From: Grizzle, Betty
To: richardeyates02@fs.fed.us
Subject: Two publications from Russian studies
Date: Monday, January 9, 2017 10:53:43 AM
Attachments: Formozov, A.N. 1963 (1946).pdf
Formozov, A.N. 1961.pdf

Hi Rick - Thanks for your time this morning.
Here are two very old, but interesting publications regarding role of snow cover. I can't remember which library we found these at, but we photocopied and scanned them. They are large files, so hopefully you will receive them through your email server.

The longer one, originally written in 1946 (at 200+ pages!), is more interesting; see page 109 for temperature measurements, but your recent draft paper is prompting me to re-look at these relative to wolverine prey rather than wolverine habitat requirements.

Happy Reading!
Betty

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SNOW COVER AS AN INTEGRAL FACTOR OF THE ENVIRONMENT AND ITS IMPORTANCE IN THE ECOLOGY OF MAMMALS AND BIRDS

by

A.N. FORMOZOV

Translated from the original Russian edition, with the permission of the author

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Originally Published in

Materials for Fauna and Flora of the USSR

New Series, Zoology, 5 (XX) 1946: 1—152

by

Moscow Society of Naturalists

Moscow, USSR

English edition published by Boreal Institute,
University of Alberta
Edmonton, Alberta, Canada.

as

Occasional Paper No. 1

Foreword

In the opinion of many northern biologists one of the truly important ecological works is Professor A.N. Formozov's book on the ecology of snow, ranking with Charles Elton's classic "Animal Ecology." The lack of an English translation has been felt keenly. Moreover, less than half a dozen copies of the original book have been available in all North America.

We started this translation in 1952. Because of our separate research and travel activities it took several years for us to complete it; partially-completed sections of the manuscript were mailed back and forth from one of us to the other. After translation, the rough copy has been used by various colleagues. It remained for Dr. William A. Fuller to initiate and drive to completion the arduous task of checking and cross-checking the many scientific and geographic names.

We are grateful to him and to the Boreal Institute for seeing this translation into print. We are also grateful to the many students and colleagues who have read and used the translation in manuscript form and who have pointed out to us sections of ambiguous or erroneous translation. We believe that this English translation of Professor Formozov's work is now in a form whereby it will be useful to many biologists.

THE TRANSLATORS.

Foreword to the English edition,

From the author

Despite a rather extensive summary in French, the contents of my book on the varying role of the snow cover in the life of mammals and birds in the U.S.S.R. remained virtually unknown beyond this country. It was published in Russian by our oldest scientific society - The Moscow Society of Naturalists.

I am most thankful to my Canadian colleagues who undertook this uneasy task of translating the book into English and to Dr. W.O. Pruitt, whose efforts resulted in the appearance of the new edition. One can hope that this book will now be accessible to a great number of readers in English-speaking countries and that it might serve as a stimulus for more detailed study of the ecology of higher vertebrates in the conditions of snowy winters in the Northern Hemisphere.

During the period that has elapsed since the publication of the first edition, the author has continued his winter observations and has published several articles, one of which he would like to mention here: "On the significance of the structure of the snow cover in the ecology and geography of mammals and birds." * Data used in this paper and my later researches indicate that at any moment of its existance the structure of the snow cover is substantially different even on small, adjacent portions of the land. These changes are determined by specific features of relief, soil and vegetation cover. Such differences, at first seemingly insignificant, can be of decisive influence upon the conditions of existence of animals and especially of small birds and mammals.

* In: Role of the snow cover in natural processes. Presentation volume to G.D. Rikhter on his 60th. birthday. Moscow, Academy of Science U.S.S.R.; 272 pp.

The state of the snow cover and weather conditions are the most important abiotic factors which create the character of the winter regime. The experience of Soviet naturalists shows that the study of this regime in northern countries deserves close attention, though the work on ecology is only just started and is still very far from completion.

Professor A.N. Formozov

Moscow
2-XII-1963

Editor's Foreword

The task of editing this translation of Professor Formozov's classical paper has occupied much of my spare time for two years. Had I suspected at the outset that it would take so long, I think that this English edition would not now be appearing. However, the task, though long and at times arduous, was not without its compensations. I was forced to begin the serious study of the Russian language, and in pouring over atlases, I learned a good deal about the geography of the USSR.

As in all translations from the Cyrillic to the Roman alphabet there have been problems in the transliteration of proper names. We do not claim to have solved those problems, but we hope that we have minimized them by, first, being as consistent as possible, and second, by including a Gazetteer (appendix D) that can lead the interested reader to the original Russian spelling if he has access to a Russian atlas.

Professor Formozov used few scientific names for plants and animals. An attempt has been made to identify the Russian common names used by him with a scientific name which has then been inserted into the text immediately after the first mention of any organism. The scientific name was in turn converted to an acceptable English common name which is then used throughout the text. Appendices A, B, and C list the English common names used and their Latin equivalents.

Material interposed by the translators (with the exception of scientific names) is enclosed in double parentheses. Footnotes added either by the editor or the translators are not so distinguished, but in every case they can be told from the original footnote by context.

In the original there are a few discrepencies in bibliographic citations between the text and the list of Literature Cited. Attention has been drawn to these, but they have not been emended.

It is a pleasure to acknowledge the help, advice and guidance of a number of individuals. Dr. K. E. Westerkov, Department of Zoology, Univeristy of Otago, Dunedin, New Zealand, suggested that the work be undertaken while he held a Post-doctorate Fellowship at the University of Alberta. Professor W.C. Wonders, and his successor as Director of The Boreal Institute, Professor R.W. Longley, gave constant encouragement and solved many technical difficulties. The clerical staff of the

Institute has had the heavy task of typing the numerous revised versions and my Boreal Ecology class of 1962-63 proofread most of the first typescript. Dr. W.O. Pruitt, Jr., gave generously of his time in checking and rechecking the original translation, and proofread the entire final typescript.

For any errors of omission or commission that may remain, I accept full responsibility.

W.A. Fuller,
Assoc. Prof. of Zoology,
University of Alberta.

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SNOW COVER AS AN INTEGRAL FACTOR OF THE ENVIRONMENT AND ITS IMPORTANCE IN THE ECOLOGY OF MAMMALS AND BIRDS.

by

A.N. Formozov

"The presence of an ice and snow cover in the biosphere is, in its direct and indirect results, one of the most important factors in nature."

V. I. Vernadski, 1933

INTRODUCTION

Vast regions of the continents in the arctic and temperate zones of the northern hemisphere are covered with snow which every year for varying periods never melts, and for centuries covers the soil with a thick shroud. The presence of this cover with its markedly peculiar physical characteristics sharply changes the conditions of existence for plants and particularly animals in every habitat where snow falls and stays. For millenia the regular annual appearance of snow cover in certain periods of the year has sharply modified the whole nature of the temperate and arctic regions of the globe. The snow cover, along with temperature, light, and humidity, has become one of the most powerful of ecological factors which has dominated by its influences the seasonal rhythms of many biological phenomena and the morphological characteristics of some organisms.

A large part of the USSR is completely within the region which is characterized, along with other climatic peculiarities, by precipitation a part of which falls as snow. In only a few parts of our land are there a few years in which snow does not fall at all (Berg, 1938). Huge areas of the north and middle regions are every year covered with deep snow for entire months. According to

Voznesenski (1930), polar climates (Group E), of two varieties, cover about 6% of the territory of the USSR. The region of cold temperate climates (D) covers up to 85% of the whole surface and can be found at all latitudes from 35 to 70 degrees north. "All this huge territory of 21,000,000 km^2 has a characteristic winter with snow cover and a no less characteristic warm summer-peculiarities which cannot always be found in other countries." says Voznesenski. Warm temperate climates (C) cover only 5.6% of the surface of the USSR.

If we take into consideration the fact that in the northern portion of the European part of the USSR the snow cover lasts more than 200 days per year, and in many places in Siberia for 250 days and more; that not less than half of all our territory is covered for about half of each year with a mantle of snow which by the end of winter has an average depth of 40 cm; that the average maximum depth of the snow cover in many places in the north is 100 to 140 cm; then it will not be difficult to imagine how important this factor is for life in nature and the (human) population of our country. "Nowhere is the question of snow and snow cover so important as it is here with us (in this country)," says Vlasov. Regretfully one has to state that some peculiar difficulties of carrying out observations on the snow cover, and possibly a lack of forethought as to its multiform importance, have deprived meteorological science of the opportunity to collect enough exact data to enable us to characterize in all aspects the nature of this phenomenon. The works which deal with the peculiarities of the snow cover of the USSR are not numerous. For many places the data are extremely scattered and not dependable or are lacking completely. If in the field of study of snow cover as a climatic and geographic factor there has been so little done, then even less has been done in the field of study of the importance of snow in the life of plant and animal organisms. Most of the existing data have been collected

by agricultural meteorologists and deal mainly with the question of holding snow cover in order to increase the harvest or the protective influence of snow on winter crops.

Observations dealing with the relationships of fauna to snow cover are not numerous and are scattered and desultory. Excepting the short paper by Stanchinski (1926) there have been no special works on the subject in question in the Russian language up to the present time. Moreover, in the newest reviews of the world literature dealing with the ecology of animals (Shelford 1939 (sic), Chapman 1931, Pearse 1926, Elton 1927, Kashkarov 1938, Hesse et al. 1938 (sic) the term "snow cover" is not given any attention at all. The explanation of this striking omission is not difficult if one harkens back to the history of the appearance and development of ecology as a science. The roots of ecology as it is now known come from hydrobiology, which is the science of life in an environment where the importance of snow cover is relatively limited.* The largest part of the factual data of the ecology of animals came from and is continuing to come from the study of invertebrates, which group is especially sensitive to the physical and chemical factors of the environment. But the invertebrates, being poikilothermal animals, are found during the cold part of the year in hibernation. Their existence depends to a lesser degree on the peculiarities of the snow cover than do the lives of mammals and birds, which are active in winter. The ecology of animals, being a very young science, has only just started on a systematic investigation of the vertebrates, and particularly the last two groups, the birds and mammals, where the snow cover has special significance. Since 1930 I have been working on expeditions to study the ecology of vertebrates and have tried to collect data which would help to explain the importance of snow cover as a factor of the environment in relation to these animals.

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*The proof that the aquatic fauna also feels the influence of snow cover as an ecological factor is the existence of winter-killing of fish under ice which is covered with a heavy layer of snow, making circulation of air difficult. The character of the spring flood of rivers depends in large extent on the accumulation and melting of snow, etc.

Being busy with teaching in the wintertime, I could not give to this work the time and attention which it without doubt deserves. My personal observations have themselves been desultory, and I have made an attempt to add to them the most valuable information from the literature on this subject.

This present work is not a complete monographical treatment but is only the preliminary result of a projected large work. However, many of its conclusions are completely new, and this first attempt to integrate collected material will serve (I think) as a stimulus for more broad and systematic works on the study of the importance of snow cover in the life of our fauna. (These lines were written several years before the start of the Second World War, which has detained the publishing of this paper. In its manuscript form this work was used by several of my students and colleagues, who have prepared and, in several cases, already published investigations which were stimulated by this work. The author was able to publish only a short paper (in English, 1939). From a large amount of additional data which I collected during recent years, this paper comprises only a part. The prepared chapters on "Snow and Seasonal Cryptic Coloration", and "Snow and Migration of Birds" will probably appear as separate articles).

In order to approach the questions of the importance of snow cover as an ecological factor, it is necessary as a preliminary to acquaint ourselves with snow as a substance, and with the peculiarities of snow cover from a climatological and geographic point of view. We will begin our presentation with a short review of these questions.

PECULIARITIES OF SNOW AS A MINERAL, AND SNOW COVER AS A CLIMATIC FACTOR.

Snow, graupel and hail are all formed directly from water vapor or by freezing of drops of liquid water. From snow to hail and graupel and then from graupel to icy rain is a whole series of

graduations. Graupel, according to Obolenski (1927), is formed from flakes of snow, which are crumpled into hard ice pellets by blasts of wind from different directions. These pellets represent the first stage in the formation of hail. Nuclei of individual hail stones have the same structure as graupel. The latter is usually precipitated by squally weather; in the middle latitudes (of Russia) more often in Spring (March, April, and sometimes May) and in the fall, but in the mountains even in summer. Graupel has the form of round white nontransparent icy pellets, approaching the size of peas (2 to 5mm) in diameter. Hail is precipitated usually in summer. In winter in company with snow, it is noted only very rarely. Snow can replace graupel, and reciprocally, graupel sometimes comes after snow. The form of snow crystal-flakes is extremely variable, but in the middle zone six-pronged, hexagonal little stars obviously predominate. Shchukevich (1910) who studied the forms of snow crystals in the vicinity of Leningrad for almost three winters, noted 246 different forms of snow flakes during 176 days of snow fall. On the average, for each day with snowfall, up to 8 forms were noted, but on some days the variety was much more, for example, on February 26, 1908 he counted 37 different forms.

It turned out that hexahedral stars were in first place in frequency of occurrence (they were noted in 37 per cent of the snow falls observed in all this time). They can be observed especially often during February snowfalls (57 per cent) and March (42 per cent); in November, December, January and April about 1/3 of the snowfalls had crystals belonging to this type. Hexahedral plates were noted in 25 per cent of all observed cases of snowfall, and were more common in February and March. Combinations of hexahendral stars and plates occurred in 32 per cent of all cases. Prisms and needles occurred in only 19 per cent of the observations. They occurred more often in December (23 per cent), January (30 per cent), and February and March.

Different forms of crystals are precipitated out by certain atmospheric conditions in the cloud level and near the earth's surface. In this manner long and thin needles were precipitated in only January and February by relatively low temperatures (averaging -7.1 C) and were never noted at temperatures above -2 C. Undoubtedly the dominant types of snow crystals will be of different forms in different parts of the region with cold winters, depending upon the particular local atmospheric conditions (temperatures, humidity, winds).

The crystals of snow, as is generally known, can be characterized as having insignificant size and small weight. Little stars have a diameter averaging 2.30 mm and thicknesses of 0.08 mm, plates — diam. 0.33 mm; needles - average length of 0.72 mm, largest diameter 0.07 mm, etc.

On the way to the earth snow flakes get covered with hoar frost and interlock or freeze together into large snow flakes (up to 1-8 cm). In order to cover 1 square meter with snow cover to a depth of 1 meter, from several to tens of billions of snow flakes are needed. They lie uncompacted on each other; air is preserved between their plates, rays, and needles. Snow cover (according to Chirvinski 1932) resembles an emulsion of air and snow flakes, or a froth. By this peculiarity the white color of snow and its low temperature transmission can be explained. The larger the snow flakes are, the less compactly they lie together; in connection with this it should be noted that the specific gravity also changes, from 0.14 for the smallest (sizes) to 0.04 for the largest, and averaging 0.09 for freshly fallen snow. The importance the size of snow flakes has for the density of freshly falling snow can be seen from the numerous determinations of Rozental' (1904), which were done in Irkutsk from 1899 till 1903. The precipitation of large snow flakes gave an average specific gravity of 0.056, middle sized flakes gave 0.091, and small sized flakes gave 0.135.

By lying a long time or by slow melting, snow gets more compacted and can be turned into ice (specific gravity=0.9162 to 0.9212). According to the investigations of Abel's, the coefficient of thermal conductivity of snow is directly proportional to the square of its specific gravity or to the square of its density. For example, at a specific gravity of 0.1 the thermal conductivity is equal to 0.004* at 0.7 the thermal conductivity will be 0.196. "If the density of snow will be taken on an average to equal 0.20, then the coefficient of its thermal conductivity will be 0.0162", says Chirvinski. "This figure is twenty times smaller than the thermal conductivity of solid ice, the density of which is equal to 0.90."

Because of these peculiarities, snow cover plays a very important role in preserving soil and plants from freezing. Its low thermal conductivity turns out to be very important in the ecology of animals.

Since the density and specific gravity of snow in any one region, as well as the depth of the cover, undergo great changes during any one season, and since frequently there are large differences in different years, then also the protecting thermal insulation characteristics of snow cover are not constant. They vary a great deal, which variation, of course, effects vegetation and animals.

Accumulated snow cover metamorphoses under the influence of a number of factors. Compaction of the snow and secondary recrystallization occur under the influence of gravity (this occurs especially in the lower layers), by partial melting and refreezing, which results in the appearance of compacted crusts and layers, and, in particular, under the action of wind which moves fine, dry snow from certain places and deposits it in others (ravines, forest borders, hedgerows), in the form of banks, hillocks, dunes etc. Drifting snow moves in the form of fine snow dust, which later forms especially compact layers under strong pressure from the wind. Cold rain and sublimation which form icy crusts, also take some part in the metamorphosis of snow. Particles transported by wind ("snowy detritus") are able to furrow and carve the surface of snow layers and even to inflict heavy damage to the

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*Given in the original as 0.00009 (Ed.)

bark of trees and bushes at the border of the tundra (Gorodkov, 1926).

The processes of "nastization" and "firnization" of the snow cover, as Chirvinski called them, have great importance in the life of vertebrates, because the conditions of locomotion of animals on the snow, the possibility of digging out food, digging into the snow, etc., are completely dependent on the hardness, granularity, and thickness of the nast, quality of firn layers in the total thickness of the cover, etc. Therefore, the snow cover is a substrate upon which, in winter, many vertebrates move, and for other species it is the matrix within which they bore their tunnels and build nests, while for other forms it is an obstacle in obtaining food, and also the only source of drinking water in the winter time. At the same time the snow cover is a marked thermo-insulating layer, which causes a special temperature regimen on the surface and in the depths of a soil which is covered with its fluffy layer, all of which plays a great part in the life of plants, invertebrate animals, and small vertebrates. Its importance is as multiform and complicated as are the characteristics of snow and its derivatives themselves. Not without reason snow has been called with us a "periodic mineral." Snow and snow cover serve as subjects of simultaneous study by meteorologists, climatologists, geographers, geologists, hydrologists, agriculturists, and people of many other scientific fields. So, the snow, because of the complexity and many-sidedness of its characteristics, has become an object of investigation by various contiguous and overlapping disciplines.

It is interesting to solve the question, what known ecological factors can one attribute to the snow cover, which periodically appears and disappears, and influences the lives of organisms from the most varied sides? From one side this is a climatic factor and therefore meteorology and climatology always include snow and snow cover within the circle of their scientific interests. From the other side, in many characteristics it becomes an edaphic factor, and quite properly

attracts the attention of geographers and geologists. At the same time it differs quite markedly from the typical climatic and edaphic factors. The importance of snow cover in the life of plants and animals is so substantial and unique that I consider it necessary to put it in a separate place between climatic and edaphic factors by separating a new group of chionic or nival factors (snow factors).

It is interesting to record that the people of the North, during centuries of having to deal with snow cover, deeply appreciate the multiplicity of its importance, and have such an abundance of terms characterizing peculiarities of snowfall and conditions of snow cover that their lexicon appears to be much richer than the dictionary of official meteorological science. It is true, however, that some of these terms have already entered or are beginning to enter the science, but many still remain unknown to the snow specialist. Doubtless, careful collecting of words dealing with snow and snow cover used in the language of northern reindeer herders, hunters of the taiga, and cattlemen of the steppes will enrich the science and will help to work out a sufficiently exact and complete terminology. I would like to recall some folk terms which have been included in the scientific lexicon: "vyuga"; "myatel"; in some places "kurritsya" (from the word "kurrit'" to smoke, i.e. blowing snow; "ponosukha" (from the word "nesti" to carry something; "buran"; "pozemka" (blowing snow, both in the upper air and along the ground); all used to define a snowfall with strong winds or the blowing of already fallen snow.

The word "nast", usually little-known to city people, and which means a thickened crust on the surface of a mature snow cover, has a whole series of synonyms. Thus, in Western Siberia, instead of nast, the word "charym" has been used; in Eastern Siberia - "chyr." From the last root the verb "zachirat'", which means to cover with crust, has been derived. A thin, icy crust that breaks noisily under the weight of a man has been called by the hunter-traders of the northern part of Gor'ki Oblast' "skovoroda" (frying-pan) or "shorokh" (rustle). The "frying-pan" with its noise is extremely troublesome while hunting; the sharp edges of the cracks wound the paws of the Eskimo dogs and also are quite destructive of foot-wear. The icy crust, which has been

formed from the layer of snow wetted by freezing rain, has been called up north and in the steppes "ozheled", "gololeditsa," or "gololedka," (glazed frost). It has a destructive effect upon many wild and domestic animals.

When deep and soft snow falls (in Eastern Siberia the people say "khlupniet"), walking on it becomes difficult. For the designation of these difficulties there is widely prevalent a precise word "brodno" (in the north), "ubrodno" (in the east), or "subrodno" (in Kostroma Oblast'). Deep and soft snow is simply called "ubrod." In the Sayan Mountains the condition of the snow which determines the difficulty of walking with skis is designated by the term "vz'em." Bad vz'em when skis sink deep, good vz'em when they do not sink very far or slide on the surface. Large animals, for example ungulates and carnivorous animals, have the same difficulties of movement on snow, therefore, the listed terms are entirely worthy of use in ecological works. A fresh fall of snow which makes hunting by tracking easier has been called "porosha", "perenova", or "perenoga" (Far East); heavy snowfall - "kid'"; snow which has been strongly compacted by the wind has been called "beaten snow" or "uboy" in the tundras of northeastern Siberia. Aeolian sculpturings on its surface have been called "zastrugi."

How extensive the vernacular is in designation of different types of snow fall can be shown with materials which were collected by Maksimov (1890) from the inhabitants of the sea-coast in the north of the European part of USSR. "If there fall large, fluffy flakes, which cover an already light covering, it is said that the "pad'" is coming down. If there is no snow coming down, but that which has fallen earlier is being dispersed in all directions by the wind, there is a "ponosukha" raging. When pad' falls with a strong wind, i.e.- when the snow is coming down from above and being whipped up by a wind, the designation is "khivus." Dense wet snow during warm weather is "ryanda." A light rain in a dense fog driven by the wind is "chidega." In Kamchatka, where the speed and possibility of communication by dog-team depends on the character of the snow cover, the

technical language is very rich in terms which denote all types of condition of the snow surface: "nast, ubrod, uboy, prolom (a thin frozen crust which breaks under sledge runners), razvod, nekat', rassol" (Derzhavin, A.N., 1916).

Geographers and geologists are often forced to be quite verbose- "the places which are cleared of snow by the wind" or "the spots of outblowing," --although there exist terms currently in use by the hunters of Altai, Sayan, and Transbaikal, as "vyduv" and "vyduva" for the designation of just such bare spots on slopes. In winter the reindeer (Rangifer tarandus) often graze on the vyduvs. In contrast to the vyduvs are "zaboys" - accumulations of snow, which has been swept by the wind into depressions of relief, where often (in the mountains) lie until the middle or end of summer. The snowdrifts, which accumulate in gullies and on the edges of a forest are perfectly anologous to the snowy zaboys of the mountains. In summer in the mountains, the reindeer often lie down on zaboys, in order to be free from blood-sucking Diptera; in the forests, varying hares (Lepus timidus) lie down on the remaining layers of the lingering snowdrifts. (S.T. Aksakov; Kirikov, 1935). The snow which accumulates on the branches of trees has been designated by the hunters of the taiga very concisely as "naves'" or "navis'" ((originated from the word "navisat'", which means to impend, or to hand over - W.P.)). In many places in Siberia it has been called "kukhta." Kukhta plays an important role in the hunting of squirrel (Sciuris vulgaris), marten (Martes martes), and sable (Martes zibellina). It has no less importance, as we will show later, in the life of vertebrates in general.

The conditions of snowiness are not the same in different landscape-zones. In order to ascertain the existing conformities, it is necessary to make at least a brief survey of the peculiarities of snow cover in different regions of the USSR.

THE SNOW COVER IN THE TUNDRAS AND THE CONDITIONS OF EXISTENCE OF VERTEBRATES

The zone of tundra which occupies the islands of the Arctic Ocean and the strip along its coast, locally penetrates deep into the continent on the woodless ridges of mountains. Here, according to Berg (1938), one has to distinguish two types of climate - eternal frost (in our country only on the most northern islands), and true tundra. Considering the vastness of this zone, there possibly exist in the tundra climate many subtypes or variants. Because of the long duration of the arctic winter, the snow remains in this zone during the greater part of the year, and in the regions with good precipitation, its layer reaches considerable thickness.

In Teriberka (Murmansk coast) the number of days per year with snow cover is 211; in Pustozersk 223 days, with an average maximal thickness of 72 cm. (Climatological Reference-Book for the USSR. Vol. I, II). In New Port (southern part of the tundra on the Yamal Peninsula) the snow cover remains for around 9 months — from the first ten days of October until the end of June; average depth in April and May is 65 cm (Davydova, M.A., 1938). On Dickson Island the snow remains an average of 266 days; average maximal depth is 30 cm (Ryazantseva, Z.A., 1936).

On the continent, the maxima of snow cover are especially great in the tundra of the western part of Siberia (on the map of Shostakovitch, 1925—over 100-140 cm); further east, in connection with the general diminution of precipitation, a smaller amount of snow falls. On the coast, near the mouth of the Yana River, the thickness of the cover hardly reaches 20 cm. Towards the east from here the average depth of the snow cover increases again. In the Anadyr Krai and on the Chukchi Peninsula it reaches 60 - 70 cm, and at Kamchatka even 90 - 100 cm.

In the open landscape of the tundra, drifting and carrying from

place to place of the dry, dusty snow, by the steadiness and great strength of the winds, are common. Urvantsov (1935), speaking of the climate of Severnaya Zemlya and of the Arctic in general, points out that flaky snow very rarely falls here. Such can only be observed on calm days during the warm part of the year (from May to September). In the time of cold, the moisture in the air precipitates out in the form of thin needle-shaped crystals with a thickness of the order of hundredths of a millimeter.* Even with weak winds, these needles, colliding with one another or the earth, are ground into extremely fine snow dust, which fills the air. With a wind speed of 5-6 m/sec there appears the phenomenon of such snow dust moving in the form of separate streams on the peaks of snowdrifts. "the streams whimsically run along, making curves, and playing like ripples on the water. All the earth's surface, especially the tops of hills and mountains, is overcast with a haze and looks as if it were smoking, With a wind speed of 6-7 m/sec most of the ground is almost covered with a complete snowy, foggy shroud to a depth of 10-20 cm. Concurrently with an increase of wind speed, the shroud rises higher and higher; at approximately 10 m/sec it reaches the height of a man, and covers all the visible horizon...." With a clear sky there results a "clear snowstorm," with low clouds and a fall of snow needles from above, a "dark snowstorm."

The fringe of the Arctic," according to V. Yu. Vize (1940), is a "classical country of storms and snowstorms. These storms are caused in general by cyclones of Atlantic and Pacific Ocean origin, however, not rarely, the strength of the wind is increased by the influence of the local relief of the earth's surface. As one moves away from the borderland Arctic inland to the central Arctic basin, the storm activity sharply slows down..." Local winds in a number of the provinces of our arctic are distinguished by extreme strength and steadiness. (For example, the bora of Novaya Zemlya has winds

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*According to Westman (cited from Chirvinski, 1931 sic), snow needles have a length of 0.18 to 2.32 mm, and a maximum diameter of 0.02 to 0.19 mm.

with speeds up to 30-40 m/sec, but separate gusts reach tremendous strength - 60 m/sec and more.) Zemlya Franz Joseph and Novaya Zemlya are distinguished by extremely high wind speeds, says Ryazantseva (1937). "Highest wind speeds are in Malaya Karmakuly, where they reach an average of 10 m/sec in the winter months. Such high averages of wind speed have not been observed as yet anywhere in our Union, except in mountainous regions." On Zemlya Franz Joseph and Novaya Zemlya the stormiest period is November to March. The average number of storms per year in the Bay of Tikhaya (Zemlya Franz Joseph) is 73; in Novaya Zemlya it is 106 at Cape Zhelaniya and 140 at Malaya Karmakuly; and on Dickson Island it is 148. In the coastal tundra of the Yamal Peninsula the yearly average speed of the wind is little abated from that noted on the coast of the Arctic Sea: New Port 7.1, Dickson 7.4., Vaigach Is. 7.5 m/sec; on the Yamal Peninsula the "cold period is distinguished by the highest speeds of the year: absolute maximum is in December, a secondary maximum is in April." The yearly average of the number of days with storms or strong winds in New Port is 75, and Salekhard (forest-tundra) only 49 (Davydova, 1938). On the continent the average wind speed is usually lower than on the coast, for example, on Wrangel Is. the yearly average is 5.2, on Cape Dezhneva (Chukchi) 7.7, and in Russkoye Ust'ye - 4.0, and in Markov (on the Anadyr), only 2.5 m/sec (Leont'eva, E.A., 1937). The winter storms in the tundras always are accompanied by snowstorm, and not rarely the snowstorms appear with a clear sky due to snow being lifted up from the earth. The average number of days per year with snowstorms of different types is 145 in Tikhaya Bay, on Cape Zhelaniya it is 131, and somewhat south at Salekhard only 51 (Ryazantseva, 1937, Davydova, 1938). Extreme "roughness of weather" (Bodman), which is peculiar to the winter weather of the tundra, an unequal distribution of the snow cover and high density of the cover are linked with the steadiness

and strength of the wind, and with the high frequency of snowstorms. "Due to strong winds and mountainous relief, the snow cover on Novaya Zemlya and Zemlya Franz Joseph lies exceptionally unequal... On the west coast of Novaya Zemlya...snow cover lies in spots and strips, not being retained on the high places. The westerly winds that prevail here sweep snow from glaciers, hills and rocks, often completely denuding them." Separate counts of the depth of snow cover on measured profiles fluctuate between very wide extremes; for example, on the survey of 15 May 1937 at Matochkin Shar, the maximum depth was 270 cm, the minimum was 0 (Ryazantseva, 1937).

L.M. Tsetsevinski, in 1932, doing special work on the ecology of arctic fox (Alopex lagopus) in the northern part of the Yamal Peninsula, thus describes the snow conditions of this region (personal communication): "In winter, the tundra is covered very unequally by snow. Quite commonly in these latitudes strong winds blow snow away from elevations and pack it into depressions. The layer of snow in the valleys of watercourses, in gullies and similar places not rarely reaches a depth of several meters, when at the same time on the tops of the hills the tips of short tundra vegetation can be seen. Snow is packed by the wind so much that it can easily hold a man. Therefore one can walk without skis all winter there. Toward the end of April, when mild nights begin, thawed patches of earth show up first on the hillocks. Most of the snow mass melts in June, but in deep gullies snow can still be found in the month of August."

A.A. Kirpichnikov, wintering in 1934 on Dickson Island, kindly permitted me to make use of some characteristics of snow conditions, which are in his manuscript, "Economic mammals of Dickson Island and southwestern coast of Taimyr." This is what he writes: "Increased wind activity helps to blow away and transport the snow cover, which leads to extraordinary density, and, in a region of dissected relief, to unequal distribution of snow on the earth's surface. The snow

measuring survey of Dickson Island, which was carried out on 28 February 1934, demonstrated correlation with this. The figure obtained is the result of 105 measurements of the depth of snow cover in different parts of the island. The average thickness of the cover is 26 cm, maximum is 156 cm, and the minimum is 2 cm."

The density of snow on Novaya Zemlya (Matochkin Shar) in January, is equal to 0.28 to 0.35. Toward May it reaches 0.39, and toward June 0.40 to 0.50. It is interesting that on the west side of the island, along with winds of less strength, the density in March was not greater than 0.27 to 0.30. Z.A. Ryazantseva (1936) for Marre-Sale (April 1921) gave the density as 0.36 and for Greater Lyakhov Island (May 1931 and 1934) as 0.34 to 0.28. On Dickson Island toward the spring it is 0.38.*

Slyunin, speaking of tundras of Okhotsk-Kamchatka Province (1900), points out that here the density of the snow after a snow storm is so high, that "an axe when knocked against it rings as if it were struck against iron." Urvantsov (1935), one of the most experienced polar men, recommends that the compacted snow of the drifts be cut with a hand saw, because the iron shovel is of little use.

Snow does not obtain such a density everywhere. In low places, arctic fox, varying hare and willow ptarmigan (Lagopus lagopus) can in case of necessity, dig in and cover themselves. The inequality of the beds of the snow cover is the reason that even low tundra plants stick out above the snow in some places. Willow ptarmigan, according to the observations of Birulya (1910 sic), in winter peck on the heads of the Arctic poppy, (Papaver) which, on small hillocks ("baidzharkas") stick out above the snow. The reindeer has the opportuntiy of walking above the dense cover of the tundra, without sinking in deep, and digging

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*According to G.F. Abel's the specific gravity of snow in drifts that will hold the weight of a man is 0.28 to 0.33.

lichen where the snow is soft, or where it lies on a less deep layer. Even such a heavy animal as the polar bear (Thalactos maritimus) can move easily on the ice, because the snow blows away from here also and packs into the depressions between the pinnacles of ice, and also at high shorelines. The polar bear can walk free on the "uboy" of the tundra, when at the same time the brown bear (Ursus arctos) aroused in the middle of winter from the nest, "plows" a deep furrow in the fluffy forest snow, and drowns in it at each step. An awakened brown bear cannot walk very long, as soon as he finds a suitable place he hurries to lie down again for the whole winter. The arctic fox, a little fox with relatively narrow paws, (Fig. I) walks on the dense tundra snow and sea ice without sinking, accomplishing long migrations. When, by emigrations, they get into forested regions with fluffy snow, these foxes as a rule perish. Cases of return migration into the tundra, as far as I know, are unknown. Thus, the peculiarities of the snow cover of the tundra explain the presence in its fauna of such a life form as the arctic fox. Morphologically closely related to the arctic fox are species of small semi-desert and steppe foxes—corsac (Vulpes corsac) and Bukhara fox (Vulpes v. daurica) which are found only many hundreds of kilometers further south, in regions of little snow or dry steppes and deserts almost without snow. The wide zone of the forests with its deep fluffy snow divides the ranges of these closely related life forms.

In spite of the high density of the tundra snow, the winds of great strength, when carrying fine snow dust, dig out holes and depressions in some places and, in others, deposit snow dunes and hillocks. These "snowy zastrugi" have sloping ascents from the sides of the prevailing winds and abrupt sides on the downwind slope. (The inhabitants of the tundra use the direction of the zastrugi for orientation in the region.) The finest snow dust, carried by the wind at high speed, has the ability to get into the smallest openings,

to infiltrate the fur and feathers of animals, making additional difficulties for winter life.

Therefore, the retention of snow cover for up to 9 months of the year, the strong reworking and compacting of it by the winds, the accumulation of large zaboys in the depressions and the presence of large vyduvs on the hills and ridges, because of which there is unequal melting of snow in the spring, - these are major peculiarities of the snow cover of the tundra. Gamberg (1907, cited from Chirvinski, 1932) called the alpine region of the mountains of Swedish Lapland the "snowy-dune zone". He proposed that the flat tundras of the arctic also be considered in this category. Joining Gamberg, and referring our tundras, because of the characteristics of the snow, to the snowy-dune zone, we want to once more point out that the chionic factors are of extreme importance for the fauna of the tundra, and therefore merit especially attentive study here.

SNOW COVER IN FOREST REGIONS

The snow cover in the forested regions of the USSR is characterized by its continuity and average maximum depth, depending on the geographical location of the region, its relief, etc. The broad-leaved forests on the plain of the European part of the USSR occupy a region with a maximum depth of snow cover which increases from southwest (Dnestr) toward the north and east (middle Povolzhia)* from 0-5 cm up to 40-50 cm. In the region of the coniferous forests of the European part of the USSR the average maximum depth of 40 cm at Karelia increases, as we go eastward, to 80-90 cm and more in the headwaters of Pechora (Shugor - 95 cm) (Shenrok, 1926). The northern subzones of the taiga of western Siberia (lower parts of the rivers Ob' and Taz) lie in a region with well developed cyclonic activity which causes abundant snowfalls, and can be distinguished by great snowiness. According to the data assembled by Shostakovich (1925), the average maximum depth of the snow here reaches 100 to 140 cm.

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*Land along the Volga River.

According to the most exact data of the Climatological Handbook (Vol. 2, 1931), Surgut has 80 cm, Turukhansk has 109 cm. In the central parts of Siberia, there is significantly less snow fall (50-70 cm), and in Irkutsk Oblast', Yakutia, and Transbaikal there is located a region of little snow; toward the month of March the thickness of the snow layer reaches, in average 37 cm in Yakutsk, 27 cm in Verkhoyansk, and in Irkutsk (February) only 22 cm (Fig 2).

Closer to the coast of the Pacific Ocean the snow cover again increases, reaching in the Okhotsk taiga an average of 50-60 cm, and on Kamchatka even 100 cm. The taiga of Priamur and Ussuri Krais, as far as the depth of snow cover goes, are reminiscent of the forests in the middle zone of the European part of the USSR (from 5 cm at Blagoveshchensk and 10 cm at Vladivostok, up to 50-70 cm. on the lower Amur). Snow cover reaches especially great depths in the mountain countries (Caucasia, Altai, Sayan, and others), where at the upper border of forests the maximum depth not rarely is measured in meters. The trees in such belts of deep snow are depressed and bent by the steady pressure on them of the large snow mass.

Therefore, the forest regions of the USSR, quite different according to their floristic contents, can be divided by the ecologist into many groups according to differences in snowiness. Overwintering conditions for mammals and birds, even within one forest botanical-geographical region, can be evaluated quite differently because of sharp differences in the austerity of winter.

A forest, as a unique environment with its own peculiar microclimate, shows a marked influence on its own snow cover. The maximum depth of snow cover, density of it, duration and date of melting, heaviness of nast and gololeditsa in the forest usually are markedly different from that observed in the open forest-free places in the neighborhood. The differences can be noted even at the first snowfall.

On the fields and meadows, where there is a lack of wind, the first snow comes down as a more or less even cover, whereas in forests a significant part of it remains on the branches of the trees. Dark-needled species, spruce (Picea), fir (Abies), stonepines (Pinus pumila and P. siberica) and to a lesser degree, pine (Pinus), and markedly less, larch (Larix), which loses its needles for the winter, hold snow more tenaciously that the broad-leaved species. At the first snow, when the forest soil gets white, there are easily-spotted places not covered by it around the bases of coniferous trees.

The largest part of a fall of wet snow, which falls directly downward from above, and sticks well to the branches, adheres to dense crowns. Below, as if in the shadows of the crown, remain snowless round spots, which show up green with mosses, dense thickets of European blueberry (Vaccinium myrtillus) and red bilberry (Vaccinium vitisidaea). Hazel hens (Tetrastes bonasia) readily feed in these cleared spots about the bases of the shrubs. Here they eat the berries of the bilberry, and twigs and buds of the blueberry, which in the glades and spaces between the trees have long since been covered with snow. Siberian jays (Cractes infaustus) and common jays (Garrulus glandarius) also often come here to look for fruits, while chickadees (Parus), crested titmice (P. cristatus) and nuthatches (Sitta) look for insects and spiders which have come down to the earth because of the cold and which were not covered with snow. (My observations in Lapland, Gor'ki Oblast' and near Moscow).

Snow gradually falls down onto the earth and under the crowns of the trees, especially on windy days, but it accumulates here very slowly, and toward the end of winter it is always thinner here by two or three times than on the glades, roads, and forest "windows." Thus, the base of the trunk of each large tree is surrounded by a sloping

snowy crater. The smallest depth of cover is near the base itself. It gradually deepens on the radii away from the trunk and sharply increases beyond the border of the zone which is protected by the tree crown. The overhanging snow or "kukhta" as it is called by hunters, during a winter's accumulation, is partially evaporated by remaining a long time on the branches, and as it melts it falls down in the form of water drops or blobs of condensed snow. During a thaw the snow under the trees is roughened and made spongy, punctured with many holes caused by the falling drops and pieces of kukhta. By this means the snow cover is somehow compacted, but does not increase at all in depth. In the first half of winter kukhta appears on the branches many times in succession, but is either knocked down by the winds or falls down during warm days. But in the second half of winter the needles and branches accumulate quite a lot of ice, and then there appear pieces of grainy snow tightly frozen to them. Fresh snow freezes to the rime or to the condensed old snow, kukhta begins to stick, and for days at a time the forest stays almost white or grey, "in silver clothes" as we often say. The calmer and colder the winter is, the more kukhta accumulates on the trees. During a time of frequent winds and warm days the branches hold only a small amount of snow. The ecological role of kukhta is quite important. It retards movements on the branches, because of its tendency to fall, therefore in the second half of winter the squirrels and forest martens rarely go "gryadoy" —on the top — but prefer to move about below, on the snow surface.

It is quite well known to the hunters of the north of the European part of USSR that the marten can be more easily trailed in the second half of winter, when he leaves an unbroken trail on the snow, but not in the first part, when the animal often goes far up in the trees without leaving any trail. Little insect-eating birds of

the forest — two species of chickadees, crested tits, long-tailed tits (Aegithalos caudatus), azure tits (Parus cyanus), kinglets (Regulus) and others — when looking for food on the branches, are forced to climb on the underside of the branches because of the presence of thick layers of snow which lie above on the knots and needly "paws." Their ability to hang to the tips of the branches or to search from below the knots, needles, and lichens which are covered with snow on top, plays an important role in the struggle for existence of these little insect-eating birds.

I would like to quote a passage from my diary about the distribution of kukhta in the spruce-fir forest which was renewed by a heavy snowfall after a thaw. "3rd. March 1935 (Shariinski raion of Kostroma Oblast'). After a snowstorm toward the end of the day the wind slowed down; clearing up. The trees held a significant part of it above. Under a large spreading spruce by the river-bank there was only 1 cm of fresh snow. On the branches of the spruce - snowy kukhta of 4 cm; it is especially thick on the lower branches of large trees and on the understory, where the wind does not reach. Little spruces are completely covered with it (Fig. 3) while the tops of the large trees (first stratum), exposed to the wind, are hardly powdered with snow. Most of the chickadees are feeding on these tops which are lacking in kukhta. In the middle stratum they are climbing on the branches, hanging and searching under the needles and lichens from below. The branches, overloaded by kukhta, are strongly bent down. If liberated from the snow by the weight of a bird alighting they straighten up like a spring. This retards movement on the branches very much. In the spruce groves the snow cover is so thin that the crust that originated after the warm period is thinly covered by new snow and makes a loud noise under skis. In the fields, where there is 8 cm of fresh snow, — a light noiseless walk." (Fig. 5)

A forest covered with kukhta becomes nearly impenetrable by wind and different sounds. In the autumn, after leaf fall, the difference can be easily noticed between a forest with leaves and

one with the leaves lost, (because of the increase of wind, and an increased hearing ability). Then, in winter, with the appearance of snow on the branches, the summer situation is reestablished. The wind almost fails to reach the thickets, which are protected by branches whose surface is expanded by the soft kukhta (Figs. 4 and 5); sounds do not carry far. The weakening of the force of the wind results in the fact that this factor is nearly negligible here in the process of snow compaction. It is generally known that the snow cover in forests is distinguished by extreme fluffiness ("brodni").

According to G.A. Lyuboslavski (1912 sic), toward the end of the winter of 1892-93, the density of snow in Lesnoye in the intervals between trees was 0.11 and in a glade was 0.13; during most of the winter it did not exceed 0.18 and only toward April did it reach 0.32. In a forest region with frequent thaws the snow is usually more dense, more strongly compacted, and not rarely covered by nast; in the continental parts of Siberia where thaws are rare, the snow cover of the taiga is distinguished by extreme fluffiness and friability. The types of hunting skis, which are distinctive of one forest region or another, reflect very well the peculiarities of its snow cover. The widest and shortest skis are made by the Evenks of Transyenisey, Siberia. Winter hunting in forests with a snow cover of more than 30-35 cm in depth is almost impossible without skis; in this connection the forest zone is sharply differentiated from the tundra and steppe zones.

The peculiarities of forest snow have been known for a long time. Thus, Middendorf (1869), in his description of travelling in Siberia, repeatedly mentions fluffiness as a specific character.

It is generally known that wind is of only slight importance in compacting snow in forests. For an illustration of this condition I would like to use one of my own observations. On 6 February 1934, (near Arzamas, Gor'ki Oblast'), the night's snow storm had heaped a new layer of snow on the fluffy cover already there. On 7 February when walking in the forest on skis, I sank in for 30-35 cm, the hound

sank into the snow almost to the shoulders (the depth of the cover was 55-60 cm). In the fields, the snow was compacted by strong winds (vyuga) so much that there was very easy walking on skis with the snow settling under them not more than 1 cm; the dog could run free, almost without leaving a trail.

The compaction of snow in a forest is due mainly to the weight of the snow itself, to thawing, and to condensation of moisture from the air. Moreover, since the forest protects the snow cover from warm, wet winds, and thus lessens the range of temperature fluctuations, the compacting and settling of snow under a forest canopy is not as great as it is in the tundra, on the fields, or in steppes.

In distinction from the tundra being a "snowy-dune zone" (snezhno-dunnaya zona), we can place forest regions into a zone of "fluffy forest snow" (lesnoye rykhlosnezh'ya). Within a forest the thickness of crust or nast is usually less than outside of it. I will give an example: 28 February 1935, in the spruce-fir forests of Shariinski raion, Kostroma Oblast', because of frosts after a continuous thaw, there had developed a crust of nast not more than 5-6 mm thick. In some places it held up well under the weight of hazel grouse and varying hare. When walking on skis with a surface of 2400 cm^2, my feet sank down for 25-30 cm (my weight with equipment - about 90 kilograms). At the same time, the crust of nast was 10-12 mm thick on the fields, and in some places held the skis so well that they did not sink into the snow at all or sank only slightly.

The property of snow to stay in the crowns of trees, and the resulting inequality of the snow cover in a forest can be illustrated by the following examples. On 28 February 1935, in the same district as before, at the bases of the spruces (20 cm from the trunk) the depth of snow cover varied between 20 and 30 cm (average 25.2), at a distance of 2 meters it varied between 40-50 cm (average 43.7), while at a distance of 3 meters, it varied between 45 and 62 cm (average 49.7). In connection with the accumulation of snow on the branches and its evaporation, the average depth of cover in coniferous plantations is markedly less than

in glades and in forests of young broad-leaved trees. Thus, in a spruce-fir forest of 0.5-0.8 density, the average depth (from 40 measurements) was 35.7 cm, in a young (10-12 years) aspen grove on a burn it was 52.5 cm (10 measurements), and in a glade in the aspen grove it was 52.8 cm (10 measurements).

Some interesting data concerning the depth of snow cover in different types of groves have been published in the forestry literature. A.V. Tyurin (1914), and P.Y. Sulkovski (1915) (cited by Chirvinski, 1935) gave interesting observations on the greatest depth of snow cover in different types of forest plantations on the Bryansk Experimental Forest Station for the winters of 1912-13 and 1913-14. Their data showing the depth of cover (in centimeters) are given in Table 2.

TABLE 2

Type of forest plantation	Snow Depth (Centimeters)	
	1912-13	1913-14
Glades (not large, in middle of forest)	33	40
Broad-leaved plantations	34	38
Pine plantations, 3rd through 6th class	24-28	32-30
Spruce plantation, 5th class	16	24
Pine plantations, 6th class, with dense spruce undergrowth	13	19

The deepest snow in both years was in the glades and in broad-leaved plantations, while in pine plantations it was much less. The pine plantations with dense fir undergrowth held the snow most of all, since the kukhta remained on the needles of the two tiers of trees; here the snow cover was two or three times less than that in the glades.

Somewhat earlier this phenomenon was studied in detail by Nesterov (1917) near Moscow, in forest tracts of the Timiryazev Agricultural Academy.

These details of the distribution of snow cover in a forest, have, as it turns out, no small importance in the life of vertebrates. From what has been said earlier, it is clear that in heavily stocked dark-needled plantations the snow cover averages less, and icy crusts are thinner, than in thinly planted and sparse ones. Therefore, many hoofed animals from musk deer (Moschus) and roe deer (Capreolus capreolus) up to deer (Cervus) and moose (Alces alces) prefer to winter and to make migrations within dark-needled plantations (spruce groves, fir groves, etc.), if the depth of snow cover in broad-leaved forests is not convenient for their movements. When the snow becomes deeper, even fox and lynx (Lynx lynx) prefer to walk in the spruce thickets, where the layer is thinner, rather than in pine groves and birch (Betula) groves. Thus, for example, 9 February 1941, according to my measurements on Losiniy Island (near Moscow), the average depth of snow cover in glades in the forest was 44.5 cm, in young birch growth it was 42.7, but in mature spruce groves with closely approximated crowns, it was only 31.4 cm. In these spruce groves there was a small herd of roe deer, and none of them ventured out on the glades. While going along the trail, I measured the depth of snow every fifty steps; the average of 54 measurements equalled 30 cm. This figure clearly indicates that roe deer carefully selected the parts of the forest with the thinnest snow.* In the same spruce groves, there were many fox trails, but in contrast to roe deer, in some places they walked out into the glades and the scattered forest.

In winter, as has already been mentioned, the snow under trees is distinguished by shallower depth and unequal density; sometimes there

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*This method of studying the relationships of mammals to the depth of snow cover was proposed by A.A. Nasimovich.

are many hard lumps of fallen wet kukhta in it. The snow in forest "windows" and in the glades is deeper and less dense, and is more convenient for making snow burrows. Hazel grouse, black grouse, and capercaillie, during their daytime rest, sometimes make shallow holes in the snow under the trees, but, when they dig in completely for the night, prefer the soft thickness of the snow of glades and clearings which are not protected by forest. This can be partly explained by the fact that the birds "dive", falling into the snow at an angle after approaching swiftly a convenient place spotted from a perch in a tree. They could not dig in in this manner under the trees because of the branches which would interfere with flight. In addition the shallow depth and the unequal density of snow under the crowns do not make a good sleeping burrow possible. Every such burrow is in use only one night. During the night in a snow burrow the bird leaves a large heap of feces. When snow melts in the spring, it is easy to note the distribution of wintering flocks and the location of burrows by these heaps.

In 1934 I tried to establish, in the forests east of the Vetluga River (Shariinski raion, Kostroma Oblast'), in what places hazel grouse spend the night. Altogether there were found traces of 102 sleeping burrows, which were distributed in the following places:

1.	Clearings with small young growth of broad-leaved spp. (Here the hazel grouse usually sleep not far from the edge of coniferous forests.....	4	burrows	(in 3 places)
2.	Roads (not used in wintertime).....	9	"	(7 ")
3.	Sparse lichen and pine forest on the dry sandy ridges ("veretia") near low places with spruce.....	11	"	(7 ")
4.	Forest "windows" (small clearings in thickets).....	13	"	(10 ")
5.	Vistas and narrow pathways (not used by man in winter).....	26	"	(20 ")
6.	Small forest glades.....	39	"	(24 ")
	Total.....	102		71

As we can see, only a small part of the total number of hazel grouse spent nights in the snow under cover of coniferous plantations. Moreover these 11 burrows were in thinned lichen-pine forests, which retained relatively little snow. All other burrows (91 or 89.2 per cent) were located in spots which were not protected by crowns of coniferous stock, but were where snow cover reached its greatest depth and fluffiness.

Nesterov (1909) conducted detailed observations for many years near Moscow on the progress of snow melting in forests and on open places. He determined that in the vicinity of the Timiryazev Agricultural Academy the period of snow melting lasts from 26 days (1904) to 57 days (1902). The melting of the snow is completed in the first 5-10 days on the fields, but in the forests it melts very slowly, and, in a definite order from the less dense to the more dense plantations. Clearings, along with the fields, are liberated first, then rather sparse young groves, then sparse oak groves on southern slopes, birch groves on northern slopes, pine plantations, and finally fir groves. By his data in 1908, the soil was completely freed from snow in the following order:

1.	On the fields, clearings, and open places in young groves.....by	9 April
2.	In young, but not dense plantations.....	11 April
3.	In sparse forest on southern slope.....	13 April
4.	In birch groves.....	16 April
5.	In pine groves.....	23 April
6.	In spruce groves.....	2 May

Therefore, dark dense groves of fir, even in the southern part of its range, have more continuous "winter" than fields and broad-leaved forests located nearby.

According to Lyuboslavski (1915), at the Institute of Forestry near Leningrad, in the winter of 1892-93, the snow cover lay 172 days in the forest, 163 days in the forest glade, and 147 days on the open field.

In connection with the course of melting of the snow in the forest, peculiarities of behaviour of some of the forest birds which pick up their food from the ground were noted during the first days after their arrival. In the middle zone (my 10 day observations refer to the part of Gor'ki Oblast' near the Volga), a number of forest species, which arrive in April, show up and stay 5-10 days on the fields, meadows and forest edges, where the snow melts relatively early, and do not come into the depths of the forest, where at this time thick layers of snow still lie. Such are chaffinch (Fringilla coelebs), brambling (F. montifringilla), green finch (Chloris chloris), fieldfare (Turdus pilaris), redwing (T. musicus), song thrush (T. ericetorum), mistle thrush (T. viscivorus), woodcock (Scolopax rusticola), stock dove (Columa oenas) and others. Only after a week (and sometimes even later after the arrival of the pioneer individuals, when thawed patches of earth of sufficient size show up, do the flocks and groups of birds get a chance to spread out into the forest. Forest birds which come after the melting of the snow in the second half of spring, flycatchers (Musicapa), warblers (Sylvia), nightingales (Luscinia), rose finch (Erythrina), golden oriole (Oriolus oriolus), and others, show up immediately in the forest in their usual nesting places.

The influence of the forest on the snow cover is more significant when the plantation is larger and thicker, with more strata. But even in plantations of one species placed in different types the changes in snow cover will not be the same. Thus, in forests which are near the upper limits of trees in the mountains or in the north near their arctic limits, thinning causes a marked increase in the role of wind, which causes changes in the snow cover. In the fir groves of central Lapland (region of Lake Imandra), according to my observations, the snow was markedly reworked by the wind, compacted and partly displaced, by the end of March 1931. Somewhat to the south of Imandra, on the vyduvs, there were many cleared spots which were left after a recent thaw. Although in March the depth of the snow cover was approaching the yearly maximum, the tops of

bilberry, dwarf willows (Salix lcp.), marsh rosemary (Ledum palustre), and other bushes were protruding above the snow. This facilitated the feeding of the willow ptarmigan. The transition from deep, fluffy, forest snow to the compacted and reworked cover of forest-tundra and tundra occurs gradually and imperceptibly. Therefore, in the northern part of the forest zone, near the border of the tundra, the snow cover has an intermediate character. The same picture can be observed at the upper altitudinal limit of the forest where the trees get smaller and grow scattered, and also in the region of the forest-steppe ecotone.

Since man, by his activity (cutting the forest, etc.), changes the aspect of forest plantations and also the character of their snow cover the conditions of snowiness in forest regions are becoming even more complicated and multiform. There will be lots of work for ecologists to do to find out all aspects of the effect of snow cover of forest regions on their fauna.

THE SNOW COVER IN STEPPES AND DESERTS

The arid regions of the USSR are complex in their climatic peculiarities, and form subdivisions with different types of climate. According to Berg (1938) all our steppes belong to that group of steppes with cool winters. Voznesenski (1930), believing that the climates of steppes are intermediate between the climates of deserts and boreal climates, delimits their typical area in the following way: "In the east - in western Siberia - they spread out in a wide strip for 1,000 to 1,200 kilometers, from Altai to Turkestan and up to 50-52 degrees north latitude; going west their distribution narrows so that on the meridian of Ural'sk they are only 400 kilometers wide. Next they increase in width in Povolzhia, on the Don, and in northern Caucasia. Between the Sea of Azov and the Donyetz Range in some places they dwindle to almost nothing. Farther west in the form of an independent complex of three kinds, the steppes

extend in a relatively narrow strip (not quite 200 kilometers wide) from the Sea of Azov to Poltava and the vicinity of Kishinev. They also cover almost all of Crimea except the small territory of the mountainous part."

According to climatic peculiarities Voznesenski recognizes:

(1) East Siberian steppes, or cold forest steppes of the foothill regions which are poor in winter precipitation. They are found in level country not less than 700 meters above sea level, in the foothills of Sayan, in Prebaikalia and Transbaikalia, (their climatic formula is DVScw), and in the Minusinsk Region (DVSbw).

(2) True steppes (I would rather call them mid-temperate steppes), which are the most widely distributed type of climate (DVSa), stretch in an uninterrupted but narrow strip 100 to 200 kilometers wide from Dzhungariya to Carpathia.

(3) A type of steppe which is transitional to forest zones (DV), colder than the previous ones. According to Voznesenski they find their most typical expression in the huge territories of Kazakhstan and western Siberia.

(4) A number of warmer varieties of steppes, which are found in small spots in Crimea, in Caucasia, and in middle Asia (type SbSa).

During very cold winters (temperature of the coldest month: Minusinsk, -19.4C, Borzya, -27.7C, etc.) the steppes of eastern Siberia are distinguished by the small amount of precipitation (24.0 to 35.0 cm),* of which the largest part falls in summer. Therefore, the maximal depth of snow cover is not large -- 20 to 30 cm -- and less. The ground is often naked in many places because the snow is strongly reworked by the wind (Fig. 6).

Typical temperate steppes can be characterized by snow cover with an average maximal depth of 20 to 30 cm, in some places in the east reaching 40 cm, and much less (0-30 cm) in the west. The region of colder, transitional steppes has a deeper snow cover (20-50 cm) which stays longer. The

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*240-350 cm in original is an obvious typographical error.

warm varieties of steppes have a snow cover with an average depth of less than 10 cm. Snow falls sporadically and in some winters its cover is completely absent. In the steppes of this type (for example, in Mil'sk Steppe in Transcaucasia) many steppe birds overwinter -- little bustards (Otis tetrax), great bustards (Otis tarda), quail (Coturnix coturnix) etc, -- flying away from the northern colder and more snowy steppe regions.

Deserts that are found well within the borders of continents of the temperate zone have a climatic type which, according to Berg (1938), is found in our country in the western half of Turkestan and part of the Aralo-Caspian lowland. The winters are relatively cold with a small amount of precipitation, the snow cover is not significant and lasts only a very short period (in Kazalinsk - 70 days, Khodzhent -18 days). According to his data, Pamir is characterized by a Tibetan type of climate (deserts of high plateaus) with sharp yearly and daily amplitudes, great aridity, and insignificant amount of snow in spite of the very cold winter (Pamir Post has a January temperature of -18.7C). The deserts and semi-deserts of Mongolia (with the climate of semi-deserts of the temperate belt) which limit our Siberia on the south have similar winter conditions. The winter of this continental region is very peculiar: during the period of greatest cold it is characterized by an almost complete lack of snow. In Ulan-Bator, where the average temperature of January is -26.6C, the winter has only 2 per cent of the annual precipitation. In Kobdo with 100 mm of precipitation in a year, 80 per cent falls in the summer and 10 per cent in the spring and the same in the fall; winter is almost devoid of precipitation and is snowless. In the environment of this cold but completely snowless winter many terrestrial birds overwinter without flying to the south, a phenomenon which cannot happen even in steppes with warmer winters (see below). Thus, the huge territory of our steppes, semi-deserts, and deserts is characterized by a meagre snow cover, or even by a complete absence of it.

