the age was precisely known, as well as those of the adders born in captivity.

In spite of not abundant data, they allow to receive general information on changes in the average body size with age, and also construct the model of this process (Table 5.2.1, 5.2.2, Fig. 5.2.1, 5.2.2). Newborn (N) males and females of adders practically do not differ by body length, Lt_H = 12.5 cm. A lot of these born in August – beginning of September can grow within 1–1.5 months, adding 4–5 cm for that time. Therefore, juveniles caught in the middle and at the end of September were always longer, than newborns, Lt_0 = 15–16 cm.

The size of a current year's young which corpses were found in June – July, on the contrary, differs from the size of those of the last year only slightly (Lt_0 = 16–25 cm), as they left wintering quite recently and grew at least during 1/3 of the warm period.

In this regard all average values of body length seem a little inexact as they are related not to the end of the growth period in a current year, but to its middle. At the same time, very wide variability of the received values for older age groups completely brings this error to naught.

Dynamics of growth can be described either as regression of body size with age (x), or by means of simulating model of change in an annual growth. In the first case it is possible to use a power, exponential or polynomial form. Each of them has significant coefficients ($p<0.01$) and lie

within the confidential borders of variation M ± 2S (tab. 5.2.1, 5.2.2). For example, a second-order parabola has the following form for females and males, respectively:

$Lt_{♀} = 13.2729 + 8.25963x – 0.401062x^2$,

$Lt_{♂} = 16.9133 + 6.87178x – 0.37215x^2$.

Parabolic dependence is chosen for two reasons. First, its coefficients characterize in detail size changing with age. According to the model, the growth of females in comparison with males begins with lower values (13 against 16 mm), takes place more intensively (8.2 against 6.9), but slows down faster (–0.40 against –0.37). In other words, females' body length increases very quickly at the beginning of life and almost stop increasing to mature age, whereas the slower growth of males proceeds more intensively in maturing years.

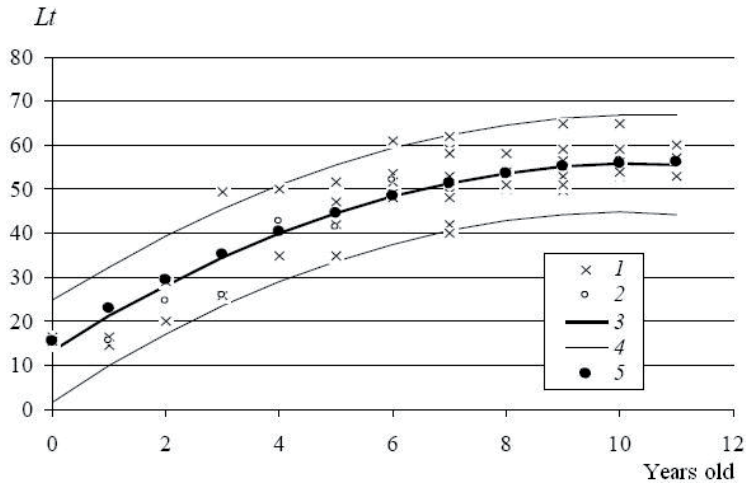


Fig. 5.2.1. Linear growth of female common viper: *1* – the original data, *2* – arithmetic average, *3* – regression polynomial Lt♀ = 13.2729 + 8.25963x – 0.401062x2, *4* – confidence interval of variants *5* – forecast of the simulation model dLt♀ = 7.933022 – 0.70997x at Lt0 = 15.6 cm

Table 5.2.1. Body length (Lt, мм) in adders' females of different age (older than 1 year – corpses)

Parameter	Age, years (H – newborns, 0 – current year's young)												
	H	0	1	2	3	4	5	6	7	8	9	10	11
n	42	4	2	2	1	2	3	7	14	11	10	8	4
M_{Lt}	12.5	15.5	15.5	24.5	25.8	42.5	41.3	52	50.5	52.8	54.9	56.4	55.8
S_{Lt}	1.1	0.71	1.41	6.36		10.6	6.03	4.57	6.47	2.98	4.59	3.94	3.4
minLt = M–2S	11.2	14.1	12.7	11.8	25.8	21.3	29.3	42.9	37.6	46.8	45.7	48.6	48.9
maxLt = M+2S	14.7	16.9	18.3	37.2	25.8	63.7	53.4	61.1	63.4	58.8	64	64.3	62.6
Prognosis M_{Lt} (polynom)	–	13.3	21.1	28.2	34.4	39.9	44.5	48.4	51.4	53.7	55.1	55.8	55.6
Gain dLt_x	–	7.22	6.51	5.8	5.09	4.38	3.67	2.96	2.25	1.54	0.83	0.12	
Prognosis M_{Lt} (model)	12.5	**15.6**	**22.8**	**29.3**	**35.1**	**40.2**	**44.6**	**48.3**	**51.3**	**53.5**	**55.0**	**55.9**	**56.0**

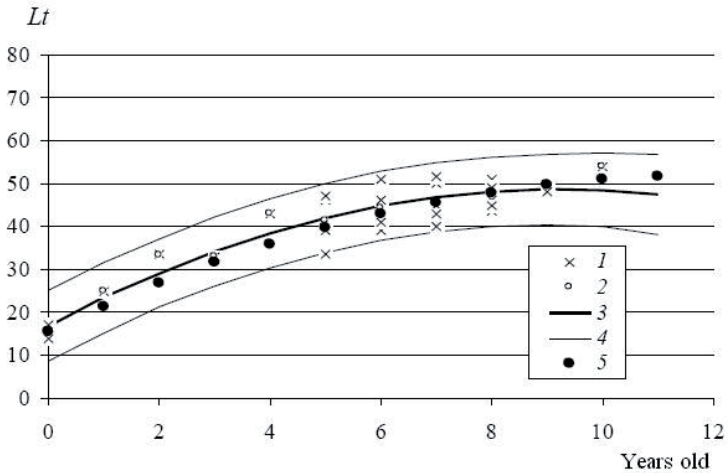


Fig 5.2.2. Linear growth of male common viper: *1* – the original data, *2* – arithmetic average, *3* – regression polynomial Lt ♂ = 16.9133 + 6.87178x – $0.37215x^2$, *4* – confidence interval of variants; *5* – forecast of the simulation model dLt ♂ = 6.333561 – 0.51065x at Lt_0 = 15.6 cm

Table 5.2.2. Body length (Lt, мм) in adders' males of different age (older than 1 year – corpses)

Parameter	Age, years (H – newborns, 0 – current year' young)												
	H	0	1	2	3	4	5	6	7	8	9	10	11
n	42	5	1	2	1	1	4	4	6	6	1	1	0
M_{Lt}	12.5	15.8	25	33.3	33	43	41.4	44.3	45.4	47.3	49.5	54	
S_{Lt}	1.1	1.38		0.35			6.34	5.38	4.45	2.93			
minLt = M–2S	11.2	13		32.5	33		28.7	33.5	36.5	41.5			
maxLt = M+2S	14.7	18.5		34	33		54.1	55	54.3	53.2			
Prognosis M_{Lt} (polynom)	–	16.9	23.4	29.2	34.2	38.4	42	44.7	46.8	48/1	48.6	48.4	47.5
Gain dLt_x	–	5.82	5.31	4.8	4.29	3.78	3.27	2.76	2.25	1.74	1.23	0.72	
Prognosis M_{Lt} (model)	12.5	**15.6**	**21.4**	**26.7**	**31.5**	**35.8**	**39.6**	**42.9**	**45.6**	**47.9**	**49.6**	**50.8**	**51.6**

Secondly, the derivative of this function is a straight line which characterizes linear change of growth rate of animals with age. Thereby, parabola takes on the role of theoretical basis for imitating model of growth rate. In this case the change in average body length can be presented as an addition of a current annual gain (dLt_x) to the size reached last year:

$Lt_x = Lt_{x-1} + dLt_{x-1}$.

As the growth rate decreases with age, the current gain can be expressed as a function of age:

$dLt_x = b + ax$.

As an initial body length of current year' young was used: 15.6 cm in both sexes. It gives the possibility to compare parameters of model for certain. In the environment of an Excel package such model was built separately for females and males. By means of optimization the coefficients for equations of growth rate dynamics were chosen (for females and males, respectively):

$dLt_{♀} = 7.933022 – 0.70997x$,

$dLt_{♂} = 6.333561 – 0.51065x$.

As well as in the case of parabolic regression (the model practically coincided with the course of the regression line), coefficients indicate the higher initial gain of body length in females, than in males (7.9 against 6.3 cm), and fast decrease in growth rate (–0.71 against –0.51). In the first year the gain of body length is 7.2 cm, but by 10 years it decreases to 0.1 cm.

Males begin with an annual gain of 5.8 cm, by 10 years it decreases to 1.2 cm. Owing to the reduction in the length growth rate, the average size of males never achieves that of the same-aged females and it is about 5 cm shorter (Fig. 5.2.3). The value of the annual gain can be expressed not only as a function of age x, but as a function of already reached linear size Lt in the form of $dLt_x = f(Lt_x)$. As the gain gradually decreases with age, for the description of its dynamics a parabolic function will be suitable (Fig. 5.2.4).

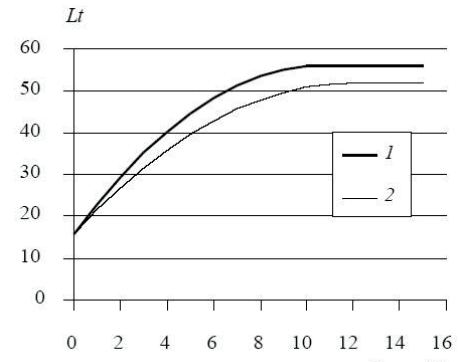


Fig. 5.2.3. Prediction of linear growth of female (*1*) and male (*2*) vipers up to 15 years

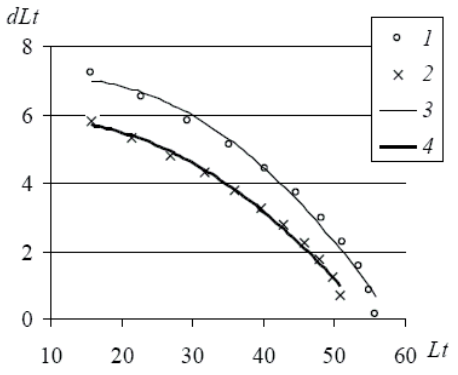


Fig. 5.2.4. The dependence of the annual model growth dLtx on body size Lt for common viper females (*1*) and males (*2*): *3* – regression of growth rate of females dLtx = –0.0033Lt2 + 0.0764Lt + 6.6124, *4* – regression of growth rate of males dLtx = –0.0027Lt2 + 0.0437Lt + 5.6725

Growth of marked animals. To determine the annual gain of body length, measurements of animals caught multiple times can be used. Such approach has both advantages and shortcomings.

The work with individual gains bring his method closer to laboratory observations, but inability to define the age of a live adder does not allow to relate it to a certain age. The only way of the analysis is to search a connection between the body size and the value of gain. As the individuals' size is only generally connected with age, a well-defined annual gain only generally can be associated with individuals' age and for this reason will never coincide with a real gain, characteristic for this age. The results of observations are presented in Fig. 5.2.3 and in Table 5.2.3, 5.2.4. For unification, all values were expressed as an annual gain, when the difference between two consecutive measurements was divided by the number of years between the dates of these measurements.

Table 5.2.3. Comparison of annual gain of adders' females on data of repeated capturing and data of animals of known age

Measurement interval	35–40	41–45	46–50	51–55	56–60	61–65
Average body length within the interval		44.0	48.6	52.8	58.5	62.0
Average gain for the interval, dLt		3.1	1.2	0.9	0.2	0.0
Calculation of gain on regression, dLt_M	4.0	3.3	2.2	1.4	0.8	
Gain of individuals of different age, dLt_x	3.8	3.2	2.1	1.5	1.0	
Difference in gain estimate, dLt/ dLt_x, %		–4	–43	–41	–68	

Table 5.2.4. Comparison of annual gain of adders' males on data of repeated capturing and data of animals of known age

Measurement interval	35–40	41–45	46–50	51–55	56–60
Average body length within the interval	38.5	43.2	47.8	51.9	57.0
Average gain for the interval, dLt	2.0	2.2	1.1	0.6	0.5
Calculation of gain on regression, dLt_M	2.8	1.9	1.0	0.7	
Gain of individuals of different age, dLt_x	2.9	2.1	1.6	1.2	
Difference in gain estimate, dLt/ dLt_x, %	–27	16	3	–18	

The first that attracts attention is a high variability of gains, including even negative values. The matter is in that it is rather difficult to measure

precisely the live but not immobilized snake alone. As practice shows, the error of a measurement of large animals can reach 2 cm. In order to avoid traumata, the violence to animals (body extension) is inacceptable as after this procedure they were let free with hope for them to be caught again. For this reason, the processing of one caught individual (photographing of a pileus, measurements of a body, tail, jaw, temperature, weighing, diagnostics of feeding and pregnancy) was carried out quickly.

As a result, the accuracy of body length measurements was poor, and estimates of gain varied greatly. Nevertheless, our data give a conception of dynamics of the linear size gain in adders. The average size gain for middle aged adders was 2–3, and for older ones – in females 0.82, in males 1.23 cm/year. The assessment of gain by means of linear regression appears to be more accurate. For the animals of observed size (35–65 cm) the gain value was (cm/year) following: (Fig. 5.2.5):

$dLt_{M♀} = 7.8 – 0.13Lt$ ($R^2 = 0.25$), $dLt_{M♂} = 9.33 – 0.17Lt$ ($R^2 = 0.23$).

The regression coefficients significantly differ from zero, $p<0.01$. Calculations of a gain on this regression approximately correspond to those for age groups with a similar average size (Fig. 5.2.5; see Fig. 5.2.4).

For both males and females forecasts for the annual gain (dLt_x) according to the model are partially within the confidential intervals for regression (dLt_M). Moreover, visually forecasts of dLt_x even better approaches to the empirical data of dLt, as they almost coincide with axes of ellipses of dispersion of received distributions. To check it, the RMA-regression was calculated (Polishchuk, Tsejtlin, 2001; Korosov, 2007б) which is focused to display a proportion between features (whereas MNK-regression displays the dependence of an average level of a feature y on a feature x). It is seen from the chart (Fig. 5.2.6) that the forecast according to the results of repeated catching in each case gives the underestimated regression values of gain. In our opinion, the reason consists only in high variability of basic data and in inaccuracy of a method of lifetime measurement. Probably, more adequate results can be received only by increasing the accuracy of measurements of animals' body length, for example applying an anesthesia.

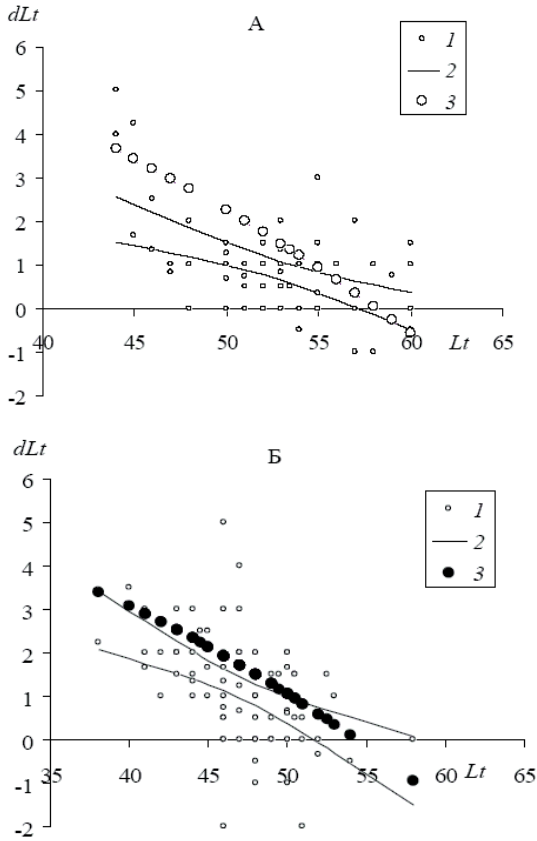


Fig. 5.2.5. The dependence of growth (dLt, cm) on body length (Lt, cm) for viper females (A) and males (B): *1* – recapture data, *2* – confidence interval around the regression lines $dLt_M = 7.8 – 0.13Lt$ (for females) and $dLt_M = 9.33 – 0.17Lt$ (for males), *3* – theoretical value of increment dLt_x, calculated by the equations of the annual growth rate (see Fig. 5.2.4)

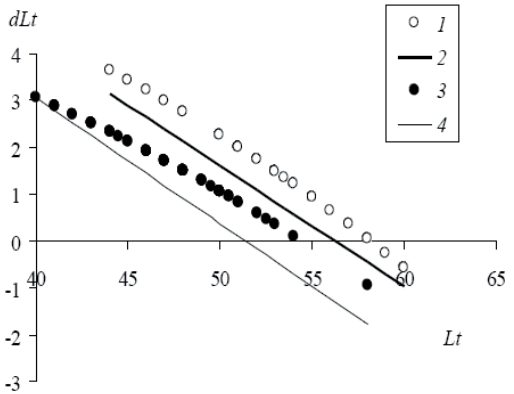


Fig. 5.2.6. Relation between growth (dLt, cm) and body size (Lt, cm) for females (*1, 2*) and males (*3, 4*) viper, expressed by the model of the annual growth rate (*1, 3*) and by the RMA-regression (*2, 4*)

Growth in captivity. The only opportunity to receive an exact description of animals' growth proposes the observations in captivity. Our experiment on the maintenance of adders in captivity was undertaken for the first time in 1978–1979 and continued in 1995 – 1998. It allowed us to obtain exact data on the individual growth (Fig. 5.2.8). To the age of 6 months the sex could not be yet defined and data on linear growth for females and males are combined.

In captivity, at a constant temperature and existence of forage ad libitum, adders grow constantly and in general smoothly (Fig. 5.2.7). With increase in age (x), the gain (dLt) decreases. The gain could be described as a linear function of age – both for females, and for males (Table 5.2.5, 5.2.6):

$dLt_{♀} = 32.45621–0.03799 \cdot x,$

$dLt_{♂} = 29.66972–0.04142 \cdot x.$

All the equations adequately describe the dynamics of growth in captivity (Fig. 5.2.8). To illustrate this statement, the results of the dispersive analysis of the curve describing growth of all individuals are given in Table 5.2.7. The total variation estimates the variability of the body size in all in-

dividuals for all months of observations (part of animals perished). The model variation is related to the values of body length calculated by the growth model.

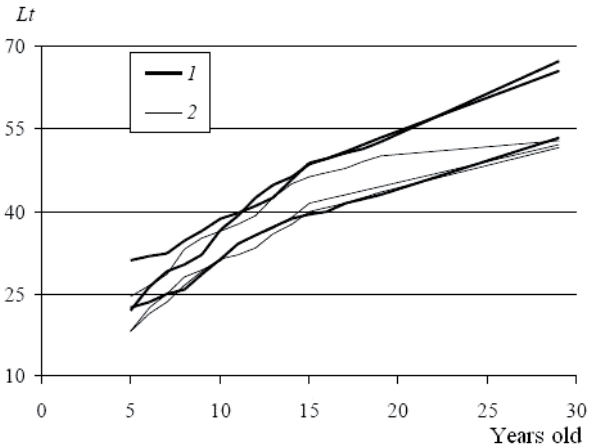


Fig. 5.2.7. Individual growth trajectories (Lt, cm) of viper females (*1*) and males (*2*) within 30 months

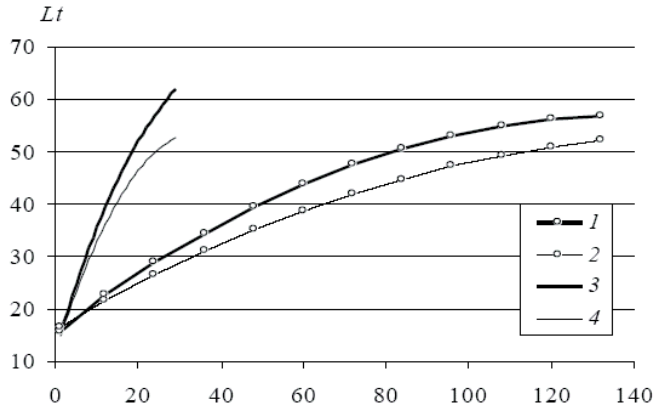


Fig. 5.2.8. Dynamics of increase in body size (Lt, cm) of adder females (*1, 3*) and males (*2 ,4*) during life in nature (*1, 2*) and in the laboratory (*3, 4*); age expressed in months

Table 5.2.5. Growth of adders' females in captivity (Lt, mm)

Age, month	Min	M	Me	dLt	Max	S	m	n
1		124	124			12.4	2.49	9
2		151	152	28		11.5	2.31	9
3	156		178	27	195	11.8	2.35	7
4	178		204	26	202	7.76	22.2	6
5	175		229	25	248	22	7.32	5
6	220	263	252	24	310	46.6	23.3	5
7	235	283	275	23	317	40.3	20.2	5
8	250	296	297	22	323	34.4	17.2	4
9	258	312	319	21	345	41.1	20.5	4
10	284	331	339	20	364	36.5	18.2	4
11	312	355	358	20	385	38	22	4
12	341	375	377	19	395	29.8	17.2	4
13	355	396	395	18	425	36.5	21.1	3
14	372	415	413	17	447	38.6	22.3	3
15	385	434	430	17	462	42.8	24.7	3
16	394	456	446	16	488	53.4	30.8	3
17	400	464	461	16	496	55.1	31.8	3
18	414	476	476	15	508	53.4	30.8	3
19	422	485	491	14	521	55	31.8	3
20	430	496	504	14	534	57.6	33.3	3
30	532	619	617		672	76.2	44	3

Table 5.2.6. Growth of adders' males in captivity (Lt, mm)

Age, month	Min	M	Me	dLt	Max	S	m	n
1		124	124			12.4	2.49	9
2		151	148	25		11.5	2.31	9
3	156		172	24	195	11.8	2.35	7
4	178		194	23	202	7.76	3.88	6
5	175		216	22	248	25.9	12.9	5
6	180	209	237	21	245	33.8	16.9	4
7	215	240	257	20	265	23.4	11.7	4
8	235	262	276	19	285	23.1	11.5	4
9	265	291	294	18	330	27.8	13.9	4
10	290	309	311	17	351	28.5	14.3	4

Age, month	Min	M	Me	dLt	Max	S	m	n
11	310	326	328	17	363	25.1	12.5	4
12	321	342	344	16	376	23.8	11.9	4
13	334	357	360	15	392	25.2	12.6	4
14	357	378	374	15	425	31.8	15.9	4
15	375	398	389	14	450	35.2	17.6	4
16	398	420	402	14	463	29.9	14.9	4
17	407	428	415	13	470	28.6	14.3	4
18	413	436	428	12	478	29.1	14.5	4
19	425	447	440	12	490	29.4	14.7	4
20	433	460	451	11	501	36.2	21.0	3
…								
30	515	521	543		528	6.51	3.76	3

Table 5.2.7. ANOVa for model of adders' male growth in captivity

Variation	The sum of squares	Degree of freedom	Dispersion	F-criterion
General	902853.6	99		
Models	182155.8	1	182155.8	20.9
Residual	720697.8	83	8683.106	$F_{(0.001,1,83)}$=11.57

Residual variation is a difference between the first two. Numbers of degrees of freedom are 1 and n – k appointed according to the statistical analysis of linear regression (Brownlee, 1977). Models for females and males have the identical significance value, $p < 0.001$.

The given equations of gain dynamics in captivity show that the gain in females initially is greater, than in males (32.4 against 29.6 mm), and the rate of gain decrease is higher in males (–0.037 against –0.41). As a result, females always are on an average longer, than males: on an average 619 against 521 mm in the 30th month of growth. Up to 12 months age female on an average increased their body length by 251, and males – by 218 mm and reached the size 375 and 342 of mm, respectively. These growth rates are significantly lower, than in adders from the southern border of an area (gain 430–475, length 590–670 mm) (Grubant et al., 1972). So strong gap allows speaking about finding one more adaptive character of the northern

populations of adders: decreased body size of poikilothermic animals in the north.

The similar impression gives a comparison of the maximum size of adders in Karelia and, for example, adders in Tambov (Kheruvimov et al., 1977); the former are about 10 cm shorter than the latter: males – 680 against 700 mm, females – 700 against 774 mm.

However, if field materials can show the positive influence of more long summer, then data on gain in the laboratory conditions testify the morphology-physiological specifics of northern populations and the selection made according to size decrease. The average dynamics of growth does not correspond to the development of any definite organism (Mina, Klevezal', 1976). It also concerns our adders (Table 5.2.8).

Table 5.2.8. Dynamics of in body length change (Lt) in group of adders aged (x, month) and parameters of model of monthly gain dLt=a·x+b in captivity

Age, month	2, ♀	4, ♀	9, ♀	3, ♂	5, ♂	6, ♂
6	310	220	225	245	180	230
7	317	263	235	265	225	253
8	323	290	250	285	250	276
9	345	302	258	330	280	288
10	364	320	284	351	292	304
11	385	367	312	363	310	318
12	395	390	341	376	340	332
13	408	425	355	392	355	345
14	425	447	372	425	368	361
15	456	462	385	450	389	378
16	488	485	394	463	415	402
17	495	496	400	470	421	414
18	508	505	414	478	429	422
19	521	513	422	490	436	435
20	534	525	430	501	445	†
30	654	672	532	528	521	
a	–0.0103	–0.05239	–0.03842	–0.19165	–0.08544	–0.02947
b	19.761	43.5797	28.0175	52.9095	47.9095	25.6271
F	40.0	66.0	22.5	23.5	26.7	23.2

Model parameters of the course of their growth show, that both its initial size and decrease in the growth rate differs individually. One can talk of slowly and quickly growing snakes. In Fig. 5.2.7 a small female and a large male are seen distinct, the male's growth rate only in a year of life in captivity became less, than in females.

Other important item is connected with higher level of adequacy of each model of an individual gain in comparison with models based on averages. It shows a really "smooth" and at that curvilinear growth course of each adder. As captivity conditions of animals were stable, the described growth dynamics has an endogenous nature.

The last item demanding discussion is the final size of animals. In 30 months of captivity, the body size of adders became close to the maximum size of animals from nature. It means that in laboratory conditions we succeeded to reproduce all "morphological" life of an individual, and these data can be used for comparison with natural growth dynamics of animals.

Comparison of growth in nature with that in captivity. Materials on intensity of adders' growth in captivity and in nature are not quite comparable. In particular, for technical reasons the body length of adders was not measured in laboratory for the last 10 months of their life, and during this period they outgrew the snakes in nature. The comparable data can be obtained if the highly significant models of growth built above are used, and to define the age of individuals at which they reach the identical (average) sizes in captivity and in nature (Table 5.2.9).

Table 5.2.9. Average (calculated) and maximal (real) size of adders grown in nature and in captivity

Conditions	Sex	Average		Maximal	
		Age	Lt, cm	Age*	Lt, cm
Nature	♀	11 years	56.8	?	68.0
				10 years	65.0
Captivity	♀	24 months	56.7	30 months	67.2
Nature	♂	11 years	52.1	?	68.0
				8 years	51.0
Captivity	♂	28 months	52.1	30 months	52.8

On an average, the adders' females living in captivity for 24 months reach the same body size as 11-year-old animals in nature (56.8 cm). As for males, they reach the same size (52.1 cm) in captivity and in nature, respectively at 28 months and by 11 years. In other words, in captivity adder's females obtain the annual "natural" gain for 2.18 months (65 days; 24 months / 11 years), and males – for 2.55 months (75 days; 28 / 11). In 65–75 days the adders living in laboratory realize growth potency as much as in 365 days in nature; for the adder 19–21% of a year is enough to realize its normal growth. 132 months (11 years) is the maximal life span of the adder in nature, so in captivity for 1 month they grow as much as in 5.5 months in nature (females; 132 months/24 months) and for 4.7 months (males; 132/28); one year of life in captivity is equivalent to 4–5 years in nature. These estimates are rather accurate as they average the linearly changing parameter, the gain. They provide for calculation of physiologically possible life span of the adder. A lot of large snakes caught at the age not less than 4–5 years lived in our laboratory in the mode of year-round activity for 5–7 years (until we lost them, generally, because of cloacitis) that is equivalent to 15–29 years of life in nature. Thus, the death because of old age (or of the diseases related with it) occurred in adders at physiological age of 25 and more years! (see section 7.6).

5.3. Weight gain

The body weight of animals is not only directly connected with the size, but widely varies depending on food supply and reproductive cycles (Mina, Klevezal', 1976). Dynamics of body weight in the adder during its life consists of the subsequent acquisitions and expenditure. The initial mass of newborn snakes (on average about 3–4 g) are higher in small broods, than in big ones (Saint-Girons, Naulleau, 1981). Newborns do not eat about 2 weeks, after that they hunt for 1–2 months, gaining additionally 1–3 g of weight before leaving for their first wintering (Popudina, 1976). The starving current year's young usually perish in wintering, but for small snakes it is simpler to feed themselves (Völkl, 1988). Further weight gain

of adders is individual in many respects: there are quickly and slowly growing individuals, size and body weight dispersion constantly increases with age (Grubant et al., 1972). Before sexual maturity (4–5 years) snakes gradually increase their weight due to feeding in warm period, the only expenditure often considered to be essential occurs in wintering (Popudina, 1976; Völkl, 1989), but at strict check it was found rather small (about 1% of body weight) (Schiemenz, 1978). Sexually matured males taking part in mating fights and pairing lose near 8% of weight in the spring (Sokolov, 1989) and restore this loss by feeding in summer (Pomianovska-Pilipink, 1974). In females 2–3-years reproductive cycle (Volsøe, 1944; Viitanen, 1967) is well expressed. Pregnant females hardly ever eat in the second half of summer (Biella, Schiemenz, 1980; Nilson, 1981).

The females keeping underdeveloped embryos from last year have the maximum weight (large individuals with large fatty supplies) (Madsen, 1989). After giving birth females lose 48–52% of body weight (Biella, 1979; Saint-Girons, Naulleau, 1981). Winter mortality of these exhausted females is higher, than in other population groups. To restore the normal weight it is necessary for the females to feed themselves actively for one or even two-three years, without participating in reproduction (Biella, 1979). The oldest individuals (both males and females) can have the weight, sufficient for reproduction, but, nevertheless, they do not participate in reproduction.

To describe weight characteristics of animals, various indicators are often used in the dependence of the body weight (W) on body length (Lt). These indexes of fatness (weight status) can be either simple $p = W/Lt$ (Yakovlev, 1985) or expressed in volume units of Ful'ton's formula $p = 100 \cdot W/Lt^3$ (Sin'dyukov, 1971); for adders a modification was proposed (Andren, Nilson, 1983): $p = W/Lt^{2.56}$. The power coefficient is applied as a correction for allometric increase in body weight when the body size rises. In our data it varies within 2.2–3.0, therefore we accepted the value 2.5; the multiplier 1000 gives integers: $U=1000 \cdot W/Lt^{2.5}$. The full information on animals sample is given by the equation of linear regression of a type $W=a \cdot Lt+b$ (Andren, Nilson, 1981), in logarithmic form –

$\log(W) = a \cdot \log(Lt) + b$ (Madsen, Still, 1988) that corresponds to the power equation of a type $W = b \cdot Lt^a$.

We see our task to characterize body weight proportions of adders on the island of Kizhi and to calculate the volume of fodder requirements in island population.

Body proportions. All the data on the linear and weight size of the adder obtained by us are submitted in the diagram (Fig. 5.3.1, 5.3.2). Body weight of mixed-aged animals in Karelia varies from 2.3 to 275 g.

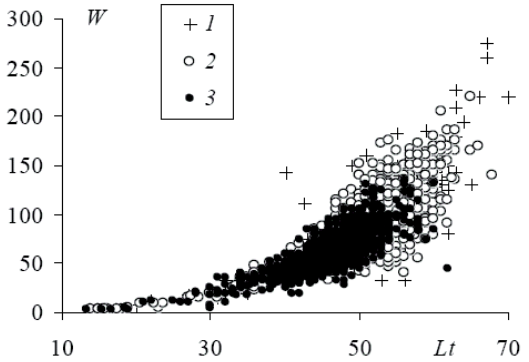


Fig. 5.3.1. Relation between weight (W, g) and body length (Lt, cm) of males and females of common vipers in Karelia: *1* – females from the mainland, *2* – females from island Kizhi, *3* – males

At that, rather accurate concordance of body weight to its length can be noted only in snakes with a body length less than 35–45 cm, in larger individuals this unambiguous connection is lost in the wide range of weight variations (50–250 g). The main reasons of so high variability are known. At first, let's consider a specific (genetic) peculiarity of a particular individual. The weight of newborns is already different (2–4 g), further the whole "fan" of individual weight growth trajectories, studied by us in the conditions of captivity (Fig. 5.3.3) is observed. By the 30th month individuals with equal opportunities for feeding differ in weight by 35 g (females) and 30 g (males). In our limited sample of animals dwelling in nature (Fig.

5.3.4) the same tendencies are seen: a trend towards weight increase is uniform in immature animals (till 4 years old) and this indicator varies widely in mature individuals. It is most pronounced in females.

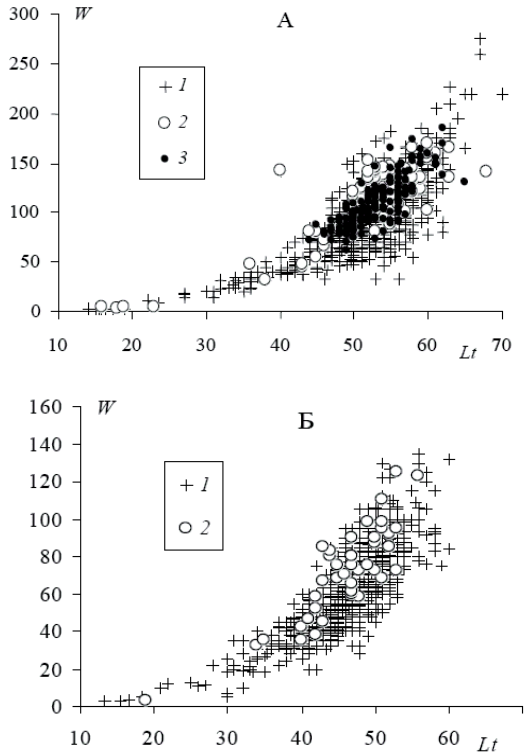


Fig. 5.3.2. Relation between weight (W, g) and body length (Lt, cm) of females (А) and males (Б) in Karelia: *1* – individuals with no apparent residual food in the stomach, *2* – individuals with apparent remnants of food in the stomach, *3* – pregnant females in July and August

Peculiarities of weight growth dynamics of females and males are readily apparent both in distinction between approximately even-aged individuals and in parameters of the regression equations (Table 5.3.1). So, the maximum weight of females is significantly higher, than that of males (275

against 135 g). Of adult animals having the same body length (40–60 cm), females are on average 20% heavier than males; their indexes of fatness are respectively 3.4 and 3.9. The power regression equations of body weight against body length in spring for individuals of both sexes differ a lot (Fig. 5.3.5): $W_{♀}=0.0012 \cdot Lt^{2.86}$, $W_{♂}=0.0082 \cdot Lt^{2.32}$.

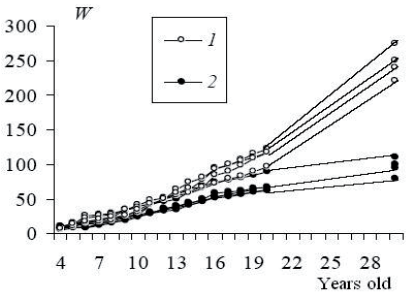


Fig. 5.3.3. Weight growth of individuals in captivity. Age is in months: *1* – females *2* – males

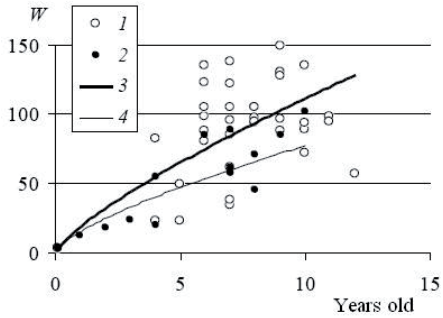


Fig. 5.3.4. Weight growth of individuals from the wild. Age is given in years: *1* – female, *2* – males, *3, 4* – power law trends

When the old-aged females came out of wintering and prepare for reproduction, they are significantly heavier than males due to the fatty stocks and large eggs.

However, in the fall after giving birth many heavy individuals sharply lose their weight, become exhausted, and as a result the regression line shifts downwards (Fig. 5.3.6); while males gain their weight to fall. As a result, in September the regression lines of both sexes practically coincide: $W_{♀}=0.0015 \cdot Lt^{2.77}$, $W_{♂}=0.0019 \cdot Lt^{2.72}$.

Table 5.3.1. Body weight and fatness of animals without food in a stomach

		Lt				W			$\frac{1000 \cdot W}{L^{2.5}}$
		n	M	min	max	M	min	max	
All females		1225	51.9	14	70	99.9	2.3	275	4.1
Pregnant		175	53.1	44	65	109	62	185	4.2
All males		1090	46.2	13.4	62	62.5	3	135	3.4
Females of size (Lt, mm)	10–21	10	16.9	14	20.5	3.9	2.3	8.5	2.8
	20–31	11	25.7	20.5	30	14.3	8.5	20	3.5
	30–41	38	36	31	40	32.3	15	55	3.4
	40–51	285	47.6	41	50.5	76.8	33	152	3.9
	50–61	734	54.5	50.5	60	108.8	33	185	3.9
	60–71	46	62.7	61	70	164.9	80	275	4.1
Males of size (Lt, mm)	10–21	6	16.8	13.4	18.5	4.0	3	4.9	2.9
	20–31	11	27	21	30	13.8	5	25	3.0
	30–41	94	37.5	31	40.5	36.4	10	60	3.4
	40–51	754	46.2	40.5	50.5	60.4	20	106	3.3
	50–61	191	52.7	50.5	60	86.5	50	135	3.4

Seasonal weight changes can be determined rather precisely as by average (and modal) values received in different seasons and according to the data of repeated capturing of marked individuals. The chart of body weight distribution shows that pregnant females (Mo=92 g) lose 42 g, or 44.5% (reproductive effort 0.445) at giving birth (Fig. 5.3.7). All females lose 16 g in the season (Fig. 5.3.8). It is theoretically possible to expect that throughout a year a stable adders' population has to gain the same weight as it has to lose. The loss of 16 g fixed by distribution, probably, is connected with that the giving birth females are absent in our captures in the spring of the next year as they leave from wintering much later, than the breeding animals (the grass grows high to this time, catching of snakes becomes difficult and we finish it).

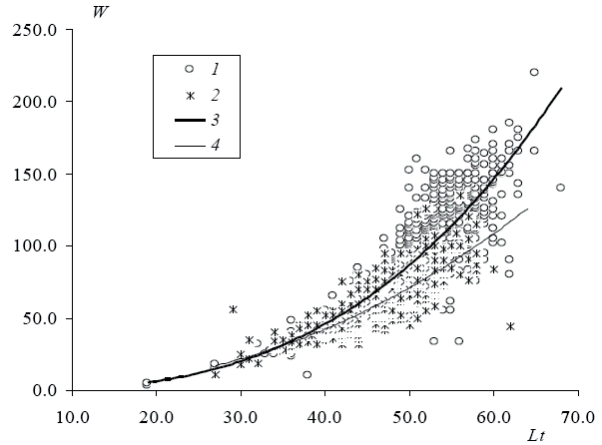


Fig. 5.3.5. Relation between weight (W, g) and body length (Lt, cm) of males and females of common vipers in May: *1* – females, *2* – males, the regression line W♀ = 0.0012·Lt 2.86 (*3*), W♂ = 0.0082· Lt 2.32 (*4*)

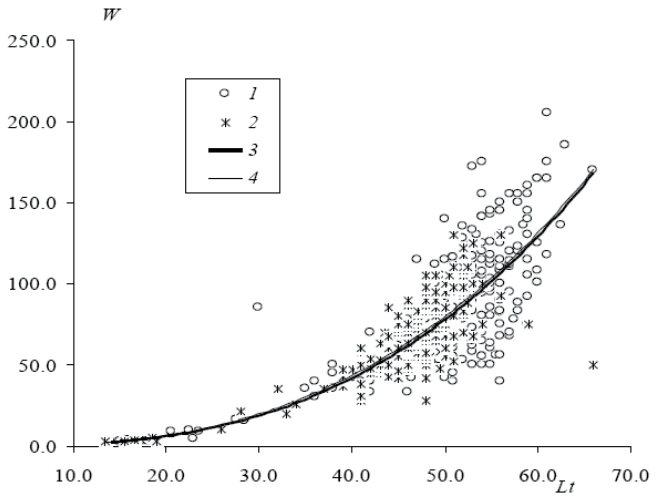


Fig. 5.3.6. Relation between weight (*W*, g) and body length (*Lt*, cm) of males and females of common vipers in September: *1* – females, *2* – males, the regression line W♀ = 0.0015·*Lt* 2.77 (*3*), W♂ = 0.0019·Lt 2.72 (4)

The females marked and repeatedly caught in a year also changed their body weight on average by –17 g (–23%): from –59 g (–54%) to +20 g (+14%) (n = 24). Integration of all weight losses and gains of all marked females within 1–3 years after the first catching gives on average –8 g, or –2% that does not differ significantly from zero (Fig. 5.3.9).

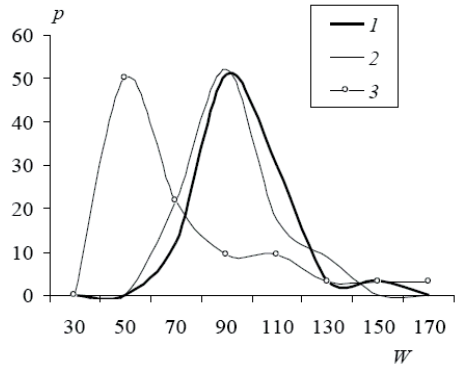


Fig. 5.3.7. Distribution of female vipers (p, %) on body weight (W, g) in August and September: *1* – pregnant females, in August, n = 79, *2* – pregnant females in September, n = 23, *3* – females have given birth in September, n = 32

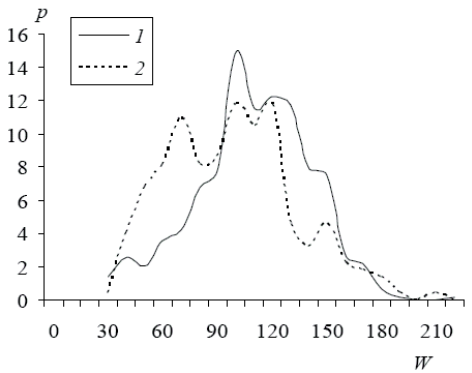


Fig. 5.3.8. Distribution of female vipers (*p*, %) on body weight (W, g) in May (*1*, n = 597) and September (*2,* n = 236)

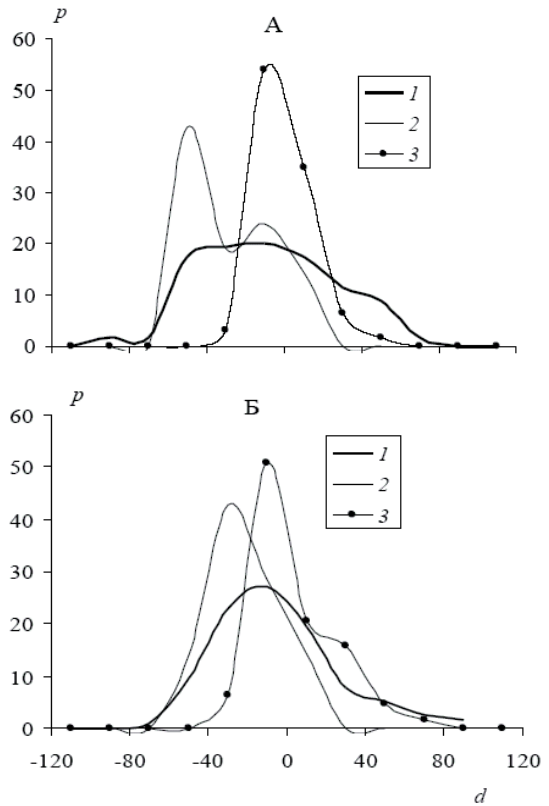


Fig. 5.3.9. Distribution (*p*,%) of absolute (А, dW, g) and relative (Б, dW / W,%) additional weight of male and female vipers: *1* – weight gain of females in one year, *n* = 24; *2* – gain of females during one-three years, *n* = 114, *3* – weight gain of males in one year, n = 64

In this case the annual loss of 16–17 g per female is explained, probably, by a three-year reproductive cycle. In the case of two-year cycle the number of the females breeding and regaining their weight for one year has to be identical and overall weigh change is zero (average losses of 42 g are compensated by same weight gain 42 g). If weight restoration after giving birth demands two years (in this case reproductive cycle is 3 years), the

share of females, which have lost weight and have not restored it yet, will be larger than a share of the restored individuals, and the general group gain will be negative. In this case the value of not gained weight has to be proportional to the share of females having three-year reproduction cycle. In our case 17 and 42 g correspond to 38 and 62%. It means that only one third of adult females are capable to reproduction, and 2/3 has not restored their losses after giving birth.

The males' weight increases on average by 26 g (37%) in a year judging by weight distribution (Fig. 5.3.10).

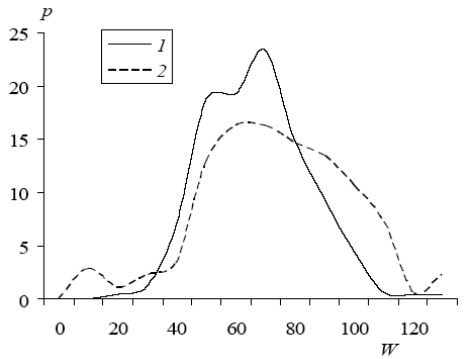


Fig. 5.3.10. The distribution of male viper (Lt > 35 cm) (p, %) on body weight (W, g): *1* – May, n = 602; *2* – September, n = 174

However, this effect is connected almost entirely with distinction in activity of diverse groups: in the spring the midsize mature individuals are active, in the fall the number of old large males grows (difference in the right slope of distribution). These are not capable to reproduction (hemipenises of such individuals are small, whitish or dried out at all). The second moment is that in spring males were usually caught as a rule after the period of mating fights and pairing, therefore they had lost their weight significantly (5–10%). In the fall this group gains the previously lost reserve of nutrients and considerably "grows heavy" (difference in the left slope of distribution). If to study the information on catching marked animals, we receive the reliable lack of an average annual gain – it was on av-

erage 2 g, or 4% (from –22 g to +43 g, from –29 to +69%). To the fall males compensate their spring expenditure for reproduction.

The main factor determining the body weight is feeding intensity. Under laboratory conditions, when animals are fed ad libitum, the weight and fatness (p = W/Lt 2.56) of individuals (with body length Lt > 35 mm) reached the greatest possible values ($W_{♀max}$ = 275 g, $p_{♀}$ = 4.9, $W_{♂max}$ = 117 g, $p_{♂}$ = 3.9) in 2.5 years. On the mainland of Karelia, where the number of victims many times higher than the number of snakes, adders also have the high rate of weight gain and fatness ($W_{♀max}$ = 275, $p_{♀}$ = 4.3, $W_{♂}$ = 125 g, $p_{♂}$ = 4.1). Under the conditions of limited food resources of the island these indicators are less ($W_{♀}$ = 220 g, $p_{♀}$ = 3.8, $W_{♂}$ = 132 g, $p_{♂}$ =3.4).

All the ratios between length and mass of an individual are reflected by the equations of power regression (Table 5.3.2, Fig. 5.3.11). To present distinctions more obvious, it is possible to build models with the fixed coefficients of proportionality (*b*) and to compare exclusively allometric coefficients (*a*). In our case coefficients *b* are close to 0.001 (b_2 = 0.001); the adjustment of models allows to compare coefficients a_2 (Table 5.3.2) emphasizing the noted differences. All differences considered above are well noted. Pregnant females seem to be the most fattened but those giving birth – the most exhausted; the weight difference between them is about 50 g over a length of the regression line.

Table 5.3.2. Parameters of model $W=b \cdot Lt^a$ for different subgroups of adder population ($_1$ – regression, $_2$ – model with fixed parameter b_2=0.001)

Group	Month	Place	a_1	b_1	a_2	m_a	b_2	n
Females	May	Kizhi isl.	2.32	0.0082	2.86	0.17	0.001	615
Females	September	Kizhi isl.	2.72	0.0019	2.89	0.26	0.001	185
Pregnant	August	Kizhi isl.	2.53	0.0064	2.92	0.43	0.001	177
Giving birth	September	Kizhi isl.	3.34	0.0001	2.81	0.27	0.001	35
Females		Karelia	2.81	0.0015	2.91	0.28	0.001	304
Females		captivity						
Males	May	Kizhi isl.	2.83	0.0012	2.91	0.22	0.001	597
Males	September	Kizhi isl.	2.77	0.0015	2.89	0,22	0.001	235
Males	May	Karelia	2.49	0.0044	2.87	0.23	0.001	173
Males	September	captivity						

The presented equations allow reconstructing weight growth in adders' females and males all over their life, accepting the maturity age equal to 5 years as well as two- three-year reproductive cycle in females (Fig. 5.3.12). In the case of two-year cycle, females become pregnant starting from the age of 5 years (weight is calculated according to equation $W=0.0064 \cdot Lt^{2.53}$), lose weight in the fall ($W=0.0001 \cdot Lt^{3.34}$), to the next fall they regain the necessary weight ($W=0.0064 \cdot Lt^{2.53}$) etc. (Fig. 5.3.12, 1). One can see that a female is likely to be pregnant four times over its life. In the case of three-year cycle there can be three pregnancies. More realistic variant assumes that from the first to the second pregnancy 2 years passes, to the third – three years, then the adult females can breed every year (Fig. 5.3.12, 2). In reality, of course, the various individual curves are realized that include from two to five pregnancies over a life, and eventually give the distributions of mass gain considered above (see Fig. 4.1.5, 5.3.9).

If the received curves of an individual trajectory of body weight are applied upon a database of the variability of this indicator within a population, it well seen that a distinct individual can realize all the range of weight variations, specific for a studied population (Fig. 5.3.13). The curve of an individual trajectory did not come into the right area of data dispersion as the weight dynamics of a midsize individual was modeled (that has the maximum size $Lt \approx 58$ cm to the age of 12 years, see Fig. 5.2.1). The area to the right of this value corresponds to the weight gain of an animals having big size (confidential interval for females aged 12 years is 44–66 cm). It is important to note that very large individuals possessing large fat stores seem to be able to breed every year and, besides, to hibernate with embryos (see section 4.2). Such individuals seem to eat during pregnancy and so they compensate the energy expenditure necessary for the development of eggs.

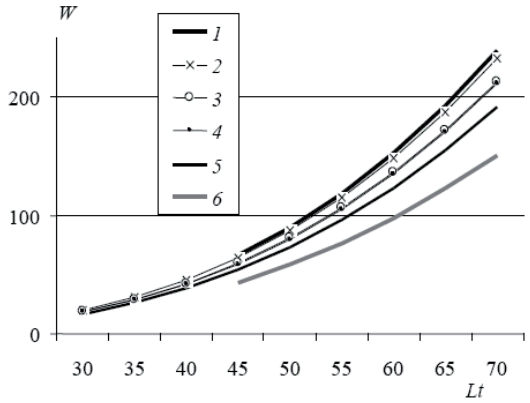


Fig. 5.3.11. Regression curves of relation between body weight (W, d) and the size (Lt, cm) W = b·Lt a for different groups of snakes at a fixed ratio b = 0.001: *1* – pregnant females in August 1998, *2* – all males in May, *3* – all females in September, *4* – all males in September (the same as 3), *5* – all females in May, *6* – females giving birth in September 1998

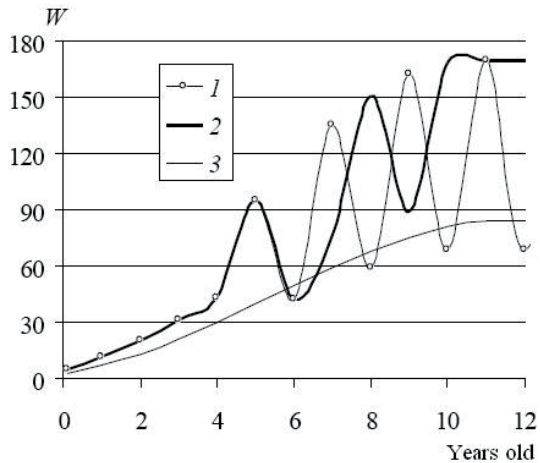


Fig. 5.3.12. Change in individual weight (W, g) with age (years): *1* – females with a two–year cycle of reproduction, *2* – females with gradually declining breeding cycle (3, 2, 1 year), *3* – males

For the verification of the received theoretical curves showing weight dynamics, the data of natural observations (Biella, 1979) were involved, they are presented on the chart (Abb.5, h. 122), scanned and digitized by us in the environment of MapInfo (Fig. 5.3.14).

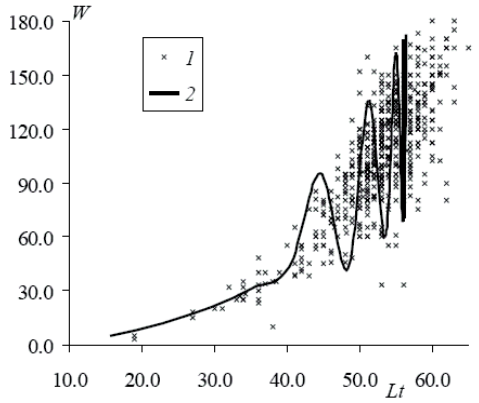


Fig. 5.3.13. Imposition of the dynamics of the mass of a separate individual (W, g) on a chart of relation between weight (W, g) and body length (Lt, cm), common viper females: *1* – all females, *2* – females with a two-year cycle of reproduction

As the real age of studied individuals is unknown, empirical series were shifted along the age scale of abscissa until initial values of observed weight is align with theoretical values. When it happened, the age of 9 years was assigned to the individual N1 by the time of the first capture, the age of 7 years – to the individual N3. The comparison of natural data with theoretical ones showed that a distinct individual (for example, N 1) for a number of years can really have wild body weight fluctuations covering all the range of values observed in nature, i.e. the model proposed by us is correct in principle. However, such dynamics is not obligatory for the adders' females especially for those breeding in 2 years or more; they can vary their weight in substantially limited range and form internal areas of females' weight dispersion.

Our data on animals, which were caught repeatedly two or three times, show a high variety of individual dynamics trajectories of body weight (Fig. 5.3.15, 5.3.16). To construct a diagram the animals' age was assigned in compliance with body length, taking into account the relationship between the size and the age considered above (see section 5.2). Despite the approximate character of the presented charts, it is well seen that the variability of adult females' mass is significantly higher, than that of males.

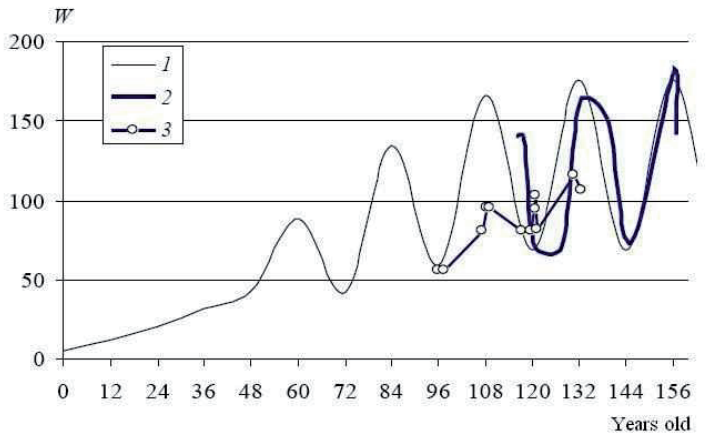


Fig. 5.3.14. The trajectories of mass (W, d) of separate common viper females: *1* – theoretical curve of mass dynamics of female with a two-year cycle of reproduction, 2, 3 – field observations (Biella, 1979, Abb. 5), *2* – specimen № 1 bred after one year, *3* – specimen № 3 bred after two years, age is expressed in weeks, the theoretical mass values are given for September

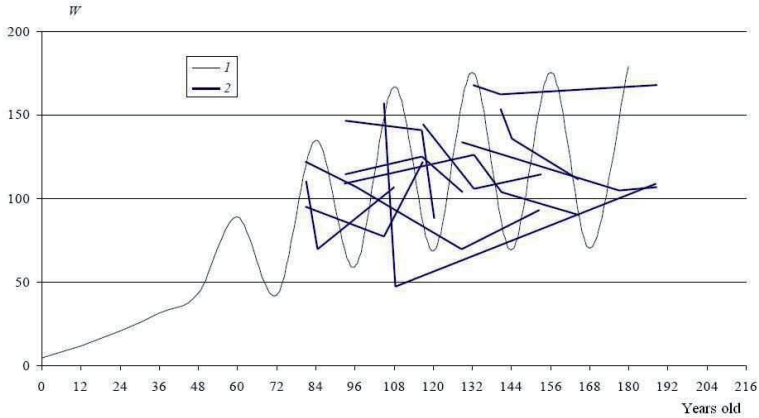


Fig. 5.3.15. The trajectories of mass (W, g) of individual common viper females: *1* – theoretical curve of mass dynamics of female with a two-year cycle of reproduction, *2* – our field observations according to re-capture, age expressed in weeks, the theoretical mass values are given for September

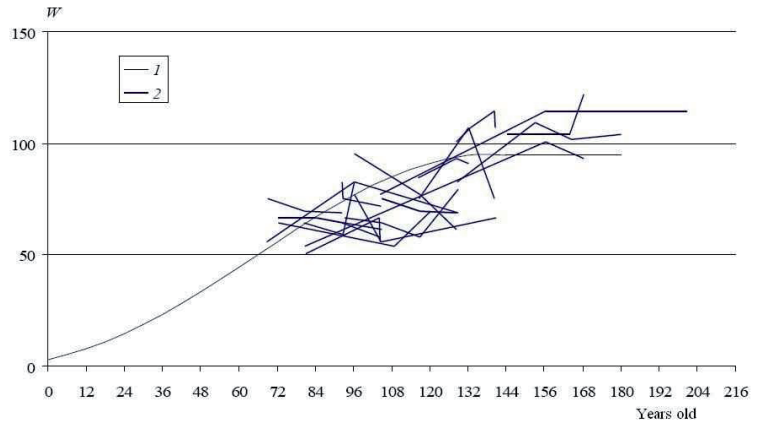


Fig. 5.3.16. The trajectories of mass (W, g) of individual common viper males: *1* – theoretical curve of mass dynamics of male, *2* – our field observations according to recapture, age expressed in weeks, the theoretical mass values are given for September

5.4. Interior characteristics

The intensity of physiological processes in an organism largely affects the size of internal organs exposed to essential modification variability in vertebrate animals (Shvarts et al., 1968). As for reptiles, especially the adder, few such researches generally deal with food objects, fatty bodies, sexual glands or embryos (Volsøe, 1944; Popudina, 1976; Nilson, 1981). We see the task in that to find out the ways of morphology-physiological "adjustment" of an organism for performing its specific function, considering general characteristics of interior indicators of adders having different status.

Materials and methods. Our research was based on the data of 47 individuals of the adder (34 females and 13 males) collected on the Kizhi archipelago (generally from islands Klimetsky and Volkostrov), decapitated and processed according to the technique of studying morphology-physiological indicators (Shvarts et al., 1968). The whole body weight was measured on spring scales (2 g), large internal organs – on cup (0.1 g) and electronic (0.01 g) scales, small internal organs – on torsion scales (0.001 g). Internal organs were determined by zootomic guid (Gurtovoy et al., 1978). The skin was peeled as "stocking", beginning with the neck; muscles partially remained on the head. Intestines were weighed without contents. To calculate the interior indexes, the total body weight was taken without food objects. To calculate the indexes of pregnant females the values of body weight were used without embryos and eggs.

The sample of animals was divided into five groups – dry females (5–11 years old, 14 ind.; there were no young females in the sample), mature females with eggs (7–10 years, 3 ind., caught in May), pregnant females (5–11 years, 20 ind., caught from July, 22th to August, 7th), young males (up to 4 years, 4 ind.) and adult males (5–10 years, 9 ind.). Interior characteristics were counted separately for each group. Indexes of a certain individual were calculated per mille (by the formula: 1000·W of organ / W of body), then for each group of statistical characteristics the arithmetic mean M and its error m (for a certain size of a sample n) were found. The regression equations of the increase of internal organs weight in ageing were calculated. To make the coef-

ficients of equations comparable with each other, the linear equations without a free member of a type W=ax, where W – the calculated body weight, x – age, a – proportionality coefficient were used. (As at zero age the mass of any internal is also equal zero)

The age of each individual in years was expressed in months beginning with the moment of birth in September. The average values of different groups were compared by Student t-test (Ivanter, Korosov, 2003). Distinctions between coefficients were considered significant if the averages for given organs also differed. The component analysis of a whole data set was carried out (without gaps, n = 33) (Korosov, 1996).

Topography of internal organs. In available literature we have not found the description of opened adder, therefore we give the illustration of the arrangement of innards in a sexually mature female (Fig. 5.4.1). Unlike many other land vertebrates, snakes use their body as a mean of locomotion. This function defines the main feature of its anatomy – all organs are located in the body cavity sequentially, they slightly overlap each other; a lot of them have identical diameter, but differ in length. The kidneys are only partially overlapped (the right one is 6%heavier on average). Intestines have no loops and its length is approximately the same as that of body (in coiled embryos it is less than body length, see: Korneeva, 1976). Mature eggs and embryos are also located sequentially in a body cavity.

Interior habitus. The general interior structure may be presented as weight ratios of a certain averaged individual, for example, a sexually mature female with the average body weight of 79 g (Fig. 5.4.2, A). Some internal organs (the spleen, the kidneys, the heart, the liver) of adult adders correspond well to the organs of the wintering females of the dark vole (*Microtus agrestis*) weighing 50 g by their size and so by physiological load (Ivanter et al., 1984).

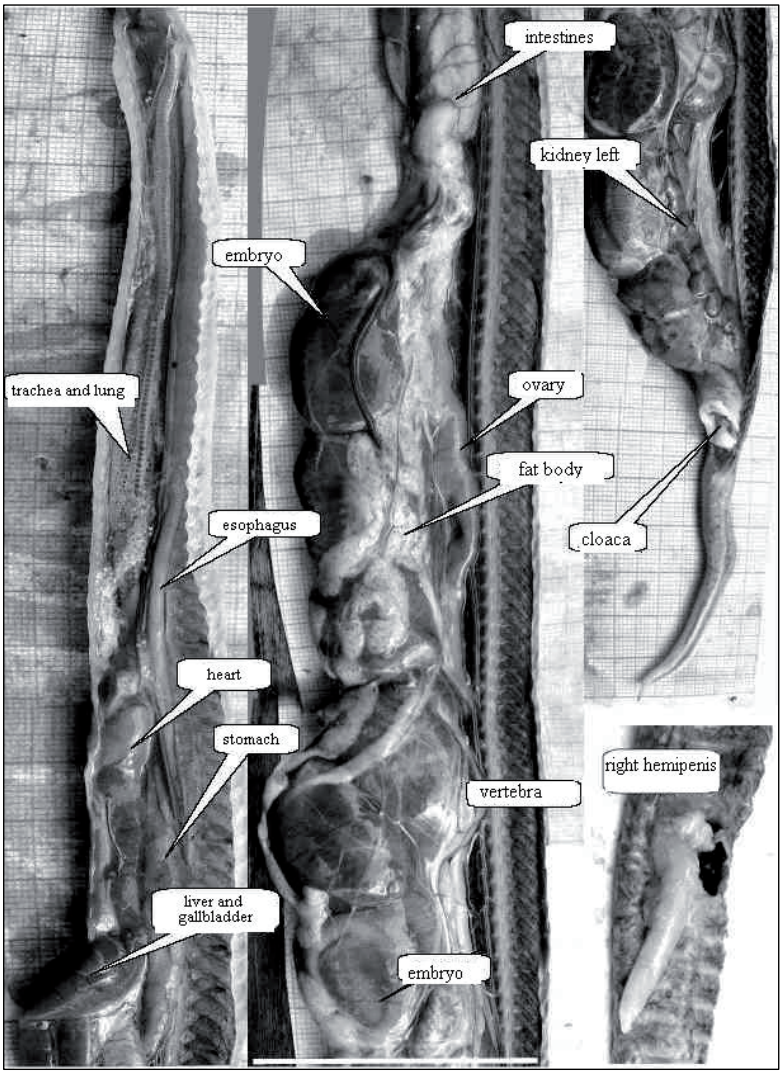


Fig. 5.4.1. Viscera of the common viper (prosection 07/08/2006)

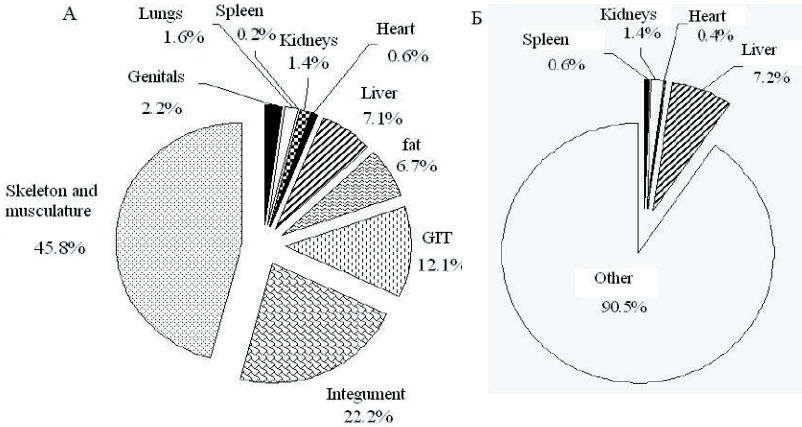


Fig. 5.4.2. Relation between weight of the internal organs of common viper (A, 14 barren females) and field vole (*M. agrestis*) (B, 9 wintered females; Ivanter et al, 1984, tab. 35)

Thus, the heart index in adders is even a little higher than in voles, but in general it corresponds to the index of all mammals, 6 ‰ (Shmidt-Nielsen, 1988). It is possible to speak about an evident hypertrophy of the heart of the adder in comparison with other reptiles having index of the heart 2.9–3.5 ‰, and even in comparison with adder snakes (3.3–5.7) ‰ (Schwartz et al., 1968). The hypertrophy of snakes' heart noted by authors is connected with a specific way of movement; as for the northern adder, an important role of the heart in thermal control providing heat exchange between external and internal areas of a body should be added.

Age dynamics of organs. As an animal grows the mass of innards also increases. Its specificity is connected with increasing general physiological load on females' organism due to puberty and pregnancy. Let's consider the changes of different internal organs of adders, beginning with females. Correlation between **the number of embryos** and the age is low ($r = 0.38$. fig. 5.4.3) and not significant ($p > 0.05$) (although the dependence between the size of a female and its fertility is real, see section 4.3). There

is also no dependence between **the mass of embryos** (eggs) and the age of a female (Fig. 5.4.4). At the same time the average weight and the index of fully developed embryos (38.1 g and 517 ‰) is almost three times larger ($p < 0.001$) than the average mass and the index of mature eggs (13.4 g and 179 ‰) (Table 5.4.1, 5.4.2).

Table 5.4.1. Indexes (‰) of an internal organs of animals of the different status (M – average, m – error of average, CV – coefficient of variation, %, n – sample size, a – coefficient of regression of change of body mass against age)

Groups		Internals										
		sexual	lungs	testises	kidneys	heart	liver	fat	alimentary canal	integuments	skeleton and musculature	eggs, embryos
Dry females	M	23.8	21.7		13	6.5	66.2	55.8	117	22.6	47.8	
	m	5.7	2.4		1.55	0.5	4.2	7.8	10.9	1.8	5.8	
	CV	90	34		14	32	22	43	25	30	44	
	n	13	5		42	15	15	9	10	14	14	
	a		0.01		0.01	0.00	0.05	0.05	0.08	0.16	0.33	
Mature females	M	23.0	24.8		8	6.1	75.2	56.0	98.7	21.7	46.2	179
	m	8.0	4.2		0.95	1.1	22.8	5.8	14.3	2.3	4.8	33.0
	CV	60	30		3	30	52	18	25	19	18	32
	n	3	3		21	3	3	3	3	3	3	3
	a	0.00	0.01		0.01	0.00	0.03	0.03	0.08	0.17	0.37	0.11
Pregnant females	M	7.2	21.5		14	5.6	42.4	41.7	204	25.1	48.7	517
	m	1.0	6.4		0.87	0.4	2.2	4.7	52.2	1.0	1.8	59.8
	CV	53	36		14	28	21	42	36	19	15	46
	n	16	2		23	16	16	14	2	16	16	16
	a	0.00	0.01		0.01	0.00	0.03	0.03	0.08	0.17	0.37	0.39
Young males	M	3.5			19	6.2	60.8	19.6		24.4	52.4	
	m	0.7			2.89	0.8	9.7	6.8		3.5	6.0	
	CV	43			4	26	32	69		29	23	
	n	4			30	4	4	4		4	4	
	a				0.01	0.00	0.04	0.01		0.16	0.38	
Adult males	M	21.3	21.5	19.4	18	5.9	56.4	61.3	131	19.7	47.5	
	m	2.9	11.3	4.2	2.97	0.4	6.8	20.4	31.4	1.9	2.9	
	CV	39	53	44	9	20	36	81	53	27	18	
	n	8	1	4	49	9	9	6	5	8	8	
	a		0.01	–	0.01	0.00	0.04	0.04	0.10	0.13	0.33	
Young males	M	3.5			19	6.2	60.8	19.6		24.4	52.4	
	m	0.7			2.89	0.8	9.7	6.8		3.5	6.0	
	CV	43			4	26	32	69		29	23	
	n	4			30	4	4	4		4	4	
	a				0.01	0.00	0.04	0.01		0.16	0.38	

It is obvious that the body of an adder embryo is built and gains weight not only due to the nutrients in an egg (as in oviparous reptiles), but also due to inflow of substances from outside, from mother's body through "placenta".

The analysis of the innards mass shows that the observed difference between the weight of embryos and weight of eggs is not compensated completely by any internal or their aggregation. Females with eggs (caught in the spring) have a little bit heavier liver and the gastrointestinal tract in comparison with the pregnant females (caught 2 months later), other innards (including fatty bodies) have almost the same weight (Fig. 5.4.5).

Nevertheless, pregnant adders are 20–25 g heavier than females with eggs. It is well seen on the graph drawn using another data (Fig. 5.4.6). For example, females with the body of 56 cm long have the average weight (with eggs) 118 g in the spring, and in July (with embryos) – 137 g.

Table 5.4.2. Average weight (g) of innards in adders

Organs	Females			Males	
	dry	mature	pregnant	young	adult
Sexual	1.49	1.7	0.56	0.06	1.38
Lungs	1.48	2	1.53	0.88	0.88
Spleen	0.14	0.15	0.1	0.1	0.35
Kidneys	0.92	0.64	1.14	0.65	2.16
Heart	0.43	0.46	0.42	0.1	0.36
Liver	4.87	6.07	3.32	1.05	3.61
Fat	4.61	4.43	3.6	0.38	3.6
Gastrointestinal tract	7.59	7.33	10.4	2	7.24
Skin	14.78	16.7	17.5	4.05	11.33
Musculoskeletal system	30.05	34.7	38.4	8.95	27.94
Eggs	13.4				
Embryos	38.1				
Sum	79.04	88.8	124.4	15.24	58.84

Where can females gain additional weight for the development of embryos? Obviously, there is one source – the food objects which adders

can consume and digest from May to June (females start eating right after they come out of wintering – see section 2.2).

Can the female gain missing 25 g (38.1 – 13.4 = 24.7) for so short period of time? The observations in nature show that they manage to do it – one needs only look at the graph showing the real weigh gaining of adders, it can reach 100 g during one season (see Fig. 5.3.14).

Taking into account the high extent of food assimilation in adders (up to 86% of fresh weight, see: Pomianowska-Pilipiuk, 1974), to gain weight in necessary proportion an adder requires additionally only 30.5 g of food, or 2–3 frogs of 15 g each (see section 5.5). At the same time, it must be kept in the mind that the discussed proportions represent average values and in reality the weight gain must not be so large for a certain individual.

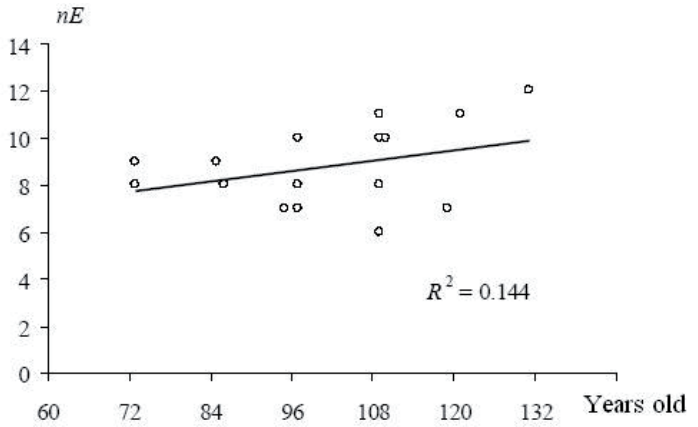


Fig. 5.4.3. Dependence of the number of embryos (nE) on age of a female viper

As a whole, the older the animal, the greater is the mass of ***reproductive organs*** (ovaries, testicles) (Fig. 5.4.7.). However, ovaries of pregnant females significantly lose weight in comparison with dry ones. Among males the minimum mass of testicles (0.8 g) was noted it the oldest individuals (9 years). The index of both hemipenises of an adult male with large testicles (1.5 g, 17 ‰) was 11.1 ‰ (960 mg).

