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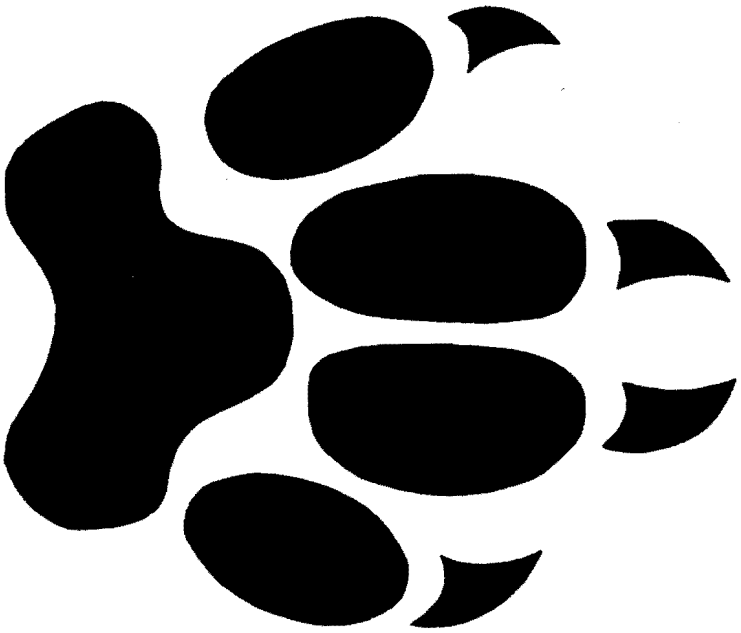

STUDIES ON MAMMALS IN GOVERNMENT PRESERVES

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СБОРНИК МАТЕРИАЛОВ ПО РЕЗУЛЬТАТАМ ИЗУЧЕНИЯ МЛЕКОПИТАЮЩИХ В ГОСУДАРСТВЕННЫХ ЗАПОВЕДНИКАХ

(Sbornik materialov po resul'tatam izucheniya mlekopitayushchikh v gosudarstvennykh zapovednikakh)

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1956

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Moskva, 1956

Directorate of Preserves and Hunting
Central Directorate of Forestry and Field-Protective Forest Belts
of the Ministry of Agriculture of the USSR

STUDIES of MAMMALS in GOVERNMENT PRESERVES

A Collection of Papers

Edited by
P. B. YURGENSON, Doctor of Biological Sciences

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INTRODUCTION

Government preserves have accumulated a vast amount of valuable scientific research material on the biology of wild animals. The results of this research are of great scientific and practical importance, particularly for the hunting trade. Researches in the field of biology do not always produce data which can be put to immediate practical use, but it does often serve as a necessary prerequisite for conducting further research. Such data, when used by other investigators in conjunction with new results, acquire immediate scientific and practical value.

The material published in this collection on the results of a number of research works on mammals of the species important to the hunting trade and industry will promote wider exchange of experience in the study of mammals and the working conditions prevailing in government preserves in particular. Such an exchange of experience is especially important and essential for scientific workers in government preserves, with many young specialists among them.

The further development of the hunting trade depends upon the correct solution of numerous problems, among them the need of determining the method of checking the individual fauna species important to the hunting trade,the ascertaining of the optimal density of their populations, and of deciding on their normative utilization limits.

The government preserves carrying out research in this direction should participate actively in the solution of these problems. The works published here cannot pretend, of course, to give the final solution of the problems raised, but yet they might be of use in solving these problems correctly.

The first three articles in this collection deal with the studies of the most valuable fur-bearing animals in the fauna of the USSR-- the sable and marten (forest and stone). A proper economic exploitation of these species cannot do without a profound and comprehensive study of their morphology, ecology, and history.

The work of G. N. Likhachev explains a number of little-known aspects of badger ecology. This study is of vital importance for the conservation of this animal, which because of its destruction of rodents and harmful insects, is so beneficial to forestry and agriculture.

M.N. Borodina summarizes in her work the results and the prospects of the measures taken for increasing the beaver population in the Oka River Basin. Besides the practical conclusions and propositions contained in this work, it will be useful to young specialists as an example for the planning and execution of similar investigations.

P. B. Yurgenson, in his article on the method of the quantitative registration of the white hare, dwells on a number of theoretical and methodical problems, which are very essential for the elaboration of quantitative registration methods.

G. F. Bromley in his monograph deals comprehensively with all fundamental ecological problems of the wild spotted deer, an animal which has become a very rare specimen in its natural area. This work will undoubtedly prove useful in planning the measures to be taken for the preservation of this rare and valuable animal; in the practical work of the deer breeding ranches, and also in the planning of the measures for the distribution of this deer species beyond the boundaries of its natural area.

G. F. Bromley

ECOLOGY OF SABLES AND YELLOW-THROATED MARTENS, WIDELY DISTRIBUTED IN THE MARITIME TERRITORY (Sikhote Alin Government Preserve)

(Materialy po ekologii sobolya i kharzy, rasprostranennykh v Primorskom Krae)

The Sable

The Sikhote Alin sables, as well as the Sakhalin subspecies Martes zibellina sachalinensis Ognev, are distinguished by a poorly-developed skull and teeth and by light-color fur with pale-yellow and rusty shades predominating. As a result of a survey of a great amount of material, B.A. Kuznetsov in 1941 distinguished the sables of the Ussuri River Basin and the mountainous parts of the Sikhote Alin as a distinct subspecies under the name Martes zibellina arsenieki Kuzn. He observed that they were of a lighter color than the Sakhalin type.

The coloration of the Sikhote Alin sables is not always uniform. Exceedingly rare dark individuals are found, but more often the fur is a rusty shade which sometimes even resembles the color of the Siberian mink. Hunters have noted that sables of the eastern slopes of the Sikhote Alin and its southern range have a much lighter coloration than those of the western slopes. The best specimens are found in the more northerly regions, along the upper reaches of the Gorin, Kurmi, Urmi, Amgun, and Kharpi Rivers. Here, dark-brown sables of a peculiar variety with good quality fur are most frequently found. To improve these qualities in the Maritime Territory, Barguzin sables were set free to mate on several occasions. Their desirable fur qualities are being transferred very slowly to the more numerous sables of the Sikhote Alin, and completely disappear under the new environmental conditions. The economic value of this method of improving the qualities of the variety has not yet been proved sufficiently.

Below are data on the percentage of the various kinds of sables caught in the upper reaches of the Samarga River in the Ternei Region of the Maritime Territory. during February 1952 (Table I).

This table clearly shows the low market value of the sables of the eastern slopes of Sikhote Alin.

Tables II and III present the weights and measurements of local sables (in cm and g). All the sables enumerated in the tables were caught in the 1947-1954 period.

From the given data it may be seen that the male sables are larger than the females.

Table I

Kind	Number of sables	% of each kind	Kind	Number of sables	% of each kind
Normal head	–	–	Collar dark	22	37.9
Nape high	9	15.5	Collar normal	11	19.0
Nape normal	13	22.4	Bright fur	3	5.2

Table II

Date	Sex	Weight	Length of body	Length of tail	Length of hind foot	Length of ear	Place of Capture
3/XII	♀	522	39.5	12.1	7.8	3.2	Ternei Region
24/XII	♀	541	39.6	12.7	7.2	3.3	" "
17/II	♀	602	40.1	13.5	8.1	3.7	" "
Average		554.7	39.7				
30/XI	♂	919	41.7	13.8	7.8	3.9	Ternei Region
28/XII	♂	750	43.0	13.5	8.5	4.3	" "
11/I	♂	754	42.0	13.0	9.5	4.2	" "
14/I	♂	847	44.2	14.2	8.5	4.1	" "
7/II	♂	782	41.0	13.5	9.2	4.1	" "
24/II	♂	771	43.5	13.9	8.5	3.4	" "
7/II	♂	635	39.3	12.1	6.8	–	Lazo Region
25/II	♂	673	43.1	12.4	7.9	3.1	" "
18/XII	♂	849	43.0	13.5	8.0	4.8	Taukhe River
Average		784.8	43.1				

Table III

Date	Sex	Total * length	Basic length	Condylo-basal length	Breadth of skull	Height of skull
3/XII	♀	73.2	67.7	72.0	36.9	32.0
24/XII	♀	72.9	66.4	71.4	37.1	32.2
17/II	♀	72.1	66.9	71.2	37.3	32.1
30/XI	♂	82.7	73.8	81.0	46.8	34.3
28/XII	♂	78.1	72.4	76.4	33.1	34.2
28/XII	♂	83.9	73.9	81.5	47.1	35.1
24/II	♂	81.3	73.0	78.2	45.0	34.9
25/II	♂	77.9	70.9	76.6	38.7	32.8

* All measurements are given in mm.

Until 1904 sables were widely distributed throughout the entire Maritime Territory. Local veterans have given many examples proving the former large numbers of these animals. One old timer, A. A. Kovez of the Taukhe River Valley (Lazo Region), said that 75 sable furs were seen pegged out for drying by the wind around one of the Chinese hunter's houses in 1908. This was the catch made by a single hunter during winter in those days. According to information received from the natives of the area in 1918, 1919, and 1920 there were so many sables in Sikhote Alin, that on the first night of a hunt they gathered around the carcass of a slain animal and very often spoiled the hunter's provisions, the raw furs, and the dried fish for dogs kept on the sledges. According to Russian immigrants, until 1930 there were more sables than Siberian minks. They were widely distributed, not only in the mountainous parts of the fir forests (taiga), as today, but also in the river valleys. About 70% of all sables of the Maritime Territory except Kamchatka, came from the middle of Sikhote Alin. Below are figures (in percentages), on the sables caught in various parts of Sikhote Alin (1920-22), based on preserve records.

Northern part of the Sikhote Alin to Samarga River	20
Middle Sikhote Alin from Samarga River to Lazo Region	40
Southern part of Sikhote Alin south of Lazo Region	10
Left bank of Amur River and other regions of the Far East, excluding Kamchatka	30
	100

In the period 1928-1930 the sable represented, financially, 60% of the State fur purchases in the Maritime Territory. However, it should be pointed out that a decrease in the numbers of this animal had already become noticeable by 1920. In the opinion of old-timer hunters, the fur trade was conducted at the expense of the basic "breeding stock" so that the sable population was seriously depleted. In spite of this fact the fur trade was not reduced but, on the contrary, increased, and just before 1928 reached unprecedented proportions. This is explained by the appearance of experienced hunters from Minusinsk from the south of the Krasnoyarsk Territory who used specially trained sable-hunting dogs. Within two years these new-comers, together with the inhabitants of the Maritime Territory, had caught almost all the sables of the more accessible parts of the taiga. The new hunters were skilled in trapping, which proved to be both simple and effective, especially during the oestral period. In the beginning of 1928, as a result of these techniques, 1000 sables were caught for State purchase in the valleys of the Sankhobe, Belimbe, and Ta-Kema Rivers (Ternei Region). In one year alone, more sables were caught than in the previous 15-year period, (1911-1926).

Because of the absence of any restrictions on fur trapping, there has been a disastrous decrease in the number of animals caught since 1930. Proof of this fact is presented in data in Table IV on the state purchases from 1928 to 1933.

As a result of the small number of sables in the Ternei Region in 1930, hunters were compelled to seek a livelihood far beyond the mountain passes in the upper reaches of the Iman River tributaries, i.e., at distances of 100-180 km from the Ternei settlement.

The rapid disappearance of the sable was due not only to excessive hunting, but also to mass deaths that occurred in 1927 from a disease of unknown origin.

Table IV

Year of capture of sable	Number of specimens caught in the Far East, excluding Kamchatka	Number of specimens caught		
		in the Iman River Basin	in the Bikin River Basin	in the Ternei region
1928/29	2318	473	93	427
1929/30	2292	180	203	190
1930/31	2160	130	152	65
1931/32	941	17	54	6
1932/33	935	8	4	0

Sable hunting was prohibited in 1933. By that time only a very number of sables had survived in almost inaccessible areas, e. g., around the sources of the Bikin and Ulyangou Rivers, among the deposits of the northern slopes of the Bogolodze Mountains, and, according to data in the preserve's archives, on the northern slopes of the Kurumi Mountain ridge. These districts were later incorporated into the vast area of the Sikhote Alin Preserve. Other areas where scattered groups of sables have survived are: upper reaches of the tributaries of the Bikina-Situkhe, Khaisan, Koltukhe, Chinga, Khandagou, Site, and Mudyu Rivers. Sables were also found in the upper reaches of the tributaries of the Tatibe-Bailaza, Chichingouza, Koloktui, Talikan, Bol'shaya Sibichi, and Malaya Sibichi Rivers. At the upper reaches of the Armu River sables survived at the sources of the Nantsa, Mikula, and Bailaza tributaries; a few sables have also survived at the Situkhe River, south of the source of the Iman River between the Daubikhe and Gilanze Rivers.

In the northern part of the Ternei Region, sables survived in the upper reaches of the Samarga and Ta-Kema Rivers. In these river basins and at the upper reaches of the Sitsa, Akhte, Chima, and Il'me Rivers, sables rarely appeared as isolated specimens. More to the south, isolated specimens remained along some tributaries of the Tunsha and Sitsa Rivers. In the Sitsa River Basin, according to data in the archives, sables were seen in 1933 around the sources of the springs Podrebesnyi "Shirokaya Pad", Goremyka, Spornyi, and the right and left banks of the Khairyuzovka. Some specimens were found on the Snezhnaya Mountain in the Ol'ga Region and the sources of the Vanchin River Basin. Further south, sables survived on the Tachin-Chtan Mountain ridge.