Even where the snow falls regularly and stays long, the character of the cover is markedly different from that which we saw in the forest. It

depends on the work of the winds, which here can be distinguished by great power. A significant part of the snow is blown by the wind into ravines, hollows, erosional gullies, etc., while elevations, slopes, and hills are almost always bare. This lack of snow is furthered by the relatively low, thin grass cover which holds snow poorly. On the places with a high cover of feather grass (Stipa) in thickets of steppe bushes (wild almond trees (Amygdalus), spirea (Spiraea) and others) snow, brought in from the neighboring bare places, lies deeper and more even. In the steppes of the European part of USSR, Kazakhstan, and western Siberia, thaws are not rare, during which time the snow melts completely or is transformed into a thin, icy crust. By small decrements with each thaw, in many regions there occurs a complete disappearance of the snow cover; therefore, the occurrence of snow is distinguished there by great irregularity.

The compactness of the snow of steppes averages markedly greater than in the forest zone. According to Tikhomirov and Ryazantseva (1939) in the steppes of Transvolga toward the end of winter it varied from 0.25 to 0.32 (averaging 0.29).

The spring melting of snow on the steppes also has its peculiarities. In spite of intense insolation, frequent dirtying of the snow by dust caused by winter denudation of the open spaces, and also the great speed of the wind, the snow melting in Kazahkstan, for example, is less rapid in the south than in more northern latitudes. In northern Kazakhstan the decrement of snow during the day is relatively great (from 1.0 to 1.5 mm); on the larger area of its steppes the decrement ranges from 0.5 to 1.0 mm; while in Turgai and Karkaralinsk regions it ranges only from 0.2 to 0.3 mm per day. "The explanation to this phenomenon, that seems strange at first sight, lies in the fact that condensed firm ice, into which the remains of the snow cover are transformed, melts slower than the uncompacted cover of more northern regions." (Reference Book, 1933).

The insignificant depth of the cover and its unequal distribution make possible the year-round grazing on pasture of a large number of hoofed animals, wild as well as domestic. Many peoples of Asia and of the steppes

the southeastern European part of the USSR have used from time immemorial the steppes and deserts with little snow cover for raising cattle without the necessity of storing hay for winter. The Arabian traveller Ibn-Fadlan a thousand years ago described travelling the winter range of Turkmen sheep; a work by Rychkov in 1762 beautifully described the "tebenevka of the herds" of the Bashkirs and Kazakhs. (Tebenevka = moving a herd from one place to another in the deserts as the grass gives out.) Przhevalski (1883 sic) well described the average conditions of the Gobi winter which allow a nomandic life on the steppes for thousands of herds of Mongolian gazelles (Procapra gutterosa), Persian gazelles (Gazella subgutterosa), and kulans (Equushemionus), and allow argalis (Ovia ammon), and Siberian ibex (Capra sibirica) to stay on the slopes of the mountains.

I will now give briefly the characteristics of the snow cover which he recorded during his crossing of the Gobi and part of Alashan' from north to south, from Ulan-Bator (formerly known as Urga) to Din-uan-in.* This information refers to the end of November through the first half of January (1883-1884) over a long, almost straight itinerary of over 1,000 kilometers length. "With our departure from Urga there commenced cold, which reached the freezing point of mercury. But the snow covered the ground only with a thin (1/4 to 1/3 of a foot) layer, and even this, in some places, was not complete. In about 150 versts (Old Russian measure of distance equalling 1.067 km) from Urga the snow cover became more irregular and half a hundred versts further on disappeared completely..." Such was the aspect of the northern steppe border of the Gobi.

"Eighteen days after our departure from Urga, we left the steppe region of the northern Gobi behind us and got into real desert near the well Dybidoba, the same desert which extends from east to west throughout all central Asia, and which extended along our route, without a break, to the frontier mountains of Gan'su... For almost a whole month we toiled across the central Gobi to the northern border of Alashan'. Besides cold and also occasional storms, the desert constantly impressed on us its unfertility and lack of water... During our travelling in the central as well as the northern Gobi the weather was

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*Now known also as Bayan-Khota

almost always clear. As has already been said, snow lay only in the vicinity of Urga and in the northern half of steppean Gobi. Further toward the south the desert was completely free of winter cover. Small snow storms again whitened the ground only in the vicinity of the city of Khurkhe and in these mountains themselves. After that the wind blew this snow away from the open places and deposited only small drifts by the bushes and stones. In the southern part of the land of Urots, in thickets of Saksaul (Haloxylon) and in other places here also, we met solid snow with depths of up to half a foot and in drifts from one to two feet deep. Calms were not rare in November, but in December, storms happened more often...." Still further south, in Alashan', "snow was encountered only locally but even in these instances usually only in small drifts by bushes and in general near objects which stuck up above the surface of the soil. In bare loose sands such little drifts were covered by a sand layer sometimes two feet deep. Nevertheless, the Persian gazelles know how to find such snow mines and, by digging in the sand which covers them use snow instead of water... The weather, as formerly, stayed clear, with cold nights and warm days, when there was no wind. The sun, in spite of its being winter, was noticeably warm, and during the calms the loose sand on the steep slopes which faced the sun warmed up to 27,5 C in spite of its being the end of December (the old style)." Undoubtedly the snow, mixed with sand and soiled with loess by the numerous dust storms, warmed up during the day and melted. Because of the extreme dryness of the air, there is marked evaporation in addition to warming by the sun, therefore, the snow cover of the desert thins very quickly after each snow fall. A large accumulation of snow does not occur here, as a rule.

Undoubtedly, because of the huge size of the region which in Europe and Asia is covered by steppes and desert, and because of the marked differences in amount of precipitation, winter temperatures, and wind, a whole series of areas can be distinguished each with a specific regimen of snowiness. There are not enough data, however, for this yet. We can note here only some of the most essential characteristics. Along with a relatively small yearly amount of precipitation, steppes and deserts are distinguished by a small amount of solid precipitation, which, moreover, after falling, is evaporated, melted, and absorbed into the soil. The snow cover of most of the arid

regions is distinguished by small amount, strong metamorphosis, great compactness, and marked variability. In winters of little snow, the importance of the snow cover becomes practically negligible in the life of vertebrates on steppes and deserts, something that does not happen even in winters which are the poorest in precipitation in the region of tundras and coniferous forests. We can call the steppes and deserts the "zone of little snow, with irregular, compact, metamorphosed cover."

SNOW COVER AS AN OBSTACLE HINDERING THE MOVEMENT OF ANIMALS

At some significant depth and at a certain degree of fluffiness, snow becomes a mechanical obstacle hindering the movement of animals. This hindering of movement depends not only on the peculiarities of snow cover e.g. its supporting ability, or, in other words, its resistance to compression, but also on height, weight and also morphology of the extremities of certain organisms. For the vole, shrew, mole, bunting or chickadee, movement on the soil surface is already obviously restricted by a fall of fluffy snow with a depth of 3 to 6 cm, while a man begins to feel inconvenienced and tired of walking in snow with a depth exceeding 20 cm. Huge moose can easily run in fluffy forest snow of a depth of 40-50 cm, a layer which its hooves penetrate to the soil. The same cover, however, causes great difficulties of movement for fox, wolf (Canis lupus), roe deer, and other middle-sized animals. Forty to fifty cm is only a small part of the length of the extremities of moose; because of the greater power of the animal the fluffy snow hinders its movement only slightly. Sinking in for 40-50 cm means that middle-sized animals thrust their extremities into the snow for the greater part of their length. They pull out the extremities at each step only with difficulty because the fluffy snow does not present dependable points of support. The swinging of the foot forward is also hindered by the resistance of the snow, on the surface of which the foot leaves a deep furrow. The animal is very often not able to lift the foot above the level of the snow because of its small size and the deep penetration of the limbs on which he is at this time supported. On his path in such cases remain not only deep holes (the prints of the feet themselves), but also long uninterrupted furrows - "povolokas" and "vyvolokas," as they are called by hunters. Everyone who has had the

experience of walking without skis on snow up to knee deep or higher knows what sort of struggles this kind of walking requires and how fast it tires one.

Here are some figures from my notebooks characterizing conditions of movements upon the snow of some common vertebrates of the middle zone.

Third of March 1935 (Shariinski raion of Kostroms Oblast'). On the fresh snow, depth 8 cm, which fell on the nast, the depth of the tracks is as follows: varying hare sinks for 4 to 5 cm; squirrel sinks for 4 cm (in this case, all four paw prints fuse into one deep hole); ermine (Mustela erminea) sinks for 3 cm; red-backed voles (Clethrionomys) glareolus and rufocanus for 1 to 1.5 cm; grouse sink for 3 to 4 cm.

Fifth of March 1935. The same place; the snow lies the same as on the 3rd of March; lynx (tracks of two old individuals) sink no deeper than varying hare, i.e. for 4 to 5 cm (possible they were supported by the crust which was at a depth of 8 cm below the snow surface); large moose sink almost to the soil, i.e. to a depth of 40-50 cm, penetrating the layer of fluffy snow and also the thickness of the crust with the granulated layer underlying it.

Sixth of February 1934. (near Arzamas, Gor'ki Oblast'). When walking on soft, slightly compacted snow, the paws of the varying hare sank into the snow for a depth of 3 to 4 cm, and a large hunting dog sank in for 35 to 40 cm. Seventh of February - After a snowstorm with a heavy snowfall the varying hare now sinks 7 to 15 cm (the latter figure on long jumps). The hunting dog sinks in almost to the shoulders, making a trail only with difficulty. The dog moved so slow that the hares, for which it was not easy either, walked very slowly when being trailed and sat down often. A weasel (Mustela nivalis), carrying a captured mole, sank in this snow for 2.5 to 3 cm; the ermine, as always, for 3 to 4 cm, while forest voles sank in not more than 1 cm. Since there had been no thaws all winter and the snow was hardly at all compacted, a man sank in, even on skis, for 30 to 35 cm (i.e. for half of the shank), but without skis one sank for 50 cm in a cover of 55 to 60 cm. The enumerated data refer to the snow cover in broad-leaved forest with a slight admixture of coniferous species.

A completely different situation occurred in the fields, where the snow, compacted by storms, supported the grey hare (Lepus europaeus) perfectly, so that it frequently did not leave distinguishable prints.

The presence on the trail of an animal of long furrows caused by the dragging of the extremities and of course the tail or the body itself through the snow, is a sign of the difficulties of movement and of insufficient adaptation of this species to walking on fluffy snow of this depth. The otter (Lutra lutra) is a good example of this. A heavy animal, very low on the feet and elongated in length, it sinks into the snow so much that it drags its belly and tail upon it, plowing a deep solid furrow which reminds one of the trail made by dragging a log. Because of this an otter progresses so slowly that a man on skis can easily catch up with it. For the otter the difficulties of moving on the fluffy snow are sufficient to make him hurry to use any path where the snow is more or less compacted. This is the basis of a method of hunting otter that is known to the forest hunters of the European part of the USSR as well as Siberia. There, where an otter moving along a river shortens the distance between bends of the river by short-cutting on a straight line across the bend, the hunter breaks a deep ski trail through the snow and sets his traps in it. When the otter encounters a ski trail, he always follows it if the direction taken by it is anywhere near that chosen by him, and thus he becomes the prey of the hunter. This method gives such dependable results that experienced hunters of the northern part of Gor'ki Oblast' promise to catch in a short time in the deep snow any "wandering" otter.

It is interesting to find out the weight load per unit of surface of the paws of the otter. I have measurements of an old male killed by me in September 1927 on Kil'din Island (Murmansk Coast). The otter weighted 8 kg. The area of the supporting surface of the hind paws was 48 cm, of the front - 32 cm. From this we find that their load per square centimeter approximates 50 g. This figure is relatively small, being close to that which is characteristic of lynx. In this case apparently the extreme height of the animal is of more importance than the area of its feet.

All existing observations tell us that the otter is not adapted for far and quick travel upon snow. In winter he avoids having to make long journeys and travels only in extreme necessity. But because of the remarkable streamlines of the body an otter can quickly and easily dig into

the snow. Caught far from water, he hides in the snow making long tunnels (observations in Gor'ki Oblast').

Good proof of the fact that fluffy snow of relatively shallow depth does not hinder the movement of animals of different height to an equal degree is seen in the method of driving wolves, red foxes and corsacs by horseback, which has long been practiced in steppes. The Yakuts drive red and arctic foxes by horseback in the soft, deep snow in the forest tundra; the Evenks do the same with a light sledge pulled by reindeer or on deerback (Jochelson, V.I., 1898). The Nenetses also drive arctic foxes in soft snow by using deer sledges. This hunting was known by the Bashkirs, Kazakhs, Kalmyks, Nogaitses, and Buryats (and in some places is practiced even now), and was adopted by the Russians from them. I will give a description of it from the words of S.T. Aksakov "Notes of a Shotgun Hunter." "If there suddenly falls a relatively deep snow of about 40-50 cm, thick and fluffy to the extent that an animal's foot penetrates down to the soil, then the Bashkirs and other Asiatic and Russian colonists bait hares in great numbers (with Borzoi dogs), and foxes and wolves are driven on horseback and killed with one blow of a thick leather lash...The animal mires in the snow almost up to the ears, soon becomes tired and exhausted; to catch up with him is not difficult. With the first thaw, i.e., with the first compacting of the snow and the appearance of a crust, without which only a rare winter can begin, any capture of steppe animals by driving is stopped."

As the snow becomes deeper and its upper layer becomes compacted from winds and thaws, small and middle sized animals gain a number of advantages over the large ones, especially the hoofed ones, the tough hoofs of which easily break through the crust. Hares, foxes, wolves, lynx, not to speak of the small carnivores and rodents, run about on the nast not only without sinking in but also without leaving the prints of their nails. The hoofed animals break through the nast and wound their legs. They avoid making extensive travels in extremely deep as well as especially nast-covered snow.

A widely known method of hunting moose, deer, maral (Cervus elaphus maral) and roe deer on the nast is based on utilizing the difficulties of movement of hoofed animals through snow with breakable crust.

In this case the nast must easily support a man on skis. How helpless the most swift and enduring deer become in deep snow can be proved by the results of olden-time unrestricted market hunting, which was especially attractive for the hunter-traders. Middendorf (1869) in his well-known work tells about two Evenk brothers who, in the Aldan Range, in three weeks of hunting on deep snow with nast, killed about 600 reindeer; Przhevalski (1870) described a case of four Golds killing 55 wapiti (Cervus elaphus xanthopygus) in two days of hunting on the nast in the forests in central Ussuri. Lavrentiev (1891) collected a number of typical examples of the destruction of hoofed animals on the nast in Siberia. I will cite here some of his data. At the end of the 1850's in the former District of Barguzin, east of Baikal, three men drove on the nast and killed 60 moose. In the same place the inhabitants of the village of Goryachinsk once killed up to 200 moose on the nast. At the end of the 1870's the inhabitants of one village 50 km from Balagansk took up to 30 roe deer per family on the nast, killing a total of up to 1500 head during a few days hunting and so forth.

It would be possible to mention many such cases. It is interesting that carnivorous animals regularly use periods with nast or extremely deep snow for hunting. Here is what the Evenks, who are some of the best observers and hunters of the taiga, say about the wolverine (Gulo gulo) of northern Prebaikalia. "As long as the snow lies deep, the wolverine does not bring down anything, but follows on the trail of the lynx. If the lynx brings something down, the wolverine takes it away. The lynx is afraid of the wolverine; as soon as he sees one he runs away and leaves his prey. But when nast comes, the wolverine hunts intensively and kills roe deer. In some mornings about 10 roe deer are killed. It eats only a little bit of each, has time only for killing. On the nast it does not eat as much as it ruins. The chief hunting of the wolverine takes place on the nast, and during the winter, the lynx exists as a worker for him." According to the Evenks, the deep snow enables the wolverine to strangle yearling deer. (Petri, E.B., 1930)

The observers of Pechora-Ylychski National Park reported to me that

in the winter of 1939-40, when snow in the Urals reached a depth of 130 - 150 cm, wolverines caught wild reindeer after two or three short jumps. The deer sank in the fluffy snow so much that it was not necessary for their predator to have the usual long stalk for success in hunting. One can imagine that with fluffy snow cover, the lynx, which has wide feet and sinks into the snow relatively little, and hunts by creeping, has a number of advantages over the wolverine, which catches hoofed animals by harassing them. Wolves in Siberia harass roe deer and deer on deep compacted snow or snow covered with nast. These same carnivores according to Dinnik (1914) destroy many deer, roe deer, chamois (Rupicapra rupicapra) and wild boars (Sus scrofa) in Caucasia," at the end of winter or the beginning of spring.., when the soil is covered by a deep and already hardened snow, into which the legs of deer or roe deer sink deeply, and into which the foot of the wolf, having a soft and wider sole sinks hardly at all..." (See also Nasimovich, 1939). A drive by foxes for musk deer in deep snow is usually successful in central Siberia, and by yellow-throated marten (Martes flavigula) in Ussuri Krai. In these ways the depth of the snow cover, in certain combinations with its fluffiness or density, plays an important role in the movements of animals in the winter time.

It can make difficult the food searching movements for some species and ease this searching for others. e.g. carnivorous ones, for which restriction of movement of their prey is advantageous. A predator which is chasing a single animal or a herd used the well trodden trail of the prey, which economizes its energy and offers advantages for the assailant. The factor of snowiness, even for this one reason alone, has a large importance in the struggle for existence of many mammals and some birds. Species that are plantigrade or digitigrade but with wide paws have, under conditions of deep snow, all the advantages in searching for food and when being pursued by enemies, as compared with digitigrade species with small supporting surface on the limbs. Of quite significant importance also is the method of progression itself. Jumps with simultaneous support on four legs at one time, which are characteristic of hares, squirrels, red-backed mice and others; and jumps with support on the two front feet, and followed by a transfer of the hind feet into the prints of the front feet, which are characteristic

of the weasel-like forms, are more advantageous of movement on the fluffy snow than the jog-trot of canids, the step of cats or ungulates, etc. (In the future for simplifying discussion we will tentatively adopt the idea that, in moving, the weight of the body of mammals is distributed on the supporting surface of four limbs at the same time, and in birds, on two). The odd-toed species - Kulan and tarpan (Equus caballus gmelini) could not exist in many snowy regions even for no other reason than because their limbs are entirely unadapted for movement on the fluffy yielding surface of snow. The species of this group never did transgress beyond the borders of the steppes with little snow and the semi-deserts. As proof of the non-adaptiveness of horses for getting food from under the snow, we can cite the periodically occurring mass decimation of the Bashkir and Kazakh herds "on the tebenevka" during winters of deep snow and icy crust (see below).

Among the even-toed ungulates, species which are completely unadapted for movement on deep fluffy snow are those with narrow small hoofs and closely approximated and scarcely movable third and fourth digits and rudimentary second and fifth digits which do not touch the ground at all. Such extremities are possessed by our steppe antelopes--Mongolian gazelle, Persian gazelle, and saiga (Saiga tatarica)--mountain-sheep, goats, and among the deer, roe deer, the various races of red deer (Cervus elaphus), and spotted deer (Cervus nippon). Mongolian and Persian gazelles, and saiga, as it is well known, are distributed only in steppes and desert regions with little or almost no snow. The distribution of some antelopes in snowy regions, chamois in Caucasia and in the Alps, etc., snow sheep (Ovis canadensis nivicola) on the ranges of eastern Siberia, Siberian ibex on the southern ranges of Siberia, can be explained, as will be shown farther on, by the peculiar regimen of snowiness under conditions of mountainous relief. How the deep snow of these regions where some of them occur influences the distribution and behaviour of the above mentioned deer will be discussed later. Here it is necessary only to mention that the musk deer is a unique species of little deer with quite widely spreading digits and a relatively wide supporting surface on the extremities, which comes up north beyond the Arctic Circle. He holds his own only in mountain regions where he can find areas of shallow snow. Two large species of deer, moose and reindeer, which are most widely distributed in snowy regions besides

having large size which aids movement on the snow, have relatively broad and well-separated third and fourth digits and well-developed second and fifth digits. Especially interesting are the extremities of reindeer.*

Even Middendorf (1869), when describing this species, pointed out that it "is distinguished from its relatives, the deer and roe deer, by the extremely wide soles of the hooves because of which the prints that he leaves are very large and markedly wide. However, he not only spreads out the true and secondary hoofs, especially on the front feet, but also walks with the whole foot, while a horse steps out with a pricking walk so to speak, as if it were on the tips of the fingers. In order to do this he bends all the joints at a sharper angle and lifts the legs higher". The legs and body of reindeer are so supple that they can stretch behind their ear with their hoof, clean their nostrils of ice which freezes to it in the winter, etc. All these peculiarities permit the reindeer to walk on very miry sphagnum bogs and deep soft snow by lifting the legs high at each step and by supporting itself on a relatively broad surface. On the compacted snow of hill tops and tundra he often does not even leave tracks.

The ability to lift the legs high above the surface of the snow while running is characteristic also of the moose. He rarely drags his hoofs in the snow. His print is "clean" say the hunters, while the maral and roe deer leave large furrows in their trail.

M. Bogdanov (1873) and Seton Thompson (1910) have pointed out the peculiar characteristics of the extremities of this species, which are of course connected with the conditions of existence in regions with long and snowy winters. The boar, even though he has well developed second and fifth digits and quite mobile and large third and fourth digits, is not adapted to movement in deep snow becuase of his low height and great weight.

All representatives of the Canidae, being digitigrade and with quite compact and relatively narrow paws, sink deeply into the snow. Thanks to

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*Formozov has in mind the ability of the third and fourth digits to separate themselves from each other when the animal is walking in the snow--translator..

the growth of a brush of hard hairs, the supporting surface of the extremities of arctic and colored foxes increases with the approach of winter, however, on fluffy snow both these animals sink in deeply, but nevertheless much less so than the wolf. The load on one square centimeter of supporting surface of the feet of foxes (from the vicinity of Moscow) is equal to 40 to 42.5 g (measurements made during the winter of 1943-44 when there were many voles and a large proportion of the wolves and the foxes were well-fed and plump). A study of the wolves from a litter which was obtained on 27 December 1940 near Maloyaroslavetz showed that the weight load on one square centimeter varied from 103 g in an old male (weight 45 kg) and 100 g in an old female (weight 31.5 kg) to 97 g in subadult males and 89 g in a subadult female. In all wolves this load is more than two times as much as is characteristic for fox. The well-known rarity of wolves in regions of deep snow, the mass emigration after large snowfalls of wolves and foxes away from the forests onto the fields, meadows, and roads where the snow is blown away and compacted by the wind, and also other facts, prove the high sensitivity of these animals to the factor of snowiness.

It is interesting in this regard to recall the observations of A. Middendorf (1869) concerning the wolf, observations which were later verified by many naturalists and travellers. "The wolf, which has a body much heavier than the fox, is afraid of deep forest snow", writes Middendorf. "This is why in Siberia one can travel several thousands of versts like I did and not encounter a single wolf track. In hundreds of settlements which keep cattle it is futile to ask about wolf damage. The fox, however, frequently occurs nearly everywhere. He searches without difficulty in snow for his prey, particularly mice of all kinds, without having to run very far. But the wolf, to appease his greater hunger, must look for his prey far away, he must trail his prey, and catch his prey by chance encounter." And moreover,"...This is why, where there is nast, compacted snow, or where there is no snow as in tundra or steppe and especially in high plateau steppes, or in places where the forests have been cut off because of agriculture, the wolf, even in Siberia, is a dreadful calamity..."

With regard to the fox, Middendorf somehow overestimated its adaptiveness to life in regions of much snow. In most of the forested parts of the north country there are not many foxes. The number of foxes increases rapidly as one goes toward the steppe and semidesert. Here is an example of how uncommon this species is in the European part of the taiga with deep snow. While counting the tracks on a long trip in the forest of Komi ASSR (the region of the headwaters of the Vychegda River, with an average maximum of snow cover of 65-70 cm, according to Shenrok) from 10th October to 17th November, an average count per 10 kilometers of the way showed 457.5 encounters of varying hare trails, 50.5 ermines, 2 wolverine, and only 1 fox. The wolf was not met at all. The count was done during the first snowfalls when the animals ranged widely and when commercial hunting had not diminished the number of individuals of this or any other species (Stakhrovsky, 1932).

Among digitigrade carnivores, all cats, both large and small but especially the small ones, are definitely not adapted to movement on deep fluffy snow. It is enough to take a look at the house cat rubbing through the drifts and sinking in up to the belly in order to appraise the helplessness of this group in the environment of regions with deep snow. It is interesting that house cats which generally go feral easily were seen by me in summer 5, 10 or even 15 kilometers from the nearest habitation, in woods and fields where they were getting their food. But I never saw a track of a cat walking in winter in deep snow for more than one or two hundred meters away from the house (cats in villages go, in winter, to barnyards for mice or into large wild bushy weeds in the fields to hunt voles and sparrows). In this connection it is interesting to mention here a calculation of the weight load per square centimeter of surface of the extremities of the Caucasian wild cat (Felis sylvestris caucasica), which is related to the house cat and not rarely hybridizes with it.

The study made by me in the field of a large female killed on 16th December 1932 (vicinity of Vladikavkaz)* showed the following: the surface

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*Changed to Ordzhonikidze and later to Dzaudzhikau

of hind foot - 16 cm^2; front - 18 cm^2; for all four extremities - 68 cm^2. This was a very large, extremely fat specimen. If we accept, according to Dinnik (1914), a weight of 6 to 8 kg for large specimens, then we will not get less than 88 to 118 g for one square centimeter of supporting surface (Fig. 7).

Dinnik (1936) not long ago described an interesting case. A hunter, who noticed an adult manul (Felis manul) plowing through the deep snow on the steppes near the village of Puri (Transbaikalia), caught him alive without special difficulty. The snow retarded the running of this cat very much. The animal was to some extent exhausted (possibly due to the deep snow), but completely healthy, because it lived a long time in captivity after it was caught. It is relevant to note that neither forest cats -- leopard, European wild cat, and far eastern forest cat (F. euptilura) --not steppe and desert species --spotted cat (F. ocreata), sand cat (F. margarita) and manul--enter regions of deep snow; the ranges of most of them are in regions of little or no snow*.

Among all our cats only the lynx is a peculiar exception. His extremities are relatively longer and wider than in other cats. The feet in wintertime are densely trimmed with fur, because of which they form a kind of snowshoe, reminding one of that which we see in the varying hare and ptarmigan (Fig. 8 and 9). Measurements made by me of a female lynx, killed on 18th February 1935 by S.I. Ognev at Station Petushki, Nizhnegorodskaya Railroad, present the following data. Supporting surface of front paw - about 112 cm^2; hind - 108 cm^2; from this the load weight of 15 kg gives about 34 g per square centimeter. This is two or almost three times less than in the wild cat of Caucasia.

A second specimen of lynx (weight 15.1 kg), obtained near Moscow, had a supporting surface on the front foot of 92 cm^2, and on the hind of 99 cm^2, giving an average load of 39 g per square centimeter. A tiger of the Korean subspecies (Panthera tigris coreensis) obtained in 1940 by the Zoological Museum of Moscow National University from Primoria had a supporting surface on the front foot of 300 cm^2, and on the hind of 155 cm^2, and an average load per square centimeter of 158 g

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*For more details concerning the ranges of cats see the chapter on Distribution of Some Groups of Vertebrates.

Most of the members of the Mustelidae, being distinguished by low height, have relatively wide feet and a peculiar type of gait, which facilitate their movement on the snow. Especially light and mobile are the weasel, ermine, kolinski (Mustela sibirica) and Altai weasel (M. altaica). Somewhat heavier than these species, but still able to move on the most fluffy snow without special difficulties, are mink (M. lutreola), black and steppe polecats (Mustela putorius and M. eversmanni), marten, sable and wolverine. It is enough to take a look at the tracks of the long and light jumps of the ermine, which succeeded in running several kilometers over the deep and plentiful snow of a forested river valley in 24 hours, to understand how little the mobility of this animal was limited by the fluffy snow cover. Sable often stay at the upper limits of the forest on the mountains in Siberia, where the snow during the winter reaches a depth of two or more meters (Sayan Range). And still its daily hunting range can be measured in kilometers, and jumps of up to 1.5 to 2 meters in length occur even on fluffy snow. All these carnivores are widespread even in the regions of our country with the deepest snow.

Among the large rodents* the varying hares are distinguished by the ability to easily move over the deep snow whereas the steppe species, European hare (Lepus europaeus) and Tolay hare (Lepus tolai) have relatively narrower paws less trimmed with fur. (According to my calculations, in the case of the European hare, the weight load for one square centimeter of supporting surface equals 22 to 24 g, in the case of the Tolay hare it is 19 g). On the appearance of a very deep and fluffy cover they get into a difficult situation. But in most of their habitats (fields, steppes, deserts) the snow is usually compacted so much by the wind that hares often walk without even leaving prints. The varying hares of the forest prefer to stay in places where there is a lot of young growth of broad-leaved trees and bushes, i.e. in conditions where the snow cover is usually especially deep and fluffy. The paws of this species are distinguished by a greater width than in the European hare, and, in winter, by a strongly developed trim of fur over the sole. (Fig. 10). The wide supporting surfaces of the extremities facilitate the

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*This was written when the lagomorphs were commonly classified as the Suborder Duplicidentata of the Order Rodentia.

running of varying hares over fluffy forest snow. One English name for the varying hare - showshoe rabbit - accurately characterizes its peculiarities.

In Table 3 are given a few figures which give an idea of the size of the weight load per one square centimeter of the sole of the snowshoe paw.

TABLE 3

VARYING HARE

Time and place of measurement	Area of surface of paws in cm^2		Weight of hare in grams	Load in g/cm^2
	Front	Hind		
1.1 June, 1929, Lake Imandra, Lapland (molting started only on the head)	41	104	3400	11.7
2.2 Feb. 1924, vicinity of Arzamas, Gor'ki Oblast'	42	106	3515	11.8
3.18 October, 1936 Shariinsky raion, Kostroma Oblast'	48	118	2780	8.4

It is interesting to note that the willow ptarmigan, the range of which in many aspects is similar to the range of the varying hare, and which is a bird that also gets white in winter, and which is also related in winter to the feeding on twigs of bushes (buds, twigs, racemes of willow, birch, and aspen) has a remarkable adaptation which facilitates running on the snow. The digits of the willow ptarmigan, which have almost flat, lanceolate nails, and which in summer are naked below, toward the fall get a dense cover consisting of compact flexible feathers, which form a wide resilient showshoe (Fig. 11 and 12). In summer the length of the claw of the middle digit of the willow ptarmigan is about 9 mm. The wide curved winter nail reaches 17 mm in length (the molting of the winter nails in the north of Europe takes place in July, together with the molting of the horny sheath of the beak, and with the appearance of the first feathers of the fall plumage).

The supporting surface of the foot in winter equals 23 to 25 cm^2; it increases several times, and the bird acquires the ability of running without sinking in deeply. According to my calculations the weight load for one square centimeter of supporting surface of the foot of willow ptarmigan is equal to 14 or 15 g. The average winter weight of ptarmigan is nearly 675 g (Rudanovski and Nasimovich, 1933). For comparison I will give data which show the weight load of the grey partridge (Perdix perdix), which is completely nonadapted to the deep fluffy snow. The average weight in winter of grey partridge is 405 to 410 g, while the supporting surface of the foot is 4.5 to 5 cm^2. On each square centimeter there is nearly 40-41 g of the weight of the bird, i.e. almost three times as much as the willow ptarmigan which has snowshoes.

The rock ptarmigan (Lagopus mutus), the form of the stony or high tundra region of the mountains, which searches for food on the bare patches and runs more often on the compacted snow, has less developed snowshoes on the digits than willow ptarmigan, which is the form of the bushy tundra, forest tundra, and taiga. In contrast to these two species, which gather food on the earth in winter and summer (willow ptarmigan flies up into trees rarely and unwillingly), other tetraonid birds have gone the other ways in their adaptation to the winter snow regimen.

Hazel grouse, black grouse, capercaillie, and spruce grouse (Falcipennis falcipennis), are birds which are terrestrial in their habits in summer but in winter become arboreal. All their food is obtained on the branches of trees (buds, catkins, berries, and needles), and they only rarely walk in the snow, but they dig into it to rest and to spend the night. The feet of these species have seasonal changes in their covering, but of yet another type than that of the willow ptarmigan. In the fall on the edges of the digits there begins to grow fringes or combs made from little elastic horny rods which reach full growth toward the end of September and the first half of October (in the central part of the country), at just about the same time that the birds begin

to feed mainly in the trees. These combs somehow increase the supporting surface of the digits and possibly partly facilitate movement on the snow, but basically their function is to facilitate climbing on very thin twigs that are covered with rime or ice, in order for the birds to procure food, which is not an entirely easy thing for large birds. (Buds, catkins, berries, needles grow only on thin twigs, and, as is well known (Formozov, 1934), thin twigs are in winter covered heavier by rime and ice than are thick ones.) In order to prove this to ourselves, it is sufficient to watch a flock of black grouse feeding during a winter day on the swaying flexible branches of a birch, or a group of hazel grouse threading their way through the icy branches of an alder tree.

In this way, during the adaptation to life in regions with continuous winters, the above listed tetraonids are forced to go over to getting their food in the trees, because of the snow cover which makes searching for food on the ground and movement there difficult. Only those species which had already perfected seasonal changes of the digital coverings could do this. The great majority of our birds which pick up their food on the earth or in trees are completely unadapted to movements on snow. Their toes are thin, their shanks, in many, are very short -- crossbills (Loxia), goldfinches (Carduelis carduelis), and redpolls (C. flammea) etc. Therefore worthy of special attention is the circumstance that only an insignificant number of species of birds that get their food on the ground over-winter in our northern regions. The great majority of birds that overwinter in snowy regions get their food on the trees and bushes or on high weeds. Among the terrestrial seed-eating and insect-eating forms, except the willow ptarmigan, there is not a single forest species that stays. All the rest are associated with open landscape where the wind compacts and blows the snow -- bunting (Emberiza), snow bunting (Plectrophenax nivalis), horned lark (Eremophila alpestris), black lark (Melanocorypha yeltoniensis), raven (Corvus corax), grey partridge and bearded partridge (Perdix daurica) -- or stay close to habitations where they feed on the scraps from the

household, etc. -- grey pigeon (Columba livia), jackdaw (Coloeus monedula), magpie (Pica pica), grey carrion crow (Corvus corone), house and field sparrow (Passer domesticus and P. montanus), crested lark (Galerida cristata) and, sometimes, the rook (Corvus frugilegus) etc.

After we made a short review of some forms of vertebrates in relation to their ability to move on deep snow, we found a number of species whose extremities are distinguished by characteristic adaptations to snow as a substrate. The lynx, snowshoe hare, willow and rock ptarmigans, and, in part, the reindeer, are worthy of great attention in connection with this. The presence of such types of adaptations, which in some of the species have a strictly seasonal character, attests the fact that the snow factor has played a large role in the natural selection and evolution of some groups. More careful study of the morphology of the limbs of northern mammals and birds and the peculiarities of their ability to move about will probably result in the discovery of a number of interesting details. Here it is necessary to note that the described adaptations of the extremities facilitate the struggle for existence in wintertime for a number of species, but by no means do they create complete independence from the factor of snowiness. On the contrary, even showshoe hare and willow ptarmigan, the best "skiers" among the vertebrates of the north, if one may express oneself in that way, sometimes suffer from excess snow. In fluffy and deep snow the willow ptarmigan sinks in up to the belly and walks among the bushes with difficulty, leaving deep furrows as a trail. In forests with much snow varying hares make trails and prefer to walk on them instead of on the fluffy drifts. On this fact is based the method of catching hares in wire snares and jump traps. If on the snow there are three or four tracks of a hare in one line then one can with assurance set a snare there. Such a trail facilitates the walking of the hare on the snow and he won't fail to use it once more. Lynx willingly walk along hare trails and therefore are often caught in hare traps. Sometimes lynx make their own trails, as wolverine and fox also do. Trails are known for European

hares, musk deer, sables, ermines, kolinskis, wolves, tiger, and others. The making of a trail is one of the interesting adaptations to life with a deep and fluffy snow cover.

In the central part of Eurasia the European hare, fox, and wolf willingly use plowed roads in deep snow. In the cited work of Petri (1930) is described the interesting method of hunting wolves used by the Tutursk Evenks. After the track of this animal has been found, some of the hunters go down the valley and watch roads, and others follow the trail. The wolf in winter always goes from the mountains where there is deep snow to the valleys with little snow, and prefers to move on the roads made by man. Therefore, he unavoidable happens upon the rifleman.

The above listed facts testify that the role of the snow cover as a factor hindering movement is more significant than it has appeared to be until now.

SNOW COVER AS A HINDERANCE TO OBTAINING FOOD

By restricting and hindering the movements of animals snow serves as a remarkable obstacle to getting food for those species whose forage is found thinly scattered. In other words, snow cover is more of an obstacle for large four-legged carnivores that hunt for mammals and birds over many kilometers in each direction than it is for small rodents which feed on rough vegetable food, stores of which are quite plentiful on the surface of a few square meters. Snow cover has even a greater influence on the conditions of existence of vertebrates in winter by covering with its thickness the larger part of the food supply, of vegetable as well as of animal origin.

When there is a small amount of snow, the insects, spiders, and molluscs which winter in dead litter, plants such as lichens, mosses, and grassy layer, seeds and fruits that are lying on the soil, etc. appear to be covered with its layer. With deeper snow semi-bushes, large grassy plants, bushes, etc. are covered. Stores of food, buried under snow, are completely hidden from the eyes of animals; in most cases it is easier to search for them not by sight but by scent. Birds, therefore, which search for food mostly by sight, must theoretically in winter find themselves in a worse condition than mammals. The reindeer, after digging several times in

the snow with his front feet and making a small hole bends to eat, and, by sniffing the air inside the small hole, "knows" by scent whether there are lichens under the snow. In the moist condition lichens of the genus Cladonia give off a strong, fungous smell which is very easily distinguished at a short distance even by a man. With the help of scent, deer find, without mistake, lichenous food that is hidden under a layer of snow 40 to 60 cm in depth. The squirrel smells the fruiting bodies of the deer truffle. (Elaphomyces), which is their common food in the fall, through a decimeter-thick layer of snow, moss cover and soil. He digs out mushrooms by making slanting "tunnels". The fox, using partly scent and partly hearing, catching the squeaking of the animals, finds with the same exactness the winter nests of voles under a layer of snow with a depth of 30 to 40 cm.

But it is not enough to find a place where food is situated; it is necessary to reach it by digging through the snow, and this often costs a lot of effort. The deeper and more compact the snow cover is the more difficult it is to dig through it for food which is situated on the level of the soil. Observations show that for many animals a thin layer of snow which is covered by nast is sometimes more dangerous than relatively deep and fluffy snow. After thaws and night frosts, when the snow gets covered with ice, one can often see on the trails of foxes blood from paws which have been cut by digging (my observations in Gor'ki Oblast', A.M. Kolosov's in Moscow Province). In the case of tundra reindeer, the front hooves which in winter do a large share of the digging out of food, are very abraded by spring, because the tundra snow is distinguished by extreme density. The grey partridge cannot dig completely through deep snow, especially when it is covered by an icy crust. He flies to the barnyards and threshing floors or to areas where snow is thin and where there are high weeds to give him food.

The small carnivores of the family Mustelidae (ermine, weasel, polecat) which have thin, elongated, strong bodies and relatively short legs, quickly make burrows in soft snow to the nests and tunnels of rodents. They capture the little animals in their retreats. When the ermine or polecat goes under the snow there is not even a trace of excavated snow on the surface because these carnivores simply penetrate with their body the thickness of the snow, compacting it at the walls of the burrow. For such snow burrows,

hunters use the characteristic term "nyrki," (from the word "nyryat'" - to dive in), which plainly suggests the sense of movement. On the hunting trails of ermine, and black and steppean polecats one can see trails of such nyrki by the tens (the word "nyrki" was introduced into the scientific literature by Zveryev, 1928). More than once I have happened to see ermine, chased by dogs, immediately disappear into soft forest snow, and reappear on the surface far to the side of the place where he just dived in. All the previously mentioned small mustelids and even mink, marten, sable, and, as was mentioned, otter, hide from danger by plunging under the snow and moving along under it for long periods without any appearance on the surface.

The animals of this group, which are apparently primarily adapted to the hunting of rodents in tunnels, are the owners of a number of adaptations that are very useful in hunting in and under snow. The smallest of the, the weasel, spends the larger part of the winter under the snow cover. He rarely comes up on the surface and does not make long journeys over the surface. The length of its trails can usually be measured in meters or tens of meters (observations in the central region of the European part of the USSR). The arctic fox, fox, and corsac, which hunt for the same small rodents, must use different methods. They make slanting tunnels with cones pointing downward trying to catch the voles in their subnivean nests. The amount of work done by a fox in getting to the nest of a common vole (Microtus arvalis) is remarkable more than the work done by an ermine or polecat for the same reason. According to A.M. Kolosov (1935), the foxes of Moscow Province make up to 20 or 25 diggings during their daily journey. Is it not this inconvenience, (together with their inability to move about well on snow), that explains the overwhelming dominance of the family Mustelidae over the Canidae in numbers of species as well as in numbers of individuals in regions with much snow? I am inclined to think that this is the correct explanation.

If there is much snow, the small species of cats, which usually also feed on small rodents, find themselves in an even more uncomfortable situation. Their peculiarly specialized extremities with strongly recurved, sharp and laterally flattened, retractable claws which serve as tools for catching prey, are not adapted to digging in snow and especially not for digging in nast or frozen soil. As is well known, they lie in wait for their prey or hunt by

stalking, using mainly sight and hearing rather than their less developed sense of smell. Cats, no matter how peculiar, are one of the most highly specialized groups of terrestrial carnivores, and, because of their above-mentioned peculiar specializations, are completely nonadapted to exist in regions with snowy winters, where for half or more of the year the small rodents are hidden under the snow. Cats can neither see nor dig them out. These circumstances, together with their difficulty in moving over the snow, make cats unfit for inhabiting regions with snowy winters. And sure enough, not a single species of the flesh-eating Felidae can be found in regions with continuous winter and a snow cover having a depth of more than 20-30 cm. ((Evidently this a lapsus calami in the original)).

Undoubtedly deep snow is a very important factor of the resistance of the environment in the case of the wild pig, whose winter food consists of fruits and nuts which have fallen from the trees onto the soil, or rhizomes and tubers which are dug out by them from the soil. A. Cherkasov for Transbaikalia, N. Dinnik and A. Nasimovich for Caucasia, and other authors for a number of different parts of the range of the pig, have pointed out the difficulties which herds of pigs have with deep snow and nast. It is interesting to note that because of the inaccessibility of the usual food (acorns, beechnuts, etc.) and because of the famine resulting from deep snow, the pigs of Caucasia are forced to switch over to branches, bark, and lichens from tree trunks, items which are the usual winter food of the other hoofed mammals.

It is important to emphasize here that browse is a most significant source of food for several species of our deer which overwinter in snowy regions, since it is one of the few available foods which is not covered by snow. Moose, red deer, maral, spotted deer, European and Siberian roe deer, and musk deer feed on browse and bark. Browse and dry grass are used by roe deer and deer during the winter in regions of little snow. Besides bark and browse, all these species (musk deer in particular) freely use lichens, plucking them off the accessible parts of trees. In forest regions with deep snow, reindeer sometimes switch over completely to feeding on lichens (different species of Usnea, and others) from trees. In summertime the above mentioned species prefer grassy vegetation, therefore winter feeding on trees can be considered to some extent forced. We meet exactly the same picture of seasonal change of food habit in

the cases of the varying hare and tetraonid birds. Therefore the unavailability of grassy foods which are hidden for the whole winter by snow has called into being the phenomenon of seasonal change in food habits to a great number of buds, browse, bark and other parts of the plants which rise above the snow. It is interesting that this peculiarity was probably characteristic for the Siberian mammoth. Hoofed animals which feed on grassy foods in the wintertime (mountain sheep, mountain goats, antelopes, horses) can successfully resist snow only if it is shallow. The northern limits of distribution of these species, as a rule never contact regions with deep snow. White sheep (Ovis dalli) and related forms on the North American continent only seem to be exceptions, since the snow conditions on forest-free mountains are quite peculiar (see below).

The process by which small mammals obtain food from under the snow has some peculiarities. For the greater number of the small species of mammals it is dangerous to be on the surface of the snow cover, because of low temperatures, danger of predation and the difficulty of getting into and under the snow cover when necessary to hide themselves. Many small mammals not only are forced to get their food by digging into snow but also to spend the whole winter in subnivean tunnels, where the temperature is usually higher than above the snow and where there is no danger from feathered predators. The voles prove to be one of the groups best adapted to life under the snow. As is well known, the sub-family Microtinae has produced several species of typical tunnelers -- common and Afghan mole-voles (Ellobius talpinus) and E. fuscocapillus), and the long-clawed mole-vole (Prometheomys schaposchnicovi) -- and includes many forms in which, to a greater or lesser degree, are expressed the characteristics of adaptation to digging and to life under the soil (relatively strong front paws with relatively large claws, short ears, small eyes, short tail, protruding incisors, behind which the hair-covered lips meet and prevent anything getting into the mouth, etc. (Vinogradov, 1926). A large number of vole species are well adapted to live under the snow getting their food during the whole winter in runways which the animals make partly in dead and grassy cover and partly in snow cover. As will be shown later (see page 108 and others), for a number of voles life under the snow is not too difficult, and they even reproduce in winter. Voles which live in the

tundra and are forced to construct runways in compact snow for 8 or 9 months, have significant seasonal characteristics on the claws of the front feet. In the case of steppe lemmings (Lagurus lagurus) and narrow-skulled voles (Microtus gregalis) the claws of the front extremities are longer and more massive in winter than in summer. In the case of Norway lemmings (Lemmus lemmus) they equal 8 to 10 mm, or approximately three times as long as in summer (S.S. Folitarek, MS). The winter claws of the third and fourth digits of the collared lemming (Dicrostonyx torquatus) are remarkable (Fig. 13 and 14), being strong and massive and with two prongs on each. Winter claws of lemmings molt in summer, as is the case in the willow ptarmigan (Dunaeva and Kucheruk, 1941).

The Ob' lemming (Lemmus obensis) which lives together with the collared lemming over the greater part of the latter's range, does not have such a sharply expressed seasonal dimorphism of the claws. This is correlated with the fact that the Ob' lemming inhabits the lower parts of the tundra which are well covered with plants and where a large amount of snow collects and where food is more plentiful than on the dry uplands which are inhabited by the collared lemming. On such upland regions the snow cover is not as deep as in the low places but is characterized by a marked density.* The peculiar adaptations of the front extremities of the collared lemming and its white coat are probably correlated with these characteristics of the snow on the high spots of the tundra. Because of the shallow depth of the snow cover on the hills and dry slopes the collared lemming must show up on the surface more often than the Ob' lemming, which is covered by the deep layers of snow in the depressions.

Other groups of small digging mammals also survive the winters very well under the snow, remaining active, which speaks well of the great importance (under conditions of snowy winters) of the adaptations to burrowing and getting food by digging. The common mole (Talpa europaea) with its subspecies, and the Ussurian mole (Mogera robusta) are active all winter; in the spring, with the

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*It was mentioned earlier that the hard snow can only be broken with an axe or cut with a saw. The suspicions of A. Middendorf that the collared lemming hibernates were unfounded. This species is active all during winter and makes tunnels.

melting of the snow, one can see the long runways made by them at the soil surface in the lower firn-like layer of the snow cover. In Kazakhstan, zokors (Myospalax myospalax) and sometimes mole-voles make similar runways in winter.

The shrews are especially common in the forested zone with its deep and fluffy snow cover. They are active all winter, sometimes showing up on the snow surface also. Because of the large number of empty spaces under the trunks of fallen trees and dry bush wood and the dense branches of small pines and firs and under the growth of large grassy plants and similar cover, shrews have the opportunity of looking for food under the snow cover of the forest, and only rarely do they resort to digging. They widely use the already present runways and galleries of voles. Winter trapping with snap traps placed deep under the snow in the empty spaces under fallen tree trunks, hillocks, hay stacks, etc. in Kostroma Oblast' and near Moscow gave me rich catches of shrews--common, masked and small (Sorex araneus, S. caecutiens, S. minutus). On all the taiga of Siberia, and in particular its far north-eastern part, different species of shrews are very numerous. Some of them come out on the tundra. Probably the snow cover of these regions is not an unsurmountable obstacle for the obtaining of food by these small but extremely gluttonous animals. A completely different picture is found in the regions of cold steppes and deserts. Shrews here are either uncommon, rare, or completely absent. Of course, because of the insignificant thickness of snow cover these animals which are forced to be active all winter appear to be little protected against adverse temperature conditions and predators. The high density of steppe snow and the not rare gololeditsas make it very difficult for shrews to obtain food on the soil surface. These peculiarities of the winter, together with a number of climatic and the resulting biotic factors, make the regions of steppes and deserts with temperate and cold winter quite unsuitable for the existence of shrews. It is interesting that the summer conditions here are quite favorable for insectivores, as is shown by the abundance of hedgehogs (Erinaceus) which spend the winter in hibernation.

Mice, gerbils and hamsters are less adapted to life under the earth than are voles, (which is shown by their peculiarities, as follows: the members of the first two groups have long tails, and all three groups have large eyes and ears, while many have relatively weak front and strong hind paws, etc.) It naturally follows that they appear to be little adapted to obtaining food under the snow cover. These animals, during the autumn, secure storages of food for themselves, thus completely obviating the necessity of leaving their holes during the winter -- common hamster (Cricetus cricetus) -- or, they have such a storage that such journeys are rare. Unlike voles, which use rough green stuff for food, hamsters, mice and gerbils mainly use grains, which are concentrated foods, and therefore are forced to resort to long journeys in search of food. It is noteworthy that species in the wintertime -- striped and long-tailed field mice and house mice (Apodemus agrarius, A. sylvaticus, and Mus musculus), and grey hamster (Cricetulus migratorius), by my own observations, and southern and tamarisk gerbils (Meriones meridianus and H. tamariscinus) by the observations of Yu. M. Rall' -- gather food either above the snow on places which are free from it, or on the large plants which still have seeds and fruits. For these rodents that are quite exacting about the quality of their food there will be no sense to dig in the snow or make snow tunnels and holes as do voles. Their needs can only be satisfied by searching for food over a relatively wide area. According to Yu. M. Rall', in winter in the sandy places of the Volga Ural region, the length of the nightly journeys of Tamarisk gerbils is as much as 3 kilometers*. According to my observations in Gor'ki Oblast', the daily journeys of field and wood mice can be measured in hundreds of meters in mild weather.

Therefore the grey hamsters, gerbils and mice are species with supraniveal activity, and for them a deep snow cover that hides the food is an unfavorable factor. Still, in summer they collect stores of food for winter, and their winter activity on the surface is often supressed by weather conditions

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*Tamarisk gerbil, a larger species able to exist on rough food (bark of bushes, etc.) goes to the surface more often and more regularly than the southern gerbil.

(frost, wind, etc.). Their winter activity, as distinguished from that of voles, is nonrhythmic (see, for example, the work of Rall', 1931). It is natural that the great majority of representatives of this group are characteristic of regions with little snow, southern woods or steppes and deserts. Mobility and speed of running, characteristics of many gerbils and mice, are particularly important when searching for seeds and fruits in exposed places with thin vegetations. Without any attempt to make a complete survey of all our small mammals in their relation to snow cover we would like to note as a summary that even within the limits of one family, the Muridae, there are groups that are completely different in their relations to the factor of snowiness. Snow cover played no less a role in the evolution of the small species of mammals and in the evolution of their ranges than it did in the history of the large hoofed animals and the carnivores.

Ermine and polecat, whose ability to hunt under the snow we just mentioned, enter traps only rarely in the fall but, towards the end of winter when the snow gets deeper and harder, they are much easier to trap. Evidently the deep and very dense snow cover interferes greatly with even their hunting, and they get hungry and come easier to the bait. The same can be said for fox, corsac, wolf, and arctic fox. I have worked over the data about trapping arctic fox on Novaya Zemlya which were written in the diary of the hunter-trader I.T. Zhuravliev for 1926-1927.* Although the number of traps in use remained unchanged all winter, the most successful catch of arctic fox was not in the fall months but from February to April when the snow cover reached a greater depth and density (Fig. 15). The layer of snow restricts the arctic fox from getting lemmings, from digging out its own stores which it had hidden in the summer in secluded spots, and from utilizing the flotsam thrown up by the sea onto the shore. In addition to this the number of arctic fox was already markedly less by spring, because of some having been caught and some having died of epizootics (probably encephalitis).

Two dead arctic foxes were found in January, one in April, and one, hardly alive, was caught by dogs in February. The progress of the hunt is shown by the following figures: caught in traps -- 111, obtained by

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*The diary is kept in the Arctic Institute and, at the proper time, it was placed at my disposal by G.P. Gorbunov.

shooting -- 3, found dead -- 3, caught by dogs -- 1, total -- 118. Of this total the monthly breakdown is as follows:

Nov. 1926	1	Feb. 1927	28
Dec. 1926	12	March 1927	44
Jan. 1927	16	April 1927	17

Thus in the first half of the season (November -January), when the arctic fox population was higher, only 28 specimens were caught, or 23.8 per cent, while in February to April, 90 were caught, or 76.2 per cent. Squirrel hunting, which is not helped by snow but on the contrary is restricted by it, presents a completely different picture. In the European part of USSR most squirrels are obtained in the latter part of October and in November, and as soon as the first snow of 30-40 cm comes, hunting ends because dogs walk through it with difficulty and also because it is pretty hard on the hunter.

The Eskimo hunting dogs ((in contrast to the sled-dogs)) being similar to the fox in size, in manner of walking and in endurance, can be used to some extent for comparison in judging the difficulties that the latter carnivorous animal meets when hunting in forest regions after a fall of deep snow. It is interesting to note that the Eskimo dog can be used again for squirrel hunting toward the end of winter when nast begins to form. He walks easily and trails squirrel well. At this time the fox also is able to hunt over a wider area, compensating in some degree for the difficulties in digging out the rodents from under the deep compact snow.

A good indicator of the deterioration with deeper snow of mouse-hunting conditions for foxes is the increased appearance of unusual food in their stomachs. According to Baranovskaya and Kolosov (1935), in the winter of 1933-1934, 4.55 per cent of the foxes examined in Moscow Province had carrion in their stomachs in December, 18.6 per cent in January, and 27.6 per cent in February. In February there is also an increased number of appearances of birds eaten (up to 24.7 per cent), while at other periods of the year they do not play an important role (mouse-like rodents had 56.8--68.6 per cent occurrence in December and January, while only 36.5 per cent in February).

If, for the mammals which are capable of doing quite a lot of digging (canids, deer, and pigs), we noted remarkable difficulties in obtaining food connected with the appearance of deep or very hard snow, it is natural to assume that this character of the earth's cover must cause an even stronger reaction in birds, which, because of peculiarities of their organization, are poorly adapted for digging. As is well known, only a few birds nest in holes dug in the earth, chosing only the softest digging soil and vertical surfaces in which it is much easier to begin digging. Birds cannot dig directly down into the depths of somewhat compacted soil, and in general they dig very slowly. The gallinaceous birds which often dig to obtain food in summer, prove to be more adapted to digging snow in winter. They dig with the hind extremities, but usually only to make temporary hiding places, and not to look for food. Only on the trails of grey partridge have I seen thin snow cover over winter-crops dug out in small spots with the feet during feeding.

The common jay digs snow with his beak when he is looking for acorns, and the nutcracker (Nucifraga caryocatactes) when he is getting pine cones from his storages. There are observations by N.A. Zarudni that black larks, when feeding on the steppes, dig with the beak when trying to break a thin ice crust. In Gor'ki and Moscow Oblasti I have seen the marks of several blows made by the beak of a raven trying to dig out common voles from under the snow cover. Still more interesting are the marks made by ravens and grey carrion crows which I have found several times at the entrances of subnivean retreats of European hares. The birds could not do anything about the hare which was hiding in the deep snow drift. They walked around for a long time but did not try to dig out his hole. Finally, there are indications that black grouse, when followed by the goshawk (Accipiter gentilis) plunge into the fluffy snow, digging in fast and deep, as they do in the evening when they hide for the night. The hawk sits down on the snow but does not make any attempt to dig down to the grouse.

Thus, only a few birds dig in snow, but they cannot do much work, because they use the beak, an organ which is poorly adapted for this purpose.

The feet of most terrestrial, and especially those of arboreal, birds are completely unsuited for digging snow. As a result of this, most birds in winter can feed only on such food as is above the snow and can easily be seen.

Owls, which have the posterior extremities as highly specialized for catching small mammals and birds as are the paws of cats, are similarly as poorly adapted as are the small cats for obtaining rodents from under the snow. It is interesting to note in connection with this that owls, which in summer feed mainly on voles, when overwintering in snowy regions are forced to switch over to hunting for species which live above the snow, i.e. -- small and middle sized birds, squirrels, hares, and even foxes, which sometimes fall victim to the eagle owl (Bubo bubo).

The snowy owl (Nyctea scandiaca) which feeds almost exclusively on lemmings in summer, often hunts birds in winter, in the central part of the country. For example, in four snowy owls opened in the winter of 1926-27 in the vicinity of Cherepovets (Bogachev, 1927) there were found only the remains almost exclusively of small birds, etc. in winter. In regions of little snow where owls overwinter, a fall of deep snow brings on a mass dying-off of these birds, caused by starvations. This happened in the Ukraine and in Germany to sedentary barn owls (Tyto alba) and long-eared owls (Asio otus) in the hard winter of 1928 (Pidoplichka, 1930).

Most birds that pick up their food from the earth cannot overwinter in the parts of the forest and tundra zones with deep snow. The number of such species (permanent residents or winter residents) increases as we go into regions with little snow, whether the winter is warm or very cold. This is proof that in a number of cases the phenomenon of migration in some birds is caused not by cold but mainly by the unavailability of food which is covered by snow. The above correlation has been noted previously by a number of authors (Sushkin, 1914; Stanchinski, 1926; Tugarinov, 1929; Kozlova-Puskareva, 1932 sic; and many others).