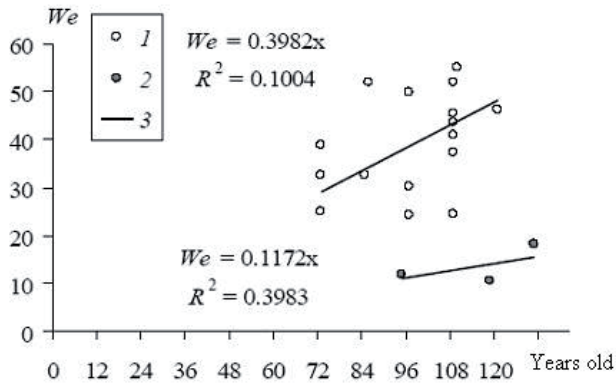


Fig. 5.4.4. Dependence of the mass of eggs and embryos on female viper age: *1* – females with embryons (July, August), *2* – females with eggs (May), *3* – Trends

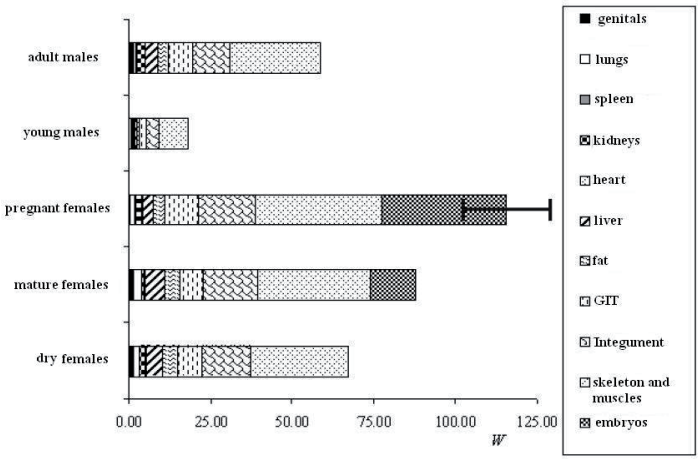


Fig. 5.4.5. Averaged summands of body weight (W, g) for five groups of common viper (delimited segment shows range of observed variability of embryons mass)

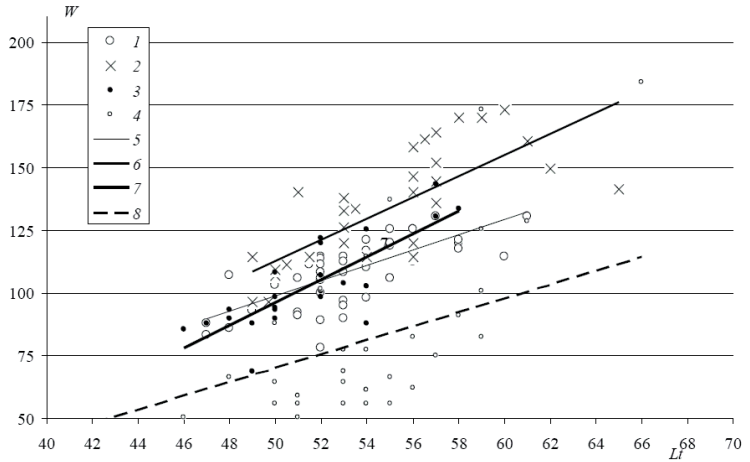


Fig. 5.4.6. Relation between weight (W, g) and length (Lt, cm) of the body of adult common viper females caught on 10–20 May (*1,* with eggs), July 20–24 (*2,* pregnant), 4–10 September (*3,* Pregnant), 6–10 September (*4*, without embryos), linear regression trends for the samples of May (*5*) July (*6*) September (*7, 8*)

The mass of the ***heart*** increases in proportion to time in all groups of adders and composes on average the same 6 ‰ in various groups (Fig. 5.4.8, Table 5.4.1). One can note that pregnant females have the maximum index. The heart index is usually considered as an indicator of locomotion activity and mobility of animals (Shvarts et al., 1968). However, in a lot of reptiles the heart has an important additional load: it provides the pumping of the blood for exchaging heat between cooler internal tissues of the body and external covering layers heated in the sun. High indexes of the heart in the adder dwelling in Karelia are connected, probably, with the increased role of the hart in thermoregulation of these snakes in the north.

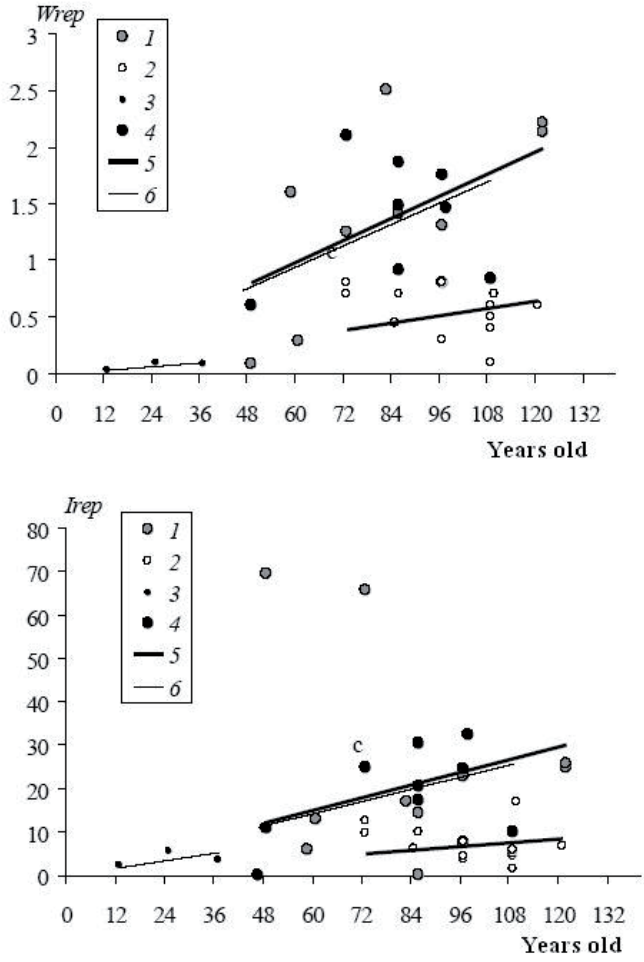
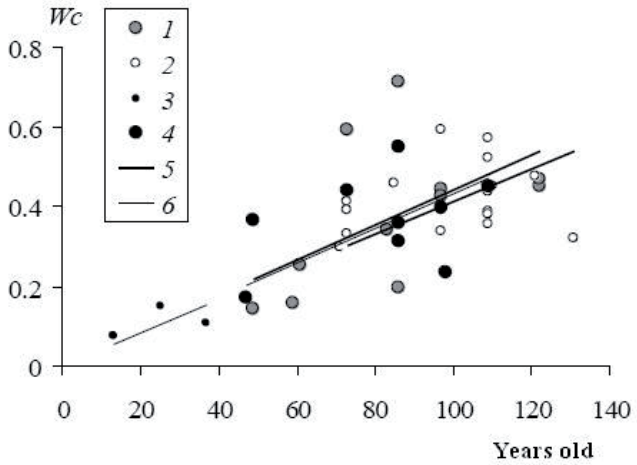


Fig. 5.4.7. Dependence of the mass (W, g) and index (I, ‰) of the reproductive organs on age of: *1* – barren females, *2* – pregnant females, *3* – young males, *4* – adult males, *5, 6* – trends for males and females



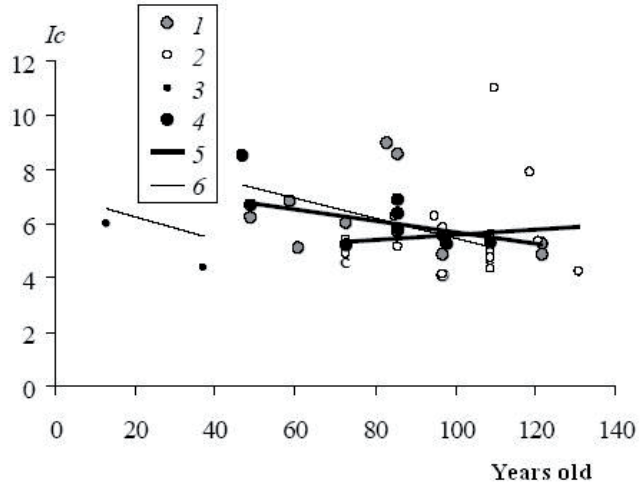


Fig. 5.4.8. Dependence of the mass (W, g) and index (I, ‰) of the heart on age (see the notation in Fig. 5.4.7)

The mass of the ***kidneys*** increases with age in proportion to the body weight, therefore the index of the kidneys remains almost the same

throughout life (Fig. 5.4.9). In pregnant females the index of kidneys is reliably lower, than in males, and in mature females with eggs it is less, than in other females (Table 5.4.1). The index of the kidneys is considered as an indicator of the metabolism intensity of an individual, which characterizes load growing on excretory system when the total physiological activity increases.

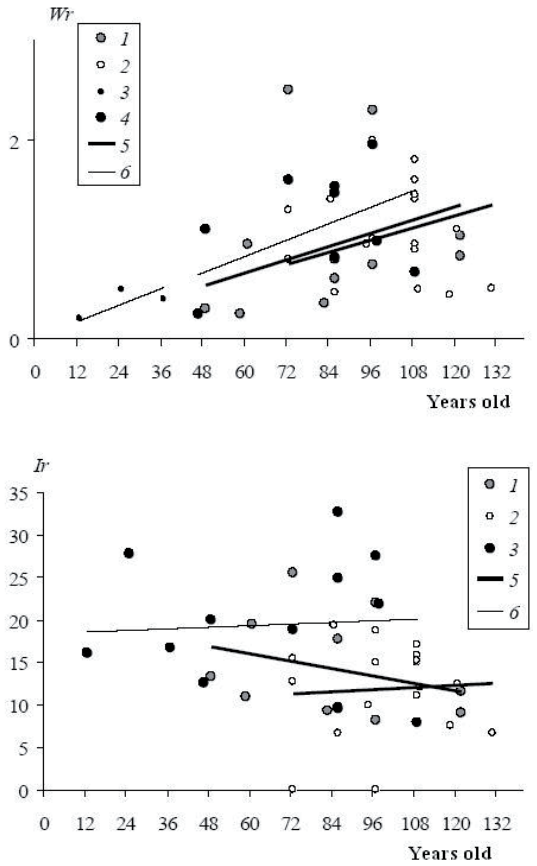


Fig. 5.4.9. Dependence of the total weight (W, g) and index (I, ‰) of kidneys on the age of vipers (notation as in Fig. 5.4.7)

However, in our case it should be assumed that metabolism is more likely to be higher just in adders' females, especially in pregnant ones. The interpretation of this inconsistent phenomenon is that even-aged males and females significantly differ in their body size. As smaller animal (males) usually have the enhanced metabolism, their relatively size of kidneys has to be higher, than that in females. If the indexes of the kidneys are compared with the general body size (weight) of animals (Fig. 5.4.10), then they do not appear to differ significantly in different groups of adders. In particular, the areas of variant dispersion became greatly expanded and the regression lines shift was not so significant. At the same time the fact of decreasing index of the kidneys in pregnant females demands additional study.

The limited data on the size of the ***right lung*** (the rudiment of the left lung of 1–3 mm size is well distinguishable) evidence its constant enlargement with age, with rates identical in adders of different sexes (Fig. 5.4.11).

The mass of the ***liver***, a barrier organ, where the reserve of glycogen and fat is kept, is defined in many respects by the intensity of vital activity of an animal (Shvarts et al., 1968). Extreme living conditions (hunger, physical exercise) lead to fast expenditure of the reserved nutrients and decrease in mass of the liver. On the other hand, constant, but not extreme increase in load (not connected with intoxication, pregnancy, adverse weather conditions) on the contrary, results in the intensive accumulation of stocks and growth of liver mass.

Our data show that in the adder the mass of the liver increases with age (Fig. 5.4.12). Thus all groups of animals have approximately identical indexes (60–75 ‰), except pregnant females (42 ‰) their indexes are significantly ($p < 0.001$) lower than others (Table 5.4.1). The reason is obvious: by the end of the second third of pregnancy (end of July) females partially spent reserves of nutrients in the liver (see Fig. 5.4.2); by September this deficiency grows more.

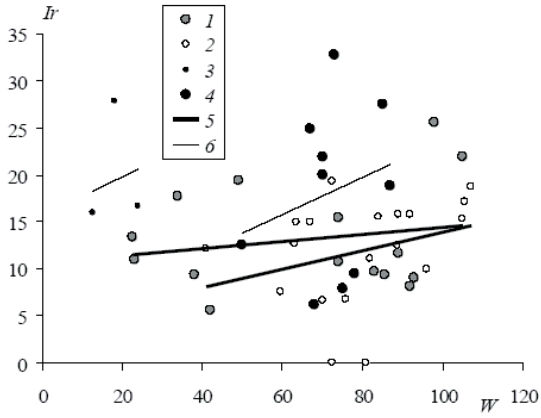


Fig. 5.4.10. Dependence of the index (*I*, ‰) of kidneys on the mass (*W*, g) of viper body (see the notation in Fig. 5.4.7)

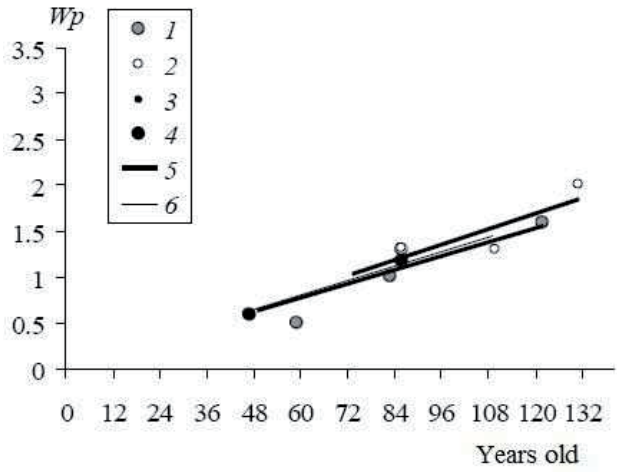


Fig. 5.4.11. Dependence of the lung mass on the age (see the notation in Fig. 5.4.7)

Abdominal fat as a reserve of nutrients can be demanded by a reptile organism with deficiency of food. Only when an animal has some necessary mass of fat, its sexual products mature and the animal becomes capable of reproduction (Biella, 1979). In the adder the mass of fat bodies increases with

age (Fig. 5.4.13). The relative mass of fat is minimum in young males (20 ‰) and pregnant females in the summer (42 ‰), but it is maximum in mature and dry females (56 ‰) (the average value of adult males is not indicative because there was one overweight fat male, but the median was 42 ‰) (Fig. 5.4.13, Table 5.4.1). However, all distinctions between groups are not significant. It is obvious that the volume of fat depot is defined both by a physiological state and by living conditions of a certain individual.

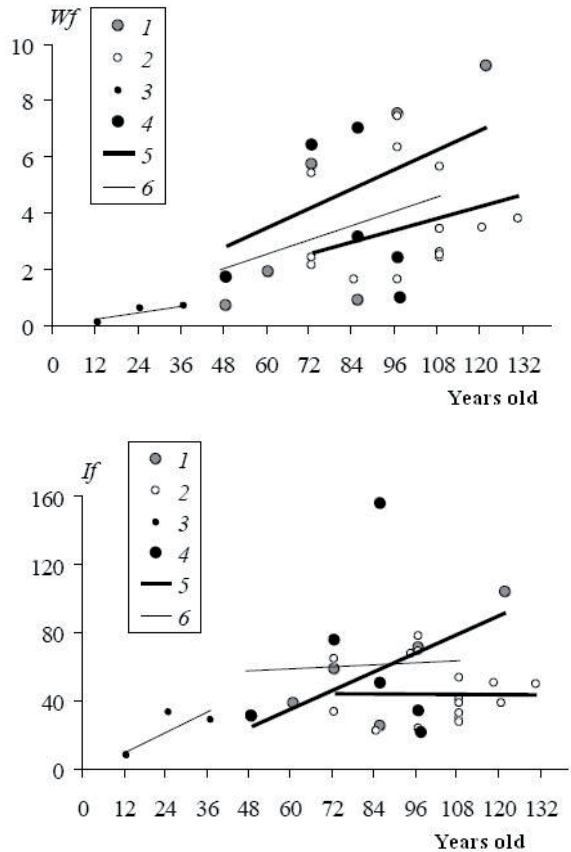


Fig. 5.4.12. Dependence of the mass (W, g) and index (I, ‰) of the liver on age (see the notation in Fig. 5.4.7)

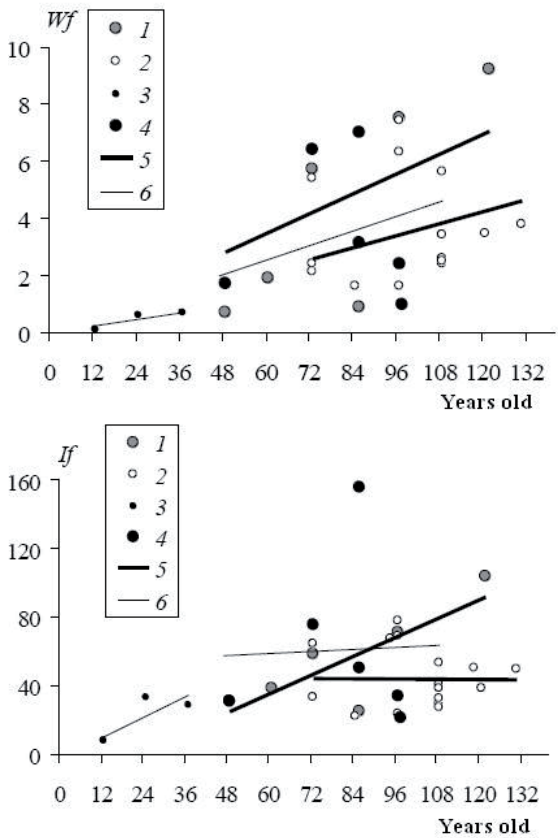


Fig. 5.4.13. Dependence of the mass (W, g) and index (I, ‰) of fat bodies on age (see the notation above)

The weight of the ***digestive tract,*** as a whole, increases with age, but its indexes have no distinction between different groups (Fig. 5.4.14, Table 5.4.1). There is no correlation with the body length ($r = 0.42$, $n = 21$, $p > 0.05$). Correlation with the body weight and fat mass is slightly higher the significance threshold ($r = 0.51$, $r = 0.62$). It suggests that the variation of mass of the gastrointestinal tract is connected to some extent with fat accumulation in the mesentery. i.e. it depends on the general fatness of an animal.

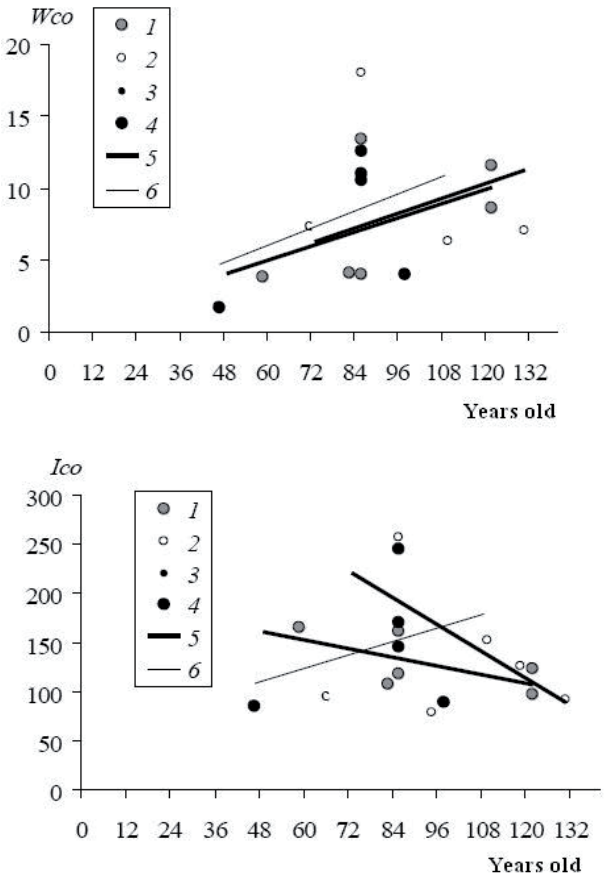


Fig. 5.4.14. Dependence of the mass (W, g) and index (I, ‰) of GIT on age (see the notation in Fig. 5.4.7)

In the adder the mass of ***integuments*** has quite definite positive dependence on age (Fig. 5.4.15). There are no significant distinctions between the integuments indexes in different adders' groups (Table 5.4.1). At the same time, the variability of this indicator is wide: CV ≈ 30%. It seems strange, because the integuments do not carry out any obvious physiological function, which

changes depending on living conditions, and for this reason the variation of skin mass has to be insignificant. The contradiction is resolved if one analyzes the graph of the dependence of the integuments' mass on the body size. The points corresponding to all observed animals lay densely in a limited zone near the curve of a power trend $Ws = 0.0016 \cdot x^{2.34}$ with the high determination coefficient $R^2 = 0.89$. The sharp decrease in variability of the considered indicator is evident. The mass of skin is defined actually only by the body size which can be very different even in even-aged animals.

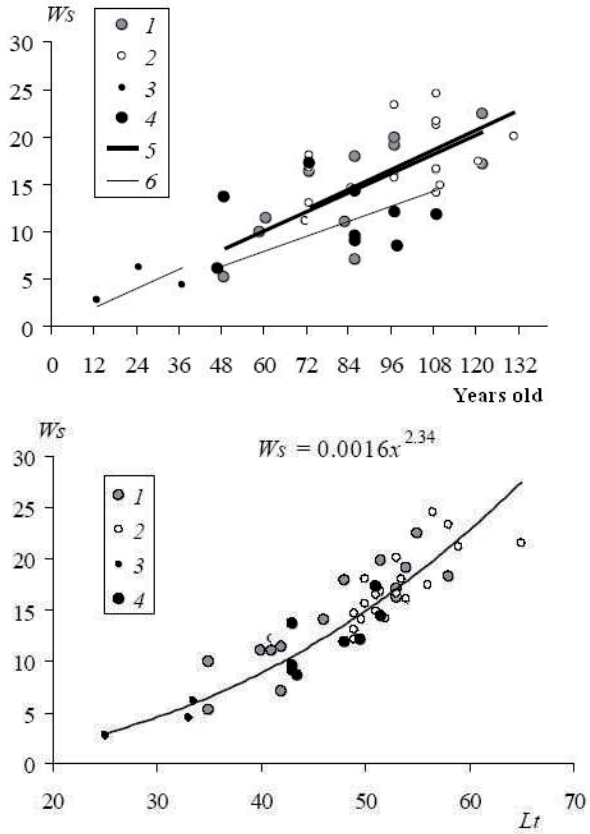


Fig. 5.4.15. Dependence of the mass (W, r) of skin on the age and body length (Lt, cm) (notation as in Fig. 5.4.7)

The joint mass of ***muscles and the skeleton*** has the same situation, as the mass of the skin. The musculoskeletal system (MS) increases in size with age, but only to the same degree as the general size of the animal (Fig. 5.4.16). The dependence of the mass of these organs on body length is clearly expressed by the power trend $Wm=0.0043 \cdot x^{2.29}$ with the determination coefficient $R^2=0.85$. Neither of the groups in the population of adders significantly breaks this simple dependence.

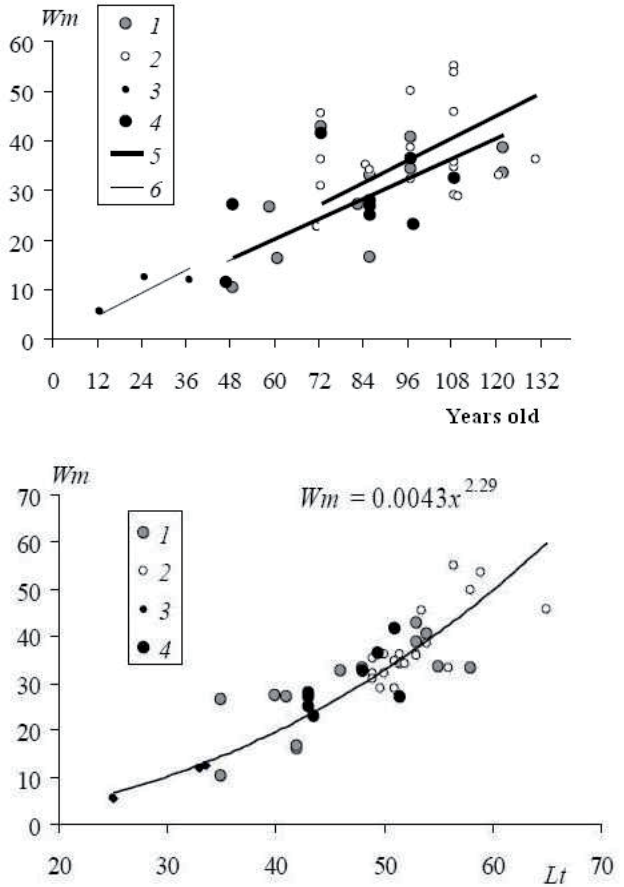


Fig. 5.4.16. Dependence of mass (W, g) of skeleton and muscles on age and body length (Lt, cm) (notation as in Fig. 5.4.7)

Interrelation of indicators. The general vectors of variability of all interior indicators were studied together by means of the component analysis. Before that, from the initial matrix of measurements those criteria, which were not defined for a lot of individuals were removed, as well as all the records (corresponding to separate individuals) containing gaps. So, the dimension of the analyzed matrix was reduced up to 9 variables and 33 individuals.

The matrix of correlations, initial for the component analysis, contains high values of coefficients; most of them are significant (Table 5.4.3). The reason is that the matrix includes mixed-age individuals, and the mass of all their innards varies widely. This fact affected the vector of factorial loads of the first component – all of them are positive and, except the mass of the genitals and kidneys, exceed the significance threshold 0.7 (Table 5.4.4).

Age variability of the initials mass of organs was expressed by the first main component keeping 65% of the general variability of indicators. On the axis of the first components the largest and heaviest individuals are in the range of great values on the right, small young – on the left. The second (also significant) component characterizes generally the condition of the genitals (without the mass of embryos).

On the chart the individuals with large innards are located in the range where the second main component is positive (on top); these are single females and sexually mature males. Individuals with light innards are located on bottom; there pregnant females are grouped. Besides the distinctions in the mass of genitals, the second main component clearly demonstrates the distinction in the liver weight ($u_2 = 0.59$); it has a smaller index in pregnant females, therefore they hold the position opposite to the vector of factorial load Wh (Fig. 5.4.17). The next in the order of size is a negative index of skin ($u_2 = –0.46$), on the contrary, shows that this indicator has the greatest value generally in the oldest pregnant females, in the largest individuals (located on bottom to the right). The index of the musculoskeletal system has the same interpretation ($u_2 = –0.33$). The rest factorial loads not considered, it should be noted that their values quite correspond to the ear-

lier revealed direction of difference between the studied groups of adders in the population.

The third component is not significant (its dispersion is less than 1).

Table 5.4.3. Correlation between the mass of innards, whole body and age of adders (the threshold of significant coefficients of correlation is 0.32 at p = 0.05)

	Body	Genitals	Kidney	Heart	Liver	Fat	Skin	MS
Genitals	0.41							
Kidney	0.51	*0.12*						
Heart	0.93	0.53	0.44					
Liver	0.71	0.65	0.41	0.73				
Fat	0.73	0.53	0.44	0.67	0.65			
Skin	0.94	*0.25*	0.47	0.85	0.51	0.66		
MS	0.93	0.38	0.53	0.89	0.53	0.66	0.93	
Age	0.73	0.39	*0.24*	0.68	0.43	0.50	0.71	0.70

Table 5.4.4. Relative factorial load of two first main components according to the data base of the innards weight in five adders' groups (see Fig. 5.4.17)

Indicator of mass		u_1	u_2	u_3
Body	W	1.00	–0.19	–0.07
Genitals	Wrep	0.58	1.00	–0.07
Kidney	Wr	0.57	–0.39	1.00
Heart	Wc	0.97	0.01	–0.12
Liver	Wf	0.83	0.25	0.22
Fat	Wh	0.79	0.59	0.31
Skin	Ws	0.93	–0.46	–0.18
MS	Wm	0.96	–0.33	–0.11
Age	x	0.78	–0.14	–0.63
Dispersion, %		65	12	9

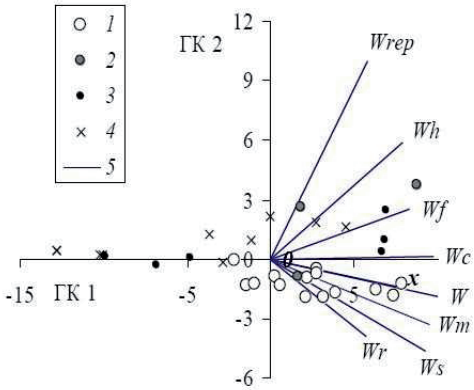


Fig. 5.4.17. Biplot of ordination of snakes on a plane of two principal components and factor loadings in the analysis of data on body and organs weight: *1* – females with embryos, *2* – females with eggs, *3* – barren females, *4* – males, *5* – projections of factor loadings (u·10)

In Karelia the common adder has a smaller body size, than on the southern edge of its area. By means of the technique of age definition it is established that the head of females and males increases in length at the same rate, but in males the rate of body length is lower. The relative size of the heart appeared to be larger, than in southern snakes that can be considered as an adaptation of thermoregulatory system to the difficult weather conditions of the North. The dynamics of body weight in adders' females is very complex and is connected with one-, three-year reproduction cycles, however these cannot be more than four during the adder's life.

Chapter 6

Metabolism

The present section is largely devoted to the ecological aspects of substance and energy exchange in an individual adder rather than physiological ones. The energetics of an individual is specific and little studied phenomenon. At the same time, the analysis of age and seasonal dynamics of the body size and weight (sections 4, 5), research of feeding in nature and in captivity (section 9), understanding of the mechanism and reconstruction of the processes of thermoregulation (section 3) provides the basis for a number of conclusions concerning the intensity of exchange processes in a certain individual and population of the adder as a whole. The energy balance equation of a poikilothermic animal (Shmidt-Nielsen, 1982) consists of the following components. The energy contained in food (consumption, C), is spent for providing the vital activity of an individual at rest (the basal metabolism, respiration, R_O), for movements and other behavioral activity (R_A), for increasing the size and body weight (somatic production, P_S) and for the formation of offspring (generative production, P_G). Besides this part of energy acquired from food (A), some share of it returns to environment in the form of excrements (E). The energy balance of population is expressed by formulas: $C = A + E$; $A = R + P$; $C = R + P + E$. Based on these formulas, the relationships between their components become the main characteristics of the features of energy metabolism of various groups of organisms. The most important of them are the coefficient of effective assimilation (A/C), efficiency of production (P/A), gross ecological product (P/C). Knowing the biomass of all population, it is possible to define the coefficient of relative efficiency (P/B) that characterizes role of the species in biocenosis.

This section deals with the search of these ratios for a concrete island population of the adder.

Energy demands of adder

Reptiles are capable to digest food very effectively (Gil'manov, 1987). The adder is able to assimilate up to 86% of the crude mass of a victim (Pomianovska, 1972; Lindell, Forsman, 1996), throwing out 14–20% in the form of semi-fluid excretes (mix of excrements and urine). The higher the body temperature, the more effective is digestion; the higher is the coefficient of assimilation (Naulleau, 1983). At a body temperature below 15°C digestion, probably, does not occur (Pomianowska-Pilipiuk, 1974). The digestion is so full that it is not possible to find almost any remains in excrement, except enamel of teeth of the victim, feathers and rings of marked chickens (Kuranova, Kolbintsev, 1983). The more food is eaten by an adder, the more is the increase in its weight. The adult individuals which have eaten during the season as much of food as their own weight (100% of own weight), spend it only on metabolism, not increasing their weight; if they have consumed 150–200% of their own weight, the increase of weight is up to 25% (Schiemenz, 1978). It is considered that current year's young have to eat three times more food, than their own weight (300%, Volkl, 1989) to receive the same gain 25% of their body weight for successful wintering. Really when an adult adder is kept in an enclosure it eats 77–225 g of food (Biella, Schiemenz, 1980). According to one calculation, the adder requires 358 kcal a year, or from 2 to 16.5 dark voles weighing 40 g each, total from 80 to 660 g of food (Lindell, Forsman, 1996). By other calculations, the annual demand of an adder is 15 rodents of 15 g each, 4 frogs of 9 g each, 5 lizards of 3 g each, in total 276 g of food (Zamolodchikov, 1993).

Large seasonal energy expenditure is connected with weight losses in males on a molting and mating activity and is about 6.6% (Sokolov, 1989) due to the energy stocks of a fat body (21.8% loss) and in the liver (12%) (Drobenkov, 2003). Females lose 48–52% of their body weight in giving birth as embryos, membranes, and liquids (Biella, 1979; Saint-Girons, Naulleau, 1981). In winter there occurs insignificant regression of fat bodies mass by 3.6%, that of the liver – by 6% (Drobenkov, 2003), the whole body – by 1% (Schiemenz, 1978), including due to dehydration. One of the

best indicators of snakes' food quality in different habitats is the relationship between body weight and its length (Leloup, 1976). For example, in the mountains and foothills of Altai the fat mass index of adders is significantly different: 13 against 9% (Yakovlev, 1983). The food supply also determines the correlation level between the length and body weight in adders. So, when the number of the dark vole was high on the islands of the Gulf of Bothnia, the correlation coefficient was $r = 0.94$; however, when the population of voles decreased, fat mass index of adders fell, destroying the correlation, $r = 0.5$, $p < 0.05$ (Andren, Nilson, 1983). To compare in detail the intensity of metabolic processes and the general wellbeing of different species of adders the regression equations of logarithmic body weight number against body length are used; in particular, more effective use of energy resources by melanists is revealed: they are heavier than colored forms regardless of their size (Andren, Nilson, 1983), although this statement is disputed (Madsen, Still, 1988). 42% of the acquired energy is used for providing the vital activity of an organism. It includes both resting energy expenditure for metabolism, and activity energy expenditure (basking, hunting, reproduction).

An essential part of energy expenditure due to the absorbed substance is energy metabolism. The normal metabolism of a large snake weighing 125 g (studied animals are relatively immobile, 25°C) require 5.2 $kcal/kg^{0.75} \cdot$days (Pomianovska, 1972). In small, young, quickly growing snakes their metabolic rate is higher (Dmi'el, 1972). The same concern embryos, therefore the metabolism intensity in pregnant females is higher, than in dry females of the same size (Birchard et al., 1984).

Carrying out recalculations of annual energy expenditure, it is necessary to remember that the rate of biochemical metabolic reactions changes following the body temperature of poikilothermic animals (Shmidt-Niyelsen, 1982). The results of such calculations will therefore depend on how well the author's notion about the species thermal biology corresponds to reality.

Of 100% energy included in food of the adder, 14% remains in the digested debris and is excreted with urine, and about 86% assimilates

(Pomianowska-Pilipink, 1974). It is a very high value which, depending on conditions and the status of an individual, can vary widely (for example, assimilation level of the moor frog varies between 6.8 and 40.1% (Ivanova, 1988). 42% of the acquired energy is used for providing vital activity of the adder's organism. The energy expenditure on physical activity of snakes, according to general opinion, is approximately equal to expenditure for metabolism (Dmi'el, 1972; Gilmanov, 1987) (another 42% of the assimilated energy). It is a very small value, as, for example, in mammals the ratio between field and basal metabolism may be 20 (Shmidt-Nielsen, 1982). The rest 16% of energy received from food are used to form the tissues of an organism and energy stocks (glycogen and fat).

To assess the adders' role in zoocenosis, it is important to investigate full energy expenditure of its population to provide its activity. Realistic estimates of energy expenditure for metabolism may be calculated, based on the specificity of thermoregulatory behavior of the adder in the North (section 6.1).

The production volumes can be estimated by investigating the body weight gain of the animals connected with the individual growth and restoration after periodical reproduction (section 6.2). Division of production into used for growth and for supporting is sometimes criticized (Vinberg, 1979), but as for the adder, it is valid, because the great energy expenditure for reproduction is readily determined. Association of these data allows in principle to find the energy balance equations for a certain individual and the island population of adders (section 6.3), as well as to calculate the volume of food, required for it (section 6.4).

In the present chapter, system logic demands more association of all fragments of scientific information than in any other. The "network" verification of one type of information by others is organized, including literary data; the assessment of the same parameters using independently received data massifs. Modeling and calculation of unknown and indefinable latent variables become an important and sometimes indispensable component. In this process no type of information is self-sufficient, it depends on other data and waits for confirmation by them.

6.1. Basal metabolism

Resting energy expenditure (basal metabolism) forms the essential part of energy balance in an individual even in poikilothermic animals. In a lot of snake species this value is about 20% of all energy received from consumed food (Gil'manov, 1987) and varies widely depending on the size and body temperature of an animal. The study of how these factors influence a basal metabolism is the main constituent of this section.

Problem of average body weight. One of the tasks of this chapter consists in calculation of energy demands of the whole island population of adders. The simple way is seen to determine metabolic characteristics for one "average" individual and, multiplying it by the number of snakes in the population, to find estimates for the whole population. The value "average body weight" is the sought parameter which is widely used in comparative and ecological researches. However, no population can function with average parameters (Korosov, 2002b). One value is not able to display a variety of life courses of its members. It is reflected, regarding the studied parameter, in the fact that although the metabolism intensity is higher in large animals, than in small ones, but between it and body weight there is not a linear, but curvilinear dependence. For this reason, the average metabolism will not correspond to the average weight, and multiplication by the number of snakes will give the underestimated assessment for the population.

Besides, there is a problem with definition of a true population indicator "the average body weight". This characteristic is often calculated on a limited sample with a random combination of mixed-aged individuals, and for this reason it does not have any ecological sense. The values calculated for such a sample generally characterize a technology of catching animals, but not the specific dimensional signs of animals, living in this territory.

A way out of this situation consists in calculation of these characteristics for physiologically (and not methodically) even-aged individuals, i.e. in restoration of the age structure of a population in general and in calculation of animals-size characteristics average for the population. Keeping reliability of calculations, the whole sample of animals can be divided into

three groups, then the group's averages can be defined, and after that the energy expenditure and food volume can be calculated in relation to these values. Thereby we divided the curve "metabolism – body weight" into some rectilinear segments within which the procedure of averaging is correct. Total population characteristics can be computed by multiplying the metabolism indicators average of the group by the number of animals in this dimensional group which can be defined much simpler (and which are more exact, than detailed age distribution).

We conditionally divided all adders into three groups – young individuals weighing from 3 to 50 g (the average value of 33 g is accepted), adults – from 50 to 100 (80 g) and old ones – from 100 and higher (120 g).

The calculation of the snakes' number in these three groups is based on age distribution (see section 8.5, Table 8.5.6) and the data on the weight gain in adders (see section 5.3, Fig. 5.3.4); all the data are given in Table 6.3.1. As is seen, the share of the females, having average body weight less than 50 g is 63%, males – 80%; the share of snakes weighing from 50 to 100 g – 28% of females and 80% of males, that of weighing more than 100 g – 10% (only females). It is obvious that these ratios can have fluctuations, especially due to the observed reduction in the island population of adders (see section 8), but we cannot receive more exact reliable values. Using these ratios, it is easy to determine the number of snakes in the studied groups at any current numbers of snakes' population. For example, in the average number of adders in the population 5200 ind., the considered groups have the following frequencies: 2000, 900, 300 ind. of females; 1600, 400 ind of males.

Caloric content of food and its assimilation. To calculate the food demands of the adder, we need the data on the caloric content of different types of a food. Some authors have performed the calculations of energy balance and corresponding food demands of an adders' population (Pomianovska-Pilipiuk, 1974; Zamolodchikov, 1993); they assumed that the caloric content of food is 5 kJ/g of live weight. At that, they proposed that the main source of food for the populations of snakes studied by them was small mammals, first of all voles. On the island of Kizhi the snakes'

diet generally consists of two species of frogs, to a lesser extent – common shrews, and even less – small birds. On the one hand, the energy capacity of these objects differs from the caloric content of voles; on the other hand, the authors give different estimates, interesting for us. Therefore, it is expedient to consider the caloric content of different types of food items. Insects have caloric content 23 kJ/g of live weight (Gil'manov, 1987), frogs – 3.9 (with water content of 80.2%) (Dol'nik, Postnikov, 1980), viviparous lizards – 4.2–7.64 (Gil'manov, Zamolodchikov, 1993), voles – 6.4 (Lindell, Forsman, 1996), house mice – 9.4 (Pomianovska-Pilipiuk, 1974). The comparison of these data based on the dominating food item of adders on Kizhi. (brown frogs) allows to accept the average figure – 6 kJ per 1 g of live mass.

Table 6.1.1. Assimilation (*A*) of food by an adder throughout one feeding cycle (the data by T.N.Hilkov)

Day	Tt°C	Weight of individuals, g					Energy exchange, joule/ind./h.				
		1	2	3	4	M	1	2	3	4	*M*
0	30	238	238	142	143	190.3	492.2	492.2	325.6	327.4	409.3
1	28.3	257.5	259	165	155	209.1	433.7	433.7	286.9	288.5	360.7
2	25.8	257.5	259	158	154.5	207.3	360.1	360.1	238.2	239.6	299.5
3	24.9	257.5	259	152	151	204.9	336.8	336.8	222.8	224	280.1
4	20.5	248	244	152	150	198.5	242.8	242.8	160.6	161.5	201.9
5	21.9	248	242	149	150	197.3	269.4	269.4	178.2	179.2	224.1
6	20.1	243	240	149	149	195.3	135.1	135.1	155.6	156.4	195.6
7	20	240	240	146	147	193.3	233.9	233.9	154.7	155.6	194.5
8	20	238	242	146	147	193.3	233.9	233.9	154.7	155.6	194.5
9	20			145	147	146.0			154.7	155.6	155.2
10	20			144	145	144.5			154.7	155.6	155.2
11	20			143	145	144.0			154.7	155.6	155.2
12	20				144	144.0				155.6	155.6
C, r		19.5	21	23	12	18.9					
P, r		0	4	1	1	1.5					
R, kJ/ind.							68.1	68.1	56.2	60.2	63.2
R, r		11.4	11.4	9.37	10.0	10.5					
A (only R/C)		0.58	0.73	0.45	0.92	0.67					0.64

The most important step is the assessment of digestion degree which in literature is defined as A = 0.86 (Pomianowska, 1974). This value is likely to be the maximum one depending on age and feeding conditions of the adder. Our simple experiments with weighing of a feeding large snake showed that the coefficient of digestion varied from 0.45 to 0.92 (Table 6.1.1).

After the ingestion of a victim (C – consumption) in the first day of a cycle and its digestion, animals reduced the weight gradually for 7–12 days. With respect to the change in preferred temperature during food digestion (see section 3.2), the expenditure for basal metabolism (R) decreased at that time from 300–500 J/ind./h. to 150–200 and amounted on average 63.2 kJ/ind. per a feeding cycle., that at the caloric content of 6 kJ/g (live weight) corresponds to 10.5 g of food. It was very little production (P), animals increased the weight very slightly (on average 1.5 g/ind./cycle); the rest – excrements. In a single feeding cycle the efficiency of assimilation was:

$$A = (P+R)/C = (1.5+10.5)/18.9 = 0.67.$$

This figure is significantly different from the value 0.86, given in literature. In essence, when the feeding cycle is once in 10 days, the food energy is sufficient only to provide only for metabolism and weak activity of large snakes. As in nature different strategy of food digestion can be realized, especially in young animals, our general belief that to accept the level of food assimilation equal to an average for several snake species, 0.7 (Gil'manov, 1987) for the further calculations.

Using these figures the formula of recalculation of energy into the mass of food objects will be the following: mass of food (g) = energy•assimilation/caloric content;$W_n = q \cdot 0.7/6$.

Calculation of metabolic indexes. In view of great complexity of the subject, we devote one part of this sub-section to the calculation technology of energy metabolism. The experimental data on energy metabolism of the adder are extremely poor and fully presented only in a few works

(Pomianowska, 1972; Pomianowska-Pilipink, 1974). Other way is to obtain data using the empirical equations of metabolism intensity constructed either for all snakes (Bennet, Dawson, 1976), or for the adder (Zamolodchikov, 1993). As different authors use various units of measure, we see the point in reducing them to a "common denominator" and show the technology how metabolic indexes of one kind are converted into another (Table 6.1.2). It should be noted that in the international SI system the unit of heat "calorie" is considered inadmissible and has to be replaced with joule, J (Sena, 1988). The recalculation given below takes into account the change in the units of mass (1000 g = 1 kg), time (1 days = 24 h.) and energy (1 kcal = 4.1868 J), respiratory coefficient (consumption of 1 ml of O_2 is equivalent to heat release of 4.8 kcal). Besides, sometimes weight is calculated per an individual, and to correct allometric dependence of metabolism on weight the power member is introduced 2/3 ($kg^{0.75}$).

In Table 6.1.2 the experimental data on oxygen consumption by adders are given (Pomianowska, 1972). For example, in the first individual this value is equal to 2.79 ml of O_2 per day related to 1 g. To find this value in kcal/$kg^{3/4}$/days, first the value 2.79 should be transferred into kilograms (·1000) and into kilocalories (·4.8/1000):2.79·1000·4.8/1000 = 13.39 (kcal/kg/days). The first individual weighs 80 g (0.08 kg) and the value $kg^{3/4}$ is $0.08^{3/4} = 0.15$ $kg^{3/4}$. As a result, instead of 2.79 ml of O_2 per day we receive: 13.39·0.08/0.15 = 7.11 kcal/$kg^{3/4}$/days.

In all studied snakes the intensity of basal metabolic rate is on average 5.23 kcal/$kg^{3/4}$/day. Just these volumes are authentically presented. (In brackets we notice that for the seventh individual the figures do not correspond to each other; the energy equal to 0.71 kcal/$kg^{3/4}$/days corresponds to oxygen consumption of 0.29 mlO_2/g/days, but not 2.91 as it is in the source table; corrections are made in Table 6.1.1.) We transfer these values into SI system units (kJ/kg/days): 13.39·4.1868 = 56.07. And we receive the average daily metabolism 37.48 kJ/kg/days.

Further let's calculate the same values with the equation of the dependence of metabolism on body weight $11.84 \cdot W_{KG}^{-0.23}$ (Bennet, Dawson, 1976). For the first individual we have $11.84 \cdot 0.08^{-0.23} = 21.79$, and on an

average – 20.32 kJ/kg/days. The reason of the lower expected value (20.3<37.5) consists in that the equation is derived for snakes with the body temperature of 20°C, and empirical data are obtained at 25°C.

Other equation (Zamolodchikov, 1993) considers both the weight and temperature of animals, however it is related to a particular individual (J/ind./h): $0.663(W_r^{0.8})\cdot e^{0.0744\cdot TT°C}$. In the example: $0.663(80^{0.8})\cdot e^{0.0744\cdot 25} = 141.8$ J/ind./h. Conversion into kilojoules (/1000), kilograms (/80, ·1000) and per day (·24) gives the value: 24·80·141.8/1000/1000 = 42.55 kJ/kg/days.

On average for all adders we receive the value 39.9, it is quite close to empirical one 37.5 kJ/kg/days. In further calculations we will use the last equation.

Formula of basal metabolism. In an example where the metabolism volume was calculated we used the empirical equation by D.G.Zamolodchikov (1993). The formula was previously used by R.M.Andrews and R.Pough (1985) for the description of resting energy metabolism in reptiles, it contains the power component W0.8, expressing the curvilinear dependence of metabolism on body weight (W), and the exponential member eT, expressing the curvilinear dependence of metabolism on body temperature (T_T).

D. G. Zamolodchikov calculated the regression coefficients for the published empirical data related to the adder by the regression analysis (least square method) (Pomianovska-Pilipiuk, 1974):

$0.663(W_r^{0.8})\cdot e^{0.0744\cdot T_T °C}$ (J/ind./h).

Unfortunately, is not always possible to describe accurately the curvilinear relationship between the variables by means of a regression analysis. The fact is that the basic least square method allows calculating a linear regression equation; therefore, before the determination of curvilinear regression coefficients the empirical data are smoothed logarithmically. This procedure gives too much weight to low values; as a result of this "automatic weighing" the values calculated with the equation poorly correspond to empirical data (Zar, 1968, cit. from: Gil'manov, 1987, p. 88; Korosov, 2002б). In our case (Fig. 6.1.1) the basal metabolic rate in the adder, ob-

tained from the given equation, not only does not cover the range of the natural variability of field data (related to the variability in body mass and to occasional variations), but the average theoretical estimates of metabolism (Fig. 6.1.1, 5) are also below the empirical averages (Fig. 6.1.1, 3).

Table 6.1.2. Recalculation of metabolism indexes of the adder (25°C), based on empirical data (*Pomianowska, 1972), on the metabolism equation for all snakes (**$11.84 \cdot W_{KG}^{-0.23}$, kJ/kg/days; 20°C; see: Bennet, Dawson, 1976) and on the metabolism equation for the adder (***$0.663(W_r^{0.8}) \cdot e^{0.0744} \cdot Tt°s$, J/ind./h.; see: Zamolodchikov, 1993) (values, discussed above are given in petit)

No of snake	1	2	3	4	5	6	7	8	9	Average
W, g*	80	108.3	104	123.5	139.5	154	68	123	123	
W, kg	0.08	0.11	0.10	0.12	0.14	0.15	0.07	0.12	0.12	
W3/4 (kg3/4)	0.15	0.19	0.18	0.21	0.23	0.25	0.13	0.21	0.21	
mlO2 / g / day*	**2.8**	0.48	1.75	3.68	2.45	3.44	0.29	1.07	0.83	1.86
mlO2/ind./day*	223.2	51.98	182.00	454.48	341.78	529.76	19.70	131.61	102.55	226
mlO2/ind./h.*	9.3	2.17	7.58	18.94	14.24	22.07	0.82	5.48	4.27	9.4
cal/ind./h.*	44.6	10.40	36.40	90.90	68.36	105.95	3.94	26.32	20.51	45.3
J/ind./h.*	186.9	43.53	152.40	380.56	286.19	443.60	16.49	110.20	85.87	189
cal/ind./day*	1071	249	873	2181	1640	2542	94	631	492	1086
kcal/ind./day*	1.07	0.25	0.87	2.18	1.64	2,54	0.09	0.63	0.49	1.09
kcal/kg /day*	**13.4**	2.3	8.40	17.66	11.76	16.51	1.39	5.14	4.00	8.95
kJ/kg /day*	**56.1**	9.65	35.17	73.96	49.24	69.13	5.82	21.50	16.76	37.5
kcal/kg3/4/day**	7.1	1.34	4.77	10.21	7.18	10.33	0.71	3.05	2.37	5.23
kJ/kg0.75/day**	29.8	5.61	19.96	42.72	30.04	43.22	2.97	12.76	9.92	21.8
kJ/kg /day	**21.8**	20.38	20.57	19.80	19.28	18.86	22.58	19.82	19.82	20.3
kcal/kg/day	5.2	4.87	4.91	4.73	4.60	4.51	5.39	4.73	4.73	4.85
J/ind./h.***	**141.8**	180.7	174.9	200.7	221.3	239.5	124.5	200.1	200.1	187
kJ/kg/day***	**42.6**	40.05	40.37	39.01	38.07	37.33	43.96	39.04	39.04	39.9

To solve this problem (accurate description of empirical data) is possible in two ways: first, to change the formula structure, second, to use another technology for the estimation of equations parameters instead of the least square method, for example, the direct forcing a model to fit the data by optimization methods (see chapter 14).

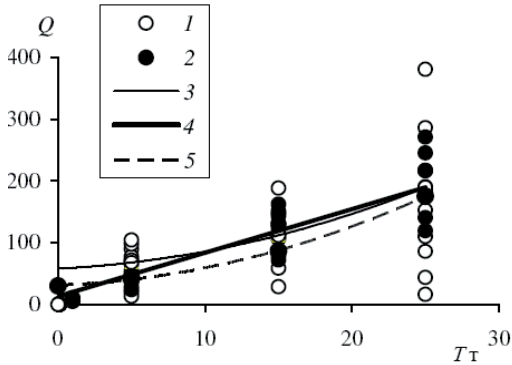


Fig. 6.1.1. . Dependence of basic metabolism of viper (Q, J / ind. / H) on body temperature (Tт ° C): *1* – empirical evidence (Pomianowska-Pilipiuk, 1974), *2* – values calculated by the formula (Zamolodchikov, 1993), *3* – empirical average, *4* – linear extrapolation of the empirical average, including the exchange at Tт = 0 ° C, *5* – average regression

As the charts shows (Fig. 6.1.2), at high temperature the first equation does not well conform to the substantial increase in metabolism of larger individuals. This allows including the weight (W) into the exponent indicator. After the coefficients identification based on empirical data, the equation became as follows:

$0.852\ (W_r^{0.8}0.8)\cdot e^{0.00049 \cdot Wr \cdot Tt\ °C}$ (J/ind./h).

Using the identification procedure, one can select coefficients to any other equation.

The second inadequate quality of the first equation is that calculated metabolism values seem to be very high at zero temperature. So, for W = 100 g, T_T = 0 °C it is $0.663\cdot (100^{0.8}) \cdot e^{.0744*0}$ = 26.4 (J/ind./h), although in terrestrial poikilothermic animals it should decrease theoretically to near zero (Schmidt-Nielsen, 1982). In other words, this equation cannot be used to calculate the metabolism in wintering adders. This problem (low temperatures consideration) could be solved, in our opinion, by the inclu-

sion of all animals at zero temperature into the empirical set of zero metabolism values. In all, therefore, the calculations involve the data on metabolism at 0, 5, 15, 25 °C (Fig. 6.1.2). The metabolism value is taken 0 J/ind./day at 0 °C.

Unfortunately, neither the new model nor the change in the data structure could help for the model description to approach the reality and they still predict high metabolic rate (Fig. 6.1.2 B) about 40 J/ind./h. at zero temperature.

Considering that in the vicinity of zero temperature the metabolism will be slightly different from zero, we eventually accepted a simple way of calculation and constructed a linear trend on empirical data (Fig. 6.1.1).

Metabolism and weather. The total basal metabolism of the adder, as that of other poikilothermic animals, is directly linked to a current body temperature. The estimates of daily respiratory volume in the adder given in literature are associated with the average body temperature. It is not quite correct, because the dependence between the body temperature and metabolic rate of poikilothermic animals is not direct, but curvilinear (Schmidt-Nielsen, 1982), so simple averaging will reduce the metabolism estimates. It seems more appropriate to use at least hourly dynamics of snakes' body temperature within 24 hours. The values of metabolism are calculated using the formula given above for each average hourly temperature, and then they are summed over 24 hours. Of course, the most accurate results could be obtained using the minutely body temperature of the adder. But calculation method based on the hourly average temperature should give good results, since the body temperature is rather inertial index, and it is maintained by the adder for a long time (20–40 minutes) even when the weather changes (see section 3.3).

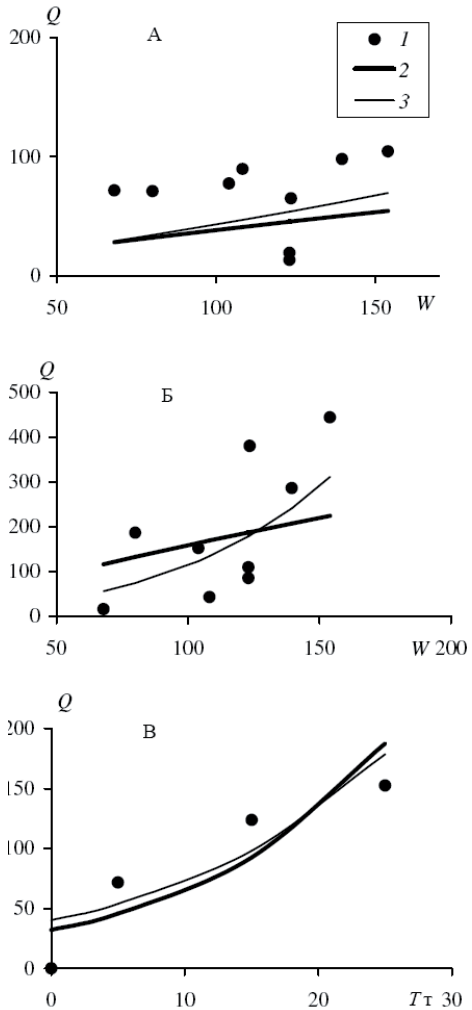


Fig. 6.1.2. Description of the dependence of viper metabolism (Q, J / ind. / H) on body weight (W, g) at body temperature (Тт) 5 ° C (A) and 25 ° C (Б) and median values for all individuals (ind.): *1* – raw data (Pomianowska-Pilipiuk, 1974), *2* – calculated by the formula $0.663(W^{0.8})\cdot e^{0.0744\cdot Тт}$, *3* – calculated by the formula $0.852(W^{0.8})\cdot e^{0.00049\cdot W\cdot Тт}$

To determine the average hourly temperature, we used our automatic models of the daily dynamics of snake's body temperature (weighing 33, 80 and 120 g) **in clear weather** (see section 3.4). As in the snakes having asmall mass the preferred temperature is lower than in large individuals (see section 3.2), we accepted as key parameters the following maximum voluntary temperatures: T_M = 30 °C for the individuals with the mass of 33 g, T_M = 33 °C for those with the mass of 80 g, T_M = 35 °C for those with the mass of 120 g. The rest parameters of the model remained the same – the minimum voluntary temperature is $T_{min.}$ = 18 °C, temperature sensitivity T_c = 8°C. For these parameters, hourly body temperature dynamics can be calculated based on a thermoregulation model and then the hourly metabolic rate on its basis and using the formula given above.

In cloudy weather the calculation of the energy metabolism is more complicated, than in clear weather, for it is necessary to take into account the share of heat that does not pass through the clouds and, accordingly, is not absorbed by snakes. These calculations are performed in section 3.4. As a result, the trajectories of the adders' body temperature under different weather conditions were obtained (Fig. 3.4.15, 3.4.16), and on the basis of them the hourly metabolism can be defined. In particular, in Fig. 3.4.17 the calculation of the daily dynamics of body temperature and basal metabolism in an adder weighting W = 120 g is shown. The total daily consumption is 3.71 kJ/ind./day, the average hourly one is 155 J/ind./h. Other figures are obtained by averaging. At the average body temperature of 19 °C the energy consumption is 130 J/ind./h, that is 16% lower than when calculating with the help of the thermoregulation model.

The value of basal metabolism per day calculated using the hourly dynamics is expected to exceed that obtained when using the average body temperature. The maximum difference is characteristic for variable cloudy, the minimum – for mainly cloudy. The general difference between the estimates obtained with our approach and averaging one (Pomianowska-Pilipuk, 1974) is 12 %. The seasonal dynamics is manifested in the fact that a basal metabolism decreases from spring to fall, following the decrease in heating time and average daily body temperature (Table 6.1.2).

In Karelia the weather is not only changeable, but mostly cloudy (see Table 3.4.5). Of 30 days in each month, the sun heats the ground well only for 7–8 days, the rest days it reaches the surface only for a limited time. The consideration of sunshine duration allows evaluating the heat conditions in any weather, and calculating the adders' basal metabolism over the summer. The values of daily metabolism in different kinds of weather are multiplied by the number of days in warm period, when this weather is observed, and the results are summed.

The presented data will allow estimating the annual metabolic rate of the adder (Table 6.1.3). For example, in Karelia of 120 days of a warm period, cloudy weather is observed on an average 34 days. An individual weighing 120 g having the daily metabolism of 3.7 kJ, only in cloudy weather consumes $34 \cdot 3.7 \approx 126$ kJ (with the accuracy to round-off error). A generalization of metabolism indexes for different weather conditions gives the seasonal expenditure for a basal metabolism equal to 432 kJ/ind./year in an individual weighing 120 g.

Table 6.1.3. Individual and group basal metabolism in adder

	Mass, g	Weather				Total
		mainly cloudy	cloudy	variable	clear	
Share of days		0.38	0.28	0.18	0.15	1.0
Days total		46	34	22	18	120
Metabolism 1 ind. kJ/ind./day	33	0.8	1.1	1.4	1.1	
	80	1.6	2.7	3.1	3.2	
	120	2.3	3.7	5.2	4.9	
Metabolism 1 ind. kJ/ind./year	33	37	38	30	20	126
	80	76	91	69	58	294
	120	105	126	113	87	432
Requirements in food, g/ind./year (1g=6kJ)	33	6	6	5	3	21
	80	13	15	12	10	49
	120	17	21	19	15	72

Winter metabolism. Most part of the year (about 240 days out of 360) adders spend in underground wintering shelters. From late September till the end of April the temperature in these shelters does not drop below –2.5 °C, because, if adders are cooled below this threshold, they die in a few hours (Terhivuo, 1967). The known data on the annual dynamics of the soil freezing temperature in Karelia (Reference book..., 1975) allow calculating the respiratory volume of the adder in winter. At the average temperature in a wintering chamber of 0–2 °C, an average individual weighting 50 g consumes the energy 2–16 J/ind./day (see Fig. 6.1.1). Over all winter one individual consumes up to 84 kJ, that is equivalent to 14 g of food, for all animals this value will be 60 000–400 000 kJ, or from 9 to 70 kg of food.

Metabolism in captivity. The energy requirements equivalent to one year of nature life can be assessed, based on the increase in body size. Earlier (see section 5) it was shown that in captivity adders' females and males require about 70 (65–75) days to increase their body size, equal to the annual natural one. Considering these timescales, it is possible to calculate the energy demands of snakes, providing an annual growth. The snakes dwelling in terrariums could choose their body temperature from 20 °C (in shade) to 30 °C (under the lamp) depending on the needs that change in feeding. The adders were fed on average 4–5 times a month or about once every 6 days. This means that for a week the body temperature of young snakes varied from 30 to 20 °C as is shown in section 3.2. The metabolism also varied following the dynamics of body temperature (Table. 6.1.4). The calculation showed that in captivity one regularly fed individual weighing 50 g consumes about 172 kJ/ind./day only for basal metabolism to provide an annual growth. These estimates differ from the natural ones (187 kJ/ind./day) only by 8 %. This very slight difference between the indexes obtained by so diverse methods and based on various data shows that our calculations are realistic. In general, the conclusion can be made about the close agreement of the adders' growth and its thermoregulatory behavior.

Table 6.1.4. Energy demands, providing the annual growth in the 3–5 year old adders, W = 50 g, $q = 0.663(W_г^{0.8})\cdot e^{(0.074\cdot TT\ °C)}$ (J/ind./h) (Zamolodchikov, 1993)

Parameter	Days after feedin (W=50 g)						Mean (M)	For 70 days
	1	2	3	4	5	6		
$T_т$ °C	30	28.3	25.8	24.9	20.5	21.9		
q, J/ind./h.	141	124	103	97	70	77	49.0	3431
q, kJ/ind./day	3.4	3.0	2.5	2.3	1.7	1.9	**2.45**	172

Metabolism of whole population. The data presented in previous sections, allow calculating the annual metabolism of the whole population of adders, and after that to move to the food requirement, providing a certain metabolic rate (Table. 6.1.5). As in wintering the losses compose about 1% of body weight (Schiemenz, 1978), they can be neglected.

Using the average energy capacity of 6 kJ/g of wet weight food, accepted earlier, it is easy to calculate the food requirement, covering the expenditure for metabolism. For example, for individuals weighing 120 g it is about 72 g (Table. 6.1.3). Using the proportions of snakes of different sizes (defined previously) in the population and taking their total number equal to 5200, we calculated the food requirement, that provide basal metabolism for the whole island population of adders; it amounted to 161 kg of food objects (Table 6.1.4).

Table 6.1.5. Food requirement for adders of three weight groups of adders for providing basal metabolism during warm season

Weather, indexes	The weight groups			Total
	33 g	80 g	120 g	
Mainly cloudy	6	13	17	
Cloudy	6	15	21	
Variable	5	12	19	
Clear	3	10	15	
For a year	21	49	72	
Share of individuals	0.69	0.25	0.06	1.0
Number	3588	1300	312	5200
Total, kg	75	64	22	161

The simulation results seemed to be contradictory to some extent. On the one hand, under similar conditions the general metabolism of large snakes is higher than that of small ones, but the intensity of metabolism is higher in smaller ones. For example, at 25 °C the hourly basal metabolism in an adder weighing 80 g is 137 kJ/ind./h and 1.7 kJ/g/h, and in an adder weighing 120 g these estimates will be 189 kJ/ind./h and 1.58 kJ/g/h. On the other hand, the number of large snakes is lower in natural populations. Combining these multidirectional features leads to that the annual metabolism and food consumption in large and small individuals are aligned (Table 6.1.4).

It makes us think whether we could use the daily dynamics of an individual having an average body weight for calculating total population metabolism. Taking into account the proportions of individuals of different sizes in the population (3600 young, 1300 adults, 300 old) and their average mass (33, 80 and 120 g), we can calculate the average mass:

$3600 \cdot 33 + 1300 \cdot 80 = 300 \cdot 120 = 50$ g.

Using the data on a seasonal requirement of adders of different size, we comprised the regression equation ($q = 3.518 \cdot W + 10.722$) and calculated the expected seasonal metabolic expenditure of a snake weighing 50 g, that is equal to 187 kJ/ind./year, and food requirement – 187 / 6 = 31 g alive/ind./year. Multiplying of these average indexes by 5200 (number of snakes) gives 162 kg, this value practically coincides with that calculated earlier. Thus, the extrapolation of energy requirement providing basal metabolism and using the average weight is quite correct and justified, but only in the case of a correct assessment of average body mass of individuals in the population. The annual basal metabolism can attain about 160 kg of food objects on a population scale.

6.2. Cost of individual's life

Let us consider the energy expenditure of one adder's female and one male from their birth to death at the age of 11–12 years (Table 6.2.1).

Production (P) of one individual was conceived of as two components: first, the sum of average annual body weight gains, second, the sum of seasonal gains, compensating expenditure on reproduction. The body weight of males increases gradually during the lifetime (see Fig. 5.3.4). The total annual gain $P = dW_{♂}$ is equal to a body weight and is 83 g in 11 years. The fat reserves in amounts of 8% are spent in spring and regained in summer, i.e. the sum of seasonal gains is 57 g/life. The growth production of females ($P = dW_{♀}$) is 120 g. The additional mass (embryos and nutrients, since 4–6 years), obtained by them during a three-year reproductive cycle is 50 g or 15 g each year ($dW_{♀}$). The sum of these components gives the female's final production of 240 g in 11 years.

The expenditure on basal metabolism (R) during lifetime was assessed using parabolic regression. It was made on the basis of the three points corresponding to the annual energy expenditure of individuals weighing 33, 80, and 120 g (see Table 6.1.2):

$$R = -0.0014 \cdot W^2 + 3.7 \cdot W + 4.3.$$

Plugging body mass in the equation, we determined the energy requirement for individuals of all ages. So, eight-year-old males weigh on average 66 g and spent on the metabolism $R = -0.0014 \bullet 66\ 2 + 3.7 \bullet 66 + 4.3 \approx 245$ kJ/year. Total metabolism expenditure in females is 2907, and in males it is 2079 kJ during their life (Table 6.2.1). The activity energy expenditure was considered to be equal to the basal metabolism.

Using the coefficients of the food assimilation (0.7) and food calorie content (5 kJ/ind.), the amount of food needed for metabolism and activity was estimated:

$$R{\cdot}2\ (g) = 2{\cdot}0.7{\cdot}\ R\ (kJ) / 5\ (kJ/g).$$

In our case: $R{\cdot}2 = 2 \bullet 0.7 \bullet 245 / 5 = 69$ g of food. Taking into account the assimilation coefficient 0.7, we transformed all the weight gains into the amount of food. In total for 11 years of life, adder female has to consume 1200 g. of food, males – 800 g.

On the island of Kizhi, the main food objects for adders are grass frogs and moor frogs. Their average weight is 14 g., therefore an adder fe-

male consumes 77 frogs, a male consumes 52 frogs. The natural variability range of the food amount for the adder can be calculated based on the variability of body size, which mainly depends on the variability of body weight, and hence the basal metabolism. The coefficient of body size variation is about 15% at any age. Applying it for estimating food requirement, we derive the range of food consumption for one individual: for females – 60 to 90 frogs, for males – 40–70 frogs

Table 6.2.1. Individual (dW, g) and total (dW • N, g) weight gain in adders of different ages, number (d, ind.) and biomass (Wd, d) of dead animals

	Age												Total		
	0	1	2	3	4	5	6	7	8	9	10	11	kJ	g	g of food
W♀, g	3	13	25	41	55	65	75	85	94	103	111	120			
W♂, g	3	8	17	29	40	47	54	60	66	72	77	83			
P = dW♀, g	3	9	13	16	14	10	10	10	9	9	9	9		120	172
P = dW♂, g	3	5	9	12	12	7	7	6	6	6	6	5		83	119
dW♀, g					15	15	15	15	15	15	15	15		120	172
dW♂, g					5	5	6	7	8	8	9	9		57	82
R♀, kJ/year	16	51	98	156	205	242	277	310	342	373	403	432	2907		
R♂, kJ/year	15	32	66	110	153	178	201	224	245	265	285	304	2079		
R♀·2, g	4	14	27	44	57	68	78	87	96	105	113	121			814
R♂·2, g	4	9	19	31	43	50	56	63	69	74	80	85			582
Total, ♀♀, g	9	28	45	66	98	104	113	122	130	139	147	155			1157
Total, ♂♂, g	9	16	32	48	67	67	75	81	88	94	100	106			782

6.3. The energetic requirements of a population

Food requirements of an adders' population in general can be determined on the basis of the long-term and seasonal dynamics of body mass growth of animals. The dramatic effect of environmental relationship "production / biomass" is that a part of a population dies (under condition of maintaining relatively stable population size and biomass). Live snakes, grown up over the year compensate this loss by their body weight gain as-

sociated with size increase; this increase makes the all-population growth production. To evaluate it is possible, first, by using the data on the growth dynamics of animals of certain age, second, using the data on animals growing in laboratory and finally the data on a specific mortality.

One of the components of the energy balance is the expenditure for increasing the body weight associated with normal growth. On the basis of the data on the dynamics of the adders weight gain (see Fig. 5.3.4) it is easy to determine the annual gain in each age group (Table 6.3.1). Taking account of the average-age body weight gain of all snakes in nature gives the total island population sum of annual weight gain (Σ dWN) about 52 kg (females – 36 kg, males – 16 kg). This value represents a production (*P*) expressed via a body mass. Since the efficiency of digestion is 0.7 (see section 6.1), about 74 (52 / 0.7) kg of food is required to provide the normal adders' population growth on Kizhi.

The annual production can be estimated indirectly given that it equals to biomass of died individuals (under condition of the constancy of the population number). The information on capture and recapture showed that the mean specific (annual) mortality of adult females is 24 %, that of adult males – 38 % (see section 7). The reconstruction of an age structure suggests that immature animals have the mortality rate 15%, mature females – 28%, males – 38 % (see section 8). Keeping in mind that the population was divided into three size groups and knowing the number of snakes in these groups (see section 6.1), it is easy to calculate what proportion of the biomass is lost in each group per year (Table 6.2.1, Wd). For example, the number six-years-old adders' females weighing 75 g is about 351. 28 %, or 98 snakes of them die within a year, it is 7 359 g, or 7.4 kg expressed in terms of biomass. The total mass of annually dying females is about 48 469 g, males – 20 084 g, and in sum – 68 kg. Using the assimilation coefficient, it follows that the renewable biomass is equivalent to the food consumption of 97 (68 / 0.7) kg of food. This estimate of production is only 25% greater than that of consumption obtained from the study of gains. It allows to assess food requirement of the island population to re-

ceive the "growth production", it approximately equals to 85 kg of food objects.

Table 6.3.1. Individual (dW, g) and general (dW* N, g) gains of mix-aged snakes, the number (d, ind.) and biomass (Wd, g) of died animals

Age	Females (d_{ad}=0.28)							Males (d_{ad}=0.38)						
	Lt'	W'	dW	N	dW·N	dN	Wd	Lt'	W'	dW	N	dW·N	dN	Wd
0	16	3						16	3					
1	23	13	9	382	3605	57	718	21	8	5	297	1353	44	331
2	29	25	13	376	4738	56	1411	27	17	9	285	2613	43	718
3	35	41	16	369	5904	55	2266	32	29	12	274	3234	41	1169
4	40	55	14	364	4978	55	3018	36	40	12	264	3153	40	1618
5	45	65	10	357	3691	100	6522	40	47	7	254	1757	38	1800
6	48	75	10	351	3467	98	7359	43	54	7	244	1591	93	5011
7	51	85	10	345	3281	96	8122	46	60	6	173	1074	66	3966
8	54	94	9	250	2302	70	6567	48	66	6	122	726	47	3104
9	55	103	9	181	1620	51	5241	50	72	6	86	494	33	2369
10	56	111	9	131	1143	37	4125	51	77	6	0	0	0	0
11	56	120	9	95	810	26	3120	52	83	5	0	0	0	0
Total				3200	35 520	702	48 469				2000	15 994	444	20 084

Generative production, or the biomass of newborn animals can be estimated by the number of giving births females, equal to 330 individuals (see section 4.3), and the average weight of a certain brood, equal to 42 grams (see section 5.4). So, the biomass of newborns is 13 kg, which in food equivalent is 19 kg.

As a whole, the annual growth of the adders' population biomass is 85 + 13 = 100 kg that is equivalent to the consumption of 143 kg of food.

The individual weight gain in different age groups of females and males is estimated as 29 + 7 = 36 and 19 + 7 = 26 kg, in total – 62 kg a year, which in energy terms is equivalent to 372 000 kJ, and its compensation requires 89 kg of food objects.

The simulation model of the adder' thermoregulatory behavior gave an opportunity to determine the standard metabolism in animals of a different age. The annual metabolism of an individual weighting 33 g is 126 kJ

that is equivalent to the consumption of 21 g of the food objects, of that weighting 80 g – 294 kJ (49 g), of that weighting 120 g – 432 kJ (72 g). Accepting that the number in each size group equals to 2500, 2000, 500 individuals, we find that in warm season the total expenditure on metabolism equals to 1 119 000 kJ, and the consumption is 187 kg of food. To this value we must add the winter metabolism expenditure – about 20 kg of food (see p. 126). The annual expenditure on all forms of activity in adders are considered to be equal to the basal metabolism expenditure (Gil'manov, 1987), which is compensated by 186 kg of food in our case.

Taking into account the growth expenditure (0.5 GJ, 140 kg), basal metabolism (1 GJ, 180 kg), and activity (1 GJ, 180 kg), the requirement of the island population of adders is 2.5 GJ in energy, 500 kg/year in food.

The energy balance of the population of adders on the island of Kizhi is as follows:

$C = A + E = R + P + E = 500 = 350 + 150 = 252 + 98 + 150$ (kg/year).

Considering the accepted value of the coefficient of effective assimilation as $A / C \approx 0.7$, we receive the production efficiency equal to $P / A = 98 / 350 \approx 0.3$, the gross ecological efficiency $P / C = 98 / 500 \approx 0.2$. Our estimates remain within the variation range of indicators for another snake species (0.06–0.88, 0.17–0.78) (Gil'manov, 1987), but they are significantly smaller than those for the common adder (0.49 and 0.42) (Pomianovska-Pilipiuk, 1974). The coefficient of relative productivity $P / B = 98 / 272 \approx 0.35$ is also close to the available data on other snakes (Gil'manov, 1987).