In 1936, at the time of the establishment of the Sikhote Alin Preserve, sable tracks were seldom seen within the former borders of this 1,800,000 hectare preserve. They were seen only among the abundant deposits and in the higher mountain areas where previously the sable could not have been caught. Observations made in 1938 proved that individual sables periodically visited the lower mountain areas of the Sikhote Alin. Their spoor was seen on the border between the Okhotsk forests and the Manchurian forests.

At the end of February 1944, the scientific worker V. D. Shamykin, traversing the trail from the Zimoveinyi Spring to the "Shirokaya Pad" Spring, discovered sable spoor around the sources of the Sitsa River Basin: Zimoveinyi, Sukhoi, Korytnyi, Kamennyi, Kholodnyi, Balobanovskii, Yuvchenko, Skvortsovskii, and "Shirokaya Pad". According to the data of V. D. Shamykin the tracks of only 13 sables were found in the area of 7,000 hectares. In 1944 and 1945, V. D. Shamykin found four fresh sable prints around the Serebryanyi and Tigrovyi

Springs, one around the Starikovyi Spring and one around the "Pereval". According to his calculations the tracks of one sable were found to be 7-10 km of trail. In 1944 the sables on the Kurumi Mountain ridges inhabited the high mountains, periodically coming down in February and March to the slopes of the foot of the mountain.

In these areas the taiga had been untouched by fires and for centuries had remained unchanged. According to V. D. Shamykin, sables had the best chance of survival in this area. As a result of his studies, in 1945, V. D. Shamykin arrived at the conclusion that the sables continued to inhabit the Kurumi Mountain ridge, and that there was no danger of their extermination.

On 11 February 1953, a special unit arrived to the "Podnebesnoe" Estate in order to register sables. From 12 to 21 February, four men in pairs going in different directions daily investigated the areas of the streams flowing from the Kurumi Mountain ridges—the Solnechnyi, Lentochnyi, Korytnyi, Kabanii, Balabanovskii, Yuvchenko, Skvortsovskii, D'yachkovskii, and Medvezhii. Sable footprints were not found anywhere. Evidently the sables in the areas either perished from epizootics or the information given by V. D. Shamykin was shown to be unreliable.

In the Sudzukhe Preserve (Lazo Region), where formerly sables had lived on the mountain peaks around the Sudzukhe and Taukhe River sources, during the period between 1936 and 1950 they settled on the shady slopes of the Chernaya and Sandagou Mountains and on the Osinovaya, Nageevskaya, and Brusnichnaya Mountain deposits.

Some sables settled on Tumannaya Hill on the seashore and around the Ta-Chingou River sources 3 km from the scientific base.

Table V shows the statistics of sable trapping in the period, 1932-1952, as a percentage of the year 1947 in the Maritime Territory.

Table V

Year	% caught	Year	% caught	Year	% caught
1932	16.8	1939	0	1946	19.1
1933	12.5	1940	0	1947	100.0
1934	18.1	1941	1.2	1948	4.1
1935	0.6	1942	7.8	1949	1.3
1936	9.2	1943	2.9	1950	3.6
1937	9.1	1944	9.3	1951	200.0
1938	0.2	1945	10.3	1952	20.0

In the Ternei Region of the Maritime Territory, the following number of sables were caught in the above period (Table VI).

It should be noted that State sable purchases are now being made in areas which are gradually being repopulated with sables. The time has not yet come to proceed with the sable fur trade on a large scale. Intensified hunting may impede restoration of this animal's stock. The sables in the Maritime Territory have not yet settled in the fir forests at the foot of the mountains, as was observed in 1927, i. e., when the extermination of the animal's basic herds began.

Table VI

Year	Number of specimens	Year	Number of specimens	Year	Number of specimens
1933	0	1940	0	1947	30
1934	1	1941	2	1948	30
1935	0	1942	15	1949	29
1936	0	1943	15	1950	30
1937	0	1944	12	1951	60
1938	1	1945	33	1952	60
1939	0	1946	53		

Table VII presents data on sable nutrition in the Ternei Region during the 1946-1954 period based on an analysis of the contents of 11 stomachs and 27 excrements. The latter data were collected around streams of the Pravaya Akhte Springs (tributary of the Velikaya Kema River).

Table VII

Feed	Number of data	% of occurrence	Feed	Number of data	% of occurrence
Mammals*	33	86.8	Flying squirrels	6	15.8
Shrews	1	2.6	Birds	3	7.9
Muridae	16	41.6	Hazel hens	2	5.2
Voles	7	18.4	Vegetable feed	4	10.4
Forest mice	8	20.8	Cedar nuts	2	5.2
Squirrels	6	15.8	Cowberries	2	5.2

In December 1953 an expedition of three men visited the best sable areas in the upper reaches of the Velikaya Kema River. As a result of a detailed study of this river's tributary, the Pravaya Akhte, this detachment succeeded in recording the following findings:

Sables can be found in individual isolated groups on the eastern slopes of the Sikhote Alin, mainly in the immediate vicinity of the ridge. Sables are not to be found in areas which have suffered from forest fires. During the cold winter months the sables on the eastern slopes of the Sikhote Alin have several temporary dens and foodstores. They do not always prepare a warm winter (permanent) den. The tendency to do so is more peculiar to the female in February. The sables also prepare warm dens near a large carcass, for instance, that of a musk deer, on which the animals live for several days. In the coldest winter months, the sables remain for 3-4 days in the dens and food storehouses, with large quantities of food.

The number of sable prints made over an interval of twenty-four hours is not constant, depending mainly on the presence and abundance of natural food and to a lesser degree on the height of the snow and temperature of the air. Around the

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* Translator's note--Apparently not otherwise identified.

upper reaches of the Pravaya Akhte Springs where the expedition worked in February 1954, we found that the average length of the daily run was 2400 m (ranging between 1200-3200 m). This observation was made on the basis of six thoroughly inspected tracks of sables when the height of the snow varied between 12-14 cm.

The "individual" realms occupied by the sables varied in size, and were not large. It is noteworthy that in winter the sables very seldom leave their selected "realms" or overstep their boundaries. For instance, it is known that in one case a sable covered a distance of 9 km from the eastern to the western slope of the Sikhote Alin through an area without forests (elevation—1400 m).

Sables are very rarely active in the daytime during the coldest winter season. They appear on the first warm days of February.

Three sketches are presented on page 8 following a sable's tracks for 24 hours at various times in the vicinity of the upper reaches of the Pravaya Akhte River (scale of sketch 1 cm = 100 m, the scale is reduced by half).

Yellow-throated Marten

On the basis of the State's fur purchases and information provided by hunters the yellow-throated marten is rarely found. The animal is quite unknown in the latitude of the branches of the Kopi, Botchi, and Tumnin Rivers, all of which flow into the Sea of Japan.

On the western slopes of Sikhote Alin, the limit of the animal's range passes through the upper reaches of the Khungari River Basin and crosses the middle stream of the Kura, Urmi, Bira, Bidzhan, Zeya, and Bureya Rivers. Its extreme northern point is on the Oldoi River, where the border of its range crosses the USSR boundary.

As in the case of the Himalayan bear (Ursus tibetanus cuvier), and the goral (Nemorhaedus goral)—(Hardwick), the yellow-throated marten must be considered one of the species which, originating in the mountainous regions of Asia, spread northward as far as the Oldoi River where they stopped for various reasons. The Himalayan bear's spreading further north was prevented by the absence of his staple food found in forests of the Manchurian-type (Mongolian oak and Korean cedar).

The barrier which prevented the spread of the yellow-throated marten farther north was the deep snow on even the steep rocks of the mountains in the north. The ability of the yellow-throated marten to climb or move through the treetops did not suffice, apparently because it obtains its principle food from the ground.

This marten may be found in the most varied regions of the Sikhote Alin from the foot to the bare crests of the mountains. The animal may be detected among the sheer rocks of the seashore, in places inhabited by gorals, in waterside scrub-oak forests with dense shrubs populated by the Manchurian hare, in places burned over by fires at various times, in centuries-old broadleaf-cedar and oak forests, in dark-needled taiga, consisting of spruce and silver fir trees, in high mountain forests of birch and Libocedrus cedars and on bare stretches covered by lichen. The yellow-throated marten may more frequently be found in the dark-needled moss-grown forests typical of the northern slopes of the hills in the Okhotsk Region, in the habitats of the musk deer, and in valleys with springs and rivulets. The marten keeps to these spots until the snow becomes too deep.

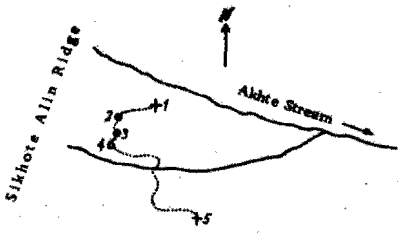

Figure 1. Diurnal track of male sable, 19 January 1954 (length of track 1316 cm; air temperature-10° up to-15°)

1-burrow in the mountain deposits; 2-picked moss; 3-ate remains of squirrel; 4-ate a mouse; 5-lay in the mountain deposit.

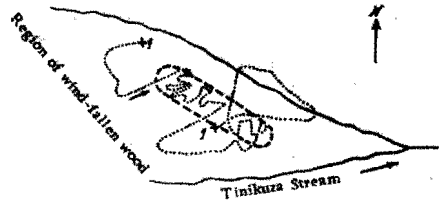

Figure 2. Nocturnal tracks of male sable, 4 November 1954 (length of tracks 3110 m; height of snow 13 cm; air temperature-12 to-6°. Sable hunting for hare 1-"nest" (place of day's rest).

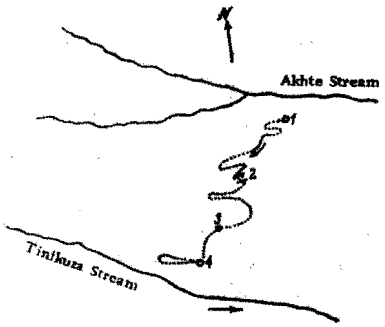

Figure 3. Nocturnal tracks of male sable, 7 November 1954 (length of track 1825 m; height of snow 12 cm; air temperature-12 to+9°)

1-nest in mountain deposits; 2-sables hunting for hazel grouse; 3-ate ten cedar seeds; 4-nest under uprooted tree.

After the snowfalls in March, when the snow is 50-60 cm deep, the yellow-throated marten is unable to walk through the snow, and starts moving through the treetops, gradually coming down to the foot of the mountains, to the zone of broad-leaf forests with little snow. The yellow-throated marten's load coefficient is 31g per sq cm; it is higher than that of the Siberian mink and the sable.

There is no foundation for the statement made by N. T. Zolotarev in 1937 that this marten is to be found only in the Manchurian type of forest but not in the needle forests.

The results of investigation of a yellow-throated marten's twenty-four-hour tracks in the Sikhote Alin Preserve are given below (Figures 4, 5, 6).

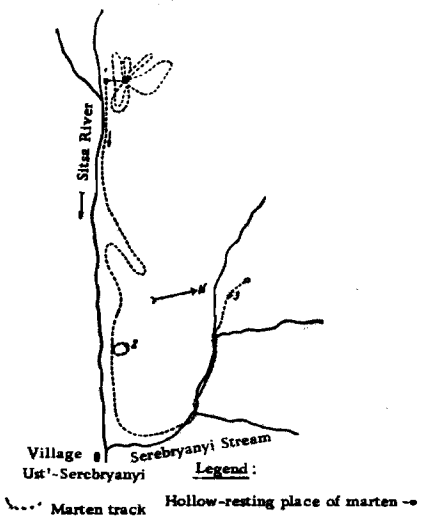

Figure 4. Diurnal track of two martens, 19 January 1953 (length of track 5296 m)

1-body of musk deer;
2-feathers of hazel grouse;
3-skin and blood of a squirrel
(scale: 1 cm = 1 km reduced three times).

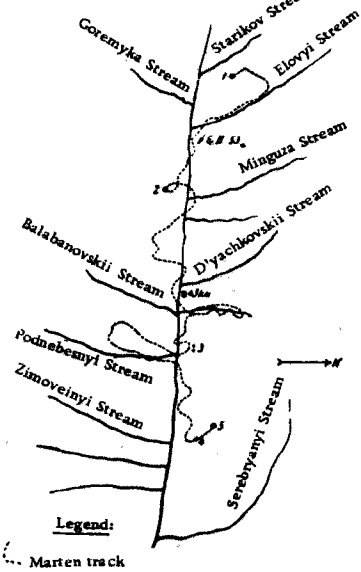

Figure 5. Track of two martens, 6 and 7 February 1953 (on 6/II covered 16 km; 7/II 18 km)

1-refuge 5-6 February;
2-refuge hollow 6-7 February (remains of Manchurian hare)
3-ate two hazel grouse; 4-remains of Manchurian hare; 5-refuge hollow 7-8 February
(scale: 1 cm = 1 km reduced three times).

The yellow-throated marten has no permanent lair and is constantly on the roam. It increases in numbers, according to the rise of the musk-deer population. These facts were disclosed by registering the number of marten tracks over several years in the Sikhote Alin and former Sudzukhe National Preserves. Conversely, martens decrease in number after large scale destruction of musk deer by the hypodermic larvae of the gadfly. These localize in the croup; as many as 1,600 have been found in one animal. Thus, at the beginning of the winter of 1940, a great

number of musk deer appeared in the Sikhote Alin Preserves; followed in 1941 by a corresponding increase in the number of martens. A marked rise in the number of musk deer followed by an increase in the number of martens was noticed in 1948, 1949 and 1950. As a result the game wardens in one year destroyed an unprecedented number (37). According to one old-timer, there were fewer martens up to 1927, since in the past, sable trapping was always accompanied by slaughter of the musk deer which is the main food of the yellow-throated marten. In trapping the musk deer, the Chinese used nooses set in glades among densely growing trees. Thus, the continued destruction of musk deer kept down the numbers of the yellow-throated marten in a given area of the forest. From 1937, when the sable trade (as well as the musk deer trade) was curtailed, the musk deer started to increase in number, so that the marten also increased in number.