There are birds in our fauna that obtain food on the trunks of trees--woodpeckers, creepers (Certhia) and some nuthatches--or on rocky cliffs--wall creepers (Tichodroma muraria) and other nuthatches--which in winter are

less dependent on the snow factor because very little sticks to the vertical surfaces. Snow that covers one side of a tree does not significantly hinder the food gathering of woodpeckers, or creepers and reduces only a little bit the amount of food available to them in winter. In the case of the wall creeper a thick hoarfrost which under some conditions covers the rocks with a thin but total layer is more important than snow. In northern Caucasia (near Vladikavkaz) in 1924, I observed a marked migration of wall creepers that were returning from the northern slopes after the appearance of thick rime there, and were going into the deep gorges of the main Caucasus Range. According to L.B. Beme, during periods of rime in the mountains, wall creepers sometimes appear even on the stone buildings of Vladikavkaz.

Birds that get their food on the branches of trees--crossbills, pine grosbeaks (Pinicola enucleata), kinglets, crested titmice, chickadees, coal tits (Parus ater), long-tailed tits etc.--are dependent on snow cover only to a relatively small degree. Many species of birds which come to us late in the spring and fly away early in the fall do not contact snow cover as a factor at all--flycatchers, swifts (Apus), orioles, yellow-breasted buntings (Emberiza aureola), etc. The time that these species remain for nesting is determined by other climatic factors: temperature, light conditions, etc. which influence the abundance of flying insects and caterpillars crawling on the branches, and also by the migration distance, etc. Among mammals, the bats, some of which hibernate and some of which fly away early in the fall from the regions with cold winters, likewise do not meet the snow cover as a factor of the environment. We can separate a significant group of species which may be called "independent of snow". Distinct from them are a number of forms which, due to peculiarities in their biology, depend on the peculiarities of the snow cover as an element of the environment to a greater or lesser degree.

Snow cover, for many species, is the most important element of environmental resistance and the struggle against this particular element is almost beyond the species' ability. Such species do not inhabit snowy regions and we can unite them into a group "avoiding snow" or "chionophobes"-the small cats,

steppean antelopes, steppean sand grouse (Pterocles), black partridge (Francolinus francolinus), many small terrestrial birds etc. This group is connected by a number of gradations with the species that can withstand winters with considerable snow. These species we can call "chioneuphores" (moose, reindeer, wolverine, wolf, fox, many voles, moles, shrews, etc.) Finally, there are forms which have characteristic adaptations (winter-white coloration, winter peculiarities of foot-coverings, etc.) which were undoubtedly perfected by snow cover taking part in selection. The ranges of these forms lie completely or almost completely in regions of hard and continuous winters with much snow (willow ptarmigan, rock ptarmigan, varying hare, arctic fox, collared lemming, etc.) "Chionees" (snowy) or "chionophiles" (snowlovers) are quite appropriate names for these forms. Of course, this classification is, to a certain degree, flexible. A snow cover of a certain moderate depth and compactness which is favorable for chionophiles can, by a great increase in depth and iciness, become harmful and dangerous even for "snow-lovers." Qualitatively the influence of the snow factor depends to a large degree on the quantitative characteristics of the cover. The limits of tolerance for snowiness do not appear equal for different species of animals and for different life forms. From the point of view of vertebrate ecology the importance of permanent continental ice is only the extreme degree of snowiness. Even snow cover which melts every year frequently has compact icy layers reminiscent of firn and sometimes the whole thickness of it is iced. Therefore the glacial periods were times with an extreme increase in the importance of snow cover as an ecological factor. Zoogeographers have, until now, acted quite inconsistently by attributing great importance to the glacial periods and by studying the influence of glaciers on the formation of faunas, while at the same time they have completely ignored the present and past role of snow cover.

Continental ice forms by the accumulation of a snow surplus which is not able to melt during the summer. The icy regions of the past were undoubtedly surrounded by wide zones having winters with much snow, comparable to the winters in similar regions today. The retreat and extinction of faunas began under the influence of this deep snow, which acted somewhat as an outpost of the glaciers. From this point of view a study of the contemporary ecological role of snow cover can cast much light on the history of faunas during glacial times. It is interesting to mention here one note by Chirvinski (1932):

"With closer acquaintance with the maps of the distribution of snow cover in the European part of the USSR it is impossible to rid oneself of the temptation to make such comparisons. It is known that during the glacial epoch the center of glaciation (maximum snowiness) moved slowly from west to east (Scandinavia and then Finland). From the maps of Vlasov one can see that today the center of snowiness lies even more to the east, namely in the region of northern Preuralia ((region just to west of the Ural Mountains)). Furthermore the maps of Vlasov show that isopleths of the distribution of snow cover are oriented as if to encompass this hypothetical center; these curves, upon the approach of winter, move concentrically toward the southwest, and at the end of winter retreat toward the northeast. By a certain boldness of the imagination one can see, in January, two snowy tongues which lie in the European part of the USSR in a position corresponding to the Dnieper and Don lobes of the glacial period ((Dnieper and Don lobes of the Third Glacial Stage, see Flint, 1957). Because of the transitory nature of the snowy periods at the present time it appears that the essential difference is that we have a continental snow cover but not a continental ice cover, that the size of it is insignificant, and that it does not show movement".

On the map of Shenrok (1926) we can see essentially the same picture of distribution of isopleths of equal depth of snow cover, reminding one of the configuration of the glacial margin. Thus the traces or weak shadow of the geographic distribution of the snowiness of the glacial period can be seen in the distribution of the winter cover of our time. This makes a deeper study of the role of chionic factors even more important and interesting.

A summation of the last two chapters results in the following basic premises:

(1) Snow cover, by impeding the movements of non-flying animals, has played an important role in their ecology.

(2) It has influenced the evolution of the extremities of a number of northern animals.

(3) Snow cover causes seasonal migrations in some forms (birds, some mammals) or seasonal changes of food habits (switching over in the winter to foods which stay above the snow) because it hinders their getting to food which is covered by its thick layer.

(4) Some forms of life (voles, burrowing insectivores, small carnivores of the weasel family, etc.) are well adapted for life in regions with much snow because of the peculiarities of their specialization. Species and individuals belonging to these groups are numerous in regions with much snow. Arboreal birds, arboreal rodents (squirrel, flying squirrel) are not very dependent on snow cover as a factor hindering food gathering: They successfully live in regions with much snow. On the contrary, the small cats, terrestrial birds of the families Phasianidae, Syrrhaptidae, and others, some hoofed animals, etc. are not able to inhabit snowy regions because of the peculiarities of their specialization. Therefore the factor of snowiness is a powerful element of the environment, which separates forms of life into those suited and those not suited for existence in regions with snowy winters. Snowiness has quite a substantial and multiform influence on the formation of faunas.

(5) The glacial period was an epoch when the importance of the snow factor was singularly increased and when it played a decisive role in the ecology of the terrestrial biocenoses of many countries. During postglacial time the importance of snowiness (aside from the Arctic regions) has somehow become smaller, but it still remains quite influential and is deserving of detailed studies.

TEMPORARY SYMBIOTIC RELATIONSHIPS BETWEEN MAMMALS AND BIRDS IN CONNECTION WITH THE PRESENCE OF SNOW COVER WHICH HINDERS THE OBTAINING OF FOOD.

Sometimes species of birds and mammals which are differentially adapted to obtaining food from under snow overwinter in the same habitats. Large strong mammals easily dig through even a compact snow cover, reaching the hidden low bushes, grassy plants, and lichens. After they feed, the deep holes remain with a part of the unused food, which is easily utilized by weaker animals not adapted to digging in snow.

Byalynitski-Birulya (1907), during a winter on the New Siberian Islands, made very interesting observations on the behavior of willow ptarmigan (northern Siberian subspecies). "I was interested," he says, "how the ptarmigan obtained their food from under the snow and partly even from under the icy crust which usually covers the parts of the tundra which had been blown free of snow by the wind. It appeared that the ptarmigan in this case used the services of the reindeer which dug the snow with their feet. On the deer pasture there are always found many ptarmigan trails. While hunting deer in the late fall one can frequently see how a flock of ptarmigan unconcernedly wandered about between the deers' feet, intensively

searching over the places dug out by the deer..." Later Tolmachev (Tugarinov and Tolmachev, 1934) observed a similar relationship between two species of ptarmigan and the places where herds of domesticated reindeer had grazed. At the beginning of May, on the way from Khatanga north to the Novaya River, he often saw willow ptarmigan near campsites, "where they gathered in order to more easily obtain food at the places which were dug out by deer." Rock ptarmigan (Siberian subspecies) were also noted in great numbers on 15th of May "on the places dug out by deer." Romanov (1934) thinks that this symbiosis is quite characteristic for the willow ptarmigan of the tundra between the Lena and Khatanga Rivers in Yakutia. "Flocks of them follow during the entire winter the herds of wild and domestic reindeer which graze on the tundra."

Kreps and Semenov-Tyan-Shanski (1934), noted that in Lapland on the Monche and Tchuma tundra, rock ptarmigan are constant companions of wild reindeer during the second half of winter. "Their usual food of berries and green parts of alpine vegetation is almost everywhere at this time of the year covered by a compacted snow which the birds are not able to dig out. At the places where the deer have dug feeding craters in the snow, they can easily get to the beloved berries of crowberry (Empetrum nigrum) and other plants..."

Similar phenomena but in other species of animals can be observed in the central part of the country. While hunting for hares in the vicinity of Gor'ki during the period from 1911 to 1918 I often saw how grey partridge had fed at the places where hares had grazed. Hares, in the middle of winter, feed more often on cover crops, especially on hillocks where the snow is not so deep. On the feeding areas in the morning one can see from afar the dark patches 1.5 to 2 meters square which have been cleared of snow. Here and there between clods of earth are present half plucked green leaves of cover crops. At sunrise grey partridge come here. Their trails lead from one set of hare workings to another. Bogdanov (1871) earlier observed this in middle Povolzhia, and more recently, A.V. Fedyushin in Belorussiya.

Similar relationships between black larks and herds of domestic cattle occur in winter on the steppes of northern Khazakstan. Although this strong little bird, according to the observations of Zarudny (1897), can

feed by digging through a thin layer of snow to the earth and may even knock through a thin nast with its strong beak, nevertheless, in deep snow it has difficulty in feeding. According to Zarudny, black larks then gather on the roads, near human habitations, or follow the herds of horses which feed by digging out the snow. The same picture can be observed on the steppes of northern Mongolia, where in winter many passeriform birds and daurian partridge come close to the camps of the Mongols. The numerous herds belonging to the latter dig snow intensively and by that act facilitate the feeding of their feathered companions.

I would hardly be mistaken if I said that in those earlier times, when many tarpans, saigas, and kulans grazed on the steppes, the little steppean birds had the opportunity of feeding near the herds in winter.

Finally, in mountainous country we can find examples of similar relationships. For a long time it has been known that the flocks of snow partridges (Tetraogallus caucasicus) congregate in winter at the places where turs (Capra caucasica) have grazed, an adaptation which can be explained by the same ease of securing food on the places where the snow cover has been even partly destoyed by the strong hoofed animals.

On the third of January 1924, in a wide mountain basin near the village of Kazbegi, I observed huge flocks of choughs (Pyrrhocorax pyrrhocorax) feeding on the places which had been dug out deeply by the flocks of sheep. There also came to these places wild grey pigeons and horned larks in flocks of 200-300 birds, with which were gold-fronted finches (Serinus pusillus) and twites (Carduelis flavirostris). The snow in the valley was very thin (about 5 to 6 cm) while all around in the mountains it lay deep.

It is interesting that steppe cattlemen for a long time have simplified the winter grazing of smaller stock by driving them to the places where large animals have just grazed.

The above described phenomena of temporary symbiosis actuated by the winter presence of deep or compact snow cover is a good example of how specific and finely attuned some biotic relationships are. Undoubtedly the destruction of deer or hares would aggrevate the wintering conditions of ptarmigan or partridge, and during difficult winters their die-off would be more frequent and complete.

SEASONAL MIGRATIONS OF MAMMALS CAUSED BY SNOW COVER

"If all food is eaten or destroyed by the difficult time of the year, or is hidden in places that cannot be reached, or is covered by a deep layer of snow, the animal that depends on this food and does not want to die from hunger must look for food in more remote places."

A. Middendorf, 1869

Middendorf, who left a great number of very exact observations and who made several generalizations dealing with migrations in the chapters of his large work paid special heed to the mammals. After him no one in this country attempted a similar summary of the wanderings of animals, although this phenomenon is deserving of the most intense attention from both the theoretical as well as the purely practical points of view. The wide enthusiasm for studying bird migration seems to have pushed into second place any interest in studying the similar phenomenon in mammals. I think because of that one fact alone it would be quite in order to have a little survey of migration caused by the presence of snow cover and the difficulties of securing food that are connected with it.

Middendorf (1869) distinguished between "migration up and down the mountains" (vertical migration) and "wandering on the lowlands" (horizontal migration). Mountain sheep, chamois, deer, roe deer, hares, and foxes, according to him, come down from the mountains into the valleys for a more or less continuous period and then in summer they climb again to the higher elevations. "Cardinal points do not mean anything here, for not rarely animals go towards the north for the winter. In the mountainous regions with heavy snow in particular there is usually pronounced migration from the mountains. Therefore, even on the northern part of the Asiatic Plateau, i.e. in southern Siberia in the Stanovoy Range, as well as the Sayan Ranges or on the Altai, mountain animals, such as roe deer for example, come down for the winter almost constantly not to the south but to the north; on the western side, however, they go toward the west, and even at 52 degrees north latitude they ford rivers by the thousands toward the south, according to the direction of the mountain range, as, for example, on the southern slope of Stanovoy Range.." A sharp

differentiation between vertical and horizontal migrations of animals is not always successful in practice, since seasonal wanderings of one type often change into movements of the second type. Therefore I will discuss them together for each species of animal.

It was not by accident that Middendorf, in the previous citation, took the Siberian subspecies of Capreolus as one of the examples. Seasonal migrations are clearly expressed in this form since it is one of the smallest of our deer. Therefore roe deer in winter are influenced to a greater degree by the thickness of snow cover as a hindering agent. Possibly its high population and its ready availability for observation facilitate recording its migrations. At the present time there is no information concerning its seasonal migrations in the European part of the USSR where its numbers are not high.*

Sabaneev (1872) had the opportunity of observing large migrations of roe deer in the Urals. "The number of bucks on the southwestern and southeastern slopes is different, depending on the period of the year," he says. "In summer most of them stay in Nyazepetrovsk and Zlatoust Forest Tracts, especially in the white steppes. In the autumn in great numbers in larger and smaller herds, up to 20-25 head, they cross the Ural and collect exclusively in the Kaslinski Mountains, where they remain until the spring, when the reverse migration begins. The reason for this migration is the same as in the case of the moose; deep snows on the western slope and the relative snowlessness of Kaslinski Mountains (Fig. 16), which in addition are covered by quite thin forests resulting in the snow being carried away by the northwesterly winds into forests and valleys with the mountain heights remaining almost bare and thus affording refuge and abundant food for the bucks, preferably through the Kychemetski and Sysert'ski Mountains where the forests have not been so deciminated.

Those which come from the west, across the Karabash Mountains in the same places, and those which come from Kyshtym, Zlatoust and Miass Mountains cross the River Vyasovka. Most of the bucks collect near Tatosh, Tashkul', and Semikul', Kozlinay, Karabash and Vishennaya Mountains."

For the lowland part of Siberia we have the recent observations of Troitski (1930), who says that in the region limited on the west by the Yenisey River (from Krasnoyarsk up to the mouth of the Angara River), on the north by the lower stream of the River Angara, and on the south by the railroad track, the roe deer

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* Michael Litvin, in the 17th century, noted migrations of roe deer in the Ukraine, from forest to steepe and the reverse. These data probably refer in part to saiga.

go to spend the entire winter near Irkutsk where the snow is thinner than in the Kansk District. The same pattern has been observed in the vicinity of the village of Uzhur in the southern part of former Achinsk District. "In October when there is already deep snow in the taiga and when there is no food, they come out on the steppes, coming quite close to the settlements and sometimes even into the villages. With the approach of spring the bucks begin to return to the taiga." According to Lavrov (1929) who worked over a large number of questionnaires obtained from hunters and naturalists, the roe deer is also widely nomadic in the former province of Biysk. In spring they appear in Beshelaksk, Kuyagan, and in the southern parts of Altai, Mikhailovski, and Soloneshenski (= Soloneshnoe) districts, and in the winter they go away to the southern Altai. A few individuals remain in the summer range.

Troitski (Kravkov and Troitski, 1930) noted regular movements of roe deer on the right bank of the upper Abakan River (near the border of the Tuvinsk People's Republic). According to personal communication from A.I. Sokolov, who worked there studying game management, the roe deer is almost sedentary within the Tuvinsk People's Republic. They wander through a very limited range and then not even every year.

Turkin and Satunin (1902) noted the yearly migrations of the roe deer in the former province of Yeniseisk; migrations which went from the headwaters of the River Tom' to Abakan in the fall and back again in the spring. The animals swan even large rivers.

Soloviev (1921) mentions the seasonal wandering of roe deer in the Sayans. Still further to the east, in the region of Prebaikalia, Zabelin (Doppel'mair, 1926) noted interesting wanderings of roe deer from the belt of deep snow along the shore up the valleys to the steppes. According to Petri (1930) each year in October the roe deer wander away from the mountainous and snowy Kirensk district into the lower parts of Tutura district which have little snow. A spring migration happens quickly within a period of two weeks. The places where the deer habitually pass are well known to the Evenks. They watch for the animals in suitable river valleys (for example, near the conjuction of the River Bireya into the River Notai). The roe deer of Tutura district are more or less sedentary. Kuznetsov (1929) collected data on periodic wanderings of roe deer in the Yablonovy Range.

For the summer they go northward beyond the range. In winter they move toward the south.

From the earlier data we would like to mention those collected by Middendorf; Bunge (vol. 2:201, 332), has described the migration of roe deer from the mountains to the lowlands and their crossing of the River Irtysh; Gedenshtrem has described the wandering of Sayan roe deer; and Middendorf himself, Schrenk, Radde, and Schwartz, have described seasonal migrations of this species on the southern slopes of the Stanovoy Range. There exists no lesser amount of information concerning the migration of roe deer in the extreme northeast of its range. Mass wanderings of roe deer were known for a long time in Preamuria and Ussuri krais.

According to the data of Vetlitsyn (1902), in Preamuria the migration of roe deer becomes noticeable in the first half of October. Gathered into herds of 6 to 12 head, the animals begin to move toward the west. Staying on the Manchurian right bank of the Amur, they move toward the headwaters of the rivers which flow into the Sungari. This part of the basin of this river is notable for having little snow. Not only roe deer collect here to overwinter, but also wapiti and pigs, after which there come carnivorous animals (tiger, wolf). The roe deer journey at night and partly in the morning, moving slowly and staying for several days in some places to feed. In the fall (before the ice covers the river) the roe deer of the left bank of the river Amur do not cross over into Manchuria but move gradually toward the west. They do not swim over wide rivers and therefore gather at the shores in large numbers. In the region of Khabarovsk the places of such gatherings were: down the Amur near the village of Voronezhskoye, by the rivers Obor and Sita, and up the river near the headwaters of Bira; on the Ussuri above Station Dichenkovaya, near Station Vidnoye, and others. In the fall, migration over the rivers begins after the ice forms.

Twice each year migrating roe deer passed through the former districts of Kumara, Yekaterininski (= Yekaterinoslavka?), Yekatrino-Nikol'skoye, and Mikhailovka-Semenovka, and also in the former Tom' volost'. ((a small administrative division including several villages)) of Zeya-Bureya region. The direction of the migrations and the routes taken are also constant here. The numbers of migrating animals are different in different years. If there is

little snow, few roe deer migrate. Each snow storm can cause an increased exodus of roe deer. The four last winters of 1898-1901, about which Vetlitsyn wrote, had little snow, and were marked by complete absence of migrating roe deer. The reverse of this picture was observed in the former province of Amur in 1888. In the winter of that year there was "an unprecedented migration of animals from the northern plateaus in the direction of Manchuria" (Supplement to the Report of the Military Governor of Amur Province of 1888. That year hunters took up to 150,000 animals.

Among later observations can be mentioned the note by F-n (1921). During several days in the middle of September, he observed a mass exodus of bucks from the Selemdzha taiga to the southward along the watershed of the River Birma (left tributary of the Zeya River) and Girbichek (tributary of the Selemdzha River). On the left side of the Amur, in its upper reaches, a greater or lesser number of roe deer stay for the winter, depending on the depth of the snow cover. "In the winter of 1921-22 there fell little snow and because of this bucks were in abundance in the vicinity of Blagoveshchensk" (hunting and Nature in Amur Province, 1922, no. 9). Besides the above information from Vetlitsyn about the migration of roe deer in Ussuri Province, there are the old data of Maksimovich (1860) and Przhevalski (1870).

Especially interesting are the observations of the latter, since he travelled in Ussuri Province during the years when the taiga still was unusually rich in animals (1867-1869). Each year in the fall roe deer moved from Ussuri Province onto Manchurian territory, and back again in the spring. "The deep snow which makes it difficult for the bucks to walk and still more difficult to get food is probably the cause of these migrations," writes Przhevalski, "Wild bucks remain the year around in the coastal regions where there is less snow than in the central part of Ussuri Province."

The fall migration occured in October and the spring migration toward the end of March and the middle of April (Old Style), after the disappearance of the snow cover. Both migrations continued for about two or three weeks, but each migration was particularly intensive only during any one week. The deer moved in herds of from 10 to 40 head, sometimes even up to 100 head, going in the fall from the lower Ussuri to the River Sungari, and from the upper and middle Ussuri to the headwaters of the River Muren' (= Mulinkhe?).

"In the winter the animals disappear from the Ussuri forests to such an extent that only very rarely does one meet single individuals, these probably being lingerers, or those not having had a chance to go with the others for some special reason. However, the distance traveled depends on the amount of snow which falls, so that in winters with little snow, the majority of the bucks remain in the mountains of the western part of Khanka Basin." The migration routes remain constant from year to year, roe deer using one and the same valley and crossing the rivers at one and the same spot. Taking advantage of this, the Gol'ds hold large community hunts during the roe deer's fall crossing of the Ussuri River (before the freeze-up), or in the spring after the river opens. Przhevalski left a vivid description which has now passed into the realm of legend because the migrations do not now have such a mass appearance since the animals have so decreased in numbers.

Near Lake Khanka the spring migration of roe deer occurred toward the end of March and the beginning of April. Part of the animals went on the northern side of the lake and thence through the Sungacha Valley to the upper Ussuri, and Daubikha, while part remained for the summer on the Sungachi flatland. Because of the swampiness of the country there were not many places convenient for migration and the bucks moved mostly on the narrow crests, which made it most convenient to watch the moving animals. The most energetic migration was noted in the morning hours (from dawn to 9 or 10 o'clock) with the deer lying down during the day. The spring migration was so intensive that one hunter-Gol'd, according to Przhevalski, killed 118 roe deer during the three weeks that it continued in 1869. The observer saw up to 10 or more herds during the morning. It is interesting to note that Przhevalski returns to the question of migration of roe deer several times in his book, yet never speaks of migration of wapiti, which was still in the Ussuri forest in large numbers in those days. We must conclude that this large deer, under the conditions of winter with relatively shallow snow, remained sedentary or almost so, while the small roe deer was forced to migrate. According to the later observations of Baikov (1915) in northern Manchuria, wapiti are limited to only local wanderings for wintering, from the deep valleys onto the sunny slopes, while roe deer arrive here in great numbers from Ussuri Province and Preamuria, and for the summer they return (excluding local individuals).

The number of references to regular seasonal migration of roe deer could be greatly increased, but there is no special necessity for it. Enough observations have been mentioned to establish the presence of regular migrations of roe deer everywhere in the snowy parts of its range, in the region from the Urals to the Pacific Ocean. Undoubtedly in earlier times migrations also occurred in the European part of the country, but they are not noticeable now because of the low density of the animal. In the central portion of the range part of the roe deer do not migrate but remain more or less sedentary and winter in convenient spots with little snow. On the southern border of its range, the location of which is determined by the border of forest islands near the edge of the steppes, because of the thin snow in this strip, roe deer are completely sedentary, and make only small movements from one habitat to another. In eastern Kentei (= Kentei-alin' Mts?), according to the observations of Kozlova-Pushakareva (1933) numerous roe deer remain in winter on the south facing-slopes where the snow quickly melts on the sun-heated slopes, thus clearing the litter. At the beginning of March when nast appears on the south slopes the bucks move onto north-facing slopes where the snow is always soft. It is interesting that in Kentei there is also no comparable clearly expressed migration of deer. Cherkasov (1867) speaks about similar local short wanderings of roe deer in southeastern Transbaikalia. According to his many years of observations, when the snow hardens the Siberian roe deer come out into "zakraikas", i.e. on the forest outskirts, where the snow is blown away by the wind. We have already mentioned how relatively sedentary are the roe deer of Tuva.

There do not exist wide migrations of roe deer in Central Asia, where because of the frequency of this species corresponding observations could of course be easily made. According to Dinnik (1905) roe deer in Caucasia do not make such regular and large migrations as they do in Siberia. In some years herd movements can be observed here, but they are only occasional. "They appear in the case of regions where there is a fall of deep snow." Dinnik has noted the migration of roe deer from the Dark Forest of Stavropol' Plateau, which is noted for its snowiness, into the valley of the Kuban' River, and he also noted migrations from the upper zones of mountains into "warm low places". The most recent observations of Nasimovich (1936) confirm this. In western Caucasia the roe deer winter in the belt of broad-leaved forest (mainly in the oak subzone).

A portion of the animals remains here sedentary. To this zone descend also animals which spend the summer in the coniferous zone. This refers to winters with a normal amount of snow, in the years of much snow roe deer are forced to make wider travels. In 1931-1932 "In Krasnopoliansk and neighboring districts roe deer came to villages in great numbers or stayed not far from the settlements."

Thus, the conditions of snowiness govern the degree of mobility of the population of this species in different parts of its range, in different zones of the mountains, and even in the same locations, depending on the severity of the winters. In regions with complex relief and unequal distribution of snow cover, the direction, continuity, and routes of migrations are quite diverse. The basic characteristic of these migrations is a movement for the winter into regions with less snow, and in the western parts of its range (Urals), the roe deer leave toward the east in the direction of the winds bringing the precipitation, as if they were rushing to hide themselves from the influence of the Atlantic Ocean; in the Far East, on the contrary, they move toward the west, hiding behind the mountain system of Sikhote-alin' from the influence of the Pacific Ocean, which furnishes moisture for this part of Asia. In both cases the roe deer rush toward conditions of a more continental winter, which is better suited for many small hoofed animals. The importance of mountainous countries in the life of hoofed animals is very significant, if only because of the fact that they form such large barriers. No less important is also the circumstance that in mountainous countries there are always some enclosed basins, valleys, and defiles, which are distinguished by an insignificant amount of winter precipitation. Such areas are notable refuges for many species of chionophobes which survive the difficult winters here as if on an island surrounded by a wide snowy sea.

Scarcer but none the less interesting are references to seasonal wanderings of forest "noble" deer (maral, wapiti), which are quite sensitive to the snowy conditions of winter since grassy foods play an important role in their winter feeding. Recently Nasimovich has begun a special study of wintering conditions of hoofed animals in the mountains of western Caucasia and has published the reports (1936, 1939) which incorporate fresh material and interesting conclusions. According to his data, Caucasian noble deer winter mostly on southern slopes of mountains within the range of the forest belt but stay only in small numbers on northern slopes. Adult males stay mostly in the coniferous zone, somewhat higher

than females and young deer, which winter in the lower part of the coniferous zone and in the zone of broad-leaved forest (mostly in the beech subzone). "Males stay on slopes which have a snow cover no deeper than 0.8 to 1.0 m...Females avoid regions with snow cover of more than 0.6 m in depth, and stay in large numbers where the snow cover does not exceed 0.2 to 0.3 m in depth. The distance from the places of summering to the places of wintering varies from 20 to 30 km. Deer migrate in two stages: In November they come out of the recesses of the mountains, and in February-March, after the heavy snow falls, they descend still lower. A reverse migration begins in April". The data of Nasimovich markedly substantiate and complement the observations of migrations of deer previously published by Dinnik.

Analogous seasonal migrations were traced in less detail in Siberia in all the parts of their range with much snow. The brothers Kozhanchikov (1924) described the fall migrations of maral in the Sayans as follows: "As soon as the first snow falls anywhere in the taiga the animals go into yards and there remain for the whole winter. This animal selects for its yards places where the snow is so thin that "pawing" is possible, i.e. scraping it with the front feet to get to the litter. Marals' yards are located in forest groves where there grows a grass called "ozagach" that remains green for the whole winter and serves as food for this animal. They do not come to the drinking spots as other animals do but eat snow. At the time of the spring thaw, where there appear patches of ground free from snow, the animals leave their winter yards and go to the warm slopes, frequently to burned-over places, and there feed on the young green vegetation."

In some parts of Achinsk region (Orlov, 1930) maral also winter in the mountain taiga, not migrating into lower regions, since near the peaks they find places almost free of snow. "In mountain taiga the snow on the peaks is blown away and carried into the ravines....Maral congregate here to overwinter on the top of Urun ((Peak)). Large bucks, which can stand the cold more easily, stay on the bare mountain tops, while younger ones, on the contrary, come from the exposed ridges down into the "warm taiga", where

they are protected from wind by the forest. Since by no means all the slopes in the "warm taiga" have a small cover of snow, then it is obvious that maral are not found everywhere. As a result many slopes are here covered with maral tracks".

Petri (1930) has collected information about the migration of deer in the regions of the north of Baikal (headwaters of the Lena). Here, with the coming of winter, wapiti begin to come down from the heights of Kirensk district and to move into lower areas "with the idea that before the heavy snowfalls of winter arrive they will be in those places where the snow cover is not very deep. This is why, in winter, wapiti willingly stay in the low-lying Tutura district, which has little snow. With the coming of the period of nast, they try to move out into tho e places where the snow is very thin."

Gassovski (1927) observed the intensive fall migration of wapiti. On the northern slopes of the Tukuringra Range, in the valleys of the Koval', Amanach, and Kerak Rivers, there appeared tracks and deer paths, leading south from the valley of the Gilyuy to the Ukran. During the first ten days of November wapiti moved fast through here, feeding on the way, and crossed through certain passes. After he had established this migration and collected information by wuestioning, Gassovski came to the conclusion that at the end of October and November "Wapiti, almost without exception, left the basin between the Stanovoy and Tukuringra Ranges, migrating on the Urkan slopes of this range and only partly through the northern and middle part of the Yankan Range into the lower stream of Ol'doy." At the end of April and the beginning of May the animals return to the summering places over the same pathways.

The American forms of these species, living in Canada and the United States, wander in winter into the steppes and forest-steppes, where the snow is not too deep. If, by the end of winter, it becomes difficult to feed on grass because of excessive snow, there is a return to the forest regions to feed on browse.

In regions of relatively little snow deer are almost sedentary even under conditions of very rigorous winter weather. Thus, in eastern Transbaikal, (Cherkasov, 1867) wapiti perform only short migrations, coming from the main ranges onto the smaller spurs of the ranges, where they stay in the thickly-forested northern slopes, forested valleys, and swamps. They come to graze

on the forest outskirts or spots warmed by the sun which are covered by dry grass. Here, in winter, they feed on grassy forage, bracket fungi on the birches, and only rarely on bush twigs. According to the observations of Kozlova-Pushkareva (1933), the marals of eastern Kentei, which lies on the border of nearly snowless Mongolia, are sedentary. Spotted deer are also almost sedentary, inhabiting the parts of the Manchurian taiga with little snow. According to the observations of Abramov (1930), who did special work on the ecology of the spotted deer of Premoria there are no widespread migrations of this animal. "If they migrate then they only go within the range of familiar territory, or in the maritime strip from the mountains to the sea and back again." The latter migrations are caused, together with other reasons also, by "falls of deep snow on the mountains and by shallow snow along the seashore, especially in spots exposed to the sunshine".

According to the latest observations (Kotovshchikova, 1936) in Crimea, the Crimean subspecies of deer prefers to stay in winter on the "southern slopes where there is little or no snow cover," but they do not make any marked migrations in the territory of the reserve.

Thus the true deer being animals which are larger and hardier, remain sedentary in those places from which roe deer are forced to migrate. The migrations of this deer in most places are shorter than in the case of roe deer, and are particularly noticeable only to the east of Baikal and toward the north of Amur, where the ranges of maral and wapiti extend especially far northward into the taiga region which has a long and snowy winter. The size, height, and strength of the animal probably play a very important role in its struggle against adverse conditions of snowiness because the males of the Caucasian deer can overwinter higher in the mountains than can the females. Does not this selective role of snow cover explain the fact that the most northerly of the deer are also the largest, (moose, reindeer)? It is interesting to compare with this the data of German naturalists which showed that the northern part of Germany was populated by a larger ecotype of the European roe deer than was the southern part. The Siberian roe deer, which is the form living in a region with longer and more snowy winters, is markedly larger that its European relative, etc.

In the literature there are also many indications of seasonal migrations of moose, correlated with movements of animals for the purpose of overwintering in regions with little snow, Sabaneev (1872) said that on the western slope of the Ural Mountains there are many more moose in summer than on the eastern slope, but at the beginning of winter "moose come in great numbers and stay here until spring. "This phenomenon is caused by deep snow on the western slope, which, in September (old style- A.F.) reaches there a depth of up to half an arshin* and two or more arshins in December. The migration of moose 'beyond the rock' is thus ended even as early as November." It is interesting to note that in this part of the Urals the carnivores accompany the hoofed animals. Lynx "also make regular migrations", writes Sabaneev, "but these migrations depend not on the depth of the snow, which is not particularly important for them, but on the migrations of moose, deer, and roe deer onto the eastern slopes of the Urals." Sabaneev reports this observation in another work (1879). It is mentioned by Turkin and Satunin (1902) more completely. In more recent times the migrations of moose in the upper Kama Forest Belt have been investigated again by Turchkov (1930). It is interesting that the only moose to migrate are those of the snowy western slopes, but the animals that summer on the lower parts of the tributaries of the Chusovaya and Sos'va rivers, where the snows are thinner than in the Urals, remain here for the winter.

L.G. Kaplanov (1935) recently has made some interesting observations in the flat taiga of Transuralia (right bank if the Irtysh River). At the end of October after the rut, moose moved to the south in groups of three to five individuals, making from 10 to 30 km per day without stopping for more than one or two days in one place. The animals come from the north, cross the river Demyanka and concentrate beyond the Big and Little Turtas rivers. The reverse migration begins at the end of winter. The moose cross the Demyanka River in April before the ice breakup. In years when there is nast the spring migration is delayed until the snow melts. The length of the route which the moose use here is no less than 300 km. The difference in the depth of snow cover between the place of summering and the place of wintering can be found from a comparison of the following data. In Surgut, from which moose leave,

*Old unit of measurement equal to 28 inches.

the average depth of snow cover is 80 cm (at the end of March), but in Tobol'sk and Dubrovnoye, which lie somewhat south of the region of the observations of Kaplanov, it is 61-51 cm. According to this author, the seasonal migrations of moose on the right bank of the Irtysh have been known for a long time (not less than 100 years). Certain places for crossing the Demyanka River remained the same for many years.

Troitski (1930) determined the occurrence of regular migrations of moose in the Chuno-Angarski district of the former province of Kansk. On the Chuna Highlands moose go in spring to the north and to the south in the fall. In Kazachinskoye district the moose migrations go from west to east and back again. They cross the Yenisey River not far from the village of Korgina where there are a number of forested islands in the river.

The same author (Troitski, 1930) when working in 1927-28 in the mountains on the right bank of the headwaters of the Abakan River noted migrations of local moose beyond the Yenisey into the lower regions of the Sayan Mountains for the winter. In the latter mountain system the members of the expeditions of Soloviev 1914-15 and the Kozhanchikov brothers in 1920-22 made observations on the movements of moose to the places of overwintering.

According to Soloviev, moose move for winter down from the limits of stone pine taiga in the mountains in the fall into the zone of subtaiga. In the spring after the ice breaks up (April, Old Style), moose move into their summer range.

Moose move relatively slowly and reach Gutarsk Lakes only toward the end of June. The fall migration begins after the end of the rut (i.e. in October) and in November the moose have already reached their winter range. Some moose remain for the whole winter in suitable spots within the taiga. "Mass migrations of the animals occur in definite places. Hunter-traders awaiting moose, arrive on the last sled road ((before snow melts)) a week before their appearance. An especially strong migration occurs on the River Krolug, the left tributary of the Mana River. The animals go there in a definite sequence; first moose, then maral and then roe deer". Soloviev gives figures showing the size of these spring migrations. In 1901, five hunters in eight days of hunting for migrating animals killed 38 moose, 4 marals and 25 roe deer, in the headwaters of the Krolug.

The data of Soloviev are very interesting in that they indicate that moose, which are common in the eastern part of Sayan, become very scarce in the southwestern part of the range and almost completely absent in the vicinity of Kazyr-Suk Forest Tract. This region, which is unsuitable for overwintering of moose, does not have convenient routes into the taiga zone, and thus moose cannot get in to it even for the summertime. As a result, the southwestern part of the Sayan Mountains appears to be uninhabited by these animals.

L. and I. Kozhanchikov, who worked in the taiga in winter, give the following interesting information: "The winter residences of moose are found each year in the same places and the animals go to these places by the same pathways and fords...The spots used for winter residence are usually on south-west-facing slopes which are covered mainly by aspen groves, birch groves, mountain ash, and other broad-leaved species, situated not far from fir groves. On such warm ridges patches of open ground appear soonest of all...In the taiga, because of the dissected relief, snow does not lie in equal depth and there are places where the snow is very shallow, and also the contrary. Thus, for example, near the River Kazyr, there is a tributary, the so-called Poperechka River, near which the snow is so thin that in the middle of winter it is almost impossible to travel by skis because the forest floor is not covered. In such spots which are especially suitable many moose gather to spend the winter."

We note a similar picture in eastern Siberia. Petri (1930) says that the moose of Kirensk district, in the middle of October, "where deep snow will soon fall" move into "the low-lying Tutura district which has little snow." The places where the migrating moose swim over the Kirenga River remain constant; here the Evenks set up blinds. Still farther to the east, Gassovski (1927) observed the fall migration of moose. In the valleys of the Koval', Amanach, Kerak, and little Dzhelkalak Rivers (to the north of Station Skovorodino), at the beginning of winter, he encountered numerous tracks of moose as well as wapiti, "all directed toward the south and, in some places, converging to become regular highways." According to him, a significant number of moose which summered in the river valleys of the basin between the Stanovoy and Tukuringra ranges, move away at the end of October and the beginning of November, following definite pathways to the southern side of Tukuringra. "However, the migration probably does not include all the moose of the district (while at the same time all the wapiti move out). A small part of the moose remain here for the winter and finally some of them, according to the Orochens, wander away in a northern

direction to the headwaters of the left ((tributaries of the)) Mogot and Getkan." In the spring a reverse migration is observed.

Cherkasov (1867) showed that, for eastern Transbaikalia, "movements (of moose) depend on the fall of heavy snows on the forested ridges. Sometimes moose come down in great numbers from the mountains into the low places where there is less snow and live there until spring." He also says, quoting Gagemeister (1854) that in 1840 there were deep snows in the Sayan Mountains and moose came down from the mountains in great numbers so that the peasants had the opportunity to kill them simply with clubs. Baikov (1915) has noted that the Ussuri moose "when heavy snows fall in Ussuri Province, cross the Ussuri River and show up in the northern part of Kentei-alin'. In summer, and even in spring, they again move away to the left bank of the Amur and the right bank of the Ussuri River."

According to Zolotarev (1935), in the basin of the River Uda (near Okhotsk coast) moose move for the winter into places with a shallow snow layer and then in the spring move onto south-facing slopes on which snow melts early. Such local migrations are found also in other parts of the range. In Karelia, according to Knize (1935), moose migrate in different directions, depending on local peculiarities of relief and forest plantations.

In the vicinity of Loukhi Lake moose go, in winter, from west to east, around Kem' from east to west, and in the southern part of the region east of Lake Onega from south to north. It is very interesting to note that in Lapland National Park (near Lake Imandra) with a fall of deep snow moose can be observed moving from the river valley up onto the slopes of the mountains to a height of 400 meters to the dry lichen-covered pine forests which are characterized by a shallower snow cover.

Finally, there are not a few districts where moose have the same ranges in summer as they do in winter. According to the latest observations, moose do not migrate in Lisino (near Leningrad), they are sedentary in the game reserves near Moscow, and in the region between the Volga and the Vetluga of Gor'ki Oblast', which is well known to me, where the maximum depth of snow cover is 45 cm (city of Semenov, cited from Nekrasov, 1935) and about 50-55 cm near Shar'ya (personal observations). Consequently, under lowland conditions moose can easily survive the winter with a snow cover reaching half a meter in depth by February or March. Because of the great height of the animal such a snow depth does not hinder movement very much, however, the hoofs of the

moose usually sink in as far as the ground. Feeding on the branches of bushes and forest undergrowth, aspen bark, and lichens hanging on the lower part of the trees, moose suffer little from snow as a factor hindering the obtaining of food. These peculiarities enable the moose to inhabit a huge forested region having a snowy and continuous winter which other of our hoofed animals, excluding reindeer, could not do. In scattered parts of their range they are forced to make migrations of sometimes up to hundreds of kilometers, in mountainous places to migrate from upper zones into lower (the opposite in the Chuna-tundra) or to cross over from one exposed slope to another. Seasonal migrations of moose are quite variable depending on the many kinds of winter snow conditions. It is important to note that they sometimes remain to overwinter in places from which wapiti migrate (Tukuringra) and easily survive in places which, because of the snow conditions, are completely unsuited for roe deer. There is every prospect of a definite correlation between the degree of intensity of migrations caused by snow cover and the ability of forest deer to inhabit regions with much snow. Roe deer, which react to a fall of deep snow by having stronger migrations than do other deer, do not invade snowy regions as far as moose which exhibit migrations much less. However, reindeer are completely separate from these considerations, being a species which, in the southern parts of its range, is extremely mobile and wanders widely.

We have already had a chance to note the number of adaptations of reindeer which facilitate their movements on deep snow. Reindeer are undoubtedly chioneuphores, i.e. snow enduring forms. Nevertheless, the effects of snow cover show to some extent in even its wanderings. On the Kôla peninsula, according to the observations of Pleske (1887), Bartol'd (1930), and the latest data of Kreps and Semenov-Tyan-Shanski (1934), reindeer come from the low forest regions in winter to the elevated mountain tundras having numerous bare patches on which they may more easily obtain reindeer lichen. This occurs when the average depth of snow cover reaches 50-60 cm in the forest. The differences in depth of snow cover in different habitats of reindeer in Lapland National Park can be seen from the following figures obtained, by measuring, by the latter two authors, Depth of snow cover on 11 March 1931:

Pine wood -- 50 cm; low spruce growth in foothills-- 56 cm: swale in tundra--29 cm; "nune" winnowed by the wind-- 11 cm.

The deer of Kamchatka (Goncharov, 1930) during snowy winters move to the naked slopes of the mountains. In the Siberian ranges of the taiga regions, which have much snow, (Altai, Sayan Mountains, mountains of Prebaikalia, Yablonov Range, Stanovoy Range, and others) the reindeer stay all winter on the tops of rocky mountains from which the snow is carried away by the winds. On the flatlands of northern Siberia reindeer penetrate deeper into the forest region if there is a windy and stormy winter. The deer wander into the forest for protection against the foul weather and also because it is easier to paw the reindeer lichens from under the soft forest snow than from the tundra's compacted snow (Naumov, 1933). Migrations connected with the appearance of snow cover of a considerable depth are also known for the reindeer of Novaya Zemlya (Zhitkov and Buturlin, 1901).

At the time of Bogdanov (1871) reindeer came each year to winter in the northwestern corner of the former province of Kazan. According to the observations of my father, N.E. Formozov, who often hunted deer in Transvolga in Gor'ki Oblast' in the last quarter of the 19th century, the number of deer always increased there in winter. Evidently, into this strip of land along the Volga came the deer from the north country and possibly from what is today Komi A.S.S.R. According to data collected by me, the annual fall migration of deer and moose from east to west was earlier in the headwaters of the Unzha River. It is interesting to compare with this, the fact that to the northeast from the middle reaches of the Volga (with an average maximum snow depth of 50 cm) lie regions with 60-70 cm of cover. These and other examples of the same kind attest that snow cover, in a number of cases, causes a migration of tundra as well as forest reindeer, and determines the time and direction of these migrations. Nevertheless, the grandiose seasonal movements of the herds of reindeer in the tundra and forest-tundra zones, which each year encompass many hundreds of kilometers, appear to be more complicated and arose, of course, under the influence of a great number of factors, among which snow plays a secondary role.

Thus all species of our deer, excluding musk deer which inhabit steep

slopes of forested mountains, migrate each year for a greater or lesser distance looking for winter grazing with the most convenient snow conditions. The degree of mobility of the population of these species depends on the biological peculiarities of the animals themselves as well as the climatic conditions of each given region of the range. The number of migrating animals, the distance and the continuity of migrations, vary even within the limits of one and the same region, depending on the flumctuations in the amount of winter snow. In some years the migration is increased so much by a fall of extremely heavy snow it attracts general attention. I will give one note from a newspaper. "The winter of 1913-1914 in Siberia appeared to be very snowy.....Moose, marals, and roe deer were forced to come down from the mountains, to leave the forests and to look for food near inhabited places. Several cases were noted in which moose...came into villages and pioneer settlements ..." (newspaper "Novoye Vremya", No. 13639). Such wanderings that can be distinguished from regular seasonal migrations, take on more the character of emigrations, i.e. eviction caused by catastrophe (forest fires, floods, etc.)

Among other hoofed animals, as one would expect, seasonal migrations in connection with snow cover have been observed in pigs, in several parts of their range. Dinnik (1910) briefly described migrations of pigs in Caucasia, saying that "with the appearance of winter when deep snow falls in the mountains, wild boars come down". Besides snow fall, the distribution of food shows an influence upon their movements. According to the observations of Nasimovich (1936) in Caucasia National Park, pigs overwinter mainly in the lower part of the zone of dark-needled forest and the subzone of beech in the broad-leaved zone. Sometimes they go even lower. Pigs go for 20-30 or more kilometers from the places where they spend the summer. Single males usually stay higher than herds of smaller individuals. In Transbaikalia towards the end of winter, when hard nast appears, the pigs (Transbaikalian subspecies) stay mostly in places that are warmed by the sun where there is no snow, since on the north slopes the pigs cut their snouts and feet bloody on the nast (Gherkasov, 1867).

According to Przhevalski (1870), during times of food shortage, or when deep snows have fallen onto frozen soil, pigs (Manchurian subspecies) in Ussuri Province "undertake migrations from one place to another, sometimes over long distances ....." Baikov (1915) referring to the pigs of the northern

parts of Manchuria, reiterates this: "When deep snow falls in the mountains they move to places where there is less snow."

Typical mountain hoofed animals, being able to move and to feed on steep slopes and rocky places, have marked advantages in comparison with hoofed animals in flat places. As has been pointed out before, only a little snow sticks on steep slopes and cliffs. The conditions of movement and feeding of mountain animals are dependent on snowiness to a relatively lesser degree than are those of lowland animals. In western Caucasia, where the inhabitants of the forests - deer, pigs, roe deer - undergo seasonal migrations of tens of kilometers in length, turs and chamois, which are forms of rocky highlands characterized by especially deep snow, migrate only within very narrow limits. According to Nasimovich (1936) the west Caucasian turs "move down the mountain slopes for several hundred meters only, not rarely staying in the same regions as in summer, concentrating themselves, however, mostly on slopes with a southern exposure."

Therefore, in winter, they can be seen both in the alpine and subalpine belts of the mountains and in the upper part of the forest belt. Wintering places in the forest must necessarily be rocky. The migrations of turs in western Caucasia were known even to Dinnik (1910). He speaks also about the fact that on the Georgia Military Road these animals in winter sometimes come down to Lars Station. From time to time there occur years when the deep snows force the east Caucasian turs of Azerbaidzhan to come down to the forest (Vitovich, 1928).

According to Nasimovich (1936), all the west Caucasian chamois move in winter from the alpine belt into the forested zone, from its upper border to the broad-leaved zone (part of the animals remain in the forest belt also in summer). Overwintering chamois usually disregard the slope exposure, but the steepness or rockiness of the slope, which governs the depth of its snow cover, appears to be quite important to them. Here they sometimes winter in company with turs. On gentle and snowy slopes they appear only as transients. According to Dinnik "In winter the chamois avoid as much as possible the places covered with deep snow and stay on the slopes, bluffs, or rocks facing south, in other words in places where there is little or no snow. But

sometimes they get into places of opposite character."

In the ridges above the Semirechka River, Siberian ibex exhibit vertical migrations that are caused by local snows (Shnitnikov, 1936), in the Altai and Sayan Mountains (Turkin and Satunin, 1902: Soloviev, 1931) and, according to personal communications from A.I. Sokolov, in the mountains of Tuva. Hoofed animals of steppe lowlands (kulans, antelopes) and mountain sheep, which inhabit regions of little or no snow, are rarely forced to migrate because of the influence of the factor which interests us. Possibly the former seasonal migrations of kulan and saiga of Kazakhstan, which went in winter to the south or southeast into the semi-desert regions with little snow and returned for the summer onto the grassy pastures of the steppes, have to be referred to the group of phenomena already analyzed. Grum-Gorzhimailo (1914) says, concerning the Mongolian gazelle, that, "In winter deep snow sometimes forces them to leave the steppes and go into the deserts, but in western Mongolia, which generally has little snow, such cases rarely occur." During the rare winters with much snow, such migrations also appear in Persian gazelles of the Transcaucasian steppes. The argalis of Pamir, which live at extreme heights under conditions of a cold mountain desert climate, usually remain more or less sendentary, correlated with the known fact that this country has little snow. According to Rozanov (1935) the argalis of some regions come down into the valleys in winter.

Among the other groups of mammals, carnivorous animals are quite widely nomadic. In Caucasia, with the snowfall, forest cats, foxes and wolves come down into the foothills which have little snow. Such carnivorous animals as lynx, snow leopard (Felis uncia) leopard (Panthera pardus) tiger, wolverine, wild dog (Cuon alpinus) and wolves, follow the migrating hoofed animals (roe deer, deer, pigs, and others) and move into their wintering places. More local migrations of corsac, fox and wolf which are connected with inequalities of the character of the snow cover in different habitats are well known to hunters.

Thus, since a significant portion of the large mammals winter without hibernation, snow cover causes in some cases a regular seasonal migration, in other cases short movements from one habitat into another, and sometimes both together. Undoubtedly with

wider winter ecological work, which is vitally needed, it will be possible to establish many types of wanderings caused by snow cover. The practical importance of these appearances is very great. Because of their quite extensive seasonal migrations, the protection of useful species in national parks, the regulation of hunting of hoofed animals, and the destruction of carnivores meet a number of difficulties which cannot be overcome without knowledge of all the peculiarities of the migrations. As is perfectly evident, study of the latter must be intimately related to the study of snow cover as a factor hindering animal movement and food getting.

Snow cover has a great importance also in the question of bird migration. However, because of the extent of the literature on bird migration, we cannot spare a necessary place for this question in the present work.

DECIMATION OF ANIMALS BECAUSE OF EXTREMELY DEEP SNOW COVER OR BY THE APPEARANCE OF AN ICY CRUST

The overwintering species of birds and mammals of each region are more or less adapted to survival of the difficult period of the year, to a struggle with the snow cover as an adverse factor.

This adaptation, however, is not absolute, but is relative and quite limited. Although able to withstand the struggle for existence with a depth and continuity of snow cover which is average for the particular region, many species meet calamity if there is extremely deep or unseasonal snow fall.

The fall of solid precipitation shows as much year to year variation as does rain fall. One may cite continuous heavy snowfalls which often cover great areas with a deep snow cover as analogous to heavy showers and "protracted" rains. Heavy showers or uninterrupted rains cause many changes in the living conditions of animals. Heavy snowfalls and winters with much snow have no less effect. They are able to cause faunal calamities over areas which may only be measured in thousands of square kilometers. Even migrations from these conditions usually cannot cause a quick enough exodus of populations of chionophobe species into regions more suited to them. Exhausted and hungry animals starve in great numbers, their population are markedly decreased, so that when they are re-established after a number of years they can be cut down again by the next winter with excess snow.

The importance of the winter snow regimen in the life of nature and of man in middle and northern latitudes is so essential that evidence of deviations from the norm occurs in the most ancient historical documents. One may find a great deal of such information in the well-known "Chronica" by Shnurrer (1823).

Such cases are especially numerous in the Russian annals. I will give several examples (Bogolepov, 1911).

"In the summer of 6916 (1408).....At that time the winter was very heavy and cold and extremely snowy....." (Tver' Annals). "In the summer of 6920 (1412) the winter was very snowy and then in the spring it flooded very much." In 1446, in the story about the escape of Vasily the Second from Dmitri Shemiaka, the chronicle says: "and they could not run away becuase the snow then was 9 pyads (i.e. about 180-190 cm) (Sophiiskaya Second Chronicle).

"In the summer of 7031 (1523).....at the same spring, on the day of Holy Trinity, there fell a heavy cloud of snow and it remained on the earth for four days, many animals died, horses and cows, and birds were dying in the forest." (excerpts from a chapter of the Novgorod Chronicle). One could give many such historical evidences but we will go to more recent times. G.P. Danilevski, a hunter well-known in his time, describes a snowy winter in the southern part of the Ukraine, where usually the cover does not exceed a few centimeters in depth. "In 1860 in Southern Russia there fell a snow that was unusually deep for the steppes. At first, when it had not compacted, a blowing snowstorm broke out, and then an upper snowstorm struck and brought piles of snow that unexpectedly filled the ravines level and farms found themselves buried, and travellers on the streets saw roofs of houses at their feet, and they started to enter the gates as if over the ramparts." (Four Seasons of the Year of Ukrainian Hunting"). After this snowfall the wolves, which had lost their chance to hunt in the steppes, appeared to be specially numerous near the settlements and were characterized by rare boldness.

L. Zotov (1884), who hunted for many years in the vicinity of Simferopol', left a good description of the great snowy winter of 1879. The two preceding years had been very good for local game breeding. But "there came a terrible winter"....from the 25th of

November on, snow piled up and continued for almost 3 days; upon these drifts snow was added for the whole winter, accompanied by frosts which were continuous and unusual for Crimea. (In shaded places remains of the drifts were preserved until April). European hares, grey partridge and great bustard suffered especially. Bustards from the steppes of northern Crimea flew over to its southern shore. It was warmer there but the snow also lay there in a solid shroud. Bustards congregated on the roads, in the vicinity of settlements, and hay lofts, looking for food in cattle droppings. Because of the lack of food, they became quite tame and allowed anyone to approach for a close shot. Toward the end of winter they died by tens from exhaustion. "Their bodies were not rarely found directly near the highways from Simferopol' to Alushta." Many black birds (Turdus merula) died in the forests. Roe deer "congregated into large herds and with forces thus combined, trampled platforms within the young forest around which they fed...Quite a few died from hunger and still more from wolves..." Because of this winter there was a sharp reduction in the number of several species. In 1878, during 7 hunts, L. Zotov took 24 European hares and 96 grey partridge, while in 1879, in 10 hunts, only 1 European Hare and 7 grey partridge. A similar hard winter was noted in Crimea in 1923-1924; unusual snowfalls and cold also occurred then over the greater part of the Ukraine. W. Rudevich (1924) who published observations from Mariupol' District* wrote that such an amount of snow had not been noted here for the last 30 years (in orchards there were depths of snow up to 70 cm). "The deep snow and frequent snowstorms were fatally reflected in the number of grey partridge says Rudevich. (About the same time, heavy snows were also reported from Podoli (Podolsky, A.D., 1924)). White-winged larks (Melanocorypha leucoptera), snow buntings and northern larks, which were wintering in southern Ukraine, suffered as well as the local steppe larks. In January, after the snowstorms, these little birds moved to the houses and "in the city covered all the yards and streets." They died by the thousands from starvation. In the steppe, Rudevich saw bodies of these birds over a distance of several kilometers. These small passerines were decimated also in the region of Askaniya-Nova, where A.A. Brauner observed a loss of rooks and crows. European hares, which occurred that year in great numbers in the Ukraine, flooded into orchards and plantations; in all places a high mortality was noted among them. In the district of Mariupol' there was observed an unusual migration of European hares, which, because of lack of food,

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*Mariupol' is now called Zhdanov.

moved out onto the ice of the Sea of Azov. Here they died en masse so that their bodies could be collected by tens. (Rudevich, V., 1924, Nezhentsev, S.N., 1924, and others).

At the end of 1924 and the beginning of 1925 in many places in Transcaucasia, there were extremely heavy snowfalls following a cold spell. Some information was published in the major newspapers and in hunting magazines. First, I will give brief selections from telegrams published in the "Central Executive Committee News" "The snow storm caught Baku napping, completely disrupting its life in all aspects. The city was covered by drifts which, in some places, reached 4 meters". (28 December 1924, Baku). On 24-27 January 1925, a deep snow fell in Novorossiysk, Gagra, Gudauta, and even in Batumi. At the same time in the region of Baku, "The snowstorm exploded with extreme force on the railroad district of Baladzhary-Chernogorka-Yamsha (= Yashma?). Here the depth of the snow was more than a man's height." From Tbilisi, on the 27th of January it was reported that in Nukha and Agada (= Agara?) districts over 1000 head of cattle perished. Strong snowstorms near Zangezur caused human fatalities. Packs of wolves invaded the cities, coming into the people's yards. Similar information arrived from Echmiadzin, Signakhi and Gori.

From Batumi on 29 January 1925, it was reported that in the canyons of the Chorokh River a great number of wild pigs appeared, which had probably been evicted from their usual habitats. Packs of jackals (Canis aureus) appeared in the vicinity of Batumi. In connection with these unusual snowfalls, the local fauna of Transcaucasia and the birds wintering there experienced most intense stresses. "Wild mammals and birds died in great numbers from the cold and lack of food," wrote Golovin (1925). "Gazelles in the Shirvan and Mil'sk steppes joined the flocks of domestic sheep. Even such strong birds as geese (Anser) and brant (Branta) flow to the settlements where they were easily caught by hand. Great bustards and little bustards lay in great numbers on the steppes, dying from lack of food and from the cold. In the case of black partridge, it must be assumed that they died off completely..... black partridge are very gentle and are completely unable to withstand cold and snow, and cannot fly in these conditions. Those which avoided death from freezing inevitably died of hunger, because the snow lay from 18 to 35 cm deep. Even sheep and the stronger cattle were unable to dig through to the earth and starved in great numbers. One must think, that at least Azerbaidzhan and the neigh-

boring regions of Iran, black partridges could survive somewhere. The snow lay... to the end of January, accompanied by freezing weather, an occurence that no one could remember. (In the two years previous to this (according to Golovin), there had been no snow at all in Baku - A.F.). And then again a snowstorm howled, and it was not known when the weather would change. Birds which overwintered in Azerbaidzhan perished in part, and in part flew away, because water surfaces froze, including small sea bays such as Kizil-agach (=Kyzylagach). On the shores of the Caspian Sea, in the places where there is little snow and birds can find food, small numbers of species which live on the sea, such as some species of ducks, brant and swans, remained near the shores. On the shallows near the shore, scattered flamingos (Phaenicopterus) can be seen. But the greater part of the water game disappeared, and probably the greater part of it died, because further south (in Iran) the same snowy and frosty weather raged." ((The whole of this citation was originally written in the present tense)).