Chapter 7.

Survival

The most important function of an individual, survival, maintains the population size and, ultimately, the existence of the species itself. Accurate estimates of survival (or mortality) of animals allow to determine sex and age composition of a population, to monitor the trends of their abundance and structure (Koli, 1979), trophic relationships in zoocenosis (Zamolodchikov, 1993; Lindell, Forsman, 1996), as well as to discuss the evolutionary tactics of area mastering. It would seem that in view of special importance, the function of survival has to be investigated first of all. However, the number of papers devoted to the estimation of natural mortality and abundance of reptiles, is rather small, especially in relation to the adder. Apparently, it is caused by the complexity of the methods of recapture and subsequent mathematical processing of data, and also by the difficulty in determining the area of extrapolation of received estimates in a continuous continental territory. In our case, only a small isolated territory of the island of Kizhi (204 hectares) was considered that allows taking into account the main factors of mortality of adders. The goal of the present part is to assess the mortality of mature adders on the small island using the capture-mark-recapture method and subsequent simulation modeling of this process. One of the important results of the work should be the characteristic of an age structure of the island population of the adder and estimation of their maximum lifespan.

7.1. Materials and methods

Capturing of snakes was carried out in May (in the period when they come out of wintering and mate) and in September (before wintering). The capture places were noted on the map, where the size, gender, color were determined, and the pileus of each snake was photographed. In order to avoid the capture of the photographed animals twice in a current season, they were marked with a

bright dot of nail enamel. In half a year these dots disappeared due to molting, but the current year re-captures are not considered. The results of 2414 captured adders and 108 found sloughs were processed. 75 individuals younger than 3 years old were excluded from the total number. The snakes with poor-quality pileus photo were also excluded from the analysis. The final sample size was 2073 individuals.

Marking and re-capture. We refused to engage in the methods of marking with aluminum plate (Viitanen, 1967), traumatic for animals, as well as the unreliable procedure of trimming the ventral shields (Brown, Parker, 1976; Belova, 1981), the laborious method of cryo-tagging (Lewke, Straud, 1974) and hot brand. Instead, we used photos of individually unique pileus of each adder as a label (Neymeyer, 1987; Drobenkov, 1989), as well as the photos and scans of sloughs' heads. In literature there is an experience of digital descriptions of phenotypes (Yakovlev, 1989). We also used the digital description of a pileus structure (the "cap" composed of head surface scales) (Korosov, 2005). It is possible to describe the individual digital adders' pileus, because it is composed of both constant components and those widely varying in number and topography. Large scales (frontal, supra-orbital and marginal) have almost no variability. On the contrary, the number of small scales lying between them changes in different individuals. The pileus of each individual was described via 14 codes. Each code figure means the number of scales in a particular area of the animal's head, and generally they correspond to the accepted classification (Bannikov et al., 1977; Pikulik et al., 1988) (Fig. 7.1.1, Table 7.1.1). The gender of an individual was also included (**s**: m, f) as well as the color (**c**: melanistic, black, dark and light blue, green, brown, grey). Fig. 7.1.2 shows some examples of the pileus encoding of few individuals.

Table 7.1.1. The description of the pileus areas used for individual tagging

Code	Scales names	Number of scales		Description of area
		Lim	Mod	
ip	Interparietal	0–3	0	Scales lie between parietal, but have no connection with frontal or frontal-parietal scales
fp	Frontal-parietal	0–5	0	Lie behind frontal scale, between frontal and parietal ones
pos	Left para-orbital	0–7	3	Lie between frontal and supra-orbital scales, in contact with them, dorsal scale touches frontal and supra-orbital ones
pod	Right para-orbital	0–7	3	Lie between frontal and supra-orbital scales, in contact with them, dorsal scale touches frontal and supra-orbital ones
pf1	Prefrontal, first row	1–6	3	Touch frontal scale in front, but do not touch supra-orbital one
pf2	Prefrontal, second row	3–8	5	Compulsorily touch edge row scales, can include lateral ones
pf	All prefrontal	4–20	9	Confined with apical scales in front, on sides – with marginal ones, behind – with frontal ones
ps	Left parietal	1–5	1	Large scale behind frontal one on the left
pd	Right parietal	1–5	1	Large scale behind frontal one on the right
a	Apical	1–4	2	Central frontal scales of edge row (frontal-nasal)
as	Left apical	1–2	1	Left frontal marginal scale (may consist of two shields)
ad	Right apical	1–2	1	Right frontal marginal scale (may consist of two shields)
pfs	Right prefrontal-marginal	1–3	2	Chain of scales between frontal and marginal ones on the right
pfd	Left prefrontal-marginal	1–3	2	Chain of scales between frontal and marginal ones on the left

All individuals' codes were added to the database in Excel environment. To search the data on recaptures the method AutoFilter was used. Taking the list of codes of an individual as a base, the similar codes were selected by obvious key codes, while found duplicates were collated using their photos. To avoid "losing of marks" in the database, the search was conducted many times with changing the priority of different keys. For the final identification of individuals the photographs were collated (Fig. 7.1.3).

The numbers of re-captured males and females from those previously labeled (empirical data) for all 17 years of observations are shown in tables 7.1.2 and 7.1.3. The left side shows the number of marked individuals in each year, and the right side – the number of re-captured adders in the subsequent years of those previously marked. For example, in 1994 67 females were captured (n), among them 63 snakes was firstly marked (M). In the next 1995 4 of them were captured (^{3}m), and the year later – 5, ..., in 2000 – 2 snakes (Table. 7.1.2).

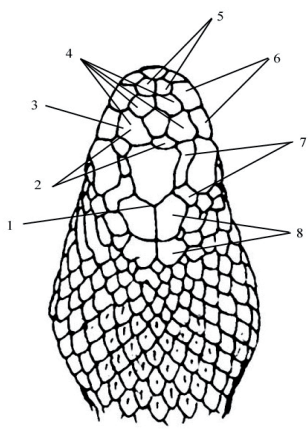
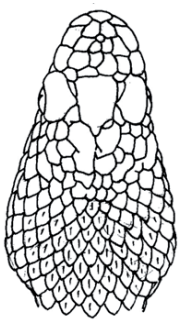
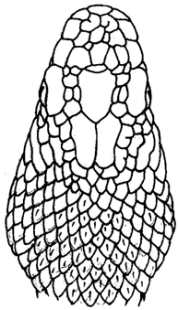


Рис. 7.1.1. Elements of a digital code of pileus of a common viper: *1 – fp*, *2 – pf1*, *3 – pfs1*, *4 – pf2*, *5 – a*, *6* – boundary, *7 – pod* , *8 – pd*.

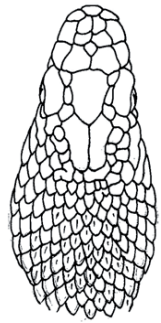
Presented individual has the code:
919, 1992, f, b, 0, 0, 3, 2, 2, 4, 6, 2, 2, 1, 1, 1, 1, 2



0 0 0 0 2 6 10 1 2 2 1 1 2 2



0 0 5 5 5 6 12 1 1 2 2 2 1 2



0 0 3 3 2 4 5 1 1 2 1 1 1 1

Рис. 7.1.2. Example of preparation of the pileus code

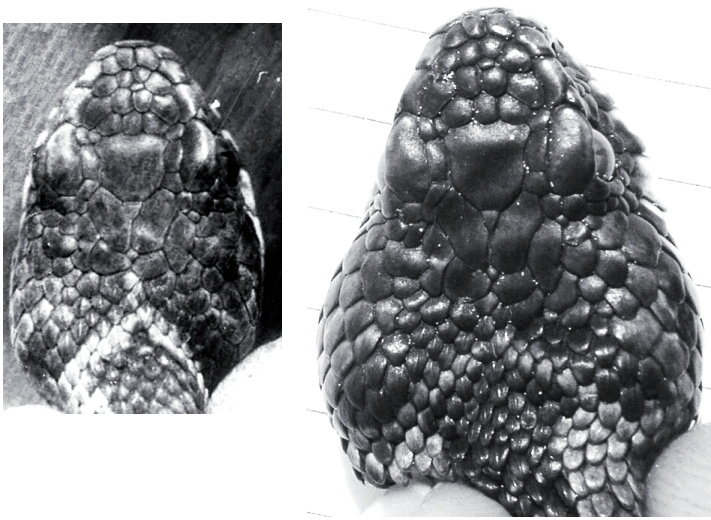


Fig. 7.1.3. Photo of pileus of female vipers caught in 1995 and 2006.
(№ 475 and 2535)

Table 7.1.2. The number (♂m, ind.) of recaptured adders' females on Kizhi in 1991–2007

Number of		Number of captured females, n ind.															
		1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007
marked		23	85	67	187	170	47	97	30	61	78	31	37	26	97	118	99
1991	8	1															
1992	22				2	2	1	2						1			
1993	85			4	8	5											
1994	63			1	4	5	2	1	1	2							
1995	17				14	13	6	7	3	1	1	1				1	
1996	14					5	3	13	7	2	3		3	1	3		
1997	35							1	1		1			1			
1998	73							5	3	4	4						
1999	15									2	2	1					
2000	50												2	1	1	2	1
2001	67										2	3		1	4		1
2002	26												1		3		
2003	31														3	3	
2004	21														1	3	1
2005	82														4	3	1
2006	10															15	3
2007	89																

Table 7.1.3. The number (♂m, ind.) of recaptured adders' males on Kizhi in 1991–2007

Number of		Number of captured males, n ind.															
		1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007
marked		25	15	79	170	81	169	140	36	32	70	36	89	40	85	57	70
1991	10			1													
1992	25	1	2	1	2		1										
1993	13				3		1										
1994	77			3	16	7	9	7									
1995	14				10	7	9	6	1		2	4	1				
1996	67						13	11	2	1			1				
1997	13						7	38	9	2				1			
1998	78							5	4	1	4	1	1	1		1	
1999	20									1	2				1		
2000	27									2	3	1	2	1	1		
2001	59										2	6	8	1		1	
2002	24												5	1	1	2	
2003	71												4			2	
2004	35														1	1	
2005	80														2	3	1
2006	47															1	3
2007	64																2

7.2. Calculation of survival on marking data

The technique of marking with subsequent capturing is used in order to observe the process of the gradual disappearance of marked individuals (marks) from a population. Assuming that the elimination rate of marked animals is equal to the mortality rate of all other individuals (of the same status) in the population, it is possible to estimate the absolute and specific population mortality and abundance (see section 8).

The most important condition for estimating demographic parameters by the method of re-capturing is that by the time of the next registration the marked animals should be well "mixed" with unmarked, thereby ensure an equal probability of capturing both (Koley, 1979). Taking into account the long periods of northern reptiles being in inactive state (Zamolodchikov, Kolosova, 1995), these specific conditions may be fulfilled only in a few months. Our calculations include the occurrence indices of marked individuals only in adjacent years; the re-captures in the year of tagging were not involved.

The main result of this work is the estimates of a *specific mortality* rate of individuals of different age, gender, status, and the calculation of the demographic tables on its basis (Koley, 1979). The term "specific" indicates that events are associated with the same time interval; in our case, it is one year: it is a proportion of snakes of a given status (sex, age) that survived the winter. As snakes were captured mainly in May and September, in fact, the period between the two captures may range from 8 to 16 months. The mortality rate expressed as a proportion is also a statistical characteristic of individuals of given age (and status) – it is the probability to die during the following year (survival rate is a probability to live one more year). Combining the data on survival with those on the number of different age groups gives the possibility to calculate the population dynamics in each age cohort (cohort means individuals born approximately at the same time, i.e. within one time interval, see: Bigon et al., 1989). In the simplest case, we get the resulting curvilinear graph of a smooth decline in the number of cohorts that was well illustrated by the

survival curves of the "populations" of marked tubes used in chemical laboratories (Pianka, 1981). The specific survival of mix-aged vertebrates often appears to be similar; their survival rate is usually distinguished in four groups: newborns (low survival rate), young (average), mature individuals (high) and old (low). In natural populations of the adder the other four groups are distinguished: newborn, young, adult females and adult males. Actually, old individuals (that cannot reproduce) are absent in the population, because the maximum physiological lifespan in adders is almost two times longer than the maximum age of individuals captured in nature. Unfortunately, young adders are almost impossible to be found, on the route, as a rule, only sexually mature females and males occur. For this reason, the survival estimates on the data of re-capturing tagged animals refer only to adults; for younger ages these values were obtained on the basis of the reconstruction of the population age structure (see section 8).

An important methodological point of the upcoming calculations is that the mortality rate was estimated as a characteristic of how fast the average proportion of marked individuals reduces in the population in one year. This required, first, to calculate correctly the proportion of marked animals, second, to average these estimates for all years of observations, and then to calculate the mortality rate. The proportion of re-captured marked individuals (p, %) was determined separately for females and males. In the simplest case, it can be represented as a ratio of the number of re-captured individuals (^{3}m) to the total number of captured ones (n),

$$p = 100 \cdot {}^{3}m / n.$$

However, the value *p* should be related to the number of recaptured animals (n) and that of primarily marked animals (M); formula is true only if M = n. In general, the captures level should be made the same, for example, 100 ind.:

$$^{3}p = {}^{3}m \cdot (100 / M) \cdot (100 / n) = 10000 \cdot m / (Mn).$$

So we obtain the number of tagged animals from 100 specimens marked in the previous year (season), among 100 specimens caught in this season (Table 7.2.1, 7.2.2). This value, twice normalized to 100, can be considered as a proportion of recaptured marked animals and it can be

expressed in percent. For example, of 173 adult females marked in 1995, 13 specimens were caught in the following 1996 among 170 captured ones. The proportion of marked snakes was (Table 7.2.1): $^{3}p = 10000 \cdot 13 / 170 \cdot 173 = 4.42 \approx 4$ %.

Table 7.2.1. Proportion (p, %, rounded off) of adders' females re-captured on Kizhi in 1991–2007 (on the data of Table 7.1.2)

Number of		Number of captured females, n ind.															
		1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007
marked		23	85	67	187	170	47	97	30	61	78	31	37	26	97	118	99
1991	8	52															
1992	22				5	5	9	9						17			
1993	85			7	5	3											
1994	63			2	3.3	4	7	2	5	5							
1995	17				4	4	7	4	6	1	1	2				0	
1996	14					2	4	9	16	2	3		6	3	2		
1997	35							3	9		4			11			
1998	73							7	13	9	7						
1999	15									22	17	22					
2000	50												11	8	2	3	2
2001	67										4	14		6	6		2
2002	26												10		12		
2003	31														10	8	
2004	21														5	12	5
2005	82														5	3	1
2006	10															12	3
2007	89																

To summarize the data for all years, the data matrix was preliminarily reconstructed: the proportion of re-captures in a current i-th year was put in the first column, that in the next i+1-th year was put in the second column, etc. for all years of observations (Table 7.2.3, 7.2.4).

Then the arithmetic means of the columns (years after capture) were calculated. Since in the first year of the study (1991) the capture level was small and somewhat distorted the whole picture, these data were not involved into the calculation of the average proportion of recaptures. So, the average mortality of females in the following year after marking is (excluding 1991) (0 + 7 + 3.3 + 4.1 + 4.3 + 2.8 + 13.3 + 22 + 0 + 14.4 + 10.4 + 0 + 5.1 + 3.1 + 2.9)/ 15 = 6.2 %.

Table 7.2.2. Proportion (p, %, rounded off) of adders' males re-captured on Kizhi in 1991–2007 (on the data of Table 7.1.3)

Number of marked		Number of captured males, n ind.															
		1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007
		25	15	79	170	81	169	140	36	32	70	36	89	40	85	57	70
1991	10			13													
1992	25	16	53	5	5		2										
1993	13				13		5										
1994	77			5	12	10	7	6									
1995	14				4	5	4	3	2		2	7	1				
1996	67						11	12	8	4			2				
1997	13						3	20	18	4				2			
1998	78							5	14	4	7	4	1	3		2	
1999	20									15	14				6		
2000	27									22	15	10	8	9	4		
2001	59										5	28	14	4		3	
2002	24												22	10	5	15	
2003	71												6			5	
2004	35														3	5	
2005	80														3	7	2
2006	47															4	9
2007	64																4

The average proportions of re-captured marked snakes obtained in such a way are not quite accurate, because the representativeness (level) of captures in different years was different. Therefore, the *weighted average proportions* of marked snakes (p_i), including the level of initial (M_i) and the current (nj) captures, was calculated and used for further analysis:

$$p_i = \frac{\sum \text{э} p \cdot M_i \cdot n_j}{\sum M_i \cdot n_j}$$

where i – the year of the first tagging, j – the year of recapturing. The technology of calculations was as follows. At first, for each pair of years (i and j) the total capture level and the weighted averages of repeated captures were calculated. So, for females captured in 1994 and 1995 (Table 7.2.1): $(M_{1994} \cdot n_{1995}) = 63 \cdot 187 = 11781$, $(\text{э}p \cdot M1994 \cdot n1995) = 3.3 \cdot 11781 = 38877.3$.

Then all the capture levels and weighted proportions for the entire period of study were summarized and weighted proportion of recaptured

marked snakes was defined (clumsy intermediate table is not shown), for example: p_1 = 420042.8 / 95014 = 4.42 %.

Table 7.2.3. Calculation of the average proportion (p) of tagged adders' females, captured in different after marking, based on the converted Table 7.2.1 (the adjusted model parameters of the is given in petit)

Year of marking	Number of marked females	Number of years after marking												
		0	1	2	3	4	5	6	7	8	9	10	11	12
1991	8	0	52.1	0	0	0	0	0	0	0	0	0	0	0
1992	22	0	0	0	4.7	5	9.5	9	0	0	0	0	0	0
1993	85	0	7	4.9	3.2	0	0	0	0	0	0	0	0	0
1994	63	2.4	3.3	4.4	6.6	1.6	5.1	5.2	0	0	0	0	0	0
1995	173	4.2	4.1	7.2	4	5.6	1	0.7	1.9	0	0	0	0.5	0
1996	145	1.9	4.3	8.9	15.6	2.3	2.6	0	5.6	2.7	2.2	0	0	
1997	35	0	2.8	9.2	0	3.6	0	0	11	0	0	0		
1998	73	6.8	13.3	9	6.9	0	0	0	0	0	0			
1999	15	0	21.9	16.9	21.5	0	0	0	0	0				
2000	50	0	0	0	10.8	7.7	2.1	3.4	2					
2001	67	3.8	14.4	0	5.7	6.4	0	1.5						
2002	26	0	10.4	0	12.3	0	0							
2003	31	0	0	10.3	8.2	0								
2004	21	0	5.1	12.1	4.8									
2005	82	5.2	3.1	1.2										
2006	106	12	2.9											
2007	89	0												
Average (1992–2007)		2.3	6.2	6	8	2.7	1.8	2	2.3	0.3	0.3	0	0.1	0
Weighted average, p_i		3.8	4.42	5.9	5.8	2.8	1.3	1.9	1.4	0.3	0.8	0	0	0
Average mortality, d_i				–0.3	0.02	0.51	0.54	–0.4	0.27	0.78	–1.8			
Model calculations, p_i'			**6.1**	4.7	3.7	2.9	2.2	1.7	1.4	1.1	0.8	0.6	0.5	0.39
$\Phi = \sum\phi = 4.99$	ϕ =		2.7	1.4	4.5	0	0.9	0	0	0.6	0	0.4	0.3	0.2

A number of average weighted proportions of recaptured marked snakes allows to calculate the annual mortality as a part of the marked snakes, lost for one year due to their death: $^{3}di = 1 – (p_i – 1/ p_i)$.

For example, the average proportion of tagged males found in the following year after tagging, is 12.3 %, and a year later – 7.2 %. So, the part of dead marked individuals: $d_{1/2} = 1 – (7.2 / 12.3) = 0.41$.

Table 7.2.4. Calculation of the average proportion (p) of marked adders' males, captured in different years after marking, on the basis of table 7.2.1

Year of marking	Number of marked males	Number of years after marking												
		0	1	2	3	4	5	6	7	8	9	10	11	12
1991	10	0	0	0	12.5	0	0	0	0	0	0	0	0	0
1992	25	16	53.3	5	4.6	0	2.4	0	0	0	0	0	0	0
1993	13	0	0	13.3	0	4.6	0	0	0	0	0	0	0	0
1994	77	4.9	11.9	9.9	6.9	6.5	0	0	0	0	0	0	0	0
1995	149	3.9	5.1	3.6	2.9	1.9	0	1.8	7.5	0.7	0	0	0	0
1996	67	0	11.5	11.6	8.3	4.4	0	0	1.6	0	0	0	0	
1997	136	3.1	19.8	18.4	4.3	0	0	0	1.8	0	0	0		
1998	78	4.6	14.3	3.8	7	3.6	1.4	3.2	0	2.3	0			
1999	20	0	14.7	13.7	0	0	0	5.9	0	0				
2000	27	21.8	15.2	10.3	7.9	9.3	4.4	0	0					
2001	59	4.6	28.3	14.4	4.2	0	3	0						
2002	24	0	22.2	10.4	4.9	14.6	0							
2003	71	6	0	0	4.9	0								
2004	335	0	3.4	5	0									
2005	80	2.9	6.6	1.8										
2006	47	3.7	9.1											
2007	64	4.5												
Average (1992–2007)		4.7	14.4	8.7	4.3	3.7	1	1.1	1.2	0.4	0	0	0	0
Weighted average, p_i		3.7	12.3	7.2	4.7	2.8	1	1	1.8	0.5	0	0	0	0
Average mortality, d_i				0.41	0.35	0.41	0.63	0.02	–0.8	0.7	1			
Model calculations, p_i' for d = 0.38			12.3	7.5	4.6	2.9	1.8	1.1	0.7	0.4	0.3	0.2	0.1	0.06
$\Phi = \sum\phi = 2.0$		$\phi =$	0	0.1	0	0	0.5	0	1.3	0	0.1			

In other words, the average mortality of males between the 1st and the 2nd year after marking is 41 %, between 2-m and 3-m – 35 %, between 3-m and 4-m – 41 %, etc. (Table 7.2.4). Since these estimates refer to males

of the same status (not young and not old adult mix-aged animals), mortality should remain approximately the same regardless of the number of years passed since tagging (most repeated captures was obtained not later than 4 years after tagging). This means that a wide variation of empirical estimates of mortality has a random nature.

To provide a generalized description of the mortality in tagged animals for all years of observations the simulating model was used. A simple dynamic model assumes a constant level of annual mortality and calculates a smooth curve of the average proportion of returned marked animals:

$$p'_i = p_{i-1} - d \cdot p'_{i-1},$$

where p'_i is the model proportion of marked snakes in the sample of the current year (i = 1, ... 17), p'_{i-1} is the model proportion of those in the sample of the previous year, d is the total specific mortality, i.e. the proportion of tagged animals dying in one year.

The value of mortality d, as well as p_i (proportion of tagged snakes, recaptured in a year after the first tagging, i = 1) served as model parameters and were calculated in the process of setting it up.

The model is implemented in the Excel sheet (Table 7.2.3, 7.2.4, lines "Model calculations"). These formulas for calculating the proportion of marked snakes for each year were introduced into the sheet cells; thus the row of model values of p'_i was formed.

Because the initial parameters were unknown, they, in first approximation, were accepted equal to d = 0.5 and p'_1 = 20 %. Then the proportion of tagged males, survived in the second year after tagging, is

$$p'_2 = p'_1 - d \cdot p'_1 = 20 - 0.5 \cdot 20 = 20 - 10 = 10.$$

In the third year it would be equal to:

$$p'_3 = p'_2 - d \cdot p'_2 = 10 - 0.5 \cdot 10 = 10 - 5 = 5 \text{ etc.}$$

A priori accepted values of d and p'_1, of course, do not correspond to reality. To assess the degree of divergence between the model dynamics of the proportion of re-captured individuals p'_i and the empirical row of average weighted proportions p_i, we found the difference for each

$\phi = (p'_i - p_i)^2$ and for all years $\Phi = \Sigma(p'_i - p_i)^2$. For the first year we have $\phi_1 = (20 - 12.3)^2 = 58.9$, and for all years $\Phi = 69.2$.

Since the model is designed to describe as accurately as possible the decline in the weighted average proportion of marked individuals in repeated samples, the task was to select such parameters d and p'_1 that the difference between the model and reality would reduce to zero: $\Phi \rightarrow 0$. The Excel module "Finding solutions" solves this problem (see section 14). (While setting, the additional condition was specified: the sum of the recaptured animals in the initial observations should be equal to the calculated row: $\Sigma p_i = \Sigma p'_i$.)

After setting module, the model acquired the following parameters: $d = 0.38$ and $p'_1 = 12.3$. Now the proportion of tagged males, survived in the second year after tagging, was: $p'_2 = 12.3 - 0.38 \cdot 12.3 = 12.3 - 4.67 =$ $= 7.5$. The difference between the model and reality for the first year was $\phi_1 = (12.3 - 12.3)^2 = 0$, and for all years $\Phi = 2.0$.

The model well describes the empirical data (Fig. 7.2.2); the coefficient of determination is $R^2 = 0.98$ (with df = 8). The similar calculations are performed for females (Table 7.2.1; Fig. 7.2.1), the coefficient of determination $R^2 = 0.76$.

It is necessary to provide the received estimates of mortality with a statistical error. When a researcher possesses several initial databases to be used to set a model and to receive a sample of estimates of some parameter, the error may be calculated directly (Bezel', 1987) by the known formula $m = S/\sqrt{n}$.

In the absence of a repeated database, it can be obtained by randomization, adding a stochastic variability into the initial database (Rozenberg, 1984; Korosov, 2002б). One of the variants to do it is a random withdrawal of a substantial part of the original values (e.g., 50 %). In our view, the accidental lack of data on the re-capturing is equivalent to the random variation of the number of re-captured animals, which is much more difficult to reproduce. The elimination process consists in following: by means of the random numbers generator to determine for each variant whether or not it will participate in setting the model with a probability of 0.5.

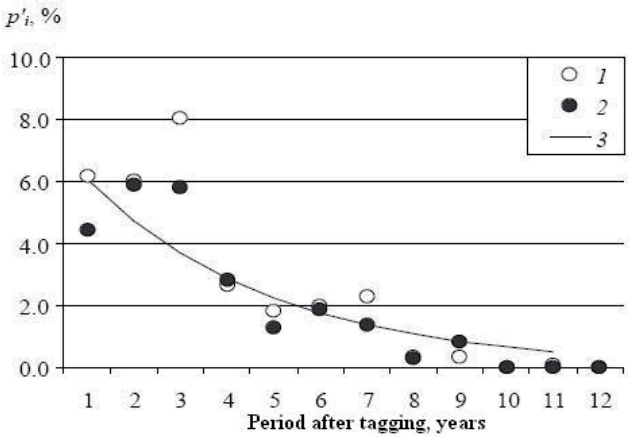


Fig. 7.2.1. . The dynamics of reduction of the share of re-captured female vipers: *1* – the average share of re-captured specimens, *2* – average weighted estimate the proportion of re-captured specimens, *3* – model description of the data (d = 0.22, p'_1 = 6.1)

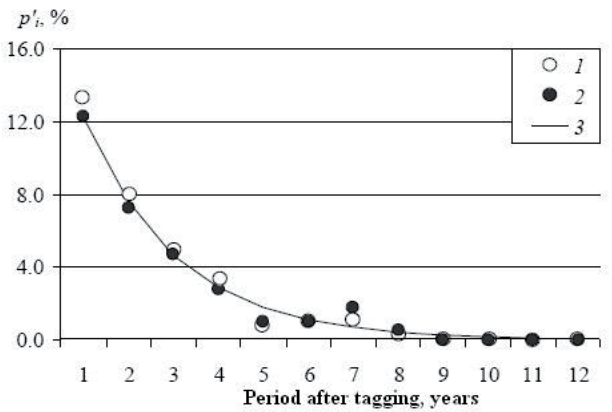


Fig. 7.2.2. The dynamics of reduction of the share of re-captured tagged male vipers: *1* – the average share of re-captured specimens, *2* – average weighted estimate the proportion of re-captured specimens, *3* – model description of the data (d = 0.38, p'_1 = 12.3)

As a result, 12 randomized (half-devastated) matrixes of recaptures both for females and males were obtained; on their base the rows of weighted average proportions p_i were calculated, after setting models – the sets of 12 estimates of mortality and, finally, the statistical characteristics were determined (Table 7.2.5).

Table 7.2.5. The statistical characteristics of specific mortality in adult adders

Parameters		Me	M	S	M–2S	M+2S	CV, %
Average annual mortality, *d*	Females	0.23	0.23	0.03	0.18	0.28	11
	Males	0.37	0.38	0.07	0.23	0.53	19
Occurrence of marked animals in the year after marking	Females	7.0	7.3	0.8	6	9	11
	Males	13.1	13.3	2.7	8	19	20

7.3. Mortality factors in adders on the Kizhi island

Among 2073 adders 469 specimens or 23% were captured twice (tab. 7.3.1). At first sight, this figure is in contrast with the data of other authors, where the re-captures level may reach 76% (Table 7.3.2).

Table 7.3.1. The level of adders' captures on the Kizhi island

	Number of specimens captured	Recaptured				The proportion in overall catch
		ones	twice	3 times	overall	
Females	1091	180	33	4	217	19.9
Males	982	199	45	8	252	25.7
All	2073	379	78	12	469	22.6

The reason is that tagging and capturing is often carried out within a short period, when active individuals can be quickly caught and tagged, although many inactive individuals do not come in view of researchers at all. To cover all animals in a population, the repeated captures should be carried out after snakes come out of shelters on the surface (after a few months). At that time the labeled snakes mix well with the mass of

unlabeled individuals and the condition of equal probability of capturing both is realized; while the proportion of recaptured individuals reduces.

Table 7.3.2. The proportion of re-captures of marked adders

Marked animals, ind.	Number of re-captured animals, ind.	Proportion of re-captured animals, %	Author
“	“	60–70	Edelstam, 1989
23	14	61	Sokolov, 1981
62	47	76	Bozhansky, Semenov, 1978
355	236	7–67	Belova, 1976
366	257	70	Belova, 1984
392	164	42	Belova, 1974
643	257	40	Belova, 1989
657	314	48	Viitanen, 1967
2073	469	23	Our data

This trend can be seen from the data of P.Viitanen (1967) and Z.V.Belova (1974–1989): the more animals could be marked (that is, the longer was the marking period), the smaller was the proportion of recaptured marked snakes. The published studies were carried out in small areas (a few hectares). Apparently, on the extensive island of Kizhi our capture levels were relatively small for the number of recaptured marked snakes to be larger. Nevertheless, the obtained data allow discussing many aspects of adders' biology.

Let's first note the fact, when adult (4–6 years) tagged specimens were recaptured in 8–9 years. This means that on Kizhi both adders' males and females may live up to 11–13 years (these estimates are consistent with the results of our studying gluing lines on the flat bones of the snake' skull, see section 8).

The data above show that the number of re-captured specimens gradually decreased both in certain years (for example, of 67 males marked in 1996 the number of recaptured ones was 11, 12, 8, 4, 0, 0, 2 ind., see Table 7.2.2) and on an average (see Table 7.2.4, Fig. 7.2.2).

Several reasons of reducing tagged animal numbers are known. The tags are given out (lost), the proportion of tagged animals is reduced because snakes withdraw from the territory of tagging, they get accustomed to the traps, and thereby the condition of an equal probability of the capture of different specimens is violated, marked individuals perish due to natural causes as well as just marking process (Koley, 1979; Makfed'en, 1965; Pianka, 1981).

These various circumstances seriously prevent from using simple methods of assessing (calculating) population demographics.

For a small island population of the adder, most of the factors discussed above are irrelevant. Long-term experience shows that the individual "tags" in snakes (pileus structure) are constant and can only be changed as a result of an injury, but it happens very rarely, as it leads to an animal's death (in total only 6 captured individuals with obvious traumatic disorders of head scales), i.e. there is no damage of tags. Water borders prevent any significant migration of snakes to the island and from it (see section 11). Traps were not used, snakes were manually-captured; in this sense it is important only the habitude of the catcher to the catching object, and not *vice versa*. In our opinion, marking does not give substantial waste of animals. First, snakes often react to capturing, measurements and photographing so calmly, that in a few minutes they can continue basking interrupted by catching. Second, in animals (32 ind.) caught and kept in captivity there was no mortality because of the possible injures while capturing, i.e. in the first two months after capture (Kudryavtsev et al., 1996)) (Korosov, Khilkov, 2008).

Of all the factors contributing the reduction in the number of marked adders on Kizhi, natural death (capture by predators, freezing, diseases, old age, etc.) as well as the result of men's activity (under wheels, direct destruction, etc) still remains the key factor. As we consider only marking and determining the number of adult snakes, puberty of young individuals is another factor. Young snakes change their behavior, start to occur on routes, increasing the samples of adults; it results in decreasing a proportion of earlier marked individuals among unmarked. Such

"recruitment" by the ripened snakes fully coincides with the reproduction process in other groups of vertebrates. Gradual uniform dying out of individuals is well described by a calculated model of geometrical regression. The part of dispersion explained by the model was R^2 = 76% for females *and* R^2 = 98% for males (at df = 8).

Curves showing the dynamics of reduction in a proportion of marked snakes differ in individuals of both sexes. So, in a year the calculated proportion of marked recaptured snakes is approximately twice higher in males (p'_1 = 12.3%), than in females (p_1 = 6.1%). The reason is that the probability of catching males (in the period of spring total reproductive activity) in general is higher than that of females (a third of which participates in pairing, see section 4). The second difference is that males eliminate from a population at a faster rate, than females: their curve of decreasing the proportion of marked individuals is smoother. In the model it is expressed with the general indicator of mortality: d = 0.22 (or 22%) for females, d = 0.38 for males.

Using randomized matrixes of initial data, statistical characteristics of these estimates were calculated (Table 7.2.3). The error of mortality estimates was 3% in females and 7% in males. Using these results, it was shown that the average mortality rate of males and females differs significantly (p = 0.0001). Average mortality estimates practically do not differ from those received earlier directly on initial data (Table 7.2.3, 7.2.4); differences range within 1%: 22 and 23% in females and 38 and 38% in males.

According to the literary data (Prestt, 1971), the estimates of mortality were also higher for adder males (32%), than for females (14%), although, due to a small sample, they do not differ significantly. The specific mortality of adult individuals derived by us corresponds to that of other authors: about 20% for 3 years (Neumeyer, 1987), 24% a year (Prestt, 1971), 34% (Madsen, 1989).

The process of disappearance in adders of different sexes also differs significantly in nature. The curve of males' mortality is almost precisely the curve of geometrical regression (Fig. 7.2.2). In females the situation is

more complex: average estimates of recaptured marked snakes vary widely from year to year (Fig. 7.2.1).

In our opinion, it is a result of cyclic changes in females' behavior in connection with pregnancy. The probability to find a female is not uniform over the years of its life: it is higher in a year of its pregnancy. Dry females are secretive, whereas the pregnant ones show active thermophilic behavior and are captured much more often. It is known that adders' females have two- (Volsøe, 1944, etc.) or even three-year reproductive cycle (Biella, 1979). It means that the majority of the females caught in each year are pregnant. In the following year they become dry and their occurrence in captures falls sharply, $p_1 = 4.4\%$ (Table 7.2.3). When in 1 or 2 years they become pregnant again, their proportion in the captures increases (in our case to $p_2 = 5.9$ and $p_3 = 5.8\%$) etc. Despite the fluctuations of pi, this process can be described with a model. We constructed another four models of decreasing the proportion of marked females (Table 7.3.3, Fig. 7.3.1).

In the first model, parameters setting (p_{1i}', d) was carried out only according to the data mainly of capturing pregnant females (maximum p_i in 3, 7, 9 years after marking); after model setting, the mortality rate was $d_1 = 0.302$ (30.2%) (Fig. 7.3.1. 2).

Table 7.3.3. Calculation of the proportion (p) of marked adders' females by three methods

		Years after marking											
		1	2	3	4	5	6	7	8	9	10	11	12
Weighted averages, p_i'		4.4	5.9	5.8	2.8	1.3	1.9	1.4	0.3	0.8	0	0	0
$d_1 = 0.302$	$p_1'_i$	11.9	8.3	5.8	4.1	2.8	2	1.4	1	0.7	0.5	0.3	0.2
$d_2 = 0.295$	$p_2'_i$	4.4	3.1	2.2	1.5	1.1	0.8	0.5	0.4	0.3	0.2	0.1	0.1
$d_3 = 0.295$	$p_3'_i$	8.3	5.9	4.1	2.9	2.1	1.5	1	0.7	0.5	0.4	0.3	0.2
Pp = 1.39	$P_p \cdot p3'_i$			5.7				1.4		0.7			
Pu = 0.53	$P_u \cdot p3'_i$	4.4				1.1			0.4		0.2		
Weighting ind.	$p_3'_i$	4.4	5.9	5.7	2.9	1.1	1.5	1.4	0.4	0.7	0.2	0.3	0.2
$d_4 = 0.285$	$p_4'_i$		5.3		2.9	1.1	1.5	1.4	0.4	0.7	0.2	0.3	0.2

The second model (p_{2i}') was set only according to the data on catching presumably dry females (points for 1, 5, 8 and 10 years after a marking); d_2 = 29.5% (Fig. 7.3.1, 3). Mortality rates practically do not differ, but not twice as it is shown in literature (Madsen, 1989), in our case they are similar (30 against 34%).

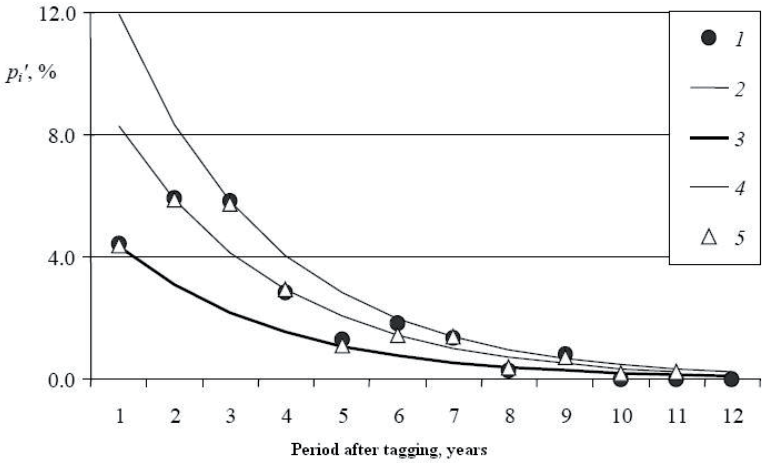


Fig. 7.3.1. . The dynamics of reduction of the share of re-captured tagged females: *1* – weighted average estimates of the share of re-captured specimens, *2* – a model primarily for the "pregnant, p1i', (d = 30.2 %), *3* – model mainly for the "barren" p2i', (d = 29.5 %), *4* – a model for all data, , p3i', (d = 29.5 %), *5* – a model for all data with corrections (d = 29.5 %, Pp = 1.4, Pu = 0.5)

To set the third model, a complete data series (1–10 years) was used, but model values for pregnant and dry females were separately supplied by the weight coefficients playing the role of a correction on probability of the different status of an individual. Thus, two rows of values were calculated: 1) average row of proportions p_{3i}' (fig. 7.3.1, 4) with mortality d, common for all groups, which has a smooth course; 2) two rows of $P_p \cdot p_{3i}$'and $P_u \cdot p_{3i}$' corrected on the probabilistic factors (Fig. 7.3.1, 5). At that four parameters

were adjusted: p'_0, d, P_p, P_u. The general mortality rate was d = 29.5%. The probabilistic factor was $P_p = 1.39$ for pregnant females and $P_u = 0.53$ for dry ones. It should be noted that corrections on probability of females' different status are common for all years of recapture. With their help it became possible to bring into precise coincidence the model points p_{3i}' (Fig. 7.3.1, 5) with empirical data p_i (Fig. 7.3.1, 1). Corrections P is to be understood so that the probability of catching pregnant female is higher than average at 39%, and that of catching dry one is lower than average at 47%, i.e. the ratio of captured females was far from 50:50%: the proportion of pregnant females is 75%, and dry ones – 25%.

In the fourth model, instead of the first three empirical values of the proportion of recaptured marked snakes p_i (4.4, 5.9, 5.8), the average weighed proportion of those in the second year after marking $p_2 = 5.3$ was used. After model's setting, the value of specific mortality was d = 28.5% (Table 7.3.3). The model variant when its setting was carried out only on the values concerning the recaptured snakes in 4–8 years, also gave the d = 28.5%.

Summarizing this section, it can be stated, as a minimum, that the average mortality of adult adders' females ranges 23–29% per year (so far let's accept the median d = 26%).

The exact average mortality is impossible to receive in principle for three reasons. The probability of death in mix-aged adult individuals is likely to be different and should increase a little as the time till recapture increases, but in our model it is not considered. In different years general natural and anthropogenic load on the population can change, causing variability in mortality. However, in our calculation method it is averaged.

7.4. Sexual structure of population

The term "the sexual structure" is often understood only as "sexual composition", i.e. a simple ratio between animals of different sexes in a sample taken from a wild population. However, the term "structure" rigorously means an assembly of relations between the elements of some

system. Speaking of a ratio between adult females and males, it must be kept in the mind, first, their initial ratio in broods (caused generally by genetic reasons), second, the relation to environment factors, which, on the one hand, cause specific behavior of individuals of different sexes and, on the other hand, cause individuals' death. As in broods the share of newborn females and males is approximately identical, we will focus on the ratio between sexes at different stages of ontogenesis that is influenced by unequal mortality rate of animals of different sexes.

The method of estimating mortality in adders, considered above, is based on the assumption that for individuals of any ages the probability of dying is equal, i.e. it was claimed that all deaths occur because of identical, random reasons. There is a rational to such conclusion, as the physiological threshold of lifespan in adders (25–30 years) significantly exceeds the maximum age observed in nature (13 years) (see section 7.6). As the found mortality rates do not depend on age of adult animals, they can be used for building hypothetical age distribution based on the adult part of a population. It has been shown (Koli, 1979) that age distribution of *stationary* (of stable number) populations coincides with the proportion of survived individuals in one cohort. Using the data on adders' mortality ($d_{♀}$ = 26 and $d_{♂}$ = 38%), the survival rate of adult individuals was calculated in one cohort when the starting number of young males and females (three-year-old) was 100 ind. each (Table 7.4.1, Fig. 7.4.1).

Table 7.4.1. Calculation of the number and proportion of survived marked individuals of adder by a certain age, based on specific mortality of females 26% and males 38%

	Age, years									Total
	3	4	5	6	7	8	9	10	11	
Females, ind.	100	74	55	41	30	22	16	12	9	259
Males, ind.	100	62	38	24	15	9	6	4	2	160
Total	200	136	93	64	45	31	22	16	11	419
Females, %	50	54	59	63	67	71	74	78	80	62
Males, %	50	46	41	37	33	29	26	22	20	38

The chart shows that the proportion of males in the population decreases with age, and that of females increases up to 80% at a maximum age. The sum of all adult males was 160 ind., and their proportion was – 38%; for females these figures were 259 ind. and 62%.

As a result, the average sex ratio determined by mortality curves turned out to be equal to 1:3. This ratio significantly differs from the parity (1:1) mentioned in any publication on the census of the adder (Chan-K'yen, 1967, etc.). Our data on the number of individuals of different sexes caught on routes (1091 females, 982 males) also approximately correspond to this proportion.

The obvious fact that the number of males is equal to that of females is connected both with the behavior influencing the probability of capturing adders of a different status and with the size of these groups. Males are less numerous, but they are more active during pairing and are more often found on a route. Females are more numerous, but only 30–40% of them (generally breeding and pregnant) could be noted. This conclusion that is true for the island population with high mortality is impossible to be extrapolated directly to mainland populations of the adder. Nevertheless, the noted significant deviation from the usual proportion between males and females makes us consider insolvent any estimates of sex ratios in the populations of given species got in route censuring.

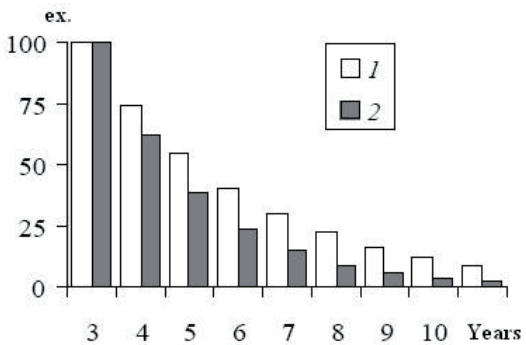


Fig. 7.4.1. Reduction of numerosity of one cohort of adult vipers during life: *1* – females, *2* – males

The analysis above allows us to make an important methodical remark on the approaches used to interpret the curves of losing marked animals. The general tendency of the graph showing the elimination rate in marked animals is defined only by their real death rate. Unlike some other authors, to assess mortality we used not the number of re-found individuals, but the fact of decreasing the proportion of marked individuals in a number of sequential repeated captures.

7.5. Life span

During individual life the irreversible changes in morphological, physiological, biochemical and other properties of animals occur. The age is the time scale characterizing dynamics of individual's conditions and allowing generalizing correctly numerous individual trajectories of ontogenesis to reveal species-specific norm.

In addition, the age is the universal indicator of population status of an individual, the characteristic of its survival ability, and the age structure describes population potency to reproduction and territorial expansion.

Large number of publications (Klevezal', Kleinenberg, 1967; Klevezal', 1988) is devoted to the problem of defining age and life span of land vertebrates. It is considered that for reptiles the most objective results are obtained by the method of calculating well distinguishable "gluing lines" between the layers of annual growth in tubular bones of the extremities (Smirina, 1974, 1989). As snakes do not have extremities, it is proposed to investigate flat bones of the skull (Bryuzgin, 1939); in this case the gluing lines can be found not using laborious operations of making slices, but only by means of discoloring in clarifying liquids. By this method the age of the grass snake, smooth shake, asp viper and another species was defined (Yemel'yanov, 1929; Castanet, Naulleau, 1985). In this section we present our experience in age defining of the adder (Korosov, Prokhorova, 1999; Korosov, 2001).

According to their size, it is possible to determine the age only in current-year young (x = 0+) and snakes up to 3 years: $L.t._{0+}$ = 14±1.3 cm,

$L.t._{1+}$ = 22±2.3 cm, $L.t._{2+}$ = 28±5.2 cm (see section 5); as for other snakes it can be said that they are older than 3 years. One of our tasks is to expand the range of ages that can be defined not only by internal, but also by external signs.

Material and methods. The adders' corpses found on the roads of the island of Kizhi (34 specimens) were collected and also 32 snakes were caught on other islands of the Kizhi archipelago (Karelia, the central part of Lake Onega) (humane considerations did not allow us to kill the larger number of snakes). The heads separated from the bodies were macerated or boiled in water, cleaned of soft tissues and dried. Flat skull bones (*mandibulare, quadratum, squamosum, pterygoideum, transversum*) were placed on a subject glass in a drop of glycerin and discolored for not less than 3 weeks. Further these preparations were covered with a cover glass for studying under a microscope (БСМ-10, Al'tami 104), photographed and scanned with the resolution from 3000 to 19000 dpi. The preparations were scanned on the little table with millimeter scale. The electronic image of the bone was imported in real size into the MapInfo program environment. This package allows to create the exact vector-based images of objects, and also to measure them in a semi-automatic mode (Korosov, Korosov, 2006). Numerical material was studied in the Excel environment both using statistics (Ivanter, Korosov, 2003), and by means of simulating models (Korosov, 2002a, b).

Bone choice. Practically in all skull flat bones studied by us it is possible to find areas with layered structure. In the coronoid process of the lower jaw (*os supraalgulare*) their differences can be seen even with a naked eye (Fig. 7.5.1). Carefully studied coronoid process (Castanet, Naulleau, 1985), according to the authors, contains not only the layers formed during wintering, but also intermediate, incomplete layers connected both with the negative impact of environment and physiological load (maturing period, pregnancy, bad weather, hunger and others) as well as with autonomic non-uniform bone formation. Apparently, therefore these authors recommended using this bone for age defining with caution. Our visual analysis showed that the sharpest and longest layers are visible

only on the front end of the transverse bone (*os transversum*) (Fig. 7.5.2). The reason probably consists in that this bone carries out the important functional load – it pushes the maxillary bone, providing abduction and adduction of the fang (Gurtovoy et al., 1978). Due to the constant load the bone substance gets thickened, and narrow layers of annual growth are well expressed. Further we used only the transverse bone. (after V.D.Bryuzgin, 1939).

Fig. 7.5.1. Layered structure on the coronoid outgrowth of a common viper mandible

Unfortunately, the anterior edge of the transverse bone is not quite flat and it is not equivalent to a slice, as the newly grown layers cover all convex forward part of the bone on its periphery. Because of that in changing the depth of focus by the micro-screw one can trace not a separate gluing line (as on a slice), but a semi-cylindrical gluing layer which in micro-photos and micro-scanning images looks as a dark band colored more intensively in the central part.

Counting layers in bones. The comparison of snakes' bones when catching snakes at the beginning and at the end of summer (Fig. 7.5.3) shows that for the warm period on the periphery of a bone a wide light layer is formed above the dark narrow one (gluing line). Wide light periosteal layers are formed in the summer and dark hyper-calcified ones – in the winter (Smirina, 1989). Counting the number of dark layers, it is possible to define the number of the winters survived by an animal.

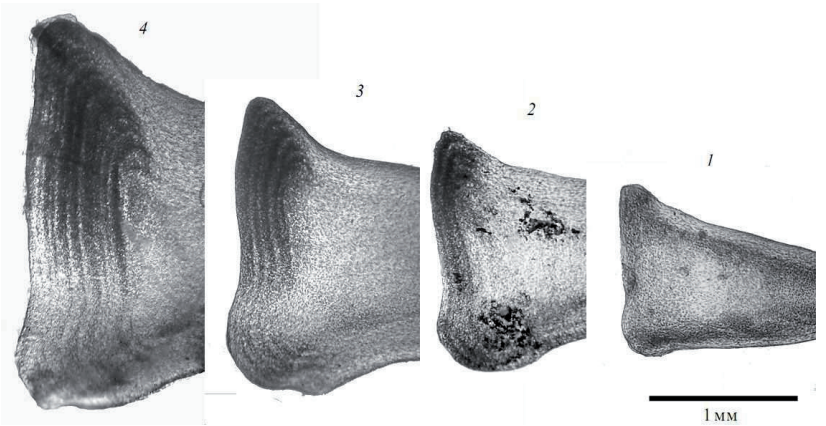


Fig. 7.5.2. Layered structure at the forefront of the transverse bone of snakes of different ages: *1* – yearlings, *2* – individuals aged 3+, *3* – 6+, *4* – 11+

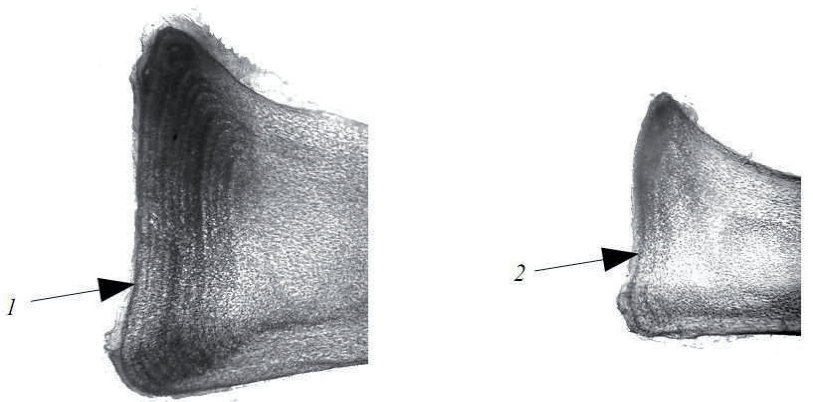


Fig. 7.5.3. The size of zone of transverse bone growth of snakes collected in May (*1* – no growth) and September (*2* – a significant increase)

To define uniquely the number of gluing lines on a transverse bone their electronic images were processed in the environment of desktop GIS Map-Info. The meaning of the procedure consisted in finding out all the layers along all preparation length (on the front edge of a bone). For this aim,

the scanned or photographic images of bones were introduced into the program environment while preserving their real size. Then over the raster image the vector lines passing in the middle of dark bands were created. At first the vector lines were drawn only over those parts of a bone where gluing lines were well distinguishable, starting with the most noticeable (not in order). Then, using the lines which had been built, the less noticeable bands were drawn. As a result, the system of smooth curves was formed and their number was counted. Of 66 preparations, the continuous lines covering the axial end and lateral parts of a bone were drawn only in a half of them. For the others, the fragments of lines were drawn; 4 more bones did not have easily detected lines and it was impossible to count them. According to the well-known classification of the layers' images (Klevezal', 1988), the photos of a frontal edge of a transverse bone can be rated as 5–4, and scanning images – as 5–3, according to their resolution.

Beginning the counting of lines, it is usually difficult to identify the initial layer which appeared after the first wintering. It is known that in tubular bones of small vertebrate animals the gluing lines related to the first two years are resorted (Smirina, Makarov, 1987; Klevezal', 1988). To find this effect in the flat bones of snakes, one-year and multiyear snakes were compared. The comparison logic consisted in that the structures, once created in flat bones, does not change significantly in their size throughout the life (Smirina, 1989), but they are covered by new layers due to periosteal activity. Because a lack of an intraosteal cavity, the resorption of inside layers does not occur in flat bones, and the first internal dark band on a transverse bone has to correspond to the first wintering of an animal. In this case the first gluing lines in one-years and multiyear snakes have to coincide in their shape and size.

To compare, 43 preparations of adult vipers' bones with the first gluing lines clearly distinguishable all along the frontal edge of the transverse bone were selected.

The comparison showed that in 30 cases (68%) the contours of the first gluing lines of one-year snakes agree closely with those of multiyear snakes (Fig. 7.5.4). In 6 cases (13%) the first lines of adult snakes were less,

than those of the "model" yearling, in 8 (18%) they were a little more than that. We relate these divergences to variation in the total size of newborns. In our opinion, we have the right to draw the following conclusion: the first gluing line is usually seen well on the preparation of the transverse bone.

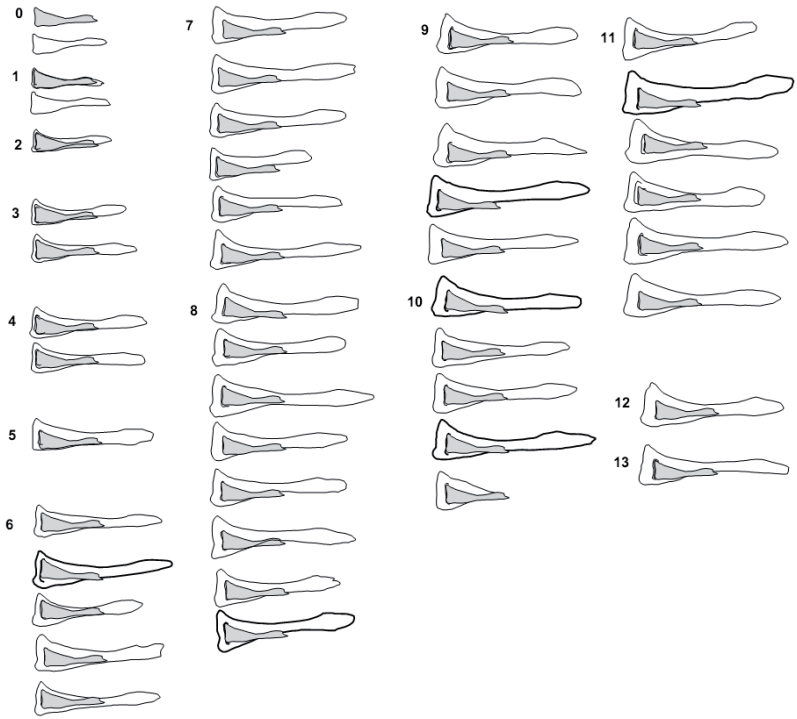


Fig. 7.5.4. The relation between the size of the of the transverse bone butt of yearlings (0) and older snakes (1–13 – number of adhesion lines). Bold line marks bones with the first adhesion line, exceeding the size of the yearling bone

As numerous authors note, one more problem in calculating the age by layered structures is that some layers can correspond not to wintering, but physiologically adverse condition of animals (illness, pregnancy,

hunger, bad weather). It is possible to solve this problem, when studying the dynamics of a bone annual gain.

The characteristic of an annual bones gain is the regularity, close layers are almost equal in their width; at the same time in mammals the gain reduces with age (Klevezal', 1988). In reptiles it is scarcely expressed, in particular in the asp viper (Castanet, Naulleau, 1985).

In Karelia the summer is very short (snakes are active about 140 days – since the beginning of May to the middle of September). If during this period a snake faces adversity causing the limited bone gain, the additional line is formed in it. In this case the width of two next layers corresponding to the gain before and after that has to be at least twice less, than the width of bands formed in normal years. At that the equality of gains is disturbed. The neighborhood of two especially narrow dark layers should indicate that between them there is an additional, but not wintering layer.

The width of gain bands was measured in the environment of MapInfo. We used the vector lines built earlier to model the position of gluing lines. Then we drew two straight lines, perpendicular to them, and, using these straight lines, measured the distances between vector gluing lines (Fig. 7.5.5).

The measuring results showed that dark layers of the almost all transverse bones alternate quite regularly, with the gain width averaging 0.062 ± 0.002 mm in females and 0.068 ± 0.0032 mm in males (statistically similar). The apparent tendency of gain decreasing with age is statistically insignificant. At the same time, the annual gain varies in the wide range – from 0.03 to 0.1 mm (Fig. 7.5.6). In our opinion, the sources of this variability are inaccuracy in drawing vector "gluing lines" in relation to real lines, year-to-year differences in gain in a snake and individual growth features (different growth rate of bones in fast- and slow-growing adders).

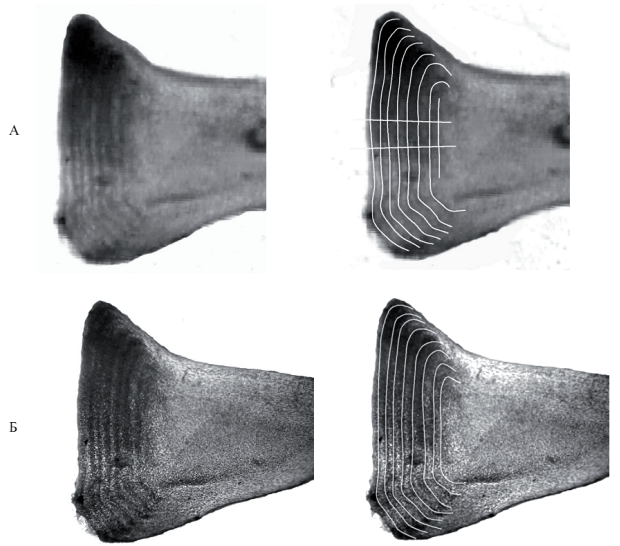


Fig. 7.5.5. Model lines of adhesion and two linear guides to measure the annual growth on a mikroskanogramme (А) and a microphoto (Б)

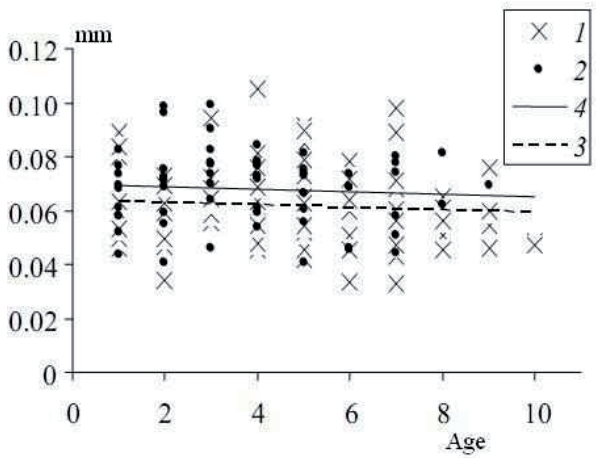


Fig. 7.5.6. Increase of the distal edge of the transverse bone of common viper: *1* – measurements for females, *2* – for males, *3* – trends for females, *4* – for males

Besides, there is no distinction in growth rate connected with sex. There are also no cases when two-year gain was registered as one (bands are well distinguishable). At last, as our data show, in ontogenesis of any individual there are no adjoining pairs of narrow zones, although the width of separate bands can be small (Fig. 7.5.7).

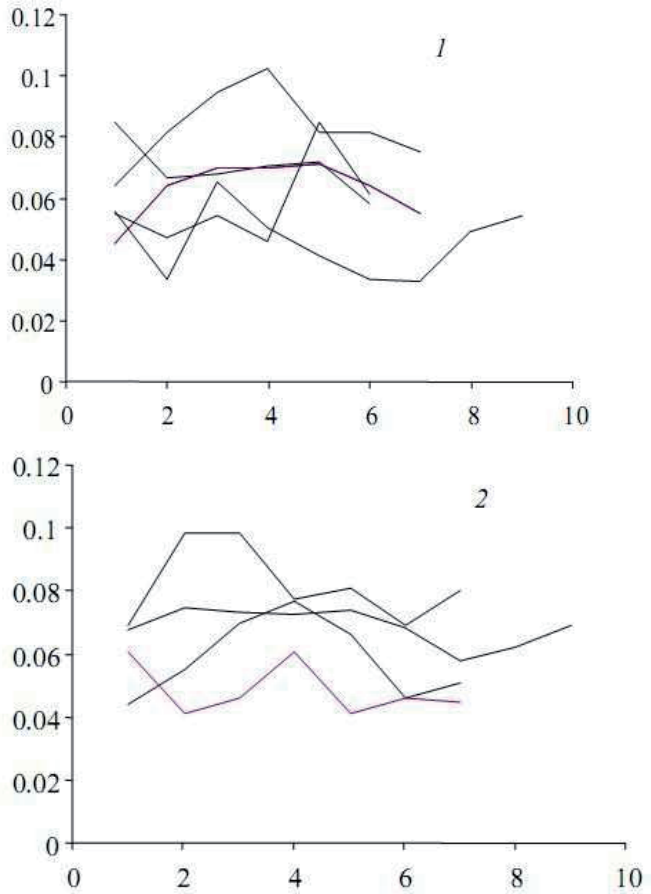


Fig. 7.5.7. Variants of the transverse bone growth dynamics of common viper females (*1*) and males (*2*)

The revealed regularity in alternation of dark and light bands indicates that if intermediate thin gluing lines exist, they are almost unnoticeable on the scanning image, and do not influence the accuracy in defining the number of survived winters.

The calculation error was determined by using triple independent definitions of lines number. It turned out that the greatest deviations of repeated calculations were observed in preparations with indistinct layered structure where dark bands were discontinuous, fuzzy, or they cannot be traced throughout all bone end-face. Such preparations were received on the bones isolated from the skull by maceration and much rarely – by boiling. In quantitative expression the error of the double calculation of the dark layers number is |0.8| years. In our opinion, the considered technique allows to define the age of adders with the accuracy of ±1 year.

Relationship between the number of layers and the size of a snake. An important practical task is to define the age of a living snake in field conditions. It is well known that on the basis of general weight and dimensional characteristics of an animal upon its achieving sexual maturity is impossible to define its age. At the same time many particular dimensional and weight characteristics can serve at least as approximate indicators of age. Among them crystalline lens of the eye of the muskrat, milling in a tooth crown or the shape of a tooth root, sizes of some morphological structures (Klevezal', Klejnenberg, 1967). We looked for similar signs in the adder. The dependence of the linear sizes of the transverse bone and the lower jaw on snake's age (on the number of found gluing lines) was considered As the proximal end of the transverse bone is very thin, it usually breaks off in making a preparation a little, and it does not allow to measure the bone length. For this reason, the bone perimeter was taken as a linear size measured in the MapInfo environment. It served as an integrated characteristic of peripheral increase in bone size. The jaw length was measured both in living specimens and on corpses by means of a plane table with millimeter scale – it is a distance from an articulation angle (posterior edge of *os articulare*) to anterior

edge of the lower jaw (Fig. 7.5.8). The error of the duplicating measurements was about 1 mm.

The ratios between the linear characteristics of mix-aged snakes are presented in Fig. 7.5.9, 7.5.10.

The growth along the perimeter of a dermal bone is quite even within the first 12 years and decreases with age a little. To describe this process, the allometric simulating model of annual gain $y = bx^a$ was composed (model type – for objects sampling, see: Korosov, 2002b) and its parameters were estimated.

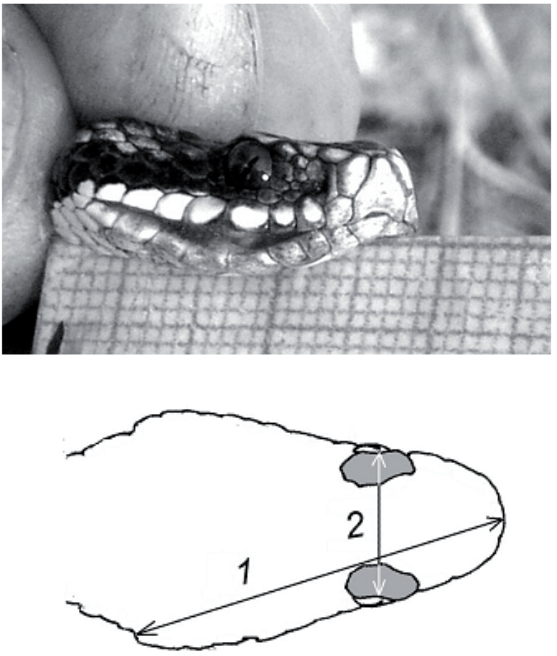


Fig. 7.5.8. Measurement of the length of the mandible (*1*, 26 mm) and width of the head (*2*)

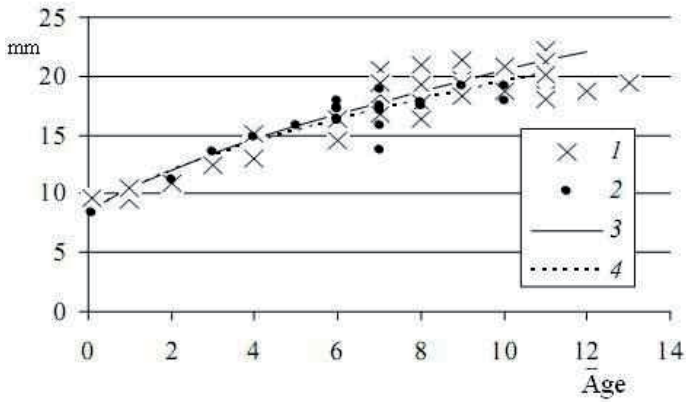


Fig. 7.5.9. Change of the perimeter of the common viper transverse bone with age: *1* – measurements for females, *2* – for males, *3* – model of growth of the perimeter for females, $R^2 = 0.85$, *4* – for males, $R^2 = 0.85$

The equation of the annual gain for females is $dP_f = 2 \cdot x^{-0.36}$, for males – $dP_m = 2 \cdot x^{-0.42}$. The average $P_{0+} = 8.5$ mm was chosen as an initial perimeter size (in current-year young). Both models adequately describe the data ($R^2 = 0.85$). Parameter b = 2 was set identical for females and males to find out the distinction in the dynamics of their bones growth; parameter *a* was adjusted in the course of optimization (see section 14).

At the first sight, the intensity of decreasing bone gain in females is slightly lower (a = –0.38), than in males (a = –0.42). However, both these coefficients and the regression lines drown for individuals of different sexes statistically do not differ (arithmetic differences are also insignificant – on average no more than 6% for the point corresponding to 11 years). In general, it is possible to state that the growth rate of the transverse bone is identical in adders' females and males, although there is a weak and insignificant (on our material) tendency to slower growth of the transverse bone in old males.

lower jaw size increases with age but there is a tendency to slow down (Fig. 7.5.9). The jaw growth decreases more slowly in females

($dLm_f = 2.28 \cdot x^{-0.48}$), than in males ($dLm_m = 2.55 \cdot x^{-0.59}$), however, the distinction between these coefficients (as well as between regression lines $R^2 = 0.85$) are not significant ($p = 0.05$) (Fig. 7.5.11).

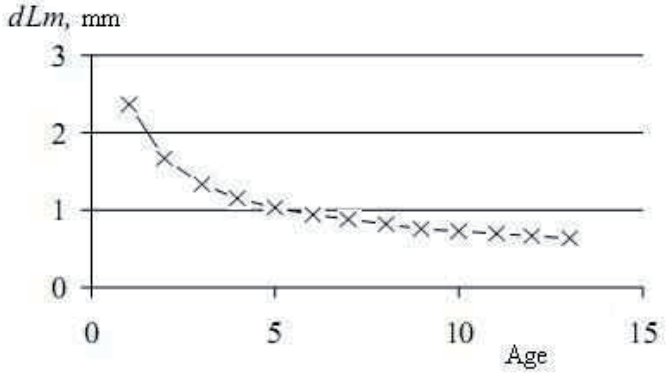


Fig. 7.5.10. Average annual value (x) of growth of the mandible $dLm = 2.35 \cdot x^{-0.508}$

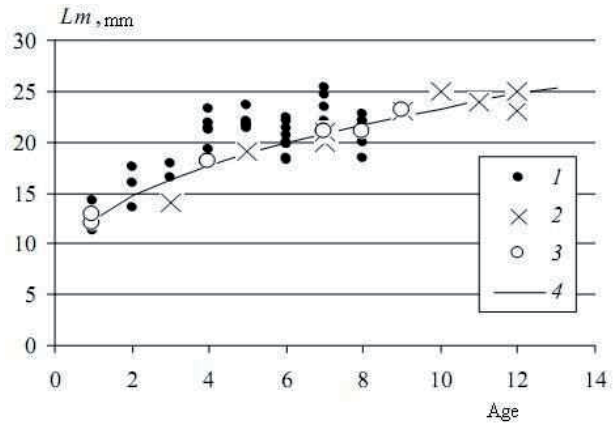


Fig. 7.5.11. Change of the viper mandible length with age: *1* – all the dead bodies, *2* – reliable measurements for females and *3* – males, *4* – model of jaw-length growth for both sexes, $R^2 = 0.85$

Measurements of the lower jaw length (Lm) produced by means of a rougher technology repeat in general the regularities considered above. The

The presented data allow drawing an unexpected and very important conclusion: the dynamics of the head growth in females and males is approximately identical; by the same age the heads of snakes of different sexes are indistinguishable by sizes. This strange phenomenon contrasts with the known opinion that females are larger than even-aged males.

However, the conclusion above is related only to the trunk of the snake (see section 5), but not to its head. One can try to use the found important ratios to describe the age structure of adders' population by constructing the equation connecting the age with lower jaw length (Fig. 7.5.12) (see section 8).

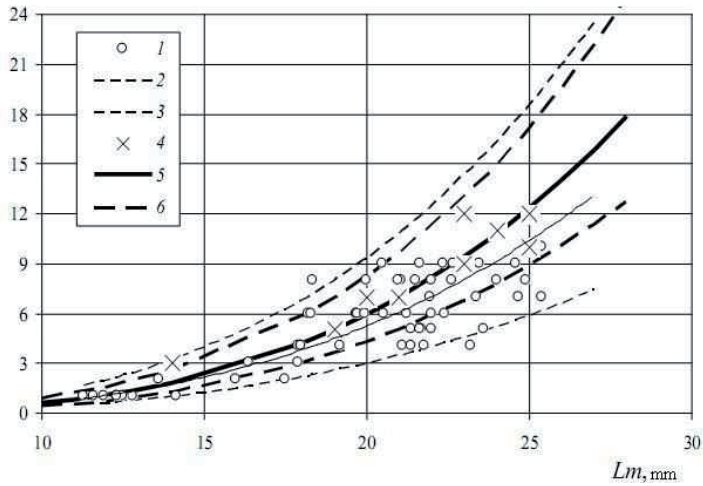


Fig. 7.5.12. Relation between individual age (x) and length of mandible (Lm): *1* – measurements of all animals, *2* – power law regression of measurements $x' = 0.000556 \cdot Lm^{3.055}$, *3* – the confidence interval for variants of $x' \pm 2S_x$ *4* – the most reliable measurements, *5* – power law regression of the most reliable measurements $x' = 0.000347 \cdot Lm^{3.255}$ and *6* – their confidence intervals $x' \pm 2S_x$

The found ratio and confidence limits give the possibility to establish at least the minimum possible age of a living individual in nature. For example, if the jaw length of an adder is 22 mm (modal value according to natural data), so the age of this snake is not less than 6 years, and on average, according to the most exact data, it is 8 years. The error of this technique of lifetime defining the adders' age is large enough (± 2–3 years) and it increases with the age of individuals, nevertheless, the approximate age is better than its total absence.

Maximum age of the adder. The greatest life span of the adder can be estimated using four sorts of data sources: monitoring animals in nature and in laboratory, dynamics of survival in marked individuals, age definition of individuals by the registering structures, approximate assessment of individual's age by relative body sizes.

As our observations showed (see section 5), newborn adders got an average annual "natural" gain in captivity in 2.2–2.6 months (65–75 days), i.e. the physiological cost of 1 month of living in captivity corresponds to 4.7–5.5 months of that in nature. At that, many large snakes caught at the age not less than 5–7 years, continued living in our laboratory in the regimen of year-round activity for 5–7 years (up to their death, generally because of cloacitis) that corresponds to 10–15 more years of life in nature. Thus, the death from old age (or its related diseases) was observed at physiological age of 15–28 years (Korosov, 2005)! Great potential life span in adders up to 20–30 years has been reported by other authors (Voženilek, 2000; T. Phelps, cit. from: Bakiev et al., 2008).

Our direct observations confirm the presented calculations (Fig. 7.5.13). Of adult snakes (at the age not less than 5–7 years) marked by us, one individual was found in 12 years (measurements were 57 and 59 cm), two – in 11 years (measurements of L. t. – 51/54 and 36/54 cm). From their size, the first two snakes were adult (older than 5 years) and their age at the moment of the second marking should be not less than 16–17 years.

Probabilistic characteristics of the maximum life span can be received, using the data on animals dying away (see section 8). The chart shows fast decrease in the proportion of marked animals within the first 4–

8 years after marking (Fig. 7.5.13; see Fig. 8.5.6), however, not all the marked animals disappear even in 9 years after the first catching. As these animals were not less than 4 years old when first captured, the data indicate that on the island of Kizhi adders are able to live up to 13 years. Applying "the agreement of 95%" (Ivanter, Korosov, 2003), it is possible to accept the age, up to which not less than 95% of individuals (in our case – marked ones) live as the statistical maximum of life span for adders. Calculations show that the proportion of survived marked females will decrease less than by 5% in 10 years (at the average specific mortality d = 26%) and males (d = 38%) in 7 years (see Table 7.4.2, Fig. 7.4.1); the difference is about 3 years. The number of gluing lines on the transverse bone showed that both among females and males there were snakes aged 12 years. Thus, the maximum life span of adders of both sexes on Kizhi is identical.