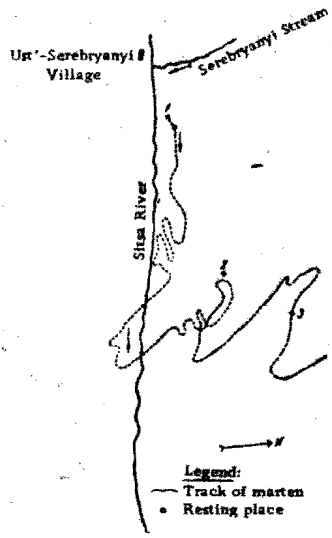

Figure 6. Diurnal track of marten, 23 February 1953

1-ate one hazel grouse; 2-killed white hare; 3- remains of woodpecker (scale: 5 cm = 1 km reduced three times).

The yellow-throated marten's fur is sparse, short (22-25 mm long) rough, and bicolored; it is sold at a low price. The government bounty of fifty roubles for each trapped marten, established in 1940, has now been abolished. Yet it is difficult and time consuming to trap. They are usually shot on chance encounter, never purposely hunted.

In Table VIII data are given on the yellow-throated marten purchased by the government in the Ternei Region in 1935-1950.

The table shows that in the Ternei Region the average annual catch was 37 martens. The annual catch of yellow-throated martens in the Maritime Territory is also small.

Table VIII

Year	Number of yellow-throated martens caught	Year	Number of yellow-throated martens caught	Year	Number of yellow-throated martens caught	Year	Number of yellow-throated martens caught
1935	54	1939	50	1943	18	1947	37
1936	55	1940	31	1944	32	1948	35
1937	35	1941	18	1945	23	1949	40
1938	48	1942	20	1946	29	1950	62

Table IX

Year	Number of yellow-throated martens caught	Year	Number of yellow-throated martens caught	Year	Number of yellow-throated martens caught	Year	Number of yellow-throated martens caught
1935	350	1939	164	1943	218	1947	119
1936	183	1940	241	1944	180	1948	122
1937	105	1941	167	1945	245	1949	86
1938	115	1942	255	1946	147	1950	184

The average annual catch is 180 specimens. As was said before, the negligible quantities of yellow-throated martens purchased by the government can be explained by the difficulties in capturing the animal. It is seldom tempted by bait. Because of its acute sense of smell it can even avoid traps set on its path. Its extreme agility aids it in escape from hounds 50% of the time.

The yellow-throated marten is large and strong and attains a length of 71.9 cm (excluding the tail). It has a thin and supple body, weighing only 5.7 kg and has been known to leap a distance of 3-3.5 m. It moves fast on the ground and in branches, jumping from the top of one tree to another so quickly that a man, overcoming all possible difficulties of the forest, is unable to reach or shoot it.

Table X and XI present data on the weight and dimensions (in cm and g) of various yellow-throated martens obtained in the Sudzukhe and Sikhote Alin Preserves in the years 1945-1954.

As is shown in the tables, the males are somewhat larger than the females. Table XII presents some measurements of yellow-throated marten skulls obtained in the Ternei part of the former Sikhote Alin Preserve.

The skulls of old yellow-throated martens have teeth which are worn down to the gums. Such martens are caught by hounds that toy with their victims before killing them.

Table X

Dimensions and weight of males

Date	Weight	Length				Chest girth	Place of capture
		Total	Tail	Hind limb	Ear		
30/X	5748	71.9	44.2	13.6	4.0	33.1	Ternei Region
11/I	3448	64.7	42.1	12.3	3.4	32.4	" "
3/III	3611	63.1	41.1	-	2.7	34.1	" "
19/X	-	69.7	42.1	12.2	3.7	-	" "
-	3450	65.0	Very old specimen			-	" "
25/XII	2760	56.0	37.0	11.0	-	-	Lazo Region
-	2367	50.0	38.0	11.5	-	-	Tachin-Chtan Mountain ridge " " " "
14/I	2463	60.0	-	11.0	-	-	" " " "
12/I	2690	50.0	-	10.0	-	-	" " " "
Average for males	3317	61.2					

Table XI

Dimensions and weight of females

Date	Weight	Length				Chest girth	Place of capture
		Total	Tail	Hind limb	Ear		
21/XII	2711	61.8	42.6	11.7	3.7	24.2	Ternei Region
24/X	3101	61.3	41.9	10.7	3.1	-	" "
19/VIII	3119	55.1	36.4	12.1	3.8	-	" "
29/XI	3819	54.9	35.4	12.3	3.8	33.1	" "
-	-	57.0	-		-	-	" "
25/X	2534	57.1	38.8	11.3	3.4	-	" "
13/XI	-	62.0	42.7	11.5	-	-	" "
-	3827	55.0	-	-	-	-	" "
-	2650	62.0	-	-	-	-	" "
11/II	2355	57.0	41.0	11.2	4.5	-	" "
25/XII	2380	57.0	39.0	10.0	-	-	Tachin-Chtan Mountain ridge
7/I	1155	50.0	-	10.0	-	-	" " " "
Average for females	2765	57.5					

Table XII

Measurements of skull (mm), weight (g), length (cm) of yellow-throated marten

Measurements of skulls \ Sex and date	11/I ♂	19/X ♂	29/XI ♀	19/VIII ♀
Total length	108.1	110.3	110.1	101.8
Basic length	98.4	99.8	99.5	96.3
Condylobasal length	106.9	109.1	109.4	99.9
Breadth of skull	66.7	67.8	64.4	61.0
Height	44.5	47.1	46.8	43.9
Weight of body	3448	-	3819	9119
Length of body	64.7	69.7	54.9	55.1

Very little is known about molting in this species of animal. Even experienced hunters cannot provide much information. On 27 September 1940, a yellow-throated marten caught in the Sikhote Alin Preserve had fur with a very marked pigment on the underhair. The underhair varied in color only on the forehead, cheeks, nape, groin, and along the tail. The pigment of the overhair appeard on the spine, nape, and both sides of the body. According to the external marks, the molting does not end in June, and summer hair is acquired only at the end of August. It is shorter, rougher, and less downy than the winter hair. In summer the fur is darker; the light spots also contain golden shades. The hair of the females in both summer and winter is usually more delicate and shorter than that of the males.

The yellow-throated marten's diet is highly varied. It can execute long leaps of up to 3-3.5 m and jump freely to the ground from heights of 12-14 m. In the tree-tops it moves easily from one tree to another 10-12 m apart. It can thus run down any fast-moving prey. Owing to its endurance, it can cover a distance of 10-12 km during day or night while hunting prey; following the footprints to the lair, its tracks are difficult to follow. The yellow-throated marten constantly changes its very extensive hunting area. Moving with uniform bounds it can cover the entire basin of a stream in a single day checking each hollow, log, and river bend for its prey. In following the tracks, one may discover the remains of hares, birds, or musk deer after 3-4 km (Figures 4, 5, 6). In February 1947, after trailing a yellow-throated marten on the coast of the Siao-Chingkow Bay (former Sudzukhe Preserve), the remains of a sable devoured by a yellow-throated marten were discovered. Fifteen to twenty days later, the skull of a sable that had been killed by a yellow-throated marten was found in the area of this bay. The yellow-throated marten is especially persistent in pursuit of the musk deer in the oak-fir forest zone and the adjacent valleys where this small deer usually hunts for lichen. The yellow-throated martens pursue the musk deer to some extent in the winter, when the fawns of the other ungulates--the red deer, Japanese sika, and roe-- are grown and difficult for the marten to kill. Numerous remains of musk deer killed by the yellow-throated marten can be found in winter over a distance of 18-25 km while crossing the frozen eastern rivers of the Sikhote Alin. When the zoologist Yu. A. Salmin, in 1936, made a winter expedition over the hummock-ice of the Armu River and its tributary the Nantsa, he found twenty-six carcasses of musk deer in a stretch of

200 km—half of them devoured by yellow-throated martens. Some victims were frozen in the ice layers so that the number of musk deer killed by the marten may have been actually much greater as it was not possible to count them all. The average number found by Yu. A. Salmin was one musk deer carcass per 7.7 km of trail covered.

The following results have been obtained through the registration of the remains of musk deer in various years along the Sitsa River (30 km trail) in places often visited by rangers and scientific workers of the reserve (Table XIII).

The uneaten remains of musk deer constitute a considerable percentage of the food of the Siberian mink in the winter.

V. D. Shamykin, who studied the ecology of the Siberian mink stated that over the year the remains of musk deer carcasses represented 6.37 % of their stomach contents. This percentage increased in wintertime as follows: January 13.61%; February 14.12 %; March 11.36%; October 2.97 %; November 3.37 %; December 10.07 %. As seen from the data, most remains were found in February (14.12 %). During that month the remains of musk deer killed by yellow-throated martens can more often found. V. D. Shamykin pointed out that in some winters the remains of musk deer carcasses provide 30 % of the food of the Siberian mink.

Table XIII

Year	Number of musk-deer carcasses found (at a distance of 30 km)	Correlation between distance covered and number of carcasses found
1937	5	1 musk deer -distance 6 km
1938	6	1 " " " 5 "
1939	15	1 " " " 2 "
1940	3	1 " " " 10 "
1941	4	1 " " " 7,5 "
1952	4	1 " " " 15 "

The yellow-throated martens are especially dangerous to the musk deer in autumn, when the young martens are almost full-grown and begin to hunt and chase live prey together. In such cases the musk deer are doomed to fall prey to the inappeasable killer.

Like many other animals, during the chase the yellow-throated martens usually move in a close circle trying to remain in the vicinity of the victim's lair. A few martens cross the musk deer's trail and reach their victim easily after 10-15 minutes. After the formation of a thick layer of ice on the rivers and streams, the yellow-throated martens, like wolves, drive the musk deer out on the ice, where they quickly run down their floundering victim.

In March, as soon as even a slight frozen crust forms on the snow, the yellow-throated martens need to pursue the musk deer for only 800-1000 m before the deer

fall victims to the smaller animals. The deer have a load coefficient of 80 g against the marten's 31 g and therefore can only move slowly over the snow. The marten has been observed creeping to the lair of the musk deer on thick snow. In 1940, at a time when there was no frost, three yellow-throated martens were seen jumping into the water to catch the musk deer taking refuge in a stream. When this happens the martens are unable to swim against the stream to reach their victim.

Two or three martens do not devour a musk deer at one feeding but return to the carcass on several consecutive days. Excrement accumulates near the roots of trees around the remnants of a carcass. Blood-stained paths leading to temporary burrows or hollows and tufts of musk-deer hair scattered by the wind can also be found. The martens often drag part of a slaughtered musk deer beneath wind-felled trees and branches or into hollows. In heavy frosts the musk deer carcasses freeze quickly and the martens leave them and look for new food.

The yellow-throated marten begin to hunt the young of the ungulate animals with their appearance in the early spring. This persecution ceases when the young reach a weight of 10-12 kg.

Red deer, Japanese sika, and goral fawns which were killed by this predator, have been found more than once in the Sudzukhe Preserve. Even a squirrel, when chased by the marten can only escape by hiding in a narrow hole. At night, the yellow-throated martens successfully catch the hare and Manchurian hare in their feeding grounds and leave the site of their repast strewn with scraps of hare skin and fur. The martens climb trees and hunt and seize the flying squirrels hidden in the broad hollows and sometimes devour their entire broods. They rarely hunt among the alluvia of the mountains and river bends. If so they cover a distance of dozens of meters under the stones and trunks of trees. They seldom catch mice or chipmunks and unlike the fox, are unable to dig in the ground. Throughout the year they kill various birds and their broods. In summer they destroy the eggs in the nests, apparently favoring those of the hazel grouse and pheasants.

Yellow-throated martens eat small spawning fish, mollusks, grasshoppers, and herbage-cedar seeds, nuts, berries, grapes, etc.

When the food is divided into groups according to animal consumption, percentages are as follows:

50%—small ungulates

30%—rodents varying in size from chipmunks to hares

5%—mice and voles

15%—other food.

The data given suffice to show how harmful the yellow-throated marten is to the hunting trade.

The following list shows the contents of the yellow-throated marten's stomach and excrements in the Sikhote Alin Preserve from 1945-1954.

Contents of stomach

2 January—flesh and fur of musk deer
3 March—fur and flesh
19 August—flesh and fur of squirrel; grapes, snails
24 October—fur of squirrel and musk deer, flesh of salmon
30 October—remains of salmon, bones of mice and flying squirrel
19 October—bones and flesh of salmon
24 October—bones and flesh of salmon, fur of musk deer, vole
13 November—fur and flesh of musk deer
29 November—fur and claw of squirrel, remains of red-backed vole
21 December—flesh and fur of musk deer

Composition of excrements

18 January—flesh and fur of musk deer
20 February—fur of musk deer and hare
4 February—fur of musk deer, claw of bird
10 February—fur of vole and musk deer
26 February—flesh (apparently of musk deer)
29 February—feathers and flesh of hazel grouse
20 February—fur and flesh of musk deer

On skinning young yellow-throated martens caught in various months of the year, it is almost always possible to find an accumulation of fat on the womb and groin. The yellow-throated marten is obviously always provided with food and never suffer from pangs of hunger during the year.