It is important to note that large snowfalls often come in the second half of winter when the snow cover already has a signigicant depth. Animals that have become exhausted during the winter cannot cope with this adversity as successfully as in the fall. Most of the known cases of mass mortality of animals come in the middle or towards the end of winter.

Winters of deep snow are repeated quite often in different parts of the country, at intervals of from 3 to 5 years. According to Shenrok (1926), the greatest depths of snow cover (for January through March) in these or other regions of the European part of the USSR were noted in 1891, 1895, 1896, 1900, 1902, 1908, 1914 and 1917. In this respect, the winter of 1891 was distinguished by deep snow in the southwestern part, in 1895 in the regions to the East of the Dnieper River, and in 1896 in the region of the Don, lower Dnieper and Volga, in 1899 the northeast and lake country, in 1900 the Western Dvina River, lakes and headwaters of the Volga, in 1902 a strip from the Western Dvina to the basin of the Kama River, in 1906 the central part, i.e. Oka River, headwaters of the Volga, of the Dnieper, and of the Don. In 1914, an unusually heavy cover was noted in a relatively narrow region on the northeast of the basin of the Kama River up to the former Ust'-Sysol'sk*. Finally, in 1917, a strip of deep snow lay from Kiev to

*Ust'-syol'sk is now called Syktyvakar.

Ural'sk, encompassing the headwaters of the Oka and Don, and on the Volga, the region from Kazan to Kamyshin. The following figures from Shenrok give an idea of the amplitude of seasonal variation of snow cover maxima. In the northeastern portion of the European part of the USSR, it flunctuates from 30-40 cm up to 100-150 cm, and in the southwest from 0 to 40-50 cm. With longer periods of observation, wider fluctuations will, of course appear. This is obvious even from the material from the chronicles in which depths of from one to one and a half meters were noted, even in the western part of the country.

In western Caucasia, according to the information collected by Nasimovich (1935) winters of deep snow which were followed by mass die-offs of wild animals were as follows: 1873-1874, 1879-1880, 1895-1896, 1906-1907, 1907-1908, 1910-1911, 1928-1929, 1931-1932. Among these, some were unusually snowy in scattered regions only, others (such as the winter of 1910-1911) were characterized by deep snow over the whole province and caused widespread disaster to the fauna.* Let us go now to the phenomenon of the die-off of mammals and birds, caused by a fall of extremely deep snow.

Reindeer, which is one of the species of hoofed animals best adapted to life under the conditions of continuous snowy winter, sometimes suffer from an excess of snow, and especially from icy crusts, which greatly hinder their obtaining food. Slyunin (1909), when speaking about reindeer ranching in Kamchatka, gave the following interesting data: "Winters that are rough and with deep snow strongly reflect on the deer. The winter of 1896 clearly showed this harmful influence; it was characterized by extreme roughness and frequent snowstorms. All the mossy tundras were buried under so much snow that the deer could not break through with their hooves. These misfortunes forced the nomads from the tundra to the seashore...but it appeared that everywhere the winter was similar. The head man of the Koryaks, from near Tigil' complained that becuase of this want of fodder, he lost nearly 400 deer that winter." Kertselli (1911) observed a similar picture on the lower Pechora. According to him, deep snows fell near Kolva in February 1909. Deer dug down to feed only with difficulty. "Hunger then began. Nast having been formed, the deer could not dig the snow

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*According to the information collected by me after the snowy winter of 1931-32, the numbers of pheasants, European hares, forest cats, and cane cats (Felis chaus) decreased in the former district of Kizlyarsk.

at all. Starvation then began and the weaker deer began to fall.." It is characteristic that both of the cases described are correlated with regions having a very deep snow cover. (The average maximum of the lower Pechora is 70-80 cm and 80-100 cm in Kamchatka).

Even with a snow cover of 50-60 cm in depth, deer can still obtain food for themselves, which is the reason that starvation because of excessive snow is so rare in other parts of the north, even when it occurs. Goncharov (1930) believed that, on Kamchatka, a snow depth of 80 cm not only retarded digging of lichen but also markedly hindered movement of the animals.

The formation of a glazed crust (gololeditsa) occurs in the fall and first half of winter in the western part of our tundras because of the invasion of warm, moist masses of Atlantic air (Vize, 1940). Gololeditsas are especially common on the islands and coast located on the western part of Barents Sea on Kolguyev, Kanin, Vaigach and Novaya Zemlya. On Vaigach they occur almost every year, resulting in the domestic deer being driven in the fall through the Yugorski Shar onto the mainland by swimming. To the east from the Kara Sea, glazed crusts occur more rarely, but were observed even on the New Siberian Islands, where the influence of the Atlantic and Pacific Oceans is lessened. At the beginning of 1929, there occurred on Kolguyev Island one of the strongest glazed crusts, a description of which appeared in the Journal "Climate and Weather" (Barankeev, 1929). Previous to that, starvation from gololeditsas occurred on Kolguyev in 1920. Occurrences of the crust began on 3 January, and continued to the 10th of the month. The maximum thickness of the crust formed was 3.1 cm. On the night of 6 January, there was a thaw with rain. The thaw and glazed crusts caused a noticeable compaction of the snow cover, an ice crust was almost everywhere and covered about 0.6 of all the surface of the island. According to the Nenets, the reindeer ranchers, the icing of the snow was especially marked in the middle, eastern and northeastern parts of the island, where there were grazing herds of deer. The change in food-getting conditions appeared to be unfavorable to such an extent that it caused the deer to begin to starve. Almost all the deer ranches suffered. Many young and old deer died. Losses reached 35 per cent of the herds.

Wild reindeer suffer with the appearance of glazed crusts as do domestic stock. In the winter of 1917-1918, on the eastern

coast of Novaya Zemlya, there was a strong glazed crust which caused a migration of reindeer to the western side of the island, and a marked reduction in their number by 1918. Because of winter hunger, the production of young was very poor in the spring. Many females appeared barren. According to the hunter-trader, part of the deer went to search for food on the ice of the Kara Sea, where they perished (I.I. Sokolov, 1933).

In 1924, gololeditsas caused total extirpation of wild deer on the island of Novaya Sibir (Pinegin, N.V., 1932). During that particular winter, the sea around the northern islands remained open until January 1925. (Usually by October the deer have gathered at the southern coast of the islands, and leave for the mainland as soon as the ice cover appears. During normal years, by the middle of November, there are no more deer on Greater Lyakhov Island). Rain, which fell after the establishment of a snow cover, hid the earth under an iron crust with an armor of solid ice, and deer perished from exhaustion because of the unavailability of food. According to approximate counts made by the herders on the island of Novaya Sibir, four or five thousand deer perished. The plague partly encompassed the islands of Fadeev and Kotel'ny.

Autumn glazed crusts formed by frost following a rain are also disastrous for deer (Beretti, 1926). Compaction of snow by wind also does not pass without affecting them; it is hard to dig for food in the tundra, it takes much time. Therefore, winter migrations of deer are short, only the strong animals eat their fill, the reindeer live from hand to mouth. In such places as Severnaya Zemlya or Taimyr, wild deer are extremely lean by springtime (Urvantsev, 1935).

Judging by the fact that during periods with glazed crust, the number of arctic fox which are caught by the traps and snares of hunters is sharply increased, the appearance of a compact crust on the snow also hinders food-getting for this species, and is catastrophic.

Examples of die-offs of hoofed animals because of deep snow are perhaps even more frequent in forested regions than in the tundra. I will quote only a few of the indications found in our literature, Cherkasov (1867), speaking about the hoofed animals (moose, maral, roe deer, pig) of the forests of Transbaikalia in general, noted that the great changes in their numbers are connected with variations in snowiness. "The longer the succession of snowless winters, the less

marked the decrease of animals, and sometimes even an increase is noted, but one extremely snowy winter, and even worse, two in succession, and a general decrease of the animals of this region becomes evident." (Cherkasov attributes the decrease in the number of animals solely to destructive hunting with pursuit on deep snow. This idea is only partly true.)

In the report of the Sayan Sable Expedition (1921), it is mentioned that the winters of 1914 and 1915 in Sayan were unusually snowy, with a snow depth reaching more than 3.5 meters, which caused mass destruction of hoofed animals. In another place in this work, it is stated that, "... in January 1915, there was such deep snow (up to 14 chetverts, i.e. - more than two meters), that wapiti could not run away when hunted by man, and thus were caught almost immediately." Finally, there is a note that in the winter of 1915, near the Yenisey River completely exhausted roe deer appeared, which were able to be caught directly by hand.

Similar phenomena are known also for the deer of North America. For example, Hewitt (1921) tells of cases of destruction of Virginia deer (Odocoileus virginianus) and black-tailed deer (O. hemionus) in years of deep snow cover. Roe deer especially appear to lack hardiness in conditions of continuous deep snow. Dinnik (1910) and Nasimovich (1936) give a number of cases when many individuals of this species perished. The latter author believes that the European roe deer in western Caucasia suffers more and perishes easier than deer, chamois and turs.

Therefore, it is not accidental that the roe deer dies off sometimes during hard winters even in the mountains of Crimea, which have a relatively mild climate.

According to Dinnik (1910), among the hoofed animals of the mountains "when a lot of snow falls," Caucasian turs suffer very much from lack of food and are forced to feed on unusual foods: tree bark, needles and lichens. By spring they are then extremely exhausted. A winter with much snow is the most difficult time in the life of a Caucasian chamois. Weakened by hunger, chamois frequently fall prey to predators.

Pevtsov (1883), when crossing the Sailyugem Mountains into Mongolia in 1878, often found skulls of the Central Asiatic mountain

sheep in the valley of Oiger. He found, according to the local inhabitants, that "in the previous hard winters, many of these animals perished from lack of food, and those remaining alive were greatly exhausted by hunger, and they became prey of wolves." Radde (1862-1863) showed that the snowy winter of 1831 destroyed the remaining Transbaikal mountain sheep in Transbaikalia which had previously suffered persecution by man. "The destruction of such large and strong animals as argali by this winter proves that nowadays, because of various conditions in which man is completely innocent, even species of large animals can become extinct, at least locally," says Radde.

The data which Dinnik (1910) collected for many years about instances of mass destruction of Caucasian pigs are very interesting. Caucasian pigs withstand well winters of mild weather and a small amount of snow. They do not even lose weight because they can easily find food. At the beginning of January, Dinnik once found about half a pail of chewed-up acorns in the stomach of a sow. The pigs also eat many beechnuts. An entirely different situation appears in years with deep snow or intense soil freezing, when it becomes impossible to dig out roots, etc. Pigs lose weight because of the lack of food, and die off by whole herds or become the prey of wolves. "In the Teberda Valley I was told that in one such unusually strong winter in the early 80's, the pigs could hardly move and they could be killed by sticks or stabbed with knives....In the headwaters of the Laba River, there were many wild pigs (in two days of hunting in 1901, nearly 150 pigs were seen). But after that, there came a succession of years, 1902, 1903, 1904, 1906, and 1908, with complete failure of crops of the nuts of the plane tree (Platanus) and acorns, accompanied by very snowy, continuous, and hard winters. These years were a real misfortune for game and for pigs in particular. They destroyed many of them in most of Kuban' Province." Cadavers of perished pigs were often found; sometimes there were seen whole herds of about 10 exhausted pigs huddled closely together and frozen. After this destruction, pigs disappeared in many places in Western Caucasia. Nasimovich (1936, 1939) also included the pig along with the roe deer as one of those animals least able to survive the snowy winters of Western Caucasia. Instances of pigs dying-off were observed in the far east (Baikov, 1915), and in Belovyezhya Forest (Kartsov, 1903).

In a MS of a friend of mine, L.G. Kaplanov, (1941), who perished tragically, and who did excellent work on the ecology of the large mammals of Siberia and the Far East, is found some interesting information about the role of snowy winters in Sikhote-Alin' National Park. The seaward-facing slopes of Sikhote-Alin' which are within the boundaries of the National Park are characterized by winters with little snow and sometimes no snow at all. In normal years, the maximum depth of the snow cover on the western slopes is from 20-70 cm. Kaplanov wrote that 1914 was a unique winter; snow depths reached 100-150 cm, causing catastrophe in the life of many animals of Primoria. "Pigs disappeared almost entirely, and for 3 to 4 years after this great snow, those animals were extremely scarce. Only a few of the strongest adults survived, which ate their younger and weaker brothers." The stock of wapiti underwent devasting destruction by hunters who killed great numbers of the animals for their tails and embryos which they sold to the Chinese. (Tails and embryos of wapiti are used in China as materia medica). Nearly 1500 wapiti were killed near Dzhigit Bay, while in Taivaz, near Terney Bay, two hunters alone killed 200 wapiti and caught 16 bulls alive. The sharp decline in the numbers of hoofed animals caused a great starvation the following winter among the tigers and lynx, and there followed a decrease in the numbers of these carnivorous animals. In 1915, a hunter, I.G. Labetski, found several lynx dead from exhaustion in the forest. In 1915, in Terney, he took part in the killing of an adult male tiger who was completely exhausted, and whose muscles were atrophied and whose intestines were empty. The carnivore was searching traps, eating kólinskis caught in them, visiting the hunting camps and trying to catch the dogs. This tiger weighed only 70 kilograms in contrast with the normal weight of 200-250 kilograms.

Winters with much snow that are disastrous for hoofed animals occur also in the southern parts of Primoria. Yankovski (1882) described the catastrophe of 1877 and 1878 that caused a sharp decline in the stock of the roe deer, spotted deer and wapiti in the country in the south of Vladivostok. Deep snow and nast facilitated pursuit by man, dogs, wolves, and tigers. In addition, a large number of hoofed animals died from exhaustion. On the first open spots in the spring of 1878, deer and roe deer were often found dead with no signs of violence. Quite recently, in 1941, a snowy

winter was noted in Preamuria. Hunting inspector, K.G. Abramov (personal communication) has observed uninterrupted snowfalls from 19 February until March 27 in the basin of the Khor River. The unusual depth of snow cover forced moose to move from the Ayansk Fir Groves onto the burns, where snow sublimes faster, and forced wapiti into the valleys where herds of them stayed close to the river banks, which had a thin snow cover (10 cm), and fed on branches of the shore-line bushes. Moose stayed on the burns having a snow depth of 80 cm but, for wapiti, 70 cm was beyond their strength. Pigs gathered at the patches of horsetail, where cases of perishing of young animals and cannibalism were noted. Small weak animals willingly used paths made by larger pigs and thus were able to obtain food.

The example of the winter with much snow when the Persian gazelles of the steppes of Transcaucasia suffered very much has already been mentioned. In the past, when wild hoofed animals occupied the wide open flatlands of the northern steppes, they probably frequently found themselves in difficult conditions in winters with much snow. As proof of this, note that even now winter calamities sometimes still appear, which take a toll of domestic herds and wild hoofed animals.

After a long succession of winters with little snow (1930-1940) which occurred in the southeast of the European part of the USSR and in the western part of the Asiatic portion of the Union, there followed a number of winters which were rich in precipitation. During the previously mentioned dry period, lakes in Transvolga, northern Kazakhstan, and the southern part of western Siberia dried up, the levels of many rivers were lowered, and the level of the Caspian Sea dropped unusually low. The first winter with rich precipitation (1940-1941) was noted in the eastern part of Bashkiria and northern Kazakhstan (in Kustanai, Pavlodar, Severo-Kazakhstan, Akmolinsk, and Karaganda Oblasti). Raging snowstorms began in Kazakhstan in October, and in some cases did not cease for 5-8 days. The edges of clumps of birches and pine groves in the steppes were heaped with drifts to a height of 6 meters. In the center of the clumps, the depth of cover reached 2.5 meters. Pond basins, covered with cane, were leveled off even with the steppe. Roe deer, which during the period of snowless winters had markedly increased in numbers in the southern Urals and in the forest-steppes of Kazakhstan,

were forced to go into the steppes where they became the prey of wolves and even dogs. In the region of Bashkiria National Park, where the snow depth reached 100-120 cm, the stock of roe deer was reduced by about 70 per cent during this winter (personal communication from S.V. Kirikov). Grey Partridge, European hares, and among carnivores, wolves, foxes, and corsacs, had a hard time obtaining food on the steppes. Many cases of the appearance of carnivores in the suburbs of settlements and cities were noted; there were reports of migrations of corsacs into the southern semi-desert regions (Materials of the Corresponding Net of Kazakhstan Biological Stations for Game Management, communicated by A.A. Sludski). For the first time after the long period of dry years, there was plenty of water in the Turgai-Sarysu and Ural Rivers, and the steppe lakes were filled up after the winter of 1940-1941. (Thus on the basis of such fluctuations of the levels of reservoirs, one is enabled to judge the degree of unfavorability of the winters for species of chionophobes and chioneuphores of the steppe and the steppe-forest zone). In the memorable winter of 1941-42 unusual snow falls were noted, which encompassed the great territory of the basins of the Volga, Ural, and Emba, reached Syr-Dar'ya, and even Murgaba. (In the spring of 1942, there was an unusually high flood on the Ural and the Volga, and the level of the Caspian Sea began to rise). Much snow occurred even in the semi-desert regions of western Kazakhstan, where the saigas and Persian gazelles suffered in early 1942. According to a communication by hunting inspector I.L. Efimov of Gur'yev Oblast' the saigas and gazelles came out toward the end of February 1942 onto the lower stream of the Ural River, from the deep regions of the semi-desert, from the outskirts of Ust'Urt on the northeastern shore of the Caspian Sea, and probably from the Volga-Ural sands. Gazelles came in groups of 500-600 head. Part of the antelope stayed 5-6 km from Gur'yev. About 15-20 March, the fishermen of Gur'yev, who were busy with their under-ice catch on the North Caspian Sea met saigas on the ice above water depths of 6-8 meters. Hungry saigas picked up hay near the fisherman's camp sites on the ice. (The saigas were probably chased onto the ice by the wolves, because the remains of mangled animals were found in several places. On the steppes, whole herds of 20-30 animals were cut down by wolves.) Towards the end of winter nast appeared, and fur on the wounded feet of the antelopes was worn completely away. In some places in the deep snow, saigas packed

trails and refused to leave them even if persecuted. Because of the lack of food, they had little fat, especially in old males and female calves. By the 15th of March, the first open spots appeared on the hills, and the surviving animals began to migrate away from the seaboard region.

In the same winter, the roe deer which had migrated from the southern border of the forest-steppe of Kazakhstan reached the railroad line between Orenburg* and Tashkent. Hares in the pre-Caspian semi-desert apparently also suffered in this winter, because in the fall of 1942, in the extensive territory of the lower Emba, A.A. Sludski (personal communication) could not find either the animals themselves or any fresh sign. There were heavy snowfalls in Kyzylkums and Kara-kums this winter. ((Kums = deserts)). In southern Turkmenia, in the summer of 1942, I encountered signs of the adverse influence of the winter of 1941-1942. In the valley of the Murgaba River, between Stations Sandykachi and Imambaba, where the winter is usually snowless, a deep snow cover stayed for four days. The local pheasants (Murgabian subspecies), after four days of hunger were weakened so much that the Turkmen found them easily in the bushes and killed them with sticks; the number of pheasants in the summer of 1942 appeared to be low.

In the days before the Kazakhs knew how to make hay and to have food stores, winter hunger and destruction of cattle because of snowy conditions in Kazakhstan was a usual occurrence, and was repeated periodically.

"One of the most difficult years in this respect was the year 1880, when 819,775 head of cattle perished in Akmolinsk Province, and 1,528,679 head perished in Turgai (70,000 of these were camels and 313,000 were horses). In 1884, in the former province of Semipalatinsk 412,000 head perished, and in Akmolinsk Province, 364,054 head perished in 1891-1892. Also, in Ural'sk Province, quite a number of cattle perished from snowstorms and ice crusts (Russia, Vol. 17, 1903). The Kazakhs thought that such calamitous years coincided with their "koyan" (Year of the Hare"), and were repeated every 10-12 years.

It is interesting to compare the following facts with these data. At the Irbit Fair where fur from the Urals, western Siberia,

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*Now known as Chkalov.

and today's northern Kazakhstan, including the former provinces of Turgai and Akmolinsk is received, the import of fox skins was very great in 1881 (600,000) pieces, and in 1889-91 (over 700-750,000 pieces, according to Turkin, 1902). As is known, fox, corsac, and arctic fox readily go into traps and snares when there is much snow, and when nast occurs, since it hinders their pursuit of rodents. Therefore, the successful catch of fox skins in the years of destruction (1880 and 1891-92), which coincides with the presence of a great number of foxes, is a quite regular occurrence. For us, even more interesting is the fact that by the next year after destruction, the catch of foxes in the Turgai and Akmolinsk steppes dropped sharply (in 1882 and 1883, 250-275,000 skins were shipped into Irbit, about 525,000 pieces in 1892-1893). Quite possibly we have here an example of the fact that adverse snow conditions markedly affect the survival and death of steppe foxes. I have no doubt that in the next few years it would be possible to collect more exact data which would allow the correlation described here to be explained in detail.

Among birds there are several species that are particularly sensitive to snow conditions. From the previous statement, it follows the first among the species to suffer are those which obtain their food on the ground. Grey partridge, a species ill-adapted to a snow cover, which hinders its obtaining food, often perishes in winters with much snow, which happen in different parts of its range. Numerous examples of this are scattered in the periodical literature of hunting, and in scientific publications. I collected a part of them in my work "Flunctuations in the numbers of economically important animals" (1935), from which I will quote an appropriate chapter, with some changes. Filatov (1915) wrote that after the winter of 1907-1908, partridge became scarce in the former district of Kaluga, where broods were not rare in the summers of 1906 and 1907. For the three years following there were none of them. The hard winter of 1907-1908 was reflected in a similar manner also on the partridge of the former Suroga District of Chernigov Province. The author does not say how the severity of the winter was expressed but from the work of Shenrok (1926), we know that in the early part of 1908, there was an unusually deep snow cover "in middle Russia", i.e. on the Oka and on the upper stream of the Volga, Dnieper, and Don Rivers. From two

separated points in this territory, there is information about deaths of grey partridge and, without doubt, the entire region outlined by Shenrok suffered in a similar manner. Shnitnikov (1913), noticed that during the years of his observations (the first decade of the 20th century) in the southern part of the former province of Minsk, there were eight snowless winters, which resulted in a marked increase in the numbers of grey partridge. He pointed out that snowy winters are disastrous for our birds, even under the conditions in Belorussiya with its generally very mild winters.

Similar indications are found in the works of Lorenz and Polyakov (1924) for Moscow Oblast', Grave (1926) for Smolensk Oblast', Sushkin (1908) for middle Kazakhstan, and a number of authors for the Ukraine. I personally observed this phenomenon in the central part of Gor'ki Oblast'. Dinnik repeatedly observed die-offs of grey partridge because of lack of food caused by snowfalls in northern Caucasia. Even the winters of the Crimean steppes and foothills are not always equally favourable for grey partridge. I.I. Puzanov (1932), says that here also partridge suffer greatly in hard winters. They disappeared after the hard winters of 1874-1875, 1878-1879, 1910-1911, and 1928-1929.

Finally, cases of grey partridge perishing in snowy winters are not rare in Germany, where Naumann had already long ago noted that it was not cold, but snow, and especially the appearance of nast, that was the essential factor which caused die-offs of these birds in winter. A marked decrease of partridge was noted in Germany in the winter of 1907-1908, 1908-1909, and 1909-1910, and, following that, during the years of the first World War.

The above noted winters were also inconvenient in Germany for the European hare, the number of which markedly diminished also. It is interesting that with us, also, in the snowy winters of 1923-1924, 1928-1929, which appeared to be fatal for partridge, a mass die-off of European hare was noted in Crimea and in the Ukraine. Grey partridge as well as European hares are linked in their feeding habits to grassy vegetation, which becomes almost unavailable for them with a fall of deep snow.

Rock partridge (Alectoris graeca) being a mountain species, is theoretically supposed to suffer less from snow because it is easier for it to find bare spots. However, in southern Kazakhstan, according to Shnitnikov (1934), "In an extremely hard and snowy winter (for example, the winters of 1918-1919 and 1929-1930), rock partridge begin to search for food on farmsteads and finally perish from hunger in great numbers when snow covers all their pastures in the windless places. Sometimes entire flocks have been found that starved to death." Kashkarov (1938) noted a decrease in the number of rock partridge in the Karatau Range after a fall of deep snow. According to Taverner (1934), bob-white quail (Colinus virginianus) which is a bird related to our partridge, suffers from snowy winters in Canada near the northern edge of its range.

Sedentary pheasants, which are unable to fly far, also suffer from winters with excess snow in the northern parts of their range. Dinnik (1886), speaking of northern Caucasian pheasants, noted that they are sharply diminished in numbers after hard winters, but their numbers are re-established after 2 or 3 easy years. Dinnik observed a die-off of pheasants in the winter of 1880 in Kuban (near the Cossack village of Samurskaya) and in the vicinity of Grozney. Such catastrophes have also been repeated there in recent times. In the winter of 1927-1928 pheasants perished in northern Caucasia (Hunter, no. 11, 1929). In the winter of 1924, pheasants (Talyshinski subspecies) as well as black partridge suffered in Lenkoran. The number of Syr-Dar'ya and Semirechka pheasants also varies greatly from year to year in agreement with the fluctuations in snowy winters. There is a marked decrease in the numbers of Manchurian pheasants in Primoria and Ussuri Krai after winters with increased snowiness (Hunter, no. 11, 1920). Shul'pin (1936) gives some data on such winter catastrophes. Thus in Primoria, in the summer of 1855, "The pheasants were so numerous, that they were found everywhere, but the heavy snow cover of the next winter, which covered the ground for a long time, and the continuous rains of the summer during the nesting period, led to a widespread destruction of this bird which became positively rare". The marked decrease in the number of pheasants about 1926 near the Korean border was caused by

an uninterrupted succession of snowy winters. According to the same work of Shul'pin, a fall of deep snow in Primoria caused a destruction of Ussuri quail, part of which remain here some years for wintering.

Many passerine birds which winter in regions with a mild climate perish in great numbers when a cold and snowy winter occurs. According to Elton (1927), hard winters are repeated in England at intervals of approximately 10 years (sometimes longer or shorter intervals). Such winters are characterized by low temperatures and a depth and continuousness of snow cover which is unusual for the Islands, while local birds that are not adapted to a winter regimen perish from cold and starvation. (As is known, most birds resist cold very well if there is an abundance of food). According to Elton, the destruction of a large percentage of the overwintering thrushes and titmice in England occurred in 1111, 1115, 1124, 1135, 1407, 1462, 1609, 1708, 1716, 1879. In 1407, the snow remained for four months (December to March) and "Thrushes and many thousands of smaller birds died from hunger and cold," says Elton. In one of the last hard winters (1916-1917), the mortality among small birds was very high, and many years were needed to re-establish their number. Such a winter occurred again in 1928-1929. According to the "Chronica" of Shnurrer, this list has to be enlarged by the addition of 1658.

The above cited facts attest that the factor of snowiness plays a very important role in the struggle for existence in many species of mammals and birds. By an increase in the unfavourable peculiarities of a snow cover (great depth, compactness, unusual continuity), populations of even very large and hardy animals perish. A long succession of extremely snowy winters can completely destroy the representatives of certain species in some parts of their range. The practical importance of this phenomenon is quite significant, since it concerns economically valuable animals or species helpful to agriculture.

Environmental resistance, which varies from year to year, and which is represented mostly by snow cover and low temperature in winter, plays a very important role in the periodic flunctuations in numbers of these forms. Therefore it is necessary to set up a system of widespread observations on the effect of variations

in snow conditions upon the overwintering of our mammals and birds. These facts are also of interest to zoogeography and paleontology. They lead us to an understanding of the disappearance of animals by an increase in snowiness accompanying the Glacial Period. They also explain to us why the spread of some species into regions having winters with deep snow meets with an insuperable obstacle in this great nival factor.

The National Parks, the system of game management biological stations and game management inspectors must constantly watch the snow regimen in order to take measures for the preservation of valuable species during hard winters. After catastrophic winters with much snow, it is necessary to set restrictions upon the hunting of certain species in areas where they spend the winter as well as areas where they spend the summer.

THE OVERWINTERING OF SMALL MAMMALS AND THE IMPORTANCE OF THE THERMAL PROPERTIES OF THE SNOW COVER

The peculiarities of the thermal regimen of snow cover and the surface soil under its protection were clearly formulated by Voyeikov (1889) in his excellent work "Snow Cover, its Influence on Soil, Climate, and Weather." Voyeikov says, "Snow, being a poor conductor of heat, always protects the soil from chilling as long as the temperature of the air and snow surface is lower than zero (centigrade)". The fluffier the snow, the stronger this influence; it is least when the snow is penetrated by water or converted into ice, when it has the structure of firn. In temperatures above zero, the influence of snow on the temperature of the soil is reversed. It continues also after melting because then the upper layer of soil is penetrated by cold water. Snow therefore lessens the fluctuations of temperature of the soil, both absolutely and relatively, i.e. there do not appear such low temperatures as appear without snow and the fluctuations are much slower.

The more continuous the snow cover is during the season of frosts, the greater is the warming influence of the snow, overbalancing the chilling effect, so that with a snow cover continuing more than six months and a cold winter, the temperature during the coldest

month at a depth of one meter is probably no lower than the average yearly temperature of soil surface. When other conditions are the same, the temperature of the snow surface is usually lower than that of a soil surface not covered by snow. This relation stems from the structure of the snow, from its color which increases radiation from the surface, from the inability of the snow surface to warm up above zero degrees because of its melting at this temperature, and from the fact that snow is a bad conductor of heat. The latter characteristic promotes the chilling of the surface of the snow, at the same time that it protects the deeper layers from chilling." For our purpose, it is not necessary to look further for a better, more concise and clear characterization of these peculiarities of the snow cover. We will just fill in with some figures. Lyuboslavski, who made temperature measurements near Leningrad (in Lesnoye) in 1893, a year which was characterized by extreme severity, obtained the following averages for January:

Depth below soil surface (cm)	0	20	40	80
Temperature under snow cover (C)	-1.9	+0.2	+0.8	+1.8
Temperature without snow cover (C)	-16.6	-14.1	-10.6	-3.6

Under snow the surface of the soil (where rodents and shrews usually stay for the winter) averaged 15 degrees warmer than soil without the protection of snow. On some days, the difference increased to 32 degrees. According to the observations of P.N. Koloskov, in Preamuria (Sumgin, 1927), the average daily temperature under snow cover was higher than on the surface of the snow by 18.9 degrees in January, by 13.0 degrees in February, by 7.9 degrees in March, and by 0.8 degrees in April. The data about daily minima are especially interesting. On the snow surface they sometimes reached, in January and February, -47.8 to -40.5 degrees, while at the same time under the snow they did not fall to below -19.2 to -14.9.

According to the observations of Tumanov near Leningrad, the temperature of the soil fluctuates sharply following changes in air temperature with a snow cover of 10 cm. But with a cover of 20-25 cm, the protective effect becomes important, and smooths the fluctuations of temperature (Nekrasov, P.I., 1937). When snow cover reaches this depth, voles begin to build their winter nests under the snow on the soil surface. In the central regions, the soil which was frozen in the fall, sometimes thaws from below upward to the surface under protection of snow cover because of the inflow of heat from deeper layers (Berg, 1935). Such soil conditions under a snow cover are very convenient for moles, shrews, and voles that feed on rhizomes--tundra voles (Microtus oeconomus), common vole, water vole (Arvicola terrestris).

The protective characteristics of the snow cover have very great importance in the lives of many small mammals, those species active during the whole year, as well as those that hibernate. Observations show that at the beginning of winter, when the temperature does not fall below -5 to -10 degrees, and the snow is still not deep, large numbers of tracks of voles, mice, shrews, and even moles can be found on its surface.

Later, with the increase in depth of the snow cover, and the arrival of the cold, the activity of most little animals goes on under the snow only. They only rarely come out onto its surface. With the first snowfall of 3-5 cm voles and shrews are already trying to mine it with runways, which soon crumble and expose them to view. However, even with such a snow depth, the small mammals which move in its thickness gain certain advantages. They appear less liable to be caught by owls, rough-legged hawks (Buteo lagopus), and other feathered carnivores, and are also protected from the unfavorable effect of the wind. With a snow cover of 10-15 cm, the snow runways of animals do not collapse, and serve them for the entire cold period of the year.

In the spring, shortly after the snow leaves, one can often see a complicated branching reticulum of bolsters and sausages on the surface of the soil near burrows, consisting of chewed dead leaves, mosses, lichens, and soil. Animals partly fill up some of the snow runways with this material at the time they make new ones on the soil surface or under the soil. When the snow melts with its lower compacted layer still preserved, one begins to see in it

clearly outlined, the winter runways of rodents and insectivores, which extend sometimes from the burrows in the soil for many meters in different directions (Fig. 17).

Such runways and depressions in the soil, which speak of winter activity, are, according to my observations, left by moles, water voles, common, field (Microtus agrestris), rat headed, pine (Pitymys subterraneosus), and red-backed voles, Norway lemmings, and in steppe regions, steppe lemmings (Lagurus lagurus) and common mole-voles. In the literature, there are records of subnivean activity by brown lemmings, zokors, and even muskrats, which one has to count as the largest rodent capable under some conditions of obtaining food by the use of snow runways.

Voles, under cover of snow in the winter, not only continue to obtain food near the surface of the soil (green leaves, stems, berries), and in the soil (rhizomes, tubers), but transfer their activity to those parts of the plant which are little available to them during the summer. They make runways going up and along branches and trunks of woody plants, and gnaw the young bark, buds, and catkins up to the height of the snow cover. In Murman (Kolski Bay) in 1929, I saw mountain ashes (Sorbus) which had all their branches completely skinned by field voles up to a height of 1.5 meters. Mountain ash often grows here under the protection of large boulders and rocks, beside which high drifts of snow accumulate. Under these conditions, the northern field vole most willingly spends the winter. When working at the end of May and June in Khibinys and in eastern Murman (1927-1929), I noted that the signs of winter activity of voles and lemmings (winter nests, winter burrows, gnawings, earth sausages, etc.) were found, in a great number of cases, in furrows, pot-holes, and places which were protected by ridges of stones, etc. In such places, the remains of snow were still lying at the end of May and the beginning of June. Voles probably prefer to winter in those places where the snow is deposited by the wind, where a protecting layer of snow is especially thick, and avoid places from which it is blown away. In the spring time, these wintering places become uninhabitable.

They are flooded out by melt water, and the voles evidently move away up onto higher places. I have observed this phenomenon, in not so striking a way, in central Kazakhstan in the region on the border between the steppes and the semi-deserts (station Dzhurun, 1933). Colonies of steppe lemmings, with accompanying signs of great winter digging are more often found in depressions in the relief, and in places which are covered by small bushes, (Caragana and others), in other words, where snow accumulates. Such distribution of animals is not noted in forests, where the snow cover lies equally thick. But in forest clearings, with broad-leaved undergrowth and grass, where there is more snow, and it is fluffier than in the forest, shrews and rat-headed voles winter in mass.

The activity of animals under snow is proved also by the results of snap-trapping. Part of the traps I set in the forest under thick fallen tree trunks, which are usually covered by snow so that the underside of the trunk remains a free space. Another part I set in deep snow, in "wells" which I dug down to the soil surface, where on the snow surface there were openings of ventilation holes. Rat-headed and field voles often make such holes which probably serve to ventilate the deeper parts of the burrow. The ventilators rise up steeply from the subnivean system of runways. After each fresh snow-fall, the voles clear these "windows", but very rarely come out of them. The success of the catch with traps set in snow is by no means lower than in the fall and spring when there is no snow. In some cases it is even higher, because the animals are hungry and willingly take the bait. I collected red-toothed shrews (Soricinae), voles, and from time to time, also mice, but not often. It is characteristic that on the frosty days of January or February, when over a distance of about 10 kilometers in the forest or the field, one meets only one or two trails of small mammals on the snow, ten traps set under the snow at 3-5 meter intervals will catch four or five animals. I will give an example.

On 2nd March 1935, in Shariinski District, Kostroma Oblast', I set out 14 traps under the snow in a forest meadow and spruce-fir forest, and caught 3 rat-headed voles, 1 red-backed vole, 2 common shrews, 1 lesser shrew, 7 animals altogether (besides having two traps sprung).

On the 4th of March, over a trail of 15 kilometers through the fresh-fallen snow which had stopped on the previous evening (night clear, -10 C in the morning), there were counted the prints of 3 common voles, 6 red-backed voles, and 1 shrew; (10 animals). It is characteristic that the length of the trails in each case was insignificant (one trail was 2 meters, two were 5 meters each, one was 6 meters, two were 8 meters each, three were 10 meters each, and 1 was 25 meters. Some trails were doubled, i.e. the animals returned to their holes over the same way. The average length of the trails was 9.2 meters. On the second day (5th March), over another trail with a length of 18 kilometers through a forest of varying types, there were found only the trails of 3 red-backed voles with lengths of 2 or 3 meters (previous night was quiet, cloudy, -12 C in the morning).

Consequently, the animals which were in abundance under the snow, avoided showing up on its surface even under forest conditions which protected them well from the wind (the fall of 1934 was characterized by a great increase in the number of voles).

To this peculiarity of the winter activity of rodents, it is necessary to add a description of their winter nests. Some species of voles (common, field, rat-headed, and more rarely, red-backed), lemmings, water voles and others, the total of which will of course be increased by future study, make subnivean nests on the soil surface instead of the summer subterranean nests. The winter subnivean nests appear only when the snow lies deep. At the time of the spring thaw, these nests appear to be already abandoned. Rodents move away from their subterranean nests in winter and use these. The winter nests are distinguished from subterranean ones by the remarkably greater thickness of the walls, the compactness of the structure, and the abundance of material used, which is a poor heat-conductor. (I have seen nests of common voles built entirely out of down or thistle leaflets). Apparently, because of the low conductivity of the snow surrounding the nest, and the compact walls of the latter, the conditions of overwintering on the soil surface are more suitable than those in the depths of the frozen soil which has a greater conductivity.

The number of subnivean nests exposed in the spring often appears to be very large. Probably the greater part, if not all, of the voles make subnivean nests in winter. This is of great importance in the lives of carnivores. Arctic fox, fox, polecat, ermine,

weasel, and others can get to them in their winter nests by digging through a layer of snow only. Conditions of winter hunting would be extremely difficult for many carnivores if, besides the snow, it was necessary to dig through frozen soil to get to the animals hiding in deep holes. It is primarily because of this that voles are so important in the lives of most of the small carnivores of snowy regions.

Thus the warm snow cover causes a transfer of the winter nests of rodents onto the soil surface. Together with this, the cover which is at one time hindering the obtaining of food by carnivorous quadrupeds (because of the necessity of digging through it), at the same time, facilitates them by liberating them from the necessity of having to deal with the less yeilding and often very hard soil.

The recent works of Strel'nikov (1933) and others have shown that small rodents have a quite limited ability for thermal regulation. The small body mass with relatively large radiating surface, even with the presence of a relatively deep fur cover, loses heat very fast. With a great loss of heat, the overchilled animals cannot avoid dying. In the central regions, I have frequently found voles which had gone only a relatively short distance on the surface in a temperature of -12 to -15 degrees. Common voles, which ran onto the snow to escape an ermine, which had dug into their nest, froze in a distance of 3-4 meters from their snow hole when there were strong frosts and winds. "Among all possible ecological conditions, rodents can live only under those conditions that enable them to undergo the smallest fluctuations of body temperature", says Strel'nikov. Snow cover, simply by lessening the temperature fluctuations, must play a very great role in the ecology of small mammals.

Because of the presence of food and favorable snow conditions, small rodents survive the winter so well under the snow that they do not stop breeding in the coldest months. Thus, in the middle of January, 1933, Kalabukhov and Rayevski (1935), found new-born young in a nest of steppe lemmings in the steppes of Precaucasia. Rall' (1931) found a gravid female of this species on 11 December, 1930, in the Volga-Ural sands of western Kazakhstan. I have found

new-born common voles in December of 1912, and in January, 1913, in the vicinity of Gor'ki. Finally, L.M. Tsetsevinski (1940), among materials collected on the ecology of Arctic fox of the Yamal peninsula, showed me newborn voles and Ob' lemmings obtained from the stomachs of Arctic fox caught in the winter, and young of social voles (Microtus socialis) found near Tambey Trading Post in winter, by the observer himself. Therefore even here, beyond the Arctic Circle, some rodents continue to breed under the snow in the conditions of the hard tundra winter.

The examples given above show that snow cover protects small four-footed mammals from harmful (and sometimes fatal) temperature conditions of winter. Without the presence of a snow cover, many forms would not be able to exist in regions with continuous and cold winters. Because of this, it is possible to explain why the forest and tundra regions of Europe and Asia have numerous shrews--very small mammals with relatively short fur cover, and extremely small body mass. We met in the taiga of Yakutia, near the Pole of Cold, the lesser shrew with a body weight of 3 g, and the tiny Cherski's shrew (Sorex tscherskii) which weighed about 2 g. Together with a host of common shrews (winter weight of 5 to 8 g) and masked shrews (averaging 3.5-4 g), these dwarf mammals remain active under the snow the whole winter, because not a single species of our Soricidae is known to hibernate. The tundra and taiga are also richly populated with a multitude of species of small voles. At the same time, in the central desert regions of Mongolia, with their snowless winters, there is an extremely small number of non-hibernating rodents. These are either gerbils which run very fast and collect stores of food in the fall, or the subterranean mole-voles which also store food, and small hamsters. Voles, which are dominant in our tundras, forests, and steppes, are numerous in Mongolia only in the northern snowy strip.

We are thus approaching the fact that the thermal insulating properties of snow have also succeeded in playing a large role in the history of faunas. The presence of snow has enabled the smallest mammals to exist actively in winter in regions where, without its warming influence, this group of animals would perish. In addition to this, snow allows four-legged carnivores, arctic fox,

fox, ermine, weasel, kolinski, sable, and others) to winter in these regions, and an appropriate fauna of rodents and insectivores supplies them with food.

The essential significance of the thermal insulating qualities of the snow cover is proved by the fact that winter-kill of mouse-like noxious rodents, which has been observed by farmers for a long time, is more complete the less snow which has fallen or the more frequent have been the thaws, which increase the snow's density and heat conductivity. In addition, with a shallow cover, not only four-legged, but also feathered carnivores destroy rodents more successfully. The reverse of this picture appears with a fall of heavy snow, and the absence of thaws; the fluffy unsettled snow perfectly preserves heat in the deep runways of rodents and hinders the hunting of carnivores (the feathered ones, particularly).

In the years with increased snow cover, one observes a die-off of mouse-eating owls because of a lack of food. In such winters, the decrease of the fall population of small rodents (and shrews) is not so marked, and many animals survive until spring. I will give you some examples. Based on his many years of observations, Nesterov (1917), says that "mice" (probably forest voles mainly) near Moscow, in Petrovski Forest Tract, "from time to time propagate in large numbers and cause significant damage, mostly in those winters when, because of an abundant snow cover, or because of mild weather, the soil under the snow remains unfrozen or freezes little." The winter of 1928-1929, which was characterized by much snow and hard frosts, was fatal for owls in Ukraine and Germany, while at the same time, the voles successfully overwintered under the protection of the snow, and in the spring of 1929 caused serious outbreaks in many parts of the Ukraine.

LACK OF SNOW AND THE RESULTANT PERISHING OF ANIMALS ("FREEZING OUT")

Winters of little or no snow appear from time to time in different parts of the country. They cause destruction of winter crops, deep freezing of the soil, damage to water systems, etc. Therefore, indications of them are quite frequent in the periodical press, and in agricultural literature.

According to Loske (1918) in 1899, in the former

province of Saratov, there was no snow at all on the fields, or just a little bit of it. The earth appeared as a totally ice-covered lowland. Farmers, who had already suffered from poor crops in 1898, were in complete despair because ther winter crops were mostly frozen out. In 1893, there was a very cold and dry January with little snow in the southwestern half of the Ukraine. There was also no snow, but several times gololeditsas appeared, and crops suffered greatly.

The size of the areas stricken by a lack of snow in one year or another can be quite variable, and the distribution of them over a country is very sporadic. Shenrok (1926), who worked over the mass of material from the meteorological net of the European part of the USSR, says that while some winters in some regions are distinguished by unusually deep snow cover, in other regions, there were extremely shallow snow depths during the same season. For example, in 1896, there were deep snows in the southeast and record low snows in the region of the middle Volga, and the headwaters of the northern Dvina and Kama. During the period studied by him "there was almost no year when a record thin cover, minimal for a given season, did not show up in some place."

Sometimes the areas with little snow appeared quite extensive; thus in 1904, an unusually thin cover was noted in the western half of the European part of the USSR, in 1894 and 1899 on the western and southern borderlands, in 1896 and 1900 on the northeastern part, and in 1905 in the region between the Oka and the middle Volga. Therefore, in one and the same winter, the advantages of (or suffering from) a low depth of snow cover will be offered the animals of only a part of their range, when at the same time in other parts of the range, the conditions of wintering can be diametrically opposite. Therefore, the fluctuations in snow conditions, which cause changes in survival and in the number of birds and animals etc., usually coincide over large, but at the same time relatively limited areas, which are only part of ecological zones and subzones.

In the 30-year data of Shenrok, the winters which are records for low cover have been noted in the northeast and east (in Northern Dvina, Pechora and up to Ufa-Troitsk), and had a snow cover of only 30-40 cm, and a complete absence of snow cover southwest of a line from Riga to Rostov-on-the-Don. In the intervening strip, the depth then appears to be only 10-20 cm. Near

Moscow in 1910-1911, there was only 13 cm of snow, and in a snowy winter (1897-1898), almost 7 times as much -- 85 cm (Nesterov, 1917).

How a lack of snow followed by frosts affect the freezing of the soil can been seen from the following example. The winter of 1928-1929, which is remembered by everyone, was extremely cold over the whole of Europe. In the region of Ufa-Buguruslan, the soil froze to a depth of 150-200 cm (Barsuk, 1929). It is explained by the fact that the beginning of winter had little snow. Thus, in Ufa, there was no snow at all on the first of December, on the 10th of December, it reached only 6 cm and 7 cm by the 31st of December. In Buguruslan, the corresponding figures were 0,4,14 cm; at Borovoye Forest Station 0,8,14 cm. However, according to Shenrock (1926), the average depth of cover over a period of many years at Ufa in the last third of December is usually 41 cm, and in the neighboring regions, not less than 20-25 cm.

In the winter of 1928-1929, the depth of soil freezing in the region of Kargopol' reached 45 cm, 48 cm in Vologda, 78 cm in Kirov, 124 cm in Novozybkov, and 50-80 cm in the former provinces of Kursk, Ryazansk and Ulyanovsk. In the extreme southeast at Stalingrad, frost reached 209 cm. As we can see from the above figures, over a large portion of the European part of the Union frost reached the level at which are usually found the nests and store rooms in the burrows of rodents. Food-gathering in the surface layers of the soil not protected from freezing was very difficult, especially for moles and shrews, which are forced to do a large amount of digging also in the winter. It is not by accident that information was received in the summer of 1929 from Bashkiria, where, as we have seen, the freezing was exceptionally deep and continuous, about the disappearance of moles, common hamsters, and small rodents. Hunters attributed this disappearance to "freezing out" of the animals; actually the process of dying-off was probably more complex. The decimating factor of low temperature was increased by the difficulties in obtaining food. The following year in Bashkiria, there was a markedly decreased harvest of the above-mentioned species. According to V.F. Isakov, to whom I am indebted for this information, judging from the tracks, weasel and ermine also experienced difficulties in the winter of 1928-1929, because of

the fact that it became harder to dig out rodents. Unfortunately, there is no information about the number of shrews, which should be especially reduced after such a winter. The store of mole skins, which, according to the Hunting Union of Bashkiria, was more than 53,500 skins during the season of 1927-1928, equaled only a few tens of skins in 1930 (it was not possible to obtain data for 1929).

From the adjoining regions (Sarapul District), during this same year, we have information about a die-off of black grouse. "The decrease of black grouse appears, in my opinion, to be due to the lack of snow and the hard winter," writes Blokhin (1929). "Last winter there was no snow until almost Christmas; it fell two or three times, and covered the soil with a thin layer of not more than 15 cm; then in January, and almost all of February, there occurred almost constant 40° of frost, after which the flocks of black grouse became very scarce....." The black grouse were unable to dig into the shallow snow cover and remain over-night under its protecting cover, which is a winter habit common in all snowy parts of their range. Probably many species of animals which use the insulating properties of snow for protection from low winter temperatures are in an extremely difficult situation, during such winters with little snow. It is interesting to note that the winter of 1928-1929, which had a scarcity of snow in the eastern portion of the European part of the USSR, was a winter of much snow with us in the west (for example, in the former province of Smolensk, there was recorded an "extremely heavy snow cover"). In agricultural regions, after a winter which causes a freezing-out of winter crops, the numbers of harmful rodents is usually negligible.

For the period 1931-1940, I possess figures relating to the abundance of shrews of the genus Sorex, and water shrews (Neomys fodiens) in the coniferous forests of Shariinski District of Kostroma Oblast'. Every year in the fall, in October (sometimes in winter and spring also), I conducted a count of small mammals by the method of trapping out with snap traps, setting out traps on the same lines in different types of forest. The fall catches of shrews show quite wide fluctuations in numbers of these little animals, and thus the years of abundance or dying-out of populations of these small insectivores follow each other without any regularity, but in rapid sequence. In Table 4 are given data on "appearance" of shrews, and average number caught per hundred trap-nights. Appearance is calculated by the proportion of trap lines having shrews in their catch, relative to the total number of trap lines. These figures reflect peculiarities

of the distribution of shrews over the forested area. The higher the number of shrews, the wider their distribution over the forest, and the more diverse habitats in which they can be found. In the fall of 1936, shrews were caught on 81.8 per cent of our sampling lines, that is, they were found in practically every type of forest and forest meadow. On the contrary, in the fall of 1939, the places inhabited by shrews represented widely separated islands scattered through wide regions completely lacking in these animals (abundance of 8.3 per cent). This low figure corresponded to a very low abundance of shrews in October 1939. For 700 trap-nights, I caught only two red-toothed shrews which made 0.28 per 100 trap-nights. This figure is especially striking when it is compared with the results of the fall count of the preceding year, which gave a record catch of shrews: 75 specimens in 662 trap-nights, or 11.2 per 100 trap-nights. On the basis of these data, during one year the number of shrews was reduced by a factor of 39. (Actually, the reduction was even greater, because the method employed in calculating the population somehow lowers the abundance indicator in years of peak numbers of animals). The catastrophic die-off of shrews between October 1938 and October 1939 was caused by abnormal weather conditions during the winter of 1938-1939 (Fig. 19). Strong frosts in the late fall and winter with an almost complete lack of snow during the first half of the season, caused the perishing of small mammals and some birds. According to my observations in Shariinski District, hazel grouse, deprived of the possibility of staying overnight under the snow, suffered greatly. N.P. Lavrov (1933), noted mass die-offs of shrews, moles, voles, mice, and hedgehogs during the winter of 1938-1939 in Shilovo district of Ryazan Oblast'. I followed a similar phenomenon in the vicinity of Moscow, as did N.P. Naumov in Tula Oblast' (correlative information arrived from many parts of the central region of the Soviet Union). In Shariinski District, according to my data, the number of shrews was reduced gradually in the winter of 1938-1939, because by trapline counts in January and February 1938, the average catch was 5.62 shrews per 100 trap-nights, with an appearance of 70 per cent (against 73.3 per cent in October 1938). By the end of January in the same region, I had already noted the sharp reduction in number of hazel grouse, jays, and some small birds which suffered from frost. This comparison leads to the conclusion that it is not a direct effect of low temperature which is manifest on the shrews, but that

TABLE 4

Shrew Census in Shariinski District of Kostroma Oblast'

Years	Total Trap-Nights	Shrews Caught	Average Catch Per 100 Trap-Nights	Appearance (in per cent)
1931	285	20	7.0	50
1932	330	23	6.9	66.7
1933	600	16	2.66	53.3
1934	562	23	4.1	50
1935	826	11	1.3	56.2
1936	486	37	7.6	81.8
1937	857	10	1.2	35
1938	662	75	11.2	73
1939	700	2	0.28	8.3
1940	764	20	2.6	57.7

it is some change in the conditions of existence that is caused by frosts with a lack of snow, probably hard and complete freezing of the soil and forest litter which hinders an animal obtaining food. In Fig. 18, the lower curve represents the average number of shrews per 100 trap-nights at the fall counts and the upper, the maximum depth of snowcover during February and March for the same years at Shar'ya Station (located 40 km to the west of the place of my observations). The graph shows a very striking correlation of the number of shrews with the conditions of the preceding winter, represented by the accumulation of snow cover.

In connection with the above-noted facts about the perishing of tetraonid birds during the period of little snow, it is necessary to say a few words about their " sleeping dens". In fluffy forest snow, the hazel grouse digs a sloping tunnel, and pokes his head up from time to time, as if he were measuring the depth of the snow cover. In such cases, there remains above the den, a row of round tracks caused by the bird's head (see fig. 20). Therefore, with a sufficient depth of snow, the thickness of the ceiling above the sleeping chamber of the hazel grouse usually exceeds the length of his neck, thus the ceiling is usually more than 12-15 cm thick. With such a thickness of snow above the den, the ceiling does not collapse, even after the bird flies out. During frosty weather, hazel hens spend not more than 2 to 3 hours feeding, and the remaining 21-22 hours of the day hiding in snow dens. Black grouse, being larger birds with more efficient heat control even during extreme cold weather, spend more time in the open air than do hazel hens, but many times per day dig into the snow for a shallow depth in order to warm up (Fig. 21). As has been mentioned above, a layer of snow more than 15 cm thick is a remarkable protection against heat loss. According to the data of V.P. Teplov (MS), in Pechora National Park, the temperature in a layer of snow at the level of the sleeping dens of capercaillie did not drop below -15 C in spite of strong frosts.

Besides the direct effect upon vertebrates, lack of snow can be reflected in their ecology by its influence upon invertebrates, which appear to be their food. Data are beginning to be accumulated which tell of the important role of snow cover in overwintering conditions for eggs, caterpillars, pupae, and adult insects in litter and soil (see, for example, Mail, 1930).

In our steppes, the depth of snow cover plays an important role in the overwintering of the egg-cluster of locusts. After winters with little snow in the northern steppes, most of the eggs of these insects appear to be dead. It was thus in 1935-1936, in the Kustanai Steppes of northern Kazakhstan. Italian locusts, which were plentiful in the summer of 1935, and which left many egg clusters were extremely rare in the summer of 1936. The winter of 1935-1936 was distinguished by remarkably little snow; in February and March in many areas, there were spots still not completely covered by snow.

A low number of locusts in the summer of 1936 was markedly reflected in northern Kazakhstan in the lives of many insect-eating birds of the steppes--little bustards, rose-colored starlings (Pastor roseus), rooks, red-footed falcons (Erythropus vespertinus) and others. It is obvious that comparable conditions in a region where small insectivorous mammals occur can also have great importance for them. Thus, the character of the snow cover during the previous winter can have a marked influence, indirectly, in the ecology of many insect-eating forms the following summer. Zolotarev (1936), showed that the appearance of Asiatic locusts to the north of their usual hatching places was governed not only by summer conditions, but by snow which allowed safe overwintering of the egg clusters. "Quite probably," says he in conclusion, "in northern latitudes, it is snow cover alone in a great number of cases that is one of the most important factors determining not only the distribution, but also the abundance of insects. This primarily concerns southern species, such as the locust, for example."

It is absolutely necessary to watch all cases of snowlessness followed by frosts and deep freezing of the soil, in order to protect and correctly utilize population reserves of tetraonid birds, moles, and weasels, and also to census and predict abundance of harmful rodents and insects.

SNOW COVER IN MOUNTAINS

As is well known, "air which rises up along mountain slopes and cools from expansion, precipitates moisture. This influence appears especially marked on mountains which rise up above deserts."

(Berg, 1938). Because of this general principle, and also due to certain local causes, the amount of precipitation following a rise from the lowlands rapidly increases, but at certain limiting heights, the increase in precipitation can stop or even the reverse process can occur - a decrease in precipitation with height. The depth of snow cover, as well as its duration increases with elevation. Here even minor elevations have noticeable effect. Thus, according to the observations of Karamzin (1901), in the village of Palibino, in the former province of Buguruslan, (elevation 108 meters) snow stays an average of 149 days, and has an average maximal depth of 34 cm, while 13 km from there, at Tikhi Farmstead (elevation 239 meters), it stays 154 days (five days longer), and has a depth of 51 cm. How snow cover increases in depth in the mountains is shown by the following example: In Mysovaya, on the shores of Baikal, the average maximal depth of the snow cover is 37 cm, while on the pass through the nearest range, (Khamar-Daban), at an absolute height of 1280 meters, and higher than Mysovaya, it is 134 cm.

The location of a range at right-angles to the moisture-laden winds causes unequal precipitation of rain and snow, however. Sometimes on non-forested peaks, snow accumulates mostly on the leeward side, where it is brought by the winds. Unequal precipitation on slopes of different exposure, transportation of snow by winds, melting of snow on sunny slopes, avalanching and rolling of snow down from areas of steeper slope, all cause a very spotty distribution of snow cover in mountainous regions. Vegetation also plays an important role here, and because of the rapid change of belts of vegetation with altitude, the snow cover of each of these belts has its own peculiarities. While lowlands covered by forests have a snow cover whose maximum depth and compactness shows only minor

changes over distances of hundreds of kilometers, the other extreme occurs in mountains. The character of the snow cover often changes markedly over a distance of only a few hundred meters.