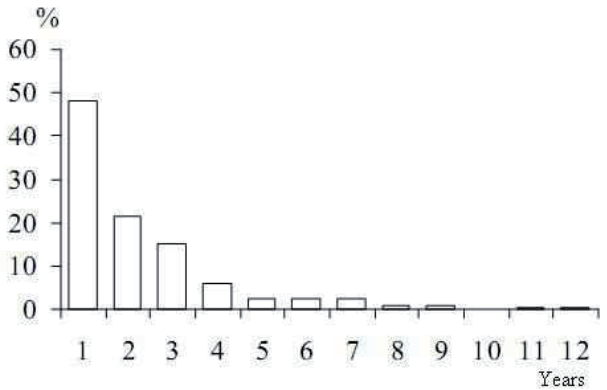


Fig. 7.5.13. Proportion of tagged individuals (% of 469 copies.) met again after a different number of years after the first capture

It is important to note that in the sample of the animals studied by the method of skeletochronology there were no individuals with the jaw length more than 26 mm, whereas in nature some individuals with a larger head size – up to 30 mm were found (see Fig. 8.5.3). They composed 3.5% (6 specimens of females and males each). The age of such individuals is likely to reach 25 years. These estimates seem possible as these animals differ a

lot from the rest of adders. They are not so long, but rather massive individuals with a broad back, their body weight is up to 170 g (without food). They are usually nonaggressive, but frighteningly large not only due to their size, but to body proportions which are almost similar as those of Levantine viper. These rare individuals, as might be supposed, realize an extreme potency of species-specific norm. In general, in the island population the proportion of long-living females is more, than that of males (see section 8). The median life span in adult females dwelling on Kizhi is 1.7–3.6 years more, than in adult males (5.9 vs. 7.6–8.5 years), although the maximum age is identical.

According to the received information, one can make the general conclusion. The physiological life threshold of the adder (25 years) significantly exceeds the maximum age, usually observable in nature (10–12 years), and even more the average age (6–8 years). These statistical indicators of age characterize not a species-specific norm (physiological possibility of individuals), but the conditions of a particular habitat, the total load of all lethal environmental factors influencing the snakes population on the island of Kizhi.

On Kizhi the maximum physiological age (25 years) of the adder and its maximum population age (12 years) differ by a factor of two that once again shows that snakes experience strong negative impact in this habitat.

In the population of the adder dwelling on Kizhi the natural mortality rate in males is higher, than in females: $d_{♀} = 26\%$ and $d_{♂} = 38\%$. Hence, eventually the parity index of newborn males to females is also disturbed in favor of females: the proportion of adult males in the island population becomes significantly less. ($N_{♀}:N_{♂} \approx 3:1$). On Kizhi the greatest life span of snakes does not exceed 11–13 years that is less than their physiological capability (25 years).

Chapter 8.

Reproduction

The reproduction of an island population (in the absence of migration) consists of dying off one part of individuals and regular reproduction of the rest of them. To describe the dynamics of this restoration it is necessary to know the population number at any particular time. In herpetology the indicators of animals abundance are widespread (Darevsky, 1987), but they hardly correspond to our goal of constructing a detailed picture of island population living. The assessment of abundance of the adder (and reptiles in general) always poses a problem, as visual methods of the census are ineffective for this goal. The most of these poikilothermic animals are constantly in shelters (Zamolodchikov, 1989; Zamolodchikov, Kolosova, 1995), therefore the route census always gives underestimate, moreover, it is also substantially incorrect. In this case the only representative method is capture-mark- recapture (direct calculation of all individuals in a population is usually impossible for wild species).

Capture-mark-recapture method is one of a few almost experimental, active field methods, with a specific feedback between the researcher and animals' population underlying it. This feedback is specific in that there is not any physical impact of an observer on a population (except the moments of catching individuals) instead, there is an information interaction: the *gradual registered* replenishment of the population with marked animals.

Due to repeated catching, the *dynamics of population response* to the impact of a researcher is formed. Studying the process helps to receive much more correct characteristics of its mechanism, than the static consideration of its results. This is evidenced by the accumulated experience of marking reptiles which allows giving substantial estimates of species number (Bozhansky, Semenov, 1978; Biella, 1979; Belova, 1985, 1989; Saint-Girons et al., 1989; Korosov, 2002a, 2008, etc.).

It is important to estimate the absolute number separately for males and females. Knowing exact quantitative characteristics, it is possible to create models of "live substance" redistribution (both in a population and zoocenosis) where parameters have clear biological sense.

*8.1. Materials and method*s

Marking technology and initial data are described in details in section 7.1. Census was carried out on 690 km-long routes on the island of Kizhi in May (in the period of coming out of wintering and mating) and September (before leaving to wintering) within 17 years (1991–2007). The standard technique on transects of 4 m wide (meadow) or 3 m wide (coppice) was used, at that the most favorable conditions in the activity period at different daytime – from 6 a.m. to 10 p.m. – were chosen (Novikov, 1953; Shlyakhtin, Golikova, 1986; Darevsky, 1987).

In total we found 4357 adders (Table 8.1.1) and 2746 (63%) of them were caught. After exclusion of snakes weighing less than 35 g (aged less than 4 years) and those identified inaccurately (pictures or descriptions of poor quality), 2073 first caught and marked adult snakes remained, among them 469 doubles were found (23%) (Tables 7.3.1, 7.2.1, 7.2.3). The marked snakes were found both in a year of marking and in the following years, even 12 years later.

According to one of the approaches, the absolute (total) number of animals on the registration square is defined as a total number of the individuals marked by the time when unmarked animals are no longer found (Bozhansky, Semenov, 1978; Sokol'sky, Kudryavtseva, 1980). Many authors note some incomplete capture of animals actually living in the place of census (Litvin, 1980; Zamolozhnikov, Kolosova, 1995).

To solve this problem can help the calculation of the absolute number on the data of catching marked individuals (Macfed'yen, 1965). The widespread methods of calculations are described by G. Koley (1979). Different assumptions of how the number of animals could changes during the investigation allowed to offer a number of algorithms, including the

method of Petersen (Lincoln), Schumacher, Bailey, Jolie – Zeber, as well as a variant of Petersen's method realized in the form of simulating model (Korosov, 2002a).

Table 8.1.1. Census of adders on Kizhi in 1991–2009 and their resulting absolute number (N) in the area of 100 hectares (meadows)

Year	Routes		Number of snakes found			Population number
	number	length, km	total, ind.	ind./km	ind./ha	estimate, N ind.
1991	2	10	21	2	5	500
1992	8	17	65	4	9	940
1993	24	48	287	6	15	1500
1994	31	77	348	5	11	1130
1995	33	81	561	7	17	1730
1996	27	65	496	8	19	1910
1997	23	57	332	6	15	1460
1998	36	56	475	8	21	2110
1999	16	22	87	4	10	990
2000	10	30	107	4	9	900
2001	21	38	224	6	15	1470
2002	10	20	88	4	11	1090
2003	8	14	44	3	8	790
2004	5	24	68	3	7	720
2005	13	49	181	4	9	920
2006	9	36	186	5	13	1300
2007	14	45	198	4	11	1100
2009	19	42.5	589	14	35	3500
Average	16	38	229	5	13	1203
Total	309	732	4357			

8.2. Assessment of relative number

The island of Kizhi has been notable long since for the abundance of adders due to the favorable conditions for their life – the existence of numerous winter and summer shelters in heaps of stones over extensive meadows and a lot of frogs (food items) in lakeside bogs (Korosov et al.,

1999). Average long-term occurrence of adult individuals of both sexes is 5 ind./km, as calculated to transect width – 12 ind./hectare (see Table 8.1.1).

Unfortunately, these density estimates do not allow estimating quite precisely the total number of the island population. Considering only dry open stations favorable for adders (100 hectares), we calculated the value – 1200 snakes (Table 8.2.1), while extrapolating to the whole island (200 hectares) – 2400 snakes. Thus, we receive different estimates of abundance, depending on the square of extrapolating.

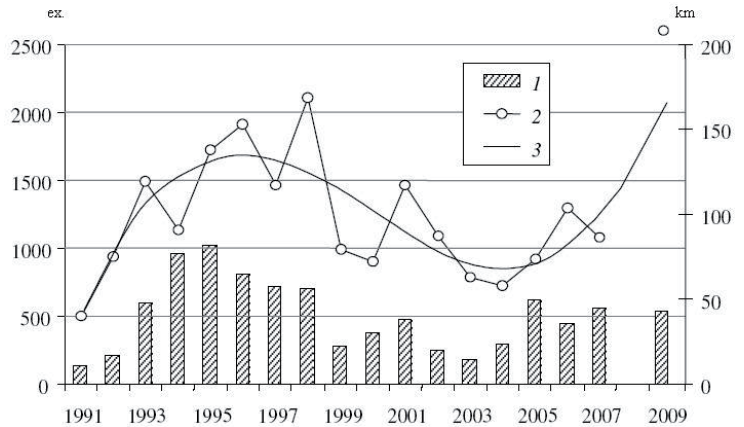


Fig. 8.2.1. Occurrence of vipers on isl. Kizhi in 1991–2007.: *1* – length of routes, *2* – evaluation of abundance(ind / 100 ha), *3* – trend (third-order polynomial)

This indicator also fails to give presentation about the dynamics of abundance. According to our data, the occurrence of snakes in a particular year correlates significantly with the route length ($r = 0.72$, $\alpha = 0.01$) and snakes number ($r = 0.85$, $\alpha = 0.001$). Instead of an abundance estimate, the census characterizes the completeness: the more carefully the territory is examined, the more animals it is possible to found, and almost regardless of a current number of species, as further calculations show! Using route census one can follow only some variations of the estimate in the vicinity of rather high and constant value – 10–14 ind./hectare, but not its

dynamics. It is known that the occurrence of reptiles is defined, besides the population number, by their current activity depending in turn on environmental conditions and seasonal cycle. Therefore, when carrying out censuses on the same dates, every year we face different temperature conditions that affect the animals' activity and their occurrence. For example, in 1995 and in 2009 the spring was late, and we could observe mass exit of adders from wintering, so their relative number (occurrence) was the highest (up to 35 ind./hectare).

It means that the seasonal censuses can hardly show the real number of animals at a given time. Nevertheless, a long-term series of censuses makes them quite representative, and the average resulting values are quite realistic.

The data on occurrence do not allow judging the sex ratio. So, the relative number of found females to males is 51 and 49% (1191:1162) respectively, but the proportion of recaptured marked individuals differs significantly ($p < 0.01$) – 43 and 57% (160 and 216 ind.).

The conclusion is obvious: snakes numbers, its changes and ratios between reptiles groups should be determined on the basis of absolute measures, which can be received by the method of repeated catching of earlier marked individuals.

8.3. Assessment of absolute number by analytical methods

In literature the ready-made formulas are offered to calculate the absolute number of animals on the data of the re-catching of marked animals (Koley, 1979). The main disadvantage of these methods is that each of them is focused on a certain limited number of re-catching – from 2 to 4. In our case observations lasted for 18 years and neither of these formulas can accommodate all the data. It means that the essential part of the received information on continuity of a population dynamics will be lost, and the estimates of the population number will not be as correct as possible. Besides, each of the methods makes a number of feasible requirements, and a deviation from them has a large impact on the accuracy

of calculations. One of such requirements is equal probability of capturing marked and unmarked animals. Unfortunately, neither of considered processing methods could satisfy our needs. Let's consider our negative experience, limiting ourselves to the analysis of a short number of observations (from 1992 to 1998) of all marked individuals, it reveals problematic points and shows a way out of the arisen situation.

Petersen's (Lincoln's) method is focused on animals' marking and the instant subsequent capture; it is based on the assumption that in the marking period there is no migration, deaths and births. The formula expresses a "chemical" proportion: concentration of marked animals in repeated tests corresponds to that in a studied population: $M/N = m/n$, where N – population number, M – total number of marked individuals, n – number of animals in a current catching, m – number of marked animals in a test. Values M, n, m are received from observations, the total number is calculated according to the formula $N = M \cdot n/m$.

Using the data in Tables 7.1.2 and 7.1.3, calculations were performed for the period 1992–1998 (Table 8.3.1). In the tables the numbers of snakes recaptured not only in a year but also in 2, 3 … 7 years are given. For example, in 1994–1995 the number of adders was $N = 152 \cdot 365/18 = 3082$, in 1994–1998 – $N = 152 \cdot 238/11 = 4020$.

Our technique of repeated censuses (in a year) does not comply with strict requirements of this method, in particular, within a year a part of individuals dies, and a part of young becomes mature and occurs in captures. Owing to this fact the estimate of population number varies widely; on average it equals to N = 4807 snakes. One of the most precise numbers is that received in two adjacent years of marking and repeated catching (the first diagonal row: 833, 2928, etc.), averaging gives the value N = 3657 individuals. Unfortunately, this assessment does not consider continuity of these long-term observations.

Table 8.3.1. Absolute number of adders on Kizhi calculated by Petersen's method

Numder of marked adders, M, ind.		Number of caught adders, n, ind.							
		1991	1992	1993	1994	1995	1996	1997	1998
		17	49	122	158	365	273	214	238
1991	17		833	–	2686	–	–	–	–
1992	48			2928	7584	4380	4368	5136	5712
1993	120				4740	4380	6552	–	–
1994	152					3082	4150	3253	4020
1995	333						6494	6478	7205
1996	241							5730	3824
1997	181								1795

Schumacher's method is more advanced, as it helps to assess "the number of animals in a population on the growth rate of marked animals proportion when more and more animals are marked" (Koli, 1979), i.e. it accumulates all collected data. However, the method also assumes that the number of animals is constant during the entire census period (Tables 8.3.2, 8.3.3).

Table 8.3.2. Calculation of abundance by Schumacher's formula (since 1991)

	Years of repeated captures							
	1991	1992	1993	1994	1995	1996	1997	1998
Captured, n_i	17	47	120	152	333	241	181	177
Marked earlier, M_i	0	17	65	185	337	670	911	1092
Occurred marked, m_i	0	2	2	9	50	36	38	66
$M_i^2 \cdot n_i$	0	13 583	491 520	5146 112	37594 368	107862 201	149886 100	210679 737
$\sum M_i^2 \cdot n_i$	0	13 583	520 872	5723 072	43541 549	151726 449	301942 150	513008 278
$M_i \cdot n_i$	0	34	130	1665	16850	24120	34618	72072
$\sum M_i \cdot n_i$	0	34	164	1829	18679	42799	77417	149489
N_i	–	400	3176	3129	2331	3545	3900	3432

The method allows estimating the snakes' number on the data of multiple catching: $N = (\sum M_i^2 \cdot n_i) / (\sum M_i \cdot m_i)$,where $\sum$ – summation sign on all i-s stages of produced work, M_i – number of the individuals marked before i-s catching, n_i – number of the individuals caught at i-s catching, m_i – number of marked individuals found out among n_i caught animals.

Table 8.3.3. Absolute number of adders on Kizhi calculated by Schumacher's method

		Captured snakes, n, ind.							
Marked snakes, M, ind.		1991	1992	1993	1994	1995	1996	1997	1998
		17	49	122	158	365	273	2114	238
1991	17		400	3176	3129	2331	3545	3900	3432
1992	48			2880	2840	2196	3440	3810	3360
1993	120				2027	1827	3155	3565	3162
1994	152					1012	2569	3035	2714
1995	333						2229	2555	2239
1996	241							1148	1136
1997	181								485

Calculated numbers have to be relevant to the year when marking began (line in Table 8.3.3) and to the year when repeated capturing was carried out (column in Table 8.3.3). Let's consider the first line. In 1992 among $n_i = 49$ caught snakes there appeared $m_i = 2$ marked snakes from $M_i = 17$ earlier marked individuals. So $sM_i^2n_i = 7^2 \cdot 47 = 13583$, $M_in_i = 17^2 = 34$, $N_i = 13583/34 \approx 400$ ind.

Calculations in each following line of Table 8.3.3 correspond to those situations as if marking would begin not in 1991, but in later terms. Thereby the number of marked animals having been collected and calculating mistakes are eliminated. For example, if marking began in 1995 (the fifth line), then in 1996 the calculated number would reach 2229 snakes. The estimates of adders number on Kizhi received by Schumacher's method also vary widely (general average is equal to N = 2546 ind.). To reveal the general tendency of changing estimates of the number is possible if one averages the values in all lines of Table 8.3.3 received for the identical moments of marking which are on diagonals. For example, the

first estimate of number received in 1992 on the data of marking in 1991 was $N_{1991/1992} = 400$ ind., and the first estimate of number received in 1995 on the data of marking in 1994 – $N_{1994/1995} = 1012$ ind. (the fourth line in Table 8.3.3). After the averaging of all first estimates (received a year apart) we have the value $N_1 = 1454$ snakes, but when considering marked snakes captured in two years, we obtain $N_2 = 2351$ snakes (Table 8.3.4).

As well as in the previous table, one can notice that the estimates of snakes' number is gradually increasing while the year a current capture is getting farther from the year of marking.

Table 8.3.4. Absolute number of adders, averaged on diagonals of Table 8.3.3

Time after marking, years	1	2	3	4	5	6	7
N, ind.	1454	2351	2751	3013	3506	3630	3432

As for this increase, it is possible to draw an unambiguous conclusion: it is caused by a gradual reduction of the number of marked animals in the population because of their death and rise of the number of unmarked individuals due to reproduction. Hence, in annual tests the proportion of marked snakes gradually decreases that creates false effect of number increase. Because of that the received estimates cannot be considered correct. At the same time, using Schumacher's method, we can receive the approximate number of adult adders on Kizhi in registration years equal to 2500.

Bailey's method, unlike those considered above, takes into account the effect of changing the number of marked animals in a population between the marking moments and allows calculating the number of deaths and births. The disadvantage of this method is that the data of three consecutive censuses are used, but not of all years. There are two necessary consecutive stages of marking and those of repeated capturing (in total three captures are carried out i = 0, 1, 2).

The method is based on the assessment of the loss rate of marked snakes and allows to calculate more precisely the snakes number $N_1 = [M_1 \cdot (n_1 + 1) \cdot m_{02}] / [(m_{01} + 1) \cdot (m_{12} + 1)]$,

the repopulation by young

$B_{12} = [m_{01} \cdot (n_2+1)] / [n_1 \cdot (m_{02}+1)]$, $b_{12} = \ln(B_{12})$

and the reduction of it due to animals death

$D_{01} = 1 - (M_1 \cdot m_{02}) / [(M_0 \cdot (m_{12}+1)]$.

In the range of our data we have calculated the number and replenishment rate for each three years group, as well as the average value for all years (Table 8.3.5).

The question if statistical averaging of number estimates is competent without the relevant weighing to capturing numbers can be laid aside, stating the general result: this estimate of absolute number of the island population is equal to N ≈ 3300 adders. The average replenishment rate calculated by Bailey's method is b = 0.15, the average mortality rate is d = 0.24. Despite its obvious advantages, Bailey's method, unfortunately, does not use all available information on tagging and capturing. Besides, owing to the low frequency of recapture of marked animals the estimates of mortality and repopulation become unreal negative values.

Table 8.3.5. Absolute number of adders on Kizhi, calculated by Bailey's method

Year	i	M_i	n_i	m_{0i}	m_{1i}	N	b	d
1992	0	49						
1993	1	120	122	2		1230	0.81	0.49
1994	2		273	1	4			
1993	0	122						
1994	1	154	158	4		2880	–0.20	0.29
1995	2		356	10	17			
1994	0	158						
1995	1	356	365	17		5430	0.24	–0.60
1996	2		273	9	12			
1995	0	365						
1996	1	261	273	12		4890	0.05	0.41
1997	2		214	8	9			
1995	0	273						
1997	1	205	214	9		2310	–0.18	0.61
1998	2		238	11	21			
On average						3350	0.15	0.24

Jolie – Zeber's method for defining the number and demographic parameters of a population is based on the data of multiple captures of the same individuals. As it was noted, the proportion of re-found snakes composes less than 23%, and the number of adders found three times is only 12 ind. (section 7.3, Table 7.3.1). So the low occurrence does not allow calculating if only representative number estimate, using this algorithm.

8.4. Assessment of absolute number in modeling

Among the ways of calculating an absolute number considered above, the Schumacher's algorithm is noticeable for its possibility to consolidate long datasets, and Bailey's method allows calculating the estimates of instant mortality and birth rate (repopulation). Analytical formulas combining these features would be too clumsy and impractical. However, there is a solution: to apply a simulating model. Unlike analytical methods, modeling fails to give a uniform universal formula of calculating the appropriate estimates on any data, but allows reconstructing model datasets characterizing such natural processes as survival, replenishment and mortality of individuals. At that time, the only requirement to the data is an equal probability of catching animals of the studied status (marked and unmarked, males and females, young and adult).

Good "mixing" of marked and unmarked snakes can be expected only in several months after marking sessions, as northern reptiles spend quite long periods of time in shelters without appearing on the ground for hunting or basking (Zamolodchikov, Kolosova, 1995). At the short-term periods of tagging and repeated catching only a part of the most active individuals will be registered and the estimates of the population number will be significantly reduced. We carried out census once in 0.5–1 year, suggesting that for that time natural rotation of animals occurs. Besides, routes are spread quite evenly over the territory of the island, excepting damp bogs (Fig. 8.4.1), but including the majority of stone ridges (896 ind.

were revealed there) in which snakes shelter. This practice also provides almost identical probability of finding different individuals.

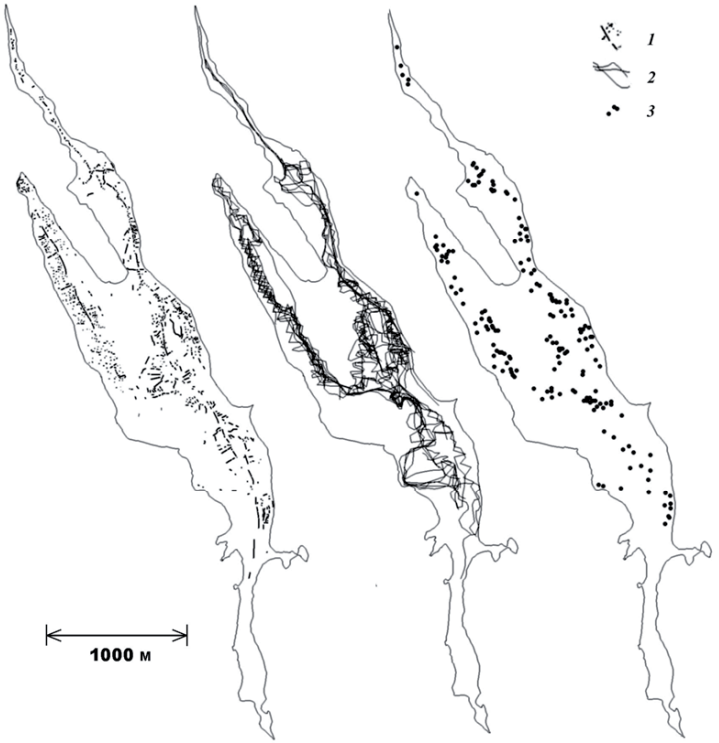


Fig. 8.4.1. The location of the stone ridges on Kizhi island (*1*), routes (*2*) and vipers (*3*) in 1995

Individuals of different sexes have significant differences in their behavior connected with reproduction (see sections 4, 11, 12), therefore females and males have various probability being found. For this reason, all calculations are performed separately for males and females.

Even more distinctions were found in the behavior of mix-aged individuals. As it is known, until their sexual maturity (3–4 years) snakes lead very secretive life and are rarely found on routes (Belova, 1978). In our samples they composed 3–4%. Therefore, it made us give up marking

young at all and exclude all the animals weighed less than 35 g from the sample.

Thus, the dynamics of the number of solely adult snakes of both sexes served as the object of the model research.

The data from section 7.1 were used in calculations. Once marked adders were found both in the year of a marking (these figures are not used in calculations), and in the consecutive years, even 10 years later. For example, in 1995 173 females were marked, 13 of them were caught next year, and 1 – in 2006.

Model structure. We possess the following empirical data for each year: the number of caught animals (n), the number of marked animals (M) and the number of repeatedly caught snakes marked in previous years (^{3}m) (Table 7.1.2, 7.1.3). The number of recaptured snakes varies due to several factors. Different model options were constructed considering some of them (mortality, birth rate, distinctive behavior of animals of different sexes). The majority of other factors (census timing, routes location, features of phenological processes, weather conditions, etc.) were considered as inevitable stochastic noise, and the simulating model was called upon to offset it.

The problem of the assessment of snakes' number was solved in two stages. At first, on the electronic worksheet of Excel the model covering all years of investigations was constructed. This model imitated the preservation of a part of individuals within each separate year, death of some of them, appearance of new mature adders, as well as primary and repeated captures of animals (Korosov, 2002a, 2008).

The main issue of simulation modeling consists in expressing known variables through unknown parameters. The simulation model has to calculate the same values that are observed in nature and experiments. Then while sorting out possible values of parameters one can choose those, at which model magnitudes of variables will coincide with the real ones. In this case, it is possible to discuss the found parameters values as the characteristic of the observed phenomenon mechanism.

For the adder population we know the number of once tagged animals (M), the number of recaptured snakes (n), number of re-captured individuals in each new test (^{3}m). The total number (N), the number of individuals dying every year (Nd) and the amount of repopulation (Nb) remain unknown (Fig. 8.4.2).

At first, the unknown model parameters (N, Nd, Nb) were appointed according to theoretical considerations and the available information.

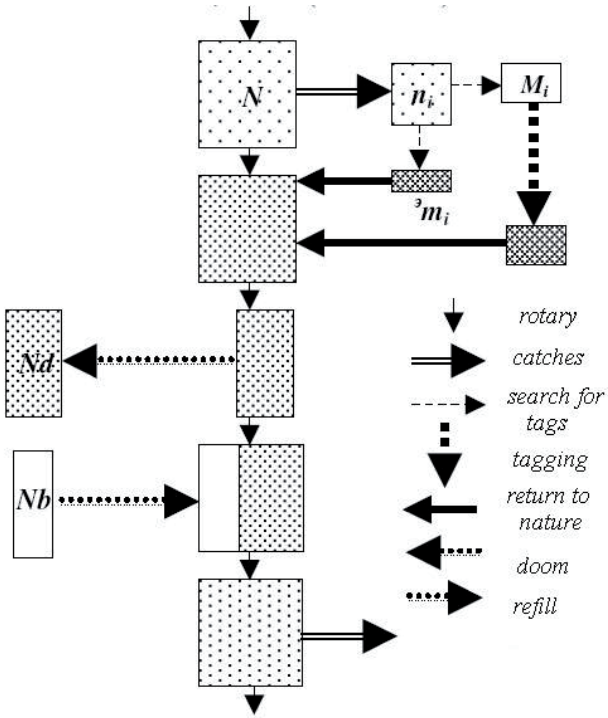


Fig. 8.4.2. The fate of vipers on Kizhi during one annual cycle of catches

In the second stage, their values were refined by means of the optimization procedure. The course of computation and final model version for females is presented in Tables 8.4.1–8.4.4; for males – in Tables 8.4.5.

The complete simulation model restores theoretical values of number, death, and repopulation in each observed year. The calculation of

long-term series of the number assessment begins with the basic value N_{1991}, which is the first parameter of the model. The population number in consecutive years is expressed by the formula including the number individuals survived from the previous year minus the number of dead snakes plus the number of snakes reaching maturity:

$N_{i+1} = N_i - Nd_i + N_{bi}$.

This method of calculating dynamics (from past to future) can be called direct. The proportion of died individuals is the (annual) specific mortality $d_i = Nd_i / N_i$. The proportion of individuals which became mature and replenished the population, is equal to $b_i = Nb_i / Ni$. So, on the island the estimated number of females in 1994 amounted to $N_{1994} = 1595$ ind., in 1995 419 snakes died, 442 females become adult, their numbers in 1995 was $N_{1995} = 1595 - 419 + 442 = 1619$ ind., the mortality rate was $d_i = 419 / 1595 = 0.26$, and the repopulation was $b_i = 0.27$ (Table 8.4.4).

In each i-th year (i = 1991, 1992..., 2006) from the population of Ni individuals ni animals were caught (for example, 187 females in 1995, Table 8.4.1). The adders captured in this year for the first time were recorded as marked (Mi). As in all catches (ni) there were previously marked individuals (mi), the number of snakes newly marked in this year (Mi) is less than the sample size Mi = ni – mi (of n1995 = 187 females captured in 1995, 2 ind. were marked in 1992, 8 and 4 – in 1993–1994, a total of newly marked snakes $M_{1995} = 173$ ind.) (Table 8.4.1). It is obvious that the mortality rate among marked individuals was proportional to a population specific mortality rate in a current year ($di \cdot Mi–1$ or $di+1 \cdot Mi$), i.e. the number of snakes marked in i-th year and surviving up to i+1-th year, is: $Mi+1 = Mi – di+1 \cdot Mi$. Thus, among 63 individuals, marked in 1994, the number of snakes surviving in 1995 is $M_{1995} = 63 – 0.26 \cdot 63 = 47$ (Table 8.4.1).

In the catches of the foremost year containing n_{i+1} snakes the number of marked individuals was equal to m_{i+1}. This value can be expressed by the Peterson's formula (Koli, 1979): $m_{i+1}/n_{i+1} = Mi_{+1}/N_{i+1}$. Hence, the number of marked animals in the sample was equal to: $m_{i+1} = n_{i+1} \cdot M_{i+1}/N_{i+1}$. So, in 1995 we get $m_{1995} = n_{1995} \cdot M_{1995}/N_{1995} = 187 \cdot 47 / 1619 = 5.4$ ind. By

inserting formulas into the cells on the Excel worksheet corresponding to all the years of capturing, we obtain the table of expected numbers of re-found marked snakes (Table 8.4.2).

Table 8.4.1. Calculated number of marked adder females (M) remaining in the population

Number of marked females, M, ind.		Number of captured females, n, ind.														
		1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006
		23	85	67	187	170	47	97	30	61	78	31	37	26	97	118
1991	8	2	2	2	2	1	1	1	1	0	0	0	0	0	0	0
1992	22	22	22	22	16	8	8	6	6	2	1	1	1	1	1	0
1993	85		85	85	63	30	30	24	24	9	5	4	3	3	3	1
1994	63			63	47	22	22	18	18	6	4	3	3	2	2	1
1995	173				173	82	82	67	67	24	14	12	9	9	9	2
1996	145					145	145	118	118	42	25	21	16	16	15	4
1997	35						35	28	28	10	6	5	4	4	4	1
1998	73							73	73	26	16	13	10	10	10	2
1999	15								15	5	3	3	2	2	2	0
2000	50									50	30	25	20	19	18	4
2001	67										67	54	43	42	41	9
2002	26											26	21	20	20	4
2003	31												31	30	29	7
2004	21													21	20	5
2005	82														82	19
2006	106															106

Setting the model. The second step of modeling is targeted at selection of such values of the initial number (N_0), annual mortality (N_{di}) and repopulation (N_{bi}) of animals, at which the estimated number of re-captured marked individuals (m) in all the years of observation would correspond as nearly as possible to the number of actually captured and marked adders (^{э}m). For this purpose, we used the program "Finding solution" that is inserted into Excel to implement numerical optimization methods (Korosov, 2002b) (see section 14). By means of this program one can derive the new values of the parameters that provide the minimal difference between calculated (m) and empirical (^{э}m) data on recaptured marked snakes.

Table 8.4.2. Calculated numbers of re-captured adder's females (m)

	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006
1991	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1992		1	1	2	1	0	1	0	0	0	0	0	0	0	0
1993			4	7	5	1	3	1	1	1	0	0	0	0	0
1994				5.4	4	1	2	1	1	0	0	0	0	0	0
1995					13	4	7	2	2	2	0	0	0	1	0
1996						6	12	4	4	3	1	1	0	1	1
1997							3	1	1	1	0	0	0	0	0
1998								2	2	2	0	0	0	1	0
1999									0	0	0	0	0	0	0
2000										3	1	1	0	2	1
2001											2	2	1	3	1
2002												1	1	2	1
2003													1	2	1
2004														2	1
2005															3

In calculating the discrepancy the Euclidean measure was used $\varphi = ({}^{э}m_i - m_i)^2$. For example, if the estimated number of snakes marked in 1994 and re-captured in 1995 was 5.4 ind., but 4 individuals were really caught, the difference was $\varphi = (4 - 5.4)^2 = 1.95 \approx 2$ (Table 8.4.3). The total difference over all years is $\Phi = \Sigma({}^{э}m_i - m_i)^2$. Before the proper setting of the model the starting values of mortality and repopulation were assigned equal and the same for all years, based on previously obtained mortality rate $d \approx 0.2$ for females and $d \approx 0.4$ for males (Korosov, 2005).

For example, at the beginning of model setting the initial value of the number was $N_{1991} = 2000$ ind. and there were16 pairs of identical values $Nd_i = 400$, $Nb_i = 400$. The optimization program changes directionally the rows of values N_i, Nd_i, Nb_i and seeks to nullify the differences between the model and reality: $\Phi \rightarrow 0$. After final model setting of this version we received $\Phi = 126$. Considering unequal representativeness of estimates of captured marked snakes ${}^{э}m$ (Tables 7.1.2, 7.1.3) obtained when the snakes number in the primary and secondary tests was different, "weights" equal to $ni \cdot nj$ were introduced into the formula. For example:

$\phi_{1994,1995} = 67 \cdot 193 \cdot (4 - 5.4)^2 = 25155$; for all years, $\Phi = 782718$.

Table 8.4.3. Difference between the empirical and the estimated number of re-captured adders' females $(^{э}m - m)^2$

	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006
1991	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1992		2	1	0	1	0	2	0	0	0	0	0	1	0	0
1993			0	1	0	2	6	1	1	0	0	0	0	0	0
1994				1.95	2	1	1	0	2	0	0	0	0	0	0
1995					0	6	0	1	1	0	0	0	0	1	0
1996						10	0	10	2	0	1	5	0	3	0
1997							4	0	1	0	0	0	1	0	0
1998								0	3	5	0	0	0	1	0
1999									2	3	1	0	0	0	0
2000										11	1	1	0	0	2
2001											1	3	0	0	2
2002												0	0	2	0
2003													1	0	4
2004														0	5
2005															0

Table 8.4.4. Calculated dynamics of the number adders' females in 1991–2006

Para-meter	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006
Ns	469	297	366	404	410	269	278	234	234	184	183	203	219	261	294	195
Nn	234	148	183	202	205	134	139	117	117	920	914	101	109	130	147	974
Np	617	391	482	532	540	354	366	309	309	242	241	267	288	343	387	256
Nd	528	834	14	0	419	558	1	173	0	468	283	155	173	18	51	595
Nb	426	158	286	150	442	0	38	0	0	269	278	234	234	184	183	203
N	185	117	144	159	161	106	109	926	926	727	722	802	863	102	116	769
d	–	0.71	0.01	0.00	0.26	0.53	0.00	0.19	0.00	0.64	0.39	0.19	0.20	0.02	0.04	0.77
b	–	0.13	0.20	0.09	0.27	0.00	0.03	0.00	0.00	0.37	0.39	0.29	0.27	0.18	0.16	0.26

Note. N – absolute number, Nd – number of individuals, dying within the year, d – specific mortality, Nb – number of individuals reaching maturity, b – repopulation, Np – number of pregnant females, Nn – number of newborn females, Ns – number of newborn females that survived the winter; starting conditions of model setting: $N_{1991} = 2000$, $Nd_1 = 400$, $Nb_1 = 400$ ind. Dash – calculations are not available.

Table 8.4.5. Calculated dynamics of the number of adders' males in 1991–2006

Parameter	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006
Nd	230	248	351	25	0	337	204	95	125	239	149	52	1	314	271	232
Nb	170	170	176	268	0	3	192	0	100	268	75	47	234	184	183	203
N	827	749	574	816	816	482	470	375	351	380	306	302	536	405	318	288
d	–	0.33	0.61	0.03	0.00	0.70	0.43	0.25	0.36	0.63	0.49	0.17	0.00	0.78	0.85	0.81
b	–	0.23	0.31	0.33	0.00	0.01	0.41	0.00	0.29	0.71	0.25	0.16	0.44	0.45	0.58	0.70
p	30.9	39	8.4	33.8	33.5	31.2	30	28.8	27.5	34.4	29.8	27.3	38.3	28.3	21.5	27.3

Note. p – proportion of males in the population (%); the starting conditions of model setting: $N_{1991} = 1000$, $Nd_i = 400$, $Nb_i = 400$ ind. Rest symbols are as in table 8.4.4.

In addition to the weights, a number of restrictions that did not reduce the potential for description, but allowed parameters to remain within the limits of realistic values, were introduced into the model. The mortality and repopulation should be positive $Nd_i \geq 0$, $Nb_i \geq 0$, and their rate – less than 1 ($0 \leq d \leq 1$, $0 \leq b \leq 1$). In addition, the number of mature adders cannot be more than that of current-year-young that were born and left for wintering 4 years ago ($N_{bi} < N_{juv.i-3}$). According to our data (Korosov, 2001) (see section 8.5), the proportion of current-year-young survived winter successfully is about 20%, L.Prest gives close value of 12% (L. Prestt (1971). The number of all newborns, in turn, is equal to the multiplication result of the total fertility (on the island of Kizhi – 7.6 ind. / female) by the number of pregnant females. Because of 2- and 3-year reproductive cycles (Biella, 1979), the proportion of pregnant snakes is about one third of all adult females in the population.

Maximum possible number of 4 years-aged individuals that were included in the adult category, for example, in 1999 was calculated as follows. In 1995, there were 1619 females (N_{1995}) (Table 8.4.4), so the calculated number of pregnant females is $Np_{1995} = 1619 / 3 = 540$, the number of newborn females is $Nn_{1995} = 540 \cdot 7.6 / 2 = 2051$ and the number of females that survived winter is $Ns_{1995} = 2051 \cdot 0.2 = 410$ ind. So, in the model the condition $Nb_{1999} < 410$ ind. must be satisfied: (in calculation for 1992, 1993, 1994 the value Nb_{1991} was used). We accepted the identical repopulation amount for both sexes ($Nb_{if} = Nb_{im}$), since in the studied broods the

proportions of newborn females and males were almost the same (44 and 56 %, respectively). Insignificant predominance in the broods either females or males has been reported (Volsøe, 1944; Biella, 1979). In the model for males the same estimated values were used as in that for females.

Depending on the starting conditions and the structure of a developed model, the set of possible trajectories of population dynamics was obtained.

Population dynamics. In our model the estimates of the number of re-captures (m) reproduce the original empirical matrix (^{э}m) having high confidence level ($\alpha << 0.01$). The correlation coefficient between these values is high and significant in all model variants (0.91–0.98). Even the simplest linear model proposing the equal amounts of loss and repopulation in each year turned out appropriate. It showed that in all years the number of females substantially exceeded the number of males and that the total number of adders on Kizhi decreased (Fig. 8.4.3, 8.4.4). In other variants, the amounts of death and repopulation were estimated separately for each year. The calculated curves of dynamics differed when the various starting values concerning the number, death, repopulation, juvenile mortality rate, were used or if the model structure was modified (Fig. 8.4.3–8.4.5).

Varying the initial values of the parameters N_{1991}, Nd_i, Nb_i, after setting up the models we received a set of very similar dynamics curves. For some years, due to the high data representativeness the estimated values of animals' number remain almost the same, regardless of the starting sets (1995–2003). So, for 1995 any model gave 1600 females (Fig. 8.4.3). In other years (1991–1994, 2003–2005) the estimated number of snakes varied widely. For example, for 1991 the number of females varied from 1200 to 3500 in different setting options.

The search for the most realistic trajectory of dynamics was performed using the device which can be called the backward calculation: the number in the last observed year (N_{2005}) was accepted as an initial value and then its value was calculated in each year by subtracting the repopulation number and adding the number of died individuals $N_{i-1} = Ni + Ndi + Nbi$. In addition, the complex model was produced. It used the snakes' number in 1995 (N_{1995}) as a reference value.

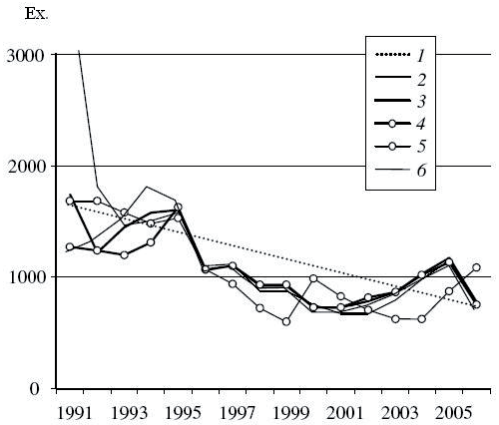


Fig. 8.4.3. Estimated population of female vipers (1991–2006) obtained by a linear model (1), direct (*2, 3, 6*), complex (*4*) and reverse (*5*) modeling techniques with different starting values of N_{1991} (*2* – 500, *1, 3, 4*, *5* – 1000, *6* – 5000 copies.)

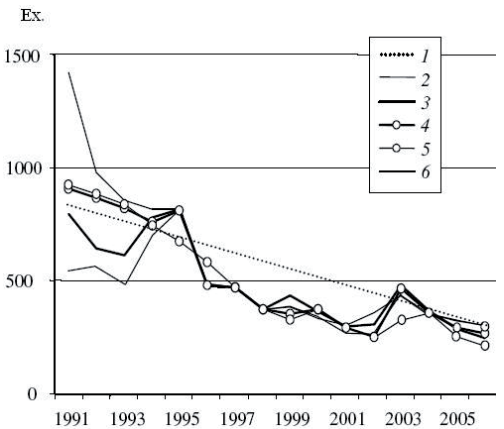


Fig. 8.4.4. Estimated population of male vipers (1991–2006) obtained by a linear model (*1*), direct (*2, 3, 6*), complex (*4*) and reverse (*5*) modeling techniques with different starting values of N_{1991} (*2* – 500, *1, 3, 4, 5* – 1000, *6* – 5000 copies.)

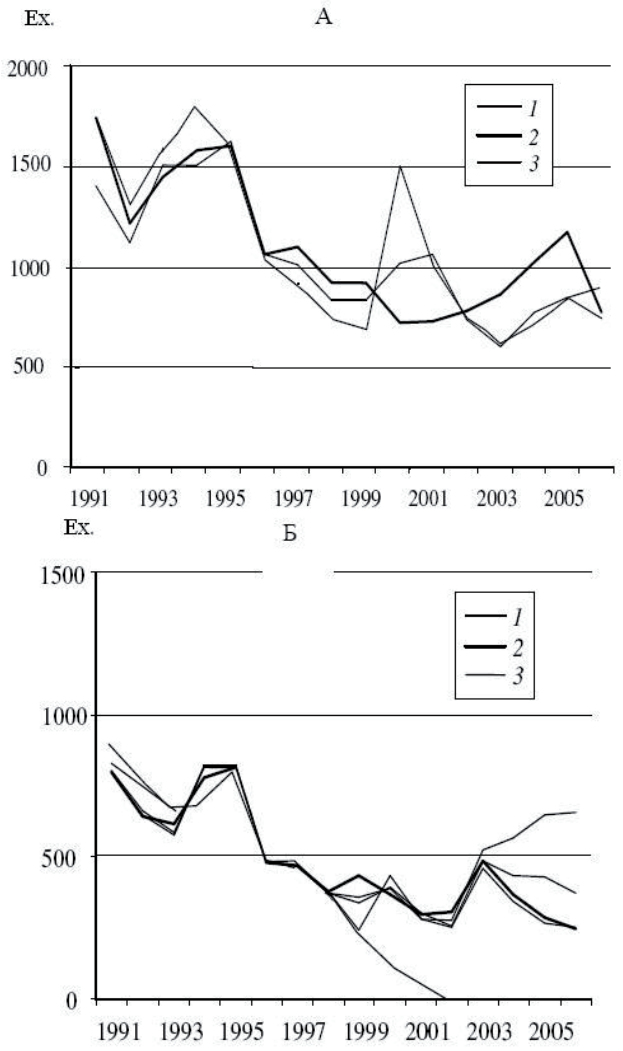


Fig. 8.4.5. Curves of population dynamics of viper females (A) and males (Б) (1991–2006) obtained by direct calculation with different levels of mortality of yearlings: *1* – 0.9, *2* – 0.8, *3* – 0.5

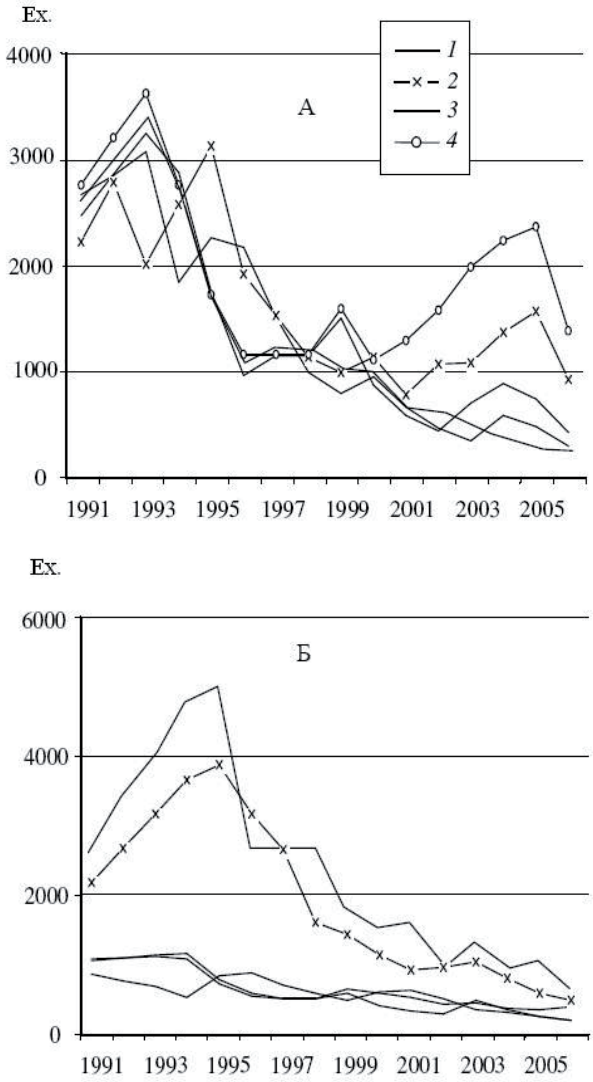


Fig. 8.4.6. Estimates of the Viper (1991–2006) jbtained by tuning the model on reduced data: А – female (*1* – to analyze only the even-numbered years, *2* – odd, *3* – random combinations, *4* – the same, without the data series for 2002–2004 gg.), Б – males (*1* – only even-numbered years, *2* – odd, *3* – random combinations)

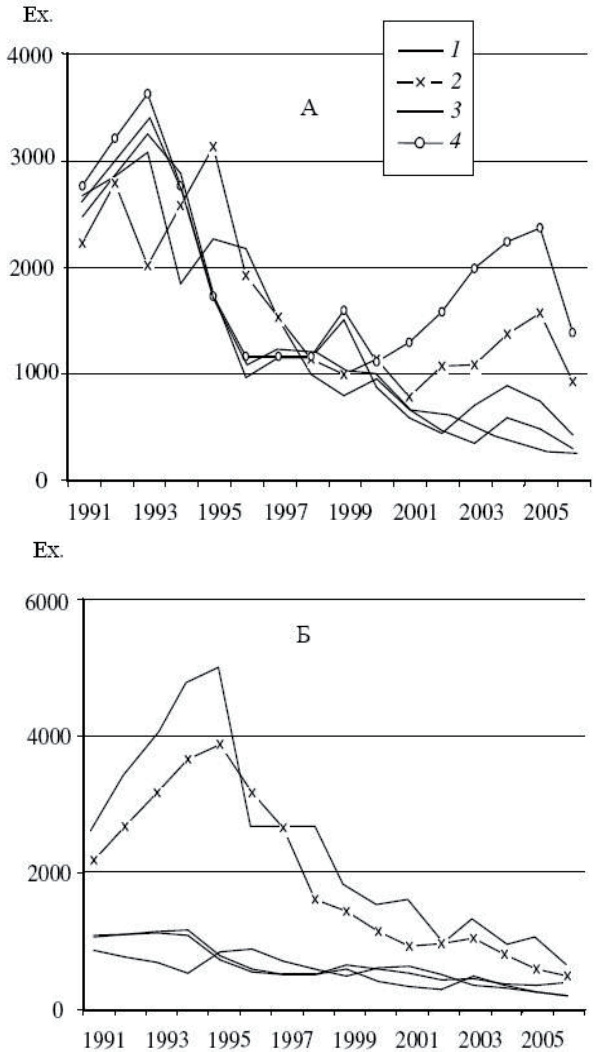


Fig. 8.4.7. Estimates of the viper population (1991–2006) obtained by tuning the model on reduced data: А – female (*1* – analysis of even-numbered years only, *2* – only odd, *3* – random combinations, *4* – the same, without the time series for 2002–2004), Б – males (*1* – only even-numbered years, *2* – odd, *3* – random combinations)

The adder's numbers up to this year were derived by using backward calculation and after this year (1996–2005) – by direct calculation. When using the "reverse" model variant, the most stable values of the initial number of females and males in 1991 (2000 and 1000 ind.) were obtained. They were used as the initial values in the proper model setting by the direct method (Tables 8.4.4., 8.4.5).

At that, in the model the juvenile mortality rate (d) was varied from 0.5 to 0.9, in so doing reducing and increasing the possible repopulation of the adult part of population in 3 years (Fig.8.4.5). It turned out that at a higher juvenile mortality (d = 0.9) model population becomes extinct, but at a lower mortality it begins varying in the range of less representative data obtained in 2003. In final calculations the mortality rate d = 0.8 was accepted.

Stability of model parameters

The most important characteristic of a model is its stability to varying initial data, the dependence of model parameters (estimates of number and mortality) on the quality and quantity of empirical results. To verify a model the initial data are usually divided into two samples: training and checking. If there is a deficiency of information, it causes both ensembles to sharply reduce their representativeness. In this case one can use the device which consists in obtaining the new sets of empirical data from the whole massif of initial information by selective elimination of datasets (up to 50% of from the matrixes with marking results, see Table 7.1.2). Resetting parameters of a basic model on the series of reduced massifs results in new dynamic curves; their analysis can indicate the "weak points" of a simulation and enhance the representativeness of initial data.

By means of this device one can obtain numerous empirical datasets from one information massif, which have a small shared part (two random samples of n/2 contain only 20% of similar magnitudes). In our case the new matrixes were formed by selecting the data for even years (1992, 1994,…, 2006), odd years (1991, 1994,…,2005, as well as their random

combinations (for example, 1992, 1994, 1995, 1996, 2000, 2003, 2004, 2005 etc.) (Fig. 8.4.7).

After the rejection of several unrealistic setting variants, when the estimated number exceeded 7000 ind., the results turned out fairly close to obtained earlier. The calculated number of females in 1995–2003 also decreased approximately from 2000 to 1000, but varied greatly at the beginning and at the end of the observation period. The decrease of representativeness had a great impact on the estimates of population number in 1991–1994. The estimated population number in 2000–2006 mostly depended on whether the representative results of captures obtained in 2001 occurred in the initial massif. If these data were included in calculations, the curve of calculated number nearly coincided with the dynamics curve obtained on valid data, or lay slightly below it (see Fig. 8.4.3 and Fig. 8.4.7, A). If there were no data in a random sample of 2001, then a "splash" of calculated females' number was observed, especially pronounced in the case of the large gap in the data of 2002–2004 – up to 2500 instead of 900 ind.

In explaining this phenomenon it is necessary to consider not only the stochastic character of observations, but also the peculiarities of the adders' female biology. They become pregnant every two or three years and dramatically change their behavior. They stop not only their free moving for food, but their secretive way of life. Pregnant females become more sedentary, they are more likely to be captured. For this reason, marked (ex-pregnant) females are re-found more often in 2–3 years than in 1 year (Korosov, 2005). When the structure of the original matrix is stochastically disturbed and it contains a few capture series obtained in 2–3 years, the proportion of recaptured marked snakes becomes artificially reduced, and the number of snakes, respectively, is overestimated.

It is much easier to interpret the results of the calculation of males' number. Their behavior is quite monotonous throughout their adult life, and their mortality is high. For these reasons, the greatest number of males is re-captured in the year following the first marking and declines rapidly in subsequent samples. When we decimate samples regularly in 1 year, in so

doing we eliminate the most representative data on marked snakes recapture. The remaining data are related to rare males' encounters and increase sharply the estimated number (up to 5000 ind.) (Fig. 8.4.7 B). When random "decimation" of the original matrix is produced, 2–3 continuous captures series in adjacent years are preserved. The estimates of number calculated on them duplicate the results based on the full matrix (Fig. 8.4.4). In general, we can assume that the model estimates are highly resistant to the data variations.

The diversity of the estimated trajectories is the evidence that there is no single optimal (true) set of possible values of snakes' number, their mortality, and repopulation (there is no global minimum of the diversity function Φ). The reason is obvious: it is the random variability of initial data associated with the insufficient representativeness of the results collected in some years: the average number (140 ind.) composed only 5–15% of all island population (1500–2500 ind.). However, in the years when the number of captured snakes was the highest (1995–1998, 2001–2003), it is estimated quite uniquely in any model variation (curves collapse into a common line), and the tendency of the population number change (decline) is the same in all cases.

So, the calculations showed that the average number of adult adders on the island of Kizhi is 1600 ind. (1100 females, 500 males), according to long-term study. Extrapolation of this value to the area of dry open stations, suitable for snakes dwelling (100 ha) gives the density of 16 ind. / ha, close to that received in the of route censuses (12 ind. / ha; see table 8.1.1). However, the calculated dynamics of absolute number is significantly different from that derived by the relative methods. For 16 years of observation, the island population of adult adders halved (from 2700 to 1100 ind.). The number of females reduced from 1800 to 800 ind., and that of males from 900 to 300 ind. (Fig. 8.4.8, Tables 8.4.4, 8.4.5). This decline is relatively gradual (the population reduced much faster after 1995 and has increased a little in recent years) and can be described by the classical equation $N_i = N_0 * e^{ri}$.

The regression equation derived for the different model rows of the population number gives the rate of increase in the number of females (r) from –0.03 to –0.07 (on average –0.04), in males from –0.05 to –0.10 (–0.07) per year (actual decline is up to 3–10 %) (Table 8.4.6).

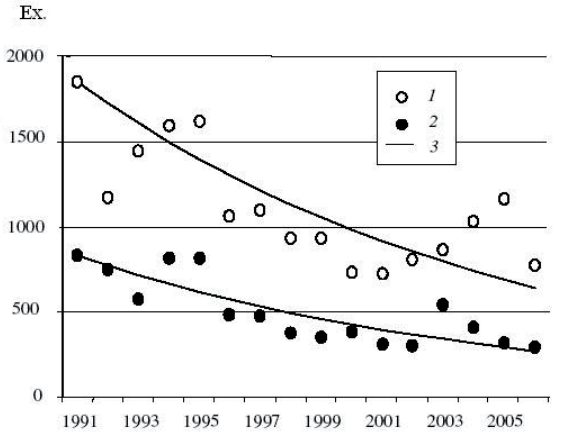


Fig. 8.4.8. Estimates of population dynamics of viper females (1) and males (2) on Kizhi and trends of the form $N_i = N_0 \cdot e^{ri}$ 3) (in both cases, the rate of growth are the same, $r \approx -0.07$)

Table 8.4.6 Rate of increase in the number of adders' island population calculated by different method

Method of calculation	Parameter	Females	Males
Direct	r*	–0.0.9	–0.10
	r	–0.08	–0.07
Direct (linear model)	r*	–0.05	–0.07
	r	–0.05	–0.06
Complex	r*	–0.06	–0.11
	r	–0.03	–0.09
Reverse	r*	–0.03	–0.10
	r	–0.06	–0.10

This is possible if in the population mortality exceeds repopulation. Indeed, the specific mortality (d) calculated in the model is 0.23–0.25 (0.24) in adult females and – 0.43–0.48 (0.46) in adult males, the average amount of repopulation is (b) – 0.16–0.20 and 0.32–0.41, respectively (Fig. 8.4.4, Table 8.4.7).

Factors of population dynamics. The decline in adders' population number is connected, primarily, with a reduction in the area of hay meadows (optimal habitat for adder), which in 1970 covered 63 % of the island territory. At present (2005), they are being replaced by a low forest, which occupies 49 % of the territory and is very fragmented. At first, the damp areas close to bogs, where there are a lot of frogs – the main adders' prey items, are overgrown with trees. At that time, most snakes concentrate in the vicinity of wetlands. While before 1995 in the 50-meter zone around wetlands less than half of all snakes (41 %) were captured, in 2001–2006 – 78 %. The second important reason why the adders' number declines on the island is the increasing recreational activity associated with tourism development and expanding the areas allotted for settlement.

The data on natural mortality of the adder is poorly represented in literature, despite a wide-spread use of capture-marking-recapture method (Viitanen, 1967; Saint-Girons, 1981; Belova, 1985, etc.). It is noted that the annual mortality rate in males (32 %) is usually higher than in females (14 %) (Prestt, 1971), the mortality of pregnant females is 34 % (Madsen, 1989). In optimal habitats the annual mortality of both sexes is less than 7% (Neumeyer, 1987). Unfortunately, in some papers, even if they contained a lot of necessary results, the estimates of specific mortality were not received or their calculation was methodically incorrect. In this case it was the number of recaptured marked animals that was used, but not the decline in the proportion of marked animals (Coley, 1979). For example, L. Prestt (1971) reports on the marking of 13 females in 1959. In the following year, 1960, 16 females were captured and 11 of them had tags, in 1961 there were 10 marked females (out of 14 captured). It follows that the sample estimate of the proportion of marked individuals in 1960 was $p_{M1960} = 11/16 = 0.69$, and in 1961 $p_{M1961} = 10 / 14 = 0.71$. It turns out that

the proportion of marked individuals in the local population did not decrease, but increased (statistically insignificant): $p_{M1960} / p_{M1961} = 0.71 / 0.69 = 1.04$, i.e. the mortality per year is 0 %. For males the situation is similar: $p_{M1960} / p_{M1961} = 1.2$. Meanwhile, the author gives the females mortality 14 % and males mortality 38 %. In contrast to those presented above our estimates were based on more extensive material and were calculated by another method, which seems to us more correct, for it considers only marked animals.

Table 8.4.7. Parameters of different dynamics models of the adders' number on the island

Calculation method	Para-meter	Females		Males		Difference between averages	
		$M \pm S_M$	(min-max)	$M \pm S_M$	(min-max)	t	α
Direct	d	0.26±0.07	(0.12-0.50)	0.43±0.08	(0.28-0.98)	1.66	0.1
	b	0.18±0.03	(0.11-0.39)	0.32±0.06	(0.20-0.73)	2.27	0.03
Direct (linear model)	d	0.22±0.01	(0.19-0.60)	0.48±0.04	(0.40-1.00)	6.35	0.0001
	b	0.16±0.01	(0.14-0.45)	0.41±0.03	(0.34-1.00)	7.10	0.0001
Complex	d	0.25±0.06	(0.13-0.50)	0.47±0.07	(0.32-1.00)	2.27	0.02
	b	0.19±0.03	(0.12-0.44)	0.36±0.06	(0.24-0.84)	2.43	0.01
Reverse	d	0.23±0.05	(0.13-0.50)	0.48±0.06	(0.35-1.00)	3.08	0.005
	b	0.20±0.05	(0.11-0.43)	0.38±0.05	(0.27-0.93)	2.49	0.02
On average	d	0.24±0.03	(0.18-0.30)	0.46±0.03	(0.40-0.52)	5.20	<0.001

The calculations showed that the estimates of the specific mortality rate in adders of both sexes reliably differ (table. 8.4.6). The average annual proportion of died females ($d \approx 0.24$) is significantly lower than that of males ($d \approx 0.46$). Previously, we obtained similar values using another technique (Korosov, 2004) (see section 7.2).

Let us consider the mortality distribution in females and males calculated using all model descriptions for all years of observation (Fig. 8.4.9). They have a symmetric unimodal shape and are shifted relative to each other. Despite wide data scatting (from 0 to 0.8), the difference of their centers (0.24 and 0.46) is statistically significant. Wide data varying reflects both the significant random variability of initial information (variation of ^{3}m) and the difference of snakes' habitats causing the different number of snakes' death in different years. They may include the duration

of a warm period and cloudy weather that affects the timing of birth of juveniles and their survival, thaws and severe cold leading to increased death of wintering snakes of all ages. However, the calculated correlation between the mortality estimates in males and females are low and unreliable, so the mortality factors in males are different from those in females. The significant difference in average mortality rates (0.24 and 0.46) indicates, in the first place, the different way of life in females and males. It seems that with such a high mortality rate, males would disappear in a few years. But in fact, the average annual repopulation of females and males remains almost the same (193 and 144 ind., direct calculation), and the number of deaths in females is even larger than that in males (267 and 178 ind.). But the proportion of died snakes is of a reverse order, calculating to the total absolute number (~2000 and ~1000 ind.).

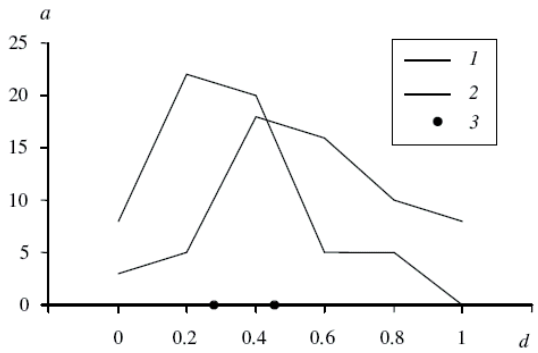


Fig. 8.4.9. Polygons of frequency (*a*) distribution of estimates of mortality (*d*) female (*1*) and male (*2*) vipers for different years, calculated in 4 models, and the average mortality (*3*)

It should be noted that the mortality rate in mixed-age groups of adult adders are obviously the same. While the maximum life span in adders is 11 years, individuals older than 8 years are extremely rare (Korosov, 2001), that is characteristic for the common adder (Belova, 1985). So, on the island the vast majority of them die not of the natural

causes associated with age or diseases, but of external factors – anthropogenic (e.g. accidental death under car wheels), the climate (wintering), or predators. All age groups equally suffer from these factors.

So, the number of males is supported by intensive repopulation (provided by numerous females), but due to high mortality in all age groups the average proportion of males in the studied population calculated on the estimates of absolute number is only about 30 %.

For 16 years of research, there were no essential dynamics of this indicator – only a small (though significant, $R^2 \approx 0.2–0.6$) decrease up to 6–11 % (Table 8.4.5) was observed. In other words, even in favorable 1991–1994, males' mortality was increased, and their proportion was less than that of females. This phenomenon can be extrapolated to the continuous area of this species. The sex ratio in the adder population was far from any of the ratios calculated by the number of males and females found on the routes as well as of the parity 1:1. It was H.Volsøe (1944) who showed the whole range of these ratios that vary during the season depending on males' activity ($n_{♂}$: $n_{♀} \sim 0.43–1.76$). The data of other authors are located within this interval (Chan-K'yen, 1967; Petzold, 1980; Kuranova, Kolbintsev, 1981; Ushakov, Pestov, 1983; Neumayer, 1987; Luiselli, Anibaldi, 1991, etc.). To find an objective ratio between the groups of animals with different mortality rate is possible only on the basis of estimates of their absolute number in given territory.

8.5. Age structure of island population

Permanent dying away of organisms and survival of fewer and fewer individuals in each age group yields an age distribution. If the ratio between age groups in a population can be established, it gives the possibility of estimating the actual population number, parameters of its reproduction, dynamics of growth processes, its coenotic value, etc. At the same time, it is quite difficult to derive the age distribution. When the age of all studied species is known, the age distribution can be yielded by counting the number of even-aged animals. It is a usual procedure, when

one can collect mass material, i.e. the species possess well-defined registering structures (Mina, Klevezal', 1970); for example, when the age is determined by the gluing lines in the bones of the extremities or phalanges (Klevezal', Kleinberg, 1967; Zug et al., 1986). In addition to bone layers, as such structures, radial clusters of sclerites on the scales, rings on the slices of otolites in fish (Zhakov, Menshutkin, 1982), the relative length of tooth roots in voles (Tupikova et al., 1970), the size of the worn out tooth surface in rodents and insectivores (Kornoukhova, 1971; Deparma, 1954; Viktorov, 1967), the weight of dry crystalline lens (Korneev, 1976), etc can be used.

There are no ectosomatic organs in the adder containing some registering structures, and determining the age of a living snake is difficult. In such a case, when there is no suitable instrumental base, or killing of the large number of animals is impossible or there are no peripheral organs, the approximate method of size-weight classes has to be used (Novikov, 1949). In this case one thing, which should be in focus, is the distribution of some metric sign, proposing that particular distributions of the sign are slightly overlapped for mixed-age animals groups. Looking at obvious tops (modes) of the distributions, the interfaces between different age groups are set in the valleys between them (Terent'yev, 1950). Unfortunately, the samples of mixed-age classes usually have a wide overlap zone (transgression of distributions), so the age of a large number of animals remains uncertain in this area (Kheruvimov et al., 1977). This is the point which causes criticism of this methodology (Larina, 1968; Karpukhin, Karpukhina, 1971), because it cannot help to define the exact age of each animal. Nevertheless, with some modification the method of the size-weight classes may be used to determine the relation between age groups in a population as a whole, without age identification of an individual, since "...the ecologist should not be concerned by determining the exact age of each individual, but the average age of the group of interest" (Shvarts et al., 1968).

Technique of age distribution reconstruction. Relying on the distribution of the dimensional sign, the age composition of the population may be reconstructed in details (Korosov, 2001). Theoretically two ways

are thought of to achieve this goal. For example, one may determine a dependence between the age of individuals (identified by registering structures in a limited sample) and the value of a stable sign as an equation "age" = f("size"). Then one may calculate the age of all animals having the measured sign in their lifetime and the occurrence of individuals of a different estimated age.

The second way is to reproduce a series of dimensional sign distributions that characterizes each age class, focusing on the average values defined previously and the sign dispersion of individuals of each age as well as the shape of the distribution.

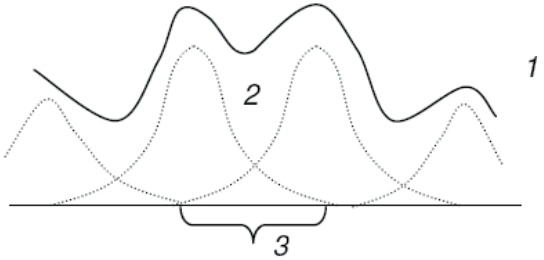


Fig. 8.5.1. Transgression zone (*3*) between adjacent distributions of the two age groups of animals (*2*) within the total (*1*) for all ages (the feature is the size of the body)

The basis for such decomposition is a reasonable assumption that even-aged individuals have the normal sign distribution. It has been shown in lots of special studies of plastic signs (see, for example: Yablokov, 1966). If normal distributions are plotted around the average values previously defined for each age using the previously defined variances, then the general distribution of the sign for all ages will look like an assemblage of local normal distributions for certain age groups overlapping each other (Fig. 8.5.1). After plotting local normal distributions, it remains to count the number of individuals composing a given age class. This task can be solved graphically by measuring the area under curves; this technology has been effectively used in the study of the smooth newt

(Bell, 1977). We used the methods of simulation modeling for the reconstruction of the series of special normal distributions; in this case, "estimating a sign is performed by examining its distribution curves in a population" (Shvarts et al., 1968).

Selection of dimentional sign. For the successful reconstruction of partial even-aged distributions, there is a need of the sign, which would provide the smallest transgression between them, i.e. it was influenced by as few random factors as possible. From dimensional characteristics of the adder, only one could apply for this role. The body weight cannot be used for that, since it depends on fatness. The tail length is not suitable due to frequent injuries of the tip of the tail, caused by the activity of ticks and frostbites. The measurements of the body length of unrestrained animals are of limited accuracy, the procedure error is up to 12 %. Thus, of all the measurements, only the jaw length (Lm) remains, which can be measured accurately both in a living snake and a corpse (see Fig. 7.5.8). However, we have started these measurements only since 1997. To characterize the animals caught earlier according to this sign, in 1991–1996 we carried up the reconstruction of the measurements of the lower jaw, using the measurements of the head width (Hc is the distance between the edges of supra-orbital scales, taken in the middle) (Fig. 7.5.8). For this purpose, we measured the jaw length in the group of animals (400 ind.) in field conditions and the head width in enlarged (×4.8) photos of pileus made in capturing. The error of measurements was about 2 %.

Further we established a correlation between the measurements (Lm and Hc) for all 400 individuals as the following regression equations that are highly significant ($r \approx 0.8$, $p < 0.05$):

$Lm♂ = 23.887 \cdot \ln(Hc) - 30.118$,

$Lm♀ = 20.279 \cdot \ln(Hc) - 21.401$.

It is interesting to note that in male and female individuals the head proportions differ. While the jaw length in even-aged snakes is the same, in females the head is wider (as reflected in the high negative value of the absolute term: –21 vs –30).

Using these formulas, we calculated the sign "jaw length" for all 1400 individuals caught in 1991–1999. To verify, how much calculated and real measurements of the jaw coincide, frequency distributions were plotted (Fig. 8.5.2).

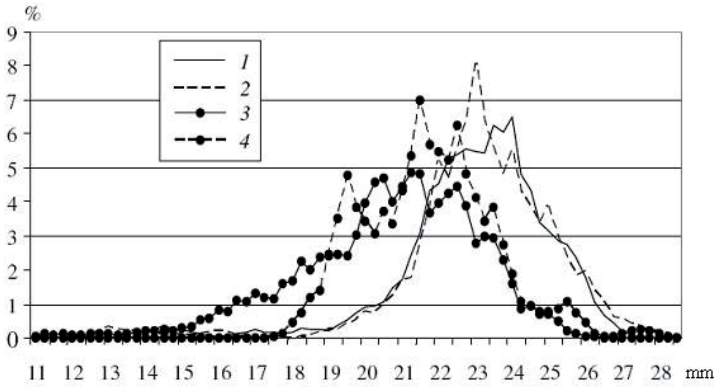


Fig. 8.5.2. Distribution of viper females (*1, 2*) and males (*3, 4*) on the jaw length directly measured in field in 1997–1999 (*2, 4*) and recalculated from the width of the head for all the years of observation (*1, 3*) (class interval width is 0.25 mm)

The diagram shows a good agreement of the adders' occurrence in the right side corresponding to large animals and there is a little deviation of the curves in the left side, which relates to small males. The fact that the right slopes of the curves are similar proves the uniformity of the real and calculated sets of values. The reason for the discrepancy is connected with the sample number: in the more numerous sample of 1991–1999 (1400 ind.) the proportion of young rarely found animals was naturally higher than that in the smaller sample (400 ind.), collected in the last three years (1997–1999). It should be noted the poorly expressed "saw-tooth" shape of the jaw length distribution, i.e. a strong transgression between adjacent age classes. Interestingly, that the females' distribution is notably shifted to the right relative to the males' distribution, towards larger sizes. Finally, the proportion of small individuals (Lm ≈ 16–18 mm) among males is significantly higher than that among females.

In 2007 we summarized the data of field measurements of the low jaw obtained in 2000–2007 (509 females and 387 males) and added them to the results of 1991–1999 years (Fig. 8.5.3).

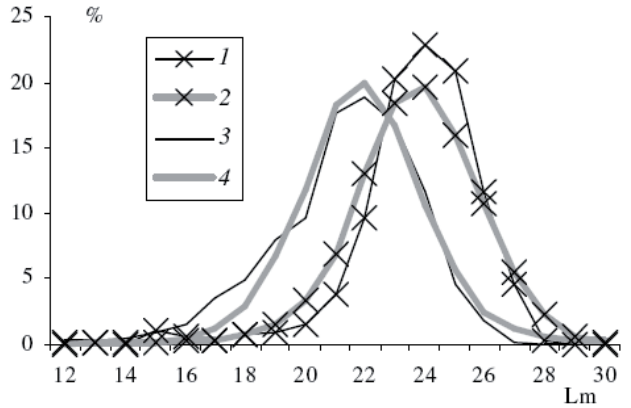


Fig. 8.5.3. Distribution of viper females (*1, 2*) and males (*3, 4*) on the jaw length directly measured in field in 1998–2007 (*2, 4*) and recalculated from the width of the head for 1991–1997 (*1, 3*) (width of class interval is 1 mm)

As the chart shows, the distribution of females and males by the lower jaw length measured in nature coincides well with the calculated width of the head. The difference is that in more numerous samples (data for 1998–2007) the proportion of largest individuals is slightly higher than that in the calculated values distributions in 1991–1997, the proportion of smaller females is also slightly higher and that of medium-sized ones is slightly lower.

These data suggest, first of all, that on the island of Kizhi in 2000–2007 no fundamental shifts of the age composition of the adders' population happened, compared with the previous decade (1991–1999). Nevertheless, in the same period the number of the island population fell by half, and this fact affected the age composition (see section 8.2). The medium-sized females were rarely found on the routes, but small and large

(young and old) ones were found more often. However, in relation to males almost nothing changed. The fact that the basic proportions of the size-age distribution remain indicates that the decline in the number was not caused by autonomous processes inside the population (similar to depression of voles), but by external adverse factors almost equally affecting the snakes of all ages. Such factors may include the increased mortality on roads due to the noticeable intensification of the restoration work at museum objects, the reduction of wintering shelters due to meadows colonization by trees, as well as the adverse weather conditions in the last years (frequent thaw in winter). According to the principle considered above, the general distribution over the dimensional sign should be composed of several even-aged distributions – each around its center with a width given by the variance. These characteristics (arithmetical average, M, and standard deviations, S) were pre-determined separately for even-aged animals (defined by gluing lines; see section 7.5). For this purpose, the regression lines were plotted for each sex. It turned out that the averages for females and males did not differ significantly, and the regression curves almost merge with each other (see Fig. 7.5.11). For this reason, the logarithmic regression lines common for both sexes were calculated for the averages (M ‘) and variances (S ‘) of the jaw length on age x:

$M' = 5.0017 \cdot \ln(x) + 11.036,$

$S' = 0.4627 \cdot \ln(x) + 0.858.$

With their help, the centers of distributions for each age group and the corresponding standard deviations were calculated (Table 8.5.1, Fig. 8.5.4).

Decomposition of dimensional sign distribution. The main goal of modeling is to describe a general distribution of animals of all ages using a set of partial normal distributions (even-aged individuals). The composition of such a model in Excel environment is fairly simple (Korosov, 2002a). Before its plotting, the whole range of dimensional sign values X is divided into k intervals (i = 1, 2, ...). In our case, it was k = 73 and the interval was dx = 0.25 mm wide. For each interval, its center X_i was calculated. Next, in

the table lines of the electronic worksheet the calculations for each age class (x = 0, 1, 2, ... m; m = 12) were carried out.