Although the yellow-throated marten is an adroit and relatively strong predator there are almost no complaints of assults on poultry-yards. The reason is that it avoids open spaces around human settlements and seldom approaches even the taiga dweller's yurts. Only old martens without teeth are sometimes forced to approach settlements to collect edible scraps in garbage piles. A yellow-throated marten which entered a bee colony in a kolkhoz in the Ternei Region in a few days succeeded in gnawing through more than 400 frames of dry beeswax, picking out scraps of honey from the combs. Another old marten was killed over the carcass of a horse on a deer ranch in the Sudzukhe sovkhoze, Lazo Region. The hungry old martens are careless and easily trapped. Young yellow-throated martens with intact teeth do not take bait and prefer the fresh meat of animals which they themselves have killed.

Hunters and veterans in various regions of the Maritime (Primorsk) Territory have indicated that the mating season of yellow-throated martens is from the beginning of June to the middle of July. At this time the male martens fight and they cease to be cautious. This information, obtained by inquiries, should be verified by large scale dissections of summer yellow-throated martens, however, these are scarce. The yellow-throated martens give birth to two, three or sometimes four kits at the beginning of May. The young apparently remain with the dam a long time in a hollow or some other sheltered retreat; they have never been seen living in nature in the summer. In autumn the kits reach full size and start to take part in the pursuit of prey.

In summer the yellow-throated marten harbors the tick Ixodes persulcatus and fleas. They are quickly picked up from the fur of slain animals. When the bodies of the yellow-throated martens are dissected (40-50% of all cases), the intestines and stomach are found to contain roundworms of unknown origin.

The yellow-throated marten is a destructive predator which should be exterminated throughout the year. Unfortunately, a plausible method of control has not yet been discovered. Nevertheless, the slight practical experience and knowledge obtained in the Sikhote Alin Preserve have proved that it is possible to combat the beast by the following methods:

Tracking and shooting yellow-throated martens trailed by specially trained hounds, for which the dog must be agile, medium sized, and not trained to chase large animals. This can be achieved by the special training of a puppy. An observer in the Sikhote Alin Preserve who owned such a dog succeeded in catching 17 martens in 1949, that is, more than 50% of all yellow-throated martens purchased by the state in this region.

The yellow-throated marten could be hunted if it were possible to use a lure imitating the voice of a strangling hare, musk deer, or ungulate calf. The yellow-throated marten is unable to listen passively to such a cry and tries to approach, coming to within 30-40 m, or quite close enough for small shot. Unfortunately, such a lure has not yet been manufactured. Also the method of using traps placed near a bait covered with honey or consisting of honeycombs should be tried. Old yellow-throated martens are readily attracted by honey especially in the winter. This method is more often used by hunters interested in catching them alive. There is no doubt that a government bounty for the extermination of the yellow-throated marten would greatly stipulate effective control of this predator.

F.D. Shaposhnikov

ECOLOGY OF THE SABLE OF THE NORTHEASTERN ALTAI*

(K ekologii sobolya severo-vostochnogo Altaya)

An appreciable increase in the number of sables began in 1940 as a result of nature conservation measures in the area in the northeastern Altai. The present study was carried out in 1950-1951 in the Altai Preserve. As a result of its rehabilitation the sable has unavoidably come into contact with the Siberian mink. The author's aim in this paper was to ascertain the chief relationships existing between these two species and their effects on the hunting trade.

The following material served as the basis for this article: 8 sables obtained by the author in different seasons of the year; 16 Siberian minks; 624 excrement analyses; data on thirty areas investigated for the purpose of ascertaining food material; data on tracks of sable and Siberian minks were followed for 140 km; registration and observation of about 1,500 km of trails; and observations made on sables kept in captivity for a period of eleven months.

Ecological Differences Between the Sable and Siberian Mink

Some characteristic features of sables and Siberian minks in adapting to the environment are peculiar with regard to behavior and types.

Under the winter conditions which prevail in the mountains and taiga regions of the Altai, when there is much snow, the sables must spend much time on the surface of the snow in order to obtain food. In hunting small mammals, it often watches its prey, steals up to hazel grouse and wood grouse sitting in the snow-holes, pursues squirrels, and looks for cedar seeds that fall and are concealed by nut-eating animals. Along the way the sable visits berry fields, climbs trees, scans the hollows, looks for food left by squirrels and owls, and hunts small birds perching for the night. Between two lairs the sable covers a distance of 5.8 km in search of food, while the Siberian mink covers only 2 km. In seeking food, the sable crawls under the surface of the snow and beneath logs 3-4 times per km of route, the Siberian mink twice as often.

It is hard to determine the undersnow distances covered by these animals. The great frequency of holes made by the Siberian mink discovered under the snow, as well as scattered observations (a Siberian mink covers a distance up to 50 m without appearing on the surface of the snow), show that the animal in quest of food makes maximum use of the hollows under the snow.

In contrast to other animals, such as the Siberian mink, ermine, and weasel, that devour mice and actively pursue mouselike rodents into their refuges, the sable makes greater use of a keen ear. It reacts to a rustle made by a slight rubbing of the palm on cloth at a distance of up to 27 m, while the Siberian mink perceives this sound only at a distance of 15 m.

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* Work carried out in 1950-1951 in the territory of the former Altai Preserve.

In our opinion the sable bests all other animals with which it competes, owing to its wider adaptation to various conditions of habitat and its ability to utilize vegetable food, resources which are unacceptable to some other related ecological forms. As a result of the combined utilization of both vegetable and animal food, the existence of this animal depends much less upon food as a whole. When there is a shortage of one food, the sable begins to use another. This characteristic is the main reason for the sable's occupation of the same region over a period of several years.

Replenishment of Sable Stocks and the Dynamics of its Distribution in the Northeastern Altai

In 1932, the year of both the prohibition of sable hunting and the establishment of the preserve areas, the sable survived in only a few regions inaccessible to trade in the Gorno-Altai district. Sable tracks were found in the Teletskoe Lake Basin, along the slopes of the Altyn-Tu and Toulok Mountains, and in the rocky canyons of the Bolshaya and Malaya Chili, and Bayas rivulets; a few sables apparently survived on the very upper part of the Bolshoi Abakan River, along the Kair and Kurumchuki Tributaries, to the southwest of these places in the Ust-Kan Region along the Kumir and Iol'd' Rivers, and along the upper reaches of the Katun' River. In the following years all these places became the breeding grounds and distribution centers of sables throughout the territory of the northeastern Altai.

In 1948 the sable was to be found in most of its normal habitats in the Bol'shoi Abakan River and Lake Teletskae Basins. In 1950 the sable occasionally appeared on the upper Bol'shoi Abakan River to its confluence with the Malaya Abakan and from there penetrated into the upper reaches of the Chul'cha and Koksha Rivers and the Kamga Valley. From the Teletskoe breeding ground the sable spread along the Kyga, the middle reaches of the Chul'cha, and from here into the middle reaches of the Shavla River; to the north and the northwest of this breeding ground the sable began to spread to the left bank of Teletskoe Lake, reached Pyzha, and to the south along the River Chulyshman, the tributary of the Shavla River, Chulyshman, reaching the Shavla Tributary.

The reinstatement of the sable began simultaneously with and in the same places as the disappearance of the Siberian mink. Table I clearly illustrates the increase in sable numbers and the decrease in mink numbers in the Bol'shoi Abakan River basin.

Table I

Number of sable and Siberian mink footprints (10 km trail) in the Bol'shoi Abakan River Basin (tributaries: Kanui and Syktyzyl)

Year	Sable	Siberian mink	Number of km covered along the trail in question
1940	0	1.4	77
1941	0	1.2	100
1942	0	3.1	38
1947	1.09	5.62	128
1948	7.9	1.3	119
1949	21.6	1.6	32 (in February)
1950	12.6	0.2	163
1951	18.43	0.09	138

In 1938, 9.4 Siberian mink footprints, but no sable tracks were recorded along 10 km in the Lake Teletskoe Basin (Ydyp River). Thirteen years later, in the same region no Siberian mink tracks were recorded but 67.0 sable footprints were noted.

During eighteen years when sable hunting was completely prohibited in the Bol'shoi Abakan River Basin, the sable ranged over 55-60 km in a straight line from the redistribution center. The numbers of Siberian mink in this area dropped over 4.5 years to single specimens.

Redistribution of the Sable and Similar Ecological Forms According to Their Principal Habitats

In the northeastern Altai the sable ranges within the forest zone from elevations of 450 m up to 2,200 m. As elsewhere, the sable in the Altai avoids areas with sparse forest stands, open swamp areas and burnt forest and mountain tundra areas.

In his typical range the sable markedly exceeds similar ecological forms in number, as is clearly illustrated from the values recorded on the basis of spoors in various stations (Table II).

Table II

Number of footprints per 10 km of trail in various stations

Station	Sable	Siberian mink	Ermine	Weasel	American mink
Cedar-fir forest along slopes of Turochak River, 1950	9.0	5.9	1.0	0.0	0.0
1951	36.6	2.0	0.0	0.0	0.0
Cedar-fir-pine sparsely growing trees in the Valley of Kamga River, 1950	0.4	9.6	1.7	6.3	2.1
1951	4.9	10.2	0.0	8.8	1.1
Cedar-larch forest along the slopes of Sur'yaza River 1950	14.0	1.2	0.4	0.4	0.0
Thickets of birch-bushes in the Sur'yaza River Valley 1950	0.0	10.5	0.0	0.0	0.0

When the sable encounters the Siberian mink and ermine, open antagonism can be observed between them.

Settling along forest-covered mountain slopes, the sable drives the Siberian mink into the open river valley spaces and tundra bush. The sable tenaciously chases the Siberian mink and ermine, hunting them doggedly. Following trails of sable spoor, we discovered three cases of dead Siberian mink and on several occasions detected the fur of this mink in sable excrement. The ermine generally escapes by hiding among the stony slopes; its fur has only been found once in sable excrement.

The greatest concentration of sables in winter is usually observed in the center of the forest zone, on northern and western slopes, mainly along the upper

reaches of rivers and streams. The mountain slopes in such spots are extremely cluttered with brushwood and rotten trunks of trees felled by the wind. Hazel grouse and wood grouse pass the night in the small glades. The snow in these places is loose and has many hollows beneath.

Food Resources and Diet of the Sable

The abundance and periodicity of cedar-seed crops are of great importance in the diet of the sable.

The majority of Altai mountain-taiga inhabitants are to some extent cedar-seed eaters and complicated food relationships exist among them (F.D. Shaposhnikov, 1950). The size of the seed crop affects the numbers of rodents, squirrels, chipmunks, gluttons, wood grouses, hazel grouses, and nutcrackers not only in a given year, but also later.

According to observations by the geobotanist, N.S. Lebedinova, a four-year cycle of fluctuations in the cedar-seed crop occurs in the northeastern Altai cedar forests; crop failures of cedar seed were noted in 1933, 1937, 1941, 1945, and 1950. Meteorological conditions, both in spring and in autumn, greatly affect the crop fluctuations. Early spring frosts destroy the ovary and cold damp in autumn harms the unripe cones, causing them to fall. We should point out that the topography of a mountain creates a variety of growing conditions, so that consecutive years of cedar-seed crop failures seldom occur.

According to N.S. Lebedinova, most sable food crops are peculiar to cedar forests lying at a level of 1,000-1,400 m absolute altitude, especially mossy cedar forests of both the bilberry and wood sorrel type, where the greatest seed crop per hectare is about 700-800 kg, or 350-400 kg of nutritive matter (1953).

An idea of the sable forage reserves in their natural ranges may be obtained from data on estimated food reserves in experimental areas established at different altitudes (Table III).

Table III

Summary of estimated sable food reserves in cedar-fir and cedar-larch forests on 28 plots of 0.25 hectares on a per hectare basis (1950)

		Cedar-fir-tree forest			Cedar-larch forest
		500-700m abs. alt.	900-1000m abs. alt.	1200-1500m abs. alt.	1200-1500 m abs. alt.
Potential crop of cedar-seeds based on kernel of nut (kg)		200	250	160	140
Actual seed crop during year of registration		30	25	0.0	0.0
Actual crop of ashberry (kg)		12	10	0.0	0.0
Actual bilberry crop (kg)		32	7.5	2	0.0
Muridae (catch per 100 hunting days)		21	17	28	9
Registered	squirrels	2	2	0	4
	chipmunks	1	2	1	0
	pikas	0	2	0	0
Seen	nutcrackers	2	1	1	4
	hazelgrouse	1	1	1	0
	wood grouse	0	0	1	0

The sable's prospects of using the vegetable food reserves depends to a great extent upon the number of other cedar-seed and ashberry eaters and meteorological conditions. The stalks of the cedar cones are pitched in the hot summer and cling firmly to the branches, then gradually fall during the winter season. The seeds of cones which fall in autumn are eaten in that season by bears, chipmunks, and rodents. The cedar cones left on the trees are eaten more gradually, especially during the hibernation period of the bears and chipmunks.

According to observations, in winters with much snow, the sable eats only the ashberry, which, being covered by snow, is protected from the small birds, the pine finches and bull finches, that customarily eat them.

The animal food reserves are much more stable, being mainly composed of rat-family rodents. The Siberian redbacked vole is most numerous among the reserves (Table IV).