I would like to quote a description of winter conditions in the mountains of Western Caucasia (Caucasia National Park), made by Nasimovich (1936), in his interesting work. "Local winter, especially in montane regions, is distinguished by great peculiaritites and contrasts in the distribution of snow cover on mountain slopes. Slopes with southern exposure, in both forest and alpine zones never have a significant cover for long. Usually, in the first sunny days, the snow either disappears, or the snow cover thins markedly, and gets covered with an icy crust on frosty nights, and again thaws rapidly during the middle of the day. The shaded north-facing slopes of mountains show quite a different aspect. Hunters call them figuratively "zakholod" ((= cold on the other side)). Snow accumulates here in huge masses. In January and February of 1934 and 1935, in and above the zone of fir forests, the depth of snow cover was almost never less than 1 meter, and in some places, for example, at timberline, reached 1.5 to 2 meters. The contrast in snow cover of northern and southern slopes often could be observed literally by walking only a few steps, that is, by passing over the crest of the ridge.

This description of the distribution of snow cover is only schematic, and in reality, is complicated by circumstances of different kinds. "In the western regions of the Main Range, in the upper part of the forest zone, and in the alpine zone, there is approximately twice as much snow on the southern and western slopes as there is on the northen and eastern, and it is brought about by the fact that this part of the Main Range stands as a barrier to winds bringing moisture from the sea, which drop most

of their precipitation on its southern and western sides. As a result, because of the thick cloud cover common in this region, the sun cannot take care of the mass of falling snow, so the snow, in spite of southern exposure, accumulates here in huge masses. In the alpine zone near Achishkho Station in the winter of 1933-1934, the depth of snow cover in March was 336 to 420 cm. In the very snowy winter of 1931-1932 in February and March, depths of up to 600 cm were noted here. In the low regions of the western part of the range, in the passes, for example, there was observed an "overflow", a transition of deep snow over onto the northern slopes. This deep snow was brought by masses of moist air penetrating here because of an absence of big barriers in their path. "On mountain slopes with a southern exposure, the depth of snow cover to a certain extent is inversely proportional to the steepness of slope, i.e., the more gentle is the slope, the thicker is the snow cover. On the northern slopes the reverse picture is observed: the depth of the snow cover, within limits, has a tendency to be directly proportional to the steepness of slope. It is obvious that the steeper the northern slope, the less sunshine falls on it. However, with great steepness of slope, the strength of cohesion between the snow flakes is not sufficient, and part of the snow slides below. Very steep and rocky slopes are not rarely completely lacking in snow because it has been blown away by winds."

We have a similar picture of inequality of cover and variations in its distribution in the mountains of Siberia. According to the observations of L. and I. Kozhanchikov, near the Buiba Biological Station in the Ergak-targak-taiga Range (higher mountains of Sayan chain), at an altitude of nearly 1370 meters, the maximum depth of snow cover in the winter of 1921-1922 was 248 cm. The snow lay from 5 October 1921 to 17 June 1922, a period of 255 days.

At the same time, the Kozhanchikovs noted that "because of the great steepness of the upper part of the range, and because of strong winds, the snow does not stay there, and is blown into the valleys, therefore, the peaks look like they are spotted, and are not totally available for ski work." In this same Sayan mountain system according to the reports of the Expedition for the study of the Sable Industry (1921), "snow falls very unequally, reaching in some places two or three meters and nearby, in neighbouring valleys, only a few tens of centimeters...In this connection, the valley of the Gutara River is particularly interesting, not more than 3-10 cm of snow fall here, and sometimes even less, and this snow is often blown away by the wind, so that horses and cows walk on feed underfoot the whole winter, and are only rarely given supplementary feed.."

In addition, I will quote data about snow cover on the ranges of northeastern Siberia. Pilot M. Shalyganov ("How We Saved the Men of the Chelyuskin") in the notes about the flight made at the end of March (21 March), when a snow cover was nearing its annual maximum, described such a picture: "We were flying over the Koryak Range. Under us were wild peaks of the range, sometimes sharp like military tents, or sometimes sloping. Some of them were covered with shiny snow, the spurs of others appeared black, and from above, looked like trees turned over with their roots up."

Farther beyond the Maina-pyl'gin and Pal'pal Ranges, on the way to Anadyr the planes passed over tundra. "The tundra is a table covered with a white tablecloth. There are no landmarks here....," writes Shalyganov. The difference in distribution of snow cover on the flatland and in the mountains is so striking that it is easily noted from a height of hundreds of meters.

The inequality of snowiness in different parts of the mountains on slopes of varying steepness and exposure creates a condition which is very convenient for a number of species of mammals and birds that

are not adapted for life under conditions of deep snow. Migration within limits of one range or mountain spur for a short distance gives them a chance to find places with little snow suitable for overwintering. This is the explanation why some typical chionophobes, such as snow partridges, several species of which inhabit the ranges from Caucasia to the Altai, Sayan, and Pamir, or rock partridge-- found from Caucasia to the Mongolian Altai inclusive-- can exist in the mountains. Musk deer, which of all our deer is best adapted to life on steep slopes and rocks, can range far to the north in Siberia, mainly because of these same peculiarities of snow on mountain landscapes. The wide distribution of snow sheep in the ranges of eastern Siberia (even beyond the Arctic Circle), the abundance of reindeer in mountains, all these are phenomena of the same type. Finally, the abundance of a number of hoofed and carnivorous mammals that are poorly adjusted or completely unadjusted to deep snow, in the mountain regions of Caucasia, Central Asia, and southern and eastern Siberia, can all be explained by the same easy wintering pecularities of mountainous landscapes.

Large mammals and all birds have great opportunities in mountains, if one may so express oneself, for undertaking different types of migrations, both vertical and horizontal, in their search for places of easy overwintering. They find suitable places with greater ease than in lowlands, where the snow cover lies with equal depth for distances of hundreds or thousands of kilometers. In mountains, there are not rarely regions, where the snow lies with a depth measured in meters, that are absolutely unsuitable for overwintering, and are therefore, uninhabited while in the immediate neighborhood can be found areas that are well protected and have little snow, and present many conveniences for survival during the cold part of the year. It appears to me that this variety of conditions which are generally good for large mammals and birds may partially explain the great faunal richness of mountain regions in comparison with the adjacent lowlands.

I would like to give some examples of behavior of some species of hoofed mammals in mountains in relation to specific conditions of snowiness. Dinnik (1910) who knew well the fauna of Caucasia, speaks about one of his regions in this way "Absence of deer, roe deer, and pigs in almost all the forests of the headwaters of the

Rioni and its tributaries can be explained by the fact that the deepest snow falls here in the wintertime. In the mountains it comes up to the tops of trees of medium height."

In the Sayan mountain country where the snow cover, as we saw, in some places exceeds two meters, the Siberian ibex, a form which feeds the whole year around mainly on grassy plants which are difficult to obtain in winter from under the snow, remain on some ranges. In the Sayan, as well as on the Altai, and on other Siberian ranges, musk deer appear in great numbers, in spite of much snow. Here is how those hoofed animals are distributed over the Sayan ranges. According to Kozhanchikov, ibex occur in the region between the mouth on the Us and Talovaya River, which flows into the Yenisey on the left side, 40 km below the mouth of the River Us, and on the Us, they come up approximately to the village of Zolotaya, 60 km from the mouth of the Us. In this part of the taiga lies the Tepsel' Range, which is distinguished for its steep and naked slopes. "In general, this region has thin snow, on the cliffs there is very little of it, and even at the end of winter, the litter is not everywhere covered. Ibex in summer and winter live on these steep slopes, and only occasionally make migrations from one mountain ridge to another".

"Steep mountains covered by forest in the valley of the Yenisey River below the Big Tepsel' River, and as far down as the Poilovaya River serve as a habitat for musk deer which do not go into the taiga far away from the Yenisey, and can be found in the valleys of the Kebezha, Oya, and Amyl rivers only as a rarity." According to the Kozhanchikovs, the favorite habitat for musk deer in this region is "cliffy mountains covered on the less steep places by fir forest, and on the steep and rocky slopes by Laborador tea (Ledum), (Sorbaria sorbifolia) and acacia. On such crests, there is a jumble of cliffs that are scattered separately, or that come down in the form of ridges from the top to the foothill of the crest... On these steep slopes, musk deer spend almost the entire year, coming a little lower in summer...In spite of deep snow in December, musk deer do not sink deep, and if the snow is packed a little bit, then the musk deer sinks only for 4 to 6 cm".

In the chapter on migration of hoofed animals, we discussed how overwintering spots for moose, maral, and roe deer are distributed in the conditions of the Sayan taiga. According to Doppelmair (1926)

the complicated picture of the distribution of roe deer on the mountainous shore of Baikal corresponds in general to the complexity of winter conditions in this strongly dissected region, and in addition to this, in some places is sometimes under the influence of the huge lake-sea.

The accumulation of huge masses of snow in some spots in the mountains, which is in itself inconvenient to animals, also causes the appearance of something peculiar only to mountain regions, namely snow slides, which have a destructive influence on the vegetation of slopes and on the animals which happen to be caught by this disaster. The importance of this phenomenon in the life of our mountain fauna has still not been satisfactorily studied. Dinnik says that not a few turs "perish during avalanches, which in many places in Caucasia are not rare, and which cause terrible destructions, destroying centuries-old forests for distances of entire kilometers. Near Besingi* glacier (former district of Nal'chik), and in Digoria, this naturalist saw sticking out from the snow, the horns, bones, and legs of several turs that had been crushed by an avalanche. He also saw cadavers of chamois that had perished under snow slides, and mentions a case when 10 crushed individuals of this species were found in the Kuban part of Caucasia.

Such cases are well known to mountaineers also. Nasimovich (1936), when speaking about overwintering of hoofed animals in western Caucasia, mentions snow slides as a factor which caused destruction of animals. "In snowy years, slides not rarely occur in places where they do not occur in normal years. Thus, for example, in the winters of 1910-11, and 1931-32 slides covered chamois and deer in many regions. Regions which are always exposed to slides, as for example, the headwaters of the Urushten, are avoided by animals." In 1924, I saw the remains of a young tur which thawed out from the snow and crushed stone of the slide at Bogosski Ridge (Dagestan) (Fig. 22). The animal was completely broken and twisted along the long axis of the body. Bearded vultures (Gypaetus barbatus) and alpine jackdaws feeding at the cadaver attracted my attention to this find. In the mountain regions of Dagestan, snow slides are of common occurrence. On the way from Nukatl' Pass to Chodokolo in July, we found signs of slides by the tens. Huge,

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*Besingi = Bezengi-village and river with glacier at its head.

snowy bridges, seeded with crushed rocks, small pieces of ground firs and bushes were lying in the deep valley of the Kudaor river. The river flowed under them after it had melted its way through the snowy mass. Above each snow bridge for whole kilometers up the slope, there were bare stripes from which the slide had brushed out everything met in its way.

The destruction of animals by snow slides was noted in many places of the Main Caucasus Range, from the western part to Dagestan. The fatal effects of snow slides have been described many times in the Alps; snow slides are also known in Khibiny, Tyan-shan, Altai, Sayan, Tarbagatai, Barguzin Ranges, and others of our mountain systems.

SNOW COVER AND LIMITS OF DISTRIBUTION OF SOME TERRESTRIAL VERTEBRATES

> "The ranges of such common animals as deer, roe deer, and pigs undergo a peculiar hiatus in central Russia...Climate is not responsible for it; one has only to consider the hard winters which these animals withstand in eastern Siberia." (A. Middendorf, 1869).

The occurrence of seasonal periodic migrations and non-periodic migrations which are caused by snow cover, the phenomena of mass die-offs of animals because of falls of unusually heavy snows, or to the contrary, unusually light snows, as well as other facts described above, all speak of the important role which snow cover plays in the lives of a number of mammals and birds.

Several references have been made above to the influence that snow has on the pattern of distribution of various groups. Several examples were also given which illustrated this situation. Let us now speak of ranges and limits of distribution of some species of chionophobes and chioneuphores.

The effect of snow is particularly marked on the distribution of species of birds which get their food from the ground, and which are not capable of flying far, that is, sedentary terrestrial forms. The mammals that do not hibernate, and that obtain their food directly from the surface of the earth, or by digging in its upper layers, will be more dependent on the peculiarities of the snowy period of the year than species capable of living under the snow, or that obtain food on the branches of trees above its deep, fluffy cover. Species with small supporting surfaces on the extremities will be hindered more, when forced to move on fluffy snow, than

will those that have developed a kind of snowshoe. In consideration of all this, we will now briefly review mainly the northern limits of distribution of some groups and species of animals correlated with the peculiarities of snow cover distribution on the continents of Europe and Asia.

Distribution of deer:

Of all our deer, the reindeer is the most resistant to snow; representatives of this species are distributed in tundras and taiga regions having degrees of snowiness varying from 20 cm maximum cover to those having 100 cm or more. It is interesting to note that the main winter food of deer - lichens - in the mountains and upland tundra, covers mostly those places with the thinnest snow cover (vyduvs, winnowed ridges, and slopes, etc.), while the places occupied by snow drifts (depressions, downwind slopes, etc.) have grassy vegetation. Wintertime use of lichens as food is in itself some sort of adaptation in the fight against snowiness. As we have seen, the reindeer has quite a number of adaptations such as this.

Within the limits of the range of reindeer, one cannot find any coincidence with the limits of distribution of snow cover of a certain depth. However, the following circumstance attracts attention. From the time that Siberia became known to the Russians, and on up to the present time, the northeastern half of this country, from Taimyr to Anadyr Province, inclusively, has been characterized by the highest abundance of deer. This part of Siberia, as one can see from the map of Shostakovich, is distinguished by relatively shallow snow cover (below 60-70 cm), while large areas here have no more than 40-50 cm of snow, and even as little as 20-30 cm during the month with greatest depth of cover. These norms of snowiness are all within the capabilities of reindeer. In the European part of the Soviet Union, the Kola Peninsula was long famous for its abundance of reindeer; over most of the peninsula there does not occur any more than 40-50 cm of snow. The region of northern Transuralia is poor in this species, and this is probably because of the unusual depth of snow cover. Thus, within the range of distribution of reindeer, there occur regions which appear to be more suited for it, because of less snow, and therefore are more densely populated.

It is not difficult to perceive similar phenomena by study

of the distribution of populations of wolf, fox, and even arctic fox, within the limits of their ranges. Separate parts of the ranges in the light of differences in continuity and depth of snow cover are characterized by unequal degrees of environment resistance. The snow cover alone divides the ranges of chionophobes and chioneuphores into "regions of similar favorability" or "regions of similar environmental resistance" (Formozov, 1935), and it sometimes plays a leading role in comparison with other ecological factors.

It is quite easy now to draw the limit of distribution of moose, (Fig. 23) because there have recently been several reviews devoted to this species. I will use the work of Yurgenson (1935), adding to it some information published later by Podarevski (1936). On the Kola Peninsula, according to the old data of Pleske (1867), moose reached 68-70 degrees north latitude. Near Lake Imandra (Sangel'ski Rectory, Uge-ioki, Tana-el'v), they are numerous even now. Near Onezhski Bay on the White Sea, moose come down to the shore line while west of the northern Dvina and Mezen' Rivers, they are known from the basin of the Peza River. In Pechora and the northern Urals, the limit of distribution dips sharply to the south. In the basin of the upper Vychegda River, they are found in significant numbers only on the Nem River, being present on the tributaries of the Ilych River - Pal'ya and Egralyaga. The limit of permanent residence of moose (not of summer invasions) passes here near 60 degrees north latitude, moose are found also beyond the Urals, in the northern part of Tobol'sk. The limit of range then runs to the headwaters of the Vakh River and toward the mouth of the Sym River on the Yenisey, that is, going below 60 degrees north latitude. From here, the northern limit of moose turns sharply to the northeast, crosses the 62nd parallel, heads toward the lower stream of the Taimura River, farther northwest toward the right side of the Kochechuma River where near 66 degrees north latitude it turns sharply to the northwest toward the headwaters of the Kureika River and then the Kheta River. After crossing 70 degrees north latitude, the limit again turns to the northeast.* As Podarevski correctly noted, the northern limit of distribution of moose, in the basin of the Yenisey, goes exactly between the iso-

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*According to Middendorf (1869) "In Taimyr Province, it is distributed up to the region of krummholz, on the border of forest vegetation (71-72 degrees)." Later, it was extirpated there.

lines of average maximum depth of snow cover of 80 and 90 cm (as they are shown on the map of Shostakovich).

Near the borders of eastern Siberia and Yakutia, moose in this way approach 70-71 degrees north latitude (within historic times they came as far as 72 degrees), penetrating even beyond the limits of forest-tundra. On the Lena, they are known up to the mouth of the Dzherdzhin River (almost to 68 degrees north latitude).* On the Yana--up to Verkhoyansk; in the basin of the Kolyma--are common along the Omolon River down to its mouth. Here the northern limit of moose goes along the 69th parallel, and coincides, with the limit of forest vegetation. But Wrangel noted moose even farther north than this, up to the shore of the Arctic Ocean itself (Cape Baranov, near 70 degrees). In the extreme northeast, moose are known from the headwaters of the Little and Big Anyui and the upper stream of the Anadyr (Belopopol'sky, 1932). ((interesting note - the phonic "anniu" means "snow" in the Eskimo dialect of northwestern Alaska.)) Here the borderline turns sharply to the south and southwest. How it runs along the Okhotsk shore is unfortunately not known in detail even yet. Probably moose do not come down to the shore, but stay in the inner parts of the country under the protection of the coastal ranges. In the vicinity of the Uda River they are common, and according to my observations (1928), are numerous in the lower reaches of the Amur (Lake Kizi). Thus, on the northern border of the range of moose, we see quite a depression, encompassing part of the basin of the Pechora, the northern Urals, the lower stream of the Ob', and part of the middle and lower stream of the Yenisey. If in the west (Kola Peninsula), and in the east (Siberia east of the Yenisey and Yakutia), the location of the northern limit of moose coincides in general with the forest limit, then in the region just described this agreement is sharply disturbed. The limit is depressed toward the south retreating to the south and flanking around the snowy region between the Pechora and the Yenisey. An average depth of snow cover of more than 90 cm appears to be a probable factor limiting the distribution of even moose, which is a typical chioneuphore or snow-resisting species. To summarize, the great forested region of the northern Urals, the lower Ob' and the Yenisey appear to be entirely unsuitable for moose. It appears to me that it would be expedient to separate,

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*On Atlas Mira spelled Dzhardzhan and located at 68° 40' N.

in analogy with the cold Pole, a center or "Pole" of maximum snowiness under flatland conditions, which would probably occur somewhere within the limits of the area just outlined.

It is characteristic that there are no moose in snowy Kamchatka. Depressions of range limits, similar to that characteristic of moose in Preuralia and Transuralia, are often readily explained by zoogeographers as being influenced by the glacial period. As we see in our example, the shape of northern range limits is entirely dependent, not on historical, but on comtemporary ecological factors, which at the same time have a great deal in common with factors acting during glacial times. It is interesting to note that moose used to reach their extreme northern limit, attaining the shoreline of the Arctic sea (near Cape Baranov) and crossing the 70th parallel in the watershed of the Yenisey and Lena, in that part of northern Asia which is distinguished by extremely cold winter, but at the same time by extremely shallow snow. The importance of the temperature factor as an element of climate determining the distribution of moose retreats to second place in comparison with the factor of snowiness.*

The northern limit of distribution of forest noble deer is also very peculiar. The increased hunting of those animals has led to a complete extirpation of them in some parts of their range, making difficult a clear definition of their former natural limits. While not pretending to great detail and exact outlines in this sketch, we will clarify peculiarities of the northern borders of distribution of this group. In the west, the European deer came up in historic times, to the southern part of the Scandinavian peninsula; from here, its northern border retreated toward the southeast to the mountain forests of Crimea (Middendorf). In this part of its range, the extirpation of deer occurred so long ago, that it is difficult now to establish the exact borderline. It can be mentioned only that as long ago as the time of Gerberstein, deer were abundant in Lithuania, and that Gueldenstaedt (1787-1791, Vol. 3) met deer from time to time on the shores of the Dnieper itself - near the former city of Yelisavetgrad on the Mius River, and Lubny on the Sula River, in the former Poltava Province. In the 11th through 15th centuries, deer occurred in the region of Kursk (Ptushenko, 1937), and according to the data of M. Bronevski (Description of Crimea, 16th Century), Jean

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*Professor Formozov has requested that we bring attention to recent changes in the limits of distribution of moose (Alces alces). Within the last 10 years moose have spread throughout the northern taiga of the U.S.S.R. Thus it appears that snow covers of thicknesses occurring today in the region are not significant factors in determining the northern limit of distribution of this species.

de Luc (Description of Perekopski and Nogaiski Tartars....), Boplan (Description of Ukraine, first half of the 17th century), there were many deer "on the steppes of the Ukraine" and in the territory of the Nogaiski Tartars who lived on the coast of the Sea of Azov up to Cherkasskoye; in the steppes near Ochakov and Perekop. Pallas (Travels... Vol. 1), mentions vaguely a Deer Creek near Dubovka (on the Volga River), called so apparently because of the remains of deer repeatedly found there, and more definitely about the Kalmyks hunting Caucasian deer in winter "on the edge of the steppe."

During the time of Middendorf, the maral still occurred in Transuralia (in the region known today as Sverdlovsk), and the author mentioned antlers seen by him that came from local, not outside, animals. Near Ufa (that is, near 55 degrees north latitude), some noble deer occurred together with reindeer in the time of Pallas. During the time of Middendorf, deer still occurred on Mt. Iremel'. Furthermore, Pallas mentions deer (probably maral) which occurred in great numbers, along with moose, near Lake Kopchi, in the forest-steppe between Ishim and Tobol Rivers, and about records of occurrence of deer near the large village of Kurtamysh, where "they are coming from the Kirgiz Steppe." Finally, Middendorf, during his travels into Barabinsk steppe, was told at that place that maral occurred there 25 years previously. Middendorf assumed, and rightly so, that the distribution of deer was continuous from the Urals, through the forest-steppe, to the range of this species in Altai. Support can be found in Rychkov (1762); "Maral are steppe animals, and are similar to moose in everything but size. On the Siberian side, they are found in the mountains where the Kirgiz-Kaisaks shoot enough of them to use them for food." Karelin found, in the Mugodzhary Mts., in spots where forest islands persisted until quite recently, quite fresh antlers of maral. Levshin (1832), Sedel'nikov and Borodin (1903), after noticing the Kazakh names for some forested mountains (Maral-tyube, Buguly) thought the maral occurred not so long ago in the former provinces of Akmolinsk, Karkaralinsk and Ust'-Kamenogorsk.

Furthermore, in the inventory of places suitable for settlement, which was compiled in 1748 by Ensign of Geodesy Pimen Startsev, there is noted the fact that "near the river Aley, where the fir forest of Irtysh ended (near the contemporary village of Lokot')...marals, moose, roe deer, and pigs occur." I have been unable to establish yet how far north maral extended here. Its limit in fairly recent

times has been along a line from Barnaul to Achinsk to Kansk to Krasnoyarsk, and farther toward Verkholensk in northern Prebaikalia (Turkin and Satunin, 1902). For the region of the Eastern Siberian provinces, we have a new survey of the distribution of maral compiled by Podarevski (1936), in whose opinion the limit of distribution has changed little here during historic times. From the junction of the rivers Mendel' and Ket', the northern limit of maral extends to the confluence of the Angara and the Yenisey, then along the left bank of the Angara to the Uda River near the villages of Vydrino and Berezovaya where it crosses the 56th parallel, and heads to the bend of the Lena River in its headwaters (near the mouth of the Chanchur River). Here the range of maral encompasses the mountains of Prebaikalia, which lie near the northern end of the lake, and the limit then goes toward the watershed between the tributaries of the Vitim and Lena (across the headwaters of the Big Minya River), from here to the headwaters of Mama River, right and left Mamakan, farther to the southern end of Nichaka Lake*, and upper stream of the Chara River below 58 degrees north latitude. Everywhere in eastern Siberia, "the limit of distribution of deer approximates very closely the limit of roe deer, from time to time interweaving with it, and sometimes lying almost exactly along it". (Podarevski).

Farther to the east, the limit of maral goes near the foothills and partially along the southern slopes of the Stanovoy Range (Gassovski, 1927). Here maral are found on the tributaries of the Ol'doi River up to 54° 46' north latitude.

Middendorf thought that the northern limit of deer in the Stanovoy Range was 55 degrees. From there the limit of wapiti has to be drawn to the headwaters of the Bureya River, where the occurrence of this species has been verified by Middendorf, and where this form persists even now, according to the data of Afanasiev (1934). In this part of northern Preamuria the wapiti according to Afanasiev extends beyond the borderlines of the range of roe deer. Deer occur on the upper tributaries of the Amgun' where roe deer do not, along the Bureya they also go higher than roe deer, still occurring in the middle stream of the Left Bureya River. They also occur on the entire upper stream of the Zeya, from

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*Probably Nechotka L. of Atlas Mira.

which they penetrate to the headwaters of the Uda River. Further, the borderline turns sharply to the south, crosses the Amur River above the village of Mariinskoye, and retreating from the sea coast, goes southward along Sikhote-Alin'. In the coastal belt, wapiti are still lacking near Kop' and Botcha (Emel'yanov, 1927) although the limit of this species was extended to the coast by Shrenk (1898) and Radde (1862), somewhat to the south of De-Kastri Bay, below 51 degrees north latitude.

Thus, the northern borderline of forest "noble" deer, (which are no more than the subspecies of one species) has an irregular outline. While penetrating far to the north in the region of the Scandinavian peninsula (within historic times up to central Sweden, and along the coastline to central Norway, that is, up to 61 or 62 degrees north latitude), noble deer probably flanked the central region of the European part of the USSR, so that the border here was sharply lowered to the south.* Judging from the fact that the range of roe deer extended without interruption along the southern border of the forests and along the forest-steppe from Poland and the Ukraine to the Urals, the distribution of European deer in this region was probably similar. In Transuralia it again penetrated quite far to the north (to the latitude of Sverdlovsk and the northern borders of the Kazakh forest-steppe, that is, to 56 or 57 degrees north latitude). Apparently in Barabinsk Steppe, the borderline was pushed somehow to the south, because the data available speak of maral as coming here only occasionally. But farther to the east, in the basin of the Yenisey, the northern frontier of the range again gives an outward curve to the north, followed by a depression to the south in Prebaikalia, and then, in the south of Yakutia, pushing out again to the 58th parallel, which is farther north than at any other place in Siberia. As in the other cases analyzed, it is typical that this agrees with the mountainous part of eastern Siberia, which has very cold winters, but a low amount of winter precipitation. The northern limit of range of true deer coincides neither with the borders of lowlands and mountainous countries, nor with landscape zones and forest types. It is always located so that it never

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*Middendorf correctly noted the presence of the southward depression of the ranges of hoofed animals in the central region, but thought that "climate was not responsible for it". As we now see, the factor is not climate in general, but snow cover.

crosses the line of average annual maximum depth of snow cover of 40-50 cm. Maral are especially abundant wherever no more than 20-30 cm of snow accumulates during the winter (Transbaikalia, Ussuri Krai, northern Mongolia, etc.)

The distribution of roe deer has been studied in a number of works in recent years, so that it is not at all difficult to compile the outlines of its range (Fig. 24). However, for the European part of the USSR, the authors (Lavrov, 1929, Dement'ev 1934, Bobrinski, 1944), did not take into consideration the historical data. Using the latter, it is necessary to introduce some corrections to the map compiled by Bobrinski, which can then be taken as a basis for our survey. On the Scandinavian peninsula, roe deer extend up to central Sweden (Miller, 1912), their limit then extends to the southern coast of Finnish Bay and Lake Ladoga (Middendorf, 1869). "From here, the northward limit, similar to the limit of deer, is depressed along the meridian to the south, so that roe deer goes farther to the east than do deer. For example, in the region of the Dnieper River, it stretches almost to Orel and Kharkov Province," writes Middendorf. According to my data, during the years 1920-1940, roe deer have been noted to the east of a line between Tikhvin, Bezhetsk, Yaroslavl', Pereslavl'-Zalesski, Balakhna (Gor'ki Oblast'), but all this was invasion by small herds. The borderline of continuous distribution of roe deer was much farther west. At the end of the 19th century, roe deer occurred in the southwestern part of Gor'ki Oblast' in the former district of Gorbatovsk (Materials for the evaluation of lands of Nizhnegorodsk Province, vol. 7, 1885). According to Guldenstadt (1787), it occurred up to Baturin and Glukhov, and was found by him near Yelisavetgrad and on the Mius. During the time of Middendorf, large numbers of roe deer were found on the left bank of the Dnieper in the vicinity of Kiev. According to Chernaya (1850), the roe deer was not rare in Kharkov Province. According to Kessler (1850) it occurred in Poltava Province. In former Voronezh Province, it occurred in old times, but later, during the time of N.A. Severtsov (1885), it was already extirpated there.

The occurrence of roe deer in the basin of the Don in the 14th Century is supported by notes on the abundance of bucks on the banks of the Don made in 1338, during the travels of the Metropolitan Pimen into Tsar'grad. According to Ognev and Vorob'ev (1924), roe deer were common in 1920-1922 in Usman' Forest of Voronezh Province, and were also found in Shipov, and Khrenovsk Forest. To the southeast

of here, roe deer were noted in Novokhopersky Forest in 1918. Probably this region, which was inhabited by roe deer in the forest steppes, was connected on the east with the part of its range west of the Volga, since we have a number of authentic records from here made by Pallas, who travelled here in 1768. These also have an ecological interest, so I will quote them in their entirety. Roe deer stayed here on the mountainous right bank, as well as on the left bank east of the Volga. Beyond the Samara (region between Alekseyevskoe and Borskoye), Pallas made these notes: "These mountainous countries are especially liked by bucks because all snow is blown away from the naked hills by the wind, and they can easily find food for themselves. The Kazakhs kill large numbers of bucks, as well as moose, every year in these places, and usually start to hunt in the month of March, because at that time, the sun has enough strength to convert the surface of the snow into a crust on which one can easily run on skis... The above mentioned animals, on the contrary, break through, and therefore are greatly hindered in running. At such times, they look for tracks, drive them into valleys in which the snow is often several feet deep, and shoot them there, or hunting dogs bring the animal to bay while the hunter, after catching up, kills it with a rogatina ((6 or 8 feet shaft with a forked spearhead)). Bucks in particular injure their feet while running, so that they are soon unable to run any farther." It is principally such barbarian hunting on nast that is responsible for such a great discontinuity in the range of the roe deer.

In the first quarter of the 19th century, roe deer still occurred in the southern part of the former district of Sengileyevsky of Simbirsky Province, on the forest tracts near the village of Dvoryanskoye (Bogdanov, 1871). In his description of the region along the Sok, Kinel', and Samara, Pallas again speaks of the presence of a great number of bucks which are of "an entirely different kind."* And adds: "It occurs in brush, in fields, and in mountains beyond the Volga."

In Transuralia, according to Sabaneev (1874), roe deer reached 65°15' north latitude, and their eastern limit was described by Middendorf in the following manner: "In Barabinsk Steppe, the northward limit of Siberian roe deer is depressed somehow to the south, while

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*According to the modern concept, this is the Siberian sub-species of roe deer.

on the Yenisey, it goes beyond 58 degrees, and still farther east, it coincides with the polar limit of deer (maral - A.F.), and in some places, the river Uda for example, crosses it to the north....Roe deer also come closer to the mouth of the Amur than do deer, crossing the river above Nikolayev, and reaching the sea near the Bay of De-Kastri (51 degrees north latitude)". According to the data collected by me in 1928, the roe deer is very rare near De-Kastri and Lake Kizi, and, according to new data (Afanasiev, 1934), roe deer do not occur in the headwaters of the Amgun' River and on the eastern side of Dusse-alin' Range. Along the Bureya River, roe deer range to scarcely above the mouth of the Tas-Khandavyt River. "It is quite possible that the depth of snow cover here plays a role which is lesser on the western, and greater on the eastern slopes of the range," writes Afanasiev. Probably the limit of continuous abundance of roe deer in this region has to be drawn much farther to the southwest than was indicated by Shrenk, Radde, and Middendorf.

According to the data of Lavrov (1920), the details of the location of the northern borderline may be described as follows: In Transuralia, the roe deer is common in the southern districts of the former province of Irbit (Blagoveshchenskoye, Tavdai, Turinsk, and others)., and in Dubrovnoye and Chernakovsky districts of the former province of Tobol'sk.* They stay in the southwestern part of the former province of Tarsk, and in Omsk Oblast', and southeastward from here, they occurred until quite recently in Rubtsovsk district, and some districts of the former province of Barnaul.

In the eastern Siberian state (Podarevski, 1936), the northern border crosses the Yenisey near 57 degrees, then goes northward to almost 58 degrees, extending along the river Shuna to approximately N((izhne)) Ilimsk. From here, it turns southward to the headwaters of the Lena and Kirenga, then again to the north, circling the northern end of Baikal, and going northeastward, reaches the lower stream of the Chara and Olekma rivers in southern Yakutia, at approximately 60 degrees north latitude. Still farther to the east, it penetrates northward even beyond the 60th parallel, but then the borderline turns sharply south-eastward to the basin of the Uda River, and the lower stream of the

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*Single roe deer come probably from beyond the Urals into Pechoro-Ilychski National Park to the mouth of the Ilych River, where they were observed in 1936 and 1937, and where I saw tracks in 1940. As a rule, these deer do not survive the winter.

Amur River. Roe deer reach the Pacific Coast only in the southern half of Primoria, and near the rivers Kop' and Botcha, for example, or they may be absent entirely or extremely rare.

In this way, the northern boundary of roe deer gives several large protrusions to the north in a manner similar to the range of forest deer. One protrusion on the Scandinavian peninsula (up to 58-60 degrees), a second on the eastern slope of the Urals, and in Transuralia (up to 64 degrees north latitude), and finally a wide tongue encompassing the south of Yakutia up to 60 degrees north latitude. This species also goes especially far north, not in the European part of the USSR, with its relatively mild winter, but in Transuralia and eastern Siberia, where the wintry part of the year is cold, but with little snow. The mountain landscape of eastern Siberia possibly created conditions that are especially suitable for this species to move along the axis of the extensive eastern Siberian region of little snow. In the northern part of its range, vegetation and temperature regimen probably affect the limit of distribution of roe deer only secondarily, in comparison with the effect of snow cover. An average maximum depth of snow cover of 50 cm is the limit of distribution of this species in the northern part of Europe, as well as the Asiatic part of the country.

Roe deer are particularly numerous in regions where no more than 10-20 cm of snow fall (forest-steppe of Transbaikalia, Ussuri Krai, Preamuria, etc.) In those parts of its range where 70-100 cm or more of snow fall on the mountains, the roe deer is, as a rule, lacking (region near Lake Baikal, upper zone of Sayan, etc.).

Spotted deer appear to be more sensitive to the winter regimen than are roe deer, and occur only in that part of the Manchurian taiga where not more than 10-20 cm of snow falls. Therefore, in our country, they never went farther north than the southern half of Primoria and Ussuri Krai. In contrast to them, the musk deer, which possesses relatively larger supporting surfaces on its hooves, and a method of running that reminds one of a hare, comes quite far into the snowy region of the taiga, but it is restricted to steep rocky slopes, where snow accumulates less. Moreover, in winter, the musk deer beats down paths for itself. Its distribution to the north in eastern Siberia coincides in general with the outlines of the wide strip of

terriotry having little snow (40-50 cm or less), which is characteristic of this region.

Distribution of Pig:

In our country, the pig is a relic of the Tertiary fauna that is preserved only under especially favorable conditions. A heavy animal, low on its feet, adapted to gathering its food on the surface of the earth, or to digging it out of loose soil, an omnivore in the strict meaning of the word, it thrives in cane-brakes of rivers and lakes, in broad-leaved forests teeming with acorns, beechnuts, and fruits as well as in the Siberian mountain taiga where the pine cones ccomprise its most valued food. (In addition to this, root stocks of grassy vegetation, insects, etc., also serve as food.) In the far East, the rich forest flora provides pigs with nutritive foods, among which the most important are the cones of the Korean stone pine, acorns of Mongolian Oak (Quercus mongolica) and winter horsetail (Equisetum). However, the northern limit of pigs agrees neither with the limit of broad-leaved species in the European part of the Societ Union, nor with the limit of the region abundant in cane brakes and stone pine forests in Siberia. The snow cover makes the larger part of our forest region unfit for pigs.

The range of this species has undergone marked changes during historic times, because of the complete destruction of pigs in the northern part of their range. In order to ascertain the natural borderlines of the range of this species, it is necessary to reproduce the picture of its former distribution.

In western Europe during historic times, it was distributed from Ireland and southern parts of Sweden and Norway to the Mediterranean Sea. At the present time, they are extirpated in the northern part of their range (Miller, 1912).

With us, the contemporary eastern boundary of the pig (according to Bobrinski, 1944, and personal data_, beginning near Riga, goes approximately to Velikie Luki, Vitebsk, and Briansk forests, Mogilev, and the lower stream of the Dnieper (Fig. 25). From here, they once in a while occur to the northeast. Thus, Kaplanov and Rayevski (1929) indicate that one pig was killed near the city of Ostashkov in about 1914. Stronganov (1934) mentions that a pig was killed about 1930 in the Peno district of Kalininisk Oblast', etc. I know of a case where a pig showed up near Moscow.

Several centuries ago, the distribution of pigs in the west of the European part of the USSR was more extensive than now. During the time of the Novgorodsky Principality, there were many pigs near Novgorod itself. Dyubyuk (1920), says that in the description of the Kostroma vicarage, which was compiled in 1792, the occurrence of wild pigs was mentioned. Dyubyuk, in turn, adds that remains of pigs are known from bone-carrying sites of old towns along the Vetluga River. The latter statement is completely wrong. I worked over about 6000 specimens found by Moscow archaeologists, when excavating the ruins along the middle and upper Vetluga, and I found the bones of domestic pig only. Neither roe deer, wild pig, or noble deer were present in Prevetluga 1000-2000 years ago. The region, however, was rich in moose, beaver, otter, and other valuable animals. The reindeer was also present, but not numerous. Even then, pigs went to the east scarcely beyond the upper Volga. They were probably also lacking in the headwaters of the Don, on the banks of which the Metropolitan Pimen, going in 1389 down to Tsar'grad, noted an abundance of roe deer, moose, bear, beavers, etc. Samuel George Gmelin who visited this region in 1763-1769, and who found wild horses (tarpans) here, does not mention pigs. However, pigs occurred until quite recently in the delta of the Don.

In the Kursk forest-steppe, pigs were quite widespread several hundred years ago, since their remains are known from many ruins (Ptushenko, 1937). During the excavation of settlements dating from the 11-12th centuries, pig bones were found in a number of places in Kharkov province (specimens in the Historical Museum in Moscow). According to Boplan, they were widely distributed in the Ukraine, including Poltava Province (in the 17th century). In the description of the Kharkov Diocese by Filaret, there is an indication of pigs in the Izyum Forests, and along the middle stream of the Donetz River (cited by Somov, 1897). Alferaki (1910), says that pigs were rare in the delta of the Don, and on the Azov coast at the beginning of the 19th century, and had disappeared completely by 1812.

According to Bogdanov (1871), within the memory of his contemporaries, pigs were found periodically along the Volga valley

up to Kamyshino, but were common only below Astrakhan' (there are quite a few remaining there yet). In the descriptions of the travels of Pallas, there are a great number of locality records where pigs were numerous in the middle of the 18th century. They were quite abundant on the Kamysh-Samarski lakes (in the Volga-Ural steppes), in the delta of the Yaik (Ural), and on the river Emba, about which Pallas says, "As is the case of all cane regions around the Yaik, so one finds here a great number of pigs also". Shortly before the arrival of Pallas, the pigs, along the left bank of the Volga reached the Buzuluk River. On the way from Orenburg* to the Iletski salt factories, Pallas noted the swampy Tongus River**. "The name of the river proves that pigs were abundant on the cane-covered banks and dells, but also today they are present farther in the steppes, and especially near the Ilek River, where they are found in large numbers, and are of extreme size."

He again mentions pigs when describing the animal industry of the Kazakhs of "Yaitski township." Somewhat earlier, Rychkov (1762), when describing the nature of the then extensive Orenburg region, said: "Boars or wild pigs appear rarely in Bashkiria on this side of the Yaik River. To the contrary, beyond the Yaik River, up along the Ilek River, and especially near those lakes around which cane grows, the Yaikski and Ilekski Kazakhs kill quite a few of them in the wintertime for food". According to Eversmann (1868), single pigs still appeared on the Ik and Sakmara Rivers, in some years increasing noticeably in numbers. Toward the end of the 19th century, they were already absent there. Zarudny (1897) says, "......at the present time, pigs occur in no parts of Orenburg State known to me". The latest records known to me of pigs killed in the southern foothills of the Urals were made by Nazarov (1887), who mentions encounters with this hoofed animal on the Belaya River about 40-45 years before him, and by Kirikov (1935), who learned from the old Bashkirs about their securing one boar which came into the vicinity of the former Voznesensky Factory, on the left bank of the Belaya River.

N. Rychkov (1772), while passing through the steppes of Northwestern Kazakhstan in 1771, left some records about the fauna in his interesting diary. One boar was killed by the Kazakhs in the region of the left bank of the river Or', about which Rychkov says.

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*Now called Chkalov

**Obviously the Donguz of Atlas Mira

Ishim and Barabinsk steppes, while near Omsk it went beyond the line where the Trans-Siberian railroad now passes. Farther to the east, the limit of boar dips sharply. According to Gebler, the wild boar formerly occurred in the southern part of Altai, even on the northern slopes of the Katunski Mountains, from which it later was extirpated. In Gebler's time, they were still found in the valley of Bukhtarma, but by the time of Kashchenko (1899), they were gone.

According to recent information (Podarevski, 1936), in the east Siberian (=Sayan) Krai, the distribution of boar is as follows. From the headwaters of the Uda and Iya rivers, they "extend along the valleys of the Tagul, Biryusa, Ognit.....into the southern vicinity of Taishet and Tulun districts, where, however, they do not remain, probably because of the excessive depth of snow". Along the foothills of Sayan, the limit of boar goes to the southeast of the southern end of Baikal, then to the northwest along the lake. (retreating quite far away from the coast itself), and along the headwaters of the rivers Turka, Gusikha, and Barguzin. From here, the northern limit goes up to the headwaters of the Vitim and its small tributaries (Tundak, Kalakan); pigs occur also in the headwaters of the Nerch and in the valley of the Uryumkan River. After the limit reaches the 56th parallel, northeast of Baikal, it heads then to the southeast to the southern spurs of the Stanovoy Range, then to the headwaters of the Bureya River, and to Lake Kizi on the lower Amur. In the Gilyuy-Ol'doi district, it goes farther north than the railroad, to nearly 54°, 30'. (Gassovski, 1927).

The data, fixed in form of borderlines on the maps of Schrenk (1858), Radde (1862), probably refer to the cases of sporadic appearance of boars beyond the limits of their permanent range. On Lower Amur (Lake Kizi), at the Tatar Straits (De-Kastri Bay), the pigs, even if they occur, do so only rarely, because in their distribution in the Far East, they are linked with Manchurian taiga, but in the places just mentioned, the Okhotskian flora is dominant. Therefore, they appear near the sea-coast in noticeable numbers only in the southern half of Primoria (on the Kop' and Botcha, according to Emel'yanov, the boars are still quite rare).

Summarizing this review, one has to note several general statements. In Europe, the range of the boar spreads farthest to the north, reaching

the southern part of the Scandinavian Peninsula (Sweden, Norway), Latvian SSR, Estonian SSR, and northern parts of Novgorod Oblast' of the RSFSR, i.e., 56-58th parallel. The eastern limit of the boar in Europe sharply drops to the south, following almost along the 30th and 33rd meridians. It coincides here with the lines of average maximum depth of the snow cover of 30-40 cm (see the map of Shenrok, 1926), without crossing them toward the east. In this region of the upper and middle streams of the Volga, the lower stream of the Oka and the headwaters of the Don River, there were no pigs in historic time. In connection with this, it is important to mention the following statement of Shenrock (1926): "The region near Oka, and the headwaters of the Volga, Dnieper, and the Don are distinguished by very great absolute depth of (snow) cover from 80 to 100 cm." But also, the average maximum depth of the snow cover in this part of the lowland is quite high, around 50-60 cm, and is close to that which is observed on the southern coast of the White Sea.

The appearance of pigs far to the north in the region of the left bank of the Volga River, and along the Ural River (up to southern Bashkiria) corresponds to the boundary of average maximum of 30-40 cm of snow cover, which here swings to the north.

Especially interesting is the former limit of the range of pigs in the forest-steppes of Transuralia, Northern Kazakhstan, and Western Siberia. In spite of the greater severity of winters (lower temperatures, strong winds, etc.), than in the middle region of the European part of the Union, boars inhabited the lakes of the west Siberian plain in great numbers coming in the region between the rivers Irtysh and Tobol, up to 55-56° northern latitude.

The map of the snow cover of Kazakhstan ("The Water Resources of the USSR") enables one to easily estimate factors which allow boars to penetrate so far to the north. It is just here, in the western part of the basin of the Ob' River, that the strip of Kazakhstanian zone of little snow penetrates farthest to the north. The borderline of the cover with an average maximum of 40 cm is located north of the city of Troitsk, thence to the north-east (probably reaching almost 60° north latitude), and then turns toward the south, passing northeast

Exactly so, the cane flood plains, which are common habitat for cane cat, in many places extend north beyond the limits of its range; and steppe regions with stone beds and outcrops extend beyond the range of distribution of manul. In all the cases, the northern borderlines of distribution of these cats agree much closer with the borderlines of snow cover of 20-30 cm, than with the outlines of the landscape or habitats typical for each species. With the exception of the lynx, the above statement can, apparently, apply also to the large cats: leopard, snow leopard, and tiger. The snow cover, especially when covered with a thin nast, apparently greatly hinders the hunting of the tiger. According to Przhevalsky (1870), the female tiger killed at the end of January (old style), 1868 in Ussuri Krai, had marks of heavy damage. The fur "on the inner side of the front and hind paws was shabby, and skin was covered with lesions from which blood was running." "Apparently, it is not as easy to walk on the deep snows of Ussuri Krai, as in the Bengal jungle", remarked Przevalsky in this connection.

Possibly, not only snow cover of shallow thickness itself, but also the abundance of ungulates connected with it makes the southern outskirts of our country most favorable for large cats. It is characteristic that from Preamuria, where the tiger comes up to 52° north latitude (the furthest appearance to the north of any other part of its range), it occurred repeatedly along the longitudinal axis on the East-Siberian zone of little snow up to southern Yakutia. Along the same strip of continental low snowiness which, apparently, in the late Quaternary Period was even more sharply expressed, the tiger spread up to the region of contemporary Lyakhov Island, and to the basin of the Yana River, i.e. it reached 74° north latitude, which is 22° farther north than in the present period.

The Distribution of Pheasants

The pheasants belong to a group of gallinaceous birds, completely sedentary, which take wing unwillingly, run perfectly, spend most of their life on the ground, and collect all their food on the ground or from low vegetation. They fly up into trees, but cannot obtain food by moving along the branches. The wings of the pheasant are small, and their flight is quite heavy and short. The digits of the feet have the same cover in winter as in the summer.

In the chapter dealing with winters of heavy snow cover, and with mass mortality of animals, we gave samples of disasters which can happen to the population of pheasants by snow cover which is too deep, and which remains on the ground too long. These birds are chionophobes. Because they inhabit the bushes on the outskirts of the forests, reeds and beds of other tall herbaceous plants, pheasants easily live in harmony with regions of intensive agriculture. The successful acclimatization of pheasants in Western Europe, North America, and here in the Ukraine speaks for sufficient ecological plasticity of these birds. However, the experiments with acclimatization of pheasants in numerous regions of middle portions of the European part of the Union ended immutably with failure. In winter with depths of snow cover of 40-60 cm, pheasants cannot exist without instensive supplementary feeding. The study of the northern limit of range of pheasants shows that in no place do they extend beyond the limits of regions with little snow, although it seems that with the presence of suitable habitats, they could spread widely. Thus, from the delta of the Volga River, pheasants could go far to the north along its valley; they could expand along with the widening of cultivated areas in the Far East, etc. Pheasants can easily endure the low temperatures of the winter, they survive well, not only in the region of Middle Amur, where the temperature of January is - 23 C (Blagoveshchensk), but also in northwestern Mongolia (Kobdo, with an absolute minimum temperature of -40C).

Pheasants were distributed in Precaucasia in historic times, along the Kuban' River, and along the southeastern coast of Azov Sea, (where the average maximum depth of snow cover is less than 10 cm); in the lower parts of the Terek and Kuma rivers, and in the delta of the Volga River, they are not rare even now. Several decades ago, pheasants occurred on the northern coast of the Caspian Sea, particularly in the delta of the Ural River.

In the "Travels" of Pallas (description of Fort Tatishchevo on the mountain plateau at the Kamysh-Samara River, near its junction with the Ural River), there is an observation on the nesting of pheasants in the middle of the XVIII Century to the north of the Caspian Sea. ("In the summer, there sometimes also occur pheasants, which nest in the hollows overgrown by bushes; these birds also inhabit the Kirgizian Steppe and the Kirgiz often wear their feathers on their hats for beauty"). The latter observation of Pallas indicates that in his time, pheasants

apparently also occurred to the north of the Aral Sea. The data of Eversmann about contemporary nesting of pheasants in the reeds along the northern shore of Aral Sea, serve to support this statement and so do the later observations of Buturlin on the occurrence of pheasants in the southern part of Turgai Oblast' and also the single observation of a pheasant around 1883 in winter near Irgiz (Sushkin, 1908).

At the present time, the ranges of the various subspecies of pheasants, which penetrate to the north further than others, go into the following regions. Aral pheasant - extends to the islands in the Aral Sea; Lower Buchara pheasant - to the lower stream of the Amu-Dar'ya River; Syrdaria pheasant - along the Syr-Dar'ya River to Aral Sea; Seven River pheasant - up to Lakes Balkhash, Alakol', and Zaisan; West Mongolian pheasant populates the region of Kobdo, Kara-us (=Kara-us-nur), Achitnor (=Achit-nur) but the borders of its range have not been studied satisfactorily (Buturlin and Demint'ev, 1935). Finally, the Amur (or Sungari) pheasant, during the time of Pallas, reached the Argun' River and Abagaitui, and now is not only common along the left bank of Amur River in its middle reaches, and further to the south within the limits of Manchuria, but also has penetrated along the valley of the Zeya River up to Mazanovsky District. A related form, the Ussuri pheasant, extends north along the valley of the Ussuri River down to the mouth of this river, and on the ocean shore up to the upper Kema River.

Thus, the natural northern limit of the distribution of pheasants in general coincides with the strip of plains, foothills, and continental dry plateaus, with a small amount of winter precipitation (Fig. 26). The line of this limit was not straight, but it formed a number of penetrations to the north: one of them in the Volga-Ural Steppes, another on the plains to the north of the Aral Sea, i.e. the regions of little snow which are already known to us, and which are characterized by far northward extensions of pig, roe deer, and other chionophobes. In Central Asia, pheasants survive near Kobdo (near 48° north latitude), with a very cold, but nearly snowless winter, and finally, they go beyond 50° north latitude near Blagoveshchensk on the Amur River, i.e. again in the region with winters which, in spite of being very cold, are relatively poor in precipitation (10-20 cm of snow).

The influence of the same factor one can see in the form of the northern limit of the range of rock partridge. Being a bird of steppe and desert rocky slopes, this fowl none-the-less avoids regions

without watering-places, and requires the presence of springs and rivers. As a sedentary species, the rock partridge is very sensitive to the winter regimen of the regions inhabited by it; it endures cold well, but cannot survive a fall of deep snow, which hinders it obtaining food from the ground. Therefore, the distribution of rock partridge encompasses the mountainous countries with low-snowy winters, and the northern limit of distribution goes from North Caucasia to Ulutau, Prebalkhashregion, and the steppe parts of Altai, to Tannu-ola and Gobi Altai, The furthest penetration to the north is again limited to the portion of Kazakhstan with little snow.

The northern part of the range of bearded partridge occupies the Semirechka, northwestern and northern forest-steppe parts of Altai, Minusinsk Krai, Prebaikalia, Transbaikalian steppe, Mongolia, Northern Manchuria, the lower part of Ussuri River, and exactly coincides with the regions of Asia with little snow. The attempts to acclimatize this forn near Krasnoyarsk (Sushkin, 1913), did not succeed, as one could predict.

It is noteworthy, that of the partridge subfamily, two species, common quail and gray partridge extend farthest north. The first is a typical migratory species and the inhabitants of the northern portion of the range of the second species make regular migrations. Thus, the ability to migrate enables them to use a wide variety of field and meadow habitats in forest and forest-steppe zones, which are wholly suitable for them in summer but unfavourable in winter after snow falls. The quail get up to 65° north latitude on the Scandinavian Peninsula and in Finland; to 60° 30' in the Urals, and up to 61° on the Yenisey River (Buturlin, 1935). It is interesting that individual quail which represent a group of species that are predominantly sedentary, often make attempts to winter even in the chernozem strip of the steppes of the European part of the USSR. Such cases have been described for middle Povolzhia, and the region of the city of Gur'yev, personally I know of cases from the Don steppes and from Voronezh Oblast'. Usually quail which stay for the winter are found until November-December on unharvested strips of millet or near stacks of millet straw. Later ((than November-December)) cases are not known to me. Probably these birds do not survive until the end of the winter. The quail remain in noticeable numbers for winter in Transcaucia and in southern Europe, while the main group winter in India, Arabia, and northern parts of Africa.

It seems to me that in the above given case, we are dealing with a species which recently has inhabited a region where it was

necessary for them to become migratory. The absence of sharp limits of winter range, the atavistic attempts to be sedentary - are adequate evidence for this. The Japanese grey quail, (Coturnix c. japonica), which is very closely related to our species, winters in small numbers even in the Transbaikalian steppes and in Ussuri Krai, which have little snow.

The gray partridge, as is known, in the European part of the country, has markedly moved toward the north, following agriculture, during the past few decades. The restoration of a picture of the vegetation of the pre-agricultural period of some parts of the Russian plain, which has been accomplished by geobotanists, shows that several centuries ago, the central part of the country was almost entirely covered by forests, and therefore, it was completely unfit for animals such as quail and gray partridge. Consequently, the whole northern part of the present range of partridge is a recently occupied region. In 1917, I saw this essentially steppe bird, nesting on the wide dry meadows of the upper stream of the Northern Dvina River. According to Buturlin (1935), the grey partridge is distributed up to 66° in Finland, up to 58° 30' beyond the Urals. Thus, it nests furthest to the north in that region where agriculture and de-forested meadows and burns have advanced far to the north. For the winter time, the partridge are forced to fly away from there.

Significant data on the seasonal migrations of this species in the eastern half of the European part of the USSR were collected by Zhitkov and Buturlin (1906). Beginning with 1930, while doing field ecological studies, I had an opportunity almost every year in October-November to observe in the forested region of Upper Prevetluzhia - Shariinsky District of Kostroma Oblast' - an intensive migration of gray partridge toward the south (Dement'ev, Formozov, Lavaden, 1934). Usually the migration coincides with the appearance of the first snow in the region of my observations, and with a noticeable southward movement of buntings, jackdaws, and buzzards. Probably they are driven away from the north by heavy snowfalls. It is noteworthy also that my observations are concerned with the eastern strip of the European part of the USSR, i.e. the region where, in the northern part of the range of partridge, especially deep snow falls (average maximum is 50-60 cm and deeper). Nevertheless, a certain number of partridge winter every year in the central part, and periodically, during years with deep snow, gololeditsa, and severe cold, the majority of them perish (see the chapter about the perishing of animals during deep snow). A decimation of the individuals

which try to remain sedentary occurs, and thus there is accomplished a selection of migratory individuals which appear to be more adapted to life in the northern part of the range. This group also appears to be most adapted for further northward advance of the species.

A brief review of the pecularities of the range of gray partridge and quail helps to appraise the circumstances that among the numerous sedentary species of partridge and of quail, neither in the Old, nor in the New World, is there a single one that penetrates the regions with much snow. The snow partridges which are inhabitants of high-mountain regions of Asia and of the Caucasus, seem to be exceptions. The peculiarities of the distribution of snow cover in mountains which are caused by the irregularities of relief, by insolation, and by the influence of winds, have already been mentioned above. These circumstances enable the snow partridge to find sections of meadows and bushes that are almost bare or with only a shallow snow cover, for pasturage. It is interesting that sometimes in winter, snow partridge come down to lower mountain belts, if the steppe slopes adjoin the alpine region. The presence of such migrations in northern Mongolia is easily determined by the abundant traces of wintering of the Altai snow partridge on the low ridges of the southern Khangai Mountains, where they do not live in summer (My observations in 1926, near Laman-Gegena). Cases are known of Caucasian snow partridges having flown out onto the grassy slopes of the ranges in mountainous Dagestan (data collected by me by questionnaire in 1924 and in 1925).

Snow partridges are distributed for the most part only in those mountains systems which have at least part of their slopes adjoining the continental regions which are distinguished by low amounts of precipitation. It is quite possible that they do not extend from the Altai-Sayan high plateau into the ranges of eastern Siberia, which go toward the north in an almost uninterrupted strip, only because of abundant snow there. There is also some undoubted significance of snow cover as a factor which limits the distribution of sand grouse, (Syrrhaptes paradoxus and S. tibetanus), which are terrestrial birds that winter on the cold high plateau of Central Asia, and obtain grain for food from the naked frozen soil.

The northern limit of range of a small sedentary steppe bird, the crested lark, as Stanchinsky (1926) has established, in the European part of the USSR coincides for some distance with the isoline of the

duration of snow cover of 140 days. Stanchinsky evidently did not delimit on the map the depth of snow cover. The comparison shows that the limit of range of the crested lark, which extends from Leningrad to Smolensk, Voronezh, Saratov, and Ural'sk, agrees very closely in this part of the country with the limit of the ranges of roe deer, boar and forest cat. At the same time, it repeats quite accurately the course of the isolines of the depth of snow cover equal to 30-40 cm. The northern limit of wintering of skylarks (Alauda arvensis) drawn on the map of Stanchinsky, is located to the south of the line of snow cover of 20 cm in depth.

I have no doubt that an extended study of the regions of wintering of birds which pick their food from the soil, the study of the ranges of sedentary terrestrial birds, will reveal still more examples of the distribution of birds being dependent on the factor of snowiness. One may be confident that the study of distribution, and in particular, distribution of populations within the ranges of a number of mammals that are to some degree dependent on snow cover, will result in many conclusions that will be interesting from the practical, as well as from the theoretical point of view. The examples taken by us represent only a small attempt to approach the work which necessarily has to be done by zoogeography and by ecology.