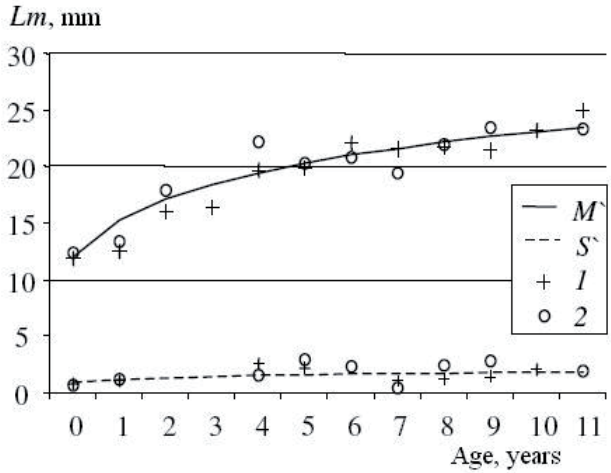


Fig. 8.5.4. Trends in mean values (M ') and standard deviation (S') for measurements of jaw length (Lm) of viper females (1) and males (2)

Table 8.5.1. Statistical characteristics of the jaw length in different age groups

Parameters	Age, years											
	0	1	2	3	4	5	6	7	8	9	10	11
min	11.3	11.6	16.0	16.4	17.9	17.5	18.3	19.2	20.0	20.0	20.0	22.0
max	12.8	14.2	17.9	16.4	23.2	23.6	22.4	22.4	24.7	25.4	25.4	24.9
M $_{females}$	11.8	12.5	16.0	16.4	19.7	19.9	22.0	21.5	21.7	21.5	23.2	24.9
M $_{males}$	12.4	13.3	17.9		22.2	20.3	20.8	19.5	22.0	23.5		23.3
S $_{females}$	0.7	1.0			2.5	2.2		1.0	1.2	1.4	2.0	
S $_{males}$	0.6	1.2			1.5	2.9	2.2	0.4	2.4	2.8		
M '	11.0	14.5	16.5	18.0	19.1	20.0	20.8	21.4	22.0	22.6	23.0	23.5
S '	0.6	1.0	1.2	1.4	1.5	1.6	1.7	1.7	1.8	1.8	1.9	1.9
n = 55	4	5	2	1	4	6	4	7	9	5	5	3

On the basis of the normal distribution law, its predetermined parameters (M', S') and an assumed number of an age class (Nx), the

occurrence of individuals of a given age in each i-th interval (n_i) was calculated (Ivanter, Korosov, 1992):

$n_i = f \cdot (Nx_{t-1} \cdot dx / S)$,

where S is standard deviation, dx – accepted interval width, Nx_{t-1} – (assumed) age class number calculated at the previous optimization step, f – probability density of the normal distribution (the ordinate of the normal curve):

$f = (1/\sqrt{(2 \cdot \pi)}) \cdot EXP\ (-0.5 \cdot (X_i - M)^2 / S^2)$,

where M is arithmetic mean, X_i is the center of a given interval. These formulas were introduced into each cell of the line corresponding to a given age class. Introducing m formulas lines for each age class, we obtain a complete description of a population composition – the table of dimensional sign distribution (Table 8.5.2).

Table 8.5.2. Fragment of an Excel worksheet used to calculate numbers (nx) of even-aged distributions before the optimization (numbers in age groups are pre-set equal, n = 100) (for even-numbered ages t = 2, 4, 6, 8 10)

k = 73		F = 1.5		t	**0**	**2**	**4**	**6**	**8**	**10**
				M ‘	11.0	16.5	19.1	20.8	22.0	23.0
				S ‘	0.6	1.2	1.5	1.7	1.8	1.9
dx = 0.5				Nx	100	100	100	100	100	100
X_i, мм	$N_{emp.}$	n_i	φ		N_0	N_2	N_4	N_6	N_8	N_{10}
…										
19	38	26	147		0	2	14	7	3	1
19.5	47	29	326		0	1	13	9	4	2
20	59	31	770		0	0	11	11	6	3
20.5	56	33	562		0	0	9	12	8	4
21	63	33	894		0	0	6	12	9	6
21.5	52	33	377		0	0	4	11	11	8
22	54	31	518		0	0	2	9	11	9
22.5	44	29	221		0	0	1	7	1	10
23	40	25	210		0	0	0	5	10	11
…										

The summation over table lines gives the number of even-aged individuals. For example, in the interval with the center X = 22 mm in the first model version the number is:

n = 0 + 0 + 2 + 9 + 11 + 9 = 31 individual.

A generalized difference between columns sums and the empirical occurrence of individuals in intervals proves the general similarity measure of the model and empirical distributions, and thus plays the role of the residual function ($\Phi = \Sigma\varphi$).

For the interval with the center X = 22 mm the number is $n_{emp.} = 54$, $\varphi = (54–31)^2 = 518$. The total residual is $\Phi = \Sigma\varphi = 14\ 518$. The Fisher's goodness fit equals to $F = 1.5$, $p > 0.3$. Obviously, the similarity of the model with reality has not occurred yet.

Summing over the table columns gives the number of individuals in each dimensional interval of the general distribution. These values over all lines act as optimized. In the calculations showed, the number of four-year old snakes (as well as in other groups) was randomly assigned as 100 ind.

The optimization procedure itself is a recurring change in the number of individuals of all age classes aimed at changing their proportions in the general distribution. Changes in a number of mixed-age individuals (n_i) affect the changes in the presence of certain age groups in different intervals of the dimensional sign, and as a consequence, the cumulative frequencies of the general model distribution change. If the residual function decreases, then the model frequency distribution gradually approaches the real one (see section 15). If the residual function ceases to change at subsequent iterations, then the optimal way of describing the general frequency distribution is achieved using the series of even-aged normal distributions. For example, after the optimization, 52 individuals got into the interval with the center 22 mm, the residual error became much lower, $\varphi = 4$, total $\Phi = 213$, the goodness of fit $F = 163$, $p < 0.001$ (Table 8.5.3).

In setting the parameters (age classes' numbers, N_m), any optimization run gave the broken rows of the age distribution, when the program gave none of animals to certain age classes. Therefore, the setting

procedure was carried out in three steps. At first, the centers of even-numbered age classes (M_0, M_2, M_4, M_6, M_8, M_{10}) was taken as a base for optimization, and the number of individuals of the even-numbered ages were determined (N_0, N_2, N_4, N_6, N_8, N_{10}) (as is shown in the Table 8.5.2). Then the centers of odd age classes (M_1, M_3, M_{11}...) were taken and the frequency of entering individuals into the odd age classes (N_1, N_3, N_{11}...) was determined.

Table 8.5.3. Fragment of an Excel worksheet used to calculate numbers (nx) of even-aged distributions after optimization (for even ages t = 2, 4, 6, 8,10)

k = 73		F = 163		t	**0**	**2**	**4**	**6**	**8**	**10**
				M ‘	11.0	16.5	19.1	20.8	22.0	23.0
				S ‘	0.6	1.2	1.5	1.7	1.8	1.9
dx = 0.5 мм				Nx	4.7	68	96	292	210	0
X_i, мм	$n_{эмп.}$	n_i	φ		N_0	N_2	N_4	N_6	N_8	N_{10}
…										
19	38	40	2.6		0	1	13	20	6	0
19.5	47	48	1.2		0	1	13	26	9	0
20	59	55	15		0	0	11	32	12	0
20.5	56	59	9.2		0	0	8	35	16	0
21	63	60	7.3		0	0	6	35	20	0
21.5	52	58	32		0	0	3	32	22	0
22	54	52	4.4		0	0	2	27	23	0
22.5	44	44	0		0	0	1	20	23	0
23	40	35	27		0	0	0	14	20	0
…										

After that, the classes were sorted in normal order (0, 1, 2,..11), the frequencies were reduced twice. In this case the sum of the frequencies became equal to the numbers of the general samples – about 670 females and 670 males. This procedure is similar to the search of occurrence in 6 classes with a consequent increasing their number up to 12, and dividing the numbers in adjacent classes by two. In our case, however, the values of partial distributions centers were not averaged, and therefore the results

should be more accurate. At the same time, when considering the results of the analysis, it is important to keep in mind the smoothed character of the frequency distribution of mixed-age animals.

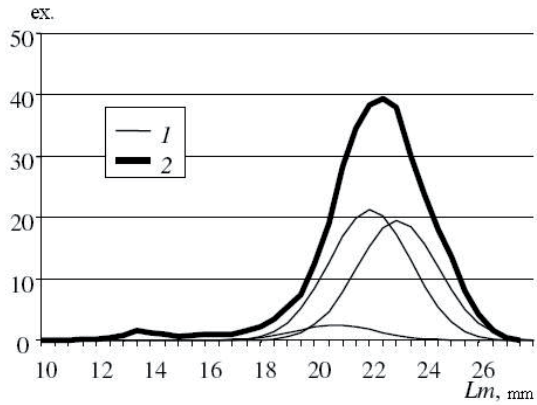


Fig. 8.5.5. Theoretical distribution of even-numbered age classes Nx (*1*) within the total (*2*)

Age composition of captured adders' sample. As a result of the decomposition of the jaw length distribution, the frequencies of different age groups, which in summation optimally correspond to the initial general sign distribution, were determined (Table 8.5.4, Fig. 8.5.6).

The data demonstrate the increased proportion of older aged females (8, 9, 10 years old). The reasons can be either the distinctiveness of the real age distribution, or methodological errors.

Systematic errors may include the uncertainty in the lower jaw measurements, the inaccuracy in determining of the medium sign value in certain groups, model functioning errors, the inaccuracy in determining an animal age and corresponding distribution centers.

The first two types of errors as typical both for females and for males. They can only increase the variance of the sign, but will not lead to displacement.

Table 8.5.4. Ratio of age groups in the visible part of the adders' population

Age	Number, ind., *n*		Proportion, %, *p*	
	females	males	females	males
0	8	2	1.3	0.4
1	10	14	1.4	2.0
2	5	35	0.8	5.1
3	0	56	0.0	8.2
4	0	49	0.0	7.2
5	18	49	2.7	7.2
6	82	148	12.2	21.8
7	160	221	23.7	32.5
8	187	107	27.8	15.7
9	146	0	21.7	0.0
10	56	0	8.3	0.0
11	0	0	0.0	0.0
Total	672	680	100.0	100.0

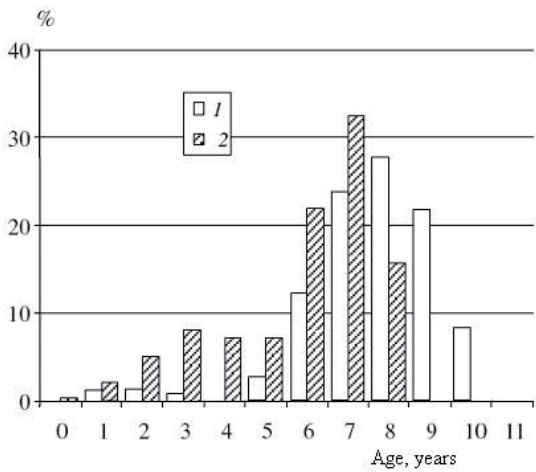


Fig. 8.5.6. Share of females (*1*) and males (*2*) of different ages (n_i) among captured in nature

Model functioning was tested dozens of times with different data sets, so we exclude the third kind of error. The age determination methods have the maximal likelihood to introduce the errors. That is not the point that the number of gluing lines can be calculated inaccurately – the same error would exist in the sample of males. In addition, the calculation was carried out by three different persons. The fact is that the gluing lines in the females' bones may occur not only in winter but also in the first (or second?) year of their two-year reproductive cycle (see section 4), when all body forces are aimed not at the own female's body growth, but at the growth and development of embryos.

Systematic errors may include the uncertainty in the lower jaw measurements, the inaccuracy in determining of the medium sign value in certain groups, model functioning errors, the inaccuracy in determining an animal age and corresponding distribution centers.

The first two types of errors as typical both for females and for males. They can only increase the variance of the sign, but will not lead to displacement.

Model functioning was tested dozens of times with different data sets, so we exclude the third kind of error. The age determination methods have the maximal likelihood to introduce the errors. That is not the point that the number of gluing lines can be calculated inaccurately – the same error would exist in the sample of males. In addition, the calculation was carried out by three different persons. The fact is that the gluing lines in the females' bones may occur not only in winter but also in the first (or second?) year of their two-year reproductive cycle (see section 4), when all body forces are aimed not at the own female's body growth, but at the growth and development of embryos.

Unfortunately, this assumption cannot be verified experimentally. At the same time, there are two strong counterarguments to criticize it. First, if the additional gluing line corresponded to the year of pregnancy, then its adjacent stripes of enhanced growth would be significantly narrower than the similar bands in a dry year of fattening. However, in the specimens of

the females' bones, there observed no special unevenness in the alternation of bands (Fig. 8.5.1).

Second, in the population there are 8–11 years old males besides old females. Another thing is that their proportion is almost negligible (less than 1%). The point is that the maximum life span of both sexes' individuals is the same, it is the species character, even though the average life span in males is 2 years shorter than that in females (according to the Table 8.5.4 it is 5.85 and 7.57 years, respectively). (Note that the estimates of life span in adders are merely illustrative, but are not correct because they do not consider the actual number in all age classes).

Summarizing the self-criticism of the presented data, it should be recognized that the shift between the age distributions related to males and females is not due to methodological mistakes but to the influence of important ecological, ethological and physiological factors.

The main reason for this shift was a higher mortality of males of all groups associated with some dangerous anthropogenic areas (roads, villages) on the island of Kizhi, where the males are brought by their lifelong behavioral pattern as "free hunters". Males of different ages are much more mobile than females (see chapters 11, 12), it makes them more prone to an existential threat especially of men. So, the majority of males cannot live up to a very old age, and among the captured snakes their proportion is much lower (see sections 7.4, 8.4).

To calculate the ***age composition according to the jaws size,*** the previously found regression equation was used

$x' = 0.000556 \cdot Lm^{3.055}$ (see fig. 7.5.11). From this formula and the field measurements of the jaw length, the age of the same 672 females and 680 males caught in 1998–2007 was calculated, and the second variant of the age distribution was plotted (Fig. 8.5.7).

Two procedures of determining the age structure of the adders' populations gave different results, while using the same data. The direct calculation of age from the regression equation (Fig. 8.5.7, 3, 4) resulted in wide distributions with the increased frequency of old animals. The minimal value is equal to 0.8 year, the maximum estimates for females –

17, for males – 13 years. The proportion of females older than 10 years is 30 %, that of males – 5 % (total 17 %). The method of reconstruction of even-aged distributions within the general sample allowed to plot a much more compact distribution where the maximum age is 11 years and the frequencies of old animals are low (Fig. 8.5.7, 1, 2).

Since both methods used the same data, the difference between the results lies only in the calculation technique. To reveal these differences, it is sufficient to consider the right slopes of the distributions. The fact is that large values of the jaw length were interpreted by the first method as those belonging to old animals (12+–16+) (see Fig. 7.5.11), but the second method treats them as the right "tail" of the size distribution of middle-aged animals (10+–12+) (see Fig. 8.5.5).

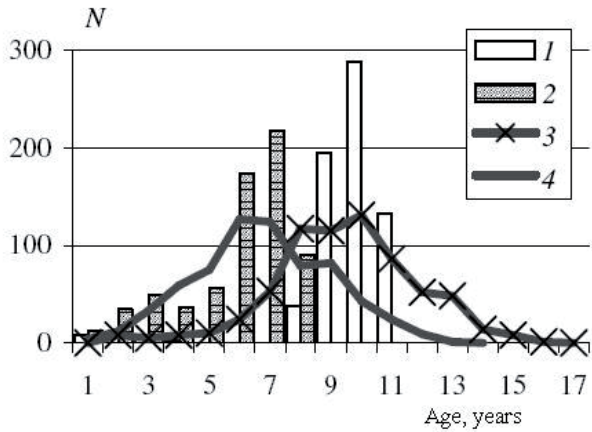


Fig. 8.5.7. The frequency polygons of age distribution, obtained by different methods on one sample of animals (672 of females – *1, 3* and 680 of males – *2, 4*): *1, 2* – calculation of the equally aged distribution frequencies, *3, 4* – direct calculation of age from the equation $x' = 0.000556 \cdot Lm^{3.055}$

The same is with the left slope: the first method "considers" that the smallest measurements belong to young individuals (1+–3+) and the second one –they constitute the left "tail" of the distribution related to the

youngest middle-aged animals' (5+). To solve the problem what method gives the most reasonable age distribution, we used additional data on skeleton-chronology, re-capturing, morphology. All of them confirmed the validity of the method of distributions reconstructions.

First, although our collection of cadaveric material contains almost the same proportion of animals older than 10 years as a calculation gave (12% vs. 14 %), however, we intentionally sought to fill it with animals of different size uniformly, so the proportion of large (old) specimens turned out inflated.

Second, at the death rate observed on Kizhi the proportion of animals that reached aged 11 years or more was vanishingly small. So, of the number of marked animals (in reproductive age for about 5 years), in 6 years less than 2 % will remain (see Fig. 7.5.13).

The conclusion is clear – the reconstruction of the age distribution of adult adders based on the decomposition of the general jaw length distribution into the series of even-aged distributions meets well the external additional criteria, it is more evidence-based than the age reconstruction from the regression equation. This result underlies the calculation of the general age distribution of the adders' population on the island of Kizhi.

Reconstruction of the age distribution of island adders' population. The data of the frequency relationship between mixed-age animals were usually related to the adult individuals that we found on the routes. The reconstruction of the number of all age classes is of the main interest of a population analysis. This would show the absolute number of island population and thereby complement the conclusions of the previous section, and also allow using these estimates to calculate the characteristics of the coenotic role of the adder.

First, let's define the absolute number of each age class on the data of the age distribution of adult snakes (Table 8.5.4, column "Number") using the formula $N_m = p_m \cdot N$ and the data on the absolute number of adult males (section 8.4). For example, the number of six years old males (m = 6) is equal to $N_{♂6} = 0.218 \cdot 900 = 196$ ind.

To restore the number of individuals of younger ages, it should be assumed that the population number is stable, and so a current age distribution corresponds to a dynamics of survival of the mixed-age cohorts, that is, the age cutoff corresponds to the dynamics of survival for each cohort (Koley, 1979). In this case, the number of a cohort surviving in each of the following m+1 years of life, calculated as: $N_{m+1} = N_m - d_m \cdot N_m$, where d_m is the mortality rate of cohort individuals at the age of m. If the population number decreases or grows, the dynamics of mortality in general does not correspond to the instantaneous age distribution. As on Kizhi between 1992 and 1997 the number of the adders' population did not change significantly, the calculations can be carried out.

To calculate the number of younger aged individuals, two anchor points need to be used: the first one is the number of the current-year-young that can be obtained from the number of parous females and their fertility (Prest, 1971), and the second one is the number of older age groups defined previously.

In the studied area the average fertility amounted 7.59 ± 0.17 (4–12) individuals per female (see section 4, table. 4.3.1). At that the proportion of pregnant females is 30 % (see section 4.1), and the proportion of females of all individuals – 70 % (see section 7.4, Table 7.4.1, section 8.4, Table 8.4.5). Using the absolute number of adders obtained previously on Kizhi in 1992–1997, 2700 ind., it is easy to calculate the absolute number of current-year-young:

$N_0 = 2700 \cdot 0.7$ (proportion of females) $\cdot$ 0.3 (proportion of pregnant females) $\cdot$ 7.6 (fertility) = 4300 ind., about 2200 animals of each sex.

The reconstruction of a possible age distribution was performed by using the simulation model. For its development, the following wide-spread ideas of the survival dynamics in vertebrates were used (Gilyarov, 1990, pp. 70–71):

• the neonatal mortality rate is the highest,

• the mortality in middle-aged animals (1–6 years) is the same and lower than that in current-year-young,

• the mortality of old animals is the same and higher than that in the previous group,

• the right slope of a general age distribution corresponds to a maximum possible lifespan of animals.

The model is a series of 12 equations for calculating the number of each age group: $N_{m+1} = N_m - d_m \cdot Nm$. The setting parameters are three values of the specific mortality rate in current-year young (x = 0), young adders (x = 0, ...4) and adult ones (x = 5, ...11):

d_0, $d_{1/4} = d_1 = ... = d_4$, $d_{5/11} = d_5 = ... = d_{11}$

The total difference between calculated and actual values of the numbers in oldest age groups is used as a residual function (in Table 8.5.6 they are highlighted grey) provided that the total number of snakes died in a year amounts 440 individuals of the visible part of the population. In assessing the population number the number of 440 ind. (about 260 females and 180 males) was identified as a total mortality of adults (see Table 8.4.4–8.4.5).

The modeling results allow to conclude that the described picture and the extinction in older age groups will occur if the mortality rate of current-tear-young is 80 %, that of middle-aged snakes – 2–4 %, that of old ones – 28–29 %. The total absolute number of the adders population on Kizhi in this case will be about 7000 individuals (35 ind. / ha) excluding current-year-young.

In addition to these mortality ratios of different-aged snakes, another calculation conditions were specified (Fig. 8.5.8).

In one of the variants it was assumed that the annual loss was the same in different-aged individuals, excluding current-year-young; at that the dynamics of extinction was adjusted only using the number of the visible population part for the ages 0, 8, 9, 10 and 11 (Fig. 8.5.8, 3).

In other variant, we removed the restrictions on the increased mortality of current-year-young and freed the mortality rate in older groups from the conditions (Fig. 8.5.8, 4). These methods gave large estimates of the island population number – 13000 and 9000 ind. In our view, these estimates are almost unrealistic. Taking into account that the number of

adults in a population is usually two times less than that of young ($2000 \cdot 3 \approx 6000$), we accepted the most realistic number – 7000 snakes.

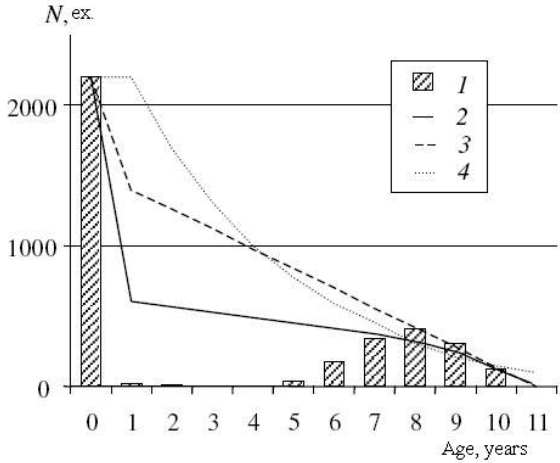


Fig. 8.5.8. Options for calculating the absolute number of all different age groups of females of a viper on Kizhi Island in 1992–1998: *1* – number of visible, *2* – $d_0 = 0.8$ $d_{1-5} = 0.04$, $d_{5-11} = 0.29$ (see Table. 8.5.5); *3* – $d_0 = 0.36$, $d_{1-11} = 140$ экз.; *4* – $d_0 = 0.0$, $d_{1-5} = 0.2$, $d_{5-11} = 0.32$

On the island of Kizhi the high rate of adders' repopulation is observed. Numerous favorable habitats and the abundant food supply provide high reproduction rate, but strong anthropogenic load causes high mortality of these animals. As a result, the maximum lifespan in adders is small (up to 11 years).

Table 8.5.5. Absolute number of different-aged groups in the visible part of the population and in the whole island population of adders as well as the annual mortality in different classes

Age	Visible part		Whole population, Nx		Mortality, dx	
	females	males	females	males	females	males
0	2800	2800	2800	2800	0.83	0.82
1	20	29	465	494	0.02	0.04
2	12	74	457	475	0.02	0.04
3	0	119	449	457	0.02	0.04
4	0	104	442	440	0.02	0.04
5	39	104	434	423	0.02	0.04
6	177	316	427	406	0.02	0.29
7	344	471	419	288	0.28	0.29
8	403	228	304	204	0.28	0.29
9	315	0	220	144	0.28	0
10	120	0	159	0	0.28	0
11	0	0	115	0	0	0
Total excluding fingerlings	1468	1445	3891	3331	0.10	0.11

Chapter 9.

Feeding

The common adder is an active predator reclaiming wide area on its feeding ways. The necessity of rather long motions while hunting is so firmly embedded into the specific stereotype of feeding, that the snakes deprived of the ability to move over long distances in laboratory terrariums stop feeding (see section 13). Different habitat conditions affect the species composition and the number of potential adders' victims. The aim of our study consists in giving a quantitative characteristic of the factors determining the specifics of the local diet of our species.

Materials and methods. Special and incidental observations of adders feeding were conducted since 1978 in the districts of Karelia different in biocoenotic conditions. These are meadows landscapes on the islands of the Kizhi archipelago, deciduous and coniferous saplings in Priladozh'ye ("Moyachino"), local forest clearings and the coast of the regulated lakes in the nature reserve "Kivach". The adders were captured and described according to standard methods (Novikov, 1953; Darevsky, 1987). To study feeding in living snakes, the ingested food was pushed out of the snake stomach by light massage (Kuranova, Kolbintsev, 1983). To avoid possible injuries of animals, these operations were conducted on Kizhi only in 1998, on other areas – permanently. All found corpses were opened. The type of victims was determined on bone remains (mammals) (Siivonen, 1979), the calcaneal tuber (frogs) and other features. In partially digested frogs the length of the femur and tibia was measured. Almost all the data on adders' nutrition are related to snakes aged over 3 years.

Hunting. The motivating stimulus for hunting is, as in other animals, the lowering level of glucose in the blood, while the maintained body temperature is sufficiently high (not lower than 12 °C). In Karelia, hunting starts at any time of the day; active snakes were found at 1, 3, 9, 12, 17 o'clock; the time of hunting does not coincide with evening or nighttime

hours. In contrast, in Karelia adders can attain the high body temperature sufficient for activity and hunting only in daytime.

The hunting snake moves slowly, analyzing the chemical traces of its prey item in the studied area by its tongue and Jacobson's organ and follows this trail to the location of the victim or its nest (small mammals). There has been noted a clear direction of adders' hunting movements toward the nests with hatching chicks. Adders do not eat eggs, but they are ready to climb the trees up to five meters to the nests with chicks. Adders are dim-sighted; at the distance of about 2 m they distinguish only large objects, nearer they see better. Detecting a small moving object visually, the snake intensely "smells" the air and puts its tongue out rather often. Out of mating season, the encountered snakes (over 2 years old) do not react to each other and after that they crawl away peacefully. Current-year-young often try to swallow their co-brothers that inevitably results in death of both the attacker (due to decomposition of not fully swallowed body) and its victim (due to asphyxia). Unlike rubber snakes (Peabody et al., 1975) adders have no ability to pull its head out of the fellows' mouth, coiling around its neck. When an adder found a prey item with a suitable size, it crawls towards the victim quickly and "interestedly", lifting its head rather high above the ground and bending its neck. Closing within the distance of spurt, it quickly bites the object once, then with effort pulls out deeply pierced teeth, and begins to watch the victim's moving. If the bitten animal moves quickly (chafes of pain), the snake bites him 1–2 times more and actively pursues, trying not to lose sight of it. If the victim passes out of sight, the snake pursues it by its scent. It is unknown whether the adder can distinguish, as the rattle snake (Chiszar et al., 1990), the individual scent of just bitten victim from that of other animals of the same kind. Waiting till the agonizing victim dies, the adder begins swallowing it – and usually from the head. To determine where the victim's head is, the snake begins to drive the tip of its muzzle along victim's body in the direction of greatest resistance of hair or feathers. Having reached the victim's head, the snake starts to swallow it. However, snakes are often mistaken, starting to swallow frogs beginning with their caudal part. Interestingly, that snakes

often swallow the victims killed not by them. We have observed when two snakes try to swallow the same frog from the opposite sides (it can lead to the death of both snakes). The time of swallowing depend on the prey size and ranges from 1 to 20 min.

When the snake is sated, its behavior changes significantly: it tends to digest food faster and therefore it heats up actively, its maximum voluntary temperature became the highest (see section 3). The digestion of a large prey lasts 4 days in optimal conditions; when the weather is variable, it lasts longer. After feeding the animals become passive for some time (4–10 days), they are not interested either in food or in high temperatures. In nature they may spend this time in light and underground shelters, rarely appearing on the ground. Then the cycle repeats. Focusing on laboratory data, it can be stated that the cycle "hunting – digestion" lasts about 2 weeks (varying between individuals of different status).

In conditions of Karelian summer, the number of feeding acts cannot be high. If snakes start feeding at the beginning of May and end it early in September, then for four months they can have 8–10 meals maximum. As for the adders on the island of Kizhi, one should bear in mind two facts. For unknown reasons snakes do not hunt small frogs, they prefer large ones, maybe they are not fast enough to bite quickly-moving small objects (many times we watched when hunting adders overshot). In addition, on Kizhi there are not a lot of prey items, except frogs, which hold to the surroundings of swamps. This means that when snakes dwell far from the marshes, it can take them a long time to find a large prey. It is reasonable to believe that on Kizhi snakes have meals less than 8 times a year.

The first hunting acts are observed in the early spring. The fact of recent feeding can be registered more often when the captured snake "shoots" the contents of its cloaca in an effort to defend itself. Dark, black, dense discharge indicates recently digested animal (less than 10 days after hunting), if the discharge is yellow, it means that the snake ate long ago (2 or more weeks ago). When males are caught after May, 15th, and females – after May, 25th, almost all of them are certain to have eaten this spring. Among the females with eggs the proportion of those having eaten by May,

15th is 50 % (see section 2.2). Hence, one can conclude that some of the males feed immediately after their exit from hibernation, but the majority of them – after mating; fertile females generally feed before mating. Judging by the growth of body mass in pregnant females, they actively feed during the first half of pregnancy (see section 5.4). Pregnant adders are not considered to eat in the second half of summer at all (Schiemenz, 1978; Biella, 1980; Nilson, 1981; Bea, Brana, 1989), but it is the obligatory rule for the Kizhi archipelago and it is corrected by habitat conditions. In particular, on the islands of the Kizhi archipelago 25.07.1998 (i.e. a month before birth) two pregnant females were found with food in the stomach, one with chicks, and the other with a frog.

Feed spectrum. The adder feeds on small mammals, chicks of small birds, sometimes lizards, amphibians (table 9.1). It is believed that the first possible prey of current-year-young can serve only young frogs (Gruband et al., 1972). We can add to the list young newts. There is no evidence of the information that young adders feed on invertebrates (Anufriyev, Bobretsov, 1996); feeding on anthropods is typical for the Orsini's viper, but not for the adder (Bea, Brana, 1989).

The species composition of victims varies widely within the area of the adult adder and is determined by the specificity of the local fauna of terrestrial vertebrates. In Karelia 23 species of prey can be reliably detected in the stomach of the adder (Table 9.2); among them there are no reptiles, but a large proportion of birds (16 vs. 12 % for other regions). The occurrence of mammals and amphibians (respectively 28 and 56 %) was within the range of variations over the adders' area. The proportion of "full" snakes among those found in Karelia averages than 15 % less per year. This is lower than that of full individuals (20–50 %) in other parts of the area. In our view, it can be explained by the fact that the researches are usually conducted in the summer, but we considered the entire warm period. However, it is just in the middle of summer that the occurrence of snakes with the full stomach is higher (55%) than in spring or in autumn (Table 9.3).

Table 9.1. Occurrence (%) of different prey items in the stomach of the adder

Mammals	Birds	Reptiles	Amphibians	Proportion of full stomachs %	Region	Authors
17		4	78		Kiev	Darevsky, 1949
57	11	19	18	33	Darvinovsky reserve	Kaletskaya, 1956
29	+		52		Belarus	Sapozhenkov, 1961
47	4	4	44		Poland	Pielowski, 1962
+		+	+		Siberia	Strelkov, 1963
+	+	+	+		Darvinovsky reserve	Han-K'yen, 1967
	+				Siberia	Irisov, 1972
+		+	+	21	Novosibirsk	Popudina, 1976
	+				Finland	Haartman, 1976
+					Yakutia	Larionov, 1977
58	6	18	18	11	Darvinovsky reserve	Belova, 1978
19			81	34	Yakutia	Prokop'yev, 1978
91	0	9	0	51	Novosibirsk	Grigor'yev, 1981
38	+	5.5	+	39	Czechia	Sebela, 1980
62	12	3	23	41	VKGZ	Garanin, 1983
0-56		17-31	6-72		Tomsk	Kuranova, Kolbintsev, 1983
83			17		Gor'ky	Ushakov, Pestov, 1983
68	+		32	24	Altay	Yakovlev, 1983
80			20		Poland	Juszczyk, 1987
76	8	11		20	Belarus	Pikulik et al., 1988
+	+	-	+		Italy	Luiselli et all., 1991
28	16	0	56	9	Karelia	Our data
0-91	0-16	0-31	0-81	9-51	All area	Lim, all authors

Table 9.4 shows how the proportion of full individuals is clearly explained the dynamics of snakes' diet during the year. In July and August the number of small mammals increases, and in June and July mass hatching takes place. At that time, accordingly, the proportion of these prey items and total filling of the stomachs of adders increase. The same can be said about the dynamics and intensity of destruction the nests of small passerine birds by adders (Table 9.5, 9.6). So, in 1985–1998 there were 4–9 % of ravaged nests and in some years – 44 % (Lapshin, 1995).

Table 9.2. Prey items of the adder in Karelia

Group	Age of animal	Proportion of full stomachs, %	Group	Aage of animal	Proportion of full stomachs, %
Amphibia		56.3	Aves		16.1
Anura		55.4	Charadriformes		+
R. temporaria	ad	42	*L. ridibundus*	juv	+
R. arvslis	ad	13.4	Piciformes		0.9
Caudata		0.9	*I. torgvilla*	juv	0.9
T. vulgaris	juv	0.9	Passeriformes		15.2
			S. communis	juv	+
Mammalia		27.7	*S. borin*	ad, juv	+
Rodentia		17	*Ph. trochilus*	juv	13.4
Cl. glareolus	sad, ad	10.7	*Ph. trochiloides*	juv	+
M. agrestis	juv, ad	4.5	*Ph. collybita*	juv	0.9
M. minutus	sad, ad	1.8	*Ph. sibilatrix*	juv	0.9
Insectivora		10.7	*E. rubecula*	juv	0.0
S. araneus	juv–ad	9.8	*S. rubetra*	juv	+
N.fodiens	sad	0.9	*T. merula*	juv	+
			T. troglodites	juv	+
			F. coelebs	juv	+
			A. trivialis	juv	+
			M. alba	juv	+

Table 9.3. Proportion of adders with full stomach

Area*	April	May	June	July	August	September	All
	Proportion of full stomachs %						
Kizhi	–	3	3	13	10	8	6
Moyachino	–	0	55	38	0	0	35
Kivach	4	2	19	26	29	0	15
All	4	2	9	17	15	7	9
	Number of examined stomachs						
Kizhi	0	347	234	164	92	144	981
Moyachino	0	5	20	13	5	3	46
Kivach	26	60	47	47	34	2	216
All	26	412	301	224	131	149	1243

The probability of that the nest will be destroyed by a snake after hatching remains approximately the same throughout the nesting period. The apparent "splash" of nests ravaging in 6–10 days after hatching is

associated only with the increase in the number of nests found by ornithologists, because the adult birds that begin feeding the nestlings become clearly visible.

Table 9.4. Change of food composition in the adder during the year

Area	Group	April	May	June	July	August	September
Kizhi	Amphibia	–	100	75	82	89	100
	Aves	–	0	13	9	0	0
	Mammalia	–	0	13	9	11	0
Moyachino	Amphibia	–	0	0	0	0	0
	Aves	–	0	82	40	100	0
	Mammalia	–	0	18	60	0	0
Kivach	Amphibia	0	33	38	33	36	0
	Aves	0	0	13	0	0	0
	Mammalia	100	67	50	67	64	0

Table 9.5. Dynamics of nests ravaging after hatching

The day of observations (0 – the day of hatching)	< –2	–2	0	2	4	6	8	10	12	16	18	Total nests	
												%	number
The proportion of discovered nests *, %	42	2	6	4	6	11	11	8	5	4	2	100	161
The proportion of ravaged nests **, %	0	0	0	14	9	18	37	7	11	5	0	100	57

Selectivity of feeding. To what extent the occurrence of victims in the adders' stomachs is relates to their feeding preferences? It is usually believed that the place of a prey item is defined by its number in a given area (Kuranova, Kolbintsev, 1983). Our data confirms this state: there is a positive correlation between the population density of a group of victims and its occurrence in the stomachs of snakes (Table 9.7). (In brackets we note that due to the wide annual variation in the abundance of natural victims' populations, estimates of density presented in the table are mainly comparative and illustrative, and are appealed for showing significant differences of the abundance of certain food items in studied regions, but they are not accurate).

Table 9.6. Proportion of nests ravaged by adders in ten biotopes of Priladozh'ye (Moyachino) (data by N.V.Lapshin, V.B.Zimin)

Species	Number of nests	% of ravaged nests
Ph. trochilus	229	9.2
Ph. trochiloides	121	4.1
Ph. collybita	132	4.5
Ph. sibilatrix	88	6.8
E. rubecula	436	5.5

The calculated correlation coefficient between two data matrixes in table 9.7 is insignificant ($r = 0.60$, $p = 0.08$). But if the dependence between the food item occurrence in the stomach and its density is calculated separately for each victim, the correlation turns out very high: $r = 0.988$ for amphibians, $r = 0.965$ for birds, $r = 0.958$ for mammals. It clarifies the situation. The fact is that in adders the availability of a prey item differs from the preference for it.

Table 9.7. Long-term average characteristic of adders' diet and estimates of average long-term population density of victims

Region	Amphibia	Aves	Mammalia
	The proportion of stomachs with prey, %		
Kizhy	83	6	11
Mayachino	0	72	28
Kivach	29	4	68
	The population density of the victims, ind. / ha		
Kizhy	200[1]	0.8[1]	7[1]
Mayachino	5[1]	5.4[2]	12[3]
Kivach	44[1]	2[4]	33[5]

Note. 1 – our estimates, 2 – (Ornithofauna of Karelia, 1993), 3 – our estimates based on hospital data in the village of Karku, 4 – estimates by M.V. Yakovleva, 5 – (Kutenkov, Shcherbakov, 1988).

So, adders mainly eat the largest of all frogs (Table 9.8), they ravage only nests that are on the ground or just above it (Table 9.9). An attempt to eat the chick of the red-winged thrush was noted, but its wide "shoulders" did not allow the snake to do it (oral presentation of T.Y.Khokhlova).

Hence, only the number of the available part of victims appears to be important, and the discussed correlation should take this into account.

Table 9.8. Frequency of finding (%) different sized frogs in the stomachs of adders

Thigh length, mm	18	22	26	30	34	38	42	Total	
								%	number
R. arvalis	0	17	17	41	17	8	0	100	12
R. temporaria	0	4	14	21	29	28	4	100	28

Table 9.9. Proportion of ravaged nests of the willow Warbler depending on their location (data by N.V.Lapshin, A.R.Tyulin)

Hight, m	0	0–0.2	0.2–0.4	0.4–0.6	0.6–1	1–2
The number of nests	480	13	19	4	3	2
Ravaged	15	4	2	0	0	0
Share, %	3	37	10	0	0	0

The correction can be introduced by two ways: either to convert the number of victims to the number of *available* victims (which seems rather complicated) or to level the effect of preference by normalizing the each victim density, according to the formula:

$t = (Xi – M) / S,$

where Xi is density of a given victim in a given area, M – average density over all regions, S – standard deviation of density over all regions (Korosov, 1996). As a result, the correlation between the occurrence of victims in the stomachs of snakes and its normalized density became high ($r = 0.970$) and significant ($p < 0.001$).

With the other conditions, the inclusion of a given victim in the adder's diet is determined by the victim's population density. At the same time, individuals of different prey groups have various chances to be eaten by adders. Despite the high number (e.g., frogs), the proportion of this food item in the diet of snakes can be relatively low. A hungry snake eats any victim it finds, but not larger than chicks of the thrush and if the prey is

neither high above the ground nor under water (although in captivity adders willingly ate fish: the whitefish and roach see section 13).

Amount of food intake. The amount of food intake was calculated based on the data of laboratory observations. Snakes were kept at a constant temperature and feeding regimen ad libitum. The results of the diet of 23 snakes are shown in the table, which is used to calculate the model of growing food intake of the kept animals with age (Table 9.10).

Table 9.10. Average volume of food (C) eaten by the adders per month in captivity

	Females			Males			C♀–C♂, %
mon.	L. t., мм	C, г	mC, г	L. t., мм	C, г	mC, г	
5	263	8.2	0	209	6.8	2.7	17
6	283	12	0.5	240	9.5	2.5	19
7	296	8.6	0.8	262	8.6	5.5	0
8	312	20	0.2	291	14	7.7	33
9	331	25.5	7.73	309	13.6	0.64	46
10	355	32.7	8.18	326	23.6	15.5	28
11	375	41.8	8.18	342	26.8	5.45	36
….							
28	600	71.4		520	39.5		45

The table shows that the food intake and body size increase with age. At that, females consume by 17–46 % more food per month than males, and their rate of food consumption rise is higher than in males. This is evident from a higher coefficient of the linear term of the equation, 1.3 > 0.4 (equations are adequate, $p < 0.001$, the coefficients are significant, $p < 0.05$):

$$C_{♀} = -0.00103 \cdot Lt^2 + 1.3297 \cdot Lt - 269.4,$$

$$C_{♂} = -0.00025 \cdot Lt^2 + 0.43247 \cdot Lt - 69.95.$$

The resulting models can serve as a basis to predict the amount of food required for animals in nature (Table 9.2), since they consider only the first three years of their life in captivity, when the age-related obesity characteristic of laboratory animals has not started yet (Kudryavtsev et al., 1991).

The obtained estimates allow calculating the food amount that the population of adders could consume in nature maintaining the laboratory diet (Table 9.11). It could be 256 + 78 = 334 kg of food per year.

Table 9.11. Food consumption of island adders' population

Age	Females					Males				
	L.t.'	W'	C, г/ экз./ год	N	C·N, кг	L.t.'	W'	C, г/ экз./ год	N	C·N, кг
0	16	7.9				17	8.3			
1	23	12	2	382	1	22	12	2	297	1
2	29	18	15	376	6	27	16	13	285	4
3	34	26	30	369	11	31	21	29	274	8
4	39	35	64	364	23	35	27	40	264	11
5	44	46	93	357	33	39	33	51	254	13
6	48	58	116	351	41	42	41	61	244	15
7	51	71	132	345	46	45	49	68	173	12
8	53	83	141	250	35	47	57	74	122	9
9	55	93	146	181	26	49	65	78	86	7
10	56	101	150	131	20	51	72	82	0	0
11	57	105	152	95	14	52	78	86	0	0
Total				3200	256				2000	78

Fatness. The relative body weight is often used as a characteristic of the well-being of snakes (Sindyukov, 1971; Leloup, 1976; Bennet, 1982). We used this coefficient of fatness to compare the food supply of snakes living on the island of Kizhi and on the mainland. As it was shown on the data of body weight changes, from May to September in males fatness grows (+2 %), and in females it reduces on average (–14 %) due to the birth of young (Table 9.12).

The most interesting is to compare the data on the snakes collected in different habitats. On Kizhi females turned out less fattened (29%, differences are significant, $p < 0.001$) than in other districts of Karelia, the same is in males (14 %, $p < 0.05$). Animals from Kizhi have equally lower relative weight (32% vs 16%) in comparison with those in captivity.

These data show that adders on Kizhi are clearly underfed, especially females. Literary data and our experience of adders' capturing show that exhaustion is the main cause of animal's death, especially during wintering

(Madsen, 1989). Therefore, there is every reason to state that the important cause of adders' mortality on the island of Kizhi is the death of exhaustion while wintering (in addition to the death under the wheels of vehicles, see section 7).

Table 9.12. Fatness of adders' males and females on the island, in the mainland and in captivity

Region and season	Females			Males		
	M	m	n	M	m	n
Captivity	6.1	0.38	7	4.9	0.30	4
Karelia, June – July	5.9	0.28	48	4.9	0.26	16
Isl. Kizhy, May	4.9	0.07	177	4.1	0.03	340
Isl. Kizhy, September	4.2	0.12	111	4.2	0.10	77
The deficit (Kizhy, May / September), %	–14			2		
The deficit (Kizhy / Karelia), %	29			14		
The deficit (Kizhy / captivity), %	32			16		

The adder is an active terrestrial predator hunting anything that moves or smells, but low above the ground and not in water. A specific feeding in any location is related only to the availability of certain prey items. On Kizhi frogs dominate, they form the basis of the diet in local snakes

Chapter 10.

Place of the adder in zoocenosis

Eating up small vertebrates (voles, mice, shrews, chicks of birds, lizards, newts and frogs), the adder acts as a second- and third-order consumer. Its coenotic role is usually estimated not more than modest – the consumption of a secondary production of ecosystems at the level of 1–2 % (Gil'manov, 1987). Sometimes, however, it is expected that its role may be more significant (Zamolozhnikov, 1993). The population of adders on the island of Kizhi is just the case. Open landscapes and plenty of shelters provide them favorable conditions for wintering and basking. To find out, to what extent the number of adders is provided by food resources (the tension of trophic relations), is the goal of this section. The water borders of the island give the possibility to solve this task. Since adders can feed only on the island, the census of their prey items is also the estimate of their potential food resources.

10.1. Material and methods

Inventory of frogs. The number of adult amphibians is determined as twofold number of their clutches (Novikov, 1953). The clutches were counted in "driving" or "trampling down" all wetlands and temporary ponds on the island of Kizhi in chemical protection suits. Clutches of grass frogs were distinguished from the clutches of moor frogs: they are larger with twofold larger spawns. There are usually aggregations from several clutches to several tens of them located mainly around the ponds (Terent'ev, 1950). Spawning places were mapped previously at night by the frogs' voices – the rumbling of grass frogs and "barking" of moor frogs. The survival of grass frogs' larvae was determined in two temporary ponds with the volume of 15–20 m^3 on the outskirts of the village Konchezero (Korosov et al., in press). In each pond the total number of shed spawns ($N_{e.}$) was determined by multiplying the number of clutches ($N_{l.}$) by the

average number of spawns per clutch ($N_{e./l.}$). To estimate $N_{e./l.}$ the volumetric method was used: the number of spawns in 100 ml of a clutch was interpolated onto the total volume of the clutch determined in a measuring cylinder. The absolute number of tadpoles ($N_{t.}$) in ponds was determined by capture-mark-recapture method (Dinesman, Kaletskaya, 1952). Larvae (533 ind.) were marked with a vital neutral red colorant, and recapturing was carried out every second day (Severtsov, Surova, 1979).

According to these data, the survival of embryos $S_{e.} = N_{t.} / N_{ov.}$ was calculated. The absolute number of current-year–young undergoing metamorphosis and settling (N_{0+}) was estimated while they were captured in two ponds surrounded with fences of plastic film. The survival rate of tadpoles $S_{t.} = N_{0+} / N_{t.}$. The overall survival at embryonic and larval stages is equal to $S_{tot.} = N_{0+} / N_{e.}$.

Inventory of birds. The observations were carried out on plots of 100 x 100 m on the area of 22 ha (Fig. 10.1.1). In the nesting season on each plot the transpositions of birds, birds with nesting material or food were observed in 3–4 points from cover. The search for nests was conducted in the morning and evening hours. All individuals detected visually or by their voices were mapped (Zimin, 1983). The number estimating is based on the data obtained on the discount plots, with subsequent extrapolation onto the entire study area. Such a recalculation is possible only in the case of a sufficiently large studied area, 25 hectares (Shishkin, 1986). In our case this condition is fulfilled. In 3–5 days of observations we finally found out the number of pairs nesting at the site. In the egg-laying period, nests are easily detected by the "rousing" method (the work by A.R.Tyulin).

The observations were carried out by the ornithologists of the laboratory of Zoology, Institute of Biology, Karelian scientific center, Russian Academy of Sciences (reports of N.V.Lapshin, A.V.Artem'yev, T.Y.Khokhlova). According to them, the nests ravaged by adders have the following characteristic features. Unlike other predators, the adder does not damage nests, it only eats chicks, sometimes not all, leaving those who died from their bite and those having a bluish discoloration.

Fig. 10.1.1. The location of deathtrap lines and sites for bird nests counting

Inventory of small mammals. On Kizhi rodents and insectivores were caught in September in break-back traps placed in standard lines of 25 pieces in each for one day (Korosov, 1994). Each year from 1993 to 2009 20–26 lines were set over the island for two weeks (Fig. 10.1.1). At the same time, trapping on the mainland (near village Pod'yel'niki) was conducted in two habitats – pine myrtillus forest with green mosses impure birch and mixed grass upland meadow. The lines of 50 traps each were set for 2–3 days (Fig. 10.1.1).

To characterize the spatial distribution of small mammals on Kizhi, in 1994–1998 and in 2006 the detailed field mapping of the areas was carried out where12 environmental components were spread. These components important to small vertebrates include: normal herbage in a

meadow (g), mowing (p), intensive grazing (v), tall grasses due to the rosebay (b), wet places around the karst ponds (w) marshes (m), reed stands (t), beds of rushes (k) or sedge (o), sphagnum (s), small-leaved and mixed woods (f), villages (d). The general map of the area was decoded ("digitized") over the network of plots of 50 x 50 m (1020 plots), and thus 12 electronic vector maps were obtained, one for each environment component. Each plot is evaluated only by two values: 0 – absence of the component in this plot, 1 – provided this component covers more than 5% of the plot (Korosov, Fomichev, 1999). Further, maps were used to assess the relationship between environmental components and occurrence of small mammals.

10.2. Number of amphibians

On the island of Kizhi only frogs are numerous, common newts are rare (12 ind.) both on the island and in the adders' stomachs (1 ind.); crested newts are absent at all. The census of adult frogs was conducted by counting the number of clutches in swamps and vernal-autumnal ponds in the spring. This clutches counting was performed by us in 1996–1998 and repeated by S. N. Fomichev in 2000–2002 (Table 10.2.1) (Korosov, Fomichev, 1999б, 2005а, 2005б, 2007; Fomichev, 2004). The efficiency of counting varied depending on the water level in Lake Onega. Very high water in 1996 and 2000 allowed investigating only some internal and vernal-autumnal ponds; these data are not presented.

Conditions of Kizhi are favorable for frogs. There are deep wintering places at the bottom of Lake Onega (some frogs were caught in basket at a depth of 3 m), and extensive non-drying swamps favorable for spawning and larvae development as well as field woodlands with a rich ground litter and the abundance of arthropods, frog's prey items (Korosov, 1996).

The choice of spawning places corresponds to frog's species stereotypes (Severtsov et al., 1998; Kutenkov, 1988; Kutenkov et al., 1990; Kutenkov, 2009). The grass frog prefers margins of large wetlands, where cows and horses have trodden numerous paths along the meadows' shore,

and fishermen – on the edge of the lake, which in spring are filled with shallow water. The clutches are also found in low-lying flooded areas of large swamps, wetlands and large pits, ruts, puddles. Clutches occur in aggregations (up to 192 units). The clutches are located in shallow water, 2–20 cm deep, but sometimes up to 40–60 cm.

The moor frog sheds the eggs in swamps mostly at a distance to the lower bank (2–20 m) as well as in slough and flooded pits over the lake periphery of large swamps. 1–2 clutches occur in one place. At low water in the lake and in marshes, frogs shed the eggs in rare deep puddles, where several dozen of clutches (up to 83) are aggregated in one place. The usual water depth below the clutch is 20–40 (up to 80) cm, but at the water shortage, the depth can be less – 5–10 cm. In total on Kizhi about 20 reproductive natural reservoirs were discovered, but almost all of them contain several large spawning areas (from 1 to 40–50) (Fig. 10.2.1). The location of spawning areas and their ordering in the spring from year to year vary depending on the weather and the water level in Lake Onega.

The normal conditions (gradual warming and filling wetlands with Onega water) in spring of 1997 provided that mass reproduction in the grass frog was finished early, by May, 12th (median date *Me*=11.5.97), and in moor frog – by May, 22th (*Me*=20.5.97) (Table 10.2.2). Rather warm weather in the early spring of 1998 followed by a sharp cold and a late return of heat combined with the low water divided mass spawning in grass frogs into two periods: first – 10–12 of May and second, 16–19 of May (*Me* = 12.5.97). The spawning of moor frogs occurred mainly in the second warming period and for the majority of individuals ended somewhat earlier (*Me* = 17.5.98) than in 1997. The total results of spawning in 1997 and 1998 were similar. The number of clutches of grass frogs was almost identical (3467 and 3649), that of moor frogs in 1998 was significantly higher (1204 vs 3211) (Table 10.2.1). The only reason of that consists in different conditions of clutches accounting. The beginning of mass spawning in moor frogs coincides with the starting of filling swamps with snowmelt water from the lake. In 1998 the water level was very high and the usual increase (40 cm) fully flooded spawning areas and made the

accurate accounting of clutches number impossible, and sometimes even the access to them (average depth was up to 60–80 cm, maximum – to 120 cm).

Table 10.2.1. Accounting of frogs' clutches on the island of Kizhi

	Roots		Number of clutches	
	number	length, km	*R. temporaria*	*R. arvalis*
1997	33	41	3467	1204
1998	42	53	3649	3211
2001	53	66	2975	2243
2002	68	85	4918	3529

Low water level and the earlier warming in 1998 cause a mass spawning of the moor frog in shallow pools at the lake periphery of swamps, and they were easy of access for accounting. As a result, the censuring was complete. The course of spring processes (filling wetlands at first by melted, and then by the lake water) in 2001 was the same as in 1997, but in 2002 – as in 1998.

Table 10.2.2. Number of frogs' clutches, shed by a specific date in the spring of 1997–1998 in all reproductive reservoirs on Kizhi

Species	Date of 1997			
	8–11.5	11–12.5	14–17.5	20–25.5
R. temporaria	811	2836	3286	3467
R. arvalis	33	129	265	1204
	Growth rate (clutch per day)			
R. temporaria		1013	90	26
R. arvalis		48	27	134

	Date of 1998							
	9.5	10.5	12.5	13.5	15.5	16.5	19.5	24.5
R. temporaria	517	620	2099	2250	2250	2423	3424	3649
R. arvalis	0	0	127	131	511	764	2956	3211
	Growth rate (clutch per day)							
R. temporaria		103	740	151	0	173	334	45
R. arvalis		0	64	4	190	253	731	51

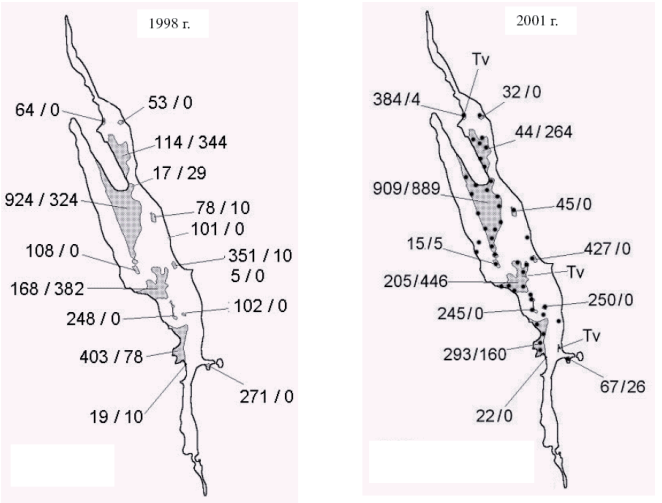


Fig. 10.2.1. The number clutches of eggs of brown frogs and moor frogs (Rt / Ra) in marshes on Kizhi Island in 1998 and 2001., places of common newt encountering (Tv) and clusters of brown frog eggs clutches (·)

The results of deriving the frogs number turned out appropriate – the undercount in 2001 and a total account in 2002 (Table 10.2.1). Based on given data (and assuming equal representation of sexes), it can be claimed that with an accuracy of about 200 animals on Kizhi there are 7–8 thousand of adult green frogs and 6–7 thousand of moor frogs.

The calculation of the absolute number of the entire population of frogs must be carried out by reconstruction of the number of young and mature animals. Assuming the constancy of the island population (proved by our estimates) and based on the known literary estimates of population parameters, it is possible to reconstruct the stationary age distribution in Excel environment and on its basis to calculate the total absolute population number. The number of current-year-young (N_1) is calculated as the proportion (s_0) of spawns, from which frogs developed and then successfully wintered, and the number of spawns (N_0) – as total fertility (e) of all adult females (N_{fad}): $N_0 = N_{fad} \cdot e$, $N_1 = N_0 \cdot s_0$.

The number of mature individuals in each class is calculated using their known proportion in the population (p_i):

$N_{adi} = N_i \cdot p_i$.

The number of each age class declined with age:

$N_{i+1} = N_i - N_i \cdot d_i$,

where N_i – the number of the i-th age class (i = 1, 2, ... 8), d_i – annual mortality at the i-th age.

Fecundity (number of spawns in clutch) in grass frogs on Kizhi ranged from 500 to 2000 (e = 910 ± 50 spawns / clutch; Table 10.2.3) and did not differ (p = 0.05) from the number of spawns in clutches of mainland frogs (village Konchezero), which averaged 1057 ± 69 spawns in a clutch; it was more than in the clutches of frogs in the North (Murmansk oblast, Solovetsky Islands; p > 0.05), and less than in clutches of frogs in the middle of Karelia ("Kivach" nature reserve) and Finland (p > 0.05; Table 10.2.3).

The average number of spawns in clutches of moor frogs on Kizhi is 674 ± 46 (range from 210 to 2112 spawns / clutch), which is lower than in the reserve "Kivach" (p > 0.05) and close to values obtained in the northern Karelia (Loukhsky region; Table 10.2.3).

Table 10.2.3. Number of spawns in clutches of frogs by our and literary data

	Area	M ± m	Min	max	Source
R. temporaria	Kizhi	910 ± 50	496	1957	Our data
	Gomselga village	1057 ± 69	313	2484	
	Kivach Nature Reserve	2404	920	3126	Ivanter, 1969, 1980
	South of Karelia	1433 ± 46	–	–	Kutenkov, Korosov, 2001
	The Solovetsky Islands	506	–	–	Surova, 1989
	Finland	1200 ± 290	650	1460	Haapanen, 1982
	Finland	1307 ± 46	625	1865	Koskela, Pasanen, 1975
R.. arvalis	about. Kizhi	674 ± 46	210	2112	Fomichev, 2004
	Kivach Nature Reserve	955 ± 49	–	–	Kutenkov, Korosov, 2001
	North of Karelia	699 ± 23	–	–	

Moreover, in a field experiment, we determined the mortality of current-year-young larvae (Table 10.2.4) (Korosov et al., 2010). Survival at the larval stage amounted $S_{sp.}$ = 1.0–1.3 %, with total survival ranging $S_{tot.}$ = 0.13–0.62 %.

Table 10.2.4. Assessment of destruction of spawn and larvae of the frog (environs of village Konchozero)

Water	Puddle № 1	Puddle № 2		Puddle № 3
Year	2002	2002	2003	2003
Nl., pcs.	189	82	58	110
Ne./ l., pcs.	1264 ± 88	895 ± 158	1159 ± 107	1254 ± 136
Ne., pcs.	238896 ± 16632	73390 ± 12956	67222 ± 17334	137940 ± 29104
Nt., ex.	3212	753+114	–	–
Se., %	1.3	1.0	–	–
N0+, ex.	–	107	86	850
Stot., %	–	0.15	0.13	0.62

The estimation of some other demographic parameters of other boreal populations was taken by us from the literature. The survival at the ontogenesis stage from spawn to fingerling is 0.16–6.0 %, of that number only 30–70 % survives to wintering, and in the first wintering half of them die. The mortality rate of mature individuals is equal; the sexual maturity in grass frogs occurs in 3–4 years, in moor frogs – in 2–3 years (Zalezhsky, 1938; Ivanter, 1980; Kutenkov, 1988; Cherdantsev et al., 1997; Severtsov et al., 1998; Severtsov, Surova, 1989; Anan'yeva et al., 1998).

Our data on the absolute number, fertility, mortality of frogs and estimation of demographic parameters from the literature allows to reconstruct the absolute number and biomass of the island population of frogs by simulation modeling. The point is that focusing on the amount of frogspawn and the number of adults to calculate the number of immature individuals (it is assumed that the population is not growing, r = 0). We accepted that the number of adults has to be 7000 individuals of grass frogs and 7000 individuals of moor frogs. After that the initial parameters were

adjusted by the optimization method, the difference between the estimated number of adult individuals and a real one acts as a residual function. One parameter – mortality – was adjusted; it is the same in all age classes older than one year. The adapted parameters are listed in Table 10.2.5, and the calculated numbers of frogs of all ages – in Table 10.2.6.

Table 10.2.5. Demographic parameters of frog's populations

Parameter		*R. temporaria*	*R. arvalis*
Amount of eggs in a clutch, pieces		910	670
Survival, %	fingerlings	0.5	0.5
	1–8 years old	56	56
The proportion of mature, %	2 years old	0	20
	3 years old	80	80
	4–8 years old	100	100

Table 10.2.6. Estimated number of all age classes in two frog's species

Age	The number of grass frogs			The number of moor frogs		
	total	mature	perished	total	mature	perished
0 (spawn)	31 50 000			20 10 000		
1 (after wintering)	15 750			10 050		1 999 950
2	8845		6905	5587	1117	4463
3	4967	993	3878	3105	2484	2481
4	2789	2789	2178	1726	1726	1379
5	1566	1566	1223	960	960	767
6	880	880	687	533	533	426
7	494	494	386	297	297	237
8	277	277	217			
Total	35 568	7 000	8567	22 258	6000	5290

The presented model allows calculating the number of dying frogs, including those eaten by adders. When the population number of grass frogs is about 36 thousand ind. and the mortality at any age $d = 0.44$, the loss per year will be about 8.5 thousand ind. Similar figures are in moor frogs: 22 thousand ind., 0.44, 5300 ind. (Table 10.2.6).

Using our data on the age distribution of frogs, the calculated values of body weight as well as the table of age diagnostics by P.V.Terent'yev

(1950, p. 68), one can calculate the total loss in the populations of frogs older than 2 years (prey items). As for the grass frog, it approaches 122 kg (Table 10.2.7). The body weight and population number of the moor frog are less than those of the grass frog, so as the mass of animals perished every year, in total 86 kg (Table 10.2.8).

Table 10.2.7. Biomass of grass frogs perished per year

Age, years	2	3	4	5	6	7	8	Total
The number of groups	6905	3878	2178	1223	687	386	217	8567
The average body length, mm	32	45	56	62	65	65	65	
The average weight*, g	2.5	7.6	15.5	21.7	25.0	25.0	25.0	
The total group weight, kg		29.5	33.8	26.5	17.2	9.6	5.4	122

Note. * Frogs were weighed after wintering

On the island of Kizhi the total biomass of the perished frogs is about 208 kg. It is obvious that only some part of these individuals can be accessible for adders as prey items. As the data confirming that are absent, we assume that the adder withdraws about 2/3 of perished individuals from the frogs' population or about 140 kg of live weight.

Table 10.2.8. Biomass of moor frogs perished per year

Age, years	2	3	4	5	6	7	Total
The number of group	4463	2481	1379	766.7	426.2	237	5290
The average body length, mm	21	38	53	55	55	55	
The average weight*, g	5.76	12.4	19.2	20.1	20.1	20	
The total group weight, kg		30.77	26.48	15.41	8.566	4.7	86

Note. * Frogs were weighed after wintering

10.3. Number of birds

The prey items composition of the adder includes chicks of small passerine birds, piciformes and charadriiformes (see section 9). On the island of Kizhi there are 20 such species of 45 (Khokhlova, Semina, 1988) (table 10.3.1).

Table 10.3.1. Number of small birds on Kizhi in spring and summer 1998

Species	Found on the areas		Counting on whole island	Counting on the routes all over the island	The average estimation of pairs number on the island
	Individuals	nests			
A. hypoleucos	0	0	0	0	1
S. hirundo	2	1	10	27	15
A. arvensis	5	0	0	6	10
M. alba	3	3	30	12	10
M.flava	3	0	0	4	3
A. trivialis	0	0	0	0	1
. rubecula	1	0	0	0	3
S. rubetra	1	0	0	4	5
Oe. oenanthe	2	1	10	2	3
A. schoenobaenus	1	1	10	1	4
A. dumetorum	2	1	10	3	4
S. borin	4	3	30	4	4
S. communis	5	3	30	8	12
Ph. trohilus	9	2	20	8	12
E. citrinella	12	1	10	3	11
E. schoeniclus	0	0	0	3	6
L. luscinia	0	0	0	0	1
T. iliacus	3	1	10	1	7
J. torquilla	1	0	0	0	1
T. troglodites	0	0	0	1	1
Всего	54	17	170	87	114

To assess the role of these species in the snakes' diet, a series of sample plots was formed. There the nests were actively searched, the found individuals were registered, and the found nests were also monitored. In addition, along the island territory a record route was mapped (12.6.1998, 16.6.1998), where individuals and voices of singing males were registered.

In addition, some species (skylark, nightingale, etc.) were registered out of the route and sample plots. This information allows estimating the absolute number of birds of different species on Kizhi as well as their proportion withdrawn by adders.

For this goal, the number estimates obtained in the sample plots were extrapolated to the entire island territory. The area of Kizhi is S = 204 hectares, it includes grasslands (100), wetlands (33), deciduous forest (24), building area (14). Sample plots with a total area of 22 hectares include meadows (18) and deciduous forest (4). The ratio between the meadows and the forests both in the plots and on the entire island is approximately 10 %. As the plot area is about 10 times smaller than the area of the island, it is suffices to multiply the number of birds in the plots by 10 to estimate the number of birds on the island.

Comparison of the calculating data with the estimates on the routes gives very low number of all species on the island – slightly more than 110 pairs (nests) (Table 10.3.1). The average population density of birds is about 45 pairs / km^2. Assuming that the average hatch consists of about 5 nestlings, the total potential food reserve is 570 chicks. How many of them get into the adder's stomach?

Of 28 nests that were monitored during the summer of 1998, only one (*Ph. trochilus*) was ravaged by an adder (six four-day chicks were eaten), another nest (*T. iliacus*) was taken by a weasel, the rest of chicks safely flied out. It turns out that about 4% of the chicks per year are accessible for adders. On an island scale it will be 20 chicks (out of 570) with a total weight of about 100 g. According to the ornithologist A.V.Artem'yev, who annually conduct the route accounts on Kizhi, the number of birds there varies from year to year within a narrow range ± 50–100 %. It means that taking nests can be more intense and 40–50 chicks can be lost. Unfortunately, our data are not sufficient for a representative statistical forecast, but one thing is clear: there are too few birds on the island of Kizhi to serve a significant food source for adders.

10.4. Number of small mammals

In the studied area the fauna of small mammals does not differ from that elsewhere in southern Karelia either in the species composition or population number (Ivanter, 1975; Korosov, Fomichev, 1999). Everywhere in the forests of the mainland, the bank vole (*Cl. glareolus*) and common shrew (*S. araneus*) dominate, on the meadows and field woodlands it is the dark vole (*M. agrestis*) (Fig. 10.4.1). For 15 years of our study populations of small mammals on the island of Kizhi has changed considerably. In the first five years (1994–1998) it strongly contrasted with the overall picture (Table 10.4.1). In meadow-boggy stations the harvest mouse (*M. minutus*) dominated for several years, the subdominants were the common shrew and dark vole (only once a bank vole and a pigmy shrew, *S. minutus* were found – in 2002 and 2005).

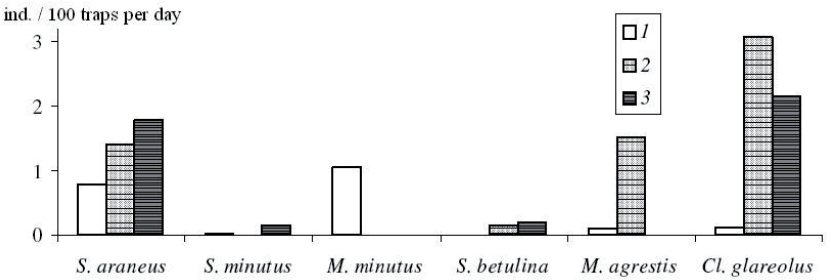


Fig. 10.4.1. Population of small mammals (*M*) averaged for 15 years on isl. Kizhi(*1*), in a meadow (*2*) and mixed pine-green moss forest (*3*) on mainland (near the village Podelniki)

Similar three-species habitat group (harvest mouse, common shrew and narrow headed vole) was noticed in the northern forest-steppe of Western Siberia (Ravkin et al., 1985). The former (Siberian) species prefers grassland habitats; in Karelia its place is taken by the dark vole, it inhabits anthropogenic grassland landscapes (Ivanter E.V., Ivanter T.V., 1983).

The harvest mouse prefers open habitats with high grass (the cultural grasses, wet meadows, marshes, reed beds), or with shrubs; these animals nestle in these plants (Stroganov, 1949; Glotov et al., 1978).

Table 10.4.1. Number of small mammals (ind. / 100 traps per day) on Kizhi (Σ – sum of animals, M – mean value, CV – coefficient of variation for the number)

Years	1994	1995	1996	1997	1998	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	Σ	M	CV
tr.p.-day	272	550	475	575	450	214	599	600	384	276	400	550	400	450	725	6920		
*sar**	1.47	0.91	0.84	0.52	1.56	0	0.83	1.83	0	1.45	0.75	0	0.25	0.22	0.83	54	0.76	126
smi	0	0	0	0	0	0	0	0	0	0	0.25	0	0	0	0	1	0.02	26
mmi	3.68	4	3.16	2.61	0	0	0.67	0.83	0.26	0	0	0	0	0	0	72	1.01	67
mag	0	0.18	0.21	0.17	0	0	0.17	0	0	0.72	0.25	0	0	0	0	7	0.11	59
clg	0	0	0	0	0.22	0	0	0.5	0	0	0	0	0	0.44	0.41	9	0.11	56
Σ	5.15	5.09	4.21	3.3	1.78	0	1.67	3.17	0.26	2.17	1.25	0	0.25	0.67	1.24	143	2.01	113

** sar – S. araneus, smi – S. minutus, mmi – M. minutus, mag – M. agrestis, clg – Cl. glareolus*

On the island of Kizhi the harvest mouse has the unique conditions favorable for reproduction – extensive meadows and marshes with reed beds. In the spring 1999 the administration of the Museum-reserve "Kizhi" decided to eradicate tall grasses and coastal reeds in the vicinity of the main exposition (as a possible source of fire hazard) and so destroyed the main habitat of this species, it lost its dominance since then, and in the last 5 years was not found at all. Gradually, as far as the territory of Kizhi was overgrown with a deciduous forest (see section 12.2), the composition of therio-fauna shifted towards the forest-meadow one. In 2004–2007 only shrews and dark voles were found on the island, but since 2008 the number of bank voles has begun to rise (up to 0.4 individuals / 100 traps per day). The number of small mammals on Kizhi is substantially lower than that on the mainland and other islands of the Kizhi archipelago (see section 12.4). Thus, their maximum number scarcely reaches 3.8, while on the mainland

it reaches the population peak of 34 ind / 100 traps-day (Fig. 10.4.2). At the same time, the continental populations' number has a larger amplitude of fluctuations, whereas on Kizhi the number of small mammals is steadily low.

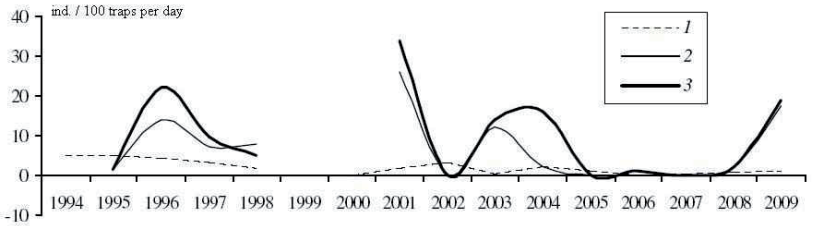


Fig. 10.4.2. Dynamics of the total population of small mammals on isl. Kizhi (*1*), in a meadow (*2*) and mixed pine green moss forest (*3*) on mainland (near the village Podelniki)

The absolute number of small mammals was calculated by extrapolation of the estimates of a relative number from local areas on the whole territory of the island and their conversion into the absolute numbers. The methodological basis is the assumption that an animal population is distributed through the territory in accordance with the distribution of "favorable environmental qualities". In the literature, it is shown that in general this assumption is incorrect (Proskurina, Krivosheeva, 1989). The number of rodents and insectivores in a certain biotope is not constant. It changes by year and season and depends both on biotopical environment and population "quality": reproductive and migration processes by the end of summer levels the peculiarities of the spring habitat groups (Korosov, Demidovich, 1987). In our case, however, the issue is not that we need to establish the impact of biotope "quality" on the animals' number, but only to receive the representative sample accounts as well as the possibility to consider the local characteristics of a small mammal population characteristic for the entire territory of the island. The limited small territory of Kizhi, homogenous landscapes, stable, and low

number of studied animals are favorable for such a forecast. By the time of censuring (September) reproduction and migration are completed, and therefore the animals' spatial distribution should be consistent with the species stereotype in regard to the choice of favorable conditions. To estimate their number, we used three methods.

To begin with, the frequency (regularity) of animals' trapping can be considered as a characteristic of their density, assuming that the average distance between captured animals roughly corresponds to the radius of their individual activity (Shchipanov, 1998, p. 30): R = (L / n) /2 where n – number of captured animals, L – total length of the traps' line. The individual area is $S_i = 3.14 \cdot R^2$, and the number of animals on the island is $N = S_{island} / S_i$. Calculating the food potential, it is worth taking the maximum estimates of a species number. Such number was registered, for example, in the common shrew in 2002 – 1.83 ind. / 100 traps-day (Table 10.4.1), in 20 lines (with the total length L = 20 · 125 m = 2500 m) n = 9 specimens were caught. The radius of the individual area is equal to R = L / n / 2 = 2500 / 9 / 2 ≈ 137 m, its area is $S_i = 3.14 \cdot R^2 = 3.14 \cdot 137^2 =$ $= 58600$ m^2, and the number of animals on the island is $N = S_{island} / S_i =$ $= 2040000 / 58600 = 35$ individuals (Table 10.4.2). The statistical error can be approximately estimated based on the following considerations. The number of caught animals in 15 (up to 25) lines of traps annually set on Kizhi, in different years are characterized by the coefficient of variation of 100–300 %, respectively, the error in the average number will be 25–70 %. Then the confidence interval for t = 2 will be 35 ± 18–48 individuals (53 to 83 ind.).