Table IV

Composition and numerical relationships of small animals in cedar-fir forests on mountain slopes (according to records on 30 plots—total of 1,093 winter hunting days of 1950/51 season)

Species of small mammals	Number in catch per 100 hunting days
Siberian redbacked vole	10.8
Redbacked vole (Clethrionomys rufocanus)..	2.8
Vole (Microtus occonomus).....	0.3
Vole (Microtus (stenocranius) gregalis).....	0.1
Field mouse	0.4
Common shrew	0.5
Pigmy shrew	0.1
Total	15.0

According to examinations of sable and Siberian mink excrement in the winters of 1949/50 and 1950/51 (when there was a good crop of vegetable food) the sable's food varied from 49.1 % vegetable food to 87.5 % animal food (Tables V-VI). The Siberian mink consumes only animal food (Table VII).

A comparison of the composition of the food consumed by the sable and Siberian mink shows clearly the sable's adaptability to a wide range of foods and its utilization of these foods according to the special features of the year in question.

Competition among animals is particularly aggravated in years of vegetable food crop failures when the existence of the two competing species depends upon one kind of food (Table VIII).

As may be seen from Table VIII, competition for food between the sable and the Siberian mink takes place mainly with regard to the ratlike rodents.

In those regions where both the sable and the Siberian mink live, the sable's animal food consists mainly of Siberian redbacked voles and that of the Siberian mink of gray voles. The shrew is more important in the diet of the Siberian mink than in that of the sable.

Table V

Composition of sable food, according to seasons of the year

Composition of diet	1950						1951						Total of all seasons		
	Winter, Nov.-Dec.			Summer, May-Sept.			Winter, Oct.-April			Summer, May-July					
	102 specimens			46 specimens			238 specimens			30 specimens			516 specimens		
	Number encountered	% of encounters to total number	Percentage in food	Number encountered	% of encounters to total number	Percentage in food	Number encountered	% of encounters to total number	Percentage in food	Number encountered	% of encounters to total number	Percentage in food	Number encountered	% of encounters to total number	Percentage in food
Redbacked voles (Clethrionomys)	7	6.9	3.4	15	32.6	15.2	148	44.1	30.0	13	43.5	22.4	183	35.4	21.4
Gray voles (Microtus)	4	3.9	1.9	18	34.8	16.2	52	15.4	10.5	9	30.0	15.5	81	15.7	9.4
Voles (unidentified)	5	4.9	2.4	5	10.8	5.1	9	2.7	1.8	3	10.0	5.2	22	4.3	2.5
Forest mice (Apodemus)	1	0.9	0.5	–	–	–	4	1.2	0.8	1	3.3	1.7	6	1.2	0.5
Shrews (Sorex)	18	17.6	8.7	9	19.6	9.1	49	14.5	9.9	6	20.0	10.3	82	15.9	9.5
Ratlike rodents (unidentified)	22	21.6	11.0	8	17.4	8.1	28	8.3	5.7	6	20.0	10.3	64	12.4	7.5
Water voles	1	0.9	0.5	–	–	–	2	0.6	0.4	–	–	–	3	0.6	0.4
Squirrels	7	6.9	3.4	3	6.5	3.0	43	12.7	8.7	–	–	–	53	10.3	6.2
Chipmunks	1	0.9	0.5	1	2.2	1.0	10	2.9	2.0	2	6.6	3.5	14	2.7	1.8
Pika	2	1.9	0.9	2	4.4	2.0	22	6.5	4.5	2	6.6	3.5	28	5.4	3.3
Flying squirrels	10	9.8	4.8	1	2.2	1.0	5	1.5	1.1	–	–	–	16	3.1	1.9
Weasels	–	–	–	–	–	–	1	0.3	0.2	–	–	–	1	0.2	0.1
Siberian mink	–	–	–	–	–	–	4	1.2	0.8	–	–	–	4	0.8	0.5
Maral (Altai wapiti)	–	–	–	–	–	–	2	0.6	0.4	–	–	–	2	0.4	0.2
Musk deer	–	–	–	–	–	–	1	0.3	0.2	–	–	–	1	0.2	0.1
Wood grouse	–	–	–	3	6.5	3.0	1	0.3	0.2	–	–	–	4	0.8	0.5
Hazel grouse	9	8.8	4.3	–	–	–	16	4.7	3.2	–	–	–	25	4.8	2.9
Nutcracker	1	0.9	0.5	–	–	–	5	1.5	1.1	–	–	–	6	1.2	0.7
Small passerine birds	8	7.8	3.8	2	4.4	2.0	8	2.7	1.6	2	6.6	3.5	20	3.9	2.3
Birds (unidentified)	5	4.9	2.4	1	2.2	1.0	17	5.0	3.4	–	–	–	23	4.5	2.7
Eggs of birds	–	–	–	1	2.2	1.0	–	–	–	–	–	–	1	0.2	0.1
Beetles (Carabidae)	3	2.9	1.4	2	4.4	2.0	4	1.2	0.8	4	13.3	6.9	13	2.5	1.5
Insects (unidentified)	1	0.9	0.5	–	–	–	1	0.3	0.2	2	6.6	3.5	4	0.8	0.5
Cedar seeds	60	58.8	28.8	21	45.6	21.2	47	19.9	19.5	17	23.3	12.0	135	26.2	15.7
Ashberry	43	49.2	20.3	–	–	–	–	–	–	–	–	–	43	8.3	5.0
Bilberry	–	–	–	7	15.4	7.1	8	2.4	1.6	–	–	–	15	2.9	1.7
Blueberry	–	–	–	–	–	–	4	1.2	0.8	–	–	–	4	0.8	0.5
Cowberry	–	–	–	2	4.4	2.0	3	0.9	0.6	–	–	–	5	1.0	0.6
Various berries	–	–	–	–	–	–	–	–	–	1	3.3	1.7	1	0.2	0.1

Table VI

Percentage composition of sable food in winter during good and bad cedar seed and ashberry crop years

Composition of diet	Winter 1949/50 (good crop in 1949)	Winter 1950/51 (crop failure in 1950)
Animal food	50.9	87.5
This comprises:		
Mammals	38.0	77.0
Including:		
Ratlike rodents	19.2	48.8
Shrews	8.7	9.9
Squirrels	3.4	8.7
Chipmunks	0.5	2.0
Pikas	0.9	4.5
Flying squirrels	4.8	1.1
Water voles	0.5	0.4
Other mammals	0.0	1.6
Birds	11.0	9.5
Including:		
Hazel grouse	4.3	3.2
Wood grouse	0.0	0.2
Other small birds	6.7	6.1
Insects	1.9	1.0
Vegetable food	49.1	12.5
This comprises:		
Cedar seeds	28.8	9.5
Ashberries	20.3	0.0
Other vegetable food	0.0	3.0

Table VII

Composition of the Siberian mink's food during year

Composition of diet	1950 Summer (May-Sept.) 10 specimens			1949/51 Winter (Jan.-April and Oct.-Dec.) 98 specimens			Total for all seasons 108 specimens		
	Number of encounters	Percentage of total number	Percentage in food	Number of encounters	Percentage of total number	Percentage in food	Number of encounters	Percentage of total number	Percentage in food
Red vole (Clethrionomys)	2	20	16.8	16	16.3	12.3	18	16.7	12.7
Gray vole (Microtus)	3	30	25.0	30	30.6	23.0	33	30.3	23.2
Vole (unidentified)	1	10	8.3	5	5.1	3.8	6	5.5	4.2
Forest mouse (Apodemus)	-	-	-	3	3.1	2.3	3	2.7	2.1
Shrew (Sorex)	-	-	-	48	49.0	37.0	48	44.0	33.8
Ratlike rodents (unidentified)	1	10	8.3	10	10.2	7.7	11	10.1	7.8
Water vole.....	1	10	8.3	1	1.0	0.8	2	1.3	1.4
Squirrel	-	-	-	1	1.0	0.8	1	0.9	0.7
Chipmunk.....	1	10	8.3	-	-	-	1	0.9	0.7
Pika	3	30	25.0	-	-	-	3	2.7	2.1
Flying squirrel	-	-	-	1	1.0	0.8	1	0.9	0.7
Weasel.....	-	-	-	1	1.0	0.8	1	0.9	0.7
Roe (carrion)	-	-	-	2	2.0	1.5	2	1.8	1.4
Hazel grouse	-	-	-	3	3.1	2.3	3	2.7	2.1
Small passerine birds....	-	-	-	5	5.1	3.8	5	4.6	3.6
Bird eggs.....	-	-	-	1	1.0	0.8	1	0.9	0.7
Bees, their larvae and bee-bread	-	-	-	3	3.1	2.3	3	2.7	2.1

Table VIII

Relative utilization of different kinds of animal food by the sable and the Siberian mink

Composition of diet	Percentage of occurrences	
	Sable (516 specimens)	Siberian mink (108 specimens)
Animal food	76.5	100
Mammals	65.3	91.5
Including:		
Ratlike rodents	41.5	50.0
Shrews (Sorex)	9.5	33.8
Other mammals	14.3	7.7
Birds and their eggs	9.2	6.4
Insects	2.0	2.1
Vegetable food	23.5	0.0

The potential euryphagia* of the sable becomes particularly apparent on feeding them in captivity. Of the thirty-three kinds of animal food which we offered the sable, it completely refused to take the flesh of the mole, the Siberian mink, and the ermine (although it does eat the latter two in the wild state) it also refused to eat eelpout fish, carabus beetles, and forest bugs. On the other hand it readily devoured the flesh of other animals: wild and domestic ungulates, dogs, rodents, shrews, birds, fish (especially fish with scales), and eggs of birds.

Of 18 kinds of vegetable food, the sable refused to take the red currant and cranberry, but accepted, albeit unwillingly, apples. They readily ate the following: bilberry, black currant, ashberry, dried apricot, grated carrot, boiled potato, white and rye bread, and various porridges made of rice, wheat, barley, and oats. Of the milk products, the sable relished cottage cheese and sour cream. It consumed its food rapidly and in great quantities. A sable can devour a bird the size of a hazel grouse or an animal as large as a squirrel in a single meal. It usually brings its food remnants into a corner of the open air cage, but the large accumulation of these hoards proves that the animals do not care to make use of them.

The speed of the sable's digestion and the frequency of defecation are remarkable. Traces of fleshy food are found in the sable's excrement 30-40 minutes after it has been consumed. Vegetable food remnants appear even faster in the excrements, after 25-30 minutes. The sable defecates on an average of 24 times per day, which explains why its excrement can be found so frequently.

The physical composition of its food is of great importance to the physiology of the sable's digestion and excretion. For normal functioning there must be some indigestible roughage in the food's composition: seed and fruit rinds, hair, feathers. Analyses of the excrement of wild animals, particularly mustelid, always reveal either small solid lumps of wool and feathers or concretions of detritus bound together by mucus which covers the sharp fragments of bird and small mammal bones. This is doubtless a protective accommodation against possible injury to the intestinal mucous membrane at a certain stage of peristalsis. As a result of our experiments for a 3-4 day period, of giving sables food free of indigestible roughage such as seed hulls, fruit rinds, berry skins, wool, or feathers, viz, the external coverings of foods constituting the sable's usual diet, it was observed that the animal's excrement became liquid. It reverted to its normal condition with the first intake of food containing roughage. Among other peculiar physiological characteristics of its digestion, it is worthwhile noting that the sable quite often vomits the indigestible parts of his food. We observed this phenomenon while following the trail of the sable's footprints. If the sable ate a vole or a mouse whose stomach was filled with thoroughly digested vegetable food, the sable vomited the entire contents of such a stomach.

It is of great practical importance to determine to what extent the squirrel, a valuable fur animal, is necessary for the sable's diet. V.V. Timofeev, a well-known expert on sable, has paid much attention to this problem. In the taiga and mountain parts of the Altai, where other kinds of food abound, the squirrel is not very important in the sable's diet. An analysis of the sable's excrement shows that squirrel remains constitute only 10.3% of all animal foods, while among the other constituents of the food, the squirrel represents only 6.2%. It should be pointed out that the presence of squirrel remains in the stomach or excrement of the sable does not explain the cause of the death of the squirrel. According to our observations, the sable eats the remains of squirrels caught by hawks and other birds of prey.

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* Translator's note - A neogism, eury = wide range, phage = pertaining to food, therefore an animal that eats many different kinds of food.

It is well known that during periods of coniferous seed crop failures squirrels leave such places en masse and only individual specimens remain. In such cases the remaining squirrels are unable to obtain sufficient food in the upper parts of the trees and descend to the ground to lead a terrestrial existence. During the hibernation period the weakened animals fall easy prey to the sable. This was observed in the Ydyp River Valley, where not a single squirrel survived during the spring, and where the remains of squirrels caught by sables were also found.

In such cases the restoration of the squirrel population can only be achieved if the animals immigrate from other regions.

Reproduction of Sables

The sables of the northeastern region of the Altai have the same periods of oestrus, mating, and bearing young as sables inhabiting other regions (G.D. Dulkeit, 1929; R.V. Kler, 1948; V.V. Timofeev, 1951).

A male sable caught on 6 June had enlarged abdominal glandules, the hair cover of which was wet by their secretions. The testicles measured 17X11 mm and weighed 2.3 g (during passive sexual periods their weight was 0.5 g). On 29 June the sexual organs of a female sable were in a condition of heat (stage 7/8, according to P.A. Manteifel).

Young sables caught on 18 June measured as follows: male 35 cm long, female 32-33 cm; respective weights 500 and 450 g at about 50-60 days of age. When these kits were seven months old, they displayed signs of sexual excitement during the last ten days of September. The male sable persistently pursued the female and repeatedly endeavored to mate with her. The female snapped at him and concealed herself in the nest. At night a noise emanated from the cage, and the male squealed continuously. Because of a fight between the animals, they were placed in separate cages.