THE SIGNIFICANCE OF SNOW COVER IN THE HISTORY OF THE FORMATION OF THE QUATERNARY FAUNA

Osborn (1910), in his well-known work, "The Age of Mammals", expressed the hypothesis that during the glacial period, the heavy winter snows, which covered the supply of natural food, had a greater effect on the extinction of animals than did the influence of cold. In witness of this hypothesis, he brought forward the observations on mass loss of herds of domestic horses and cattle on the plains of the west of the United States of America during the heavy snowfalls. Apparently, the concrete facts of extinction of quaternary vertebrates under the influence of snow cover were unknown to Osborn. However, with attentive study of the conditions of quaternary time, it is easy to find indubitable proofs of the importance of snow cover in the process of the formation of the mammal fauna. In this respect, the division of vertebrates into groups of chionophobes, chioneuphores, and chionophiles, which we did, will play a certain role. The dying out of chionophiles, and chioneuphores will manifestly speak in favor of the snow cover as a basic factor of

selection. The presence of paleontological evidence concerning the wide distribution of chionophobes tells of the winters in a given area and age as having little snow. More than that, knowing the limits of snowiness that at the present time limit the distribution or cause wide distribution of species, we can possibly restore with certain approximations, the picture of the distribution of snow cover in the past.* From this point of view, of particular interest is the picture of the extinction of the rich fauna of large mammals of the northern part of Yakutia, which, at the end of the last glaciation, was known to consist of arctic fox, musk-ox, moose, reindeer, marmot, ox, bison, a certain sheep, goat, roe deer, horse, mammoth, and others.

Tugarinov (1927) rightly thought that the condition which allowed the simultaneous existence of species of tundra, steppe, and montane mammals was the presence of a markedly continental climate which was similar to the contemporary climate of Transbaikalia or Northern Mongolia, where we now can see similar animal communities. "The only change of the climate which has altered the desert landscape has been moistening. The encroachment of forest has begun, which has forced out the animals of the open spaces, causing some of them to move south, and isolating the others on the extreme north" says Tugarinov. It is characteristic, that among the species of this fauna that became extinct in the north, maral, reindeer, saiga, sheep, goat, there are not only chionophobes (saiga), but also chioneuphores, which usually reconcile themselves to the presence of a snow cover of 20-40 cm (roe deer, maral). It is difficult to agree with Tugarinov, that only a simple forest invasion was the cause of the dying out of the majority of species of an open landscape, since, in addition to them, typical forest forms (maral, roe deer) have also died out. Areas of tundra, meadows, and forest-free mountains are numerous in Yakutia even now: larch forests are light, thin, and are scarcely to be considered taiga in the usual understanding of this word. The findings of Sukachev (1914), obtained as a result of the study of the remains of plants which were found in the stomach and on the teeth of mammoths from the River Berezovka (320 km (sic) to the northeast from Srednye-Kolymsk), are extremely important. They showed that "during the age of the mammoth, the meadow vegetation differed little in its composition from contemporary meadows of the middle stream of Lena River, and that the larch forest was distributed then the way it is now" Komarov, 1927). Judging by these arguments, the plant cover of the country did not undergo such significant changes as one would expect. The increase in humidity of the climate about which Tugarinov speaks, should, first of all, show up as an increase in the thickness of snow

*This method has special interest also for archaeologists studying the Neolithic and Paleolithic.

cover, because from November until March, only solid precipitation occurs here. Maximum average depth of snow (during the month with the greatest cover) is 47 cm in Nizhnye-Kolymsk in April, in Srednye-Kolymsk, 47 cm (March), in Rodchevo, 49 cm (March), i.e., it just approaches those standards that limit the northward penetration of maral as well as of roe deer (see above). At the same time, there exists up to the present time, in ths basin of the Yana River, quite a large "island" with a snow cover of 30 cm and even 20 cm in the lower stream of Yana River (in Verhoyansk, there is 27 cm in March, in Bulan, 21 cm for April,etc). It is possible that this scarcity of snow, peculiar for such a northern region, and similar to that characteristic of steppean Transbaikalia, and northern Mongolia, which are located far to the south, must be regarded as a kind of relic, a slight hint as to the conditions that existed there during the Post-Pliocene time. It is not by accident that just here, in north central Yakutia, the snow sheep, musk deer, and moose at the present time penetrate farthest beyond the Arctic Circle.

The presence in such high latitudes of this group of hoofed animals, which represent a fragment of the former very rich fauna, is correlated with these partly preserved conditions of the past of scarcity of snow. It is very interesting to note that the described Post-Pliocene fauna has existed longest of all in the continental region of Eastern Siberia, which remains up to the present time a region of relatively little snow, and which is characterized by the furthest penetration toward the north of many hoofed animals. Tolmachev (1929), who analysed in detail the distribution and the causes of the extinction of the mammoth noted a number of interesting situations. The mammoth was absent, or was very rare on the Scandinavian Peninsula (at that time, a region of deep snow), but was very abundant in northeastern Siberia, and on the nearest islands. Tolmachev points out that neither the climate nor the vegetation of this region, which was well suited for mammoth, have changed markedly from the time when this animal was still existing. From these observations, he makes the conclusion that the changes of physical-geographical conditions in northern Siberia could have only local importance, and that neither of these external conditions could bring on the extinction of the mammoth.

The statement is not entirely correct that the vegetation of Yakutia has not changed at all since the Pleistocene. The newest works of the study of forests of Yakutia show that the Daurian larch, which is the continental species, and which survives well even on the southern borderline of forests near the outskirts of the Gobi deserts in Mongolia,

and which forms forest islands in the depths of the tundras of Eastern Siberia, has begun to retreat before pressure of more mesic tree species. The Siberian larch was the first afforester of the steppe in the high eastern foot-hills of the Southern Ural (Tyulina, 1931), the Daurian larch in the continental regions of eternal frost during the time the glaciers covered the larger part of that territory of Yakutia which was not occupied by firn (Grigor'yev, 1930). This species, which is tolerant of physiological dryness of the substratum, as well as to dryness of the air, formed zeric larch forests in the region of the arctic steppe or semi-desert. The time of its dominance has already past, as well as the time of the mixed forest-steppe fauna of Yakutia, which was rich in ungulates. However, the vegetation reacts less noticeably to the increase of snow cover from 10-15 cm up to 40-50 cm, therefore, the past climatic changes are reflected more strongly on the fauna which included both chionophobes and chioneuphores. The location of the Yakutian form of Saiga (described by Cherski), remnants of which are known from the mouth of the Olenek River (72° 30' latitude), and from Lyakov Island (73° north latitude), is separated from the range of typical saiga, (a range which, during the historic times, stretched from Kazakhstan to northwestern Mongolia, an area with a depth of snow cover of 10-20 cm), by a wide zone of taiga with an average maximal thickness of snow cover of 40-50 cm and more. For the mammoth, which needed food in huge quantities, and which was in constant movement because of the poorness of northern pastures, the appearance of fluffy snow cover, which hindered walking and the search for food, might well have been fatal. The structure of the trunk which was markedly different from that of the contemporary elephants (K.K. Flerov, 1931), leads us to conclude that grassy food was dominant in the diet of the mammoth. As we know, herbivorous forms that use arboreal and bushy food to only a small extent coincide poorly with snowy regions.

The less snow-enduring a given species was, the further it retreated to the south from the extreme north of Yakutia, where it had happily existed during Post-Pliocene time. As before, reindeer were preserved in the fauna of the New Siberian Islands: moose which is also a snow-hardy form, exists even closer to the coast than other forest deer, but roe deer and maral retreated far. The northern borderline of the saiga and tiger have been moved especially far to the south. It is quite possible that the niveal factor has played an important part

not only in the dying out of the mammoth, but also in the disappearance from the North of Asia of musk-ox and wooly rhinoceros. It is desirable to undertake some special works in this direction. The study of the ecology of contemporary large herbivorous and carnivorous animals indicates that one has to look to the role of snow cover as a determinative factor of environmental resistance for a clue to the marked reduction of the ranges during the quaternary period of forms surviving to-day, and for the cause of the complete extinction of a number of Post-Pliocene species.

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Legends of Plates

Fig. 1 The winter claws of the front paw of the Arctic Fox (Alopex lagopus) are developed relatively more than in the case of the common fox (Vulpes vulpes). Adaptation for the digging of the compacted snow of the tundra. (Spring specimen from Western Siberia).

Fig. 2 Average duration and depth of snow cover in two different taiga-regions of Siberia. The upper curve is for Turukhansk, 67°47'N 80°4'E. It rperesents a region of heavy snow cover, where even moose cannot exist. The lwoer curve is for Irkutsk, 82°16'N 104°19'E. Low-snowy winters of Irkutsk are favourable for moose (Alces alces), maral (Cervus elaphus) and roe deer (Capreolus capreolus).

Fig. 3 Kukhta on the spruce trees of the second stratum in mature birch plantation. The height of the trees is 8 to 9 m. Shariinski District, Kostroma Oblast', January 30, 1939.

Fig. 4 Kukhta on the fir undergrowth 1.5 to 2 m. high. Same locale as Fig.3.

Fig. 5 Linden 3.5 m. high, covered and bent by snowy kukhta. Feb. 3, 1939. Same locale as Figs. 3 and 4.

Fig. 6 Average duration and depth of snow cover in two regions of the steppe zone below 51°N. The upper curve is for Buturinovka (50°50'N 40°36'E), representing the climate of moderate steppes; the lower curve is for Station Oloviannaya (50°36'N 115°36'E); representing the climate of the east Siberian steppes, in the region of Oloviannaya the winter is favourable for corsac, manul, Daurian partridge and other "chionophobes".

Fig. 7 Front paw of Caucasian Forest Cat. Dec. 16, 1923, Northern Caucasia.

Fig. 8 Ventral surface of front paw of lynx (18 Feb. 1935, Moscow Province).

Fig. 9 Middle toe of front paw of lynx, laterial view, The long elastic hair covering the lower surface of the toes is clearly seen. (December 1940, Moscow Province).

Fig.10 Left - Sole of hind foot of varying hare in winter pelage, somewhat worn. (wgt. 3400 gms., 1 April 1920, Lapland).
Right - Same of European Hare of heavy weight (wgt. 4200 gms., 18 Nov. 1944, Moscow Province). The larger European hare has a markedly smaller sole surface.

Fig.11 Sole of foot of white ptarmigan.
Left - in summer.
Right - in winter.
Small elastic feathers of the foot are depressed; in this position of the foot of the bird moves forward easily, furrowing the fluffy snow with a smaller surface.

Fig.12 Foot of white ptarmigan in winter plumage supporting itself on the substrate. The small elastic feathers of the sole are extended; the supporting surface has increased.

Fig.13 Front paw of collared lemming with winter claws. 5 April, 1934, Yamal.

Fig.14 Winter and summer claws of the third digit of a collared lemming (from the specimen from Yamal).

Fig.15 Graph of catch of Arctic foxes with steel traps by months winter 1926-27 (From the notes of the hunter I.T. Zhuravliev, Novaya Zemlya).

Fig.16 Differences in average duration and depth of snow cover on western and eastern slopes of the Urals. Upper curve- Perm (58°1'N). Lower curve - Sverdlovsk (56°51'N). Near Sverdlovsk roe deer are common, near Perm they are absent.

Fig.17 Winter runways of moles, constructed under the snow on a plot 15 meters square. Only a small part of the area occupied by the animal's runway system is drawn. 28 April, 1937, meadow, edge of spruce-fir forest. Village of Kiseliovo, Chariinsky District, Kostroma Province.

Fig.18 Fluctuations in the number of shrews in the forests of Shariinkky District, Kostroms Province, according to data obtained from traplines for 1931-1940. Lower line of graph - average number of shrews per 100 trap-nights; dotted line - maximum depth of snow for the winter. Snow data from Station Sharia.

Fig.19 Snow cover in Shariinsky District for three winters showing different degrees of suitability for shrews. Winter 1936-37 remarkably little snow; alternating thawing and freezing (Great winter die-off of shrews).
Winter 1937-38 deep and fluffy snow cover (Successful everwintering of shrews). Winter 1938-39 late accumulation of snow cover (from the second half of January) and strong frosts with little snow at the beginning of winter (mass die-off of shrews).

Fig.20 Tracks at grouse's overnight stay in a snow hole. (13 Jan. 1939. Shariinsky District, Kostroma Province). The tunnel is straight, 1 1/2 m. long, and directed downwards under the snow. The grouse left in four places holes made by its head while "measuring" the thickness of the ceiling. Bottom of sleeping chamber at a depth of 23 cm.

Fig.21 Tracks at overnight stop of Blakc Grouse, 21 Jan. 1941. Zvenigorodski District, Moscow Province. This tunnel is curved, 95 cm. long. At the entrance of the tunnel may be seen the print of the tail which was left by the bird upon diving into the snow, the prints made by the wings upon flying out. Temperature at night -30°c: bottom of sleeping chamber at a depth of 40 cm. with a depth total snow cover of 46 cm.

Fig.22 Young Dagestan tur smashed by snow avalanche and eaten by mountain birds. Dagestan, Bogosski Ridge, 22 July, 1924.

Fig.23 Northern limits of the range of moose in USSR (Upper solid line) and reconstructed northern limit of pig (lower solid line). Dashed lines - limit of average maximum snow cover of 30, 50 and 90 cm (According to Shenrok, 1926, Shostakovich, 1925 and others. Schematic).

Fig.24 Reconstructed northern limit of roe deer in European part of USSR (dashed line) and average depth of snow cover of 50 and 70 cm. (According to Shenrok, 1926). Arrows - places of most advanced penetrations of roe deer into regions of much snow.

Fig.25 Distribution of pig in eastern half of European part of USSR and average maximum depth of snow cover of 50 and 70 cm. (According to Shenrok, 1926). Black dots - Recent occurrence records: circles - distribution in historic times: triangles - greatest penetration of pigs in recent years.

Fig.26 Map of depth of snow cover near northern limit of range of pheasant in European part of USSR. Upper line - Ural'sk, most northerly region in which the pheasant has occurred in historic times. Middle line - Akhtubs, conditions characteristic of Volga delta. (Pheasant occurs here consistently but not in large numbers). Lower curve - Khasov-Turt (Flat part of northern Dagestan). Winter conditions are always favorable for pheasants.

Fig. 1

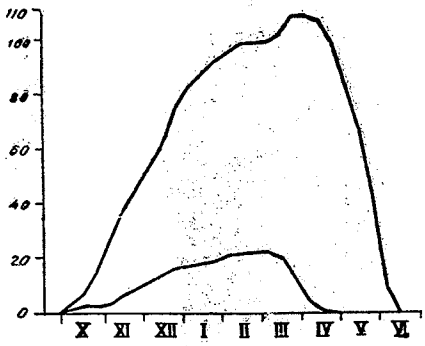
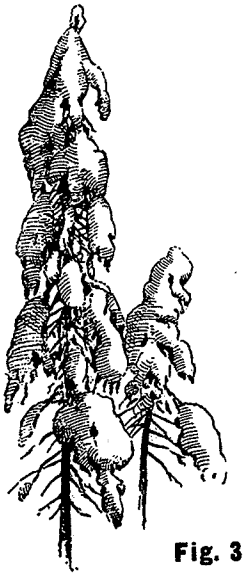


Fig. 2



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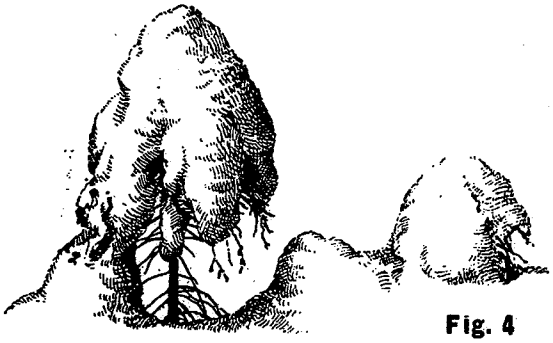

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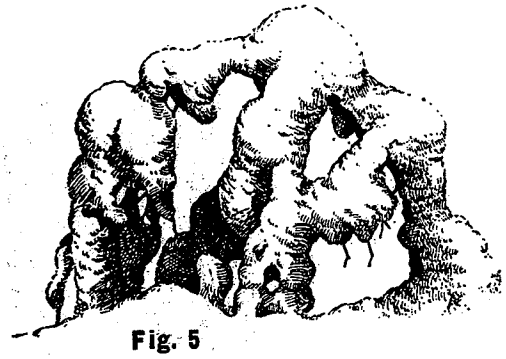

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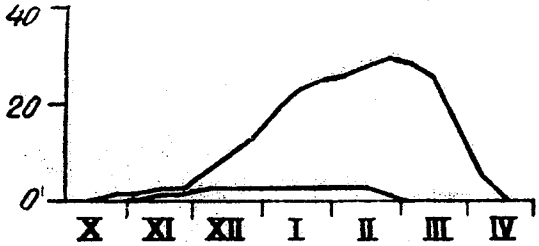

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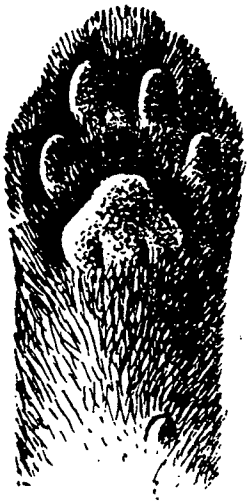

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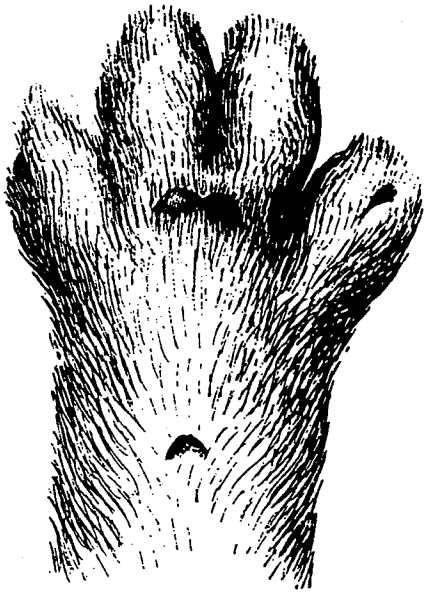
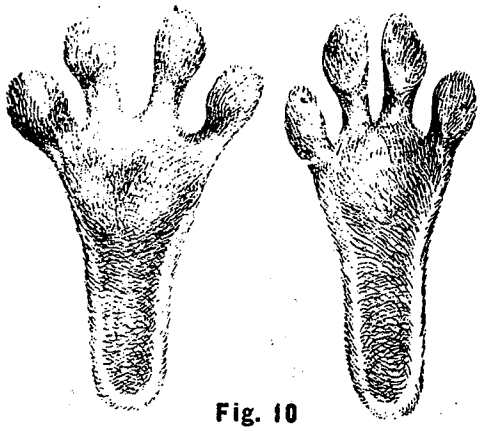


Fig. 8

Fig. 9



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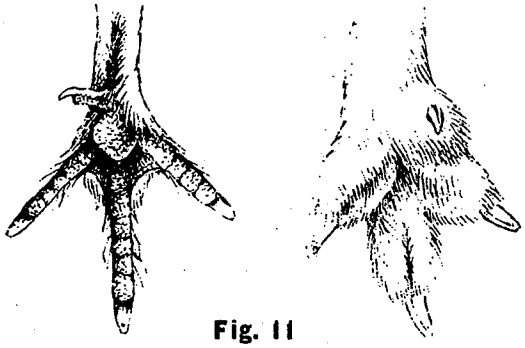

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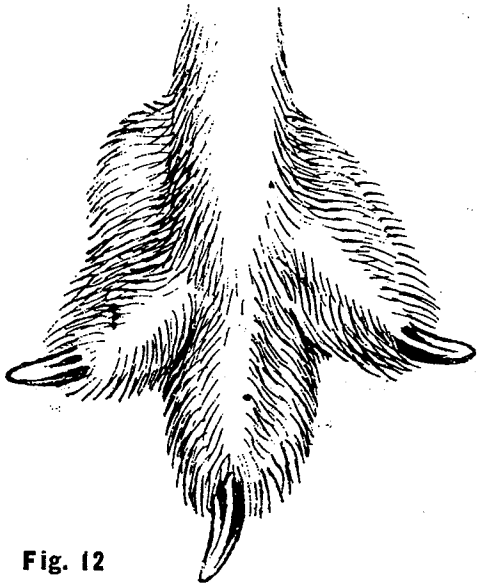

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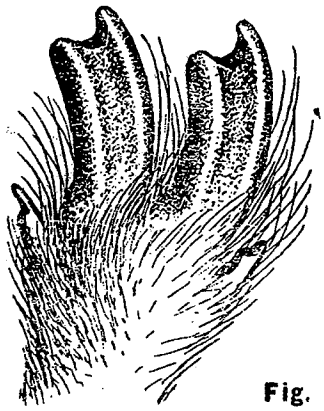

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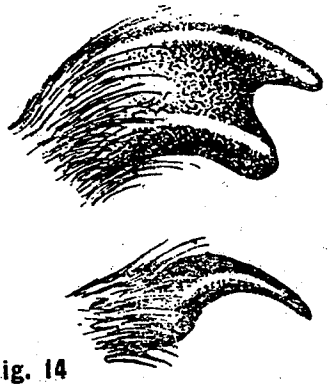

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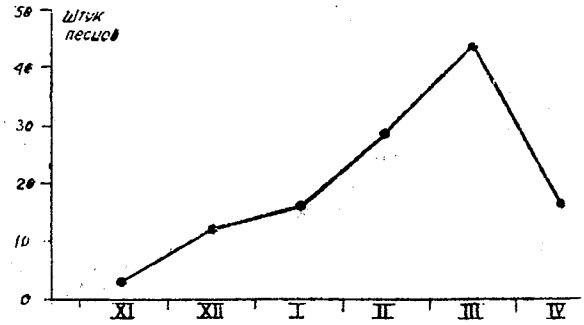

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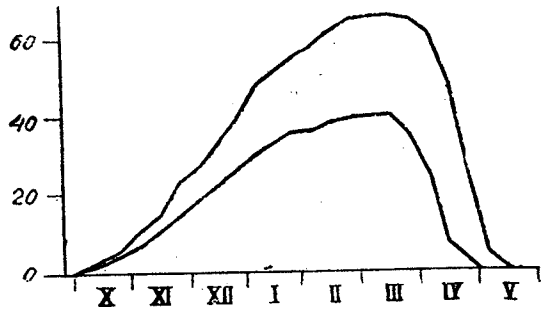

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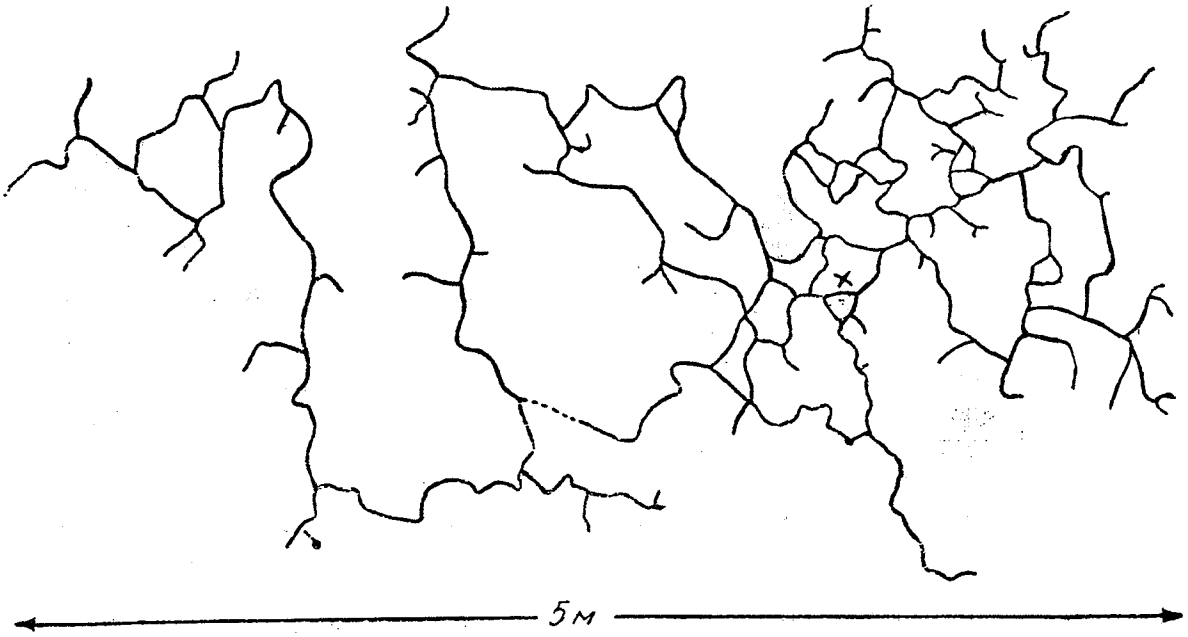

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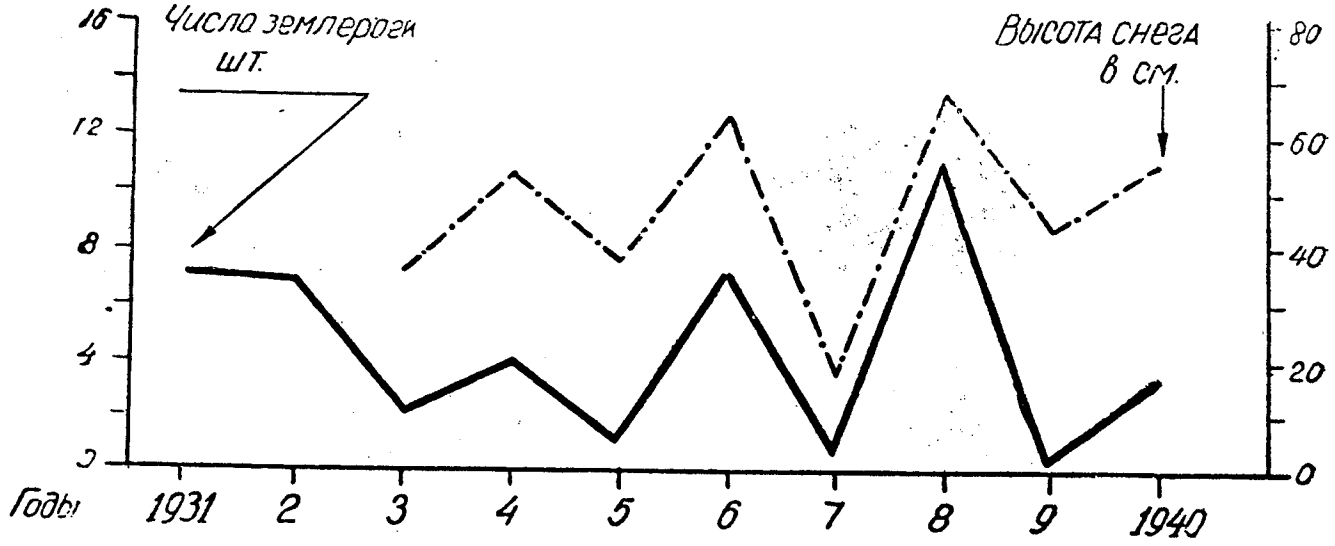

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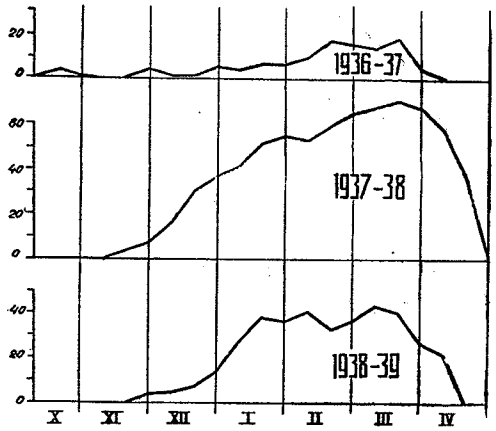


Fig. 19

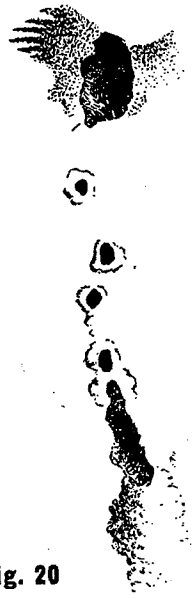


Fig. 20

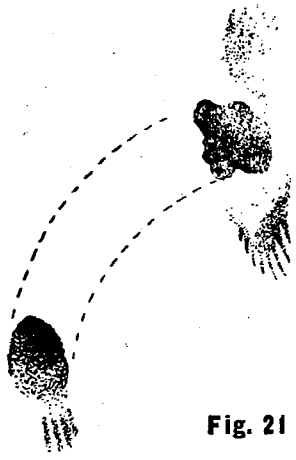
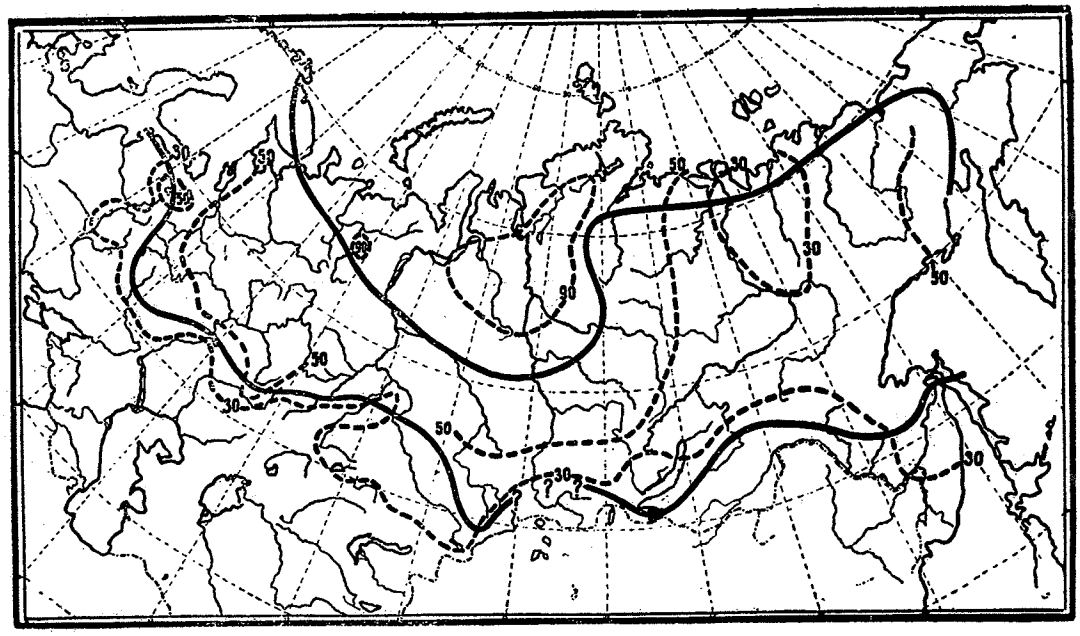


Fig. 21

Fig. 22



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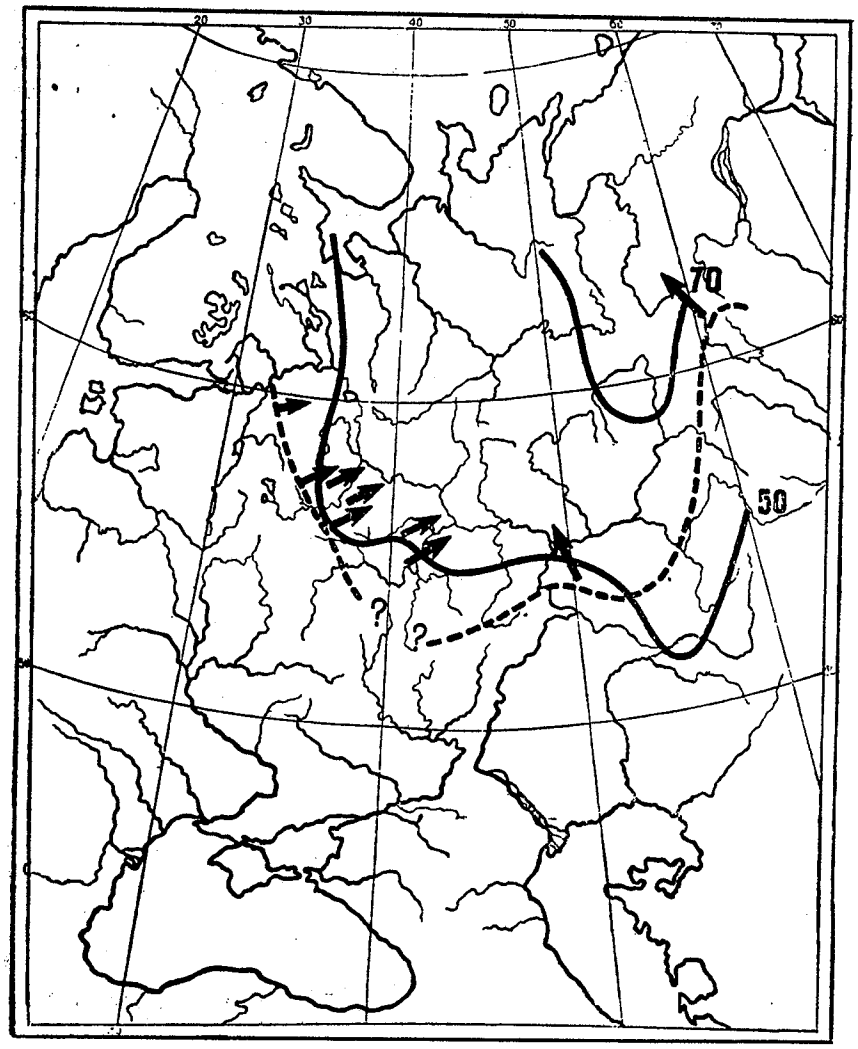

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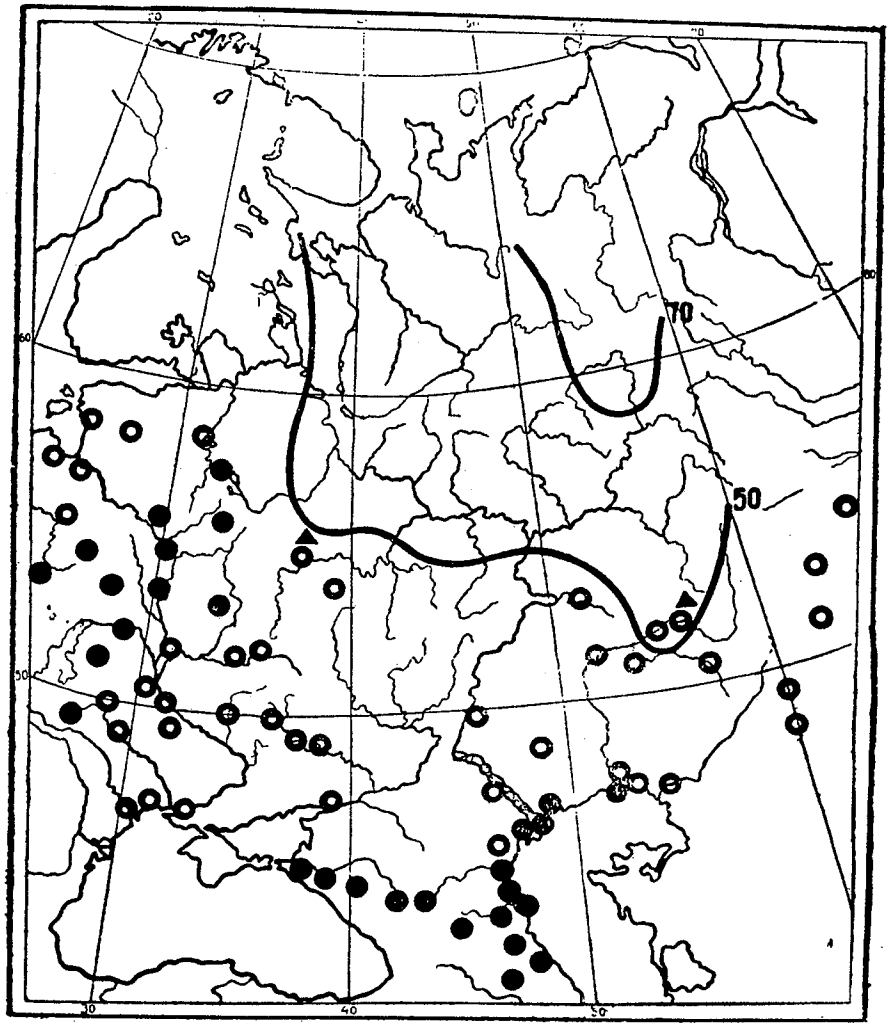

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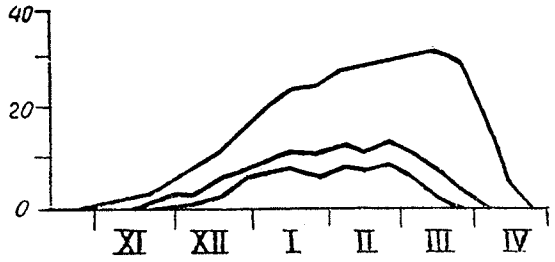

Fig. 26

APPENDIX A

Latin and English names of mammals mentioned in the text mostly by Russian common name. Authorities for these equivalents include subsequent papers by Formozov; Ellerman and Morrison - Scott, 1951 Check list of Palaearctic and Indian Mammals, British Museum (N.H.); and Mohr 1961 Glossarium Europae Mammalium Terrestrium.

Argali	Ovis ammon
Bear, brown	Ursus arctos
polar	Thalarctos maritimus
Boar	Sus scrofa
Cat, cane	Felis chaus
Caucasian	F. sylvestris caucasica
European	F. sylvestris
Far Eastern	F. euptilura
sand	F. margarita
spotted	F. ocreata
Chamois	Rupicapra rubicapra
Corsac	Vulpes corsac
Deer, black-tailed	Odocoileus hemionus
musk	Moschus moschiferus
red	Cervus elaphus
roe	Capreolus capreolus
spotted	Cervus nippon
white-tailed	Odocoileus virginianus
Dog, wild (dohle)	Cuon alpinus
Ermine	Mustela erminea
Fox, arctic	Alopex lagopus
Bukhara	Vulpes v. daurica
Gazelle, Mongolian	Procapra gutterosa
Persian	Gazella subgutterosa
Gerbil, southern	Meriones meridianus
Tamarisk	M. tamariscinus
Hamster, common	Cricetus cricetus
grey	Cricetulus migratorius
Hare, grey	Lepus europaeus
Tolay	L. tolai
varying	L. timidus
Hedgehog	Erinaceus

Ibex, Siberian	*Capra sibirica*
Jackal	*Canis aureus*
Kolinski	*Mustela sibirica*
Kulan	*Equus hemionus*
Lemming, collared	*Dicrostonyx torquatus*
Norway	*Lemmus lemmus*
Ob'	*L. obensis*
steppe	*Lagurus lagurus*
Leopard (common)	*Panthera pardus*
snow	*P. uncia*
Lynx	*Lynx lynx*
Manul	*Felis manul*
Maral	*Cervus elaphus maral*
Marmot	*Marmota marmota*
Marten, pine	*Martes martes*
yellow-throated	*M. flavigula*
Mink	*Mustela lutreola*
Mole, common	*Talpa europaea*
eastern	*Mogera robusta*
Mole-vole, Afghan	*Ellobius fuscocapillus*
common	*E. talpinus*
long-clawed	*Prometheomys schaposhnicovi*
Moose	*Alces alces*
Mouse, striped field	*Apodemus agrarius*
house	*Mus musculus*
long-tailed field	*Apodemus sylvaticus*
Musk-ox	*Ovibos*
Otter	*Lutra lutra*
Polecat, black	*Mustela putorius*
steppe	*M. eversmanni*
Reindeer	*Rangifer tarandus*
Sable	*Martes zibellina*
Saiga	*Saiga tatarica*
Sheep, snow	*Ovis nivicola*
white	*O. dalli*
Shrew, Cherski's	*Sorex tcherskii*
common	*S. araneus*
lesser	*S. minutis*
masked	*S. caecutiens*
water	*Neomys fodiens*
Squirrel	*Sciurus vulgaris*

Tarpan	Equus Caballus Gmelini
Tiger	Panthera tigris
Tur, Caucasian	Capra caucasica
Vole, bank	Clethrionomys glareolus
common	Microtus arvalis
field	M. agrestis
narrow-skulled	M. (Stenocranius) gregalis
pine,	Pitymys subterraneous
rat-headed	M. (oeconomus?) ratticeps
red-backed	Clethrionomys rutilus
social	Microtus socialis
tundra (root)	Microtus oeconomus
water	Arvicola terrestris
Wapiti, Mongolian	Cervus elaphus xanthopygus
Weasel, Altai	Mustela altaica
(common)	M. nivalis
Wolf	Canis lupus
Wolverine	Gulo gulo
Zokor	Myospallax myospallax

APPENDIX B

Latin and English names of birds mentioned in text mostly by Russian common name. Authority for these equivalents was MacLennan, J.M. 1958. Russian English Bird Glossary. Canadian Wildlife Service.

Blackbird	Turdus merula
Brambling	Fringilla montifringilla
Brant	Branta
Bunting	Emberiza
snow	Plectrophenax nivalis
yellow-breasted	Emberiza aureola
Bustard, great	Otis, tarda
little	O. tetrax
Capercaillie	Tetrao urogallus
Chaffinch	Fringilla coelebs
Chough	Pyrrhocorax pyrrhocorax
Creeper (in general)	Certhia
wall	Tichodroma muraria
Cross-bill	Loxia
Crow, grey carrion	Corvus corone
Dove, stock	Columba aenas
Falcon, red-footed	Erythropus vespertinus
Fieldfare	Turdus pilaris
Finch, gold-fronted	Serinus pusillus
green	Chloris chloris
rose	Erythrina
Flamingo	Phoenicopterus ruber
Flycatcher	Musicapa
Goldfinch	Carduelis carduelis
Goose	Anser
Goshawk	Accipiter gentilis
Grosbeak, pine	Pinicola enucleator
Grouse, black	Lyrurus tetrix
hazel	Tetrastes bonasia
sand (common)	Pterocles
sand, Pallas'	Syrrhaptes paradoxus
sand, Tibetan	Syrrhaptes tibetanus
spruce	Falcipennis falcipennis
Hawk, rough-legged	Buteo lagopus
Jackdaw	Coloeus monedula
Jay, common	Garrulus glandarius
Siberian	Cractes infaustus
Kinglet	Regulus

Lark, black	Melanocorypha yeltoniensis
crested	Galerida cristata
horned	Eremophilus alpestris
white-winged	Melanocorypha leucoptera
Magpie	Pica pica
Nightingale	Luscinia
Nuthatch	Sitta europaea
Nutcracker	Nucifraga caryocatactes
Oriole, golden	Oriolus oriolus
Owl, barn	Tyto alba
eagle	Bubo bubo
long-eared	Asio otus
pygmy	Glaucidium passerinum
snowy	Nyctea scandiaca
Partridge, black	Francolinus francolinus
chinese	Perdix daurica
grey	Perdix perdix
rock	Allectoris graeca
snow	Tetraogallus caucasicus
Pigeon, grey	Columba livia
Ptarmigan, rock	Lagopus, mutus
willow	L. lagopus
Quail, bob-white	Colinus virginianus
(common)	Coturnix coturnix
Japanese grey	Coturnix c. japonica
Raven	Corvus corax
Redpoll	Carduelis flammea
Redwing	Turdus musicus
Rook	Corvus fragilegus
Skylark	Alauda arvensis
Sparrow, field	Passer montanus
house	P. domesticus
Starling, rose-coloured	Pastor roseus
Swift	Apus
Thrush, missel (mistle)	Turdus viscivorus
song	T. ericetorum
Tit(mouse), azure	Parus cyanus
coal	P. ater
crested	P. cristatus
long-tailed	Aegithalos caudatus
marsh	Parus palustris
Twite	Carduelis flavirostris
Vulture, bearded	Gypaetus barbatus
Woodcock	Scolopax rusticola

List of plants in the text with approximate Latin equivalents. Most of these names were verified by Professor B.A. Tikhomirov in Edmonton in October of 1962.

Almond (tree)	Amygdalus
Ash, mountain	Sorbus
Bilberry	Vaccinium myrtillus
Birch	Betula
Crowberry	Empetrum nigrum
Fir, (silver)	Abies
Grass, feather	Stipa
Horsetail, (winter)	Equisetum scirpoides or variegatum
Huckleberry	Vaccinium vitisidaea
Larch	Larix
Oak, Mongolian	Quercus mongolica
Pine	Pinus
Plane tree	Platanus
Pondweed	Potamogeton
Poppy	Papaver
Rosemary, marsh	Ledum palustre
Saksaul	Haloxylon
Sorbaria	Sorbaria
Spiraea	Spiraea
Spruce	Picea
Stone-pine (Siberian)	Pinus sibirica & P. pumila
Korean	P. koraiensis
Willow	Salix

APPENDIX D

Gazetteer of Russian place names mentioned in text and located in Atlas Mira (1954). Those with asterisks are also in The Times Atlas of the World (1959).

	Lat.	Long.
	o '	o '
*Abagaitui	49.35N	117.55E
*Abakan, R.	53.40N	91.30E
Abyshkan	54.40N	76.20E
Achishko	43.40N	40.10E
*Achinsk	50.15N	90.30E
Achitnor, Lk. (= Achitanur)	49.30N	90.30E
*Akmolinsk	51.10N	71.30E
*Aksuat, Lk.	51.25N	64.30E
*Aktyubinsk	50.20N	57.10E
*Alakol'	46.00N	82.00E
Alashan', Mts.	38.30N	105.40E
*Alekseyeoskoye	55.20N	50.05E
*Aley, R.	52.50N	83.40E
Altai	53.30N	91.45E
*Alushta	44.40N	34.30E
*Amgun', R.	52.55N	139.40E
*Amu-Dar'ya, R.	43.30N	59.00E
*Amyl, R.	53.50N	92.50E
*Anadyr	64.40N	177.30E
*Angara, R.	58.10N	93.00E
Anyui, Big R.	67.00N	160.40E
Anyui, Little R.	67.00N	161.00E
Argun', R.	53.20N	121.30E

	Lat.	Long.
	o '	o '
*Arzamas	55.20N	43.50E
*Askaniya Nova	46.30N	33.50E
Astrakan'	46.25N	48.05E
Ayansk	56.30N	138.10E
*Azerbaidzhan	40.00N	38.00E.
*Baku	40.20N	49.59E
*Baladzhary	40.25N	49.45E
*Balagansk	53.40N	103.20E
*Balakhna	56.25N	43.35E
*Balkash Lk.	46.00N	74.00E
Barabinsk Steppe	53.00N	78.00E
Baranov, Cape	69.40N	164.00E
*Barguzin	53.40N	109.30E
*Barguzin, R.	53.25N	109.00E
*Barguzin, Mts.	54.30N	110.20E
*Barnaul	53.20N	83.15E
*Batumi	41.40N	41.40E
*Baturin	51.20N	32.50E
*Belaya, R.	55.35N	51.30E
Belovyezhya Forest	52.30N	24.00E
Berezovka	67.40N	155.15E
Besingi (=*Bezengi Glacier)	43.05N	43.10E
*Bezhetsk	57.45N	36.45E

	Lat.	Long.
	o '	o '
Bira, R.	48.10N	133.20E
Birma, R.	51.30N	128.40E
*Biryusa, R.	57.40N	95.15E
*Biysk	52.30N	85.15E
*Blagoveshchensk	50.20N	127.30E
Blagoveshchenskoye	58.10N	62.55E
*Bogosski, Mts.	42.20N	46.15E
Borovoye	51.10N	27.15E
Borovoye	51.40N	28.00E
*Borskoye	53.00N	51.45E
*Borozya	50.25N	116.30E
Botchi	48.00N	139.30E
*Bryansk	53.15N	34.10E
*Buguruslan	53.40N	52.30E
Buiba	52.40N	93.20E
*Bukhtarma, R.	49.40N	83.30E
Bulun	70.40N	127.20E
*Bureya, R.	49.30N	129.30E
*Buzuluk, R.	52.50N	52.15E
*Chanchur, R.	53.50N	107.00E
Chany, Lk.	54.50N	77.30E
*Chara, R.	60.15N	121.00E
Cherepovets	59.10N	37.50E
Cherkassk	48.35N	38.55E
Cherkassk (=*Cherkasskoye)	48.50N	37.25E
*Chernigov	51.30N	31.20E
Chorokh, R.	41.40N	41.40E
Chu, R.	42.30N	76.10E
*Chukchi, (=*Chukotski)Penn.	66.00N	174.00E
*Chuna	61.20N	93.00E
Chunozero	67.40N	32.30E

	Lat.	Long.
	o '	o '
*Chusovaya, R.	58.05N	56.40E
*Daubikha	44.50N	133.30E
*De Kastri, Bay	51.30N	140.45E
*Dem'yanka, R.	59.40N	69.20E
*Dezhneva, Cape	66.10N	169.30W
Dickson, (=*Dikson) Isl.	73.30N	80.30E
*Digora	43.10N	44.10E
*Dinnuan'in, (=Bayan-Khota)	38.50N	105.40E
Dnieper, (Dnepr), R.	46.30N	32.20E
*Dniester, (Dnestr), R.	46.10N	30.20E
*Don, R.	47.10N	39.15E
Donets, R.	47.35N	40.55E
*Dubovka	49.05N	44.50E
*Dubrovnoye	58.00N	69.20E
Dusse-Alin', Mts.	52.00N	135.00E
Dzelkalak (=Dzeltulak?)	55.00N	125.10E
Dzherdzhin, R.	68.40N	124.00E
*Dzhurun	49.15N	57.30E
*Echmiadzin	40.10N	44.20E
Egra-lyaga (=Ydzhig-Lyaga)	62.30N	59.00E
*Emba, R.	47.30N	56.40E
Ergak-targak-taiga, R.	53.00N	94.30E
Fadeyev, (=*Faddeyevski) Isl.	75.00N	144.00E
*Gagra	43.20N	40.15E
Gan'su, Mts.	38.00N	103.00E
Getkan, R.	55.10N	124.40E
Gilyuy	54.00N	127.00E
Girbichek, R.	51.50N	129.10E
*Glukhov	51.40N	33.50E
Gobi Altai, Mts.	44.00N	102.00E
*Gorbatov	56.05N	43.10E

		Lat.	Long.
		o '	o '
Gori		42.00N	44.10E
*Gor'ki		57.45N	45.05E
*Goryachinsk		53.00N	108.20E
*Grozny		43.20N	45.40E
*Gudauta		43.10N	40.10E
*Gur'yev		47.10N	51.50E
*Gusikha, R.	(?)	58.20N	108.45E
Gutara, R.		54.50N	97.25E
Ik, Lk.		56.05N	71.30E
*Ik, R.		51.50N	56.20E
Ilek, R.		51.35N	53.25E
*Ilych, R.		62.30N	56.45E
*Imambaba, Lk.		36.45N	62.25E
*Imandra, Lk.		67.50N	33.30E
*Irbit		57.40N	63.05E
Iremel', Mts.		54.40N	58.45E
*Irgiz		48.40N	61.20E
*Irkutsk		52.15N	104.20E
*Irtysh, R.		58.15N	68.20E
*Ishim, R.		57.40N	71.00E
*Iya, R.		55.30N	102.10E
*Izyum Forest		49.15N	37.20E
*Kaban'		54.40N	66.30E
Kaban'ye, Lk.		56.10N	71.25E
*Kalakan		55.10N	116.45E
*Kalinin		56.50N	35.55E
Kaluga		54.30N	36.15E
*Kama, R.		55.10N	49.20E
*Kamyshin		50.05N	45.24E
Kamysh- Samarski, Lk.		48.50N	50.00E

	Lat.	Long.
	o '	o '
Kanin, Penn.	68.00N	45.00E
*Kansk	56.15N	95.50E
*Karabash	55.30N	60.15E
*Karaganda	49.50N	73.05E
*Kara-Kum	40.00N	60.00E
*Karatau, Mts.	43.30N	69.00E
Kara-us, Lk.	48.00N	92.00E
*Kargopol'	61.30N	38.55E
*Karkaralinsk	49.25N	72.25E
*Kasli	55.50N	60.45E
*Katunski, Mts.	49.45N	86.40E
*Kazachinskoye	57.45N	93.15E
*Kazalinsk	45.45N	62.00E
*Kazan'	55.45N	49.10E
*Kazbek (=Kazbegi), Mt.	42.40N	44.30E
*Kazyr-Suk, R.	52.40N	92.20E
*Kema, R.	45.25N	137.15E
*Kem'	65.00N	34.30E
Kentei-alin', Mts.	45.00N	131.00E
Kerak, R.	53.55N	125.10E
*Ket, R.	58.20N	90.05E
*Khabarovsk	48.30N	135.05E
*Khamar-Daban, Mts.	51.40N	106.00E
Khangai, Lk.	48.00N	98.00E
Khanka, Lk.	45.00N	132.30E
*Khatanga, R.	73.00N	106.00E
Kheta, R.	71.50N	102.20E
*Khibiny, Mts.	67.45N	33.30E
*Khodzent	40.15N	69.50E

	Lat.	Long
	o '	o '
*Khora, R.	47.50N	134.40E
*Khrenovoye, Forest	51.10N	40.20E
Khurke, (=Khurkhe), Mts.	42.30N	105.30E
*Kiev	50.30N	30.30E
*Kil'din, Isl.	69.20N	34.15E
*Kinel', R.	53.15N	50.30E
*Kirenga, R.	57.40N	108.10E
*Kirensk	57.45N	108.05E
*Kirov	54.05N	34.25E
*Kishinev	47.00N	28.50E
Kizi, Lk.	51.40N	140.20E
*Kizlyar	43.50N	46.45E
Kobdo	48.00N	91.40E
*Kochechum, R.	64.20N	100.30E
Kola Bay	69.15N	33.30E
Kola, (=*Kol'ski) Penn.	68.00N	36.00E
*Kolguyev, Isl.	69.00N	49.00E
*Kolva, R.	66.00N	57.15E
*Kolyma, R.	69.30N	162.00E
*Koryak, Mts.	62.00N	170.00E
*Kotel 'ny, Isl.	75.00N	140.00E
Krasnopolyanski	53.30N	61.00E
*Krasnoyarsk	56.00N	92.50E
*Kuban', R.	45.20N	37.20E
*Kuma, R.	54.50N	46.55E
*Kumara	51.40N	126.40E
Kureika, R.	66.30N	87.10E
*Kurgal'dzhin, Lk.	50.30N	69.20E
Kurgan	55.30N	65.20E
*Kursk	51.45N	36.15E

	Lat.	Long.
	o '	o '
*Kurtamysh	54.55N	64.25E
*Kustanai, Steppe	53.20N	63.30E
Kuyagan	51.45N	84.50E
*Kyshtym	55.40N	60.30E
Kyzylagach (= Kizil-gach) Gulf	39.15N	49.00E
*Kyzyl-Kum	42.00N	66.00E
*Laba, R.	45.15N	39.40E
Lapushek	54.45N	67.15E
*Lenkoran	38.45N	48.50E
*Lokot'	51.10N	81.15E
Loukhi, Lk.	66.15N	33.20E
*Lukny	50.00N	33.00E
*Lyakhov Isl. Greater	73.30N	142.00E
*Lyakhov Isl. Lesser	74.00N	141.00E
*Malaya Karmakuly	72.25N	52.50E
*Maloyaroslavets	55.00N	36.30E
*Mama, R.	58.20N	112.50E
*Mamakan, R.	57.45N	114.00E
Mana, R.	56.00N	92.10E
Mangut	55.45N	70.45E
Mariinsk	51.40N	140.15E
*Mariupol' (=*Zhdanov)	47.05N	37.35E
*Markovo	64.40N	170.30E
*Marre-Sale	69.40N	66.55E
*Matochkin Shar	73.15N	56.30E
Mazanovo	51.40N	128.45E
*Mendel', R.	58.20N	90.05E
*Mezen	65.50N	44.20E
*Miass	55.00N	60.05E
Mikhailo-semenovski (?)	50.40N	127.20E

	Lat.	Long.
	o '	o '
Mikhailovski = (*Mikhaylovskiy)(?)	51.40N	79.45E
*Mil'sk, Steppe	39.50N	48.00E
*Minsk	53.50N	27.40E
*Minusinsk	53.45N	91.40E
Minya, R. (Big)	56.40N	107.45E
*Mius, R.	47.15N	38.45E
*Mogilev	53.55N	30.20E
Mogot, R.	55.20N	125.00E
Monche , Lk.	68.00N	32.45E
*Mugodzhar, Mts.	49.00N	59.00E
Mulinkhe (=*Muling), R.	45.50N	133.30E
*Murgaba, R.	36.20N	62.35E
Nakh, R.	61.00N	77.00E
*Nal'chik	43.30N	43.35E
*Nem, R.	61.35N	54.50E
*Nercha, R.	51.55N	116.40E
New (=*Novyy) Port	67.40N	72.30E
*New Siberian Islands	75.00N	140.00E
Nichaka (? =*Nechatka), Lk.	57.45N	117.30E
Nikol'skoye	50.55N	128.20E
N(izhne) Ilimski	57.15N	103.20E
*Nizhne-Kolymsk	68.30N	161.00E
Notai, R.	55.00N	107.00E
*Novaya, R.	72.30N	103.00E
*Novgorod	58.30N	31.20E
*Novokhopersk, Forest	51.05N	41.35E
*Novorossiysk	44.45N	37.40E
*Novozybkov	52.30N	32.00E
Nukatl', Pass	42.10N	46.30E
*Nukha	41.15N	47.10E
*Nyazapetrovsk	56.05N	59.30E

	Lat.	Long.
	o '	o '
*Ob', R.	66.40N	70.00E
Obor, R.	48.30N	136.30E
*Ochakov	46.40N	31.35E
*Odessa	46.30N	30.45E
Ognit, R.	54.30N	99.15E
Oirotia	43.15N	73.30E
*Oka, R.	54.20N	40.50E
*Ol'doy, R.	53.30N	123.20E
*Olekma, R.	60.20N	120.40E
*Olenek, R.	72.30N	120.00E
*Omolon, R.	68.40N	158.30E
Onega, (=*Onezhskaya) Bay	64.30N	36.00E
Onega, (Onezhskoye) Lk.	62.00N	35.00E
*Or', R.	51.20N	58.30E
*Orel	52.55N	36.05E
*Orenburg (=Chkalov)	51.40N	55.10E
*Ostashkov	57.10N	33.10E
*Oya, R.	53.25N	91.50E
*Pal-pal, Mts.	63.00N	170.00E
*Pavlodar	52.20N	77.00E
*Pechora, R.	68.30N	54.00E
Pechoro-Ilychski, Nat. Park.	62.20N	58.00E
Peno	56.55N	32.45E
Perekop	46.20N	35.00E
*Pereslavl'-Zalesski	56.35N	38.50E
*Petropavlovsk	55.00N	69.00E
*Peza, R.	65.40N	45.00E
*Poltava	49.40N	34.30E
Puri	50.45N	118.05E
*Radde	48.40N	130.40E
*Riga	57.00N	24.00E

	Lat.	Long.
	o '	o '
*Rioni, R.	42.10N	41.45E
*Rodchevo	66.05N	151.00E
Rostov	47.15N	39.40E
*Rubtsovsk	51.40N	81.10E
*Russkoye - Ust'ye	71.00N	149.00E
*Ryazan	54.40N	39.40E
Sailugem, (=*Saylugem), Mts.	49.30N	88.30E
*Sakmara, R.	51.50N	55.20E
*Salekhard	66.35.N	66.35E
*Samara, R.	53.15N	50.00E
Samurskaya	44.15N	39.50E
*Sandykachi	36.40N	62.30E
*Sarapul	56.30N	53.45E
*Saratov	51.30N	46.00E
*Sarysu , R.	46.00N	67.00E
*Selemdzha, R.	51.45N	128.50E
*Semenov	56.45N	44.30E
Semenova	51.40N	127.40E
*Semipalatinsk	50.20N	80.20E
Semirechka, R.	53.15N	94.10E
*Sengileyevski, (=Sengileyeskaya)	45.05N	41.45E
*Severnaya Zemlya	79.00N	98.00E
*Shar'ya (= Sharia)	58.20N	45.30E
*Shilovo	54.20N	40.55E
*Shirvan, Steppe	40.20N	48.00E
Shugor	64.20N	57.30E
*Signakhi	41.40N	45.55E
*Sikhote - Alin'	48.00N	138.00E
*Simferopol'	44.55N	34.10E
Sita, R.	48.40N	136.30E
*Skovorodino	54.00N	124.00E

		Lat.	Long.
		o '	o '
*Smolensk		54.45N	32.05E
*Sok, R.		53.25N	50.10E
Soloneshenski (?=*Soloneshnoye)		51.40N	84.40E
*Sos'va, R.		59.35N	62.20E
*Sredn(y)e - Kolymsk		67.30N	153.30E
*Stalingrad		48.45N	44.30E
*Stavropol'		45.00N	42.00E
*Sula, R.		49.15N	32.45E
*Sungacha, R.		45.05N	132.50E
Sungari, R.		47.40N	132.30E
*Surgut		61.15N	63.15E
*Sym		60.30N	90.00E
*Syr-Dar'ya, (=*Syr-Daria), R.		46.00N	61.00E
*Sysert'		56.30N	60.45E
*Tagul, R.		55.40N	97.40E
Taimura, (=*Taymura), R.		63.45N	98.00E
Taishet, (=*Tayshet)		55.55N	98.00E
Talyshinski, Mts.		38.30N	48.30E
*Tambey		71.30N	71.50E
*Tannu-Ola Mt.		51.00N	93.00E
Tara		56.55N	74.25E
Tarbagatai Mt.	(?)	46.30N	82.30E
Tarbagatai Mt.	(?)	49.20N	86.30E
*Tashkent		41.20N	69.20E
Tatishchevo		51.45N	54.15E
*Tavda		58.00N	65.15E
*Taz, R.		67.30N	79.00E
*Tbilisi		41.40N	44.45E
*Teberda		43.30N	41.50E
Temir, R.		48.30N	57.20E
Tepsel, R.		52.25N	92.25E

	Lat.	Long.
	o '	o '
*Tereka, R.	43.40N	47.30E
*Terney, Bay	45.00N	136.40E
*Tigil'	57.50N	158.40E
*Tikhaya, Bay (= Bukhta Tikhaya)	80.20N	53.00E
*Tikhvin	59.40N	33.30E
Timiryazev	57.05N	42.20E
*Tiraspol	46.50N	29.40E
*Tobol, R.	58.15N	68.15E
*Tobol'sk	58.15N	68.15E
*Tom, R.	56.50N	84.30E
*Troitsk	54.05N	61.40E
Tsar'grad (=*Istanbul)	41.00N	28.55E
*Tukuringra, Mts.	54.30N	125.00E
*Tula	54.10N	37.40E
*Tulum	54.35N	100.35E
Tundak	55.15N	117.10E
Tunguska, (*R.)	63.40N	90.10E
*Turgai' (=*Turgay)	49.40N	63.20E
Turgai (=*Turgay)	51.45N	72.40E
*Turinsk	58.05N	63.40E
*Turka, R.	52.55N	108.15E
*Turtas, R.	58.20N	70.00E
*Turukhansk	65.25N	88.00E
*Tutura	54.45N	105.10E
*Tyan'-Shan', Mts.	42.00N	80.00E
*Ubagan, R.	54.20N	64.45E
Uda, R.	56.05N	99.40E
*Uda, R.	54.30N	103.15E
*Uda, R.	54.40N	135.00E
Ufa.	54.45N	55.55E

	Lat.	Long.
	o '	o '
*Ulan-Bator	48.00N	107.00E
*Ulu-Tau (=Ulutau)	48.40N	67.00E
*Ul'yanovsk	54.20N	48.25E
Unzha, R.	57.20N	43.10E
*Ural'sk	51.15N	51.20E
*Urkan, R.	53.20N	126.55E
Urushten, R.	43.55N	40.40E
*Uryumkan, R.	52.30N	120.10E
*Us, R.	52.10N	92.15E
*Usman'. Forest	52.00N	39.40E
*Ust'- Kamenogorsk	50.00N	82.40E
Ust'-Sysol'sk	61.40N	50.50E
*Ust' Tara	56.45N	74.40E
*Uzhur	55.20N	89.45E
Vaigach, Isl. (=*Vaygatch)	70.00N	59.00E
*Velikiye Luki	56.20N	30.30E
*Verkholensk	54.10N	105.30E
*Verkhoyansk	67.35N	133.25E
*Vetluga, R.	56.20N	46.30E
Vidnoye	47.10N	134.20E
*Vitebsk	55.10N	30.10E
*Vladikavkaz (=Daudzikau)	43.00N	44.40E
*Vladivostok	43.10N	131.55E
*Vologda	59.15N	39.50E
*Vychegda, R.	61.20N	46.30E
*Wrangel, (= Vrangelya) Isl.	71.00N	180.00E
*Yakutsk	62.10N	129.50E
*Yana, R.	71.30N	136.00E
*Yankan, Mts.	54.30N	124.00E
Yaroslavl'	57.35N	39.50E

	Lat.	Long.
	o '	o '
*Yashma (= Yamsha)	40.45N	49.25E
*Yekaterinoslavka	50.20N	129.10E
*Yenisey, R.	71.00N	83.00E
*Yugorskiy Shar	69.40N	61.00E
Zaisan, Lk.	48.00N	84.00E
Zanguzur, Mt.	40.00N	46.00E
*Zemlya Franz Joseph	81.00N	56.00E
*Zeya, R.	50.20N	127.30E
*Zhdanov (=Mariupol')	47.05N	37.30E
Zhelaniya, Cape	77.00N	69.00E
*Zlatoust	55.10N	59.40E
*Zolotaya	52.05N	92.40E

Place names used in text but not listed in Atlas Mira. In most cases the approximate locality is evident from the context.