Table 10.4.2. Estimates of the absolute *maximal* number of small mammals on the island of Kizhi, calculated using different methods

Species	ex. / 100 tr. p-day	R	S, ha	N1	N2	N3	N
S. araneus	1.8	137	5.9	35	1122	169	506
M. minutus	4	1000	1.2	1	3264	335	1879
M. agrestis	0.72	63	37.9	166	739	173	314
Cl. glareolus	0.5	347	78.5	5	510	127	268

To criticize the reliability of the obtained values it should be noted that the basic information, the number of caught animals (n) is not defined correctly. As is supposed by the author of the method, a number n must correspond to the number of sedentary animals and must be defined for a long time (for about 5 days of capturing). In our case, capturing was always carried out within one day to avoid the reduction of already low number of animals. Therefore, the resultant absolute number (N_1) is significantly underestimated.

The second method of extrapolation of the animals' number onto the whole island can be constructed on the basis of known coefficients used to convert the estimates of relative number into those of absolute number (Marin, 1978; Sokolov et al., 1978; Resume..., 1980; Tupikova, 1983; Korosov, 1986). These coefficients vary widely (from 0.2 to 10) depending on the phase of population dynamics and animal's species. We took the maximum estimates of the number. For shrews, the coefficient 3 is recommended (the shrews' density, ind. / ha, is three times more than the value of relative number, ind. / 100 traps-day), for voles the coefficient is 5, for harvest mice there is no available data, so we take the value 4. Multiplying the calculated density to the area of Kizhi (204 ha), we receive the resulting estimates of the absolute number (Table 10.4.2). They turned out much higher – up to N_2 = 3264 mice. This value should be corrected significantly, because it gives the forecast of sampling captures on the island clearly distorting the specificity of the habitats. The area ratio of meadows, marshes, forests (49 : 12 : 16 %) is not the same as spacing of lines over the same habitats (9: 9: 7 lines, or 36: 36: 28 %). Extrapolation of accounts should be carried out considering the quality of habitats.

This is the essence of **the third method**: all relevant environmental factors are described in the form of 12 maps, consisting of 1020 squares including the environmental characteristics. Among them there were 52 plots where the animals were trapped (each of the 26 lines is 125 m long and occupies approximately two plots). Focusing on the values of the considered environmental factors on these 52 plots and the number of

species in the peak year, the polynomial dependences of the animals' number on biotopical environment were built:

$$N = a_1 \cdot e_1 + ... + a_i \cdot e_i + ... + a_m \cdot e_m,$$

where N is the number of a given animal's species in the plot, m is the number of environmental factors, e – presence (expression) of the factor in the plot, a_i – coefficients.

The following polynomial equations with significant coefficients ($p < 0.05$) for the factors were obtained:

1) for the harvest mouse (1995)

$N = 1.02 \cdot$ reed $+ 0.34 \cdot$ rosebay $+ 0.49 \cdot$ cane;

2) for the common shrew (1995)

$N = 0.15 \cdot$ forest $- 0.14 \cdot$ pond $+ 0.21 \cdot$ rosebay;

3) for the dark vole (2004)

$N = -0.07 \cdot$ grazing $- 0.09 \cdot$ pond $- 0.04 \cdot$ swamp $+ 0.04 \cdot$ meadow $+ 0.24 \cdot$ reed $+ 0.22 \cdot$ rosebay;

4) for the bank vole (2008)

$N = 0.083 \cdot$ forest $+ 0.17 \cdot$ pond $+ 0.11 \cdot$ rosebay.

From these equations the number of animals in all plots, where capturing was not produced, was calculated. The values of the average relative number over all plots were summed and multiplied by conversion factors discussed above, receiving the third variant of the estimates of the absolute number, N_3 (Table 10.4.2).

The presented models underline specific features of the territorial distribution of small mammals. The most eurytopic species, the common shrew, is widespread (Fig. 10.4.3). Narrow stenotopic species, the harvest mouse, is concentrated in a few beds of reed adjacent to swamps (Fig. 10.4.3, Б). Both species of voles are confined to field forests, but dark voles also inhabit the overgrown moor edges (Fig. 10.4.3, В, Г).

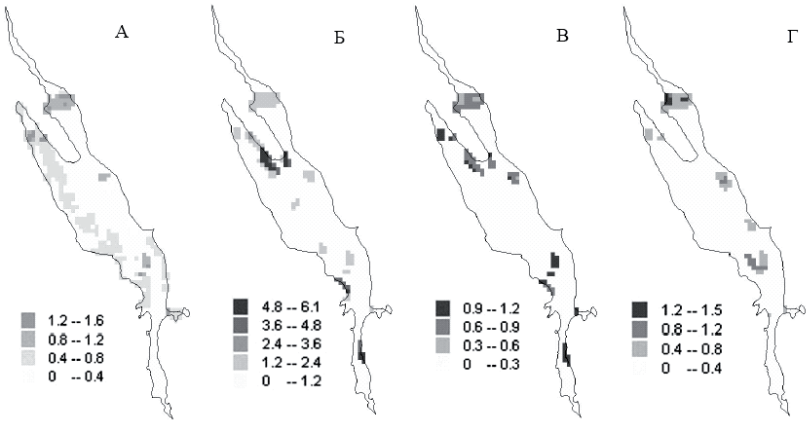


Fig. 10.4.3. Cartograms of estimated abundance (ind / ha) of the common shrew (А), harvest mouse (Б), field (В) and bank voles (Г)

Unfortunately, in each of the presented models the coefficient of determination did not exceed 0.1. This extremely low value is due to the fact that the island territory is rather homogeneous in relation to main environmental factors: it is small, and originally it was a plough-land, consequently, there is no any pronounced habitat specificity between separate plots. In addition, all species of mammals living on the island are eurytopic. Even the harvest mouse, being at the peak phase of population number in late summer, settled almost over the whole territory of the island, and in winter (according to natives) this species can be seen in the attics and basements of residential facilities. Taking into account the low predictive power of the discussed regression models, it should be concluded that the estimates of the animals' absolute number obtained by the third method are significantly undervalued. Perhaps, the averaging of all three estimates can give the number of small mammals on Kizhi closest to the true value. Probably in the years, when the number of small mammals is maximum in September their absolute number will amount 1000–2000 individuals. In 1994–1996, they were mostly harvest mice and shrews, in the later period – shrews, dark and bank voles.

Estimation of the number of animals eaten by adders is a serious problem, because it is only one of the numerous potential factors of mortality, which is extremely difficult to estimate in natural conditions. However, a way of calculating the animals' mortality rate due to adders can be proposed. To do this, one should assume that the withdrawal of some part of individuals by adders is burdensome on the island population in comparison with the usual mortality in the populations of small mammals in those places, where the number of snakes is low. Our long-term censuses of small mammals in different parts of the Kizhi archipelago allow us to make such a comparison. So, in the meadows of mainland (village Pod'yelniki, 1 km from Kizhi) and in swamps of Klimenetsky island (cape Voyguba, cape Klimenetsy), where adders are rare, the number of small mammals is significantly higher than on Kizhi (Table 10.4.3, 10.4.4).

Table 10.4.3. Number of small mammals in different areas of the Kizhi archipelago

Species	Kizhi isl.	Maedow on Continent					Swap
	M	1996	1997	1998	M	± m	1997
S. araneus	0.8	2.0	0	2.4	1.4	0.7	1.8
M. minutus	0.02	0	0	0	0	0	0
M. agrestis	1.0	6.0	10.0	2.4	4.9	2.2	4
Cl. glareolus	0.1	2.0	4.0	2.4	1.4	0.6	2.2
S. betulina	0.1	2.0	0	0	0.7	0.7	0
Total	2.0	12.0	14.0	7.1	8.5		8
Traps per day	6920	50	50	42	142		178

Table 10.4.4. Dynamics of dark vole number on the mainland and on the island of Kizhi

	Continent					Kizhi isl.	
Month	Nz	Njuv	Njad	Nad	N	dN	N
May	0.05	0.19		0.05	0.24	0.02	0.18
June	0.03	0.49	0.10	0.13	0.62	0.1	0.30
July	0.01	1.00	0.25	0.26	1.26	0.14	0.41
August	0.00	2.00	0.52	0.52	2.52	0.18	0.54
September	0.00	3.97	1.03	1.03	5.00	0.24	0.72
Total						0.67	

On account of that, the aim of a simulation will be to calculate the number of voles withdrawn from the population on Kizhi during the warm season, which causes their number typical of mainland change to typical of the island. As it is a long process, it is impossible to calculate the number of withdrawal by simple subtraction. It is necessary to restore the dynamics of their number changing during the season. Let us start with the dark vole (table 10.4.5).

Simulation model of population dynamics of the species number was based on the data of E. V. Ivanter (1975, p. 180–189). After the model was composed, the mortality coefficients were adjusted in each age group: overwintered (Nz), newborns (Njuv) and additional adults (Njad), based on the condition that by the fall the population number becomes 5 ind. / 100 traps-day. In spring the average mainland population number is 0.05 ind. / 100 traps-day. We found first newborn voles in the adders' stomachs on May, 22th; totally by September voles were able to produce four generation of additional animals, with each cycle lasting about 40 days (lines in Table 10.4.4). The proportion and number (Nz) of overwintered animals falls rapidly (at an estimated speed of 44 % in 40 days). The mortality of fingerlings (Njuv) is 27 % in 40 days. In summer the matured young animals (Njad) having the mortality of 48% in 40 days begin to reproduce. Overwintered and matured additional snakes form the group of adults (Nad) with fertility of 5.2 ind. / female (modal fertility for Karelia). These parameters provide the growth of voles' population (N) up to the observed average value of 5 ind. / 100 traps-day in September. The monthly increase in the number is 50–60 %.

The death of the voles from adders can be represented as an irretrievable withdrawal from this gain, which affect the reproduction of voles so that the population hardly reaches the value of 0.72 individuals / 100 traps-day by September (maximal estimate on the island of Kizhi in 2004).

The simulation modeling undertaken by us shows that if the predator impact (additional mortality) on each generation is 33 % in 40 days (dN), then to achieve the resulting number 0.72 individuals / 100 traps-day, the

extent of withdrawal from the population of the dark vole will amount 0.67 (not 4.28 individuals / traps-day as could be obtained at a simple subtraction). Such a large difference is explained by the exponential growth of the rodents' populations: when the predator impact is very strong, the population cannot reach the ascending branch of the curve of population dynamics.

The total number of eaten up individuals of dark voles can be calculated from the relationships defined previously. If the relative number 0.72 individuals / 100 traps-day corresponds to the absolute number of 314 specimens (see Table 10.4.2, *N*), then the value of 0.67 individuals / 100 traps-day corresponds to the number (314 · 0.67 / 0.72 =) 292 ind. Since the error of accounts is about 50 %, the number of voles eaten up during the season can vary (M ± 2m) from 0 to 600 ind. Comparing these values with the absolute number of the species, we can say that during the season adders kill approximately 93 % of the number of voles reached in September (100 % · 292 ind / 314 ind).

The population of the bank vole on Kizhi is less than that of the dark vole, but it inhabits other biotopes, and probably it is accessible for adders to a lesser extent. The annual withdrawal of these animals can be estimated as 200 ind. (at the phase of the pick number).

The reproductive potential of mice, and especially of shrews, is much lower, as their additional animals practically do not participate in breeding (Ivanter, 1975, p. 42, 105). Therefore, the proportion of these animals withdrawn by adders will be lower than that of dark voles. The number of common shrews on Kizhi (from 0.76 to 1.47 ind. / 100 traps-day) on average is slightly lower than in other parts of the archipelago (1.4 ind. / 100 traps-day) (Table 10.4.3). Calculations similar to those presented above show that during the summer such a reduction is provided by a withdrawal of 12 % of the shrew number or 61 ind. of their number in September. It may seem strange that when the number of shrews is twice as much as the number of dark voles, the intensity of their withdrawal due to adders is almost 10 times lower. But there is a fairly simple explanation for this. The dark vole inhabits the same biotopes as the adder: edges of the

forests and marshes. It is in these places that the plentiful grass damage occurs in spring. For this reason, dark voles afflict with snakes. Similar situation is observed on the islands of the Baltic Sea (Lindell, Forsman, 1996). Shrews, by contrast, are confined to the habitats with a fairly defined bedding and weak tussock (Makarov, Koosov, 1996), i.e., to the forests, fields, tussock bogs. Adders avoid these habitats because of the adverse thermal regime (shadow) and lack of shelters. The ways of adders' feeding migrations lead to shrews more rarely than to dark voles.

It is hard to predict the withdrawal of the harvest mouse because there is not anything on Kizhi to compare their number: in the other parts of the archipelago we could not catch any mice. We can say definitely that their proportion should be higher than 12 and lower than 190 %. The fact is that the habitats of mice only partially (on meadow edges of marshes) overlap those of adders, and in many ways they are isolated from them, because mice nest at the places that are inaccessible for snakes, quite high above the ground on thin stems of reeds and tall grass.

On account of the same number of voles and mice found in the examined stomachs of adders – 2 ind. of each species, we can assume that during the summer the number of voles eaten up by adders is almost the same as that of mice (255 ind. ± 255), or 19 % of the total number of mice (100 % · 255 ind / ind 1346). This estimate is close to real one because at mortality rates above 35% the majority of species are not able to maintain its high number, and the harvest mouse does have the high number.

It turns out that on Kizhi in the years, which are the most favorable for small mammals snakes can consume about 800 animals (300 dark and 200 bank voles, 60 shrews and 250 mice). Considering the average body weight of dark voles (32 g), bank voles (20 g), common shrews (7) and harvest mice (8), one can state that the biomass of prey eaten up by adders per year amounts 16 020 g, or 16 kg. As different types of mammals reach a high number in different years, the average annual weight of this food resource for snakes is hardly more than 5 kg.

Besides the mentioned estimates of the amount of prey items, our data are also interesting as they show the adder up as a predator, having a

major impact on prey populations. On the mainland, small predators generally have a little impact on victims such as voles (Erlinge et al., 1988), and the snakes also cannot significantly influence the number of their victims (Gil'manov, 1987, p. 148). However, on the islands snakes (including adders) often become a major regulating factor (Lindell, Forsman, 1996), sometimes causing the complete extinction of victims' populations (Rodda, Fritts, 1989). Our case supplements the short list of exceptions. The average number of dark voles on Kizhi differs by a factor of 5 (0.1, 4.9) and the maximum number – by a factor of 10 (0.72 and 10) from those on the mainland) (see Table 10.3.1, 10.3.3).

10.5. Total volume of food resources

The maximum total number of potential victims of adders on the island of Kizhi is about 58 thousand frogs of two species, 200 birds of 20 species, 1500 small mammals of 5 species, whereof the adders consume about 10 thousand (140 kg) of frogs, 20 (100 g) chicks, 800 (16 kg) mammals, in total up to 10 800 ind. (150 kg). Considering that the total number of adders is about 2700 ind., for each adder there are 3–4 victims / year, or 60 grams of food.

It is important to define if zoocenosis is capable to meet the adder's needs of food. As it was shown in sections 3.7 and 3.9, to ensure the normal annual increase in body mass and respiration of adders' population on Kizhi it is necessary, respectively, about 60 kg and 160 kg of food items. Since the energy expenditure on physical activity is roughly equal that on respiration (Schmidt-Nielsen, 1982) and equivalent to additional 160 kg of food, the total *estimated* nutritive need of adders' population on Kizhi is approximately 500 kg. This estimate is close to the adders' need in relation to the food consumption in captivity (see section 9), estimated as 334 kg.

The estimates of accessible and required food resources do not coincide, but differ only by a factor of 2 (220 and 500 kg). As in a sustainable population a balance between nutrition and expenditure must be

maintained, the error is in determining the estimates. Significant sources of error can be found only in precision of the accepted values of the total absolute number and age distribution in adders' populations: the model estimates vary within the range ± 30 % (see section 8). The estimates of the frogs' number also may be undervalued.

However, another thing is important. The assessment of snakes' needs and capability of zoocenosis do not have many-fold differences, they are very close. It is of evidence that the population of adders on Kizhi must consume almost all food resources, but they are not sufficient. Such a ratio does not exist either on the mainland part of Zaonezh'ye and on large afforestated islands where the victims' number exceeds the feeding needs of adders by one or two orders of magnitude (Korosov, 2003). No less interesting that with such a high abundance of predator as on Kizhi, it has to have a strong impact on its victims.

On the island of Kizhi (and on some other islands of the Kizhi archipelago) a more or less stable equilibrium developed between the predator and victims: the number of adders turned out so great that it began to restrict the populations of victims (this is particularly notable on the example of voles and meadow birds' species). The decrease in the number of victims, in turn, limits the number of predators. This can be traced on the feeding data: on Kizhi adders are not as well-fed as those in the mainland districts of Karelia and those kept in captivity. The food deficiency always causes increased mortality. In particular, on small islands a recurring starvation leads to an increased mortality of adders' females (Andren, Nilson, 1989). The ratio between the populations of victims and predator on Kizhi attained by 1998 is apparently limiting. For the majority of adders it gives a stochastic opportunity of finding the minimum required number of victims to maintain their own living, thereby ensuring the existence of the population of the predator. At the same time, this ratio allows terrestrial vertebrates to reproduce more or less normally. There is every reason to believe that the adders' number on Kizhi cannot achieve higher value for lack of prey items.

On the island of Kizhi the adders' population had reached its maximal number (about 5000 snakes) and biomass of 1.3 kg / ha (272 kg / 204 ha) by 2000, consuming almost all the production of zoocenosis of small terrestrial vertebrates. The ratio between the biomass of the predator and that of the accessible victims on the island is less than 1:10, whereas on the mainland it is from 1: 100 to 1: 10000.

Chapter 11.

Spatial movement

The spatial movement of animals provides many important physiological and population functions. If the pattern of the mobility of a given animal species is known, it is possible to identify the causes leading to animal death or survival and reproduction, to understand the mechanism of the population number dynamics. As for the adder one can observe and describe the following manifestations of motor activity:

– movement in wintering shelters depending on the ambient temperature (see section 2.2),

– thermoregulatory behavior on the ground surface (see section 3),

– reproductive behavior leading or not to mating (see section 4),

– hunting and feeding (see section 9),

– migration from wintering sites to reproduction and feeding ones,

– settlement of juveniles (see sections 7, 8),

– spontaneous activity (see section 3.3).

The types of motor activity considered above (hunting, migrations, settlement) lead to a gradual redistribution of animals within the island, its main feature is that they are virtually unable to leave the island. Water border returns animals to the same habitats, to the same hazards. One of the major adder life hazards on Kizhi is people – both travelers, who are afraid of snakes and so eager to kill them and motor vehicles. The main aspect of this section can be formulated as a dependency of population mortality on the individual mobility of animals.

Materials and methods

The distance between the points of two or several successive captures was accessed as the main characteristic of the snakes' movement. All points of animals capturing in the field were mapped (usually it was stone ridges; the capture points numbers were written down in the diary),

then they were carried over a MapInfo electronic map, where their coordinates were determined with the help of special operators. Then the database of repeated captures was implemented into the MapInfo environment (see sections 7, 8). This database contained the numbers and characteristics of individuals and the numbers of the capture points. Using the SQL-query the fields of points coordinates related to two consecutive captures of each individual were composed, and then the distance between them was automatically calculated. The average size of the ridge is about 3 m, but in the database, the coordinates of the snake's finding out correspond to those of the ridge center. If the snake is re-caught at different slopes of the same ridge, its displacement will be 0 m; if it is recaptured on different ridges, the displacement will be taken as the distance between the centers of the ridges. Consequently data on the movements of 206 females and 244 males were obtained and processed in different time periods.

One of the analysis variants having a great visibility is as follows (Zimov, 1993). Coordinates of the first capture of a given individual were taken as a datum (0, 0) and those of the second capture were determined as the difference between the coordinates of two concessive catches (X2–X1, Y2–Y1). The mapped points display a picture of the snakes' moving from one standard point. Thus, there is a possibility to perform the analysis of a settlement using graphical operators MapInfo. For that, the circular concentric regions ("buffers") of different radiuses (50, 100, 200 m...) were built. Using them, the number of captured snakes was automatically counted, and the characteristics of snakes caught in one or another radial zone, i.e. those moved one or another distance between concessive captures, were selected from the database. In fact, almost all the data refer to mature animals.

11.1. Total characteristics of movement

The general results of physical activity of the common adder are known. As a free terrestrial hunter, for warm season it can move over a distance of hundreds of meters up to 2–3 km (Table 11.1.1). Pregnancy

seriously hinders free female's movement: fertilized females, as a rule, do not leave the area of 1 m^2 during the whole breeding period (Madsen, 1989). Dry females, males and immature animals migrate freely in search of food and favorable conditions (Saint-Girons et al., 1989).

Table 11.1.1. Limits of variation in displacement distances of adders (m)

Females	Males	M		Period between captures	Source
1–900		50		season	Belova, 1974
1–750				for summer	Belova, 1976
1–3000				2–3 years	Belova, 1984
600–700				for summer	Larionov, 1977
0–100				season	Biella, 1979
		up to 576		for summer	Sokolov, 1981
0–		up to 530		for summer	Ushakov, Pestov,1983
50–500				season	Edelstam, 1989
		< 1 (♀ ad)		season	Madsen, 1989
0–3000				season	Moser, 1989
0–2000				2–3 years	S.-Girons et al., 1989
0–1656	0– 2186	50	100	up to 8 years	Our data

It is shown that in homogeneous environment, where the resources necessary for survival and wintering are spaced more or less evenly, seasonal migration activity is not manifested; in heterogeneous environment (where wintering shelters and feeding areas are rare) migration is well expressed (Viitanen, 1967; Biella, 1978, 1979; Völkl, Biella, 1988; Belova, 1984; Kosov, Bozhansky, 1989; Moser, 1989).

Our data provide a more detailed characterization of adders' moving (Table 11.1.2–11.1.9, Fig. 11.1.1–11.1.5). On their basis, the following picture of the snakes' movement was reconstructed.

On the island of Kizhi the mobility of adders is somewhat less pronounced than it has been described in the literature (less than 3000 m per season; Table 11.1.1), probably, due to the small area of the island. The scatter band of distances between the most separated points of recapture is 1656 m for females and 2186 m for males (Table 11.1.3, 11.1.6, B).

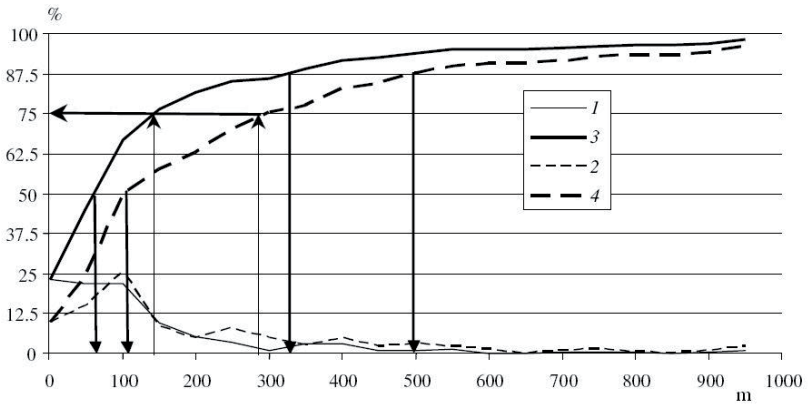


Fig. 11.1.1. Distribution (%) of distances between successive capture of common viper females (*1*) and males (*2*) and cumulatives of frequencies for them (*3, 4*). Bold arrows indicate the distances at which 50 and 88% of males and females crawl away; thin – 75%

Average movement distances for them are also different – 139 and 231 m (Table 11.1.4, 11.1.7). Unfortunately, arithmetic averages are not suitable to characterize the most typical values of those signs, which do not conform to the normal distribution (movement distance is quite the indicator). In this case the best statistical characteristics are the median and median standard deviation (Zhivotovsky, 1991). The median is a value in the middle of an array of numbers; there are 50 % of sample variants both on the left and on the right of it. The main difference of it from the average value is its high invariance; i.e.it is almost independent on the addition or removal of the extreme values. The median describes a reaction of a half of studied individuals to a given factor. In the same way the indicator of the reaction of a greater part of individuals, for example 88 % can be used (Fig. 11.2.1). For this purpose, a graph of accumulated frequencies (cumulate) is constructed using frequency distributions, a normal is dropped from the point where the curve intersects the corresponding ordinate and takes the reading on the x-axis (Korosov, 2007).

Table 11.1.2. Number of repeated captures of adders' females

Marking date		Number of half-year periods from the date of marking																	
year	season	1	3	5	7	8	9	10	11	12	13	14	15	16	17	19	25	26	Total
1991	spr	0	1																1
1992	spr					1	1	2		1		1	1					1	8
1993	spr			4	5	4	5												18
1994	spr		1																1
1994	aut		3	1	1	4	1	1	1		1	2							15
1995	spr	3	11	5	2	2	2	2	1	3	1	1					1		34
1995	aut		5	1	2		1	3					1						13
1996	spr		4	2		4	7	4	2	2			2		1	1			29
1996	aut		1		1	1	1		1			1			2				8
1997	spr			1		1							1						3
1997	aut							1											1
1998	spr		5	1	2	1													9
1998	aut		2	2	3														7
1999	spr		2	2		1													5
2000	spr					2		1	1		2	1							7
2001	spr		2	1			1	2			1								7
2001	aut		2				1												3
2002	aut		1			3													4
2003	spr				2		3												5
2003	aut			1															1
2004	spr		1		3	1													5
2005	spr			3	1														4
2005	aut																		0
2006	spr	15	3																18
2007	spr																		0
Total		18	44	24	22	25	23	16	6	6	5	6	5		3	1	1	1	206

The median of the distance from the place of marking (Fig. 11.1.1, Table 11.1.8) amounted 57.4 for females and 106.4 m for males. This estimate is two times smaller than the arithmetical average (139 and 231 m). But it has a more apparent interpretation. Regardless of the time elapsed from the moment of release, half of females was found no farther than 57 m from that point, and half of males – no farther than 106 m. The maximum movement distance of 88% of females and males amounted to about 330 and 505 m (Fig. 1.1.1); females are almost two times less mobile than males.

The minimum movement distance between the captures after a different number of half-year periods equals to 0 m (animals were caught at

the same ridge both times), but while the observation number reduces to 5–10 per half year, D_{min} increases. This is a purely statistical effect: the sample number is not sufficient for the manifestation of a full natural range of variability, including minimum values. Average (and median) distances between the points of consecutive captures of snakes vary, but remain more or less constant (Fig. 11.1.3), especially for the first 3–4 years, when 20–60 observations were carried out. It would seem that over the time snakes have to crawl in all directions (and the average distance between captures has to increase), but it does not happen.

Table 11.1.3. Minimum (A) and maximum (B) movement distances of adder females between captures

Marking date		Number of half-year periods from the date of marking																**A**
year	sea-son	1	3	5	7	8	9	10	11	12	13	14	15	17	19	25	26	Min.
1991	spr	0	117															0
1992	spr					378	0	47		47		0	171				91	0
1993	spr			0	0	0	0											0
1994	spr		122															122
1994	aut		39	20	74	0	56	395	18		23	80						0
1995	spr	0	0	0	9	0	19	44	0	17	34	17				142		0
1995	aut		26	16	51		0	0					392					0
1996	spr		33	0		21	0	0	0	80			123	95	33			0
1996	aut		107		66	64	8		8			70		46				8
1997	spr			22		215							95					95
1997	aut							415										415
1998	spr		30	19	57	275												19
1998	aut		17	0	0													0
1999	spr		34	0		42												0
2000	spr					113		162	0		44	50						0
2001	spr		0	0			53	0			12							0
2001	aut		0				20											0
2002	aut		55			0												0
2003	spr				54		13											54
2003	aut			73														730
2004	spr		53		85	14												14
2005	spr			68	183													68
2005	aut																	
2006	spr	0	0															0
2007	spr																	
Minimum		0	0	0	0	0	0	0	0	17	23	0	95	4	33	142	91	0

Marking date		Number of half-year periods from the date of marking																**B**
year	sea-son	1	3	5	7	8	9	10	11	12	13	14	15	17	19	25	26	Max
1991	spr	0	117															117
1992	spr					37	0	97		47		0	17				91	378
1993	spr			46	103	42	10											103
1994	spr		122															122
1994	aut		369	208	74	83	56	39	18		23	12						395
1995	spr	21	657	932	45	40	87	79	0	55	34	17				142		932
1995	aut		536	168	464		0	53					39					536
1996	spr		108	162		86	30	90	12	82			17	95	33			108
1996	aut		107		66	64	8		8			70		96				107
1997	spr			229		21							95					229
1997	aut							41										415
1998	spr		373	19	138	27												373
1998	aut		64	1279	324													127
1999	spr		58	92		42												92
2000	spr					11		16	0		18	50						500
2001	spr		295	0			53	34			12							295
2001	aut		52				20											204
2002	aut		55			71												71
2003	spr				154		30											307
2003	aut			730														730
2004	spr		53		322	14												322
2005	spr			195	183													195
2005	aut																	
2006	spr	13	165															165
2007	spr																	
Maximum		21	165	1279	103	86	30	90	12	82	18	50	39	96	33	14	91	165

There are two obvious reasons – a small size of the island of Kizhi and a species stereotype. Striking the water barrier on the way of their individual migrations, adders change their direction, scattering stochastically in a confined space, and may return to the point of their first capture a lot of times. On the other hand, some snakes behave as inactive animals, limiting the area of their life space to about 1 ha (100 x 100 m). (Items of available individual area in adders and proportions of mobile and sedentary individuals are described in section 11.3.)

Table 11.1.4. Average movement distances of adder females between capture

Marking date		Number of half-year periods from the date of marking																Median
year	sea-son	1	3	5	7	8	9	10	11	12	13	14	15	17	19	25	26	
1991	spr	0	117															58
1992	spr					378	0	72		47		0	171				91	72
1993	spr			17	252	134	42											88
1994	spr		122															122
1994	aut		161	208	74	28	56	395	18		23	103						74
1995	spr	73	191	197	27	20	53	418	0	30	34	17				142		43
1995	aut		223	168	257		0	227					392					225
1996	spr		341	81		255	82	242	62	81			149	95	337			122
1996	aut		107		66	64	8		8			70		71				66
1997	spr			229		215							95					215
1997	aut							415										415
1998	spr		175	19	98	275												136
1998	aut		41	639	134													134
1999	spr		46	46		42												46
2000	spr					113		162	0		116	500						116
2001	spr		147	0			53	17			120							53
2001	aut		26				204											115
2002	aut		55			35												45
2003	spr				104		190											147
2003	aut			730														730
2004	spr		53		175	14												53
2005	spr			125	183													154
2005	aut																	
2006	spr	16	552															284
2007	spr																	30
Median		25	195	180	158	121	77	227	25	50	82	132	191	79	337	142	91	139

The maximum estimates of movement between catches, on the contrary, clearly reduce with time, both in females and males (Fig. 11.1.2, 11.1.4, 11.1.5, Table 11.1.4, 11.1.6, B). In other words, in a few years after marking snakes can be found in the immediate vicinity of the place of their first capture. If only two of the above-mentioned mechanism functioned (spatial redistribution and coincidence to “home”), the maximum estimates would remain almost the same all the time, but it is not the case.

Table 11.1.5. Number of repeated captures of adders' males

Marking date		Number of half-year periods from the date of marking													
year	season	1	3	5	7	8	9	10	11	12	13	14	15	16	Total
1991	spr	0			1										1
1992	spr		2		1	2				1					8
1993	spr				3	1				1					18
1994	spr		2	5	1	1	2	3		2	1				1
1994	aut	1	4	5	2	2	5	1	3	1					15
1995	spr	2	7		3	4		2	1				1	2	34
1995	aut		2	2	5		3		1		1		2		13
1996	spr			5		5	2	1	1						29
1996	aut		6	2	4		1					1			8
1997	spr	4	3	27	3	7	2						1		3
1997	aut		4	1	1										1
1998	spr	3	2	3	1	2	1	1	1		1			1	9
1998	aut		1		1										7
1999	spr		1	2						1					5
2000	spr	2	2	1	1	1	1	1	1						7
2001	spr		1	1	3		1								7
2001	aut	1	4	2	1				1						3
2002	aut		3		1	1		1							4
2003	spr	2	2				2								5
2003	aut														1
2004	spr				1										5
2005	spr	1	1	3	1										4
2005	aut														0
2006	spr	1	3												18
2007	spr	2													0
Total		18	18	44	24	22	25	23	16	6	6	5	6	5	244

Table 11.1.6. Movement distances (Min. – **A**, Max. – **B**) of adders' males

Marking date		Number of half-year periods from the date of marking													**A**
year	season	1	3	5	7	8	9	10	11	12	13	14	15	16	Min
1991	spr	0			271										0
1992	spr		314		53	47				0					0
1993	spr				62	429				38					38
1994	spr		79	75	286	481	46	94		96	1010				46
1994	aut	912	14	12	53	75	0	75	30	32					0
1995	spr	31	95		75	37		145	141				432	375	31
1995	aut		34	36	38		49		355		62		259		34
1996	spr			22		33	940	0	197						0
1996	aut		46	0	60		65					83			0
1997	spr	0	62	0	0	0	0						194		0
1997	aut		64	62	62										62
1998	spr	118	16	41	117	73	363	42	233		228			78	16
1998	aut		75		708										75
1999	spr		90	217						714					90
2000	spr	30	0	383	0	403	403	97	776						0
2001	spr		100	316	85		97								85
2001	aut	2186	0	23	23				58						0
2002	aut		73		270	106		120							73
2003	spr	201	0				90								0
2003	aut														0
2004	spr				157										157
2005	spr	0	542	162	398										0
2005	aut														0
2006	spr	54	0												0
2007	spr	0													0
Minimum		0	0	0	0	0	0	0	30	0	62	83	194	78	0

Marking date		Number of half-year periods from the date of marking													**B**
year	season	1	3	5	7	8	9	10	11	12	13	14	15	16	Max
1991	spr	0			271										271
1992	spr		1390		53	89				0					1390
1993	spr				961	429				38					961
1994	spr		1003	282	286	481	536	123		128	1010				1010
1994	aut	912	465	171	245	83	1113	75	898	32					1113
1995	spr	354	310		127	575		928	141				432	432	928
1995	aut		243	64	247		1298		355		62		282		1298
1996	spr			1339		878	940	0	197						1339
1996	aut		537	89	1258		65					83			1258
1997	spr	97	238	526	942	675	30						194		942

Marking date		Number of half-year periods from the date of marking													**B**
year	season	1	3	5	7	8	9	10	11	12	13	14	15	16	Max
1997	aut		578	62	62										578
1998	spr	526	79	218	117	77	363	42	233		228			78	526
1998	aut		75		708										708
1999	spr		90	678						714					714
2000	spr	79	75	383	0	403	403	97	776						776
2001	spr		100	316	325		97								325
2001	aut	2186	341	260	23				58						2186
2002	aut		169		270	106		120							270
2003	spr														
2003	aut	559				714									714
2004	spr				157										157
2005	spr	0	542	383	398										542
2005	aut														
2006	spr	54	148												148
2007	spr	61													61
Maximum		2186	1390	1339	1258	878	1298	928	898	714	1010	83	432	432	2186

It seems that in time snakes creep up to the place of their first marking, but this assumption has not any meaningful explanations yet. Another point is more likely – the gradual extinction of snakes, tending to continuous moving (or having the largest individual areas). Only the most "settled" adders remain.

The important reasons for the increased death rate of snakes on the island of Kizhi are known, they are transportation and people mostly on the roads. This hypothesis is supported by the results of the comparison of mobility and mortality in females and males. In adult females, the average annual mortality is almost two times lower in comparison with males (see sections 7 and 8), whereas the median distance between two captures is almost two times shorter (57 vs. 106 m), and maximum time between two captures is two times longer in females (30 vs. 16 half years, Fig. 11.1.5). Because of their greater mobility, males crawl longer distances than females, and therefore more often fall under the wheels of cars or are exposed to other hazards, and as a result they do not live long. At the same time, the groups of males and females are also heterogeneous.

Table 11.1.7. Average movement distances of adders males

Marking date		Number of half-year periods from the date of marking													Median
year	season	1	3	5	7	8	9	10	11	12	13	14	15	16	
1991	spr	0			271										136
1992	spr		852		53	68				0					61
1993	spr				417	429				38					417
1994	spr		541	192	286	481	291	108		112	1010				289
1994	aut	912	232	81	149	79	281	75	330	32					149
1995	spr	192	225		97	184		536	141				432	403	209
1995	aut		138	50	148		489		355		62		271		148
1996	spr			459		292	940	0	197						292
1996	aut		276	44	496		65					83			83
1997	spr	41	121	111	325	233	15						194		121
1997	aut		235	62	62										62
1998	spr	278	47	111	117	75	363	42	233		228			78	114
1998	aut		75		708										391
1999	spr		90	448						714					448
2000	spr	55	37	383	0	403	403	97	776						240
2001	spr		100	316	182		97								141
2001	aut	2186	107	141	23				58						107
2002	aut		118		270	106		120							119
2003	spr	237	280				402								280
2003	aut														
2004	spr				157										157
2005	spr	0	542	301	398										350
2005	aut														
2006	spr	54	74												63
2007	spr	30													30
Median		273	221	170	248	219	355	173	306	168	433	83	292	295	231

Table 11.1.8. Statistical estimation of adders' movement for different time periods

Sex	Period	Me	S_{Me}	m	Me – 2m	Me + 2m	n
Females	spring	0	8	2	0	17	18
	spring-autumn	117	17	4	82	151	23
	autumn-spring	86	15	4	55	116	12
	1 year	55	11	2	32	77	23
	1.5 year	45	11	3	23	67	14
	2 years	83	10	2	63	103	27
	2.5 years	48	7	1	34	62	22
	3 years	109	21	4	67	150	24
	3.5 years	18	8	4	2	34	5
	4 years	47	14	4	19	75	11
	4.5 years	15	5	4	5	25	2
	5–7 years	82	10	2	61	102	19
	8–12 years	95	18	7	59	130	7
	According to all data	**57**	4	0	**50**	**65**	207
Males	spring	61	14	3	33	88	17
	spring-autumn	188	26	6	137	240	18
	autumn-spring	127	19	4	88	165	20
	1 year	79	10	1	59	98	65
	1.5 year	169	22	4	125	213	24
	2 years	136	18	3	99	173	31
	2.5 years	119	23	5	72	165	18
	3 years	92	9	2	74	110	18
	3.5 years	248	50	18	148	348	8
	4 years	97	14	6	69	125	5
	4.5 years	50	5	2	40	60	4
	more than 5 years	246	44	12	157	334	14
	According to all data	**106**	6	0	**95**	**118**	244

Table 11.1.9. Statistical characteristic of females' mobility

	Dry (U < 0.5)			Pregnant (U > 0.5)		
	(definitely without eggs)	all	all without Max.	one season	one season	one season, without Max
M	303	159	119	311	184	135
Me ± m	79	94±45	89±25	247	75	65
Min.	0	0	0	92	0	0
Max.	1656	1656	793	657	1080	464
n	9	42	42	4	19	18

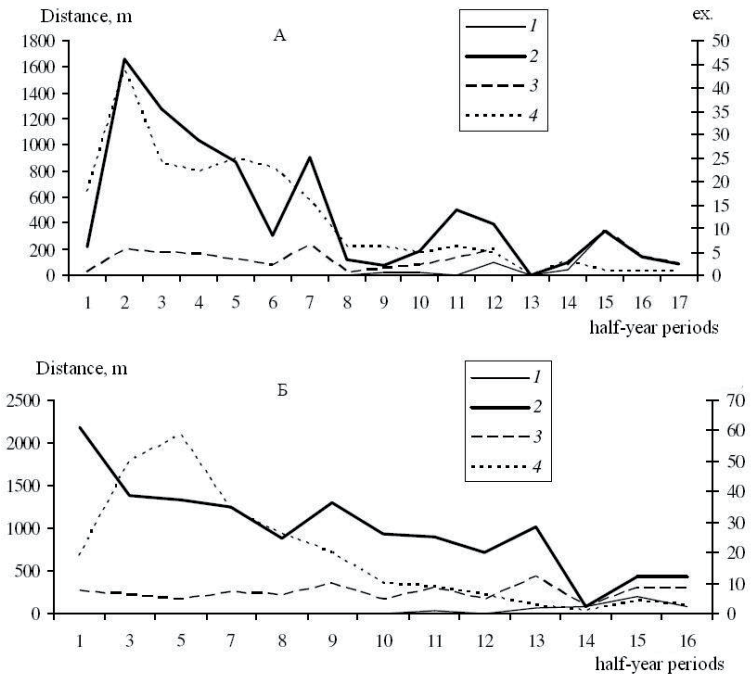


Fig. 11.1.2. Distances between points of two successive catches of viper females (А) and males (Б) after different number of half-year periods: *1* – minimum *2* – maximum *3* – average, *4* – number of observations

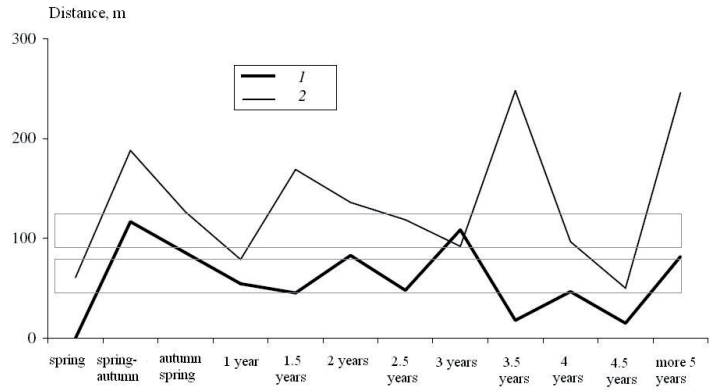


Fig. 11.1.3. The median distance between two successive catches of viper females (*1*) and males (*2*) through different time periods. Bands displayed the confidence intervals around the overall median (based on Table. 11.1.4)

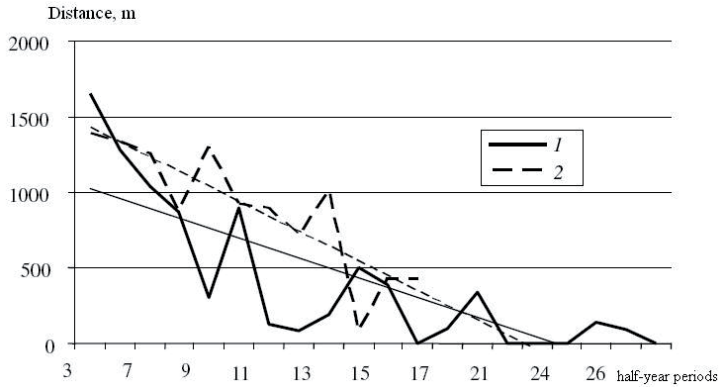


Fig. 11.1.4. Trends of reduction of the greatest distance between the points of two successive catches of males and females after different number of half-year periods (the maximum values, see Fig. 11.1.2)

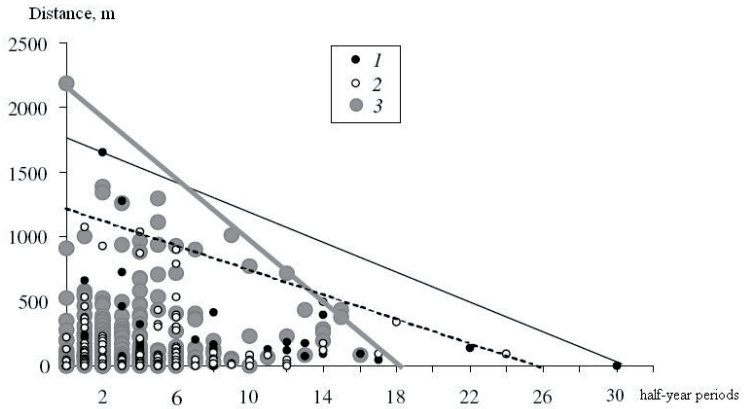


Fig. 11.1.5. . Envelope lines for the greatest distances between the points of two successive catches of viper females (*1* – all females, *2* – only pregnant females) and males (*3*) after the different number of half-year periods (all data)

11.2. Individual mobility

Among females and males there are individuals with different moving tendency. Within one warm season adult females carry eggs and eat very little (see sections 4, 5.4, 9), but in one or two following seasons they actively move and hunt restoring their mass. In the food-constrained conditions on the island of Kizhi reproduction takes place more often once in two years. The question is to what extent the status of a female affects its behavior. From a methodological point of view it is hard enough to distinguish living pregnant females from dry ones. In the spring mature eggs have a liquid consistency and almost could not be palpated, in the fall the developed embryos are well-palpable, however, we rarely used this technique because of the hazard of intra-cavity injuries of the marked individuals.

Using sparse data and discriminatory analysis it was established that the fatness of pregnant females (U = W / L. t. 2.5) usually (in 82% of cases) is greater than the value U = 0.5, and that of dry females is less. Using this

criterion, the movement distances of pregnant and dry females during one warm season were selected as well as those of non-pregnant females for 2 years preceding pregnancy. It turned out that during the periods of pregnancy and fattening, the behavior of snakes is almost the same. Judging by the median, pregnant females are less mobile (Me = 65 m) than dry ones (Me = 89 m), but these differences do not overrun the confidence interval (table 11.2.1). It is important to note that when using different selection criteria, the median distances are always lower for pregnant females.

Table 11.2.1. Statistical characteristics of adder females' mobility

	Dry (U < 0.5)			Pregnant (U > 0.5)		
	(without eggs)	all	all exept Max.	one season	one season	one season, without Max
M	303	159	119	311	184	135
Me ± m	79±203	94±45	**89±25**	247±136	75±28	**65±15**
Min.	0	0	0	92	0	0
Max.	1656	1656	793	657	1080	464
n	9	42	41	4	19	18

The reason for the vague differences is, apparently, that females of different status physiologically are very similar. So, by the end of fattening period dry females gain a lot of weight, in the womb large eggs develop. In the first half of next summer, these females with eggs, which develop normally, and fertilized in the spring, do not change their behavior – they move, hunt and digest food as well as dry females. Only in the second half of summer, when the embryos reach a certain stage of development, the females almost stop feeding and become inactive. However, our method of animals' registration twice a year cannot reflect this detailed dynamics and finds out only the traces of gradual shifting of the pregnant females from the active way of life (hunting) to passive one (only basking). Median estimates (65 and 89 m) presented in Table 11.2.1 are significantly higher than those obtained for all females (57 m, Table 11.1.8). The reason is that

these data were selected according to the criteria of recapturing animals in the same year or 1–2 years after marking. As it seen from our data (Fig. 11.1.2), in this period a lot of animals moving long distances are caught, and median values are large. In the years following marking the proportion of adders, which do not move long distances and return to their former shelters increases; therefore, the general median distance between the catches becomes lower.

Besides the physiological aspect, a question of a genetic basis for moving appears: whether it is possible to distinguish both more and less mobile females in the population? The data of three consecutive captures of marked snakes will help to answer this question (Fig. 11.2.1).

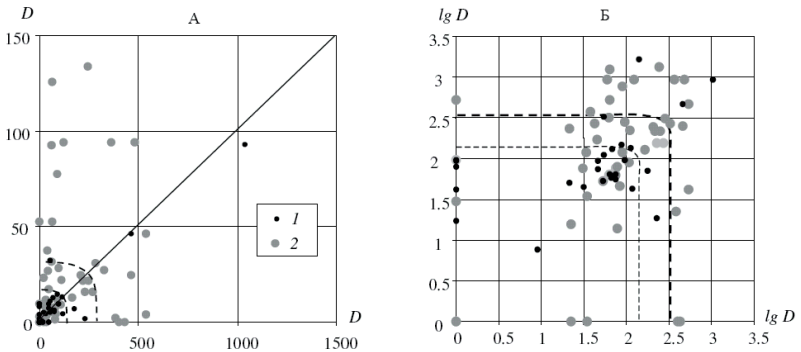


Fig. 11.2.1. Relation of distances (D, m) between the first and second catches (horizontal axis) to distances between the second and third catches (ordinate axis) of female (1) and male (2) vipers in the normal (А) and logarithmic (Б) scales. Dotted line marks area of points accumulation for females (lg 2.2 ≈ 158 m) and males (lg 2.5 ≈ 316 m)

It can be assumed that "fidgety" individuals will move different distances (including long ones) after each capture and their corresponding points will be widely scattered over the chart field. More "settled" snakes will form a relatively dense cluster of points near the coordinate origin (0, 0). For females, this boundary turned out more or less distinct and equals to

about 150 m. Using Fig. 11.1.1, it is easy to define that about 75% of all marked females are within this radius. The remaining 25 % are different in their behavior and throughout their life they move very long distances. To present detail description, the number of snakes, which occur within the increased radius zones around the release point, was calculated by means of cartographic technique. From the computational results a smooth simulation approximation was constructed (Fig. 11.2.2, 11.2.3). Similar constructs were performed for all years after the first animals marking (Fig. 11.2.4). It turned out that during the entire period of their life the proportion of females, exploring different by its size living space, varies but remains almost constant (Fig. 11.2.4 A): in the area of 50 m, about 45% of the marked females were found repeatedly, in the area of 100 m – 67, 200 m – 82, 500 m – 94, up to 1000 m – 98 %.

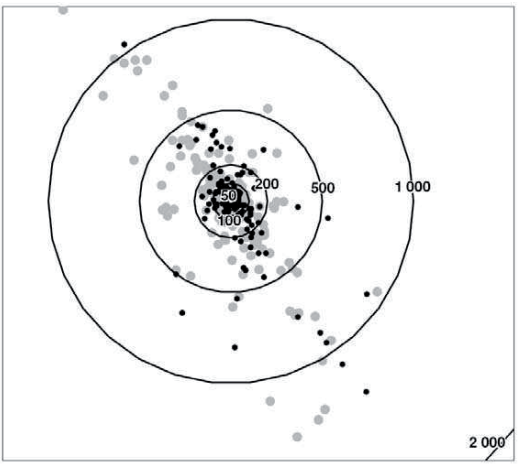


Fig. 11.2.2. Distribution of viper recapture points around the relative central point of the first capture within six concentric zones with radius of 50, 100, 200, 500, 1000 and 2000 m

Adult males are more diverse in their moving tendency than females. In the diagram, where the distances between two points of recapture are compared, the densest cluster is formed by the males, which do not leave

the zone with a radius of about 320 m ≈ log D = 2.5 (Fig. 11.2.1 A and B). The fact is pointed that the radius obtained for males is twice as large as that for females. Using Fig. 11.1.1 or 11.2.1, we find that the proportion of males in the 320 m-radius zone is about 75 % of the total observation number. The remaining quarter of males (the same proportion as in females!) is more adhere to long journeys than the most snakes. The ratio between "settled" males and "migrants" remains quite constant for 4 years of observation after marking: in the area of 50 m about 24% of the tagged males are re-found, in the area of 100 m – 47, 200 m – 62, 500 m – 88, up to 1000 m – up to 97 %. In the fifth year the proportion of less mobile species increases, probably, due to the death of "mobile fraction" (Fig. 11.2.4 B).

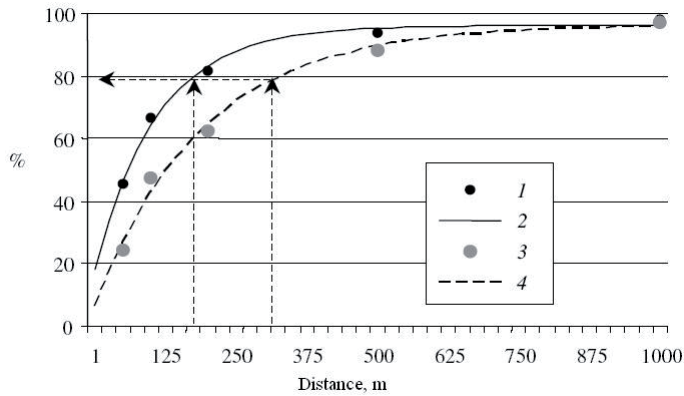


Fig. 11.2.3. Proportion of vipers (%) crawled from the place of the first capture no more than 50, 100, 200, 500 and 1000 m, calculated from Fig. 7.11 (*1, 3*) and approximated model for all years of observations (*2, 4*). The arrows indicate the proportion of females (*1, 2*) and males (*3, 4*), falling in Zone 160 and 320 m

Underneath these proportions (75% and 25%) is some undefined regularity, a general law of the behavior of random variables, which is realized in different way for two heterogeneous samples (individuals of both sexes) that have general parameters distinct from each other. For its

approximate description, one can use the simulation equations obtained by us. They show what proportion of adders (p_{i+1}, %) will be in the next (i +1) circular area of the radius increased by 25 m ($R_{i+1} = R_i + 25$) compared to the previous (i) area of the radius R_i: $p_{i+1} = p_i \cdot a + b$.

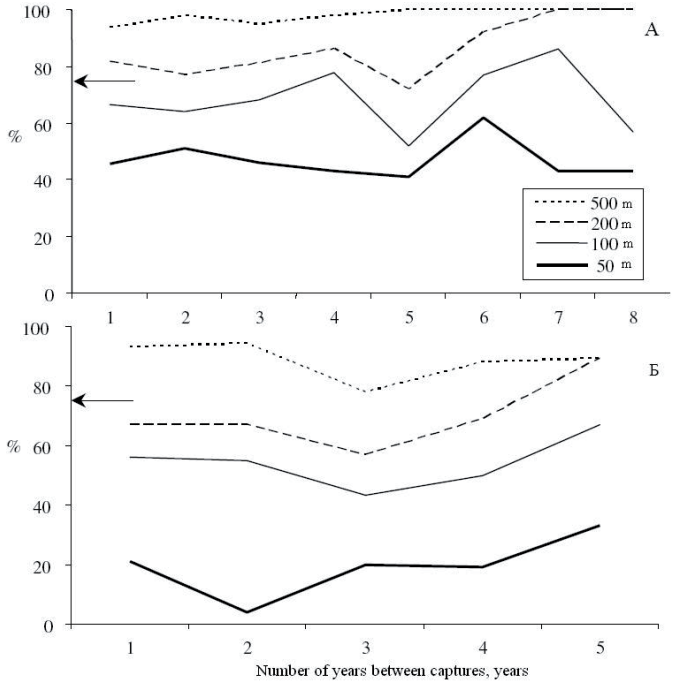


Fig. 11.2.4. Proportion (%) of viper females (А) and males (Б) found in the zone of specified radius after a different number of years. The arrows indicate the zone, covering 75% of the movement of females (160 m) and males (320 m)

Beginning with the area of 1 m radius, where $p_1 = 18.3$ % of individuals were found, the equation for females was: $p_{i+1} = p_i \cdot 0.79 + 19.3$. For males, starting with $R_1 = 1$ m and $p_1 = 6.5$ %, we obtained: $p_{i+1} = p_i \cdot 0.88 + 11.6$.

All these parameters (p_1, a, b) were obtained from the real calculations with the help of simulation technology (Korosov, 2002a); they have a clear meaning. In the first zone (0–1 m) there are more females than males (18.3

and 6.5 %). When the radius is increased by 25 m (zone of 1–25 m), the proportion of females will be: $p_{f2} = p_1 \cdot 0.79 + 19.3 = 18.3 \cdot 0.79 + 19.3 = 34$, that of males: $p_{m2} = 6.5 \cdot 0.88 + 11.6 = 17$ %. The parameter b indicates the growth rate of the proportion of the individuals; it is higher in females than in males (19.3 vs 11.6). The parameter a shows a reduction in the growth rate, it is lower in females than in males (0.79 vs. 0.88). This is natural, because both curves approach the same maximum value, 100 %; but the curve for females is more curved.

11.3. Death on the roads

The resulting equations enable to calculate the probability of snakes' moving from the places where they were found. It allows calculating the probability for adders to occur in the most dangerous areas of the island of Kizhi. If we know the coordinates of adders' capture points and the location of roads, where a lot of these animals were killed, we can calculate the probability of snakes having different mobility to die under the car wheels. This problem was solved by plotting the circular buffer zones of different diameter around all snakes' habitats (about 1000 ridges on Kizhi). Then, using geographic criteria of MapInfo environment, it was determined how many times the zone was crossed by the road. In fact, it was the assessment of risk for those snakes that dwell in this habitat and have a given radius of individual activity to be run over by a car. Naturally, that the zones of a small radius are crossed by roads less frequently than those of large radius (Fig. 11.3.1). It turned out that areas of 25 m radius are crossed by roads 10 times less than those of R = 500 m (Fig. 11.3.2).

Using a cartographical technology, it is possible to calculate the number (and proportion) of inhabited ridges, where adders crawl different distances and can get on the road, including the main busy road on Kizhi (Fig. 11.3.3).

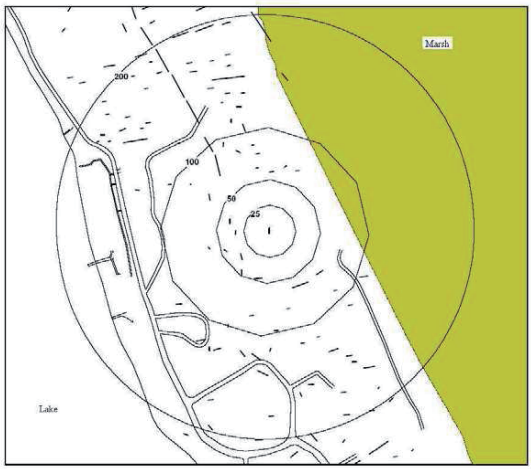


Fig. 11.3.1. Four separate zones around vipers habitats

These facts can be interpreted as a probability of an individual to get under the wheels. We have no data how often a snake visits different places of its limited areal; by convention the estimates of the probability of death on the road can be related to 2–3 seasons. There are good grounds for that. If the total number of males is near 500–1000 ind. and their specific mortality is 46%, there should be about 200–400 ind. perished per year. The route accounts of dead adders on the roads gave half as high estimates of the annual death – 100–200 ind. This may mean that half of the males had no time to explore their whole habitats, and they could crawl to the road next year. As is seen in Fig. 11.3.3, if their average movement radius D = 60 m, the females may die under the wheels with a probability of 27 %, and in males (D = 106 m) this probability is 45 % that is almost two fold. Since the estimates of the specific mortality of females is almost 2 times less than that of males (0.26 vs 0.38), we may conclude that these differences are mainly caused by the high mobility of males, affected by the eliminative anthropogenic factor (roads with transport) more often.

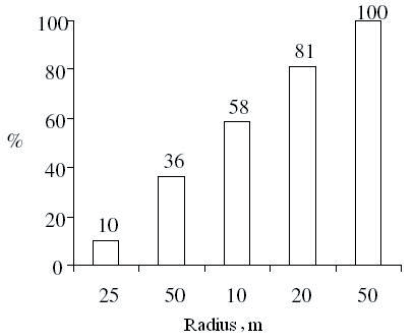


Fig. 11.3.2. Relative frequency of crossing of roads and zones of different diameter, constructed around vipers habitat

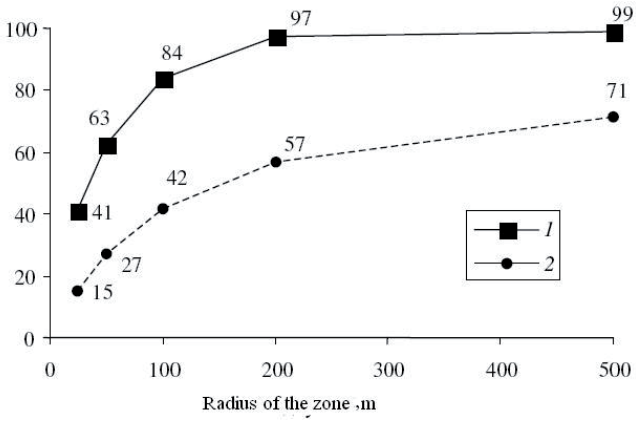


Fig. 11.3.3. Probability (p, %) for the vipers with a different radius of individual activity to cross the road at isl. Kizhi: 1 – any road, 2 – paved roads with active traffic

Our data prove that on the island of Kizhi adders move quite freely all over the island in all directions, although there are three restrictions. The island lies 5.6 km from North-Northwest to South-Southeast; its maximum width is 700 m, hence, the most adders move in these directions. The increased number of people and vehicles on the roads of Kizhi in recent years leads to a rise in accidental deaths of snakes and decrease in their population.

Chapter 12.

Distribution

Water borders give certain distinctness to the movement of adders on the island. They are forced to explore a small area, where they can repeatedly return to various habitats that are both favorable and hazardous for them. In this regard, it is possible to formulate a number of research questions:

– what is the nature of adders' distribution on the island (uniform, random, aggregated);

– what are the factors of the spatial distribution of adders, including the most significant;

– if the mortality of animals depends on their spatial distribution.

Material and methods

The points of animals' captures in the field were mapped, after that they were transferred to a MapInfo electronic map, and their coordinates – into the database. Assessment of adders' environment was carried out in two ways – as a characteristic of shelters (stone ridges), and as a characteristic of the surrounding landscape. On the island of Kizhi we have quantitatively described 896 ridges: numerical or volumetric estimates were given to 33 rating factors: exposure, slope angle, exposure to wind, length, width, height, profile, ridge shape, prevailing stone sizes; incidence of lichens, mosses, 11 species of dominant herbaceous plants, 4 wood species; hay-mowing, southward opacity, type of biotope within 30 m radius (description was presented by S. N. Fomichev).

Using GIS-technology (Korosov A.V., Korosov A.A., 2006), various territorial allotments were plotted, which characterize different adders' habitats on the island of Kizhi and other islands of the Kizhi archipelago, including the mapping of old-arable allotments.

To compile vector maps of the allotments of main habitats on Kizhi, the field survey (1994–1998) was carried out, and aero photographs taken in 1969 and 2004 were decoded. Besides, the whole territory of Kizhi was divided into 4 zones encircling swamps by bands of 0–50 m (zone 1), 50–100 m (zone 2), 100–200 m (zone 3) and wider 200 m (zone 4). The map of altitudinal belts was also plotted with 5 m step size. The similar analysis was carried out on 18 islands of the Kizhi archipelago (2004–2006), as a result, the maps of their biotopical allotments were received. They served as a basis to form samples characterizing the occurrence of adders on various areas of Kizhi and other islands of the Kizhi archipelago.

12.1. Adders' habitats on Kizhi

The modern landscape of the island of Kizhi is a result of human activity. For centuries before 1964 crops (rye, oats) were grown on the greater part of Kizhi. The amalgamation of the collective farms in the early 1960s changed the way of land use, as a result, arable lands turned into grasslands, which were gradually overgrown with small-leaved young stand (Fig. 12.1.1, Table 12.1.1). Clearing the soil on the moraine, farmers put stones in piles ("rovnitsy", localism) and built real boundary fences ("zabor'ya", localism) around the allotments and along the roads (Fig. 12.1.2 A). These stone ridges have become good shelters for adders (Korosov, 1996).

The observed decline in the number of adders' population has two distinct causes. With the changes in the economic system of Russia since 1994 agricultural exploitation of the territory of Kizhi virtually has stopped. Hay-making has brought to a stop, and the area of hay meadows (optimal habitat for vipers) is declining rapidly. While before 1969 they occupied 63 % of the whole territory of the island, now they are forced out by the undergrowth and have reduced up to 49 % (2004) (Table 12.1.1).

The wet areas near bogs are overgrown more rapidly: these are places with abundant food reserve for adders (frogs). Alongside with the degradation of the cultural landscape, the tourist industry is developing,

and restoration works of the Museum complex "Kizhi" are constantly expanding. The Museum staff and the number of tourists visiting the island increases, the number of vehicles and the intensity of their movement on many roads rises, stone ridges (snakes' shelters) are disassembled for housing foundations. All this leads to the direct death of animals (in 2003 in the autumn builders accidentally dug up the "ball" of the 60 adders left for wintering by an excavator and then specially destroyed it). At present on Kizhi the following habitats can be distinguished: Museum space, meadows, "rovnitsy", field woodlands, forests, swamps, ponds, housing and industrial areas.

Table 12.1.1. Area of the biotopes on the island of Kizhi and the proportion of captured adders

	Area, %		Proportion of adders in accounts, %		
Biotope	1970	2004	1991–1995	1996–2000	2001–2006
Museum sp.	7	6	0	0	0
Meadow	63	49	55	75	77
Field wood.	5	7	9	6	3
Forest	4	12	30	13	15
Swamp	17	16	0.0	0.6	2
Ponds	1	1	0	0	0
Housing	2	7	0.3	0.5	0.4
Divestiture	0.4	1	5	5	2
Total	204 ha		1159 ind.	1564 ind.	1838 ind.

The allotments listed above divide the territory of the island (total area of 204 hectares) in proportion 6, 49, 1, 7, 12, 16, 1, 7, 1 %. Roads and trails with a total length of 18 km and an area of 6.8 hectares pass over meadows, with the most busy roads being 6 km in length and 3 ha in area (Fig. 12.1.2 A). On the island of Kizhi, the common adder finds the most important components for its normal life: open spaces with numerous shelters, vast swamps with food (brown frogs) as well as the constant disturbance and destruction factor – roads and hostile attitude of most tourists and workers (although there is an order of the Director of the Museum-reserve "Kizhi" forbidding categorically to kill snakes).

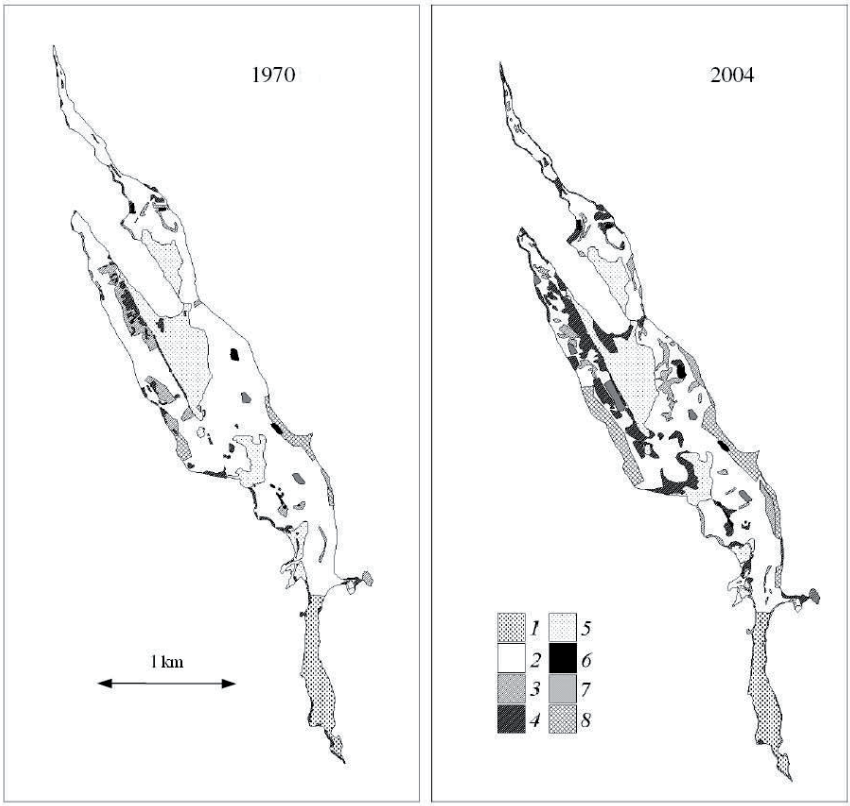


Fig. 12.1.1. Overgrowing of meadows on isl. Kizhi during 35 years: *1* – exhibition of the museum, *2* – meadow, *3* – woods (undergrowth), *4* – deciduous and coniferous forests, *5* – bogs, *6* – karst ponds, *7* – the area of rejection (industrial sites, dumps, cemeteries) *8* – construction (housing)

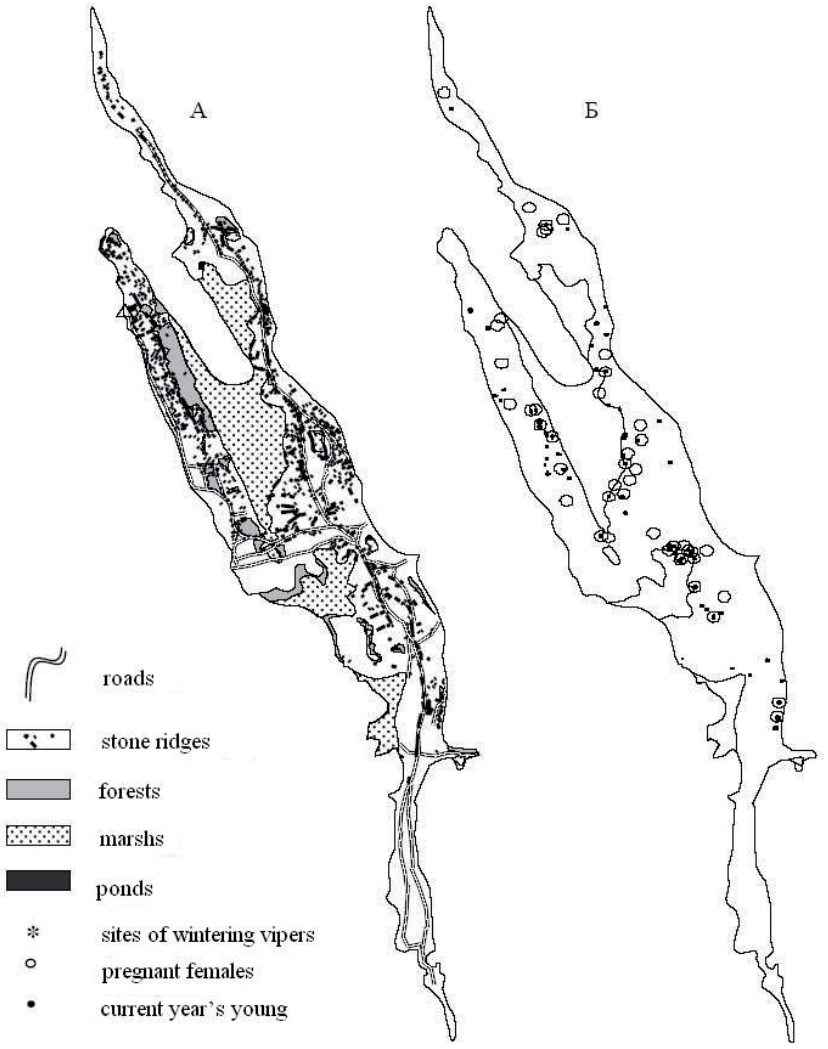


Fig. 12.1.2. Biotopic sites (А, 1996), points of vipers encountering at wintering sites (Б)

To solve the problem the technical basis was used to establish the database, combined with the electronic map of Kizhi, which contained all adders' shelters, places of their capture for all the years of work, habitats, altitudes, and buffer zones around significant objects.

12.2. Allocation of adders on the island of Kizhi

We found the vast majority of snakes either on the stone ridges or in the immediate vicinity of them (1–2 m); these observations are mainly related to the moments of basking or breeding, much less – to migrating adders. Only a few places were hundreds of meters apart from the ridges. At that, the location of stone ridges on the island is determined by the type of soil and the places where farmers threw stones, namely on the high places (moraines). At the edges of swamps and on the lake shores there are a lot of ridges, whereas on bottom and marshy areas ridges are almost absent (Fig. 12.1.2). This enables to make the first conclusion: adders are not uniformly distributed on Kisi and coincide to their shelters.

At once, in the summer adders actively move between shelters; that is daily confirmed by the traces on dusty roads. The second question in this regard – if they give preferences to some ridges – is the question of the uniformity of snakes' distribution over all investigated ridges.

There are three main known types of spatial distribution of individuals (in our case – over shelters): uniform (regular), aggregated (group) and random (Gilyarov, 1990), and a lot of their variants (Odum, 1975; Yablokov, 1987).

The aggregation of individuals is associated both with the uneven spatial distribution of environmental resources (feeding areas, shelters) (Timofeev-Resovsky et al., 1973), and with behavioral adaptive strategies (reproduction, defense, etc.) (Panov, 1983). The uniformity is ensured by competitive interaction, protection of individual area (Odum, 1975). Random distribution means the lack of both priorities and reasons to avoid certain habitats.

One can distinguish a random location from the others by using chi-square criterion. If a separate plot (in our case – ridge) is considered as a variance, numerically equal to the number of individuals found on it, then in the case of random allocation of snakes the frequency distribution of individuals over all ridges must be in agreement with Poisson's law (Gilyarov, 1990). When the allocation is uniform, we get a strict unimodal distribution, and, when it is apparently aggregated – the bimodality (Ivanter, Korosov, 2003).

To construct the adders distribution over the ridges we used two data stores: first, the total number of snakes found on ridges for all years, second, the average number of snakes found on a ridge at a single visit (each of 1000 ridges was observed from 1 to 30 times, on an average 3–4 times). Then the conformity of the distribution to the empirical Poisson's law was checked (Ivanter, Korosov, 1992).

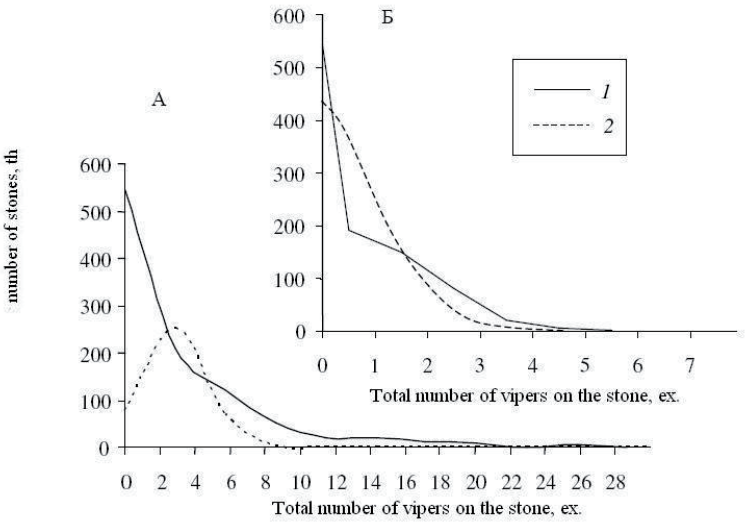


Fig. 12.2.1. The number of stone pile with different total number of snakes encountered during all (А) and during one visit (Б): polygons of empirical: *1* – and theoretical *2* – frequencies corresponding to the Poisson distribution

Our data (Fig. 12.2.1) show that each variant is significantly different from the Poisson's distribution, that is, the allocation of adders over ridges is not random ($p < 0.0001$). The distinction between empirical and theoretical frequencies consists in that really the ridges without snakes and those with aggregations of 2–4 snakes are more common than they should be for accidental reasons (544 vs 433 and 102 vs 50). At the same time, the ridges with a small number of snakes are found much more rarely (192 vs 361). The value of 1.5–2 snakes on a ridge per a single visit is a turning point; the ridges with the number of snakes above this threshold occur more often than the random allocation supposes. There are 144 such ridges. It can be assumed that adders do find some particularly favorable conditions in these places. So, the distribution of snakes over stone ridges is non-random, because there are no snakes at the majority of ridges and there are aggregations of them at a limited number of specific ridges. Hence, the question follows, whether it is connected with a restriction on the freedom of movement (migration) between the ridges or it is determined by the quality of the environment.