The excitement of the male ceased at the beginning of October. The second period of sexual excitement was observed in the middle of May. The male became restless and attempted to mate with the female, but at first she paid no attention to his advances, and only after a few days did she also become excited. The abdominal glands of the male became noticeably swollen, but no changes were observed in the external sexual organs of the female. At that time the sables were eight months old. Unfortunately, at the end of May the two sables were released due to circumstances beyond control.

In the natural environment, the sables in the Altai Region, as those of other regions, showed signs of the oestral cycle in February (G.D. Dul'keit, 1929; V.V. Raevskii, 1947; V.V. Timofeev, 1951).

According to a study made by R.V. Kler (1948), during that period the female undergoes placentation of the impregnated ovule, which until then had been in a latent stage.

Molting and Hair Coloration of Altai Sables

The characteristics and periods of molting by the Altai sables, like their sexual cycle, are similar to those of sables of other regions. The hair begins to change in March. The winter hair first changes on the head and then gradually on the body. Remainders of the sable's winter fur may be found until May on hind parts of the limbs. The summer underfur is 13 mm long and the winter underfur

32-33 mm, the length of the overhair in summer is 23 mm and in winter 48.4 mm. The winter hair starts growing at the end of August and in September the sables become more downy. During November and December, fur of the sable is downiest with a silken luster. At the end of January the fur loses its luster, fades, and begins to shed in places.

Owing to its coloring and fluffiness, the fur of the Altai sable belongs to the typical "neckpiece" variety. According to old trappers who have been hunting sables for 50-60 years, the darker specimens of this animal have more often been found close to the upper border of the forest among the stony deposits.

Peculiarities in Sable Behavior and the Methods of Hunting the Sable in the Past

In his monograph on the sable in the Konda-Sosva Preserve (1947), Raevskii notes four types of sable lairs:breeding or spring, summer, winter and temporary lairs. The sables of the Konda-Sosva Region had one permanent lair during the cold period of winter in January-February. The sables of eastern Siberia behave similarly, according to observations by V.V. Timofeev (1951). We were unable to ascertain the permanent nature of the winter lairs of the sables in the mountain and taiga areas of the Altai. After following the spoor of the same sable for several days it was impossible to state with certainty that this sable had a permanent lair. On the contrary, sables as a rule change their resting places every day, and very rarely keep the same one for more than 2-3 consecutive days.

What is typical of the Altai sable is its reoccupation of the same region and winter lair—that is, after a certain period, 2-3 or even more days, the sable returns to the lair it occupied previously. In all probability, this may be explained by the fact that the winters in the Altai are milder than in the Konda-Sosva Preserve and northern Siberia. A drop in temperature to -20° or -23° has seldom been observed in the region of our work. The abundance of hiding places in the mountain taiga is also of great importance. According to our data, per hectare of cedar-larch forest there was an average of ten wind-uprooted tree trunks in whose hollows and pith cavities the sables liked to hide themselves.

Adult sables behave differently toward the lair than do young 2-3 month old sables. When the adult sable senses that its lair has been detected, it leaps headlong from it at the earliest opportunity, and when the lair cannot be destroyed, the sable will remain there until smoked out of his hole. The young sable remains in the nest until it is possible to take him out with one hand. On 18 July a couple of young 2-month old sables were in a hollow of a rotten fir tree uprooted by the wind beneath the upturned roots of this tree. The trunk of an old cedar that had previously fallen was found, and inside this the main breeding lair had been established. A block one meter long was cut from the trunk of the fir-tree in which the young sables were lying and they were thus carried,in the arms of those who found them, to the boat four km away. The young sables clawed at the cordate knots of the hollow and all efforts to remove them failed. However, they were smoked out and ran into a portable cage placed under the trunk. The next morning we discovered a hole that had been gnawed through in the zinc net by a young sable. The cage was put on the ground close to the cordon's house wall, with the forest 150 m away. No one paid any attention to this cage which was filled with the dust of rotten wood from the nest. A sable kit sleeping in it was discovered by chance when the cage was about to be sent back into the forest for the purpose of sable hunting. The second sable kit which had escaped through the gnawed hole was found by the observer's children under the granary floor. This incident proves to what extent the kits reflex of holding the breath or the imitation thereof is developed in the lair.

The sable's daily food in Altai, as in other places where they live, depends

chiefly upon the kind and abundance of the food available. We have no foundation whatever for describing the sable as a nocturnal or diurnal animal. In years with abundant vegetable foods, the sables are active during the day and night. When the sables eat animal food, they usually hunt during twilight. After a successful hunt the sable as a rule goes straight to his lair regardless of the hour of the day or night. Its activity decreases with weather changes and frosty days; according to our observations, this results from the changing activity of their prey, especially the ratlike rodents.

Modern methods of hunting sables resemble those used decades ago. Of the Altai methods, trapping is worth mentioning. The trap is placed where sable tracks cross. In order to get the sable definitely trapped, a suitable place is chosen where the animal jumps over a log or stones. The trap must be covered by a light material or paper so that its outline may not be seen on the snow.

For smoking sables out of holes under large stones, old hunters of the Altai blew the smoke into the crevices through a tube, using the usual smoker with sulfur added. In places inaccessible to smoke and snares, the hunters did not molest a sable already in a hole, but waited patiently some distance away with his gun ready until the animal looked out of the hole. In our work we have successfully taken advantage of this sable peculiarity of looking out from the hole or shelter from time to time. However, the chief sable hunting method at any time of the year requires a specially trained sable-hunting husky, which is an irreplaceable assistant both to the trade and to scientific workers.

CONCLUSIONS

1. Because of its ecological peculiarities, the sable in the northeastern Altai may be considered a form broadly adapted to various habitats in the forest zone of the mountain taiga. The utilization of both vegetable and animal food by the sable creates an advantage for it in its competition with similar ecological forms.

2. In regions where the sable appears, the Siberian mink soon disappears, as a result both of its destruction by the sable and of its being driven into open unforested spaces. To ensure the preservation of the Siberian mink as a commodity in the interests of the hunting trade, the sable should not be admitted into large tracts of unbroken forests.

3. The competition between the sable and the Siberian mink becomes particularly fierce in years of vegetable food crop failure, when both these species consume animal food, in which the ratlike rodents are of paramount importance.

4. The squirrel does not play an important part in the diet of the sable, except in years of coniferous seed crop failure, when the squirrels remaining in the area are annihilated by the sable; hence the delayed restoration of the squirrels' numbers in such regions.

5. The approach and duration of the periods of the biological cycles of the sables in question—reproduction and molting of hair—does not differ perceptibly from the biological cycles of the sables in other regions.

6. The sable quickly restores its numbers when conservation measures are employed. During the 18 years that reserves have been established the single specimens that survived in 3-4 limited areas bred and dispersed over the greatest part of the forest zone of the territory of the northeastern Altai mountains.

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P. B. Yurgenson

COMPARATIVE SURVEY OF SABLES AND MARTENS

Postglacial History of Area of Distribution of Martens and Sables in European USSR

(Ocherki po sravnitel'nomu izucheniyu sobolya i kunits)

Fossils of martens (genus Martes) occur among the fauna of the Paleolithic period in only six Upper Paleolithic Stations (Kluchevskaya, Ust' Katavskaya, Akhshtyrskaya, Sakazhliya, Shan-Koba, and Kanevskaya). Although more than 300 fossils have already been found in the USSR to date, the fragments in our hands do not enable us to make a determination as to the species level (V.M. Gromov, 1948; V.I. Gromova, 1948; I.G. Pidoplichko, 1951). It is notable that all the above areas are situated on the periphery of the East European Plain (the central and southern Urals, Crimea, and Caucasus) and, at the same time, outside the territory covered by Quaternary glaciation.

It is an important fact that a considerable Quaternary separation occurred between the areas of distribution of the marten and the sable, and also between the ranges of the Caucasian races of pine or forest and stone marten and their ranges in Western Europe. We may agree on the appearance in the southern Urals of a disruption in the region of the Ural race of the pine marten, but there are still not enough data for this. At the same time, we may affirm that the environment of the majority of the Paleolithic zones was unfavorable as a habitat for the marten genus. I.G. Pidoplichko, 1951, is undoubtedly correct in indicating that the junction between the regions of the pine or forest marten and sable is of comparatively recent origin and was formed as a result of the disappearance of some Quaternary barrier. Undoubtedly the ranges of these species were juxtaposed in the Pliocene and early Pleistocene.

The presence of the cedar in the substage layers of the Velikie Luki Oblast' (N.N. Sokolov, 1949) indicates that in the Paleolithic period extremely favorable conditions existed in the forest zone of the European USSR for sable habitation. The cedar grew as part of fir-deciduous forests along with a rich hazel subforest. The occurrence of cedar pollen in individual layers ranged from 0.5 to 16%. It is notable that the fir trees in those times were more related to the Siberian species, which Academician V.N. Sukachev pointed out in 1928. As in the Neolithic period the ranges of the sable and pine or forest marten again touched one another. We may state that the process of settlement of the East European Plain by sable and pine marten took place in the period between the Upper Paleolithic and Neolithic. Unfortunately the length of this period is not known to contemporary archeology. However, the material evidence permits us to speak of the history of the distribution of the sable and forest marten from the time of the Neolithic epoch. The Neolithic culture of the European USSR is dated mostly within the limits of 4,000-800 B.C. However, most of the Neolithic zones, the fauna of which has been studied, dated according to the newest data (A.Ya. Bryusov, 1952), from a narrower interval of time, or approximately from the middle of the third to the beginning of the second millenium B.C., i.e., within the limits of 1.5 thousand years.

Marten representatives were discovered in the osteological material of 14 habitation zones situated between the valley of the Oka River, on the south to 60° N.lat., and on the north and from 24 to 43° E. long. (Table 1).

The sable (in all cases together with the marten) was determined in the fauna of three areas: Ladoga (Professor A.A. Inostrantsev); Kolomtsy, Il'men Lake (Professor V.A. Gorodtsev); Yazykovskaya (Kashin Raion, Yaroslavl' Oblast'); (V.M. Gromov). The bones which were found with the digging up of the pile settlement on the Modlona River, Charozerskii Raion, Vologda Oblast', 60° N. lat., belonging to 9 individuals (A. Ya. Bryusov), could belong to either martens or sables. The material of the Kolomtsy site was determined by V.A. Gorodtsev, and was not preserved. In the material at the Ladoga site, A.A. Inostrantsev discovered the mandible of the forest marten (pine marten) and of one sable. According to our investigations, there are no marked differences in size and proportion between the lower jaws of the sable and forest marten. In the osteological material of the Yazykovskaya site, V.I. Gromov determined 93 sable bones and 58 bones of the forest marten. We re-examined this interesting material in 1941. Having established in advance that the length of the lower jaw of the martens constitutes 67% of the condylobasal length of the cranium on the basis of 15 mandibles found in the Yazykovskaya site, we determined the approximate condylobasal length of the skulls here, finding them equal to 74.6-83.8 mm (average 80.3); the average length of the femur was 41.8 mm (9 specimens). The average length of the tibia was 75.2 (12 specimens). The coefficient of the ratio between these bones, 0.95, coincides with that of the North Ural sables. That of the local marten equals 0.85. The only large fragment of the posterior portion of the cranium (No 36) was undoubtedly from a sable, according to a number of diagnostic proportional features (P. B. Yurgenson, 1948).

This unambiguous data permit a clear determination of the previously doubtful data of V.A. Gorodsev and A.A. Inostrantsev. The sable of the Yazykovskaya site was small.

In the osteological material of the Vladychinskaya site, (Spas Klepiki Raion, Ryazan Oblast'), in the Meshchera lowland, for the first half of the second millenium (B.C.), determined by Solotkevich (PIN, Paleontological Science Bulletin of the Academy of Sciences, USSR), we discovered 18 skulls; one of them (No 1268/3770) was fully preserved; the rest were partly damaged or consisted of large fragments. A detailed study of this material enabled us to establish in this series the remains of the hybrid of the sable and forest marten, the so-called "kida"* together with forest martens.

Thus, the forest of the left bank of the Oka and Upper Volga Rivers, was a region of concurrent habitation by these species. The boundary between the ranges passed somewhere through here in a wide belt. Both species were encountered together within the boundaries of the region.

The phenomena of heterosis is often manifested in considerably larger dimensions than in the initial species of the given locality. The report by K. Glyuk concerning the very large tibia of the forest marten found near the city of Pyarnu (Esthonian SSR, K. Greve, 1909) also suggests that there too he was dealing with the kidas [hybrids]. The station is dated 6-7 thousand years B.C.

Three Neolithic stations — Volosovskaya, with the remains of individuals of the marten genus, the Panfilovskaya, and the Neolithic strata of the "Kropotovskoe gorodishche" [Kropotovskoe, ancient city] —lie in the valley of the Oka River, which

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* Translator's note - Name assigned to hybrids between forest marten and sable.

we have already established as the boundary line between the ranges of the sable and the forest marten.

The stations of the Lower Veret'e, Kubenino (Onega Krai), Modlona pile settlement, and Fedorovskaya (on Lake Chukhloma, Kostroma Oblast'), lie north-east of the boundary determined by us. Thus, the remains in these stations were more probably those of sable than of marten. The species of the remains of the Bologoe site are still in question. Both sables and forest martens could have existed here.

Great interest is attached to the remains of martens found in the fauna of the ancient (6–7 thousand years, B.C.) Neolothic station of Lammemyagi (Kunda), in the Esthonian SSR (A. Ya. Bryusov, 1952). The possible presence of the remains of kidas still further west (City of Pyarnu) and the general character of the forest vegetation make habitation by the marten at this time quite plausible. A determination of sable habitation in the early Neolithic period on the shores of the Baltic Sea could be of extremely great importance for the history of the fauna. It could also be a fresh confirmation of the autochthonism of the postglacial fauna of European USSR.