Agadsk
Amanach
Berezovaya
Beshelaksk
Bireya, R.
Buguly
Chalkar, Lk.
Chebarkul, Lk.
Chernakovski
Chernogorka
Chodokolo
Chushka-Kul', Lk.
Chushkaly, Lk.
Dichenkovaya
Dvoryanskoye
Dybidoba
Dzhigit , Bay
Getkan,R
Gutarsk, Lk
Isel'
Kaminskaya
Kamysh-Samara, R.
Kebezha, R.
Kop'
Kopchi, Lk.
Korgina
Koval,' R.
Kozlinaya
Krolug, R.
Kudaor, R.
Kuvan'
Kychemetski
Laman-Gegena
Lars
Lesnoye
Maina - pul'gin, Mts.
Maral-tyube
Mysovaya
Oiger
Palabino
Pal'yu, R.
Petushki
Podoli
Poilovaya, R.
Poperechka, R
Sangel'ski
Semikul
Shipovoy, Forest
Sidyashevoy, Forest
Simbirski
Surozhki
Taivaz
Talovaya, R.
Tana - el'v
Tarsk (=Tara)
Tashkul
Tas-Khandavyt, R.
Tatosh
Tikhi
Uchansk
Uge-ioki
Urots
Urun
Ust' Ust
Vishennaya
Voronezhskoye
Voznesenski
Vyazovka, R.
Vydrino
Yelisavetgrad

THE SIGNIFICANCE OF SNOW COVER IN THE ECOLOGY AND GEOGRAPHICAL DISTRIBUTION OF MAMMALS AND BIRDS.

by

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in

The Role of the Snow Cover in Natural Processes.

Institute of Geography, Acad. Sci. U.S.S.R., Moscow, 1961.

Memorial volume in honor of G. D. Rikhter.

M. I. Iveronova, Editor.

Translator - E. Issakoff

Editor - W. A. Fuller

THE SIGNIFICANCE OF SNOW COVER IN THE ECOLOGY AND GEOGRAPHICAL DISTRIBUTION OF MAMMALS AND BIRDS.

In any geographical region, where sufficiently steady snow cover remains for at least three or four months of the year, its significance in the life of the plant cover and of the great majority of animals is doubtlessly very great and diverse. But up to now we know in fact very little about the ecological role of this sometimes light and porous, and sometimes more compact, snow layer which periodically covers the earth, as we know very little about the way in which its geographical distribution effects the distribution of animals.

We have more data in our literature than other countries but in general these data elucidate only a few questions, in particular the influence of the snow cover on the conditions of movement of animals and the possibilities of their getting food, on the seasonal migrations of ungulates, as well as the role of the hard spring crust (nast) which in some years leads to the exhaustion or to the destruction of a series of species of animals and birds (Formozov 1939, 1946; Kirikov, 1946, 1952; Nasimovich, 1955; Dulkeit, 1957 and others).

The variability of the height and of the structure of the snow thickness in different geographical regions, or on different kinds of soils in the same region and the same habitat, but at different periods of the winter, in different years make the study of the ecological role of this factor a very difficult problem. The difficulty of its study is also connected with the fact that the lengthy subnivean life of many small mammals does not lend itself easily to direct observation. Ways to study the conditions which are created in the sleeping dens of

gallinaceous and other birds have also not been worked out as yet. That is why the relationship between the study of the snow cover, the ecology and the ecological geography of the animals is at present in the state of a gathering of factual material and hardly pretends to make broad generali-
p.167 zations. This article has also the character of a preliminary communication and deals especially with "suspended" and "ground-in" snow crusts. (Prof. Formozov calls "suspended" crusts those that are carried on layers of snow. Such crusts include crusts which form on the surface of the snow cover and those which, covered by a layer or layers of fresh snow, become interlayer crusts in the thickness of the snow. "Ground-in" crusts are those formed directly on the ground, covering it as a shield.) As is generally known these crusts appear very often under snow cover on a great part of the territory of the U.S.S.R. The existence of such hard interlayers in the thickness of the snow cannot but influence the conditions of life of animals especially the small mammals, which are active in winter, as well as the life conditions of resident birds which spend the winter in our lands.

The described observations have been made during systematic trips at different seasons in 1948-1959 to the Pushkin, Zagorsk and Zvenigorod rayons of the Moscow Oblast' and separate winter trips to the Vologod and Kostroma Oblasts. In the neighborhood of the villages Zelenograd and Sofrino in the Pushkin rayon of the Moscow Oblast', there has been made at least every seven or ten days snow measurements on separate parts of the usual itinerary which led through open spaces as well as through forests of different character. Several times during winter, in the field, in the spruce forest, and in clearings in forests, the structure of snow cover in

sections in special digging holes has been studied. As to its characterization we used with certain changes the classifications suggested by G. D. Rikhter and L. D. Dolgushin (1950). The observations of the behavior of animals and birds made at the same time, as well as the constant study of the tracks of animals and of their activities, gave us the possibility to judge of the ways in which the snow cover of a definite thickness and structure affects the life of the winter fauna. In addition to these observations, in spring, as soon as the snow began to go, we surveyed the places where the small animals had wintered as well as their subnivean trails and nests. This has given us a series of additional biological data which we could not have obtained during the winter tracking of animals along their trails.

The smaller the animal the weaker is its muscular energy and the more difficult becomes its fight for existence, which is conditioned by the varying compactness of the snow, the thickness of icy crusts and the time these remain icy, as well as by the diversity of the structure of the snow cover in different habitats and even in varying parts of the same habitat. For small animals the existence of even a very thin ice crust is a serious obstacle while drilling through the snow vertically or while making long sloping trails.

We shall give an example explaining this situation very well. Near the village of Lutsina, Zvenigorod rayon on January 22, 1941, we saw a track of a small shrew (Sorex minutus) which came out of a damp pinewood adjoining a sphagnum bog and attempted, with temperatures at -30 C and no wind, to cross a field of 300 meters in width beyond which there was a wood of a mixed variety of trees. The ice crust 2-3 mm in depth, which had

p.168 been formed on the field after a thaw, was on the day of the observation covered by a 3-4 cm layer of fresh snow on which the tracks were distinctly seen. For about 110 meters the little animal ran fast, but as soon as the frost made itself felt it tried to dig itself into the snow to warm itself up. The compact ice crust, thin as it was, prevented the shrew from getting into the depth of the snow beyond the boundary of the extremely cold surface layer. On the next 150 meters the shrew attempted to dig itself in four times, then abruptly turned back to the spruce forest, making on this last lap of 100-120m ninemore stops attempting to dig itself in. (Fig. 1). At the end of this trail it lay under the layer of light snow on the ice crust, frozen and shrunken into a small clot hard as ice. In the forest, the ice crust which was very thin and hardly noticeable at all, occurred in patches between the trees, but under the crowns of spruce trees and pines it was completely absent. In such conditions, small shrews easily get onto the surface of the snow and dig themselves into the snow as deep as the frozen ground. Having gone out into an open field when it was very cold the little animal perished because the structure of the snow cover in the field was somewhat different than that of the snow crust in the forest.

As it will be shown further, cases where small animals perish while migrating on an ice crust or layer of snow hardened by the wind sometimes reach mass proportions, but even for very large animals the conditions of the structure of the snow cover are far from being indifferent. An easily crumbling or breaking ice crust hinders a predator sneaking up to a watchful victim. It lacerates the feet, renders movements difficult, and obliges it to change the place of the hunt. The hard, next-to-the-ground crust, shielding grass, fallen leaves and the flora of lichens

leaves the ungulates and rodents without food.

p. 169 The moose, the largest ungulate animal of our woods, easily overcomes the deep, light, powder snow if it does not reach up to its belly, but "gololeditsa" or even a thin crust of snow that has been soaked with water and then frozen, especially if such a crust is lying on the frozen soil, sharply diminishes the moving capacities of the moose who avoid treading on a slippery or lacerating substrate. A.A. Liverovski, who has observed moose during a series of years near Leningrad (in the Lisinski Forest), informed us of a very characteristic case. A group of moose was freely moving about in November and in the first days of December, 1946, over light, not deep, snow during a thaw. But on December 7, when they were in a small wood, measuring about 300 x 400 m, the temperature fell during the night to -14 C. In spite of the fact that on the next morning on three sides of this wood there began the felling and dragging of trees, burning of branches and driving of a three-ton truck, the moose did not venture onto the hardened snow, although they could have moved along a narrow belt of trees to the central part of the wood which was undisturbed by anything.

The well known Danish zoologist, Vibe, (1958), has made extensive studies of the variability in the numbers of the mammals in Greenland during this period of time. He found in particular that a great number of musk-oxen (Ovibus moschatus) perished a few years ago in one of the regions of eastern Greenland because a definite and clearly expressed warming up of the climate has taken place. This change of climate has produced the falling of rains during winters and this resulted in the formation of compact ice crusts and among them evidently, low lying crusts carpeting the ground. The musk-oxen easily dig grass and the lichens from under

comparatively light snow with their hooves but they cannot break the ice. The gololeditsa has doomed them to death from hunger. Cases of mass death of wild reindeer from hunger provoked by gololeditsa are known to have occurred in Novaya Zemlya and Novosibirsk Islands. Much more seldom are recorded in the literature cases of such catastrophes occurring to animals of the deserts of the southern regions of the land. We shall quote an interesting communication given G. I. Ishunin and E. P. Korovin (1945): "The winter of 1934 in Badkhyz (in the extreme south of the Republic of Turkomenia) had been especially hard and was distinguished by the formation of gololeditsa. The ground was covered with ice for a long period of time and the cold wind blew dry, light snow over the ice crust. During this winter in the sectors of Islam-Cheshma and Salt Lake a great number of kulans perished. A wild mountain sheep (Ovis orientalis)was taken without a shot. It had slipped on an icy slope and had fallen. The Asian gazelles suffered more than other ungulates. Near the sectors of Kara-Changa and the Cheguretsk pits, as well as near Dunguzla, bodies of these antelopes were often found on the slopes (sometimes as many as
p.170 thirty head on one spot). According to hunters there were very few gazelles after that winter."

These examples show that temporary sharp changes in the structure of the snow differing from the long term normal, are capable of producing changes in the numbers of large animals and possibly even affecting the boundaries of their distribution. As to what concerns the small animals and the birds, one can say without exaggeration that in middle and northern latitudes, the fate of these wintering populations is often fully dependent on the constantly varying rigor of the weather as well

as on the strength and the structure of the snow cover. Climatologists and ecologists still seldom use indices of the severity of the weather, for the calculations of which, according to the formula of Bodman, data about the speed of the wind and the temperature of the air are necessary in addition to two constant coefficients. As these are different at the same hour in different sectors of the same region, for accurate ecological studies one cannot fully rely on the data of meteorological stations, even if these are situated in the neighborhood. Unfortunately, we have not ourselves made observations of the velocity of the wind when we studied the winter life of animals, and therefore we must forego the use of indicators of the rigor of the weather in spite of the fact that it is very important for the understanding of the conditions of loss of warmth by homeothermic animals with a small body mass and with a comparatively large body surface as is the case with the majority of small mammals and birds. So it happens that in our observations there exist deplorable lacunae but one can presume that our observations, as they are, will be useful for further studies.

The Structure of the Snow Cover in the Winter Life of Small Rodents and Insectivora.

The belief that with the coming of winter all the activities of animals not subjected to winter sleep is concentrated on two levels is rather widely spread. It is believed that the activities of animals are conducted either only above the snow or on the level of the ground under the protection of the snow cover which softens subzero temperatures. This belief is right only in part. In reality, under the snow cover, the whole snow thickness from top to bottom is full of signs of life, of animal and bird trails, of diggings, chambers and hollows, of every dimension and intention. This is especially characteristic for the snow cover of forests, forest-steppes, and steppe zones in years when the number of rodents is great, and to a lesser extent for the tundra where the great hardening of the snow cover by the winds makes it difficult for the lemmings and the voles to make their trails beyond the horizons of light powder snow.

Already in the first hours of the first snow fall the small animals begin to make trails in the fresh, light, snow cover. Sometimes because
p.171 of a change of weather, so common in the beginning of winter, one can observe in thawing, two or three days old snow, separate trails 100-150 m long and longer made by immigrating gray voles (Microtus arvalis). Already when the depth of the snow cover measures about 2-3 cm the voles, lemmings, and shrews prefer to move about under its protection, that is, to dig through the light thickness and not move openly on the surface, where, against the white background they can be clearly seen by any predator.

When the snow is not very thick they do not always succeed and we have more than once observed how the gray voles and the steppe lemmings cut into the thin layer of snow with their bodies evidently supposing they will dig through it.

Migration and collecting of food under the snow naturally diminish the danger of attacks by bird predators. On October 23, 1946, in the neighboring of Sofrino, the height of the snow cover on the winter crops did not exceed 1-3 cm, on the stubble and fallow fields it reached 5-6 cms, and in some furrows 35 cm, whereas on the edge of the forest, in the valleys, small drifts had already accumulated. On this day, we met many tracks of the subnivean migration of gray voles from the fields from which the harvest had been taken away, towards the edges of woods and places where trees had been felled. The little animals were going across meadows that had been mown, and there, where the layer of snow was too thin, the roofing of the trail passages sometimes collapsed. In five of such places we saw in the snow that magpies had been digging, attempting to catch the voles which had become visibile in the collapsed parts of the trails.

This speaks for the fact that predators watch very attentively the movements of small animals and if it were not for the protective layer of the snow very few small animals would reach places favorable for spending the winter. As the thickness of the snow layers grows the system of trails spreads out in both horizontal and vertical directions. Not seldom in connection with the distribution of food supplies and the condition of movement, a network of galleries on several levels is established in the thickness of the snow layer. These galleries are connected by vertical and sloping passages.

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1. See for instance the data of S. N. Varshavski (1937), about the death rate of the field mice migrating on snow in the Don Steppes.

Even the mole, feeding in winter as well on earthworms and soil insects, which he gets from out of the frozen floor of the forest, the moss cover, or the soil, makes from time to time long snow passage trails on the level of about 20-30 cms above the surface of the earth, as well as an intricate net of passages threading through the next-to-the-ground layer of snow. (Part of them has only the "ceiling" made of the snow and the bottom and sides of earth or moss). The walls of mole's snow galleries are made compact by the energetic movements of the small animal's muscular body. They always become icy whereas the floor of the galleries is smeared with the earth the mole carries along on his feet. Such passage galleries lead through light snow from one hunting ground of the mole to another, through places poor in food, or covered with a compact next-to-the-ground crust of hardened snow.

p.172 The passage trails of small animals dug before the start of the winter become gradually wider and wih time become lightly coated with ice. If strong thaw does not occur and the passages are not flooded with thaw water, followed by frost, the endless net of snow passage trails is used all through the winter by small animals of the most varied species.

So for instance, it has been established by trapping and the studying of tracks, that snow galleries made by the gray voles are used by rusty voles, shrews, weasels, the ermines and the moles.

In early spring, passage trails coated with ice, as well as the furrows bitten through the turf by voles or dug by moles in the dead floor of the soil become passages for the drainage of thaw water and play a substantial part in the transport of the plant detritus, that is,

of small parts of leaves cut up by the little animals, and broken up parts of the humus horizon. This affects the processes of soil formation. The thermal conditions in the next-to-the-soil layer of snow through the greatest part of the winter are more favorable for the small animals than those in the higher layers of snow. However, in the end of the winter when the sun begins to shine with greater strength, part of the long wave solar radiation begins to penetrate the upper 10-20 cm of the snow thickness and the little animals often move higher up to warm themselves. Some of them even run about on the surface of the snow. In moderate zones, this is especially characteristic of shrews, rusty voles, wood mice and pigmy mice. These daytime vertical migrations towards the surface of the snow are most easily observed in the case of small animals inhabiting stacks of hay or straw. In the casing of snow which clothes these, in the sunny days of February and March, on the south and southwestern side, a great number of passage trails made by voles and mice appear.

But contrary to the conditions of temperature, the composition of the air in the lower, next-to-the-earth layer of snow, is less favorable for the little animals than those in the upper layers; moreover the diffusion of gases through the thickness of the snow is slowed down to a great degree (Rikhter, 1948). This especially obliges many species of small animals which live in winter only under layers of snow, leading a rather sedentary existence, to drill through the snow thickness vertical ventilation passages which open up on the surface. We have suggested that these snow passages be called "air vents" (Formozov, 1937) and this term has now been accepted by many zoologists. The little animals regularly prolong the air vents, and clean them of snow which falls in to keep them open, but they use them very rarely as ways of communication

with the surface. However, on the very highest lap of such an air vent the little animals appear very often and rather constantly spend there a certain amount of time, being evidently attracted by fresh air. The temperature gradient between the deep part of a passage trail and the surface of the snow provokes a flow of air upwards and owing to this the p.173 air vent functions as an air sucking chimney. During prolonged bright and freezing weather the outlet of an air vent is sometimes encircled by small shaft or tube composed of large crystals of hoar frost. They are formed by the cooling of water vapors which come from the passage trail of the little animals which thread through the lower, next-to-the-earth, warm layer of the snow thickness. The existence of the little shaft at the outlet of the air vents is a most convincing proof of a current of air moving from below upwards.

Our conjectures as to the ventilation role of air vents has been recently confirmed by N. B. Bashenina (1956) who has established the existence of a great quantity of carbon dioxide gas in the air under the snow in places where gray voles generally spend their winters. It is characteristic that air vents are encountered especially frequently where there are colonies of gray voles (M. arvalis), field mice (M. agrestis) and root voles (M. oeconomus). These colonies are situated in meadows where there are large supplies of green herbaceous plants. The gray vole makes air vents in the snow if it winters on clover and winter crop fields. Much more seldom are encountered air vents made by the rusty voles (Clethrionomys glareolus) and shrews. In the places where bushes, or thick stemmed herbaceous plants grow and surmount the surface of the snow, the snow does not usually settle evenly and compactly. The swaying of the plants by the wind contributes to this. The hollows which are formed evidently facilitate the exchange of air and the little animals

often forego making air vents in such places. The mole clears a small number of his vertical passage trails in the snow cover only during the first months of the winter but later open passage trails resembling the air vents of the voles have been encountered extremely seldom. There is reason to consider that moles, as highly specialized underground animals, are not so sensitive to the lack of oxygen in the air and are therefore less in need of regular airings of their undersnow passage trails. Finally, the ermine and the weasel during their hunt for rodents in colonies of voles, not infrequently bore vertical passages through the thickness of light, powdered snow but evidently only to look out and watch that the scared little animals do not escape over the surface of the snow.

The existence of air vents on the colonies of the voles of the genus of Microtus is a fact which at first glance might seem unimportant but in reality it has great importance in the question of the distribution of the wintering population of owls. Observations in Stavropol'ya, winter 1946 and 1947, have shown that the steppe brown owl often watches for voles while sitting on a high place (a pole, some bushes and so on), 2-3 meters away from an air vent. In the Voronezh Oblast' in the winter of 1951-1952 when great numbers of grey voles had been noticed, we had, during two excursions, registered in the fields more than ten cases of bog owls (Asio flammeus) watching for these rodents. The owls
p.174 wait for the appearance of the little animal in the air vents always from the backside of the trail, and at a distance not greater than 20-30 cm from it. Often on the tracks of an owl near an air vent we have found drops of blood or thrown out bowels of the vole that had been

caught by the owl. In the same year in the Voronezh state reserve, we frightened away long-eared owls (Asio otus) patiently waiting on tree stumps or lower branches of trees for the appearance of the rusty vole in an air vent.

As is known, during the heavy snow and frost period of the winter, small rodents move along the surface of the snow very unwillingly (Formozov 1946). Often the region may seem quite devoid of grey voles or root voles, whereas in reality on every hectare many scores of these little animals spend the winter. In these conditions, only the existence of the air vents made by the field mice gives the owls a chance to get the necessary amount of the little animals and to winter successfully, during prolonged cold spells and snow storms. A bog owl which was shot by us in the Voronezh Oblast' in January, 1952 in the place of its hunt for voles, was very well fed. On the contrary, a male owl found frozen in January, 1947 on one of the sites in Stavropol'ya was completely exhausted and weighed 232 grams. At this season, the number of voles and mice in most of the regions of Stavropol'ya was very small and owls perished from hunger.

In the second part of the winter, after a hard snow crust has been formed on the surface of the snow, the number of air vents above the colonies of voles diminishes sharply and often they are completely absent. This may indicate that the entire population has died out or has been exterminated by predators, according to the opinions of some researchers. But sometimes, as far as we have been able to observe, this is due to a better aeration in the next-to-the-ground layer of snow,

after the formation of the light snow horizon, a fact which makes the upkeep of air vents unnecessary. Finally, very often this disappearance of air vents indicates that the little animals have moved elsewhere because of the formation of a "compressed" crust, as a result of flooding by thaw waters. So, for instance, in the beginning of the winter of 1958-59 on small meadows in the kitchen gardens of the suburbs of Moscow, the snow passage trails of voles were distributed comparatively evenly. After a series of strong thaws and numerous floodings, on January 10, 1959, when the average snow cover on this sector reached 41 cm, we were able to observe only three air vents and all the three were situated next to the walls of the sheds. At that time there were in the whole thickness of the snow cover, two interlayer ice crusts, the upper one from 8-9 mm thick, the lower one 6 mm thick. A third crust, 20mm thick, was firmly bound with the sugar snow which lay directly on the ground. Two weeks later, on January 24th, the height of the snow cover
p.175 reached 54 cm and the number of crusts was augmented by one more, and all air vents disappeared. One could have thought that all voles had perished, but in reality, the majority of them had come to live in the barn where, along logs that had been laid in a heap they penetrated into the hay which was lying in the loft. In the hay they spent the second half of the winter. This could easily be established by the traces of their life activity. When the snow had gone, several winter nests of voles were found on the site; in two of them were tufts of fur and pieces of skins of small animals, a fact that indicated that bodies of perished animals are eaten up by others of the same species.

The appearance of a deep horizon of light snow, and of hollows under

the hard snow crust that has been formed under the influence of wind is a rather common phenomenon. It is well known to hunters that in the fields even when using rather wide skis the upper compact layer of snow suddenly gives way with a loud noise and sinks over the space of some 100-150 m. This noise prevents the hunters from sneaking up to watch for animals and birds and renders hunting more difficult. (S.T. Aksakov has picturesquely described this a long time ago.)

Much more seldom does such a sudden sinking of the surface layer of snow occur in forests and hinder the hunters because the trees and bushes everywhere hold up the snow crust that has been frozen to them on a permanent level[2]. Under the surface of the snow layer are formed whole labyrinths of connected hollows. This is especially characteristic of forest sectors with a strong undergrowth consisting of silver firs, pines, junipers, spreading cedars or young spruce trees or leafy trees on clearings or burnt out flats. On such sites one encounters usually a lot of high stemmed herbs such as willow herb, bear's pipe, meadow sweet and others also holding up the snow. Here it always lies very unevenly and great hollows appear under branches and tufts of grass after the very first heavy snow falls.

Snow crusts, those on the surface of the snow cover, or forming interlayers in the thickness of the snow, as well as those lying directly on the ground, also are distributed in such places unevenly, in small patches, and are always distinguished by a greater weakness than those on open spaces. This insures better aeration and in some places where the snow is less compact, evidently also, more favorable temperature conditions in the next-to-the-ground layer of the snow thickness, and what is not less important, a good penetration of the snow thickness in all directions.

2. In case of a strong wind around the stems of trees, cracks often appear with radiating branches and sometimes two or three rows of circular ones. This indicates that the swaying of tree trunks has an influence on the structure of snow cover.

In the forest-steppe, and the steppe thickets of bushes, patches of high feather grass and spear grass, patches of wild growth on places where trees have been felled, fields with high stubble, protected strips of wood, are distinguished by a higher and less compact snow cover than the fields of winter crops, pastures and cleared areas. Under the
176 protection of thickets and high stubble which holds up the snow, the small animals find the best conditions for spending the winter if they have enough food on the spot. But in the conditions of open landscape with a flat relief, the snow cover is always of a more even height, compactness and structure than on forested sites of equal dimensions. That is why one can conjecture beforehand that the appearance of glare ice or next-to-the-ground ice crusts must exercise a more steady and strong influence on populations of small animals and birds in the field than on the animal populations of the woods.

The conditions of aeration in the next-to-the-ground layer of the snow cover are certainly much more varied and complicated in separate types and sections than they are in non-forested spaces with similar relief. The question of composition of air in the snow and under the snow in the case of a different density and structure of the snow cover, and differences in the specific composition and condition of herbaceous plants, as well as the condition of the dead litter and of the soil, deserves special study as it would serve to elucidate the as yet obscure conditions of the winter life of small vertebrates.

Further observations of the distribution of air vents and the length of time of their existence, might give material to be used as an indicator of the conditions of populations of some of the species of voles and even

of the conditions of their existence during this or that period of the winter in thelower layers of the snow cover. These small animals play an important part in the damage done to the fields and woods. Very great is their role in the keeping alive of the natural reservoirs of a series of illnesses of humans and animals. At the same time, the winter period of their lives, often playing a decisive part in the perpetuation in the numbers of their population, is especially difficult to study. That is why new research methods must be sought.

The significance of the snow cover in the winter life of small animals is in general very great especially as the layer protecting them from the direct influence of low temperatures and the wind, a fact which, together with the existence of fresh green food preserved by cold, creates conditions fully favorable for the life of certain species. Very telling is the fact that forms that feed on coarse bulk food and the seeds of arboreal species begin to reproduce again during the frosty months after an autumn interval.[3] In the tundra zone subniveen reproduction in winter has been established in the case of the Norwegian and the Ob' lemmings and the varying lemmings (Lemmus lemmus, L. obensis and Dicrostonyx torquatus) and the large narrow-skulled vole (Stenocranius gregalis major) and of a series of lemmings inhabiting North America. Young born in winter have been found in the following animals: the water rat, the red vole and the rusty vole (Arvicola terrestris, Clethrionomys rutilus and Cl. glareolus) the wood and the yellow necked mice (Apodemus sylvatica, A. flavicollis) of the forest zone; the grey and narrow-skulled voles and the steppe lemming (M. arvalis, Stenocranius gregalis, and Lagurus lagurus) in the forest-steppes and steppes. In the forest zone of the

3. In the case of some species, the autumn period of reproducing is followed directly by the winter period.

western Caucasus after a good harvest of nut-bearing trees, an intensive winter reproduction has been established in the case of species feeding on concentrated foods, such as the wood and yellow-necked mice (Apodemus sylvatica, A. flavicollis). When the winter ecology of rodents is more carefully studied, a series of other species will probably be added to the list.

Evidently, neither the lack of sunlight nor the comparatively low temperatures can hinder the reproduction of lemmings and voles if the height of the insulating snow cover is great enough and if food is abundant. Successful reproduction in winter when the destruction of rodents by predators is sharply diminished, or mass death caused by unfavorable winter weather are decisive factors in the fluctuations in the numbers of small animals which play a dominant part in the biocenosis of numerous landscapes. That is why observations of the subnivean life of rodents and insectivores and the assessment of the ecological role of the snow cover are absolutely necessary for establishing accurate prognoses of the members of harmful species as well as the valuable fur animals which feed on rodents, to forestall certain epizootics and mass winter damage done to fruit trees, tree nurseries and young shoots of valuable trees by voles.

T. N. Dunaeva and V. I. Osmolovska (1948) have suggested an ingenious method of the prognosis of numbers of arctic foxes a year in advance, using as an indicator the finding of new-born lemmings in the stomachs of arctic foxes caught in winter. The hunting of arctic foxes is used in this case as a factor facilitating to a high degree the observations of what goes on in the lemming nests under the thickness of

the snow. Frequent findings of young lemmings dug out by the arctic foxes from nests testifies to an intense winter reproduction of lemmings. In such winters, the mating period of arctic foxes occurs in good food conditions and in summer the feeding of the young fox cubs coincides with the period when the numbers of lemmings attain their maximum. This insures a good increase in the number of arctic foxes and a good hunt for them in the next hunting season.

Sometimes, as a result of an intensive reproducing of field m ice during one winter period, there occurs a striking change in the aspect of animal populations. For instance, in the summer of 1945, according to our
p.178 observations in the steppes of the southern part of the Kustanaiski Oblast' there were few lemmings and grey voles and the birds of prey so characteristic of the steppes--harriers and bog owls which are specialized mouse eaters--were correspondingly very rare. Having returned to the region in the beginning of the summer of 1946, we were astonished even on our way there by the unexpected abundance of bog owls and steppe and meadow harriers. It became clear that the numbers of rodents had grown sharply during this single winter. It became known that after the mild autumn of 1945, which was rich in precipitation, rather large amounts of green plants had grown under the snow and the little animals could easily use these food supplies owing to a rather deep and light snow cover. Everywhere amidst the growth of grasses and wormwood, the snow blown by the winds had accumulated. We found nests of grey voles with signs of winter reproduction. In the summer of 1946, the appearance of the animal populations of the Kustanaiski steppes was quite different from that in the previous year.

Returning to the question of the usage of the thickness of the snow cover for making passage trails, one must note that small animals constantly penetrate into the upper layers, not only arranging the air vents, but also looking for food or else moving to new places. This enhances the ecological significance of the changeability of the structure of the snow cover. In the forest zone, the winter dropping of seeds of birch, ash, maple and lime trees, as well as the cutting of cones of spruce, pines, larch, and berries of mountain ash and juniper by some species of birds and mammals, create in different layers of the snow thickness, supplies of valueable food for other species. Sometimes a snow crust that bacame compact after a thaw and was coated with ice ever since the beginning of winter, makes many thousands of cones thrown down in autumn by cross-bills nearly inaccessible to small animals. In these cones, as is well known, a considerable part of the valuable seed, which is distinguished by high food values, remains untouched. The cones thrown down in a frosty period sink into light snow and here, protected from cold and attacks of the owls, the rusty and red voles constantly use the remaining spruce seeds. Therefore the thickness of the snow under the spruce trees on which crossbills have fed, is usually threaded with passage trails of the voles, whereas on the surface one encounters only footprints of chickadees and crested tits (Parus atricapillus and Parus cristatus) which are searching for the few seeds lost by crossbills.[4]

).179 In this way the snow cover, depending on the number and the strength of compact crusts, may regulate the use of a variety of grasses, seeds, and as will be shown later, animal foods for certain groups of mammals and birds. Among the small mammals, this concerns not only the rodents and

4. Until the scales of the cones open, and this happens usually in March or at the end of February, the seeds are inaccessable to tits. The tits begin to hang on the cone and pull out the seeds only in spring before these are ready to fly out, and then gather them in masses from the surface of the snow.

insectivores, but precisely the mass inhabitants of the forest, the shrews (Sorex araneus, S. Minutus, S. macrogynaeus) which willingly eat up the seeds of spruce, pines, larch and birch trees. So, for instance, where the linnets have fed on the birches and have thrown down onto the snow many scales and small winged seeds, one constantly encounters footprints of shrews, especially the small species. The small animals use these patches of seed food even after they have been completely covered up by snow. Of definite significance for the shrews is the fact that in late autumn, for a long time, the insects and the spiders migrate vertically, descending from the crowns of trees to spend the winter in the forest litter. Not seldom does a part of these invertebrates descend onto the snow when the temperatures are already from -2 to -5 C. Alternating warm periods and snowfalls during frost, bring about a stratified distribution of caterpillars, insects and spiders in the thickness of the snow cover and corresponding to it, a dense net of hunting trails of the shrew is also distinguished in layers which contain food. (Fig. 2).

The snow accumulated on the branches falls off from time to time but this snow, which is soaked by moisture during the period of thaw, and during an incursion of comparatively warm, moist, sea air, becomes heavy, and when falling carries with it lichens, fir needles, and bits of bark together with the caterpillars wintering in them and their eggs. This forest fall-out, clearly seen on the snow, is carefully, but for a short time, searched by tits and then for a longer time by shrews which drill through the snow in the patches under the projection of the crown of the most densely branched trees. Leaves that have fallen to the surface of the snow are picked up by musk deer and forest voles (Clethrionomys).

The latter search for them in the thickness of the snow cover even after new snow falls. Finally in the snow along the trunks of young trees or in the undergrowth and young shoots, small rodents make vertical passage trails eating up the bark, small branches, and buds.

In this way, according to the degree of accessibility and the location one must distinguish not only the subnivean and surface foods, but those in the very thickness of the snow cover. The peculiarities of the snow cover may facilitate or render more difficult the activity of the little animals searching for food. For the moles which during the whole winter search intensively for food in the forest litter and in the upper layers of the soil, the most essential layer of snow is the lower one, about 20-30 cm thick. When the snow is light the mole easily creates a star shaped system of short snow dens above his vertical trails leading underground, some of which he then fills with earth thrown up from deep galleries. When the snow is light it is
p.181 easier for him to drill through the floor litter and the moss cover. When the lower layers of snow are icy, the mole is obliged to dig deeper trenches in the floor litter and arrange emplacement for the thrown out earth considerably higher in the layer of light, soft snow. The earth thrown out by the mole remains until spring in the guise of large mounds and is usually more rapidly washed out when the snow thaws than the earth lying on the ground. The digging of a vertical passage trail in firn snow and the transport of the earth higher requires considerably more effort on the part of the little animal.

Much more sensitive to the appearance of hard interlayer crusts in the snow thickness are the small shrews. These very small and exceedingly greedy little animals are during the winter ceaselessly

on the go, searching for food in the dead litter of the forest floor and into the snow cover itself. The round-the-clock need for food of various kinds of these insectivores is inversely proportional to the weight of their bodies. For instance, a least shrew (Sorex tscherskii) with its body weighing from 1.8 to 2.9 grams consumes round-the-clock an amount of food equalling 400% of its body weight.

As the lower layers of snow grow more compact it is the representatives of the smallest species that experience the greatest difficulties. It is more difficult for them to manage the making of passage trails than it is for the strong common shrew (Sorex araneus). This is indicated by the great amount and the length of the snow tracks of the least shrew which is obliged to search for food on the surface when it cannot get any under the snow. Judging by the foot prints this little animal is more often subjected in winter to attacks by the moss-footed owls and magpies than its stronger and larger relatives (according to observations in the Moscow and Kostroma Oblast's). It is sufficient to recall the frequent appearance of compact next-to-the-ground ice crusts in steppe zones and in the ploughed-up regions of the forest zone to become convinced how much more favorable are the living conditions of this little animal in forests. Evidently, this is one of the peculiarities of the forest zone which is the cause of a great number of species and individuals of shrews inhabiting this zone, while they are extremely scarce in the steppes and deserts.

It is generally known that after the appearance of a sufficiently strong next-to-the-ground ice crust the numbers of most species of

voles diminish sharply. There exists an opinion that the destruction of these animals is caused by ice corks which close the entrance of dens. Experimental studies of the activities of voles and observations amidst nature have shown that these small animals--consumers of coarse bulky foods--have a definite rhythm of very frequent feeding excursions. With such a type of activity, the basic passage trails of dens are regularly cleared out and only in exceptional cases may they become impassable because of ice formation. Apart from this a number of voles live in winter in nests situated in the snow sometimes at a height of 20 to 30 cm above ground level where ice corks cannot be formed at all. The next-to-the-ground ice crust with food plants such as green shoots of perennial cereals, wormwood, and the small leaves of winter crops frozen into it, renders the feeding of the little animals extremely difficult. The biting through of the ice or of the hard frozen snow which shields every leaf and shoot demands tremendous expenditure of energy, all the more so as the round-the-clock need for food of the small animals is comparatively great (depending on the food value and its assimilibility they consume an amount of food equaling 80-150% of the weight of their body.)

The small animals, which suffer hunger because of the inaccessibility of food, go out onto the surface of the snow if possible, and not seldom does the whole population of enormous areas come into disorderly movement. While attempting to find more favorable conditions, part of the voles get into straw copses, haystacks, and stores of hay where they find refuge and an abundance of food. Part of the mice reaches growths of bushes or edges of forests, where, as we have

already indicated, the snow crust is distributed in patches and they can penetrate under the snow and feed on bark. But the majority of the little animals freeze to death on the surface of the snow or perish from exhaustion and illnesses that become acute during periods of hunger or else become a prey of the predators.

Very characteristic in this respect was the winter of 1954-55, exceptionally warm in the northern part of the Black Earth Belt of the European part of the USSR. After the December snow falls rain fell and the following frosts transformed the soaked snow into ice with plants frozen into it. I.Vasil'ev (1955) has pointed out that in February the next-to-the-ground crust in a series of regions reached the thickness of 15 cm and winter crops in the Kursk Oblast', for instance, had been under the ice crusts for over two months.

The map (Fig. 3) shows the size of spaces in the limits of the European territory of the USSR which had an ice crust in the third decade of January 1955. About the influence of the conditions of this winter on the life of small rodents, (basically grey voles, and in part house and field mice) there have been received many reports from the agronomists of the MTS and the State farms of the Orlov, Kursk, and Lipetsko Oblasts.[5] Information about the next-to-the-soil crust being from 15 to 20 cm thick and to the mass destruction of rodents came from the Sudzhansk, Mezdinsk, L'gov, Kastorensk, Solntsevsk, Zerbynsk, Khvorostyansk, Novo-dereven'e, Streletsk and other rayons of the above mentioned Oblasts. In some places up to

5. The information came as answer to questionnaires sent out by V.V. Gruzdev, a co-worker of the Biology and Soil Faculty MGU who placed them at our disposal.

p. 184 60% of the area of the fields had been flooded by snow water which soon was transformed into ice. The death rate of the little animals was noted since January in the periods of glare ice as well as after a fresh snow fall. Dead animals were found in great numbers on the surface of the snow and by their tracks one could judge of their unsuccessful attempts to get away from these very unfavorable places. Only a few succeeded in reaching stacks of straw or belts of forests. The voles were perishing in such masses that their numbers could not be restored during summer and remained very low in autumn 1955. Information sent by correspondents fully confirmed the data of special investigations that have been carried out in the region of Kursk Oblast' by the sanitary-epidemiological stations.

V. P. Mosolov (1936) has established that the former Kursk Province was one of the provinces where winter crops perished from ice crust the most frequently. On his map characterizing the distribution of areas where winter crops perished because of ice crusts during a period of 35 years (1899 to 1934) this province is situated in regions where such cases occur most frequently (six times in the mentioned period of time). In the Kursk Province there have also been frequent cases of winter crops freezing out because of intense cold which followed upon periods of thaw, a fact which, according to our observations, exercises an unfavorable influence not only on plants but on small rodents. The damage done to winter crops was frequently so considerable that in 1902 it had been necessary to sow anew on 25% of the area under winter crops. The same was necessary in 1907 on 20% of the area and on 40% in 1908. Probably the numbers

of voles on the fields of the whole Oblast' which is frequently damaged by ice crusts must be unsteady but we cannot speak about it in a positive way as yet because of the unsufficiency of data.

The ice crust as a cause of a mass destruction of small rodents was alluded to in different oblasts of our country many a time. So G. P. Gorbnov (1929) wrote that in 1926 on Novaya Zemlya were encountered many arctic foxes and they seemed to be well supplied with food, as toward the autumn, there appeared many lemmings. But when the snow fell a thaw began and then suddenly severe frost struck, the earth was covered with an ice crust and the arctic foxes were left without food. In winter an epizootic broke out among the arctic foxes which resulted in a great death rate among them.

In the summer of 1923 in the steppes of the southeastern Ukraine social and grey voles (Microtus socialis and Microtus arvalis) appeared in exceptional numbers and house mice were also very numerous. We were able to observe a phase of such a mass reproduction during our work in the reserve of the Askaniya Nova. According to reports of A.A. Braunera (1928) the number of exits from dens of rodents attained towards autumn about 40,000 per hectare, 13,000 exits being encountered very often. In the winter of 1923-24 nearly all the voles and mice perished because the high snow cover had thawed twice and the earth was covered by a thick layer of firn under which the small animals could neither move nor breathe and in 1924 there were no inhabited dens (except in one place). N.M. Semonov (Semenov et al, 1955) mentions facts concerning the death of grey voles and house mice in

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the Volgo-Akhtubinsk basin. In the winter of 1941-42 (period of mass reproduction of the little animals) because of strong snow storms, a fall of deep snow, and a following formation of glare ice, the numbers of rodents in open steppes began to decrease sharply as early as the first days of December. This process continued later as well, as the glare ice conditions returned several times. In the year 1948 in Kharabalinsk, Enotaevsk, Prevolga, and Sasykol'sk rayons and on the islands of the delta of the Volga was noted a mass reproduction of rodents (predominantly the house mouse--90%, the second place was occupied by the field mouse--8-10%, with a few grey voles--about 1%). In the second 10 days of November, their number began to decrease because of rains, severe cold and glare ice. Their reproduction was stopped and the glare ice conditions produced mass deaths. According to V. P. Khrustselevski (1954) even in the southeastern Transbaikalia with its definitely continental climate the formation of glare ice in the steppes may lead to a sharp decrease in the numbers of the Brandt's voles (Microtus(Phaiomys) brandti). Such a case was noted for instance in 1950. In the semi-desert part of southeastern Precaucasia a strong formation of glare ice was the cause of the destruction of the social vole.

As may be seen from data in the literature the significance of glare ice is very great in the conditions of a landscape with a very low and weak plant cover, (grasses and lichens) which may completely freeze into the ice crust. Not a small importance have the peculiarities of the soil cover. So for instance, in those deserts where autumn and winter precipitations are predominant (for instance, in Karakum) on the

sands the ice crusts scarcely ever form at all whereas in the same Oblasts but on clay soils an ice crust is a common phenomenon. Sand quickly absorbs rain and snow water and no layer capable of forming an ice crust remains on the surface. The absence of glare ice makes sands an especially valuable pasture land for the grass eating ungulates, (gazelles and saiga antelopes) as well as for domestic animals (sheep and horses). This peculiarity is favorable also for the small rodents which are not subject to winter sleep, for the endemic shrew of our sand deserts--the "putoraka" (Diplomesodon pulchellum) and for the Tolay hare which is especially numerous within the boundaries of sand deserts.

Our observations testify to the fact that the appearance of glare ice in steppe conditions exercises strong influence on the rusak (a species related to the Tolay hare). So in the winter of 1951-52 till January 5 there was scarcely any snow at all in the Voronezh Oblast' but the fields were covered with an ice crust 2 to 3 cm thick. When fresh, new snow fell on January 9 and 10 we were convinced that the rusaks could not get the winter crops and feed on dry weeds (goose foot and others) along the edges of fields and valleys. Literature data confirms the same. According to the report of Yu.A. Loman (1895) in the beginning of December 1894 in the neighborhood of the Ratsynsk forestry (Khersonsk Province) there was a strong glare ice formation which lasted for two weeks and all the herbaceous plants were covered with an ice crust. The hares changed over completely to feeding on the bark of trees, biting it off on the side where it was not coated with ice and causing a great deal of damage. There hardly remained an

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undamaged maple, oak, or honey locust and fruit tree nurserys had also been badly damaged.

The endemic of the sand deserts of Central Asia--saksaul jay (Podoces pandori)-- is a resident bird that procures food during all the winter by digging it out from the sand with its beak. Its food consists in this season of seeds, beetles and soil larvae. On its winter tracks are encountered hundreds of small diggings to the passage trails of the larvae. Apart from this, beginning in the autumn the jay buries in the sand supplies of food (chiefly seeds of grains) which it used up during the winter. The resident existence of this comparatively weak-beaked bird in the sand deserts would be completely impossible if glare ice or next-to-the-ground ice crusts of frozen through snow formed often there. This example shows that the structure of the snow cover may influence the distribution of animals. It is probably not by chance that a species related to our jay, the Mongolian desert jay (Podoces hendersoni) a stronger beaked form living in conditions of the nearly snowless climate of Central Asia has occupied not only the sands, but also the clay and broken-rock desert with bushes. Its range is situated in the region where the possibility of formation of glare ice is practically nil. The common jay (Garrulus glandarius) in the Moscow Oblast' easily gets acorns from under light snow but those that have been frozen into the glare ice remain inaccessible to it; it only lightly pecks at the upper parts of the acorns protruding from the ice.

Even the tree climbing rodent, the squirrel (Sciurus vulgaris), suffers from glare ice in some cases. So for instance on January 30 1949 during the tracking of squirrels in the Zvenigorodsk rayon of

the Moscow Oblast' (in the neighborhood of Lutsina) it was easy to see they often moved about on the ground as fresh harvest was absent from the trees. We often encountered diggings of squirrels to the cones which had been thrown down by cross-bills in the previous year, but in more than 20% of the cases the small animals could not get them from out of the ice crust which lay on the ground. It was curious to observe that one squirrel digging for food in a thin spruce-birch plantation went four times below the snow, mining the light layer
p.187 that overlaid the hard crust. It had passed under the snow for 30 m and on this lap of its track there were only three short exits onto the surface and several where the ceiling of its passage trail had fallen in. The shape of the passage trail under the snow, the straightness of it, and its very length testified to the skillful drilling of the snow cover, something that one does not easily expect from the small tree-climbing animal with a tall delicate fur and a long fluffy tail.

On December 31, 1958, in the spruce forest neighboring on fields (near the station Zelenograd) we walked along a track of a squirrel which had nowhere climbed onto trees. The height of the snow cover in this spruce forest reached from 8-14 cm, (12 cm on the average.) The winter of 1958-59 was extremely poor in food for the squirrels--during the preceeding autumn on these spruce trees there was no harvest at all, pine trees bore seed cones only here and there, one could have assessed its harvest not higher than two or three points, and there were extremely few acorns on the oaks. The squirrels searched for the spruce cones that had been thrown down by the cross bills as well as for mushrooms, but the next-to-the-ground ice crust at the edges,

where the warm winds easily penetrated, was so hard that here the little animal could not use the cones it had found. There is no doubt that the searching for fallen acorns and hazel nuts, constituting in some years the basic winter food of the squirrels living around Moscow, was exceptionally difficult during this winter in many regions. This hungry winter became exceptionally hard for the squirrels because of the number of interlayer ice crusts in the thickness of the snow and the next-to-the-ground crust which was observed in some types of forests. By the end of January when the height of the snow cover reached in the spruce groves from 30-50 cm (45 cm on the average) and from 60-70 in the clearings (65 on the average) in its thickness on the clearings there were 6 interlayer hard crusts. The majority of them remained to the end of March.

In certain years voles do a lot of damage to fruit trees and nurseries of forest trees. According to our observations a measure of such damage depends on the number of voles as on the conditions of their wintering and in particular on the structure of the snow cover and on the freezing through of the soil. The root vole (Microtus oeconomus) and the dark field vole (Microtus agrestis) and in some habitats the grey one (Microtus arvalis) dig out from unfrozen soil rhizomes and tubers of perennial herbaceous plants.(willow herb, angelica, wild radish, chicory, dandelion, some buckwheat plants and many others.) In spring after a mild winter one can find thousands of shallow funnel shaped holes remaining on the emplacements of destroyed rhizomes. If the seasonal frost is not interrupted by thaw from autumn to spring the foods below the surface of the soil remain

inaccessible for these voles. The appearance of a neat-to-the-ground crust renders the digging-out of parts of plants remaining green through the winter more difficult. In these conditions the grey vole can exist only on emergency food--the bark of trees and branches.

p.188 In autumn 1950 the number of grey voles was very great (according to visual calculations up to 5 points) and this in Pushkin rayon of the Moscow Oblast' as well as near Zvenigorodsk where winter buzzards (Buteo lagopus). (These carrion vultures winter in the neighborhood of Moscow only in years when voles are numerous and easily accessible.) On April 1, 1951, when after 5 days of intensive thawing about 80% of the field surface was free of snow it became evident that this had all been dug up and cropped by the voles. There were few winter nests on the stubble fields but lots of them on the clover fields. The soil had not thawed as yet. On April 9 the fields were already completely bare of snow but in spruce forests it still remained on 20-30% of the area. On this day, we again carefully examined many places inhabited by voles. We encountered many cases of the winter cropping of grass but not a single case of damage done to trees. Finally, on April 21 of the same year on our itinerary of 20 km we found only in two or three places tops of aspen trees broken by the snow that had been gnawed by voles.

In this way while the numbers of the voles (Microtus arvalis) were very great and the soil had been frozen through, no damage was done to trees. This happened because of the fact that the autumn of 1950 had been mild, had lasted a long time with occasional rain falls

and so many plants had gone under the snow in their fresh green state. Thaws that alternated with frost had created already in the first ten days of December the situation that obliged part of the voles to migrate along the surface of the snow (on December 10 we noticed many traces of immigration). But the next-to-the-ground ice crust was absent that winter and the lower layer of snow did not hinder the mice from eating the green plants.

In Autumn 1948 the number of small rodents and especially the grey voles in the Pushkin and Zagorsk regions was also very great (5 points). On the first fresh snow in October there were many foot-prints of voles and mice. In spring 1949 after the snow had gone on the stubble fields near the village of Sofrino, there were about 50 winter nests of grey voles to a hectare. Here, in the nests there were no traces of the death of the little animals. On another field where the left-over stubble was high (near the village of Rakhmanova), the density of the winter population of grey voles was considerably greater; 131 nests per hectare, and about 20% of these nests had been destroyed by a fox during winter while in another 20% there was found tufts of fur and skins of voles indicating that the bodies of dead voles had been eaten by others of their species and in 2.9% of the nests were found bare skeletons of voles. In some nests were found traces of reproduction (probably in autumn under the snow) but only in 1.4% of the nests did we find definite traces that a least weasel had visited them. (It is extremely difficult for this predator to penetrate into the winter nests of field mice when an early next-to-the-ground ice crust has been formed.)

Spring assessments have shown us that on the fields of rye where the rye has been harvested in autumn and clover has been sown

and where there has been an exceptionally great number of voles in autumn, the number of inhabited spring nests proved to be from 12 to 15 times smaller than the number of winter nests had been. This testifies to the sharp decrease in the numbers of the small animals. This was not only the result of the activity of predators but rather of the death rate of the voles in winter and early spring and also of their migration to growths of bushes and edges of forests. In the beginning of May when the snow had gone in the forest, one could see everywhere aspen branches, the bark of which had been gnawed off by voles. These branches had been left on places where trees had been felled. The bark of young trees had been gnawed off the trunks to a height of 70 cm. The next-to-the-ground ice crust had prevented the voles from drilling through the dry grass and obtaining green shoots and leaves in the fields as well as on forest clearings. Because of a mild winter and of a high snow cover voles which had migrated to the forest and were obliged to feed on bark of trees had time to damage many young trees and bushes.

Similar traces of the winter activity of grey voles and of the damage done to young aspen trees were noted in the neighborhood of the station Buzhenina on the Northern Railway and further to the north east on the boundaries of the Moscow and Vladimir Oblasts. Evidently the area over which similar conditions of wintering prevailed was very great.

We were able to observe in the spring of 1941 in the Pereslav

region of the Yaroslov Oblast' (to the west of Pleshcheyevo) considerable damage done to the bark of trees including pine trees by root voles and rusty voles, but the conditions under which the little animals had wintered remained unknown to us.

From the 19th to 22nd of April, 1953, on the River Nepl' in the neighborhood of the village of Rogozinin we had noted the greatest damage we had ever witnessed done to trees by the gnawing of the young trees on slopes of hillocks that were surrounded by damp meadows and marshy valleys. The flooding of low lying areas by thaw waters in the beginning of winter, and the formation of ice on patches of sedge growths had chased the voles away (according to left-over traces and bodies found in spring mainly Microtus agrestis and Microtus oeconomus), to slopes grown with brush where trees had been felled which were poor in grass but densely covered with young leafy growth. We encountered here districts measuring several square hectares where there were many young aspen trees (with a diameter of the trunk measuring from 1-3.5 cm) whose bark had been completely gnawed off. On the sites where trees had been felled, the majority of the young, growing trees looked as though their lower parts had been painted with light paint and this whiteness was noticeable from afar. The damage done to the bark began on some trees at the level of the soil and on some at a height of 15-20 cm., evidently in the places where there were patches of compact snow. Many trees had all their lower branches cut off, gnawed into short pieces and completely bared of bark. These bare bits of branches,

light as matches, had been firmly packed into the winter passage trails so that after the thaw of the snow they lay there like
p.190 miniature stacks of wood. Besides the aspen trees, young willows, shoots of hazelnut, oaks and spindle trees were also badly damaged. According to calculations made by N. V. Bashenina, who visited these regions in June of the same year in order to assess the percentage of dead trees, (in spring before the appearance of leaves this had been impossible) on the average 36.7% of aspen trees, 28.8% of hazelnut shoots, 12.5% of young oaks and 5.8% of honeysuckle had been damaged out of the whole number of trees surveyed on the experimental plots and strips. Of the number damaged, 80.6% of hazelnut shoots and 63.3% aspen trees perished.