Dependence of the snakes' allocation on the quality of shelter.

The study of habitat conditions of adders in the vicinity of their shelters (stone ridges) was performed in three directions: description of the ridge location, description of its abiotic characteristics and that of its floristic environment. The main task was to find the factors responsible for the apparent unevenness of snakes' distribution within the island and over ridges. It would be natural to solve such problems including multiple characteristics of studied objects (ridges) by means of multivariate statistics methods. We applied the method of principal components (Korosov, 1996) and discriminate analysis (Ivanter, Korosov, 1992).

Preliminary correlation analysis showed a complete independence of the snakes' number on all the factors, except the distance to marshes (zone near the swamp), and also showed weak correlations with the exposure of the landscape to wind (wind) and with the density of fireweed and nettle (Table 12.2.1).

Table 12.2.1. Rank correlation between the characteristics of ridges and the total number (N) of snakes found at the ridges as well as the average number of snakes per visit (n)

Factor	n	N	Factor	n	N	Factor	n	N
Biotope	0.05	0.05	Moss	–0	–0.03	Nettle	0.08	0.11
Wind	–0.13	–0.15	Crassula	0.01	0	Rosebay	0.14	0.16
Shadow	–0.01	–0.03	Bilberry	0.09	0.11	Chervil	0.05	0.07
Exposition	0.01	0	Short grasses	0.01	0.02	Raspberry	0.08	0.1
Angle	0.03	0.05	S.John's-wort	0.07	0.08	Willow	0	0.02
Length	0.1	0.11	Strawberry	0.03	0.03	Birch	–0.02	–0.03
Width	0.08	0.08	Horsetail	0.12	0.09	Alder	0.03	0.04
Height	0.04	0.05	Lime grass	0.02	0.06	Rowan-tree	0.02	0.04
Profile	–0.03	–0.02	Herb	–0.04	–0.02	Pine	0.04	0.03
Stones	–0.07	–0.07	Mowing	–0.06	–0.01	Swamp zone	–0.32	–0.34
Soil	–0.01	–0.01	Tall grasses	0.02	0.03	Number, N	0.92	1
Lichens	–0.04	–0.05	Bracken	0.02	0.02	Quantity, n	1	0.92

Negative correlation between the number of snakes and the zone near swamps means that the higher is the zone number (the farther it is from the swamp), the less snakes are found at the ridges. Similarly, the fewer snakes, the more open is the landscape ($r = –0.13$), the more the nettle ($r = 0.08$) and fireweed ($r = 0.14$) in this place.

The component analysis also showed a weak correlation of varying, but allowed concentrating the information on variability by the rejection of unimportant factors (Table 12.2.2). In one variant of the analysis, in addition to the distance from a swamp, the ridge size turned out quite significant (but not decisive) factor, in the other variant it was the openness of the landscape. It is obvious, that the component analysis has not simplified the picture.

In the discriminate analysis the number of snakes on a ridge (n) was selected as a diagnostic sign; ridges with more than 2 snakes formed one group, with $n < 2$ ind. – the other. The number of 2 was chosen, because in this point empirical and theoretical frequencies coincided (Fig. 13.3.2): the amount of ridges with less than 2 snakes was not randomly lower and that with the number above 2 – not randomly higher.

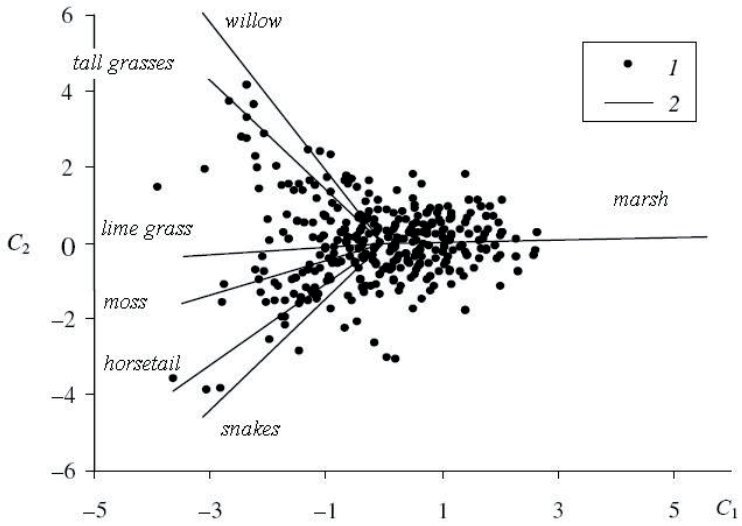


Fig. 12.2.2. Biplot diagram of component analysis of viper habitat conditions: *1* – value of the component (*C*) for separate ridges, *2* – vectors of the accounted factors loads (*U*)

Table 12.2.2. Two variants of decomposition of the original data matrix in the frame of the component analysis of varying factors of the adders' number on ridges

		Component 1	Component 2
Variant 1	Number, n	–0.93	–0.66
	Zone near swamp	1.00	0.50
	Width	–0.65	0.89
	Length	–0.54	1.00
	Dispersion, %	35	27
Variant 2	Number, n	–0.99	0.32
	Zone near swamp	1.00	–0.26
	Wind	0.58	1.00
	Dispersion, %	45	31

The results of the analysis (Table 12.2.3) not only emphasized the already listed factors partially responsible for the changes in the number of adders on ridges, but also helped to calculate their ranks: the coefficient of canonical correlation is equal to r = 0.3. This equation allows predicting correctly the "preferable" ridge only in 2/3 of cases that is not much different from ½, corresponding to complete uncertainty. The other variants of the canonical analysis (the attempt to explore a larger number of groups) do not improve discrimination. The results interpretation is quite clear, because almost all the factors are interrelated. There are more snakes where a swamp is nearer, habitat is more closed, ridges are wider, where there is a less amount of nettle, alder and small grasses but more tall grasses. A lot of such ridges are found on the left edge of the Moss bog in the central part of the island of Kizhi (Fig. 12.1.2).

Table 12.2.3. Standardized coefficients in the equation of ridges' discrimination according to the adders' number

Parameter	Coefficient
Zone near the swamp	0.88
Biotope	0.34
Wind	0.26
Width	–0.24
Nettle	–0.22
Alder	–0.21
Small grasses	–0.31
Tall grasses	0.39
Correlation	0.299
Forecast, %	67
Significance, p	0.00001

The discovered trend becomes evident if we look at the proportion of animals found in different zones around bogs over the years of observation (Fig. 12.2.3).

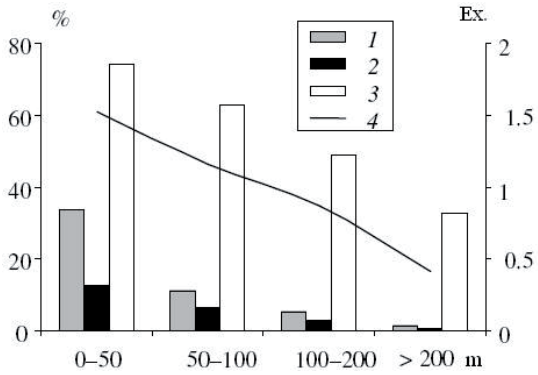


Fig. 12.2.3. Proportion (%) of vipers with different status (*1–3*) encountered in different zones around wetlands and their average number (specimens) on a single ridge (*4*): *1* – pregnant females, *2* – young individuals, *3* – all individuals

The question arises: why marshes are attractive to adders, and we can assume that in their vicinity there are a large number of prey items – frogs. Night accounts of frogs carried out in September in open meadows showed the number 0 ind. / ha, on the fringes of the forest and meadows around marshes (50 m) – 200–430 ind. / ha, on the edge of a sedge marsh – up to 900 ind. / ha (Korosov, Fomichev, 1999).

The analysis also showed that the present character of snakes' distribution around the swamps did not always exist. In recent years, the apparent trend for the concentration of snakes around marshes is emerging (Fig. 12.2.4).

An indirect illustration of the same effect is the distribution of snakes throughout the altitude. The largest proportion of the "populated" ridges is in the vicinity of lowland lakeside marshes (Fig. 12.2.5, 12.2.6).

We see two main reasons for such a situation. First, more and more areas overgrow with small-leaved secondary forest, where habitat conditions (shading) are not favorable for adders. When forest covered a small area (a fraction of hectare), snakes were found both in these clumps of trees and at the periphery. The formation of large fully stocked forest

(several hectares) completely expelled the snakes out of the woods to the meadows (Fig. 12.2.7).

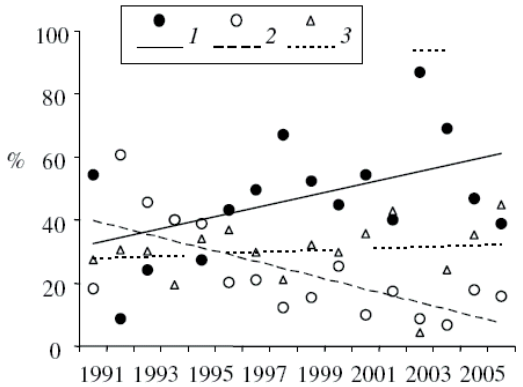


Fig. 12.2.4. Change of the proportion of ridges (%) where viper are encountered: *1* – zone 0–50, *2* – zone of 50–100, *3* – zone of 100–200 m

The second reason of changing the spatial distribution of snakes is the declined total number of these animals on Kizhi. Most of the remaining animals concentrate on edges of marshes, close to the most favorable places with abundant food reserve and better wintering shelters.

Allocation of wintering shelters. On the island of Kizhi adders spend winter in stone ridges. The constantly blowing wind forms very large snow-drift sites all round the ridges. As a result, by the coldest period of the late winter the snow-drifts 10–30 cm higher than ridges are formed around them, with a total height measuring 40–300 cm depending on the size of the ridge.

As a result, surface winter shelters of snakes inside the ridges are well thermally insulated and the temperature there is always positive, since in the south of Karelia the isotherm 0 °C lies in the soil not lower than 1.6 m (Handbook on the climate in the USSR, 1975). These conditions provide successful wintering for the majority of adders in any part of the island, because the ridges are located everywhere on Kizhi. An additional positive feature of setting the wintering shelters is long history of their formation.

The stones, which were placed on the fields' edges along by marshes and lakes in annual plowing and "smoothing" of arable land, formed bold, stony shores 2–3 m high. Such shelters are covered with a rather thick layer of soil. In winter, this layer serves as an additional buffer between the wintering place and outside air.

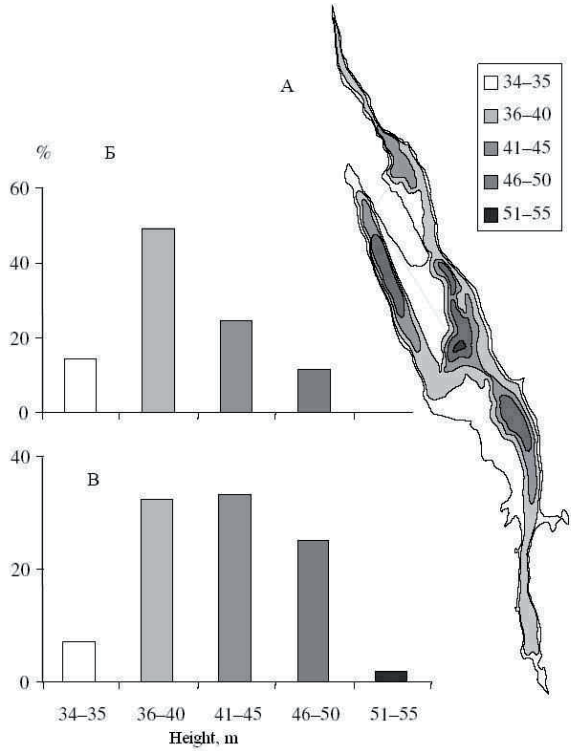


Fig. 12.2.5. Distribution of vipers on heights (34–55 m.a.s.l.) on isl. Kizhi: А – hypsographic map of isl. Kizhi (height given in meters), Б – fraction (%) of the total number of vipers (n), В – fraction of the total abundance (n / S)

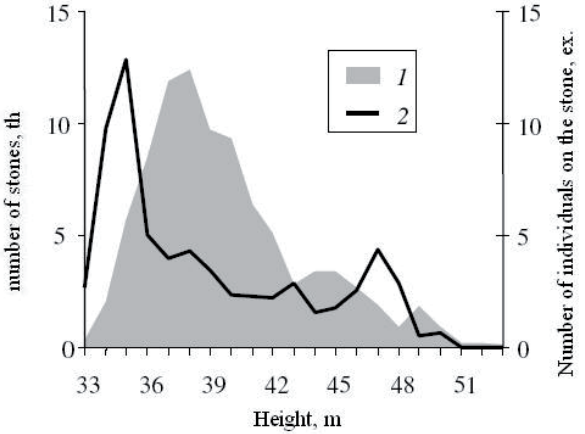


Fig. 12.2.6. Distribution of viper shelters on heights of isl. Kizhi: *1* – number of stone pile at a certain height, *2* – the average number of vipers, met on a ridge

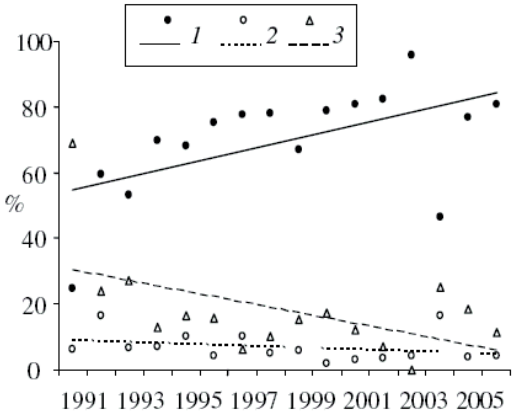


Fig. 12.2.7. . Proportion of vipers (%) found in different habitats: *1* – meadow, *2* – woods (undergrowth), *3* – forest

Due to the variety of suitable wintering shelters, the distribution of adders in autumn (before wintering) and in spring (after wintering) may be quite random, not aggregated; we have not observed either large snakes' aggregations in certain places (near wintering places) or large-scale migrations of animals toward or away from them. In other points of the area the aggregations of snakes in the wintering places can be very large, and the spring and autumn migrations are the most important seasonal events in adders' life (Viitanen, 1967).

However, not all ridges are large enough to prevent freezing of wintering snakes. How do adders choose these particular shelters favorable for wintering? We have no answer to this question. Adders are assumed to crawl to the place of their birth to winter (Völkl, Biella, 1988). In late autumn they are likely to choose those ridges which retain heat accumulated during the daytime longer than the others; hence they are larger and potentially effective as wintering shelters.

Assessment of mortality in current year's young. The revealed trends in the adders' spatial distribution (swamps impact) enable to define what role this phenomenon plays in the mortality of the least studied age group – wintering current year's young. As was shown, the average number of snakes at the ridges and the proportion of ridges, where adders were noted, smoothly diminish when moving from swamps to open grasslands (Fig. 12.2.3). Against this background, the proportion of ridges with pregnant females declines with the same gradient *significantly* ($p < 0.001$) more sharply than in all snakes. Apparently, this indicates the distribution of wintering places: wintering shelters are in those ridges where pregnant females dwell.

When there are abundant shelters, females need not to migrate in search of special basking places, as in the case of shelters shortage (Viitanen, 1967). Besides, a lot of females ready to breed feed in the surrounding bogs immediately after hibernation (see sections 5.3, 5.4), after that they digest food and mate at surrounding ridges. After mating the pregnant females, most likely, do not leave their wintering places and dwell at the same ridges up to the moment of birth of issue. One evidence is that

the habitats of pregnant females and newborn snakes coincide (Fig. 12.1.2 B). This assumption is indirectly confirmed by the changing occurrence of both sex individuals: at the same ridges males can be found before breeding, fertilized females – 2–3 days after spring "lek".

If the assumption of inactive pregnant females is correct, then the ridges, where they are found, are both the wintering places and survival stations for newborn snakes.

The newborns crawl away in different directions from their birth place and concentrate in its vicinity of it (Table 12.2.4). In terms of the indiscriminate migrations of juveniles, their distribution over ranges should be random. When they get to a good shelter (to the ridge with a pregnant female), they successfully survive. When they get to another ridge, they die.

Table 12.2.4. Occurrence of adders around marshes on the island of Kizhi

Proportion of ridges (%) where there were	Zone around mashes, m				Total
	0–50	50–100	100–200	>200	
Pregnant females	34	11	5	1	11
Young (< 3 years)	12	7	3	1	5
Males	63	50	35	22	41
Females	65	46	39	24	42
Snakes of different status	74	63	49	32	53
More than 2 individuals	14	26	18	12	1
Number ind. / at the ridge	1.53	1.16	0.87	0.41	0.96
Number of ridges in the zone	121	199	278	157	755

This logic suggests a way of calculating the newborn number that can survive in winter (Table 12.2.5). Using the proportion of ridges with young animals one can calculate their distribution over zones and their number in each zone. In particular, of 100% of individuals 55% should settle in the first zone; since in the autumn about 1500 newborn females appear in total on the island of Kizhi (see section 4.3), in the zone adjacent to swamps there will be 829 specimens. They settle at 121 ridges of this zone (Table 12.2.4), by the spring only 34 %, or 280 ind. will survive, and

in all zones there will be 264 young females (23% of all newborns) (Table 12.2.5). As our practice shows in captivity about 5% of young adders die from cloacitis, i.e. only 23 – 5 = 18 % of young or 264 individuals (females or males) really survive. The estimate found in the literature (Saint-Girons, 1981) is close to ours – 14.3 %.

Table 12.2.5. Calculation of mortality of current year's females

Indicator	Zone around mashes, m				Total
	0–50	50–100	100–200	>200	
Proportion of wintering places, %	34	11	5	1	
Proportion of ridges with young, %	12	7	3	1	
Distribution of young over zones, %	55	29	13	3	100%
Number of current year's females in zones	829	437	192	43	1500 ind.
Number of current year's females in wintering places	280	49	10	1	339 ind.
Average proportion, % (on average 18%)	34	11	5	1	264 ind.
Error, %	4	1	1	1	
Minimal, %	26	7	3	0	174 ind.
Maximum, %	42	15	8	3	354 ind.

Note that the obtained number practically coincided with that of over-wintered current year's young calculated on the age distribution (see Table 8.5.6, 4.6.5). Taking into account the statistical error of estimating the proportion of wintering shelters in different areas, from 174 to 354 individuals of each sex can survive. In our view, it is crucial that the number of yearlings calculated using different methods and different data sets were the same order. This suggests that the number of the adders' population increases up to certain limits, which are determined by abiotic environmental factors – the deficiency of shelters suitable for juveniles' wintering. At that, the probability of mass death from food deficiency (Völke, 1989) should be rejected as a vast abundance of frogs' young in the island bogs cannot leave the young adders hungry.

12.3. Distribution of adders over the islands

Our researches showed that on a lot of islands of the Kizhi archipelago (Eglov, Volkostrov, Kizhi, Olen'yi, Bukol'nikov, partly Klimetsky) the estimates of adders' occurrence are by two orders higher than on average in south Karelia (6–14 ind. / ha against 0.04 ind. / ha; Korosov, Fomichev, 1999; Korosov, 2005; Korosov, 2009), and approach the density in the center of the area (Pikulilk et al, 1988). The reason is that there's a large number of good summer and winter shelters ("rovnitsy"), the abundance of prey items (2 species of frogs, densely dwelling in lakeside swamps) and vast open meadows. Hence there are three necessary conditions: insolation, wintering, food. Over the last century agricultural industry was decreasing that has led to the degradation of cultural lands. At first, arable lands turned to grasslands, which were overgrown with tall grasses, shrubs and some tree species. These processes intensified in the last decade. Therefore, the conditions for adders are deteriorating significantly (the area of open spaces is reducing, stone ridges are mossing) and the number of the species began to decline steadily. Whereas in the last 15 years the number of adult adders on the island of Kizhi decreased from 3000 to 1000 ind. (see section 8), on other islands the situation is even worse. Whereas at the beginning of the XX century most lands on the islands of the Kizhi archipelago were arable fields, and swamps – hay lands, now they are almost completely covered with secondary undergrowth (Fig. 12.1.1; 12.3.1).

To characterize comprehensively the quality of adders' habitats, the vegetation mapping of the islands with open habitats (farmlands, bogs) suitable for vipers was performed on a series of different sized islands of the Kizhi archipelago. The study also included the counting of the prey items (total counting of the clutches of two frog species, see section 10) and the route accounts of the number of adders (Table 12.3.1, Fig. 12.3.2).

As it appears from the data above, whereas at the beginning of the XX–th century the area of habitats favorable for the adder on the "middle"

island was about 70 %, at the present time it is not more than 10-20 %, i.e. it is several times less. The same is about inland waters (depression puddles, karst ponds) that serve as reproduction places of grass frogs: they are overgrown with the forest and shaded, so they became unsuitable for spawning and development of tadpoles (Korosov, Fomichev, 2005).

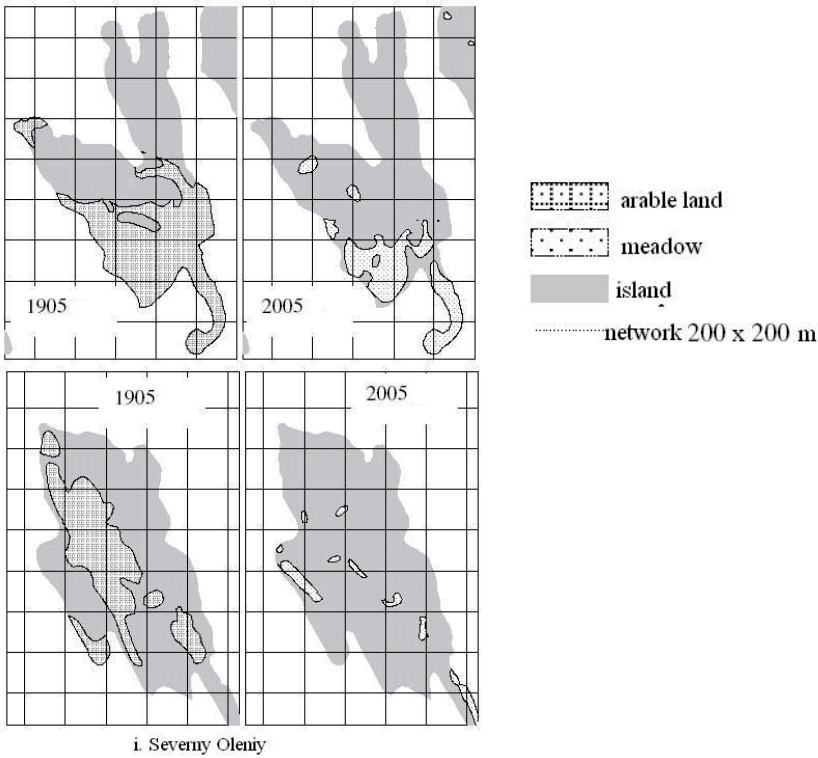


Fig. 12.3.1. Reduction of farmland on two islands of Kizhi archipelago during the century

Table 12.3.1. Characteristics of adders' habitats on the islands

Island	Island area, ha	Proportion (of total area), %				Number of		Routes accounts, km
		arable land[1]	forest[2]	meadow[2]	swamp[2]	clutches[3], units/ha	snakes[4], ind./ha	
Mulych	1.2	100	99	0	1	0	0	1
Lebyazhiy	1.2	84	99	0	1	0	0	1
Gazhiy	1.6	82	90	9	1	0	0	1
Sigovets	1.7	100	95	5	1	0	0	1
B.Sato	2.4	85	89	10	0	0	0	1
Yablon'	3.9	86	87	13	0	0	8	1
Krestniy	5.7	54	100	0	0	0	0	1
Mal'kovets	26	69	5	64	31	26	0	1
Myal'	31	56	87	11	3	3	0	5
Karel'skiy	32	40	93	1	6	9	0	3
Kerkostrov	36	94	2	84	8	6	10	6
Lyudskoy	40	59	87	1	12	70	0	3
Sychevets	41	82	80	17	3	17	2	2
Dolgiy	43	72	83	0	17	7	3	6
Kalgostrov	49	26	77	4	18	6	0	2
M.Lelikov	57	90	14	76	10	11	0	6
Bukol'nikov	65	44	75	19	6	20	7	5
S. Oleniy	74	30	92	5	3	8	9	8
Y.Oleniy	90	44	83	14	3	4	5	19
Eglov	97	54	76	14	10	12	1	22
Ernitskiy	102	27	89	2	9	2	0	3
Volkostrov	198	80	24	60	17	51	6	108
Kizhi	204	82	26	56	18	34	14	600
Average	52	67	72	20	8	12	3	35
Median	40	72	87	10	6	6	0	3

Note. [1] Estimates of the beginning of XX-th century, [2] the recent data, [3] for two frog species, [4] estimates for meadows.

Proceeding with the analysis of this situation, it is important to note that different islands were excluded from the scope of economic interests at different time and therefore represent a varying set of biotic conditions, restoring in basic terms the entire history of the degradation of the once dominating agricultural landscape.

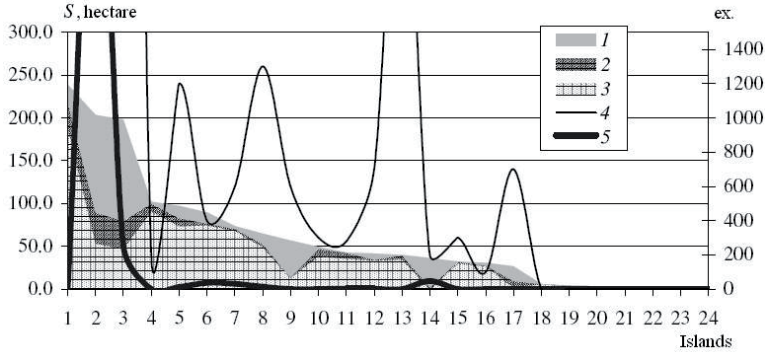


Fig. 12.3.2. Relation between of the total size of the island (S, *1*) swamps (*2*) meadows (*3*) and the absolute number of (ex.) frogs (*4*) and viper (*5*) on the islands of Kizhi archipelago

For example, on the island of Kerkostrov till 2007 100% of meadows were mowed clean, on Volkostrov – 30%, on Kizhi – 10 %, on Mal'kovets grazing continues. At the same time, on the islands Severniy Oleniy and Dolgiy distant from inhabitable villages agriculturally used lands were abandoned about 90 years ago.

As correlation analysis showed (Table 12.3.3), the area of the island is of great importance for the adders' population (only on a large island a sustainable population of adders can exist) as well as the proportion of open habitats (meadows). Colonization by trees has a significant negative impact on snakes. Despite the evident dependencies, the correlation coefficients are not high. The causes of this phenomenon can be revealed in detail by means of the component analysis (Table 12.3.3, Fig. 12.3.3). The analysis showed that the data variability can be reduced to three components (with variance $S^2 > 1$). The first component (PC1) reveals a significant correlation of the abundance of adders (–0.62) with all factors except the area of arable land (–0.15).

It is clear, because for adders not the type of soil, but the level of insolation is important, with it being equally low both on the inarable land in the forests and on the arable land overgrown with forest. In order of their reducing significance for adders such factors are important: the proportion

of meadows, proportion of bogs, area of the island, number of frogs' clutches. This kind of variability is the clearest from the ecological point of view: the more expressed the conditions favorable for adders on the island, the greater is the number of snakes. In this respect, the relatively large islands of Kizhi, Volkostrov, Kerkostrov with forests and meadows are the most favorable (Fig. 12.3.3). They are located at the upper left of the diagram. Opposite, on the right, there are small, overgrown with forest islands characterized by a low number or absence of adders, besides occasional penetrations of some individuals from the neighboring larger islands. The second component (PC2) is not associated with the number of snakes and expresses the islands variability by the area of arable land.

Table 12.3.2. Correlation between the number of snakes and environmental factors on the islands (significant coefficients at $\alpha = 0.05$ are highlighted in bold type)

Factor	r
Island area	**0.56**
Proportion of arable land	0.06
Proportion of forests	**–0.40**
Proportion of meadows	0.43
Proportion of swamps	0.11
The number of frogs' layings	0.20

Table 12.3.3. Factor loadings of the first four components calculated on the data of table 12.3.1

Variable	PC1	PC 2	PC 3	PC 4
Island area	**–0.80**	–0.50	0.43	0.07
Proportion of arable land	–0.15	**1.00**	0.02	0.63
Proportion of forests	**1.00**	–0.34	0.21	0.31
Proportion of meadows	**–0.94**	0.48	–0.07	–0.29
Proportion of swamps	**–0.81**	–0.31	**–0.65**	–0.22
Number of frogs' clutches	**–0.69**	–0.42	–0.23	1.00
Number of snakes	**–0.62**	0.00	**1.00**	–0.12
S^2	3.39	1.44	1.01	0.66
S^2, %	48	20	14	9

The third component (PC3) reveals a negative correlation between the number of adders and the area of bogs: some islands, such as Mal'kovets, M. Lelikovsky, are not inhabited with snakes despite the extensive marshes and meadows. This situation required a certain explanation. The fact is that the existence of an autonomous island population of adders depends on the number of frogs on the island. In turn, the abundance of frogs is determined by the area of reproductive water basins and the availability of wintering places. Grass frogs spawn mainly in temporary puddles, but not in flooded lakeside swamps (see section 10); their current year's young winter in the forest litter, but older frogs – at the bottom of ponds. The island M. Lelikovsky in question has only one puddle of 5 m diameter and one swamp (5 hectares) located in the lowland of the island, where there are no stone ridges. There only few clutches of green frogs were found; apparently, the absence of woods and stone ridges around the reproductive water bodies does not provide sufficient survival of current year's young in winter. Moor frogs prefer the lakeside bogs for spawning (see section 10), however, they winter in the forest litter, almost absent on M. Lelikovsky, and their number is also extremely low (only 20 clutches were found). Thus, on M. Lelikovsky there is no sustainable population of adders due to the lack of prey items.

In the graph with the first and the third components plotted along the axes, M. Lelikovsky (with extensive meadows) is located at the bottom left, opposite to the forested islands inhabited with adders. Here (upper right) the S.Oleniy islands are highlighted that have small favorable to adders sites of natural (sel'gi, rocks) and anthropogenic origin (meadows, barrens) among continuous forest. Taking into account the current trends of anthropogenic landscapes degradation on the islands of the Kizhi archipelago, it can be stated that the island populations of the adder will reduce permanently and eventually remain only in natural habitats – on "sel'gi" and shores.

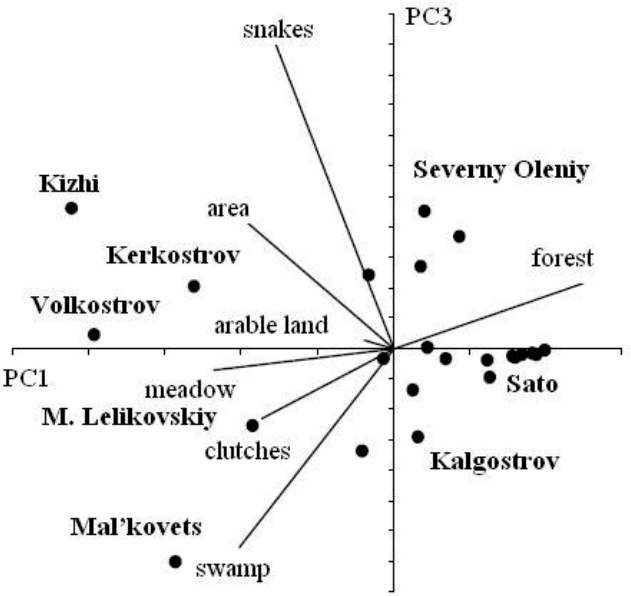


Fig. 12.3.3. Biplot, built on the results of component analysis of the viper habitat characteristics on the islands of Kizhi archipelago. Lowercase letters sign all axes of the factor loadings, petite signs the points corresponding to values of the principal component for some islands

Despite a rather uniform distribution of convenient shelters on the island of Kizhi, adders are met for the most part in the meadows, in the vicinity of bogs, in biotops inhabited by frogs. The dependence on the number of frogs and quality of habitats is observed and on the other islands of the archipelago: a lot of snakes are found where there are a lot of meadows, bogs and frogs.

Chapter 13.

Keeping adders in captivity

The common adder is so sensitive to the changes of living environment, it is so maladaptive to captivity that it scarcely occurs in the expositions of zoos or animal facilities. Our long-term experience of keeping adders in captivity allows us to propose the items for optimization of animal care (Korosov, 1988; Khilkov, 1998; Korosov, Khilkov, 2008). In the basis of our report there lie the observations made in 1978–1979, 1990–1991, 1993–1998 over 28 adults and 58 newborn individuals of the adder that were kept in the laboratory of the Department of Zoology and Ecology of Petrozavodsk state university.

Terrarium. Adder, as an active land predator, should be able to straighten at full length for its well-being in the terrarium; the terrarium size must be not less than 60 cm. Focusing on the well-known recommendations (Chernomordikov, 1950; Makhlin, 1966; Care of poisonous snakes..., 1972; Kudryavtsev et al., 1996), we have tried with the equal success terrariums of different size (length x width x height): from 60 x 30 x 20 up to 80 x 50 x 50 cm. In the summer in nature the shelters with low temperature (below 15 ° C) and surface plots heated by the sun to 40 ºC are available for adders. Similar conditions were provided in terrariums: there was a shaded remote camera (10–20 ºC), and the area illuminated and heated by a filament lamp (40–75 W) located at the height of 5–20 cm (35–40 ºC). Due to the steady illumination of the chambers a temperature gradient was maintained. The wood-cabinet terrariums with glassy walls of illuminated camera were equipped the removable (often glassy) cover having air holes. In the low-walled tank water was changed ones in two days. The bottom of the terrarium was covered with plastic, oilcloth, or thin layer of dry moss-sphagnum. In this case, to keep a terrarium clean is very simple, the cleaning of terrariums was performed at least once a week, moss was changed every 2–3 weeks; in addition moss may be washed and reused. The density of snakes in the terrarium ranged from 500 cm^2/ ind. (4

snakes in a small terrarium) to 4000 cm^2/ ind. (one snake in a large terrarium). Terrariums' characteristics in the given band provide normal vital functions (nutrition, shedding) of adult snakes. It is more convenient to keep one snakes in the large terrariums, but in this case, they take up too much space. At the same time, it is preferable to keep newborns and young snakes (up to the length of 30 cm) separately. Otherwise a "passive" cannibalism is observed among juveniles when two snakes tried to swallow the same prey item. At that both snakes die: one (swallowed) – from suffocation, the second – from intoxication, not being able to digest so large prey. Among juveniles kept together the cannibalism amounts 30 %. It is better to keep quarantine juveniles (which are fed artificially) and sick snakes separately.

Feeding. When an adder gets into captivity, it stops eating (Biella, Schiemenz, 1980). This fact makes almost impossible keeping snakes in captivity. There are some methods of nutrition stimulation using artificially organized short-term hibernation and the withdrawal from it. We have opted for training the snakes to self-feed using artificial feeding (Makhlin, 1970). The overall results were as follows. After 2 (1–5, 15) months of artificial feeding, the adder, captured in nature, begins eating by itself. Mortality will be about 5 % when using the most benign methods. Crude feeding methods cause damaged mucosa in the oral cavity and the snake dies of stomatitis in 2–3 weeks. To avoid diseases is possible if to sterilize the tools for feeding, to divide the victim's body into pieces on joints for the sharp bone fragments or fishes' prickly fins not to stick out, to feed whenever possible without violence over an animal, which is better to be slightly chilled. A small prey item is introduced into the mouth, pushed by forceps into the esophagus and by massage brought into the stomach. Swimming contributes to swallowing the food, so after feeding it is useful to place a snake in a tub. Sometimes it is enough to place the food into the snakes' mouth, as she starts to swallow it by itself. This behavior shows that next time the adder will take food itself or will actively hunt. The snake trained to artificial feeding willingly takes food from forceps, even not trying to bite. However, moving live victims, especially small

mammals, stimulate the awakening of the hunting instinct. The snakes began self-eating on average after 5 artificial feedings. For the artificial feeding the following kinds of food were used: the fragments of frogs, small fish (whitefish), pieces of frog's meat, even meat-egg pasta inserted through a catheter, it is better to use solid food than liquid one. Later snakes were offered live or slain frogs, white mice, fish (whitefish, roach). Newborn snakes in nature starts to eat 2 weeks after birth. Their first victims are current year's young of frogs (Grubant, Rudaeva, Vedmederya, 1972) and those of common newts (Korosov, 2000). Adders born in captivity were offered pieces of frogs' meat with skin fragments or pieces of fish rubbed over the frog's skin. In the absence of live current year's young, they usually gave up feeding. Current year's young were fed artificially with the pieces of meat without bones, but very carefully: the piece of food was placed only in the mouth and no further. At that 36% of juveniles died from cloacatis possibly associated with unusual food. Young adders begin self-eating in a month, i.e. faster than adult vipers.

Following a meal plan *ad libitum,* adders hunt about once a week (consuming on an average 10–20 g of food), i.e. 2–3 times more often, than in nature. In captivity similar sized females turn out better-fed than those in nature (see Table 9.4.3). Due to constant activity and feeding in captivity animals grow 2.5–2.9 times faster than in nature; for the calendar year in captivity, they reach the size of a normal 4–5-year-old individual (see section 5).

Shedding. The change of integuments happens in nature 3–4 times a year, in captivity – once every 30 days, but some specimens usually shed once every 60 days (see section 5.1). Shedding is a good indicator of adders' health. The emergence of solid horny covers, "stockings" 5–7 days after eyes clouding is the evidence of a good health and fatness of an animal. Stayed fragments of skin indicate health problems of snakes. Warm baths (25 °C) help to get rid of the remnants of the old skin; it is important, because the old skin prevents following shedding and hinders snake's movements. In captivity, shedding snakes eat less often than shed ones.

Taming. In reptiles, conditioned reflexes are developed very badly. All their "ethological" life is a series of manifestations of the reflex reactions, realization of specific stereotypes more or less oriented to the environment. Therefore, taming of adders is not the same as domestication of mammals. Under normal conditions, a snake attacks the man's arm giving it food with the same aggression for many years; it's the fact, proven by practice, including bites. The only way of "taming" consists in converting the holder of a terrarium into one of the environmental factors that the animal tolerates because cannot avoid it, and therefore "do not notice". For adders, the main way to communicate with their environment is its poor eyesight, thermo-location, tactile sensations and an acute sense of smell. Experience shows that when the adder becomes acquainted to the smell and touch of the snake's "owner", it ceases to exhibit aggressive behavior, do not hiss and bite. This, however, requires a special period of adaptation to the researcher. In the wild this is impossible, because the adder always attacks and keeps off. So, in captivity the conditions should be changed in such a way that to suppress aggression. This can be achieved by lowering the temperature and not feeding a snake for some time. In our case, at room temperature (18–20 °C) 2 weeks after capture adders scarcely react to touch, they allow to manipulate them, to move from place to place, etc. After once "assure" itself of the safety of the procedure (this happens without feeling of pain), the adder stopped responding to the "owner", which became for it a kind of external environment, such as a bush branch vibrating in the breeze. A two-weeks fasting is not dangerous for the adder, normally feeding 1–3 times a month. However, the snake becomes disaccustomed to the terrarium holder more quickly than it has been accustomed to him: 10 min. after their release of the terrarium into the wild, snakes become so aggressive that they were at the moment of capturing 8 – 10 months ago.

"Taming" of snakes eliminates a lot of problems of their keeping concerning artificial feeding, bathing, moving, cleaning and disinfection of terrariums, measuring, weighing and carrying out experiments.

In conclusion, it is important to note that the simplicity of the described technique of taming is deceptive, because at early stages it requires extreme caution, great experience in contacting snakes and understanding the nature of their behavior. At the same time, the adder is calm and "preventive", because before biting it always hisses (in truth, sometimes for a very short time).

Safety. Snakebites are inevitable for herpetologists studying this species in nature and especially in captivity, if snakes are not “tamed”. The main source of danger connected with the snakebites is a compromise between the harsh manipulations with snakes (preserving a herpetologist) and applying limits on these operations preserving a snake. Most of these bites are "defective", made by one fang and penetrating into the soft tissues of the finger for a shallow depth. Further, 20 cases of biting observed by us are summarized. If after a "full" bite no measures are taken, a local swelling of the forearm will develop (expressed completely in about 4 hours). It is accompanied by pain in the joints and extremities, sometimes dizziness. If the *Vipera berus* venom antiserum is injected immediately after the bite (*Vipera lebetina* venom antiserum is inappropriate), edema does not develop, but after another bite the severe allergic reaction appears – redness, swelling and itching of the skin, redness of the eyelids, and risk of anaphylactic shock. The same is observed after repeated bites without the serum injection.

Another method consists in cutting the bite place within 30 s after the bite and squeezing the blood with the venom penetrating it. At that, swelling is limited to one finger; subsequent allergic reactions do not develop. The instrument must be sterile, since the depth of the incision should correspond to the length of the adders’ fang (3–4 mm), and an infection may penetrate the wound through a dirty knife. After the procedure, the wound must be disinfected in the usual way. Our practice suggests another effective way of avoiding bite consequences: venom should be squeezed out immediately (not later than 10 seconds!) after a bite. A snake’s fang makes a hole in the tissue, which is filled with a drop of venom. If you press on the edges of the wound, most of the venom

immediately comes out in the form of amber-red drop, and you can simply wipe it out by your arm and continue squeezing for a few more minutes. After that, you should put a pack with vodka on the wound for an hour. If the first moment is missed because of fare or anger, the venom will penetrate into the tissues. In any case, after the adders' bite one should consult the doctor.

We strongly recommend nature lovers against keeping adders at home; in any case this will lead to an injury, and even death – either of the snake or of its owner.

Chapter 14.

Technology of simulating

Simulation modeling is considered by us as a computer technology to give a quantitative description of a data array characterizing the "behavior" of studied biosystems (Korosov, 2002a, 2002б, 2007). The main point of the operations discussed below is to determine model parameters – the coefficients in the equations relating the studied variables. In a lot of cases, these coefficients can be given the meaning of dynamic characteristics of the studied biological phenomenon. The proposed technology enables to create models of two types: static and dynamic. Static or descriptive models are similar to regression models with the difference that their coefficients are assessed by the optimization procedure (fitting) but not by the least square method. This optimization on frequent occasions allows not only to determine the coefficients more accurately, but to reconstruct the model quickly, if the selected equation is not suited to the data. Dynamic models reconstruct the process of biosystem's "living" and in principle cannot be replaced by regression analysis. As our practice shows, both model types are useful in ecological investigations.

14.1. Development of dependence (descriptive model)

The dependencies expressed by "non-standard" equations are very difficult for the regression analysis. For example, to characterize the basal metabolism of poikilothermic animals the formula (see section 6.1): $R = a \cdot W^{0.8} \cdot e^{bT}$ is proposed. To estimate the parameters a and b quickly enough, adjustment can be used. Initial data on the adders' metabolic rate were borrowed from the work of I. Pomianovska-Pilipiuk (1974). 9 adders of different size at three different temperature regimes – 5, 15, and 25 °C have been studied. On these data, the regression equation was obtained by means of the least square method (for a = 0.663 and b = 0.0744): $R = 0.663(Wr^{0.8}) \cdot e^{0.0744 \cdot TT°C}$ (Zamolodchikov, 1993). However, the

dependence was not suitable for determining the metabolic rate in wintering snakes: at 0 °C the value of metabolic rate significantly exceeded zero (see Fig. 6.1.1). It was logical to assume that at zero temperature the metabolism of wintering adders, as poikilothermic animals, ceases. Then, introducing these additional hypothetical values into the initial data array, it would be possible to construct a new model that would include the metabolic rates in a wider range and enable to calculate the metabolism at the temperatures close to zero. In other words, the particular task is to form an equation of the dependence of basal metabolism on adders' body weight (range: 80–154 g) and temperature (at 0, 5, 15 and 25 °C).

Then we launch VS Excel and input the names and values of the initial data (number of specimen, body temperature in experiments, snakes' weight, basal metabolism values obtained experimentally) in an electronic worksheet into the columns N, T, W, R (columns A, B, C, D) (Fig. 14.1.1).

E8 fx =E$1*(C8^0.8)*EXP(E$2*B8)

	A	B	C	D	E	F	G
1				a =	0.663		
2				b =	0.074		
3				Обмен. Дж/ экз. / ч.			
4	N	T	Wг	**Rм**	Мl		
5	7	**0.01**	80	**0**	22		
6	1	**0.01**	108	**0**	28		
7	3	**0.01**	104	**0**	27		
8	2	**0.01**	124	**0**	31		
9	8	**0.01**	140	**0**	34		
10	9	**0.01**	154	**0**	37		
11	4	**0.01**	68	**0**	19		
12	5	**0.01**	123	**0**	31		
13	6	**0.01**	123	**0**	31		
14	7	5	68	72	28		
15	1	5	80	71	32		
16	3	5	104	78	40		

Fig. 14.1.1. Fragment of an Excel sheet with the original data and calculations before tuning of the model parameters (full array reaches line 40)

To calculate the exponent, instead of zero temperature a value of 0.01 was accepted. Then an metabolism values array was received using the formula

$R_M = 0.663(Wr^{0.8})\cdot e^{0.0744\cdot TT°C}$

Tabular programming rules require that the model values for each sample unit (or one time step of the model) should be calculated explicitly. The value of parameter *a* was introduced into the cell E1, the value of the parameter *b* – into the cell E2 and stereotypical formulas containing relative references to the cells with variables T and W, and absolute references (with prefix $) to the cells with parameters *a* and *b* – into the block of cells E5:E40.

At the beginning the first formula was inserted into the cell E5:

=E$1*(C5^0.8)*EXP (E$2*B5),

where E$1 – absolute address of the cell with a parameter a value,

E$2 – absolute address of the cell with a parameter b value,

C5, B5 – relative addresses of the cells with the values of variables N and W,

*, ^, EXP() – signs of of multiplication, exponentiation, and calculation of exponent.

After pressing the button Enter, the cell will contain a calculated metabolism value of adder with mass C5 = 80 g at a temperature of B5 = 0 °C at current values of a and b:

$=E\$1*(C5^{0.8})*EXP (E\$2*B5) = 0.663\cdot 80^{0.8}\cdot e^{0.0744\cdot 0.01} = 22$ (j / ind. / h).

(In parentheses we note that, after entering one formula into the cell E5, it is just enough to run "Auto completion" up to the cell E40).

It turned out that the estimated metabolic rate at 0 °C (19–37 j / ind. / h) was almost equal to its estimates at 5 °C (22–54 j / ind. / h), but that theoretically must not be.

At the next stage, the previous model should be readjusted so that it would correspond better to the entire array of empirical data. At first, we shall calculate the total deviation of the the model from reality. For this aim

the squared difference between each pair of values: model – reality can be used:

$\varphi = (\text{Mod.}–\text{Real.})^2 = (R_{Mi}–R_i)^2$.

On the Excel worksheet, this formula will be written as (Fig. 14.1.2):

F5 = (D5– E5)^2 = $(0–22)^2 = –22^2 = 488$.

Using the procedure “Auto completion”, it is easy to calculate the similar values for all pairs of variables *R* and *R*M (to check it needs to click D5 and press "F2"). Let us denote the obtained graph as "φ". Then we should enter the formula to calculate the sum of all squared differences between real and model variables into the cell F2:

$\Phi = \Sigma\varphi$ or E2 =SUM (F5:F40) = 177173.

The value Φ=177173 characterizes the generalized difference between the calculated model values of a sign and the initial data. Such a large value suggests that the model conforms poorly to the initial data. It may be assumed that when other coefficients are used, the model will describe reality more accurately and the discrepancy function (the value in cell D8) will diminish. This consideration enables to start searching for the best values of the model parameters, changing them by using the built-in program (macro), which performs the procedure of finding the best parameters and the optimization procedure. It will be called with the command "Finding solutions" in the menu "Service" (Fig. 14.1.3).

F7 =(E7-D7)^2

	A	B	C	D	E	F
1				a =	0.663	
2				b =	0.074	177173
3				Обмен^ Дж/ экз. / ч.		
4	N	T	Wг	R	Rм	ф
5	7	**0.01**	80	**0**	22	488
6	1	**0.01**	108	**0**	28	793
7	3	**0.01**	104	**0**	27	743
8	2	**0.01**	124	**0**	31	978
9	8	**0.01**	140	**0**	34	1188
10	9	**0.01**	154	**0**	37	1392
11	4	**0.01**	68	**0**	19	376
12	5	**0.01**	123	**0**	31	972
13	6	**0.01**	123	**0**	31	972
14	7	5	68	72	28	1903
15	1	5	80	71	32	1519
16	3	5	104	78	40	1444
17	2	5	108	90	41	2398

Fig. 14.1.2. Calculation of the difference between model and reality

If it is impossible to find the command "Finding solutions" in the menu "Service", this procedure most likely is either not connected or not installed. To connect the macro "Finding solutions" it is necessary to call a new window "Add-in" of the menu "Service", where to put a tick against the heading "Finding solutions". After that, the command will appear in the menu "Service". If there is no title "Finding solutions" in the window "Add-in", it is necessary to use the installation disk MS Office, select "Add / Remove / Microsoft Excel / Add-in", put a tick in the window "Finding solutions" and then connect the procedure.

The macro window that appears on-command "Finding solutions" must be correctly completed (e.g. via a mouse) (Fig. 14.1.3):

– Set the target cell: $F$2,

– Equal to 0,

– Changing the cells: $E$1:$E$2 (containing parameter values).

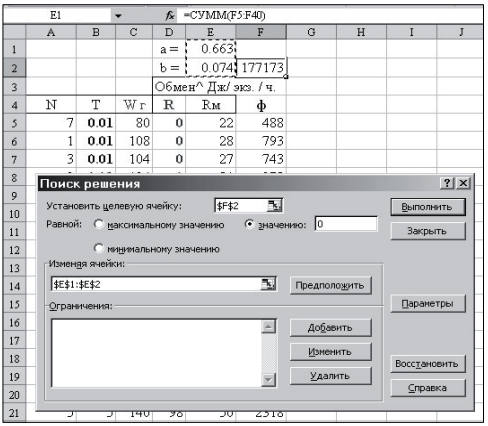


Fig. 14.1.3. Set up of the macro "Solver" window

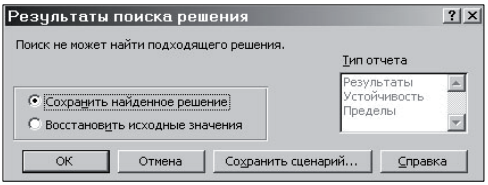


Fig. 14.1.4. Window with the results of solution search

After clicking the button “Run”, a window (Fig. 14.1.4) warning that the search could not find solution, will appear. This is natural, because the task of module was to nullify the diversity function, but the procedure was able to reduce it only to Φ = 172761 (cell F2). With macro "point of view" (see section 14.3) the found solution is unsatisfactory, i.e. the obtained values of the coefficients are inaccurate. However, from the ecological point of view, the decision could be quite acceptable if the values in columns R and RM became close (the statistical significance of the differences between them needs to be investigated by statistical methods – see: Korosov, 2002). Unfortunately, despite some variations in the model parameters (a = 0.771, b = 0.072), the adjustment results cannot be considered as satisfactory, because the predicted basal metabolism at 0 °C varied from 26 to 43 j / ind. / h and did not diminished (Fig. 14.1.5). Therefore, the structure of the equation that cannot give a zero metabolic rate at zero temperature must be reviewed.

	A	B	C	D	E	F
1				a =	0.771	
2				b =	0.072	172761
3				Обмен^ Дж/ экз. / ч.		
4	N	T	Wг	R	Rм	ϕ
5	7	**0.01**	80	**0**	26	660
6	1	**0.01**	108	**0**	33	1071
7	3	**0.01**	104	**0**	32	1004
8	2	**0.01**	124	**0**	36	1321
9	8	**0.01**	140	**0**	40	1606
10	9	**0.01**	154	**0**	43	1881
11	4	**0.01**	68	**0**	23	509
12	5	**0.01**	123	**0**	36	1313
13	6	**0.01**	123	**0**	36	1313
14	7	5	68	72	32	1557
15	1	5	80	71	37	1172

Fig. 14.1.5. Fragment of an Excel sheet with the original data and calculations after tuning of the model parameters

14.2. Reconstruction of the process (dynamical model)

To describe the speed and result of the process, a dynamic model is used. It characterizes a causal mechanism of the process behavior, as it gives the possibility to focus on the study of any moment of process implementation. Unlike the single equation of descriptive models, the dynamic simulation models are represented by at least two equations. One of them expresses the process speed; it is used to calculate the partial momentary result of the process attained at any specific time:

$dy_i = f(y, x,... , a, b,...);$

The second formula is used to generalize partial results obtained in all previous steps

$y_i = y_{i-1} + dy_i,$

where y_i – current value of the variable (characteristic of state), y_{i-1} – value of the variable in the previous (i–1-st) time step (characteristic of previous state), dy_i – variable gain for the i-th time step determined by the function f(y, x,... , a, b,...), y, x,... – studied variables, properties of a studied object, a, b,... – proportionality coefficients, model parameters, i = 1, 2,..., T – index of model time steps.

Using this technology, we have calculated, for example, the dynamics of marked animal mortality (see section 7.2). The problem was set to determine the coefficient of annual mortality (specific mortality) of adders, using data on gradual reduction of the proportion (%) of re-captured snakes. In this case, the model equation is written as:

$dp_i = d \cdot p_{i-1}$,

$p'_i = p_{i-1} - dp_i$,

where p_i – proportion of marked animals found in i years after marking, p_{i-1} – proportion of marked individuals found in a previous year (in the i–1-th year after the first capture), dp_i – proportion of individuals died in the past year, d – specific mortality, the required model parameter, i = 0, 1, 2...– number of years passed after the first capture (0 – index of re–captures in the marking year).

In the Excel worksheet, the complete model occupies several blocks of cells (Fig. 14.2.1). All formulas are entered manually only into the upper cells, and lower ones – using the auto-complete method. Block A3:B12 contains initial empirical data (see Table 7.2.4). The formula for calculating the proportion of died animals per year (dp_i) was introduced into the block C3:C13; in the Excel worksheet, the formula will be, for example, for the third year =D5*$C$1 (Fig. 14.2.2, A). The cell C1 contains the value of a model parameter – specific mortality. This parameter will be defined in the process of model setting. However, at the beginning it should be given a hypothetical initial value, for example d = 0.5 (50 %). As in all time steps the same value of mortality was used, the reference to the cell with this parameter must be absolute, i.e. it must contain prefixes $. For example, if on average two years after marking 5% of marked individuals are caught, at the mortality of 50 % the number of perished adders amounts:

$dp_2 = d \cdot p_1$ = C6=D3*$C$1 $0.5 \cdot 5 = 2.5$ (%).

D4				=C2	
	A	B	C	D	E
1		d =	0.5		Φ =
2		$p1$ =	10		21.36
3	i	p	dp'	p'	Φ
4	1	12.33		10.00	5.41
5	2	7.24	5.00	5.00	5.02
6	3	4.73	2.50	2.50	4.96
7	4	2.79	1.25	1.25	2.37
8	5	1.03	0.63	0.63	0.16
9	6	1.01	0.31	0.31	0.48
10	7	1.81	0.16	0.16	2.73
11	8	0.55	0.08	0.08	0.22
12	9	0.00	0.04	0.04	0.00
13					

Fig. 14.2.1. Model of the extinction dynamics of tagged male vipers before setup

The formula for calculating the proportion of individuals surviving in a current year (p_i) was entered into the block D3:D12; in the Excel worksheet, the formula for the second year will be written as follows: =D5–C6 (Fig. 14.2.2, B). For example, if in the third year after marking the losses amounts 2.5 %, then $p'_3 = p'_2 – dp_3$, = 5 – 2.5 = 2.5 % of marked individuals will survive. As the starting value of p_1 is unknown, it appears as the second adjusted parameter of the model (it is inserted into the cell C2, the first value of the model is accepted equal to this parameter D4 =C2, see Fig. 14.2.1). p_1 = 10 is pre-installed (in a year after the first capture, 10% of marked individuals is found).

Using the parameters d = 0.5, p_0 = 10 the model dynamics of extinction of marked individuals (p') is in a bad agreement with the empirical data (p) (Fig. 14.2.3). For example, in the fourth year after marking, the corresponding values equal to 1.25 and 2.79, and on the eighth year – 0.08 and 0.55.

The sum of squared differences between these values for each year of capture $\Phi = \Sigma\varphi_i = \Sigma(p'_i – p_i)^2$ (block of cells E1:E13) enables to assess the overall difference of the model from empirics (Fig. 14.2.2, C).

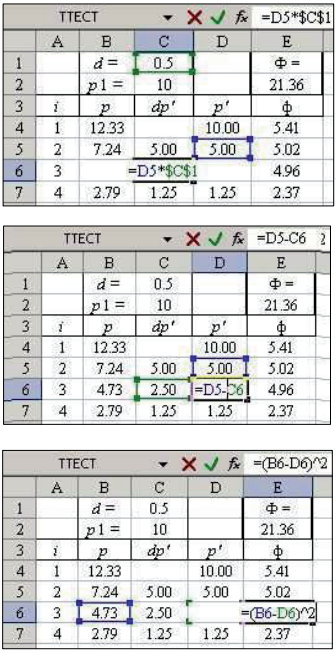


Fig. 14.2.2. Formula for calculating the model variables: А – Calculation of the proportion of dead tagged animals, Б – Calculation of the proportion of survived tagged animals, С – calculation of difference between model and empirical values

Since the model with roughly set parameters poorly corresponds to reality, the next procedure will be model setting using macro optimization, which is initiated on-command Service / Finding solutions. In the window (see similar example in Fig. 14.1.3) the target cell $E$2 is set equal to 0 via a mouse, changing cells $C$1:$C$2, and then one clicks the Run button. In the appeared query results window (see Fig. 14.1.4) one clicks the button Save.

After setting, the coefficients changed significantly (Fig. 14.2.4), and model values p' coincided very accurately with the empirical dynamics (see Fig. 7.2.2).

On the island of Kizhi the specific (annual) mortality in adders' males turned out about 39 %; this value reflects a significant pressure exerted on snakes by the environment, primarily anthropogenic factors. The second parameter (occurrence of marked animals in the second year after

marking) refers to the death of animals, but to a greater extent of the proportion that constitute the marked animals in the island population – 12 %. Since every year about 100 males were caught and 12 % of them were marked, then on the island the total amount of males is equal to 1200 ind., more precisely, taking into account a mortality rate of 39 % – 732 ind.

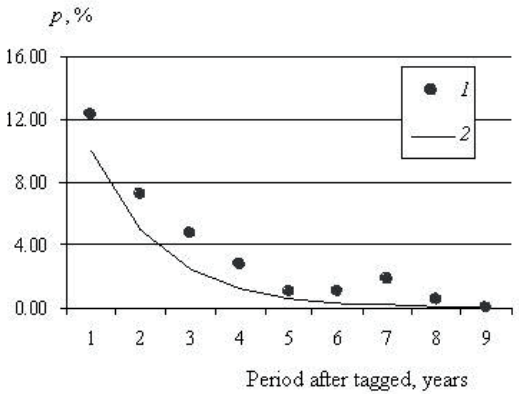


Fig. 14.2.3. Calculated dynamics of reduction of the share of re-captured tagged male vipers: *1* – the average share of re-caught specimens, *2* – a model description of the data (d = 0.5, $p'_1 = 10$) before setup of the model parameters

As it seen, while constructing a dynamic model to calculate values at any particular time (in a given step, in a separate cell in Excel worksheet) one should restore the whole process from the very beginning. A model seeming "lives" on its own and depends only on the values of starting parameters. In conclusion we note that the process speed function $dy_i = f(y, x,... , a, b,...)$ can be assigned by different type equations – linear ($dy_i = ay_{i-1}+b$), exponential ($dy_i = by_{i-1}^a$), etc. In addition, the process speed can be defined both by autonomous reasons (dependence on the previous state; $dy_i = f(y_{i-1})$) and by external factors (dependence on the environment;

$dy_i = f(x1, x2,..., yi–1))$, or the interaction of simultaneous processes ($dy_i = f(z_{i–1}, y_{i–1})$, $dz_i = f(z_{i–1}, y_{i–1})$) (see: Korosov, 2002b).

E2 | =СУММ(E4:E14)

	A	B	C	D	E	F
1		*d* =	0.3903		Φ =	
2		*p*1 =	12.232		2.00	
3	*i*	*p*	*dp'*	*p'*	ϕ	
4	1	12.33		12.23	0.01	
5	2	7.24	4.77	7.46	0.05	
6	3	4.73	2.91	4.55	0.03	
7	4	2.79	1.77	2.77	0.00	
8	5	1.03	1.08	1.69	0.44	
9	6	1.01	0.66	1.03	0.00	
10	7	1.81	0.40	0.63	1.39	
11	8	0.55	0.25	0.38	0.03	
12	9	0.00	0.15	0.23	0.05	

Fig. 14.2.4. Model of the extinction dynamics of tagged male vipers after setup of the model parameters

14.3. Parameters of macro "Solver"

Information about the order of using and changing macro settings "Finding solutions" is presented in several tabs of "Reference system" of MS Excel package (the question mark on the main menu bar). In "Contents" it is a point "Sampling and data analysis / Nonlinear multiple optimization", in the "Subject index" – rubric "Finding solutions". In the tab "Search" a new information can be found by key words "Finding …". "Help" button provides basic tips in the macro panel window.

The optimization procedure is called on-command "Finding solutions" in the menu "Service". In the resulting window, it is necessary to make some changes to make macro working as needed. In general, the supplemental information covers all stages of the process quite well. Some variants of filling the macro main window "Finding solutions" have already been considered in the previous sections. It is important to make a few additions concerning control over the progress and results of setting procedure.

"Run" is the button of run macro. It would seem unnecessary to explain its meaning, after clicking the button it starts a model optimization. The trick is that sometimes to set the model it is worth calling up the program many times! At that, each new attempt improves the model, sometimes two stable sets of parameters appear, one of which is better than the other. The reason for this phenomenon is that at every new start the value of optimization parameter gain used to calculate a new "search" values of the objective function, is defined anew. The new gain is calculated automatically and is determined by starting "atmosphere" of a model. The change of the initial parameters values (after each new setting) entails a gain change and the kind of optimization. For this reason, the results of successive setting acts may differ. It is true that differences persist only during 3–5 iterations. However, it happens by no means always, but only in the case of models having a "soft" frame, a few latent variables or poorly structured data.

"Limitations" – the dialogue of entry, delete and change of the boundary conditions of changing variables and parameters. In the context of the simulation system this macro property is used simply as an output filter. In fact, the program allows solving problems of mathematical programming. Some conditions may be imposed both on certain values and blocks of cells, both on parameter values and model ones. Limitations should be used in two cases. First, based on theoretical considerations, one can set a biologically plausible range of probable parameters and variables. For example, lots of natural characteristics cannot be negative (number, dimensions, weight, concentration), however, they can be derived from the model equations. Second, one can correct computational errors, if in setting the model unit is filled with the signs of sharp (##, they hide the errors messages: **#DEL/0!, #NUM!**). The window "Results of finding solutions" appears containing the text that warns about the error (Fig. 14.3.1).

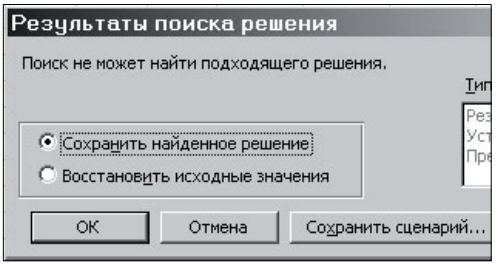


Fig. 14.3.1. Error message about setup of the model parameters

Sources of errors in arithmetical models are almost always the same: division by zero, an attempt to calculate logarithm or take the root of a negative number. It is the only way out – to cancel setting results and establish the conditions that would limit the range of values which have caused the error. To do this, one should click the button "Add", and selecting cells (or cell) via a mouse, establish the boundary values for them (for example, "greater or equal to zero, > = 0).

"Parameter" is a window call (Fig. 14.3.2) for changing the way of macro functioning. Let us discuss the most important of them. "Limit number of iterations" is the limitation of setting duration. A single iteration consists in twofold recalculating the residual function (with basal and modified parameter values), calculating the direction of basal parameters changes and the value of these changes, calculating the new values of basal parameters. Each iteration improves the model. Well-structured models converge for less than 10 steps; poorly structured ones try to overcome the barrier of 100 iterations. If a window appears "Current status of finding solutions" with the question "Continue?", hence, the model considers that "something is wrong" and requires critical revision.

"**Convergence**" is the extreme minimal difference between the values of the objective function obtained in adjacent iterations, e. After it achieving, the model setting stops. The larger the value e, the faster the setting ends, the rougher the model description will be. This is a relative parameter; it controls the speed of objective function changing. For bio-ecological models the value of e = 0.1 is sufficient, but default value e = 0.001 is assigned. This value gives slightly more accurate results, almost without affecting the procedure duration. This parameter may never be changed.

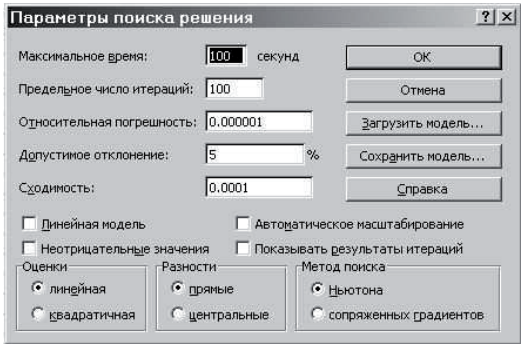


Fig. 14.3.2. Window with macro settings

"Relative error" (or precision) is the round-up of the residual function values while the difference between them is calculated. This parameter, like the previous one, also substantially determines the course of setting, but this is an absolute indicator, it establishes not the extreme speed, but the maximum deviation of the objective function from a specified level.

"**Acceptable deviation**" is a difference between the value to which the objective function strives (it is preset), and its value reached in the optimization process. This parameter influences not the setting course, but the ability to display its results. When the difference between *achieved* and *planned* values of the residual function does not exceed the "acceptable deviation", in the window "Results of finding solutions" the text "Solution is found, all the conditions and constraints are optimally accomplished" appears. It gives the possibility to create a report on the results, with the appropriate item being selected in the window "Report type ", for example, "Limits" (Fig. 14.3.3).

When a deviation is greater than the acceptable, the text in the window "Results of finding solutions" reads: "Search cannot find the appropriate solution" and the access to the report selection is not granted. Since in simulation modeling the planned value of the objective function usually equals to 0 (which, of course, is never reached), then the model adjuster always sees only the latter window.

Generally speaking, in simulation model setting these messages are indifferent, because the simulation system has the block of adequate assessment, which gives a meaningful answer how close is the model to reality. However, if the user wants to obtain reports on setting results in any case, the following should be done. At first, the model should be set using the macro "Finding solutions" with automatically adjusted settings. Then one should re-run the macro "Finding solutions" and “set the target cell equal to a value” with the value of the residual function just obtained from an Excel sheet; click "Run". Immediately a window "Results of finding solutions" of the first type opens.

"Linear model" is the way of preliminary, quick and rough estimation of model parameters. In our view, the “method of biological likelihood” is more productive, it means the primary assignment of a parameter based on the knowledge of the subject and theoretical grounds.

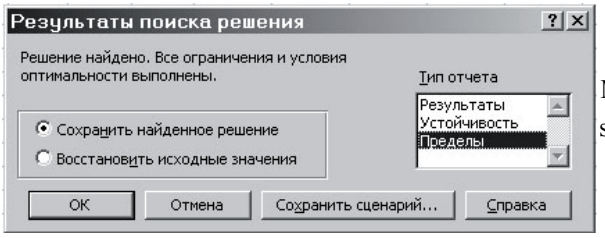


Fig. 14.3.3. Message about the successful setup of the model parameters

"Newton's method" is a calculating procedure of the optimum search directions discussed above. It is characterized by a large amount of computing work, but a higher speed of finding solutions. It is acceptable for most tasks, but it can miss the global extreme having a narrow base in the conventional landscape of the objective function.

"Method of conjugated gradients" is one of procedures calculating directions of optimum search. Unlike Newton’s method, it suggests smaller amount of computational work in each step, but a relatively low speed of finding solutions. It is acceptable for most tasks because it examines the structure of the objective function landscape in more detail (hence, slower). For the considered models, both methods gave the same results.

"Assessment", **"Derivatives"** are the variants of the optimization technique slightly influencing the results of setting considered models.

Simulation modeling provides a synthesis of an author's theory with actual data and thus is the highest manifestation of a systemic thinking, philosophy of empirical biology. Our method of spreadsheet programming in Excel (Korosov, 2002b) enables any biologist having computer competence to construct models of any complex biological phenomena.

Conclusion.

The common adder was studied in peculiar conditions, on the north island; therefore, three aspects of species ecology – common, northern and insular – were touched upon. The originality of the received information is associated with the use of labor-intensive field methods, and laboratory instrumental research methods combined with effective procedures of mathematical data processing.

General ecology. The maximum (physiological limited) age of adder is documentary considered as 28 years. (In captivity old snakes die of intestinal obstruction of different etiology.) However, in nature snakes rarely attain the age of 13–16 years, most of them die before 11 years, and the average age of the visible (adult) part of population is 7.6 years in females and 5.9 years in males. The gap between these values is connected with that the specific (annual) mortality in females is significantly lower than in males (26 vs. 38 %).

The reason is consistent high mobility of males, which is expressed, in particular, in that for a year 50% of males moves no farther than 106 m, and females – 57 m, 88% of individuals – no farther than 505 and 330 m, respectively. Females are on average twice less mobile than males, but only due to pregnancy, when they lead inactive way of life. Mobility of non-pregnant females is almost the same as that of males. It is interesting to note that the "mobility" does not have a continuous character. Both among females and males, there are two groups: 75 % of the individuals are relatively inactive, and 25 % are very mobile. In general, males are more active, crawling from the places of birth, they often became subject to adverse and disastrous circumstances both in the areas without wintering shelters and on the roads where they can be run over by vehicles. A more rapid decline in the proportion of males with age results in that the ratio of females and males in the sexually mature part of the population is on average 3 : 1. This true ratio cannot be received on route censuses: due to the increased mobility of males, their occurrence seems the same as in females, and the ratio – parity (1 : 1).

During visual accounts of adders another wrong impression appears that (gray-multicolored) males are significantly smaller than (brown and green) females. Actually, the even-aged females and males slightly differ in their body length (at the age of 8 years, the average difference is 53.5 – 47.9 = 5.6 cm), and in the length of the whole body with tail – less than 4 cm. To find these differences visually is rather difficult. However, the described impression has an objective nature. It is connected with that found (i.e. more active) males are mostly younger than females, because they mature earlier and eliminate faster from the population. Detailed morphological analysis showed that despite the small differences in the body length of even-aged females and males the head length (bones of the jaw apparatus) is the same, the females head is a little wider, though.

It is also impossible to make any firm conclusion concerning the differences in the body weight. During pregnancy and for a preceding year, the mass of females is greater than that of males. However, after giving birth it falls below the male weight. In general, the range of weight variability in females is about 5 times wider (50%) than in males (8 %). Giving to the embryos a lot of efforts and nutrient reserves (in the liver and fat body), females recover for more than one year. Probably the normal chronology of the adult life stages can be considered the following: maturity and the first pregnancy at the age of 5–6 years, fattening for 2–3 years, the second pregnancy at the age of 7-8 years, fattening for 1–2 years, the third pregnancy at the age of 9–10 years, fattening for 0–1 year, the fourth pregnancy at the age of 11–12 years, death. During its life the female can bear up to 4 broods, with an average lifespan of 8 years – only 1–2. Successful wintering with embryos (in a particularly adverse year) is accessible only to very large females aged 11–13 years, but their proportion in the population is less than 3.5 %.

In spite of good fatness of females with mature eggs and ready to breed, they often begin to feed before that, immediately after they come out of wintering, and continue feeding after mating till the mid-late July. During this time embryos weight increases 3–4 times compared with that of eggs, mostly due to females feeding, but not their nutrient reserves. These

resources are spent in August and September, when females stop feeding, but that becomes dangerous both for fat and inactive females and for large embryos enclosed in a too thin membrane.

Successful development of embryos, efficiency of digestion, the normal growth of the common adder is ensured by maintaining a certain body temperature significantly higher than in the environment (record registered by us was + 28 °C). Observations show that the adult adder is active heliotherm receiving heat mainly from solar radiation. During the summer day, only due to its behavioral thermoregulation the adder is able to maintain a certain, fairly constant body temperature. At that there are a very small number of external and internal variables forming its thermoregulatory behavior, which an individual registers. The adder has a good ability to thermo-location, through which it finds the substrate areas with a higher temperature more favorable for basking. This ability can be expressed as the difference between the temperature of its body and that of the surface area (shelter), where the snake tends to from a less favorable shelter. This value is T_L = 5–8 °C (the first parameter) when the distance is 20–30 cm. The adder can heat up until the body temperature reaches the "maximum voluntary temperature" varying significantly in animals of different status and condition. In well-fed adult animals of both sexes, it equals to the species-specific limit 34.5–35 °C. Field measurements of the "optimal" body temperature are considered not as physiological parameters, but environmental statistical characteristics, and while comparing the representative large samples of females and males they also do not differ. In young snakes and those that have already digested the food, the threshold of voluntary temperature is substantially below 28 °C. In a summer day, this body temperature is achieved even in shelters of medium density (between stones, in grass bunches). This means that small and well-fed snakes are not motivated to crawl out in the blazing sun, the most part of the day they neither appear on the ground surface, nor occur in route counts. In clouds shadow adders tend to preserve the accumulated heat and change their poses (up to 10 times per hour or faster), gradually assembling in dense nodes; it helps to save up to 20 % of heat. Snakes leave for

shelters when their body temperature drops to 18–12 °C. Illnesses, injuries disturb the "regular" physiological parameters and a sick adder "node" can be found on the ground surface at +6 °C.

Within a year an individual must provide some energy and nutrients to support its activity (basal metabolism), mobility, normal growth and restoring reserves after hibernation and reproduction. The medium-sized adder (80 g) requires 294 kJ / individuals / year on basal metabolism, the same amount is spent for mobility. For 11 years of life, the food intake in one female equals to 1200 g, in one male – 800 g. On the island of Kizhi the main prey items for adder are grass and moor frogs. These species have an average population body mass 14 g and caloric content 4 kJ / ind. During its life an adder's female consumes 77 frogs, and male – 52. The total consumption of the whole adders' population containing 2–3 thousand of snakes (as on Kizhi) is 150 kg or 11 thousand of small vertebrates.