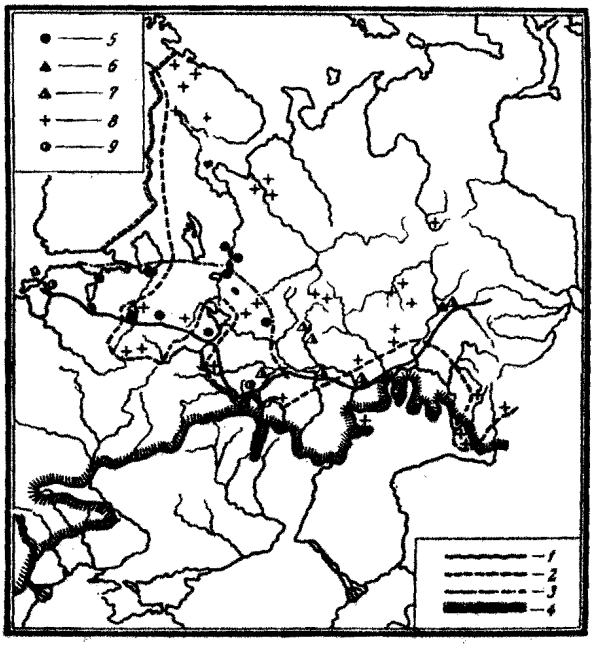

Figure 1. Schematic map

1–reconstructed boundary of the range of the sable in the Neolithic period; 2–reconstructed boundary, on the basis of relict habitation sites of the unbroken range of the red vole; 3–northern boundary of range of the wild boar in the Neolithic period; 4–schematic boundaries of the forest zone; 5–places where sable were found from the Neolithic period; 6–same during period of Anan'in culture; 7–places of finding kidas from period of Anan'in culture; 8–contemporary most southern areas where micelike (Muridae) rodents are found in the taiga complex; 9–places where kidas were found from the Neolithic period.

Table I

Mammals of Neolithic Stations of the European USSR forest zone

Station / Animals	Kunda	Pyarnu	Yargobskaya	Shigirskaya	Lyalovskaya	Yazykovskaya	Bologovskaya	Kolomatsovskaya	Ladozhskaya	Modlon settlement	Lower Veretе	Voronsovskaya	Dubrovichskaya	Pastilovskaya	Kropotovskaya	Vladychinskaya	Fedorovskaya	Volosovskaya	Kubelino	Baulovskii cemetery	Kholmogovskii cemetery
Brown bear	+	+	+**	+	-	+	+	+	+	+	+	-	-	+	+	+	-	+	+	*	+
Badger		****	-	-	+	-	-	-	-	+	-	-		+	+	+	-	+	-	+	+
Otter	+	+	-	-	-	+	+	+	+	-	-	-	-	-	-	-	-	-	-	-	-
Sable	-	-	-	-	-	+	-	+	+	-	-	-	-	-	-	-	-	-	-	-	+
Forest marten	+?	-	-	-	-	+	+?	=	+	+?	+?	-	-	+	+	-	+?	+?	+?	+	+
Kidas (hybrid)	-	+?	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-
Polecat	-	-	-	-	-	+	-	-	+	-	-	-	-	-	-	+	-	-	-	+	-
Wolf	-	+	-	-	-	-	-	-	+	-	+	-	-	-	-	+	+	+	-	-	+
Fox	-	+	+	-	-	-	-	+	+	-	-	-	-	+	+	-	-	+	-	-	+
Seal	+	+	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	+	-	-
River beaver	+	+	+	-	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	-	-
Hare	+	-	+	-	-	+	+	-	+	-	-	+	+	+	-	+	-	+	-	-	+
Squirrel	-	-	-	+	+	-	+	-	-	-	+	-	-	-	-	-	-	-	-	-	+
Dormouse	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Water rat	-	-	-	-	-	-	+	-	+	-	+	-	-	-	-	-	-	+	-	-	-
Field mouse	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Red deer	-	+	-	-	+	-	-	-	-	-	-	-	-	+	+	-	-	+	-	-	-
Roe deer	+	-	-	+	-	-	-	-	+	+	-	-	-	-	-	-	-	-	-	-	-
Elk	+	+	+	+	+	+	-	-	+	+	+	+	+	+	+	+	+	+	+	-	-
Reindeer	+	-	-	+	-	+	-	-	+	+	+	-	-	-	-	+	+	+	-	-	+
Giant deer	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Aurochs	+	-	-	-	-	-	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-
Flat-forehead bull	-	-	-	-	-	-	-	+	+	-	-	-	-	-	-	-	-	+	-	-	-
Boar	+	+	-	-	+	+	+	+	+	+	-	+	+	+	+	+	+	+	-	-	+
Musk sheep bull	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	***
Mammoth	+	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Date of settlement	7-5,000 B. C.		10,000 B. C.	Middle of 2nd millennium B. C.				Middle of 3rd millennium B. C.		Beginning 2nd millennium BC	3rd millennium BC	Second half of 3rd millennium B. C.		2,000 B. C.	2,000 B.C.			2,000 B.C.	Second half of 3rd millenium and beginning of 2nd millennium BC		

* Lynx
** Cave bear
*** Fauna of the Fakyanov cemetery of the Kua'minovskii on the Dubna River (2-3 thousand years B. C.):
Bear
Fox
Wolf
Lynx
Reindeer
Hamster
Cow
Horse
Dog
Goat
Glutton
**** Found by Glyuk in the Parma
Neolithic

Fat'yanov culture approximately 2 millennium B. C.

Legend: + Remains exist - No remains exist +? Species unknown

The data given are quite sufficient to establish with certainty the western boundary of the sable range in the Neolithic period, from the city of Pyarnu on Lake Il'men, to the Kashin Raion, the Kalinin Oblast', and then to the valley of the Oka River including its left bank (the Ryazan' Meshchera), to the east from the mouth of the Moskva River and up to the city of Murom; further to the east the osteological material of a somewhat later period permits us to determine the boundary between the sable and the forest marten (see map).

Confirmation of the above-mentioned on the character of the forest vegetation of the Quaternary period may also be considered by the fact that the southwestern boundary of the range of the Siberian red vole (Clethrionomys) also extends at the present time, along the water divides of the Volga and Western Dvina Rivers and then along the left shore of the Upper Volga. Another representative of the fauna of the Siberian taiga, the forest lemming, has also been found recently in the Il'men Lake region (S.I. Ognev, 1948) and on the water divides of the Volga and Western Dvina (P.B. Yurgenson, 1955). The relict and sporadic habitation sites of the Siberian red vole were also discovered considerably to the south, in the pine forests of the Mordov Preserve (1951) and in the Zhiguli, where the vole was discovered by E.M. Snegirevskaya. This compels us to assume that taiga elements in the postglacial fauna of the Central Russian Plain were not less and perhaps more ancient than the elements of the broadleaf forests of the Western European type (P.B. Yurgenson, 1955). It is probable that they may be considered as autochthones of the East European Plain.

Data by G.K. Goldsmaier and V.D. Kraft (S.I. Ognev, 1940), report finding the chipmunk in the Sarov and Trans-Sura Region forests. As a result of the discovery in the Sarov forests and the Zhiguli pine forests of the red vole these data are no longer in doubt.

Neolithic fauna east of the Volga in the forest zone of European USSR has only been known to exist in peat bogs. There are no remains of martens there. For the Trans-Volga we must thus employ information based on a somewhat later fauna of the ancient towns of the so-called Anan'in culture, which is dated in the period 700- 200 B.C. Thus, this fauna is only several hundred years younger (Table II).

The wild fauna of the 14 ancient cities and settlements of this culture is known to us. Remains of "martens" were found in eight of them. In the fauna of the Vetluzhskie cities, and also of the Odoyevskii, Bogorodskii and Chertov areas, A.N. Formozov (1927) and P.B. Yurgenson (1948) have determined clearly distinct kidas. The material from these cities is very extensive. Well preserved skulls are present. (Figure 2).

In the osteological material of the old city of "Sorochi Gory", at the mouth of the Kama River, we also discovered a kida skull with typical traits of heterosis; we obtained the same type of skull near the city of Murom. The dimensions of these skulls exceed those of the largest of the Kamchatka sables.

We discovered the undoubted remains of kidas and sables in the osteological material of the ancient villate of Kontsegorsk near the mouth of the Chusovaya River (fragment of skull No 1/20357 of the Osteological Division of the Zoological Institute of the Academy of Sciences USSR, excavation of A.V. Zbrueva).

We had no opportunity to investigate the remains of "martens" from the fauna of ancient cities near the Kama River the Svinogorskii, Pizhemskii, Galkinskii, Sabanchikar, etc (A.V. Zbrueva, 1937).

Table II

Mammal fauna of the ancient cities of the Anan'in culture

Species \ City	Vetluga	Sorochi Gory	Svino-gorskoe	Tizhem-skoe	Gaikin-skoe	Saban-chikar	Kontse-gorskoe	Annin Isl.
Brown bear	+	+	+	+	+	+	+	—
Glutton	—	—	—	—	+	—	—	—
River otter	+	—	+	—	—	+	—	—
Sable	—	—	—	—	—	+	—	—
Kidas	+	+	—	—	—	+	—	—
Forest marten	+	—	+?	+?	+?	+?	+?	+?
Lynx	+	—	—	+	—	—	—	—
Wolf	+	+	—	—	—	—	+	+
Fox	+	+	+	—	—	—	—	—
Forest beaver	+	—	+	+	+	+	+	+
Hare	+	—	+	—	+	—	+	—
Hamster	—	+	+	+	+	—	—	—
Elk	+	+	+	+	+	+	+	+
Reindeer	+	—	+	+	+	—	—	+
Roe deer	—	—	+	—	—	—	—	—

As a result of the above-mentioned data, it is unquestionable that the boundaries of the ranges of the sable and forest martens until the beginning of our era extended from the valley of the Oka River to the mouth of the Kama River. Further east they probably continued along the valley of the Kama up to the mouth of the Chusovaya River. The presence of the kidas in the middle reaches of the Vetluga and also at the mouth of the Chusovaya, indicates that from the first half of the second millenium B. C., forest martens succeeded at times in advancing considerably eastward. There is no question in our minds that this resettlement of the forest marten chiefly took place by skirting south of the sable range.

In the first millenium of our era, the boundary between the sable and forest marten ranges was still for the most part unchanged. Among the osteological material of the subfossil fauna of the "Bychki" (Steer) cave on the Chusovaya River we discovered the remains of kidas and sables with heterosis phenomena(a possible condylobasal length of 95.6 mm). We also established the certainty of kidas in the fauna of the old city of Malakhai on the boundary of the Chuvash and Mari, ASSR.

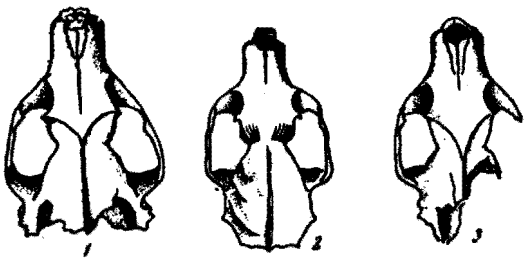

Figure 2. Skulls of subfossil kidas with signs of heterosis

1—skull of a kida from excavation near Murom City; 2—skull of contemporary forest marten (male), from Moscow area; 3—skull of a kida from excavations of Sorocha Mountain, at the mouth of the Kama River.

In the fauna of the old city of "Volna" near the city of Yaroslavl' (4th century A. D.), we determined a forest marten, as we did in the forests of the ancient city of Kondrakovskii, near the city of Murom (E. G. Andreeva, 1941). We did not examine the "martens" of the fauna of the Upper-Volga cities of the first millenium B. C. —Pekunovskii, Babenskii, and Gorodnya (V. I. Bibikova).

Toward the tenth to twelth centuries, the forest marten, undoubtedly assisted by man, who exterminated the sable, managed to move further northward along the valley of the Kama River. The remains of kidas of rather large dimensions (possible condylobasal length, 91 mm; length of the femur, 79 mm), were discovered by us in the fauna of the "city of Rodanov", Chernovskii Raion, Molotov Oblast'. Thus, in 1,000 years, it moved approximately 100 km further north (No 19943, Zoological Institute of the Academy of Sciences, USSR).

The fact that the forest marten chiefly skirted the range of the sables on the south was also proven by the fact that, penetrating into the Trans-Urals in the same manner, it also skirted the region of dense sable distribution in the basin of the Konda and Sos'va Rivers (V. N. Skalon, E. S. Zhbanov, and V. V. Raevskii, 1940). This is also confirmed by data of P. Pallas (L. P. Sabaneev, 1875) regarding the fact that the forest marten had already been encountered in western Siberia by the eighteenth century.

During the first half of the seventeenth century, as shown by P. M. De Lamartinier ("Voyage into Northern Countries in 1653". Russian translation by V. M. Semenkovich, 1912, Records of the Historico-Archeological Institute, Vol 15), the forest marten was taken together with sables in the basin of the Mezen and Pechora Rivers. Thus, in the store at Pustoozersk, the leaders accompanying De Lamartinier bought five sets of sables, two of which were black as pitch and of the best quality, and 200

martens of an ash-gray color. In a 6-hour trip from the city of Pustoozersk eastward they purchased from local chieftains eight more sables. Local chieftains prepared sables in their own districts only, and hunters afraid of the chieftain did not dare to make sales themselves. The origin of the sables bought in the city of Pustoozersk are thus not open to question.