The winter migration of root voles from boggy, low-lying patches to places where trees had been felled in the depths of the forest, occurs basically under the protection of the snow and that is why the structure of the snow cover has a substantial significance for the expansion of the migrations of small animals. It also determines to a great extent whether they shall damage trees or not. The following example illustrates this. In the autumn of 1943, in the boggy district of the Moscow State Reserve there were many root voles. In the spring of 1944, it became known that in the neighborhood of the flood plains in the basin of the River Pushta, these field mice had badly damaged the new growth and had penetrated even into the nurseries with young larch trees. These nurseries were traversed by a trodden path which was used in winter aswell and led from the administration building of the reserve to one of the sectors. Yound larches were found to be damaged only on the district lying between the forest and the path. The bulk of hard trodden-down snow along

the path stopped the further penetration of the root voles into the nurseries.

It is known that the heaping of snow around the trunks of fruit trees and stamping it firmly down creates a sufficient protection from attacks by grey voles which are capable in years of winter migration, and when they are very numerous, of doing an enormous amount of harm to young orchards. In the note of S. Nagibin (1918) is described one of the cases of the mass reproduction of grey voles in the black earth belt. In the winter of 1916-17, there were so many of these little animals that the snow cover, both in the forests and in the orchards, was discovered in spring during thaw, to be threaded through by canals of mice passage trails and the soil, bared of snow, and not yet covered up by growing plants, was found to be completely dug up by dens. In the gardens and forests the mice had done a lot of damage by eating the bark of trees. In one orchard the bark on the majority of young apple trees had been gnawed off in a ring thus the trees were doomed to perish. Not only young trees but 15-year-old ones with hardened bark had been damaged.

The trodden down, compact snow of ski trails constitutes also a serious obstacle to the under-snow movements to small animals. Not seldom can one observe the passage trails of rusty voles and shrews open up on the soft edge of one side of a ski trail and go under on
p.191 the other side. The rusty voles and the shrews migrate much more often along the surface of the snow than do the voles of the genus Microtus. That is why meadow barriers do not constitute such a serious obstacle to them as they do for the grey, field and root voles.

In the winter of 1958-59, the flooding of some sectors of forests and meadows by thaw waters, and the appearance in the thickness of the snow of a whole series of hard crusts, provoked exceptionally large migrations of the small animals including under-snow migrations. In the spring of 1959 when the thawed out snow passage trails of grey voles, which stretched for hundreds of meters along the forest meadows near the hamlet of Zelenogradskaya were surveyed, it was easy to notice that reaching a trodden winter path, these passage trails turned aside, continued along its edge, branched out into different directions and even turned back, but never crossed the path.

In the winter of 1952-53, the number of grey voles in the Pushkin rayon was low (1-2 points). After the snow had fallen it was difficult to find winter nests even in the large areas of the fields where wheat had been harvested in the previous autumn and in clover fields, but in some places, for instance, in the wheat fields near the village of Talitsy there were found small patches rather densely populated by grey voles (up to 100 winter nests in one hectare). In the forests there were scarcely any rodents at all, but noticeable damage to the trees had been done by the rusty voles (Clethrionomys glareolus).

On April 11, at the time of the thawing of the last snow on the itinerary from the village of Zelenogradskaya to the village of Fomkino, there were encountered many aspen trees which had been broken by the snow, and from which the bark was gnawed off for a distance of 4-5 m by rusty voles.[6] The same little animals had gnawed young trees and many spruce cones that had been thrown down by crossbills.

6. After several heavy snowfalls in the first days of December 1952, many trees had been bent and broken by the snow including spruce trees and pines.

The cones were lying in the upper layers of the snow cover and were used by the little animals during the second half of the winter. At this period the rusty voles settled among the dense branches of the willow and ate a lot of its buds. On a clearing we found a winter nest with the remnants of a body of a rusty vole; all of this indicates that the conditions of wintering were hard.

Actually, after heavy snow falls in the end of November and the first half of December 1952, there was a strong thaw and the thaw water covered the frozen earth in many places; the compact snow turned into a hard crust. On December 21st, on the freshly fallen snow which had covered the firn snow on the surface we noticed an exceptional number of tracks of rusty voles and shrews. Ten days later tracks of rusty voles predominated and there were fewer shrew tracks. We noticed the trail of a rusty vole leading from a den to a place where squirrels had gnawed at many spruce cones (searching for seeds lost by the squirrels). On January 4, 1953 an icy crust appeared on the trees and the snow. On January 19th after several snowfalls, the height of the snow cover in the meadows and in the forest reached 46 cm (on the average 43 cm) and in the groves of spruce 15-35 cm (28 on the average). Usually when the snow is light and of such a height, all the life of the small animals goes on under the protection of its cover, but on this day, we encountered trails of rustly voles and shrews making their way through to the upper layers of snow while others were moving to great distances or were looking for food on the surface of the snow--all this showed that the under-snow foods were very difficult to get. This was indicated by the character of the trails of the least weasel--they were exceptionally long, because the interlayer and surface snow crusts prevented the

weasels from getting into the nests and passage trails of the rodents. These observations indicate that mass damage done to the trees and bushes does not occur every winter when the number of voles is large. Of great importance is the fact of the little animals being supplied with a sufficient quantity of green and seed foods and the accessibility of these foods. This last factor depends on the structure of the next-to-the-soil layer of the snow cover.

The conclusion that only a hardened snow crust remaining for a long time obliges the voles to feed on the bark of trees is confirmed by observations made by L. G. Dinesman in the western Kazakhstan Oblast'. The summer of 1955 was there dry and grass developed badly. In winter, the ground was covered by a compact crust 12 cm thick (Fig. 4). L. G. Dinesman worked in the district of Station Dzhanybek and noted that the root voles had, during this winter, badly gnawed the bark of the trees and bushes on field protection plantations and even climbed along stems of elm trees to smaller branches, the tender bark of which was also found to be gnawed off. The data of G.F. Bromley (1958) concerning the damage done to trees and bushes by mouse-like rodents in the forests of the Primorski Kray indicate the same thing. The red-grey vole (Clethrionomys rufocanus arsenjevi), the red vole (Clethrionomys rutilus) and the Asiatic field mouse (Apodemus speciosus) after repeated harvests of nuts of the Korean stone pine inhabited the Taiga of Primoria in exceptional numbers. But, as G. F. Bromley indicates, during winters poor in snow they use as food various nuts, acorns and seeds of herbaceous plants and scarcely damage the bark of trees even at times of mass reproducing. Small animals begin

to gnaw the bark only after the snow has become compact after frequent snow falls with intervals of rain. In spring 1948 there were a lot of signs of such damage. In the winter of 1947-48 the height of the snow cover on the Tagin-Chtan Mountains amounted from the end of November to mid-April to 80-102 cm and the small animals in the course of 4-1/2
p.193 months fed on bark. But years of great numbers of small rodents seldom coincide here with winters abundant in snow. And the mass damage done to trees is not a frequent phenomenon.

The worsening of the conditions of existing under the snow, the insufficiency of food,(that often happens after a dry autumn and a strong freezing through of the soil) and the limited amount of green grass because of the peculiarities of the structure of the lower layer of the snow cover, often oblige the voles to migrate. The migration of grey voles occurs especially frequently before the winter and in early spring when thaws are strong and the thaw waters flood the low lying meadows, drainage hollows and edges of forests where, from the time of autumn, a lot of green grass remains and attracts the small animals. In the second half of the winter the insufficiency of food occurs not infrequently. The migrating voles leave in different directions.

Usually their way over the surface of the snow cover is intricate and complicated with many loops and zig zags; it is quite unlike the tracks of animals intent on definite migrations. The vole wanders about the field evidently acting blindly; the length of its winding way is sometimes two or four times longer than would have been a straight line from the exit from under the snow to the new passage trails made by going into the snow thickness again. (Fig. 5). The success of such a movement

depends first of all on the distance to the nearest haystacks or valleys or edges of forests and secondly on many other causes amongst which, not in the last place, is the severeness of the weather during the movement and the structure of the snow cover. In conditions of frost and wind, the vole cannot stay on the surface of the snow for a long time because of its great loss of warmth. Having run over a few tens of meters, it must dig itself into the snow to the depth of 20-30 cm to warm itself up again; apart from this it must reach food as soon as possible because the grey voles cannot stand prolonged hunger. One interlayer hard crust situated near the surface of the snow is sufficient to cut off the vole which has left its den from the deepest layers of the snow cover with its comparatively mild "subnivean climate" and with its supplies of food.

On December 30, 1950, near to the village of Sofrino we followed the trail of a grey vole which had left a harvested clover field. Having penetrated through a crust of hard, icy old snow, it drilled through the layer of fresh snow lying on it for a distance of 3 m and finally got onto the surface. On its trail, 55 m long, the vole made 10 attempts to dig itself in but everywhere it was prevented from doing so by the ice crust. After a short drilling, the little animal returned to the surface and ran further. Finally, it dug into deep snow and continued making its way along the surface of the hard crust. Another vole had left the clover field and made its way over 50 m to a meadow near the shores of the river, having made on its way 6 unsuccessful attempts to dig itself in.

Migration in unfavorable conditions causes the death of many voles from cold or attacks of predators, but how these migration losses affect population dynamics of separate populations is not quite clear up to now. The mass emergence onto the snow, as it was described for instance by I. G. Pidoplichka (1935) or noted by us according to reports of agronomists during the winter of 1954-55, results in a sharp decrease in the numbers of voles. In the neighborhood of Moscow, the winter of 1947-48 which began with the numbers of field mice being at their highest (visual assessments 5 points) was very interesting in this respect; in spring after the snow had gone, one could assess their numbers in the Pushkin rayon as being not higher than 2 points.

This rather mild winter was distinguished by frequent alternations of snow falls, strong thaws and cooling off. The thaw at the end of October which had been provoked by the incursion of a comparatively warm polar sea air mass, resulted in the flooding by water of the surface of the ground. On October 27 near the villages of Sofrino and Rakhmanova, Pushkin rayon, in growths of young trees, and on sites where trees had been felled, there was that day seen an endless net of trails of common and lesser shrews (the latter was exceptionally common) and partly of grey and rusty voles. Evidently the entire populations of small animals had come into movement. Never before had we seen such long migration trails.

On December 8, under large spruce trees there was still no snow and on the periphery of the projection of their crowns, the earth was covered by glare ice. In dense growths of young deciduous trees and bushes, to which had frozen crusts, which did not allow the later fallen snow to accumulate, the height of the snow cover reached on that day from 20-30 cm. Under the hard inter-layer crust were noticed hollows

and light sugar snow. In this way, the small animals had here the best conditions for moving about and for existence. On clearings in the forests the height of the snow cover did not exceed 14 - 18 cm (the thickness of the freshly fallen snow reached 0.8 cm below which lay an ice crust 6 mm thick with layers of sugar snow one cm thick frozen onto it from both sides, and deeper still large-grained sugar snow with bits of crumbling crust in it). On fields of winter crops the thickness of the snow cover varied from 0 on mounds of earth to 25 cm in furrows. Here the thickness of the crust reached 3.5 cm.; in some places the whole thickness of the snow froze together to a compact mass firmly welded together with the earth. On December 10, it rained all day long, forming an ice crust. The snow cover grew even more compact from top to bottom.

On March 21 near the village of Talitsy (close to Sofrino) we walked more than 300 m along the trail of one of the grey voles which were moving from the rice stubble field into the forest. The snow cover in the field was so hard that it easily held the weight of a man without skis. The frozen-together snow with a density of 0.32-0.33 g/cc froze as a whole layer to the ground and was only lightly powdered with fresh snow. The vole crossed the winter crop field and went under the crust in a patch of young trees having found a small hole near the stem of a tree. On April 4, after several days of radiational thaw, we found on the meadow not far from the edge of the forest three voles that had perished at the end of March. They were lying on the surface of the crust in different places and had thawed out of the light snow that had fallen during the last March snow storms. Studying of the bodies of

the little animals in laboratories of medical zoology and parasitology proved that they had perished from cold. The migrating little animals were evidently soon buried in the snow and this gave us the possibility of finding them before the birdsdid. The raven, the grey crow, the magpie and from the moment of its return, the rook also, carefully watch the fields over which they fly in the period of the thawing of snow and eat up the majority of dead voles, therefore only a very small part of the victims of unsuccessful migrations fall into the hands of zoologists.[7]

We have more than once seen the tracks of corvine birds near darkened leaves that had flown a long way from the forest, and melted out of the snow to small clods of earth and near to sharp tree stumps that began to show from under the snow; every dark object which, by its dimensions and form resembled a frozen vole is certain to attract the attention of a raven, magpie or crow. These facts testify that for the corvine birds the eating up of small animals which have perished during unsuccessful winter migrations is something usual which creates in them a characteristic feeding reflex. At the same time it is an indirect proof of a rather great consistency in the perishing of voles on the surface of the snow during winter.

The following observations proved that voles obtained food with difficulty during the winter of 1947-48. On April 4, we found on a patch where cabbage had been planted, near the village of Nikol'ska, Pushkin rayon, several deep diggings made by hares to the cabbage stumps. From the air vents of the dens of grey voles to these diggings

7. These birds also successfully hunt for running or swimming voles at the moment when their dens become flooded with thaw water and open up thawing winter nests where they also look for bodies of voles that perished during winter.

led the passage trails of these rodents which had been attracted by bits of cabbage leaves left by the hares. Judging by the quantity of tracks the voles had for a long time made use of the food that they were able to get only because the hares had in several places dug through the hard snow. For the life of the shrew, as has already been indicated above, sometimes even a thin icy crust or a crust of snow hardened by the wind may have a decisive significance; only in light powder snow can they easily make their passage trails and find refuge from danger.

On December 10, 1944 a heavy rain fell during the whole day which froze immediately on the snow and on branches; the height of the snow cover on that day was from 18 - 25 cm. The ice crust that formed on the fields was 6 mm thick, and on the under side of it a layer of hoar frost 6-8 mm thick had firmly frozen. The crust that was thus formed was from 12-14 mm thick and very hard. In the forest the crust did not exceed from 1-2 mm but even that did not allow an ordinary shrew to dig itself in in one place. Only when it had reached the spruce trees with dense branches, the little animal found under them a place with light powder snow and immediately disappeared under its protection. If a prey bird had chanced upon the shrew while it was in the clearing the fate of the little animal would have been decided in a few seconds. This same winter on February 17 near the village of Fomkino we saw the tracks of a jay which had attacked a common shrew (Sorex araneus) which was running in the snow near a tree trunk. The little animal at once sank into light snow easily drilling through its thickness. The attempts of the jay to dig out

the shrew remained unsuccessful. On this day on clearings in the forest, the snow was 56 cm thick on the average and under the spruce trees from 25-30 cm thick.

On the 25th of February, 1953, lesser shrews frequently ran about on the snow. We cought one of them which had fallen into a deep, ice-coated furrow and could not get out of this trap. We attempted to photograph the shrew in its natural surroundings but the little animal, having run up to the top of a small spruce tree covered with snow at once went into the depth, going down into the snow vertically along the trunk of the small tree. On this day the snow thickness on clearings was from 59-74 cm, (on the average 63 cm.) and among the spruce trees from 36-62 cm, (on the average 52 cm); in the depth of the snow cover there were interlayers of hard crusts but there were
198 none under the branches of spruce trees and they could not hinder the shrew. It drilled through these layers of snow sinking into hollows which were situated at the level of all of the whorls of the stem.

On the 24th of December, 1944, we followed the tracks of a common shrew which was migrating from a harvested clover field. The little animal making zig-zags and turnings crossed the field and approached a hay stack. The attempt to get into the stack did not succeed as its lower part from the wind side was protected by hardened snow. Continuing on its way the shrew came upon our old footprings and attempted several times to get under snow through their hollows but unsuccessfully. The floor of the footprints had been strongly coated with ice. Only when it had reached a dense patch of

young tree growth, did it dig itself in next to a tree trunk.

One can observe quite different pictures during winters with heavy snow falls and without strong thaws. The entire life of small animals is then concentrated in the next-to-the-ground layer of snow. Their tracks appear very seldom on the surface and are usually very short. So for instance in the neighborhood of Moscow during the winter of 1955-56 which was abundant in snow, on February 25th, we walked on skis over 10 km on the itinerary Zelenogradskaya to Fomkino and returned along a different parallel route. On this sunny day the temperature was -5C . We met only one short track of a lesser shrew, two rather long, but not fresh, tracks of least weasels and one short and fresh one: the predator chased a rusty vole which tried to escape but the weasel caught it 3 m away from the snow den and dragged it the same way under the snow. The height of the snow cover on this day was, among the spruce trees, from 60-75 cm, and in the young undergrowth, from 75 to 90 cm, on the fields from 60 to 75 cm with, in some places, a rather weak crust which had formed under the influence of the wind. In the undergrowth the profile of the snow thickness (the height was 71 cm) was as follows: on the top a layer of powder snow 3 cm thick, then a layer of large-grained sugar snow 15 cm thick, and deeper to the ground a layer of granular, very porous and unstable snow, (like quicksand). When paths were trodden down the snow sank to about 20 to 25 cm. The movement of foxes was clearly rendered difficult by the lightness of the snow; they preferred to move along ski trails, paths, or old hardened foot tracks. Only in dense spruce groves they walked on the fresh snow, winding their way from tree to tree.

Their hunting went badly, as was indicated by the marked increase in the area of their activity. But the least weasels easily managed the drilling of the snow in the forests and their under-snow hunt: and we saw their tracks with "drag marks" (traces of their having dragged along captured rodents) on the the 6th and 11th of January and again on the 27th of February.

On December 29, 1946, on the itinerary Sofrino to Rakhmanova to River Talytsa (near Nikol'skoye) it struck our sight that all the tracks of gray voles were encountered either in bushes or along ditches on edges of fields or on slopes of overgrown ravines where rather a lot of snow had been accumulated, and finally on edges of forests and in the forests themselves. The tracks were not short ones as though in search of food, but very long ones which indicated that a migration was in progress and the voles had left plowed-up fields and meadows but had not settled yet in their new habitats. Quite out of the ordinary was the appearance of tracks of moles and water rats. What happened was that the whole second ten days of December had had steady freezing weather (from-14C to -25C) and a rather weak, frozen, snow cover. The fast and deep freezing through of the soil was the cause of the migration of small animals that had begun and had been influenced by the existence of the ice crust as well. In the forest on that day, the layer of frozen soil was 7 cm thick; in fields it was considerably deeper. The average height of the snow cover in spruce groves was 7 cm, on a rice stubble field 17 cm among sparce desiduous forests 24 cm; on a clearing grown with bushes 26 cm; under a layer of fresh powder snow 16 cm thick there lay an ice crust 1 cm thick and then 9 cm of granular snow.

A mole which had left its den on the edge of a forest clearing made its way for about 150 m in the forest, got onto the field and into the cold. Here, making loops, it wandered for about 350 m and returned to the forest. On its way it had made 16 attempts to dig itself in-4 times in the forest and 12 times in the field, but everywhere it came up to the surface again. In this field, out of its 12 attempts only 2 succeeded in cutting through the ice crust, the others were done in soft snow. The compact ice crust and the frozen earth prevented this mole and another one, which moved from a plowed field into the forest, from quickly finding a place where they could get food and not suffer from the cold. In similar conditions enforced migrations usually cause the death of the weakened moles unless they happen to get onto a patch of thawed soil near to the emergence of ground waters onto the surface.

The majority of water rats change over to feeding on rhizomes and roots of plants in the autumn. In winter these rodents, like the moles, make passages in the earth, which is why a deep freezing through of the soil could not but affect their conduct. It is not by chance that on December 29th a very long (hundreds of meters) winding track of a water rat was encountered crossing a field from where wheat had been harvested. In winter, this rodent appears on the surface of the snow only in exceptional cases, being obliged to do so either under attack by an ermine or by extremely unfavorable abiotic conditions. We did not succeed in unraveling the trail of this little animal to its end because the snow began to drift and it grew impossible to track it further.

It is significant that out of the eight samples of droppings of

foxes gathered that day along the tracks, two contained bones and
200 fur of water rats and one of the root vole. This shows that these little animals, obliged to migrate and deprived of the possibility of digging themselves in because of the ice crust, become an easy prey for the fox. (In normal times the water rat in winter is nearly inaccessible to the fox). But this same ice crust made it more difficult for the fox to hunt for its usual victims the grey vole. While tracking trails of foxes on December 29, we encountered 23 diggings in the snow; out of these only six were connected with hunting for voles: five diggings on edges of forests led to under snow passages of these rodents and one to the nest of a grey vole at the bottom of a small hollow which was covered with snow 24 cm deep. The remaining 17 diggings were made to human excrements near paths and roads.

For the foxes inhabiting the neighborhood of Moscow, this is the usual food during the last period of winters abundant in snow. At the described time, the greatest efforts of the foxes were directed to getting it notwithstanding the fact that in the fields the height of the snow did not exceed from 8 to 20 cm. The peculiarities of the snow structure on the frozen soil evidently prevented the foxes hunting for voles. It is interesting to note that on December 8th, 1946, that is 3 weeks before the described trip and two days before the settling in of steady cold weather, the calculations of diggings made by foxes in the same region gave different results: in 10 cases they led to passage trails and dens of small animals (9 to passages of grey voles and one to a den of a mole) and only one digging led to exrements.

Certain Particularities of the Winter Life of Predatory Mammals in Connection With the Structure of the Snow Cover

The least Weasel

For the least weasel, the smallest of our predators, light powder snow which it can easily drill, is the most favorable. The height of the snow cover in the absence of hard crusts is not of great importance. In the neighborhood of Moscow, for this little animal, winters with strong thaws are very unfavorable. The thawing of snow and the following frost diminish the number of rodents and apart from that, the appearance of crusts makes hunting much more difficult for the least weasel.

In the first 10 days of December, 1946, a thaw lasted for over a week. After a frost an icy crust reached a thickness of 2 cm in the fields and large crystals were frozen to its under side; all the thickness of the snow sank and became much more compact. On December 8th, on the fresh snow we say in the neighborhood of the villages Sofrino and Rakhmanova, many tracks of small animals. This was an indication of their difficulties caused by compact firn clothed with a hard crust. The least weasel that was rushing about on the rye field seeking for vole nests, had tried in scores of places to penetrate under the snow, but after making in the top layer of soft snow a passage from 10 to 40 cm long, which protruded like a small ridge, it always came up to the surface and ran further. It penetrated under the snow only over plowed land, in places, where the snow had loosened itself from clods of earth, between which passages were formed. The earth in the field was frozen and the least weasel did not succeed in moving fast

p.201 enough along the passage trails of the den of the mouse. The rodent

The rodent had time to jump out onto the snow and after having run over 300 m. disappeared into the first den it saw. Continuing on its way, the least weasel tried to get under the snow on old human footprints but even these after the thaw had been coated with ice. The average height of the snow cover on the field reached 10 cm on that day in the fields, 4 cm in dense spruce groves and on the clearings where the grass had not been cut 18 cm, but the moles that day were throwing up earth through the thickened crust of snow. Evidently, this strong earth digger was not embarrassed by the necessity of digging a passage through hardened snow.

When there is a large number of rodents and their nests are easily accessible, the tracks of the central Russian least weasel (especially of the smaller female) along the surface of the snow, are usually very, short. When the tracks get markedly longer, it is an indication of the fact that either the number of rodents has decreased, or that hard snow crusts have been formed. Instead of tens and hundreds of meters the weasel tracks are measured in thousands of meters. On december 22, 1949, we walked over 2-day-old snow along fields and sparce forests near the village Sofrino. The earth was frozen, the height of the snow cover reached from 30 to 40 cm and there were only from 12 to 16 cm of light snow, under which lay compactly frozen snow. On the fields, air vents of voles were rare, not more than 2 or 4 per Km. Everywhere among the bushes and sparce trees there were a lot of very long tracks of least weasels; they came there from the fields, as among bushes it is easier to penetrate into the depth of the snow cover, but still the least weasels moved more on the surface of the snow rather than drilling through

it.

On January 25, 1953, we noticed that weasels went under the snow only next to tree stumps or in tufts of high grass, in other places, the snow cover was too compact. Very long least weasel tracks were also encountered in the winter of 1958-59 which was distinguished by heavy snow falls and frequent thaws. Towards the end of January, near the village of Zelenogradskaya in the thickness of the snow which reached on the fields 70 cm, (65 on the average) there were six inter-layer hard ice crusts and one next-to-the-ground crust. During this winter, traces of migration of shrews and rusty voles were very numerous as well as traces of movements of grey voles. Evidently, the least weasel does not differ much from its victims as to the degree of sensitivity to the changes in the structure in the snow cover. Observations over the first falls of fresh snow show that chasing the vole in light soft snow, the least weasel makes lots of passages that spread out starwise before it catches its prey. Not seldom does it throw itself into the pursuit of a little animal that had jumped out onto the snow surface then plunges into the snow again following up its pursuit. With this system of hunting the ease of drilling, that is the degree of resistance of the snow in its thickness to the winding movements of the weasel, is of decisive significance. It becomes interesting to note that the numbers of least weasels are subjected to sharp fluctuations along the
p.202 years resembling the fluctuations characteristic of the populations of shrews and voles.

Sable

G. D. Dulkeit (1957) owing to his laborious tracking and studying

of the tracks of sables in the Taiga of the eastern spurs of the Sayan Mountains (on the Big & Little Arybee -tributaries of the River Mana) has ascertained how snow covers of different strength and structure affect the movements and the length of hunting trips of predators during one day of successful hunting for food.

In the Taiga of Sayan in the winter diet of the sables, an important part is played by the stone-pine nuts, which is connected not only with a wide distribution of stone-pine trees but also with the time when the nuts fall. The falling of the nuts takes place earliest on the lower slopes of the mountains & proceeds upwards while the formation of a constant snow cover moves on the contrary from the heights downwards. In years when nuts ripen and cones fall early, the snow covers them up, creates favorable conditions for voles and mice which choose stone-pine nuts, and until the end of the winter, makes the remnants of the nut harvest nearly inaccessible for the sable. The higher the mountains the more cones fall onto the snow and remain in its thickness.

In the top levels of the forest belt, the gradual falling off of ripening cones insures for the sables a supply of nuts during the whole winter regardless of the height of the snow cover because part of the cones stays on the surface or not too deep in the snow. The sables are capable of finding the cones covered by a layer of soft snow 50-65 cm thick, but in general they dig out nuts from lesser depths (on the average from 30-32 cm.)

So, for instance, in the end of February or the first half of March 1955, when the average height of the snow cover was 110 cm (from 102-165 cm.) the sables got the cones from a depth of from 12 to 50 cm. In the end of October and beginning of November 1954, in the

basin of the Big Amybee River there were thaws and prolonged rain falls. The 40 cm thick layer of snow soaked with water together with the cones which were in its thickness were firmly frozen on the 6th and 8th of November when temperatures fell to -21.6C and especially on the 11th and 15th of November with the temperatures at -31C. The hardening of the snow cover sharply diminished the accessibility of the cones; towards the second half of November the number of nuts eaten by the sable during a 10 km long hunting trip, fell to an average of 4. But the continuing falling of cones onto the snow and the stopping of heavy snowfall on November 19th again ameliorated the conditions of the getting of this important food and in the first half of December there were already 10 nuts eaten on a 10 km long hunting trip of the little animals (accurate indicators remained till the end of the winter).

From the conclusion of D. Dulkeit based on lengthy observations, we shall mention what follows:

"As a rule, a stone-pine cone is taken from under the snow by the sable and the nuts are eaten on the surface of the snow. [5]A cone that
p.203 is firmly frozen into the snow is not willingly taken by the sables. The sable seldom climbs trees and does not pick the cones off trees itself" (page 25). In this way the use of this important food by the sables apart from other reasons depends to a high degree on the strength and structure of the snow cover.

The Fox

These conditions have no less significance for a larger predator, the fox.[8] The basic food of the fox in all parts of the country is small rodents. In the neighborhood of Moscow, of the greatest importance

8. The weight of an average Russian fox is from 4 to 7.5 kg, that of a sable from 0.8 to 1.8 kg.

is the grey vole which lives in winter, as has already been indicated, under the snow in special winter nests, or in earth dens which have been built during the warm part of the year. Numerous trackings along winter trails and frequent observations show that the fox hunts, digging up the dens of field mice, only until the earth is not frozen. As soon as the earth freezes even to 3 or 4 cm depth, the fox stops its attempts to dig voles from out of their dens and does not return to them until spring. The most frequent digging leads to the under-snow dens where it catches grown up rodents and sometimes eats the helpless young, while less frequently it catches the little animals in their snowy food passage trails. Not seldom does the fox also dig out bodies of voles which have perished from illness, exhaustion or cold. Nearly always it is obliged to dig through the whole thickness of the snow. It must be noted that nests of voles and lemmings are situated as a rule in deep furrows, ditches, holes, depressions, growths of tall grasses, and in bushes where the snow cover is higher than in the neighborhood.

It is understandable that the structure of the snow thickness has a great importance for the predators during their hunting by digging into the snow. A compact crust hardened under the influence of the wind or glare ice crusts, evidently worsens the conditions of the penetration of smells from below to the surface of the snow. Observation of a fox which was hunting for mice in the second half of the winter show that it uses hearing rather more than smelling. Evidently it can better hear the squeaking of voles or the sound of their cracking up dry grass in the passage trails than smell the little animals.[9] Not

9. While fox hunting with an artificial call, it was established that a fox hears the imitation of the squeaking of mice from the distance of 250 meters and more.

infrequently the fox sits for a long time over a colony of voles before throwing itself toward a definite spot and beginning to dig in great haste.

At the intradepartmental conference arranged by the Geographical Institute, Acadamy of Science of the U.S.S.R. in December 1954 in connection with the study of snow, during the discussion of our information, one of the members who had worked for a long time in the Arctic as a meteorologist reported that arctic foxes also often hunt for
p. 204 lemmings in the tundra in the winter by hearing. One can constantly observe how this animal inclines its head to one side or the other attentively listening to what goes on in the thickness of the snow under its feet. According to the opinions of the same observer, the reindeer evidently also does not detect the smell of the lichens through a thick layer of snow and scrapes the snow with its hooves at random, in connection with which, one often finds unsuccessful empty diggings. It is clear that the question of the penetration of smell through snow covers of different depths and structures is doubtless an interesting question which deserves to be attentively studied.

Returning to the winter life of a fox, let us note a series of other circumstances. If the layer of snow is deeper than from 40 to 50 cm and there are snow crusts, the fox, even digging at the full speed it is capable of, cannot always catch the vole- the prey hears very well the crunch of the snow scraped by the claws of the fox and runs away along the deep passage trails. The great difficulty is also constituted by a very fluid, over-crystallized, dry, lower layer of snow which, from all sides, spills into the excavation under the

feet of the fox (or of another digging animal). In such circumstances even a motionless piece of carrion or body of a small animal is dug out by the fox with difficulty. Small animals, voles, shrews, least weasels, ermines, drill through such a snow although even for them its peculiar qualities are not indifferent. The ecological significance of a layer of over-crystallized snow, characteristic of the vast spaces with steady frosts during winter, has not been completely studied as yet and represents an interesting field for future research (in particular one can elucidate a lot by experiments with animals subjected to tests).

So it happens in regions where there is a lot of snow, and especially during certain winters, that the foxes go hungry for weeks, and even months, because the hunting of small animals proves to be difficult. In these circumstances they are obliged to change over to different kinds of emergency food and not infrequently transfer their hunting grounds from the fields to other places. Around Moscow the common emergency food of foxes is human excrement for which the fox constantly searches in the woods or along paths and roads leading to the villages. But here also the significance of a fresh layer of snow is apparent. The foxes do not touch frozen fecal masses on the surface of the snow and dig them out from the lowest layer of snow where they are thawed because of the warmth of the soil.

Let us give a few examples.

In the first half of the winter of 1944-45 (till the end of December), there was very little snow around Moscow with strong thaws and glare ice. In the region of the village of Sofrino the first glare ice was noticed on the 15th - 17th of November, even before the first snow had fallen (the first snow fell on this glare ice). On November 27 when

the snow cover in the fields reached 6 - 8 cm, there fell a heavy rain,
205 the snow sank, and then froze to the soil. On December 10 when the depth of the snow cover was 18-25 cm, a cold rain fell during all the day. It froze at once on the snow and on branches. In the fields, long needles of hoar frost froze from underneath to the ice crust. (0.6 cm thick) which formed a slab that was from 1.2 to 1.4 cm thick and very compact. On clearings in the forest the thickness of the ice crusts with a needle-like layer of crystals frozen to it was only from 0.1 - 0.2 cm, while under the protection of the crowns of spruces lay a rather light, soft snow. On February 22 we followed the tracks of a fox near the village of Sofrino, where the depth of the snow cover was 40 cm in the fields. From among the diggings of the fox, six led to the nests of grey voles and eight to their under-snow dens. It is interesting that three nests were found to be enclosed in peculiar icy capsules that were so strong that the fox could not destroy them. To survey these nests, we had to hack the ice with a hunting knife. In half of the diggings to the passage trails of the voles, the fox went only as far as the surface of the ice layer where the little animals were beneath its protection. In these conditions the hunt for rodents was not very successful. All the other 19 diggings of the fox we surveyed on February 22 indicated that they led to excrement.

The next winter - 1945-46 - was also characterized by the existence of a compact icy layer in the lower part of the snow cover on fields. Already in the beginning of March, the collaborators of the biological station M.G.U., situated near Lutsina in the Zvenigorod rayon, reported to us that the foxes were suffering from hunger. The predators began to appear frequently near the refuse dumps in the villages. On March 5, near the biological station, the body of a very exhausted fox killed

by a dog was found. Near the village of Sharapovo a forester, having laid the head of a dead horse opposite the window of the stables of the collective farm as bait, killed three foxes in a short time (in usual conditions foxes do not approach bait laid near villages).

The measuring of the snow and the tracking of foxes carried out near the village of Lutsina on March 9th and 10th showed the following: the snow cover on a field with short rice stubble was 30 cm deep (from 29-51 cm.), on the high wheat stubble with patches of weeds, 38 cm (from 31 to 60 cm.). The lower part of the snow cover consisted of a hard next-to-the-ground crust which was from 17-19 cm thick on the stubble field and had the consistency of firn which could not be broken with fingers. (On comparatively low-snowy patches the depth of the snow cover did not exceed from 10-15 cm.) In mature spruce groves with a density of 0.3 to 0.4, the average height of the snow cover amounted to 24 cm (from 15-37), and on places where trees had been felled amidst an undergrowth of young aspens and birch trees - 52 cm (from 46-64). On a profile of the snow thickness in an excavation dug in a forest clearing were easily distinguishable an upper layer
p.206 11 cm thick, then on an ice crust a few millimeters thick lay a layer of fine grained snow 14 cm thick, while under it lay a layer of coarse-grained sugar snow 32 cm thick, more dense in its higher levels and comparatively loose near the surface of the earth. On forest clearings and on patches of undergrowth, a next-to-the-soil crust did not exist, but it was replaced by an icy crust at a higher level and a layer of coarse-grained snow. The majority of fox tracks were found to be in the forest where the height of the snow cover and the inter-layer hard crust did not hinder the movements of predators and the absence of the next-to-the-ground crust facilitated the digging out of food. In the

fields, there wasn't a single digging towards the nests of rodents although voles were encountered here and there. We found air vents on a wheat field, where the little mice had stayed in autumn, as well as on a damp meadow near the edge of undergrowth and near a stack of rye straw (on March 9th, the voles cleared the air vents more than once as a snow had begun to fall in the night and continued through the day).

It is worth mentioning that in the lower layer of the snow cover the diameter of the passage trails was like that of the trails of a mole. Evidently the walls of the passages had melted considerably during a thaw and had then become coated with ice. It was possible to widen them only at the cost of great effort, tearing small pieces of firn off with one's fingers. On this day, we found two diggings of foxes, one in the rye straw at the base of the stack, and another at the bottom of a hay stack.

Evidently a hard, next-to-the-ground crust of the above-mentioned strength safely protects the nests and the passages of the voles from the foxes. These were suffering from hunger because they were rather numerous, whereas the number of voles was below the average (according to visual calculations, equalling 2 or 3 points), and the structure of the snow was also very unfavorable for hunting in the fields. Let us remember that in the Pushkin rayon that winter the ice crust rendered the hunting of the foxes very difficult as early as December.

On March 16, 1947 near the village of Nikol'skoye, (Pushkin rayon) in dense spruce groves, the average depth of the snow cover reached 58 cm (under the crowns of the trees, 49 cm), in growths of young leafy

trees - 78 cm, and on the fields 60-65 cm. In the thickness of the snow, beginning from a level of 5 cm below the surface and down to 45 cm, there were 7 ice crusts of which 6 were up to 1 cm thick and only the upper one 0.5 cm. On this last crust lay a layer of fresh powder snow 19 cm thick. The round-the-clock trips of foxes in these days were very long but we found no traces of prey having been caught. From the three diggings of foxes which we encountered, two led to droppings at a depth of 45 cm and one to carrion (a piece of skin of either a dog or a calf which the fox ate up without leaving any remains.).

The winter of 1951-52 was comparatively warm, mild and with little snow until February, then followed a period abundant in snow and March proved to be the coldest month of the cold half of the year. In the beginning of this month on March 5, on forest clearing near the villages of Sofrino and Fomkino the depth of the snow cover reached 90 cm and
p.207 in its thickness there were 5 ice crusts, the lowest of them being very hard. Everywhere, even under spruce trees, there was a next-to-the-ground ice crust. On March 24, we tracked a large male fox near the village of Fomkino. From the first digging it had made to a depth of 70 cm at the edge of a forest clearing, the fox got and ate the nearly rotten body of a mole, having left on the snow one front paw; two other diggings went as deep as the earth to tufts of fur of moles which had evidently perished during a summer epizootic, and the fourth digging led to human excrement. This winter was very hard for many animals, in particular for the jays which could not get food because of the quantity of snow and the number of ice crusts. In spring we found bodies of dead jays in three places in our region of observations; they were also found further to the northeast in the Perlyaslavski rayon of the Yaroslavski Obl.

In this way the snow cover around Moscow, in which crusts frequently appear, makes the hunting very difficult for the foxes nearly every winter. Only the presence of small fat reserves kept from the autumn and the capacity to feed for a long time on refuse, and to suffer hunger for lengthy periods of time permits this predator to exist in the conditions of a landscape poor in game and distinguished by long winters abundant in snow.

Conclusion

The structure of the snow cover at every given moment is substantially different even on small, neighboring districts, depending on various reliefs and on the plant and soil cover. The differences in the structure of the snow thickness which seem insignificant at first glance may exercise a decisive influence on the life of birds and those mammals which are active during winter. Larger animals, the fox for instance, visit during a single day a series of districts the snow cover of which differs sharply in height, compactness and structure, and choose those which are most favorable to movement and hunting. The inter-layer and next-to-the-ground ice and snow crusts have a greater influence on the small animals than on the large ones.

Analysis of the described facts leads to the conclusion that when studying the winter ecology of mammals and birds in parts of the country with winters abundant in snow, the research zoologist and biogeographer must at all costs use numerous special measurements and descriptions of the snow cover and its structure in various biotopes and landscapes, and this in excess of the data given by meteorological stations. It is essential to continue to study the snow cover and at the same time to assess systematically the distributions, numbers, and peculiarities

208 of the life activity of animals because the elucidation of their various reactions allows one to judge the positive or negative influence of a snow cover of a given strength and structure on the conditions of existence of the winter fauna.

Study of the ecological role of the snow cover and its structure requires observations during many years. Such observations will give answers to a series of questions which are important for the preservation of valuable animals, for the rational organization of hunting for them, for the establishment of prognoses as to the numbers of harmful rodents, prognosis of the probability of their damaging of winter crops, fruit trees, protected plants, nurseries and so on. It is expedient to make such observations in special establishments while also making the simplest experiments on animals which are caged under open sky.

Literature Cited

23 titles in the Cyrillic alphabet plus one in Danish.

Figure 1 Scheme of the trail of a little shrew which perished from frost 22 January 1941. The dots show places where the shrew attempted to bury itself in the snow.

Figure 2 Small part of the network of trails made by a shrew in fresh snow.
1) bases of the trunks of firs 2) the same, lindens
3) the same, chokecherries and their shoots.

Figure 3 Map of the distribution of surface and interlayer ice crusts in the third 10-days of January, 1955. (from data of the Institute of prognoses).
1) Surface ice crust. 2) Interlayer ice crust

Figure 4 Map of the distribution of surface and interlayer ice crusts in the first 10 days of February 1956. (from data of the Institute of prognoses)
1) surface ice crust 2) interlayer ice crust

Figure 5 Scheme of the trail of an evicted grey vole (total length about 350 m) which was wandering in thick snow on fields ploughed in autumn and partly in a dry valley with shrubs. Dotted line shows the boundary between the field and the dry valley.

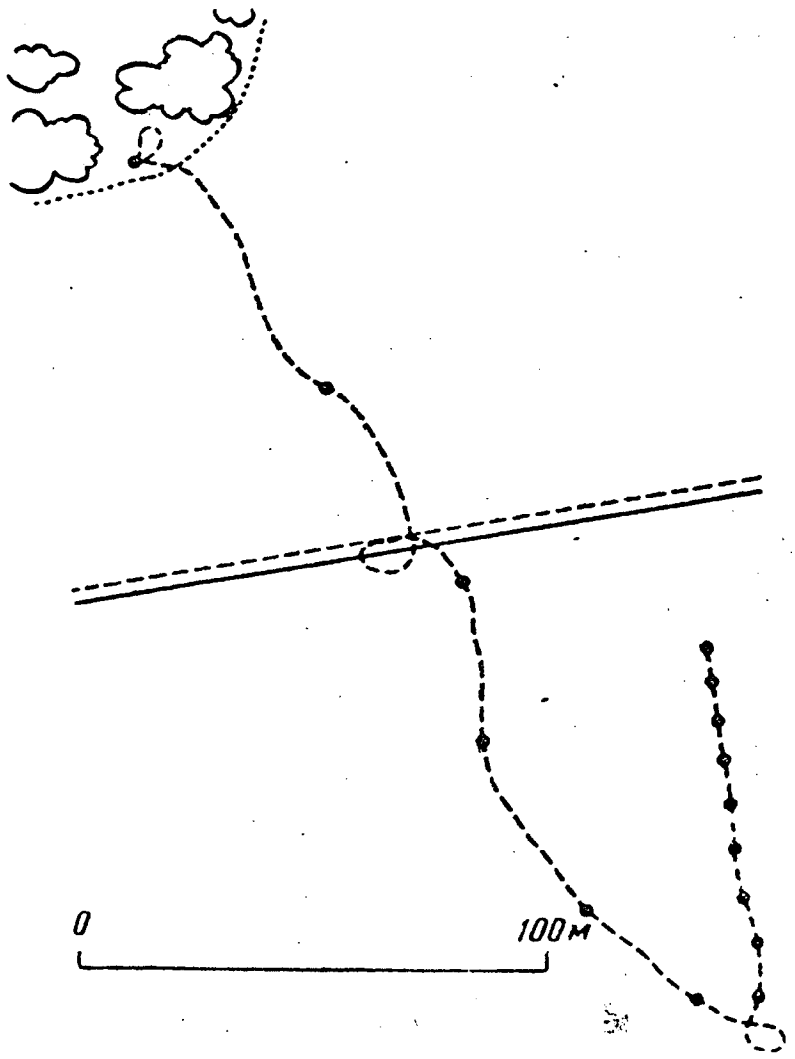

Рис. 1. Схема пути малой землеройки, погибшей от мороза 22 января 1941 г. Точками показаны места, где землеройка пыталась зарыться в снег

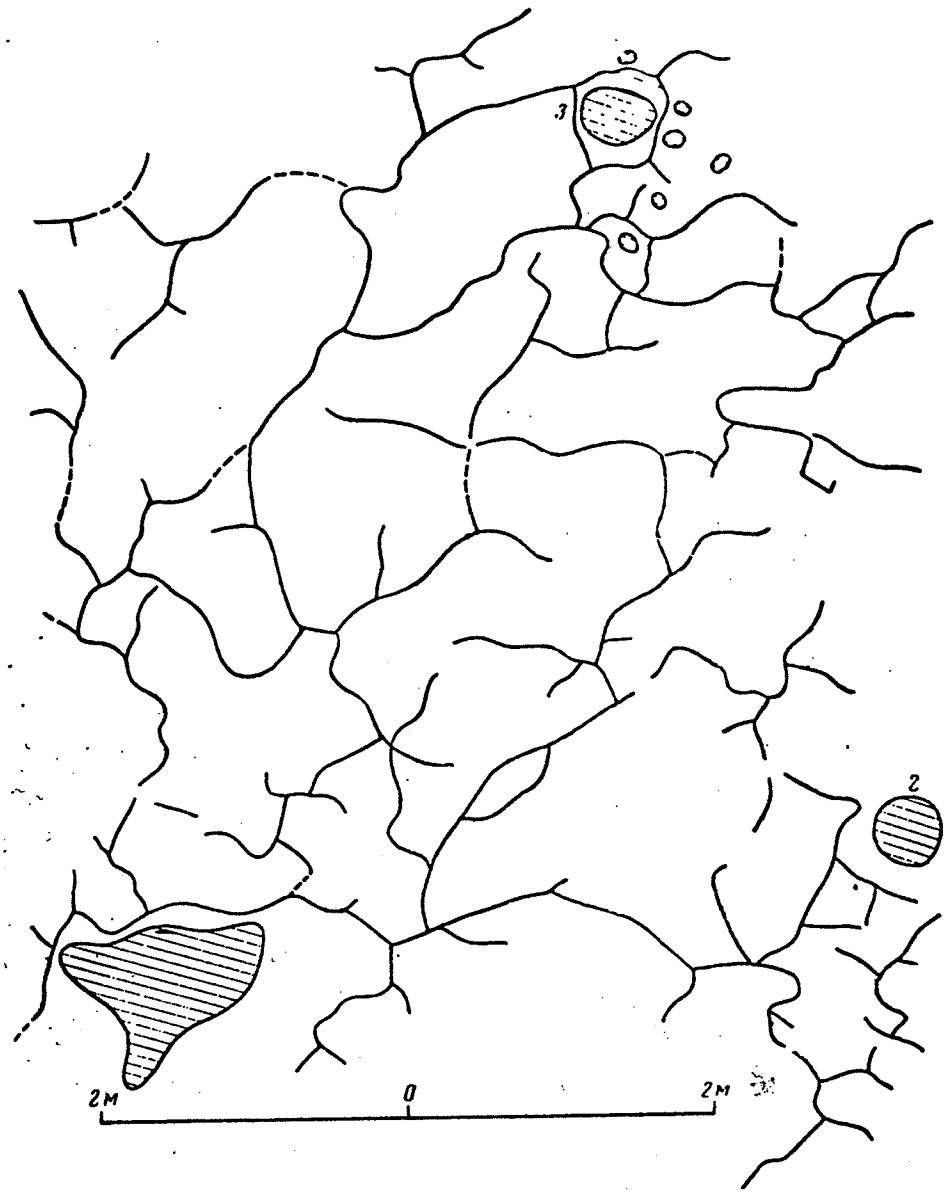

Рис. 2. Небольшой участок сети ходов, проложенных землеройкой в свежем снегу

1 — основание ствола пихты; 2 — то же, липы; 3 — то же, черемухи и ее поросли

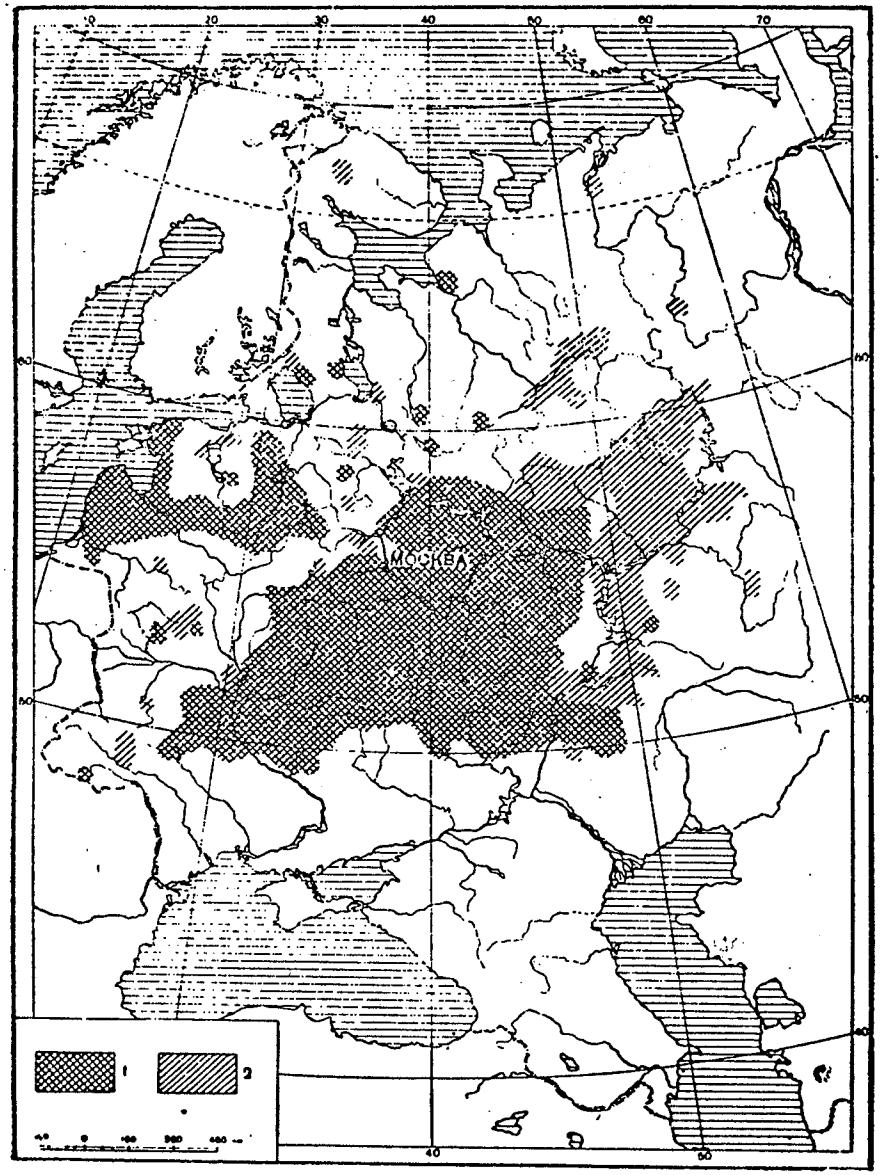

Рис. 3. Карта распространения притертой и взвешенной ледяной корки в третьей декаде января 1955 г. (по данным Института прогнозов)

1 — притертая ледяная корка; *2* — взвешенная ледяная корка

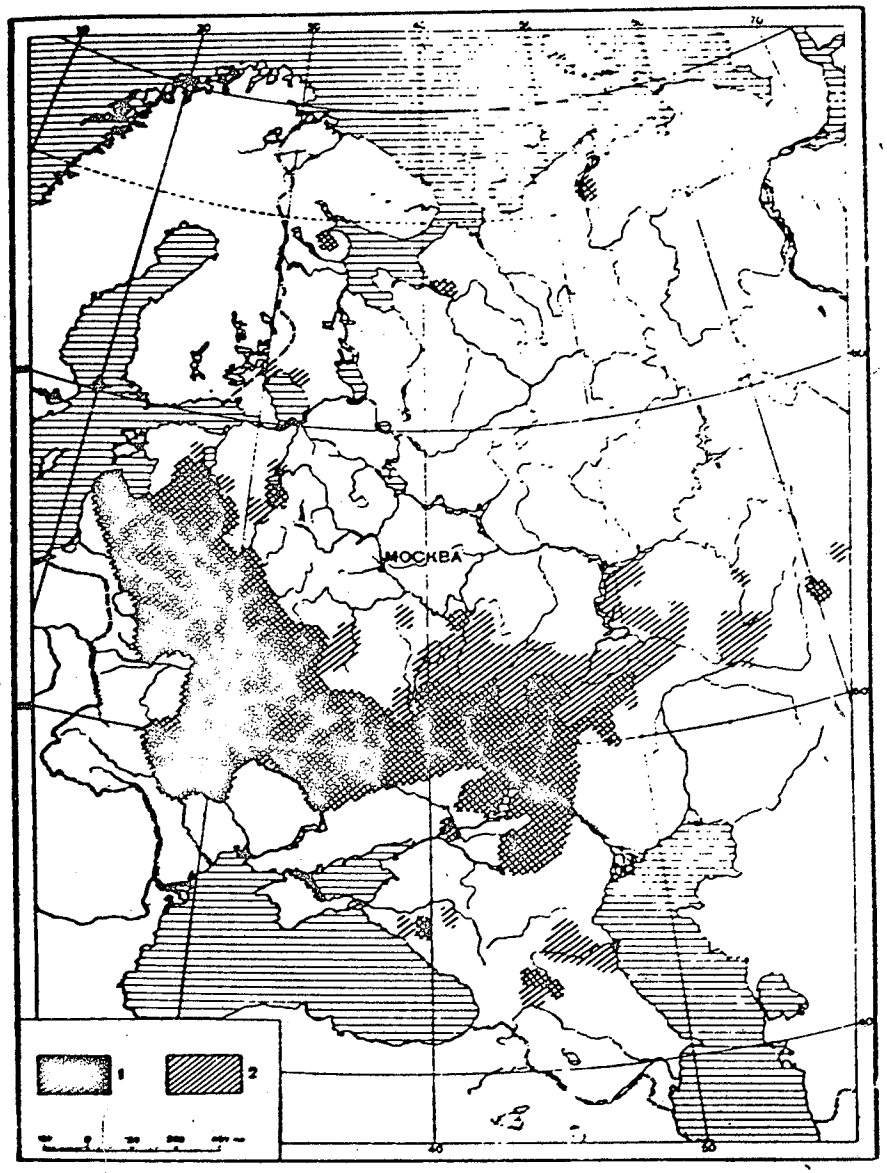

Рис. 4. Карта распространения притертой и взвешенной ледяной корки в первой декаде февраля 1956 г. (по данным Института прогнозов)

1 — притертая ледяная корка; *2* — взвешенная ледяная корка

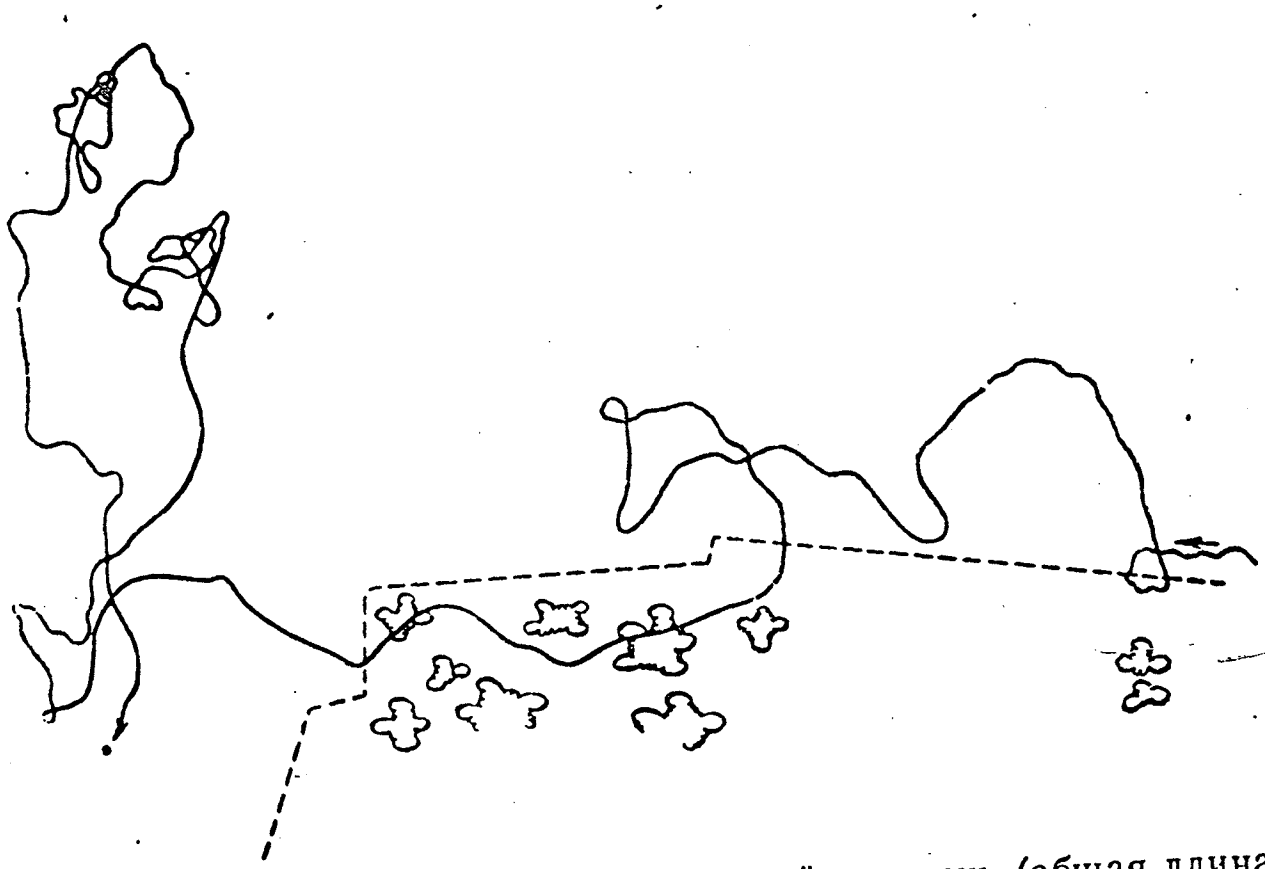

Рис. 5. Схема пути, выселявшейся серой полевки (общая длина около 350 *м*), блуждавшей при плотном снеге на зяби и частично на суходоле с кустами. Пунктиром показана граница между полем и суходолом.