Northern peculiarities. The obvious phenological peculiarities of the North (short warm season and long winter) influence the functioning of adders' populations. In the taiga zone the spatial distribution of these animals has a clear focal character. In the North snakes are much more xerophilous and heliothermic than in the south of their area. Only while combining the following three main factors the formation of sustainable adders' settlement is possible – open habitats (meadows, shores), wintering shelters (rock crevices, faults, stone ridges) and neighboring reproductive ponds of frogs (only their current year's young can be prey items of adders' young). The mentioned combination of factors mainly presents on the man-acquired territories (the White Sea coast, Zaonezh'ye, Priladozh'ye), whereas in the vast plain-marshy and forested inner territories of Karelia there are no snakes. The destruction of age-old peasant way of life, extinction and desolation of villages lead to the widespread reduction in the abundance of adders. Recently, a new wave of species expansion has been observed in dacha communities where the land was developed for private households in the 70–90-ies of the last century.

Short warm period apparently has affected the morphological identity of animals: in laboratory keeping the adders from Karelia grow

slower than those from the southern borders of the area (Kharkov) and at the same time females and males are 7–8 cm shorter. Besides the dimensions, the fertility in the North is reduced (up to 12 in Karelia, up to 18–20 in the central part of Russia). At that, in Karelia adders' females reach sexual maturity 1–2 years later (5–7 vs 4–5 years). However, the maximum lifespan in captivity is approximately the same – 11 years. There is a reason to believe that in the northernmost habitats the adder reproduce less often than every 2–3 years, because the relatively favorable conditions for bearing offspring develop there not every year. In these regions, wintering with embryos is also observed, and it may be of more significance than in its habitats southward.

Another feature of northern snakes is significantly higher cardiac function index. The data on adders from the southern borders of the area are not available, but comparing adders with southern species of snakes, it was found that the average cardiac function index is 50% higher in the north and it is closer to the index of mammals (6 ‰), but in pregnant females it is even higher (up to 12 ‰). The increased load on the heart may be related to the fact that this organ, pumping the blood, provides a rapid heat exchange between sun-warmed integuments and the innards, providing quick heat redistribution in the adder's body. This is especially important at low temperatures usual in Karelia and typical weather – "clouds and sun".

Adaptive features of the island population. Two behavioral stereotypes of the adder ("the urge of moving" and "hydrophobia") make adders' island habitats very specific. Water borders are almost impassable for the snakes (swimming or moving on spring ice was sometimes observed by us, but it was never widespread). At a sufficiently high fertility (about 2200 newborns each year with a total population of 5200 snakes on the island of Kizhi), the population density of adders must have increased rapidly in any area. However, this does not happen in mainland territory, but only on the small meadow islands of Zaonezh'ye. Normally adders are prone to spontaneous displacements and spread widely over surrounding habitats. In Karelia with the acute shortage of favorable habitats, the majority of these snakes perish in the winter. Only a small part of the

animals finds new comfortable habitats, or return to old ones. Water borders of the small islands of Zaonezh'ye prevent the snakes from leaving these uniform favorable habitats, save them from death and help to maintain a unique high number. In homogeneous optimal habitats on the island of Kizhi there is no seasonal migration of adders at all, since both the place of feeding and best wintering shelters are located in any part of the island. At the same time, the motor activity of individuals does not change – the maximal distance of seasonal movements is 2.5 km, as in other parts of the area.

However, the enclosed space of the island has its disadvantages, because there is nowhere to escape from the island to avoid the eliminative man's pressure (transport) enhancing on Kizhi every year. Random but intense death of moving adders has led to the situation when in the studied island population there are almost no individuals older than 8–9 years. Only on those islands where this kind of anthropogenic impact is absent, very old individuals are found. So, on the island of Kerkostrov, the adder female (L. t. = 67 cm) the largest in Karelia was captured, and on Volkostrov – the largest adder male (L. t. = 68 cm).

Another consequence of a high number of island populations of adders is that this predator exerts a sharply increasing pressure on the populations of victims, especially those that occupy similar habitats. For example, on Kizhi the number of dark voles is in 2 orders of magnitude lower than that in similar habitats of other islands (Maly Lelikovsky) and mainland territory (vil. Pod'yelniki), where there are no snakes or their number is very small. The large population of adders has also a strong impact on the population of frogs: eating away the oldest (largest) frogs results in a sharp shift of their size-weight distribution to the left. The reduction in victims' number and the increase in abundance of predators within the island (even in the presence of good conditions for wintering and basking) also negatively influence the predator itself. Calculations show that on Kizhi adders withdraw almost 100% of the production of the victims' populations (all yield). The relationship of the number and biomass of the adder and those of its prey items on Kizhi becomes smaller

than 1 : 10, whereas in the mainland territory it ranges from 1 : 100 up to 1 : 10000. The adders do not have enough food (by 1999) – fatness of the snakes on Kizhi is on an average 10–30 % lower comparing with those in mainland territories and in vivarium. Low fatness is probably one of the reasons that on Kizhi the maturation of females is shifted to the age of 6–7 years.

Despite a long history of independent existence on the island of Kizhi, the local adders' population has no clearly defined genetic specificity: in all the studied morphological (dimensions), phenetic (shielding) and genetic (LDH and venom esterase) characteristics the variability of local adders covers all the variability range of adders from the mainland territory.

The common adder is a very conservative species; its adaptations to the habitat in the North or on the island do not fall significantly outside the limits of the vital manifestations that were noted in southern populations. The main difference of northern adders consists in the reduced size of individuals, increased cardiac function index, increased recovery period in females after parturiation. The key parameters of behavior, including thermoregulatory one, remain unchanged.

Bibliography

About food of the adder, Priroda. 1949. No. 7. P. 64–65.

Altuhov Yu. P. Genetic processes in populations. M.: Nauka, 1983. 280 p.

Analysis of the results of observations. Razvedochnyy analiz. M.: Mir, 1981. 693 s

Anan'eva N. B. Borkin L. Ya. Darevskiy I. S. Orlov N. L. Encyclopedia of Russian Nature. M.: ABF, 1998. 576 p.

Andersson S. Freeze tolerance in the Boreal adder Vipera berus, L. // Second Asian Herpetol. Meeting. Ashgabad, 6-10.9.1995. Ashgabad, 1995. P. 13.

Andersson S., Johansson L. Freeze tolerance in the boreal adder Vipera berus // Second World Congress of Herpetology: Abstr. Adelaide, 1994. P. 6.

Andren C. Reproductive behavior in Vipera berus berus (L.), Bull. Soc. Zool. France. 1975. 100. No. 4. P. 683–684.

Andren C. The rule of vomeronasal organs in the reprodactive bechavior of the adder (Vipera berus), Copeia. 1982. No. 1. P. 148–157.

Andren S, Nilson G. Reproductive success and risk of predation in normal and melanistic colour morphs of the adder, Vipera berus, Biological Jounal of the Linnean Society. 1981. Vol. 15. P. 235–246.

Andren C., Nilson G. Reproductive tactics in an island population of adder Vipera berus (L.) with a fluctuating food resources, Amphibia-Reptilia. 1983. Vol. 4. No. 1. P. 69–79.

Andren C., Nilson G. Reproduction in the adder, Vipera berus, and the effect of prey density, 1st Wold Congr. Herpetol. Canterbury, 11–19 sept., 1989. Canterbury, 1989. P. 0.

Andrews R. M., Pough H. Metabolism of squamate reptiles: allometric and ecological relationships // Physoil. Zool. 1985. Vol. 58. № 2. P. 214–231.

Anufriev V. M. Bobrecov A. V. Amphibians and reptiles. Fauna of the European North-East of Russia. T. 4. SPb.: Nauka, 1996. 130 p.

Atlas of the Karelian ASSR. M., 1989. 40 p.

Atlas of the Leningrad Region and the Karelian ASSR. L., 1934. 50 c.

Bakiev A. G. Malenev A. L. Chetanov N. A. Zayceva O. V. Peskov A. N. The adder Vipera berus (Reptilia, Viperidae) in the Volga Basin: materials on biology, ecology and toxinology, Byul. Samarskaya Luka. 2008. T. 17. No. 4 (26). P. 759–816.

Bannikov A. G. Darevskiy I. S. Ischenko V. G. Rustamov A. K. Scherbak N. N. The determinant of amphibious and reptilian fauna of the USSR. M.: Prosveschenie, 1977. 415 p.

Baranov A. S. Marking with fens of different scale of intraspecific groupings of different rank, Fenetika prirodnyh populyaciy. M.: Nauka, 1988. P. 170–177.

Bartholomew G. A. Physiological control of body temperature // Biol. Reptilia. Vol. 12. Physiol. C. Physiol. Ecol. London e. a.: Acad. Press., 1982. P. 167–211.

Bea A., Brana F. Feeding strategies in Vipera spwcies from temperature zones of Western Europe (Reptilia, Viperidae) // 1st Wold Congr. Herpetol. Canterbury, 11–19 sept., 1989. Canterbury, 1989. P. 0.

Beckman W. A., Mitchell J. W., Porter W. P. Thermal model for prediction of a desert inguana's daily and seasonal behavior // Pap. ASME, 1971. NWA/HT-35. 7 p.

Belanovskiy A. S. Physics with the basics of biophysics. Ch. 1. Gemodinamika, akustika, termodinamika. M., 1984. 92 p.
Bell G. The life of the smooth newt (Triturus vulgaris) after metamorphosis // Ecol. Monogr., 1977. Vol. 47. № 3. P. 279–299.
Belova Z. V. Territorial distribution of adder in the Darwin Reserve, Vopr. gerpetologii. L.: Nauka, 1973. P. 35–36.
Belova Z. V. Individual sites of the adder (Vipera berus L.) in summer, Byul. MOIP. Otd. biol. 1974. T. 74. Vyp. 3. P. 146–148.
Belova Z. V. Spatial structure of populations of the adder, Ekologiya. 1976. No. 1. P. 71–75.
Belova Z. V. Accommodation and change in the number of the adder (Vipera berus L.) in the Darwin reserve, Ohrana i racional'noe ispol'zovanie reptiliy. M., 1978. P. 13–25.
Belova Z. V. The movement of the adder on the territory during an active period, Nauchnye osnovy ohrany i racional'nogo ispol'zovaniya zhivotnogo mira. M., 1984. P. 74–77.
Belova Z. V. Study of the lifespan of the adder with the help of tagging, Ekologicheskie osobennosti ohrany zhivotnogo mira. M., 1985. P. 81–84.
Belova Z. V. Repeated meetings in the nature of labeled vipers, Vopr. gerpetologii. Kiev, 1989. P. 27–28.
Bennet A. F. The energetics of reptilian activity // Biology of the Reptilia. 1982. Vol. 13. № 9. P. 155–199.
Bennet A. F., Dawson W. R. Metabolism // Biology of the Reptilia. Academic Press; NY; L., 1976. Vol. 5. Physiology A. P. 127–223.
Berdibaeva Zh. Sh. To the biology of the adder, Fauna i ekologiya zhivotnyh Kazahstana. Alma-Ata, 1981. P. 31–33.
Berk M., Heath E. An analysis of behavioral thermoregulation in the lizard, Dipsosaurus dorsalis // J. Therm. Biol. 1975. Vol. 1. № 1. P. 15–22.
Bezel' V. S. Population ecotoxicology of mammals. M.: Nauka, 1987. 130 p.
Biella H.-J. Beobachtungen zur Vergsellscheftung der Kreuzotter (Vipera b. berus, L.) wahrend der Aktivitatsperiode (Reptilia, Serpentes, Viperidae) // Zool. Abh. Statl. Mus.Tierk. Dresden. 1978. Vol. 35. № 1–14. P. 219–221.
Biella H.-J. Untersuchungen zur Fortpflanzungsbiologie der Kreuzotter (Vipera berus L.) (Reptilia, Serpentes, Vipiridae) // Zool. Abh. Staatl. Mus. Tierk. Dresden. 1979. Vol. 36. P. 117–125.
Biella H.-J., Schiemenz H. Beobachtungen zur Naturunsaufnahme der Kreuzotter (Vipera berus berus L.) im Freiluftterrarium // Zool. Grat. 1980. Vol. 50. № 1. P. 15–16.
Bigon M. Taunsend K. Ecology. Individuals, populations, communities. T. 1. M.: Mir, 1989. 667 p.
Birchard G. F., Black C. P., Schuet G. W., Black V. Influence of pregnapcy on oxigen consumption, heat rate and hematology in the garter snake: implications for the «cost of reproduction» in live bearing reptiles // Comp. Biochem. And Physiol. 1984. A 77. № 3. P. 519–523.
Bozhanskiy A. T. Ecology of adder in an anthropogenic landscape, Ohrana i racional'noe ispol'zovanie reptiliy. M., 1978. P. 37–56.

Bozhanskiy A. T. Pischeev V.A. Influence of some forms of economic activity on the distribution and abundance of the adder, Zool. zhurn. 1978. T. 57. Vyp. 11. P. 1695–1698.
Bozhanskiy A. T. Use of resources of the adder in the north-west of European Russia, Voprosy prikladnoy ekologii (prirodopol'zovaniya), ohotovedeniya i zverovodstva. Kirov, 1997. P. 70–72.
Braunli K. A. Statistical theory and methodology in science and technology. M.: Nauka, 1977. 468 p.
Brodskiy D. A. On the issue of behavioral thermoregulation of a viper in summer in nature, Upravlenie povedeniem zhivotnyh. M.: Nauka, 1978. P. 42–44.
Brown W. S., Parker W. S. A ventral scale clipping system for permanently marking snakes (Reptilia, Serpentes) // J. Herpetol. 1976. № 3. P. 247–249.
Bryuzgin V. D. To the method of studying the age and growth of reptiles, DAN SSSR. 1939. T. 23. No. 4. P. 402–404.
Capula M., Luiselli L., Anibaldi C. Complementary study on the reproductive biology in female adder, Vipera berus (L.), from Eastern Italian Alps // Vie et Milieu. 1992. Vol. 42. № 3/4. P. 327–336.
Castanet J. Etude histologique des marques squelettiques de croissance chez Vipera aspis (L.) (Ophida, Viperidae), Zoologica Soripta. 1974. Vol. 3. P. 137–151.
Castanet J. Quelques observations sur la presence et la structure des marques squelettiques de croissance chez les Amphibians, Bulletin de la Sociele zoologique de France. 1975. Vol. 3. P. 603–620.
Castanet J. Age Estimation and Longevity in Reptiles, Gerontology. 1994. Vol. 40. P. 174–192.
Castanet J., Naulleau G. Donnees experimentales sur la valeur des marquos skelettiquee comme indicateur de l'age chex Vipera aspis (L.) (Ophidia, Viperidae), Zool. Scr. 1974. Vol. 3. P. 201–208.
Castanet J., Naulleau G. La squelettochronologie chez les Reptiles.II. Résultats experimentaux sur la signification des marques de crossance squelettiques chez les Serpentes.Remarques sur la crossance et la longevite de la Vipere aspic. (1), Ann. Natur. Zool. et Biol. Anim. 1985. Vol. 7. No. 1. P. 41–62.
Cherdancev V. G. Lyapkov S. M. Cherdancev E. M. Mechanisms of formation of fecundity in Rana arvalis, Zool. zhurn. 1997. T. 76. Vyp. 2. P. 187–198.
Cherlin V. A. Methods of adapting the reptiles to the temperature conditions of the environment, Zhurn. obsch. biol. 1983. T. 44. No. 6. P. 753–764.
Cherlin V. A. Population aspects of thermal adaptations of reptiles, Itogi nauki i tehniki 1970–1988. Ser. Zoologiya pozvonochnyh. T. 17, VINITI. M., 1984. P. 135–172.
Cherlin V. A. Condition and evolution of thermoregulation in reptiles, Voprosy gerpetologii. Kiev, 1989. P. 278–281.
Cherlin V. A. Methods of research on thermobiology of reptiles, Pozvonochnye zhivotnye Uzbekistana. Tashkent, 1991. P. 70–79.
Chernomordikov V. P. How to keep reptiles, Moskovskiy zoopark. M., 1950. 40 p.
Chiszar D., Melcer T., Lee R., Rodcliffe Ch. W., Duvall D. Chemical cues used by prarie rattlesnakes (Crotalis viridis viridis) to follow trails on rodent prey // J. Chem. Ecol. 1990. Vol. 16. № 1. P. 79–81.
Climate of Petrozavodsk. L.: Gidrometeoizdat, 1982. 214 p.
Comparative physiology of animals, Pod red. L. Prosser. M.: Mir, 1977. T. 1. 608 p.

Contents of poisonous snakes of Central Asia in captivity, Red. G. P. Sultanov. Tashkent, 1972. 178 p.
Cossins A. R., Bowler K. Temperature biology of animals. London; New York: Capman and Hall, 1987. Y. 339 p.
Darevskiy I. S. Amphibians and reptiles, Priroda Leningradskoy oblasti. L., 1983. P. 125–131.
Darevskiy I. S. Method of studying reptiles in reserves, Amfibii i reptilii zapovednyh territoriy. M., 1987. P. 25–32.
Dawson W. R. On the physiological significance of the preferred body temperature of reptiles // Ecol. Stud. 1975. Vol. 12. P. 443–473.
Demidov I. I. Quaternary deposits of the reserve "Kizhi skerries", Ostrova Kizhskogo arhipelaga. Biogeograficheskaya harakteristika: Tr. KNC RAN. Ser. Biogeografiya Karelii. Vyp. 1. Petrozavodsk, 1999. P. 11–15.
Deparma N. K. To the method of determining the age of moles, Byul. MOIP. Otd. biol. 1954. T. 59. Vyp. 6. P. 11–25.
Devyatova E. I. The natural environment and its changes in the Holocene. Petrozavodsk, 1986. 110 p.
Dinesman L. G. Kaleckaya M. L. Methods for quantifying amphibians and reptiles, Metody ucheta chislennosti i geograficheskogo raspredeleniya nazemnyh pozvonochnyh. M., 1952. P. 329–340.
Dmi'el R. Relation of metabolic to body weight in snake // Copeia. 1972. № 1. P. 179–181.
Dol'nik V. R. Allometric "arrangement" of the energy of reptiles, Zool. zhurn. 1999. T. 78. No. 11. P. 1330–1339.
Dol'nik V. R. Allometry of reproduction in poikilotherms and homoiothermal vertebrates, Izv. akad. nauk. Ser. biol. 2000. No. 6. P. 702–712.
Dol'nik V. R. Standard metabolism in vertebrate animals: what are the causes of the differences between poikilothermic and homeoothermal classes, Zool. zhurn. 2002. T. 81. No. 6. P. 643–654.
Dol'nik V. R. Postnikov S. N. Caloric content of food objects and nutritional needs of birds, Energetika pitaniya i rosta zhivotnyh. Sverdlovsk: Izd-vo URO RAN, 1990. P. 131–140.
Drobenkov S. M. The method of individual labeling of the adder (Vipera berus L.) on the basis of morphological variability, Voprosy gerpetologii. Kiev, 1989. P. 83–84.
Drobenkov S. M. The thermoregulatory behavior of the adder (Vipera berus L.) in the conditions of Belorussia, Dep. red. zhurn. Izvestiya AN BSSR. Ser. biol. nauk . Minsk, 1990. 18 p.
Drobenkov S. M. Ecology and social organization of adder (Vipera berus) in winter period, Aktual'nye problemy gerpetologii i toksinologii: Sb. nauch. tr. Vyp. 5. Tol'yatti, 2001. P. 45–50.
Drobenkov S. M. Morphophysiological adaptation of the adder to the winter period of the life cycle, Zmei Vostochnoy Evropy: Mater. mezhdunar. konf . Tol'yatti, 3–5 fevr. 2003 g. Tol'yatti, 2003. P. 13–15.
Dubinin N. P. General Genetics. M.: Nauka, 1986. 560 p.
Edelstam C. A long-term study of snake populations // 1st Wold Congr. Herpetol. Canterbury, 11–19 sept., 1989. Canterbury, 1989. P. 0.

Elina G. A. Filimonova L. V. Stages of development of vegetation and climate in eastern Zaonezhie in postglacial Holocene, Ostrova Kizhskogo arhipelaga. Biogeograficheskaya harakteristika: Tr. KNC RAN. Ser. Biogeografiya Karelii. Vyp. 1. Petrozavodsk, 1999. P. 21–27.

Elmberg J. Factors affecting male yearly mating success in the common frog, Rana temporaria // Behav. Ecol. And Sociobiol. 1991. Vol. 28. № 2. P. 125–131.

Elmberg J. Long-term survival, length of breeding season, and operational sex ratio in a boreal population of common frogs, Rana temporaria L. // Can. J. Zool. 1990. Vol. 68. № 1. P. 121–127.

Emel'yanov A. L. Snakes of the Far East, Tr. Vladivostokskogo otd. Gop. Russkogo geogr. ob-va. Vladivostok, 1929. T. 3 (20). Vyp. 5. P. 757–765.

Erling S., Goransson G., Hogstredt G., Gansson G., Liberg O., Loman G., Nillson I. N., von Schantz T., Sylven M. More thoughts on vertebrate predator regulation of the prey // Amer. Natur., 1988. Vol. 132. № 1. P. 148–154.

Fedorov N. V. Uzenbaev S. D. Znamenskiy S. R. Influence of the mowing on the mesofauna of the grassland of the meadows on. Kizhi, Biologicheskie osnovy izucheniya, osvoeniya i ohrany zhivotnogo i rastitel'nogo mira, pochvennogo pokrova Vostochnoy Fennoskandii. Petrozavodsk, 1999. P. 105.

Fish F. E., Consqrove L. A. Behavioral thermogregulation of small American alligators in water: postural changes in relation to the thermal environment // Copeia. 1987. № 3. P. 804–807.

Fomichev S. N. Ecology of island populations of brown frogs of Karelia: Dip. … kand. biol. nauk. Petrozavodsk, 2004. 188 p.

Fomichev S. N. Korosov A. V. Specificity of the Species Structure of the Amphibian Population of Zaonezhie, Bioraznoobrazie Evropeyskogo Severa: Tez. dokl. Petrozavodsk. 3–7 sentyabrya 2001 g. Petrozavodsk, 2001a. P. 202–203.

Fomichev S. N. Korosov A. V. Comparison of estimates of the relative and absolute numbers of the population of the brown frog, Biologiya – nauka XXI veka. 5-ya Puschinskaya konferenciya molodyh uchenyh. Puschino, 2001b. P. 306–307.

Fromhold E. Die Kreuzotter. Wittenberg, 1969. 88 p.

Fukada H. Body temperatures of snakes in the fields.1. Elaphe quedrivirgata // Jap. J. Herpetol. 1985. Vol. 11. № 1. P. 25–32.

Ganschuk S. V. Body temperature and its dynamics in two species of lizards and two species of snakes, Voprosy gerpetologii , Mater. Pervogo s'ezda Gerpetologicheskogo obschestva im. A. M. Nikol'skogo. Puschino, 4–7 dekabrya 2000 g. Puschino; M.: Izd-vo MGU, 2001 (stendovyy doklad).

Garanin V. I. Amphibians and reptiles in the nutrition of vertebrates, Prirodnye resursy Volzhsko-Kamskogo kraya. Zhivotnyy mir. Kazan': Izd-vo KGU, 1976. Vyp. 4. P. 86–111.

Garanin V. I. Amphibians and reptiles of the Volga-Kama region. M.: Nauka, 1983. 176 p.

Gavrilov V. V. Algorithm for recalculating the time budget into the energy budget in the ecological energy of sandpipers, Aktual. probl. ekol. i zookul'tury, Mosk. gop. akad. vet. med. i biotehnol. M., 1995. P. 122–127.

Gibson A. R., Smucky D. A., Kollar J. The effect of feeding and ecdysis on temperature selection by young garter snakes in a simple thermal mosaic // Can. J. Zool. 1989. Vol. 67. № 1. P. 19–23.

Gil'manov T. G. Introduction to quantitative trophology and ecological bioenergy of vertebrates in terrestrial ecosystemsCh. 1. Osnovnye modeli. Poykilotermnye zhivotnye . M.: Izd-vo MGU, 1987. 180 p.
Gilyarov A. M. Population Ecology. M.: Izd-vo MGU, 1991. 191 p.
Giplin M. E. Spatial structure and viability of populations, Zhiznesposobnost' populyaciy: Prirodoohrannye aspekty. M.: Mir, 1989. P. 158–173.
Glotov I. N. Erdakov L. N. Kuzyakin V. A. Community of small mammals of Baraba. Novosibirsk: Nauka, 1978. 231 p.
Golubev A. I. Geological structure of the Kizhi skerries reserve area, Ostrova Kizhskogo arhipelaga. Biogeograficheskaya harakteristika: Tr. KNC RAN. Ser. Biogeografiya Karelii. Vyp. 1. Petrozavodsk, 1999. P. 4–10.
Goncharenko A. E. Ecology and patterns of reproduction of the Rana arvalis (Rana arvalis Nils.) in the conditions of the Yuzhny Bug river basin, Vid i ego produktivnost' v areale. M.: Nauka, 1983. P. 82–88.
Graves B. M., Duvall D. An experimental study of aggregation and thermoregulation prairie rattlsnakes (Crotalus viridis viridis) // Herpetologia. 1987. Vol. 47. № 2. P. 259–264.
Grigor'ev O. V. To the ecology of amphibians and reptiles in the flood plain of the Ob ', Sukcessiya zhivotnogo naseleniya v biocenozah poymy reki Obi. Novosibirsk: Nauka, 1981. P. 154–160.
Grubant V. N. Rudaeva A. V. Vedmederya V. I. Growing of juvenile adder in captivity, Ekologiya. 1972. No. 5. P. 85–87.
Grubant V. N. Rudaeva A. V. Vedmederya V. M. Perspective method of growing an ordinary viper, Vopr. gerpetologii. L., 1973. P. 75–77.
Gtriffits I. Skeletal lamellae as an index of age in heterothermous tetrapods // Ann. Mag. Nat. Hist. 1961. Vol. 4. № 4. P. 449–465.
Gurtovoy N. N. Matveev B. S. Dzerzhinskiy F. Ya. Practical zootomy of vertebrates. Amphibians and reptiles. M.: Vysshaya shkola, 1978. 407 p.
Haapanen A. Breeding of the common frog (Rana temporaria L.) // Ann. zool. fenn. 1982. Vol. 19. № 2. P. 75–79.
Haartman L.von. Huggorn plundrar fågelholk // Ornis fenn. 1976. Vol. 53. № 2. P. 48–51.
Heruvimov V. D. Sokolov A. S. Sokolova L. A. To the definition of sex and age of the adder, Vestnik zoologii. 1977. No. 6. P. 39–44.
Hilkov T. N. Experimental ecology of the adder Vipera berus L: Dip. … kand. biol. nauk. Petrozavodsk, 1998. 105 p.
Hilkov T. N. Korosov A. V. Thermal transfer behavior of the adder, Aktual'nye problemy biologii: Tez. dokl. 4-ya mol. konf. 11–12 aprelya 1996. Syktyvkar, 1996. P. 133.
Hilkov T. N. Korosov A. V. Factors of daily activity of the adder, Problemy ekologii i toksikologii. Petrozavodsk, 1997. P. 118–126.
Hofer R., Ladurner H., Gattringer A., Wieser W. Relationship between the temperature preferenda of fishes, amphibians and reptiles, and the substrat affinities of ther trypsins // J. Comp. Physiol. 1975. B 99. № 4. P. 345–355.
Hohlova T. Yu. Birds of the Kizhi skerries of Onega Lake, Ostrova Kizhskogo arhipelaga. Biogeograficheskaya harakteristika: Tr. KNC RAN. Ser. Biogeografiya Karelii. Vyp. 1. Petrozavodsk, 1999. P. 107–112.

Hohlova T. Yu. Semina O. V. Nature of Kizhi skerries. Petrozavodsk: Kareliya, 1988. 104 p.
Igolkina Vol. A. Breedind the Lebetine viper ssp (Vipera lebetina turanica and Vipera. l. obtusa) at Leningrad Zoo // Int. Zoo Yb. 1989. Vol. 28. P. 183–189.
Irisov E. A. The case of an attack of a viper on a nest of rosefinch, Ornitologiya. 1972. Vyp. 10. P. 334.
Ivanova N. L. Growth, development, energy supply of the larvae of the Rana arvalis, contained on different feed rations, Vid i ego produktivnost' v areale. Mater. 5-go vsep. sovesch. 10–12.11.1988 g., Tbilisi. Vil'nyus, 1988. P. 131–133.
Ivanter E. V. Population ecology of small mammals of the taiga Northwest of the USSR. L.: Nauka, 1975. 240 p.
Ivanter E. V. Amphibians and reptiles. Petrozavodsk, 1975. 96 p.
Ivanter E. V. To the study of the northern populations of the grass frog, Materialy k 3-mu Vsesoyuznomu soveschaniyu «Vid i ego produktivnost' v areale». Vil'nyus, 1980. P. 67–68.
Ivanter E. V. To the study of feeding of the brown frog (Rana temporaria L.), Ekologiya nazemnyh pozvonochnyh Severo-Zapada SSSR. Petrozavodsk, 1981. P. 5–12.
Ivanter E. V. Amphibians and reptiles. Petrozavodsk, 1988. 96 p.
Ivanter E. V. Faunistic analysis and problems of zoogeographical regionalization, Biogeografiya Karelii: Tr. KarNC RAN. Ser. B. Biologiya. Vyp. 2. Petrozavodsk: Izd-vo KarNC RAN, 2001. P. 76–81.
Ivanter E. V. Ivanter T. V. Ecological structure and dynamics of the population of small mammals of Lake Ladoga area, Fauna i ekologiya ptic i mlekopitayuschih Severo-Zapada SSSR. Petrozavodsk, 1983. P. 72–99.
Ivanter E. V. Ivanter T. V. Tumanov I. L. Adaptive features of small mammals. L.: Nauka, 1985. 318 p.
Ivanter E. V. Korosov A. V. Introduction to quantitative biology. Petrozavodsk: Izd-vo PetrGU, 2003. 304 p.
Ivanter E. V. Korosov A. V. Basics of Biometrics. Petrozavodsk, 1992. 168 p.
Ivanter E. V. Korosov A. V. Amphibians and reptiles. Petrozavodsk, 2002. 160 p.
Ivanter E. V. Marvin M. Ya. On the results of the study of the fauna of terrestrial vertebrates of Karelia, Razvitie nauki v Karelii za 50 let Sovetskoy vlasti: Uchen. zap. Petrozavodskogo un-ta. Petrozavodsk, 1968. T. 16. Vyp. 4. P. 175–180.
Iverson J. B. Patterns of relative fecundity in snakes // Fla Sci. 1987. Vol. 50. № 4. P. 223–233.
Juszczyk W. Płazy i gady Krajowe. Częšč 3. Gady. Reptilia. Warszawa, 1987. 214 p.
Kaisila J. Herpetologische Notizen.1. Die Zauneidechse, Lacerta agilis, in ostfennoskcandien // Arch. soc. zool. bot. Fenn. «Vanamo». Helsinki, 1949. № 3. P. 143–150.
Kalabuhov N. I. The technique of experimental studies on the ecology of terrestrial vertebrates. M.: Sov. nauka, 1951. 177 p.
Kaleckaya M. A. To the biology of the adder, Priroda. 1956. No. 5. P. 101–102.
Kaleckaya M. L. Fauna of amphibians and reptiles of the Darwin Reserve and its changes under the influence of the Rybinsk Reservoir, Rybinskoe vodohranilische. Ch. 1. M., 1953. P. 176–186.

Karpuhin I. P. Karpuhina N. M. The weight of the lens of the eye as a criterion for the age of the red squirrel (Sciurus vulgaris), Zool. zhurn 1971. T. 50. Vyp. 2. P. 274–277.
Kashkarov D. N. Fundamentals of animal ecology. M.; L., 1938. 602 p.
Kataev G. D. Makarova O. A. Change in the fauna of terrestrial vertebrates of the Lapland Reserve for a half-century period, Monitoring prirodnoy sredy Kol'skogo Severa. Apatity, 1984. P. 75–92.
Kaufman B. Z. Preference behavior of ectothermic animals. Petrozavodsk, 1989. 149 p.
Kessler K. Materials for the knowledge of Onega Lake and Obnezhsky Krai, mainly in zoological terms. SPb., 1868. 144 p.
Klevezal' G. A. Kleynenberg S. E. Determining the age of mammals in the layered structures of teeth and bone. M.: Nauka, 1967. 144 p.
Klevezal' G. A. Recording structures of mammals in zoological studies. M.: Nauka, 1988. 285 p.
Koli G. Analysis of animal populations. M.: Mir, 1979. 362 p.
Koreneva L. G. Stages of development of embryos of some snakes on the time of egg laying, Arhiv anatomii, gistologii i embriologii. 1976. Vyp. 12. P. 75–81.
Korneev G. A. The possibility of using the weight of the lens of the eye as a criterion for the age of a large gerbil, Zool. zhurn. 1976. T. 55. Vyp. 3. P. 443–444.
Kornouhova N. G. Determination of the age of gray and black rats, Ekologiya . 1971. No. 2. P. 71–76.
Környei N. M. Observations on Vipera ammodytes and Vipera berus during the pre-sloughing period // Bulletin of the Chicago Herpetol. Soc. 1982. Vol. 17. № 4. P. 85–95.
Korosov A. V. Results of taking into account the absolute abundance of forest voles in the Southern Baikal region, Vsesoyuzn. sovesch. po problemam kadastra i ucheta zhivotnogo mira. M., 1986. P. 134–135.
Korosov A. V. To the ecology of the adder in Karelia, Fauna i ekologiya nazemnyh pozvonochnyh. Petrozavodsk, 1988. P. 15–23.
Korosov A. V. Organization of summer practice in zoology of vertebrates. Petrozavodsk, 1994. 68 p.
Korosov A. V. Reptiles, Krasnaya kniga Karelii. Petrozavodsk: Izd-vo «Kareliya», 1995a. P.184–187.
Korosov A. V. Borders of reptilian habitats in Karelia and their determining factors, Ekosistemy Severa: struktura, adaptacii, ustoychivost'. M., 1995b. P. 114–126.
Korosov A. V. Ecological applications of component analysis. Petrozavodsk: Izd-vo PetGU, 1996a. 152 p.
Korosov A. V. Anthropogenic landscapes of the Kizhi archipelago are optimal habitats of the adder, Krupnye ozera Karelii – Ladozhskoe i Onezhskoe: Tez. dokl. mezhdunar. konf. Petrozavodsk, 1996b. P. 59–61.
Korosov A. V. Bogdanova A. A. Ilyuha V. A. Genetic polymorphism of Karelian populations of the adder, Kontrol' sostoyaniya i regulyaciya funkciy biosistem. Petrozavodsk, 1995. P. 15–18.
Korosov A. V. Development of a systematic approach to the study of island animal populations (on the example of the adder, Vipera berus L.): Dip. … dokt. biol. nauk. Petrozavodsk, 2000a. 333 p.
Korosov A. V. Reptiles of the Karelian-Kola region, Biogeografiya Karelii: Tr. KNC RAN. Petrozavodsk, 2000b. Vyp. 2. P. 96–102.

Korosov A. V. Age composition of the island population of an ordinary viper, Voprosy gerpetologii: Mater. Pervogo s'ezda Gerpetologicheskogo obschestva. Puschino, 4–7 dekabrya 2000 g. Puschino; M.: Izd-vo MGU, 2001. P. 130–132.
Korosov A. V. Simulation of ecological objects in the environment of the Microsoft Excel package, Ekologiya.. 2002a. No. 2. P. 144–147.
Korosov A. V. Simulation modeling in MS Excel environment (using examples from ecology). Petrozavodsk, 2002b. 212 p.
Korosov A. V. Snakes of Valaam Island, Biogeografiya Karelii (flora i fauna taezhnyh ekosistem). Vyp. 4. Petrozavodsk, 2003. P. 224–226.
Korosov A. V. Analysis of mortality in island populations of the adder, Sovremennaya gerpetologiya . T. 3/4. Saratov, 2005a. P. 71–83.
Korosov A. V. Reptiles of the Kizhi Archipelago, 10 let ekologicheskomu monitoringu muzeya-zapovednika «Kizhi». Petrozavodsk, 2005b. P. 127–131.
Korosov A. V. Reptiles and amphibians, Krasnaya kniga Respubliki Kareliya. Petrozavodsk: Izd-vo «Kareliya», 2007a. P. 219–222.
Korosov A. V. Special methods of biometrics. Petrozavodsk, 2007b. 364 p.
Korosov A. V. Dynamics of the number of the island population of the adder (Vipera berus), Zool. zhurn. 2008a. T. 87. Vyp. 10. C. 1235–1249.
Korosov A. V. A simple model of the adder basking (Vipera berus L.), Sovremennaya gerpetologiya. 2008b. T. 8. Vyp. 2. P. 118–136.
Korosov A. V. Distribution of the adder on the islands of the Kizhi archipelago, Tr. KarNC RAN. Ser. Biogeografiya. Vyp. 9. Petrozavodsk, 2009. P. 102–108.
Korosov A. V. Two-loop negative feedback and the viper thermoregulation model, Uchenye zapiski Petrozavodskogo gosudarstvennogo universiteta. Ser. Estestvennye i tehnicheskie nauki. 2008c. No. 1. P. 74–82.
Korosov A. V. Wintering of the adder (Vipera berus) with embryos, Principy ekologii. 2012. No. 1. P. 54–59. DOI: 10.15393/j1.art.2012.321
Korosov A. V. Demidovich A. P. Structural features of the population of small mammals of anthropogenic zones of the southern coast of the lake Baikal, Ohrana i vosproizvodstvo zhivotnyh v Pribaykal'e. Irkutsk, 1987. P. 8–17.
Korosov A. V. Fomichev S. N. Cadastral characteristics of the population of small mammals of the Kizhi archipelago, Ostrova Kizhskogo arhipelaga. Biogeograficheskaya harakteristika: Tr. KNC RAN. Ser. Biogeografiya Karelii. Vyp. 1. Petrozavodsk, 1999a. P. 100–106.
Korosov A. V. Fomichev S. N. Fauna of amphibians and reptiles of the Kizhi archipelago, Ostrova Kizhskogo arhipelaga. Biogeograficheskaya harakteristika: Tr. KNC RAN. Ser. Biogeografiya Karelii. Vyp. 1. Petrozavodsk, 1999b. P. 96–99.
Korosov A. V. Fomichev S. N. Leading factors in the location of amphibians on the islands of the Kizhi archipelago, 10 let ekologicheskomu monitoringu muzeya-zapovednika «Kizhi». Petrozavodsk, 2005a. P. 120–126.
Korosov A. V. Fomichev S. N. Territorial location of brown frogs during the breeding season, Ekologiya. Eksperimental'naya genetika i fiziologiya: Tr. KarNC RAN. Vyp. 11. Petrozavodsk, 2007. P. 85–92.
Korosov A. V. Fomichev S. N. The structure of trophic relations in island zoocenosis: dominance of an ordinary viper, Mater. III s'ezda Gerpetologicheskogo obschestva im. A. N. Nikol'skogo (17–22 sentyabrya 2006 g., Puschino-na-Oke). SPb., 2008. P. 191–197.

Korosov A. V. Fomichev S. N. Trophic relations in island zoocenosis, Strukturno-funkcional'nye osobennosti biosistem Severa (osobi, populyacii, soobschestva): Mater. konf. (26–30 sentyabrya 2005 g., Petrozavodsk). Petrozavodsk, 2005b. P. 190–193.

Korosov A. V. Hilkov T. N. Experience in captivity of an ordinary viper, Voprosy populyacionnoy biologii: Tr. PetrGU. Ser. biol. Vyp. 2. Petrozavodsk: Izd-vo PetrGU, 2008b. P. 39–47.

Korosov A. V. Hilkov T. N. Fomichev S. N. Kizhi is a mecca of reptiles, Ostrova Kizhskogo arhipelaga. Biogeograficheskaya harakteristika: Tr. KNC RAN. Ser. Biogeografiya Karelii. Vyp. 1. Petrozavodsk, 1999. P. 91–95.

Korosov A. V. Hilkov T. N. Quantitative characteristic of daily activity of the adder, Uchenye zapiski Petrozavodskogo gosudarstvennogo universiteta. Ser. Estestvennye i tehnicheskie nauki. 2008a. No. 4. P. 52–55.

Korosov A. V. Ivanter E. V. Variability of phenological phenomena in the life of a viper in the conditions of Karelia, Zmei Vostochnoy Evropy. Tol'yatti, 2003. P. 34.

Korosov A. V. Korosov A. A. GIS introduction technique: Application in ecology. Petrozavodsk: Izd-vo PetrGU, 2006. 186 p.

Korosov A. V. Prohorova T. A. Number and age composition of the island population of the adder, Biologicheskie osnovy izucheniya, osvoeniya i ohrany zhivotnogo i rastitel'nogo mira, pochvennogo pokrova Vostochnoy Fennoskandii: Mezhdunar. konf. i vyezdnaya nauchnaya sessiya otdela obschey biologii RAN, Petrozavodsk, 6–9 sentyabrya 1999 g. Petrozavodsk, 1999. P. 84–85.

Korosov A. Vol., Zamber N. S., Fomischev S. N., Uzenbaev S. S. A common frog's (Rana temporaria, L.) spawn and tadpoles survival rates in small transient basins // Ученые записки Петрозаводского государственного университета. Сер. Естественные и технические науки. 2010. № 2. (в печати)

Koskela P., Pasanen S. The reprodactive biology of the female common frog, Rana temporaria L., in northen Finland // Aquilo Ser. Zool. 1975. Vol. 16. P. 1–12.

Kosov S. V. Influence of some abiotic factors on the daily and seasonal activity of the green snake, Voprosy eksperimental'noy zoologii. Minsk.: Nauka i tehnika, 1983. P. 86–90.

Kosov S. V. Bozhanskiy A. T. Dynamics of the Viper's normal density (Vipera berus L.) as a criterion in the development of rational use regimes, Dinamika zoocenozov, problemy ohrany i racional'nogo ispol'zovaniya zhivotnogo mira Belorussii. Minsk, 1989. P. 275–276.

Kudryavcev S. V. Frolov V. E. Korolev A. V. The Terrarium and its inhabitants. M., 1991. 296 p.

Kuranova V. N. Kolbincev V. G. Bloodless methods for studying the feeding of snakes, Ekologiya nazemnyh pozvonochnyh zhivotnyh Sibiri. Tomsk: Izd-vo TGU, 1983. P. 161–169.

Kutenkov A. P. Reproduction and some features of the ecology of Rana Arvalis in Middle Karelia, Vid i ego produktivnost' v areale. Ch. 5. Voprosy gerpetologii. Sverdlovsk, 1984. P. 25.

Kutenkov A. P. Amphibians and reptiles, Fauna zapovednika «Kivach». M., 1988. P. 9–11.

Kutenkov A. P. Ecology of reproduction of tailless amphibians of Karelia and the Kola Peninsula, Nazemnye pozvonochnye zhivotnye v zapovednikah Severa Evropeyskoy chasti RSFSR. Petrozavodsk, 1990. P. 54–70.

Kutenkov A. P. On the role of the weather factor in the dynamics of the population of the grass frog (Rana temporaria) in the north, Ekologiya. 1998. No. 1. P. 49–54.
Kutenkov A. P. Factors determining the dynamics of the number of tailless amphibians of Eastern Fennoscandia, Biologicheskie osnovy izucheniya, osvoeniya i ohrany zhivotnogo i rastitel'nogo mira, pochvennogo pokrova Vostochnoy Fennoskandii. Petrozavodsk, 1999. P. 86–87.
Kutenkov A. P. Ecology of the brown frog (Rana temporaria L., 1758) in the North-West of Russia. Petrozavodsk: Izd-vo PetrGU, 2009. 140 p.
Kutenkov A. P. Korosov A. V. Materials on the biogeography of amphibians of the Karelian-Kola region, Biogeografiya Karelii. Petrozavodsk, 2001. P. 103–109
Kutenkov A. P., Mosiyash S.S. On the dinamics of population of common frog (Rana temporaria) in the north-west of Russia // Russian Jornal of Herpetology. 2000. Vol. 7. № 2. P. 123–134.
Kutenkov A. P. Panarin A. E. Shklyarevich F. N. Ecology of tailless amphibians of Karelia and the Kola Peninsula, Nazemnye pozvonochnye zhivotnye v zapovednikah Severa Evropeyskoy chasti RSFSR. M., 1990. P. 54–70.
Kutenkov A. P. Scherbakov A. N. Mammals, Flora i fauna zapovednikov SSSR. Fauna zapovednika «Kivach». M., 1988. P. 36–43.
Kuz'min S. L. Amphibious former USSR. M.: Tovarischestvo nauchnyh izdaniy KMK, 1999. 298 p.
Kuznecov O. L. Brazovskaya T. I. Stoykina N. V. Flora, vegetation and genesis of bogs in the protected area of the Kizhi Museum-reserve, Ostrova Kizhskogo arhipelaga. Biogeograficheskaya harakteristika: Tr. KarNC RAN. Petrozavodsk, 1999. P. 48–54.
Lakin G. F. Biometrics. M.: Vysshaya shkola, 1973. 344 p.
Lapshin N. V. The nesting results of 4 species of chiffchaff species of the g. Phylocsopus in Karelia, II Mezhdunar. nauchno-prakt. konf. Ch. 1. Perm': Izd-vo KNC RAN, 1995. P. 58–59.
Larina N. I. Methods of field studies of the ecology of terrestrial vertebrates. Saratov, 1968. 54 p.
Larionov P. D. To the ecology of the adder (Vipera berus) in Yakutia, Zool. zhurn. 1977. T. 56. Vyp. 6. P. 919–923.
Lasos J. B. Postures of the military dragon (Ctenophorus isolepis) in relation to sulstrate temperature // Amphibia-Reptilia. 1987. Vol. 8. № 4. P. 419–423.
Leloup P. Methode simpe poure calculer approximativement et comparativement les matieres de reservedes serpents vivants // Acta. zool. et pathol. antverpion. 1976. № 64. P. 91–94.
Lewke R. E., Stroud R. K. Freeze branding as a method of marking snakes // Copeia. 1974. № 4. P. 997–1000.
Lindell L. E., Forsman A. Density effects and snake predation: Prey limitation and reduced growth rate of adders at high density of conspecifics // Can. J. Zool. 1996. Vol. 74. № 6. P. 1000–1007.
Litvin V. Yu. Gray and mountain voles, Itogi mecheniya mlekopitayuschih. M.: Nauka, 1980. P. 221–247.
Litvinov N. A. Thermobiological studies, Zmei Volzhsko-Kamskogo kraya. Samara: Izd-vo Samarskogo nauchnogo centra RAN, 2004. P. 109–146.
Litvinov N. A. Body temperature and microclimatic habitat conditions of reptiles of the Volga basin, Zool. zhurn. 2008. T. 87. No. 1. P. 62–74.

Litvinov N. A. Ganschuk S. V. Methods of research of amphibians and reptiles. Perm': Izd-vo PGPU, 2003a. 49 p.
Litvinov N. A. Ganschuk S. V. Thermobiology of Serpents of the Volga-Kama Region, Zmei Vostochnoy Evropy: Materialy Mezhdunar. konf. Tol'yatti, 3–5 fevralya 2003 g., In-t ekologii Volzhskogo basseyna RAN. Tol'yatti, 2003b. P. 50–53.
Litvinov N. A. Ganschuk S. V. Thermobiology of the adder (Vipera berus, Reptilia, Serpentes) in the Volga basin, Izvestiya Samarskogo NC RAN. 2009. T. 11. No. 1. P. 89–95.
Litvinov N. A. Sipatov N. N. Thermobiological characteristics of snakes of the Lower Volga Region, Aktual'nye problemy gerpetologii i toksinologii, In-t ekologii Volzhskogo basseyna RAN. Tol'yatti, 2006. No. 9. P. 115–118.
Luiselli L. M., Anibaldi C. The diet of the adder (Vipera berus L.) in two alpine environments // Amphibia-Reptilia. 1991. Vol. 12. № 2. P. 214–217.
Lukashov A. D. Relief and education conditions Kizhi Island, Ostrova Kizhskogo arhipelaga. Biogeograficheskaya harakteristika: Tr. KarNC RAN. Ser. Biogeografiya Karelii. Vyp. 1. Petrozavodsk, 1999. P. 16-20.
Lukashov A. D. Demidov I. I. Conditions for the formation of the relief and quaternary deposits of Karelia in the Late and Postglacial periods as the basis for the formation of a modern natural environment, Biogeografiya Karelii: Tr. KNC RAN. Ser. Biologiya. Vyp. 2. Petrozavodsk, 2001. P. 3–11.
Lysenko S., Gillis J.E. The effect of ingestive status on the thermoregulatory behvior of themnophis sertalis sertalis and T.s. parietalis // J. Herpetol. 1980. Vol. 14. № 2. P. 155–159.
Madsen Th., Still B. The effect of size dependent mortality on color morphs in male adders, Vipera berus // Oikos.1988. Vol. 52. № 1. P. 73–78.
Madsen Th. Ecology of Vipera berus: careful mother stay put // 1st Wold Congr. Herpetol. Canterbury, 11–19 sept., 1989a. Canterbury, 1989. P. 0.
Madsen Th. Female adder in southern Sweden recorded giving birth in spring // Amphibia Reptilia. 1989б. 10. № 1. P. 88–89.
Mahlin M. D. Terrarium. M.: Lesnaya promyshlennost', 1966. 153 p.
Mahlin M. D. Artificial feeding of poisonous snakes in captivity, Priroda . 1970. No. 1. P. 124–125.
Makfed'en E. Ecology of animals. M.: Mir, 1965. 376 p.
Marin Yu. V. About a technique of definition of number of wood microtine rodents, Vtoroy s'ezd Vsesoyuzn. teriol. o-va. M.: Nauka, 1978. P. 157–159.
Marvin M. Ya. Amphibians and reptiles of the Karelo-Finnish SSR, Izv. Karelo-Finskoy nauchno-issled. bazy AN SSSR. Petrozavodsk, 1948. No. 2. P. 61–83.
Mayr E. Population, species and evolution. M.: Mir, 1974. 460 p.
Medico-biological reference book of the Karelian ASSR. Petrozavodsk, 1990. 196 p.
Miheeva K. V. Pavlov B. K. Kulikov A. N. Bezel' V. S. Smirnov A. I. Experience in determining the spatial structure of a species within a continuous range (by the example of a squirrel), Populyacionnye mehanizmy dinamiki chislennosti zhivotnyh. Sverdlovsk, 1979. P. 15–22.
Mil'to K. D. On the spread of the green snake (Natrix natrix) in the north of the European part of Russia, Sovrmennaya gerpetologiya [. 2003. T. 2. P. 100–123.
Mina M. V. Klevezal' G. A. Principles of Investigating Recording Structures, Uspehi sovrem. biol. 1970. No. 3 (6). P. 341–352.

Mina M. V. Klevezal' G. A. Growth of animals. Analysis at the level of the body. M.: Nauka, 1976. 291 p.
Morev B. Yu. The preferred temperature of the medium and the behavior of lizards in the desert, Temperaturnye kompensacii i povedencheskiy gomeostaz L.: Nauka, 1980. P. 101–105.
Moser A. Seasonal movement of the adder (Vipera berus L.) in the Swiss Alps: a telemetry study // 1st Wold Congr. Herpetol. Canterbury, 11–19 sept., 1989. Canterbury, 1989. P. 0.
Naulleau G. Effects of temperature on 'gestation' in Vipera aspis and Vipera berus (Reptilia, Serpentes) // Studies in Herpetology / Proceedinds of the European herpetological meeting (3rd ordinaral meeting of the Societas euripaea herpetologica, Prague. 1985). Prague, 1986. P. 489–494.
Naulleau G. The effect of temperature on digestion in Vipera aspis // J. Herpetol. 1983. Vol. 17. № 2. P. 166–170.
Naulleau G., Marques M. Etude biotelemetrique préliminare de la thermoregulation de la degestion chez Vipera aspis // C. r. Acad. sci. 1973. D276. № 2. P. 3433–3436.
Neumayer R. Density and sesonal movements of the adder (Vipera berus, L., 1758) in a Subalpin environmrnt // Amphibia-Reptilia. 1987. Vol. 8. № 3. P. 259–276.
Niel'sen K. Physiology of animals. Prisposoblenie i sreda. M.: Mir, 1982. T. 1–2. 800 c.
Nikol'skiy A. M. Reptiles and fish. SPb., 1903. 872 p.
Nilson G. Ovarian cycle and reprodactive dynamics in the female adder, Vipera berus // Amphibia-Reptilia. 1981. Vol. 2(1). P. 63–82.
Novikov G. A. Field research on the ecology of terrestrial vertebrates. M.; L., 1953. 602 p.
Odum Yu. Fundamentals of Ecology. M.: Mir, 1975. 742 p.
Orlov N. L., Ananjeva N. B. Distribution of amphibians and reptiles and their relict populations in the Gulf of Finland and Lake Ladoga // Memoranda Soc. Fauna Fennica. 1995. Vol. 71. № 3–4. P. 109–112.
Ornithofauna of Karelia, Red. V. B. Zimin. Petrozavodsk, 1993. 220 p.
Panov E. N. Behavior of animals and the ethological structure of populations. M.: Nauka, 1983. 424 p.
Pavlov A. V. Seasonal phenomena in the life of the steppe viper (Vipera ursinii) in the extreme northern point of its habitat, Zmei Vostochnoy Evropy: Mater. mezhdunar. konf. Tol'yatti , 2003. P. 62–65.
Pavlov A. V. Garanin V. I. Bakiev A. G. The adder Vipera berus (Linnaeus, 1758), Bakiev A. G., Garanin V. I., Litvinov N. A., Pavlov A. V., Ratnikov V. Yu. Zmei Volzhsko-Kamskogo kraya. Samara: Izd-vo Samarskogo nauchnogo centra RAN, 2004. P. 49–61.
Peabody R. B., Johnson J. A., Brodie E. D., Jr. Intraspecific escape from ingestion of the rubber boa, Chazina bottae // J. Herpetol. 1975. Vol. 9. № 2. P. 237.
Petzold H.-J. Statistisches uber die Geburtsgewiche von Kreuzotter (Vipera berus, L.) // Milu. 1980. Vol. 5. № 3. P. 443–448.
Pianka E. Evolutionary ecology. M.: Mir, 1981. 400 p.
Pielowski Z. Untesuckungen uber die Okologie der Kreuzotter (Vipera berus L.) // Zool. Jahrb. Abt. F Syst., Okol. v. Geogr. Tiere, 1962. Bd. 89. H. 3/4. Vol. 5. P. 479–500.

Pikulik M. M. Kosov S. V. Phyenogeography of background species of herpetofauna of Belarus, Fenetika prirodnyh populyaciy. M., 1988. P. 125–132.
Pikulik M. M. Baharev V. A. Kosov S. V. Reptiles of Belarus. Minsk, 1988. 166 p.
Pokrovskiy V. M. Korot'ko G. F. Natochin Yu. V. Human physiology. T. 2. M.: Medicina, 1997. 368 p.
Pomianovska I. Metabolic rate in adder (Vipera berus L.) // Bull. Acad. Pol. Sci. Ser. Sei. biol. 1972. Vol. 20. № 2. P. 143–146.
Pomianovska-Pilipiuk I. Energy balance and food requirement at adult vipers Vipera berus (L.) // Ecol. polska. 1974. Vol. 22. № 1. P. 195–211.
Popov P. L. Synthesis of evaluation information when overlapping areas of different thematic content, Mezhdunar. konf. «Geoinformatika: tehnologii, nauchnye proekty». Irkutsk, 15–22 iyunya 2008 goda (URL: http://www-sbras.nsc.ru/ws/GeoIn/).
Popudina A. D. Peculiarities of the viper's habit of life in the south of the forest zone of the Ob region, Fauna i ekologiya zhivotnyh Priob'ya. Novosibirsk, 1976. Vyp. 133. P. 51–54.
Pough F. H., Gans C. The vocabulary of reptilian thermoregulation // Biol. Reptilia. Vol. 12. Physiol. C. Physiol. Ecol. London e. a.: Acad. Press., 1982. P. 58–66.
Prestt L. An ecological study of the Vipera berus (L.) in Southern Britain // J. Zool. sound. 1971. Vol. 164. № 3. P. 373–418.
Prokop'ev L. V. To the ecology of the adder (Vipera berus L.), inhabiting Yakutia // Вестн. зоол. 1978. No. 1. P. 83–84.
Proskurina N. S. Krivosheeva N. V. The use of graphs to study the conjugation of the spatial structure of the population of small mammals and spatial heterogeneity of the environment, Metod grafov v ekologii. Vladivostok, 1989. P. 66–81.
Ravkin Yu. S. Gureev S. P. Pokrovskaya I. V. Spatio-temporal dynamics of the animal population. Novosibirsk: Nauka, 1985. 207 p.
Reference book on the climate of the USSR. Vyp. 3. Karel'skaya ASSR, Leningradskaya, Novgorodskaya i Pskovskaya oblasti. Ch. 1. Solnechnaya radiaciya, radiacionnyy balans i solnechnoe siyanie. L.: Gidrometeoizdat, 1966. 81 p.
Reference book on the climate of the USSR. Vyp. 1. Vologodskaya oblast' i Karel'skaya ASSR. Meteorologicheskie dannye za otdel'nye gody. Ch. 6. Oblachnost' i solnechnoe siyanie. L.: Gidrometeoizdat, 1974. 332 p.
Reference book on the climate of the USSR. Vyp. 3a. Karel'skaya ASSR. Meteorologicheskie dannye za otdel'nye gody. Ch. 8. Temperatura pochvy. L.: Gidrometeoizdat, 1975. 210 p.
Resovskiy N. N. Yablokov A. V. Glotov N. V. Essay on the Study of Populations. M.: Nauka, 1973. 278 p.
Resovskiy N. V. Voroncov N. N. Yablokov A. V. Brief essay on the theory of evolution. M.: Nauka, 1977. 297 p.
Reynol'ds R. Sullers A. Meteorological models and climate data sets, Distancionnoe zondirovanie v meteorologii, okeanografii i gidrologii. M.: Mir, 1984. P. 354–394.
Rodda G. H., Frits T. H. Predator prey cycling on Guam following the catastrophic introduction of the brown tree snake, Boiga irregularis // 1st Wold Congr. Herpetol. Canterbury, 11-19 sept., 1989. Canterbury, 1989. P. 0.

Rozanov A. S. Mechanisms of formation of spatial genetic structure of a species, Uspehi sovremennoy genetiki. 1983. T. 11. P. 58–63.
Rozenberg G. S. Models in phytocenology. M.: Nauka, 1984. 265 p.
Rozhkov Yu. I. Pronyaev A. V. Microevolutionary process. M., 1994. 364 p.
Saint-Girons H. Observations preliminaires sur la thermoregulation des Viperes d'Europe, Vie et Milieu. 1975. Vol. 25. Fasc. 1. ser. C. P. 137.
Saint-Girons H. Thermoregulation comparee des viperes d'Europe. Etude biotelemetriaue, Terre et vie. 1978. Vol. 32. No. 3. P. 417–440.
Saint-Girons H. Quelgues observations sur la dispersion des nouveau-nes ches Vipera berus et Vipera aspis dana le bocaqe at lautigue, Amphibia-Reptilia. 1981. Vol. 19. No. 2(3). P. 590–613.
Saint-Girons H., Duguy R., Naulleau G. Speto-thermal aspects of the annual cycle of temperature Viperinae, 1st Wold Congr. Herpetol. Canterbury, 11–19 sept., 1989/ Canterbury, 1989. P. 0.
Saint-Girons H., Duguy R. Un exemple de predation atypique et de gestation hivernale chez Vipera aspis (L.), Ann. Soc. Sci. natur. Charente-Naritime. 1973. Vol. 5. No. 5. P. 379–381.
Saint-Girons H., Naulleau G. Poids des nouveau-nes et strategies reproductives des Viperes europeenes, Rev. Ecol. (Terre et vie). 1981. Vol. 35. P. 598–616.
Sapozhenkov Yu. F. Amphibians and reptiles of Belarus, Fauna i ekologiya nazemnyh pozvonochnyh Belorussii. Minsk, 1961. P. 183–194.
Schiemenz H. Zur Ökologie und Bionomie der Kreuzotter (Vipera berus L.) Ergebnisse mehrjahriger Beobachtungen Tieren (Teil 1: Abulte Mannchen und Weibchen) // Zool. Abh. Staate. Mus.Tierk. Dresden. 1978. Vol. 35. № 1–14. P. 203–218.
Schiemenz H., Biella H.-J. Die Untalle durch Kreuzotterbisse (Vipera b. berus L.) in den Jahren 1955–1975 in Cachsen // Zool. Abh. Staatl. Mus. Tierk Dresden. 1978. Vol. 34. № 2. P. 229–243.
Schipanov N. A. Functional organization of populations (on the example of small mammals): Dip. … dokt. biol. nauk. M., 1996. 609 p.
Sebela M. The diet of the common viper (Vipera berus L.) in the area of mt. Králický Sněžnik // Folia Zool. 1980. Vol. 29. № 2. P. 117–123.
Sena L. A. Units of physical quantities and their dimensions: Uchebno-spravochnoe rukovodstvo. M.: Nauka, 1988. 432 p.
Severcov A. S. Lyapkov S. M. Surova G. S. The ratio of ecological niches of the Rana temporaria and Rana arvalis (Anura, Amphibia), Zhurn. obsch. biol. 1998. T. 59. No. 3. P. 279–301.
Severcov A. S. Surova G. S. Dynamics of the number of brown frogs in the Moscow Region, Zemnovodnye i presmykayuschiesya Moskovskoy oblasti: Mater. soveschaniya po gerpetofaune Moskvy i Moskovskoy oblasti. 9–10 noyabrya 1987 g., Moskva. M.: Nauka, 1989. P. 110–120.
Shilov I. A. Physiological ecology of animals. M.: Vysshaya shkola, 1985. 328 p.
Shine R., Seigal R. A. Reproductive strategies in snakes a preliminary synthesis // 1st Wold Congr. Herpetol. Canterbury, 11–19 sept., 1989. Canterbury, 1989. P. 0.
Shishkin G. V. Efficiency of accounting for species composition and abundance of forest birds on test plots, Vsesoyuz. sovesch. po problemam kadastra i ucheta zhivotnogo mira. Ch. 1. M., 1986. P. 210–211.
Shlyahtin G. V. Golikova V. L. Methodology of field studies of ecology of amphibians and reptiles. Saratov: Izd-vo Saratovskogo un-ta, 1986. 79 p.

Shmal'gauzen I. I. Growth of animals. Growth and overall body size due to their biological significance. M.; L., 1935. P. 61–73.
Shvarc S. S. Ecological patterns of evolution. M.: Nauka, 1980. 278 p.
Shvarc S. S. Smirnov V. S. Dobrinskiy L. N. Method of morphophysiological indicators in the ecology of terrestrial vertebrates. Sverdlovsk, 1968. 387 p.
Siivonen L. Mammals of Northern Europe. M., 1979. 232 p.
Sindyukov A. P. Determination of the fatness of lebetina viper, Ekologiya. 1971. No. 4. P. 101–103.
Slip O. J., Shine R. Thermophilic response to feeding of diamond python, More liasispilota (Serpentes, Boidae) // Comp. Bioch. and Physiol. A. 1988. Vol. 89. № 4. P. 645–650.
Slonim A. D. The evolution of thermoregulation. L.: Nauka, 1986. 76 p.
Smirina E. M. Prospects for Determining the Age of Reptiles from Layers in Bones, Zool. zhurn. 1974. T. 53. Vyp. 1. P. 111–117.
Smirina E. M. A technique for determining the age of amphibians and reptiles by layers in the bone, Rukovodstvo po izucheniyu zemnovodnyh i presmykayuschihsya. Kiev, 1989. P. 144–153.
Smirina E. M. Makarov A. N. On the establishment of the correspondence of the number of layers in tubular bones in amphibians to the age of individuals. Zool. zhurn.. 1987. T. 66. Vyp. 4. P. 599–604.
Sokolov A. S. On the issue of migrations of the adder, Vopr. gerpetologii L.: Nauka, 1981. P. 124–125.
Sokolov A. S. Moult sexually mature males of the adder in conditions of the Tambov region, Voprosy gerpetologii. 3-ya Vesoyuzn. gerpetol. konf., 26–29 sentyabrya 1989 g., Kiev. Kiev, 1989. P. 240–241.
Sokolov G. A. Shvecova V. Ya. Balagura N. I. Experience in accounting for the absolute abundance of small mammals in the forests of the Western Sayan, Ekologiya populyaciy lesnyh zhivotnyh. Novosibirsk, 1974. P. 77–86.
Sokol'skiy S. M. Kudryavceva E. N. Tagging of proteins in the Pechoro-Ilychsky Reserve, Itogi mecheniya mlekopitayuschih. M.: Nauka, 1980. P. 109–123.
Spaendonk Vol. G., Damme Vol. R., Verheyen R. F. Thermal ecology of the adder (Vipera berus L.) // Belg. J. Zool. 1990. 120. Suppl. № 1. P. 62–63.
Spaendonk Vol. G., Damme Vol. R., Verheyen R. F. Thermal relations of the adder (Vipera berus L.) // Societas Eur. Herp.: the 6th O. G. M. Budapest, 1991. P. 83.
Spotila J. R., Lommen P. W., Bakken G. S., Gates D. M. A mathematical model for body temperature of large reptiles: implications for dinosaurus ecology // Amer. Natur., 1973. Vol. 107. № 955. P. 391–404.
Still B., Madsen Th., Hiklasson M. Multiple peternity in the adder, Vipera berus // Oikos. 1986. Vol. 47. № 2. P. 173–175.
Strelkov E. I. Studies on the comparative ecology of vertebrates in Western Siberia. Tomsk, 1963. 187 p.
Stroganov S. U. The determinant of small mammals of Karelia. Petrozavodsk, 1949. 199 p.
Suley M. E. Survival thresholds: maintenance of adaptability and evolutionary potential, Biologiya ohrany prirody . M.: Mir, 1983. P. 177–197.
Surova G. S. Features of the structure of the population of the brown frog (Rana temporaria) at the northern boundary of the range, Voprosy gerpetologii. 1989. P. 245–246.

Systematics and ecology of the adder (Vipera berus L., 1758): Avtoref. dip. … kand. biol. nauk. L., 1967. 14 p.
Terashima S., Goris R. C. Electrophysiology of snake infrarad receptors // Progr. Neurobiol. 1974. Vol. 2. № 4. P. 309–332.
Terent'ev P. V. Frog. M.: Sovetskaya nauka, 1950. 346 p.
Terent'ev P. V. Herpetology. M.: Vysshaya shkola, 1961. 336 p.
Terent'ev P. V. Some quantitative features of calf frogs and tadpoles, Zool. zhurn. 1960. T. 39. Vyp. 5. P. 779–781.
Terhivuo J. Provisional atlas and status of populations for the herpetofauna of Finland in 1980–1992 // Ann. Zool. Fennici. 1993. № 30. P. 55–69.
Terhivuo J., Korosov A.Vol. Lacerta agilis// Red Data Book of East Fennoscandia. Helsinki, 1998. P. 267– 268.
The results of tagging mammals. M.: Nauka, 1980. 300 p.
Tlenbergenova L. N. The rates of heating and cooling in various representatives of lizards, Tr. nauch. konf. mol. uchen. In-ta fiziol. AN Kaz. SSR. Alma-Ata, 16.11.1982 . Alma-Ata, 1982. P. 173–185.
Tlenbergenova L. N. Isabekova S. B. Adaptive behavior of heliothermal lizards under the action of light and temperature stimuli, 1-y s'ezd fiziol. Sredney Azii i Kazahstana. Ch. 2. Nauch. sovesch. AN SSSR, AMN SSSR po fiziol. naukam . Dushanbe, 1991. P. 125.
Tupikova N. V., Sidorova T. A., Konovalova E. A. Opredelitel' vozrasta lesnyh polevok The determinant of the age of forest voles], Fauna i ekologiya gryzunov [. 1970. Vyp. 9. P. 145–169.
Tupikova N. V. Ratio of the absolute and relative abundance of red voles, Gryzuny. 4-e vsesoyuz. sovesch. M., 1983. P. 461–463.
Ushakov V. A. Pestov M. V. To the biology of the adder in the Gorky region, Vid i ego produktivnost' v areale. M.: Nauka, 1983. P. 76–82.
Vainio J. Vorbereitung und Biologie der Kreuzotter, Vipera berus, L., in Finland // Ann. Zool. Soc. Vanamo. 1931. Vol. 12. P. 1–19.
Viitanen P. Hidernation and seasonal movements of the viper, Vipera berus (L.), in southern Finland // Ann. Zool. Fennici. Helsinki. 1967. Vol. 4. № 4. P. 472–546.
Viktorov L. V. Determination of the age of the common shrew (Sorex araneus), Byul. MOIP. Otd. biol. 1967. T. 72. Vyp. 6. P. 151–152.
Vinberg G. G. Formation of ideas about products, Obschie osnovy izucheniya vodnyh ekosistem. L.: Nauka, 1979. P. 114–119.
Vitt L. J. Body temperatures of high latitude reptiles // Copeia. 1974. № 1. P. 255–256.
Völkl W., Biella H-J. Traditional using of mating and breeding plases by the adder (Vipera berus L.) // Zool. Abh. Staate. Mus.Tierk. Dresden. 1988. Vol. 44. № 3. P. 19–23.
Völkl W. Prey density and growth factors limiting the hibernation success in neonate adders (Vipera berus L.) // Zool. Anz. 1989. Vol. 222. № 1–2. P. 75–82.
Volsøe H. Structure and seasonal variation of thr male reproductive organs of Vipera berus (L.). Copenhagen, 1944. 157 p. / Spolia zoologica Musei heuniensis.Surifter udg Uviv Zoologiske museum Kobenavn. 5.
Voženilek P. Ty Zmije. Praha: MŽP, 2000. 78 p.
Wirminghaus J. O. Observations on the behavior of the girdled lizard Cordylus cordylus (Reptilia, Cordylidae) // Z. Natur. Hist. 1990. Vol. 24. № 6. P. 1617–1627.
Yablokov A. V. Variability of mammals. M.: Nauka, 1966. 364 p.

Yablokov A. V. Population Biology. M.: Vysshaya shkola, 1987. 303 p.
Yablokov A. V. Larina N. I. Introduction to population phenetics. M.: Vysshaya shkola, 1985. 159 p.
Yakovlev V. A. Materials on the biology of the adder (Vipera berus L) in the Altai Reserve, Ekologiya nazemnyh pozvonochnyh Sibiri. Tomsk, 1983. P. 151–160.
Yakovlev V. A. Amphibians and reptiles of the Altai Reserve: Avtoref. dis…. kand. biol. nauk. L., 1985. 24 c.
Yakovlev V. A. A digital method for describing the phenotype of amphibians and reptiles, Voprosy gerpetologii: Vsesoyuz. gerp. konf., Kiev, 26–29 sentyabrya 1989. Kiev, 1989. P. 303–304.
Yumashev I. Yu. Thermobiological indicators of the adder in the Upper Volga basin, Pervaya konferenciya gerpetologov Povolzh'ya: Tez. dokl.. Tol'yatti, 1995. P. 63–65.
Zalezhskiy G. To the dynamics of the number of some amphibian, Sbornik nauchnyh rabot nauchnyh studencheskih kruzhkov Moskovskogo universiteta. M.: Izd-vo MGU, 1938. T. 2. P. 3–28.
Zamolodchikov D. G. Seasonal activity and estimation of the number of viviparous lizards, Zemnovodnye i presmykayuschiesya Moskovskoy oblasti. M.: Nauka, 1989. P. 141–146.
Zamolodchikov D. G. Dynamics of populations of reptiles: the experience of system analysis, Zhurn. obsch. biol. 1993. T. 53. No. 5. P. 592–607.
Zamolodchikov D. G. Kolosova O. V. Dynamics of populations of reptiles: an empirical verification of the bioenergetic model, Zhurn. obsch. biol. 1995. T. 56. No. 2. P. 165–171.
Zhakov L. A. Menshutkin V. V. Practical training in ichthyology. Yaroslavl', 1982. 112 p.
Zhilina T. V. Solomatova E. A. Soil cover of the islands of the Kizhi skerries, Ostrova Kizhskogo arhipelaga. Biogeograficheskaya harakteristika: Tr. KNC RAN. Ser. Biogeografiya Karelii. Vyp. 1. Petrozavodsk, 1999. P. 34–41.
Zhivotovskiy L. A. Population Biometrics. M.: Nauka, 1991. 271 p.
Zimin V. B. Some techniques facilitating the search for nests of forest terrestrial nesting passerines, Fauna i ekologiya ptic i mlekopitayuschih Severo-Zapada SSSR. Petrozavodsk, 1983. P. 3–11.
Zimin V. B. Kuz'min I. A. Ecological consequences of the use of herbicides in forestry. L., 1980. 175 p.
Zimov S. A. The alphabet of drawings of nature. M.: Nauka, 1993. 125 p.
Znamenskiy S. R. Current state and attempt to forecast the development of meadow communities of the island of Kizhi, Ostrova Kizhskogo arhipelaga. Biogeograficheskaya harakteristika: Tr. KNC RAN. Ser. Biogeografiya Karelii. Vyp. 1. Petrozavodsk, 1999. P. 66–74.
Zuffi M. A. L. An ecological analysis of activity patterns of the Asp Viper, Vipera aspis, in a Mediterranean enviroment from Central Italy // Progr., and Abstr., 8-th Ord. Gen. Meet. Sol. Eur. Herpetol. Bonn, 1995. P. 111–112.
Zug G. R., Wynn A. H., Ruckdeschel C. Age determination of loggerhead sea turtles, Caretta caretta, by incrementtal growth marks in the skeleton // Smithsonian Contrib. Zool. 1986. № 427. 34 p.

Buy your books fast and straightforward online - at one of the world's fastest growing online book stores! Environmentally sound due to Print-on-Demand technologies.

Buy your books online at

www.get-morebooks.com

Kaufen Sie Ihre Bücher schnell und unkompliziert online – auf einer der am schnellsten wachsenden Buchhandelsplattformen weltweit!
Dank Print-On-Demand umwelt- und ressourcenschonend produziert.

Bücher schneller online kaufen

www.morebooks.de

OmniScriptum Marketing DEU GmbH
Bahnhofstr. 28
D - 66111 Saarbrücken
Telefax: +49 681 93 81 567-9

info@omniscriptum.com
www.omniscriptum.com

OMNIScriptum