In the year 1738 the historian F. I. Miller (Sammlung Russischer Geschichte) wrote that sables were found near the cities of Pustoozersk and Chernin only in ancient times. Thus, it is less than 400 years since they have been found here. There is no doubt that the rate of settlement of the marten was considerably increased as a result.

In the first half of the seventeenth century sables were still encountered on the Kola Peninsula. The same De Lamartinier relates that from local hunters in Moscovite Laplandia they purchased martens among other furs, but not of such good color as those caught in Barandeya, Samoves', and Siberia.

Johann Sheffer (1673), referring to reports by Olay the Great and Johnson, wrote that "the supply of them is small and even very rare" (B. M. Zhitkov, 1937). B. M. Zhitkov was not sure that this phrase referred to animals of the local fauna or to the accumulation of the sable furs circulating among the population. However, the data of De Lamartinier indicate that sables were obtained by local hunters (Lopars by nationality). The expedition of the "Northern Trade Company", in which this author participated as a surgeon, occupied itself exclusively with the purchase of furs. He witnessed all such operations and thus his data are undoubtedly correct.

Within the limits of northern Europe, the sable maintained itself in insignificant numbers up to the middle of the last century. A series of factual data on this point is presented in the article by B. M. Zhitkov. Thus, according to the "Description of the Russian Empire" of 1845, sables were rarely found in the Mezen County, whereas in the Vologda Province (today Vologda Oblast') they were common together with the beaver, but are now absent. According to Academician I. F. Brandt (1856), sables were killed near Kholmogor and Kem', on the Pechora, and in the Mezen County. The newspaper "Peterburgskie vedomosti", No 79, 1840, reported the taking of sables in the Arkhangelsk and Kem' Counties district (14 sables were taken).

In 1933 (P. B. Yurgenson) data were presented by E. Dyubyuk to the effect that a number of names of villages and natural features of the Upper Volga undoubtedly testified to the previous and evidentally very rare habitation of sables there. Indications by the same author that the sable was encountered near the city of Uglich in the fifteenth century are highly important.

We may conclude that these data coincide with the data on the distribution of the sable in the Neolithic period and at the beginning of our era. They also indicate that the process of displacing the sable beyond the Urals proceeded very slowly, gradually speeding up proportionately with the growth and improvement of the hunting trade. The subsequent stages of this process were connected with the use of the bow and arrow by man in the Neolithic period by the fact that pelts of fur animals attained commercial value, with the sable fur acquiring a monetary unit value in the State of Moscow, and with their recognition as a government monopoly.

The forest martens expulsion of the sable in accordance with the hunting trade plan, has also occurred recently. Thus, in the Pechora Preserve region in the eastern Urals, according to I. I. Mezentsev, only sables were obtained. Some years later the same forest martens began to appear as were obtained on the western slopes. The exclusion of the sable was also hastened by the absorptive hybridization of the sable with the forest marten and the kida with the forest

marten. Experiments in zoos (A.T. Portnova, 1941; A.L. Ponomarev, 1946) indicate that such hybridization produces fertile offspring.

In the kidas we have been able (P.B. Yurgenson, 1948) to trace the presence of intermediate features as well as the phenomena of heterosis. Later in the Pechorskaya race of the forest marten we also succeeded in finding not only a shortened tail but also a series of other intermediate features in skull structure and limb skeleton. We discovered forest marten skulls with the features of sables (absence of the posterior ocular swelling of the skull capsule and others) in the former Kirillov County of Novgorod Province, the former Vytegra County of the Olonetsk Province, and in Bashkiria (vicinity of Belorechensk); we consider this oddity to be the result of the hybridization of sables in comparatively recent times (100—200 years ago). At the same time this confirms the boundaries of the former distribution of sables. In Bashkiria, the forest marten undoubtedly met the sable not too long ago. Similar skull features convince us that concurrent habitation by these species also took place north of the former Novgorod and Olonetsk Provinces (skulls of the forest marten, Nos 16344, 16345, 5564, and 9557 of the Osteological Division of the Zoological Institute).

Let us note that reports of Arab geographers of the tenth century stating that sables were obtained in the country of the Boortases (Middle Volga reaches) which formerly seemed doubtful to us are confirmed today by the finding of subfossil kidas between the mouths of the Oka and the Kama Rivers. Thus here also the displacement of the sable occurred in historical times.

Our data on the developmental history of postglacial landscapes of the East European Plain are very scarce and fragmentary. We know that in 12,000 B.C., according to the absolute chronology of DeGeer (K.K. Markov, 1939), the territory of Leningrad happened to lie outside the glacial area.

Soviet archeologists (A. Ya. Bryusov, 1952, and others) have established that the increase in the amount of peat in the forest zone amounted to 4—5 cm per hundred years. From this it follows that the data mentioned above (12,000 years) and the data of the analysis of the pollen from depths of not less than 6 meters agree.

According to data on studies of the Tosno peat areas (I.P. Gerasimov and K.K. Markov, 1939) forest vegetation—fir, pine, and birch trees—grew near the edge of the glaciation, not only at this time but also considerably earlier (depth above 8 meters).

In addition at the depth of 6—7 meters, we find pollen grains of species of broadleaf forests. This was the time of the "lower fir" and the transgression of Baltic glacial lakes.

The supposed "forest tundra" near the glaciation undoubtedly did not so much resemble the arctic high latitude forest tundra as it did the high mountain tall-trunked sparse forests of the northeast Altai, where the stands of the roundleaved lumber birch spread extensively, often adjacent to the mountainous tundras where partridgeberries grow. The climate here is completely different from the sub-Arctic, and the occurrence of birch is associated with low soil temperatures and earth which is not constantly frozen (3—4° at a depth of 40 cm).

Ten thousand years B.C., on the Yargoba River in the Sheksna Basin, the trees included maple, English elm, and alder (A. Ya. Bryusov, 1952). In the northeast of the Velikie Luki Oblast' ("Katin mokh", according to the data of T.T. Trofimov), at approximately the same time of the year the forest consisted of pine (40%), birch (45%), fir (9%), willow (10%), and alders (1%). Somewhat

earlier at a depth of 6.25–6.50 m, it was possible to find fir and pine trees, amounting to 20%, birch up to 54%, willows to 4%, and alders to 2%.

In Ivanovo Oblast' (V.S. Dokturovskii, 1932), at the same time, pine tree, pollen predominated (50%–70%), followed by birch (up to 30%) and spruce (15%). The pollen of the broadleaf species amounts to 8%, that is, the zonal distribution of the forest vegetation is very clearly followed. Numerous points remain unclear; for example, the reason why spruce trees are displaced by pine and birch. Their temperature requirements are approximately similar. However, the requirements of these genera with regard to soil, humidity, and light differ distinctly. No one has attempted to evaluate the true significance of the change of the forest genera on the basis of the data obtained from pollen analysis. Actually temperature change only affects the broadleaf varieties.

The fauna of the Yargoba Station includes a number of species typical of the Quaternary period, the cave bear, the giant deer, musk ox, and mammoth, as well as such animals as the fox, hare, river beaver, and elk. As shown they survived the glaciation, lived in fir or pine forests mixed with broadleaf tree varieties.

The next stage is data of the early Neolithic stations–Kunda and Pyarnu in Esthonia, which are dated from 6,000 to 7,000 B.C. Forests at this time consisted of pine (53–67%) and birch (33–37%), with a mixture of alders (2.5%), elms (2%), and hazel (2–3%), in the subforest. The combination of elm and hazel gradually increased and linden appeared, but oak and spruce trees were not yet present.

In the fauna of these stations, of which the Kunda is somewhat more ancient, there are animals typical of Quaternary fauna, such as the mammoth, brown bear, glutton, river otter, seal, wolf, fox, kida, forest marten (?), river beaver, hare, red deer, roe deer, elk, reindeer, aurochs, and wild boar. Faunal elements of the pine tree taiga are encountered here among those of the broadleaf forests. Thus, the conjunction of the ranges of the forest marten and sable in the Pre-Baltic had already occurred around this time, and in the epoch of the developed Neolithic period these species were in close juxtaposition for several thousand years.

This period also corresponds to the data of pollen analysis from depths of 3.5–4 meters.

At this time, in the Velikie Luki Oblast' ("Staroselskii Mokh [moss]"), according to pollen analysis carried out by S.V. Katz), discoveries of pine tree pollen fluctuate between 60 to 35%; spruce, 25–20%; birch, 35–13%; broadleaf genera, 3–5%; hazel, 20–4%. The same depths, at a distance of not more than 10–15 km, according to data from "Katin Mokh", convey a somewhat different picture. Pine trees are 34–23%; birch, 48–1%; spruce 19–7%; broadleaf species, 18–11%.

In Ivanovo Oblast' birch pollen predominates in the analysis (50%); pine tree amounts to 20–25%, broadleaf genera to 16–17%; and spruce less than 10%.

In Moscow Oblast', in the Neklyudovskoe Marshes (V.S. Dokturovskii, 1932), the picture changes We find the pollen of broadleaf species to be greater than 40%, spruce and pine at 10%, and birch at approximately 20%. Thus geographical zoning also took place in this period. It is interesting to note that while there were no spruce or oak trees at that time on the shores of the Baltic, in the Moscow area the broadleaf species predominated in some places. The conclusion to be drawn from this is that in the Moscow area at that time it was warmer and drier than at present, but in the region of the Baltic it was colder.

The majority of the Neolithic stations, from the Oka River Basin and northward up to 60° N. lat. (reaches of the Onega River), are dated at 2,000 to 3,000 B. C.

The list of mammalian fauna of the Neolithic stations is presented in Table I, and will not be repeated here. We will dwell merely on individual features which are important for our purposes.

M.E. Foss (1941), has presented the general characteristics of the natural conditions of the region of the Station of Mizhneveret'e (Lake Lago, 35 km from the city of Kargopol, in Vologda Oblast'). At this time, pine, birch and spruce predominated in the eastern part of the northwestern regions, whereas in the western portions spruce, pine, and birch predominated in that order. The station was situated on the boundary of these regions where mixed forests of pine, spruce, and birch grew, with a mixture of alder, oak, English elm, willow, and hazel. Approximately the same species are encountered at the present time in the northwestern part of Velikie Luki Oblast'. This was the beginning of the second "upper" [i.e., northward] maximum of spruce. A milder climate is also confirmed by the presence of thermophilic fishes in the fauna of the basins of the White Sea rivers —rudd, minnows, bream—no longer encountered north of the Volga River Basin. However, there too they constitute no more than 4% of all finds, and the majority of the bones at the station belonged to species which also inhabit the area today.

Somewhat to the south, on the Modlona River, in the Charozerskii Raion of the Vologda Oblast', below 60° N. lat, at the beginning of the second millenium B.C., at the junction of the so-called Sub-Boreal and Sub-Atlantic periods, a pile settlement of fishermen-hunters existed. According to data of A.Ya. Bryusov (1951), birch-spruce-pine forests grew here. The trees also included alders, elms, ash, linden, and juniper. Linden and elm exist up to the present day. In more ancient strata than that of the settlement, the pollen of spruce constituted 60—70%; pines, 20—30%; birch, 10—20%; and forest species, 2—3%. The level of the water pools was lower than at present and the climate was drier.

According to data from excavations by A.A. Inostrantsev along the southern shores of Lake Ladoga, spruce, birch, alders, and oaks grew to a size of 1.6 meters in diameter and to an age of 250 years.

The period of 3,000—5,000 B.C., corresponds to layers of peat at a depth of 1.5—2.5 meters. The upper maximum of spruce and broadleaf species in the Leningrad vicinity in the Tosno Marshes belongs to the beginning of this time. According to the data from the peat of the Nikol'skoye Marsh in Leningrad Oblast' (V.S. Dokturovskii), the upper maximum of spruce lies above 1.5 meters (1.30 m), whereas the maximum of broadleaf species is at 2—2.25 m. The maximum of broadleaf species in the region of the "Galitskii Mokh Marsh" in Kalinin Oblast' (15—17%) also falls in the beginning of the period we are examining, whereas the upper maximum of the spruce occurs at the end of this period. The same result is obtained from the pollen analysis of peat from the Katin-Mokh marsh (broadleaf species 15%, rarely the hornbeam) and from "Staroselskii Mokh" (broadleaf species 18—23% at the beginning of the period and spruce 60% at the end). An analogous picture is also seen in Ivanovo Oblast' (broadleaf species 18%). In Moscow Oblast' (Neklyudovskoe Marsh) in the given period spruce was at a level of 40% between the two maxima (50—60%). The maximum number of broadleaf species which occurred here at the beginning of the period was also 18%, penetrating the deepest layers.

Thus, in this period, the northward movement of the elements of the leafy forests had already reached its limits and a reverse process set in.

Fir trees and spruce-pine forests with the usual mixture of birch, alder, and a varying percentage of broadleaf species of wood complexes also extend north of the valley of the Oka River at present. The intensity of development of the hazel subforest differed. Undoubtedly the distribution of the small forest elements and hazel was closely connected, as it is today, with the degree of soil richness and moisture. The predominance of the main species, pine and spruce, was determined on this basis.

The needle-broadleaf forests extended everywhere, penetrating somewhat further north than they do today. Only occasionally, somewhere near the latitude of Moscow and principally west of Moscow, do we note any very considerable proportion of elements of the small broadleaf forest. This area was somewhat drier and the top level of the rivers and lakes was lower than it is today. In summer, in July, it was 1.5—2.0° warmer. In winter the frosts were not severe enough to damage the oak, hazel , and other species, as was observed in a number of regions in 1940- 1941. The majority of the fauna of the Neolithic stations do not permit us to draw any generalized ecological conclusions. These were the widely distributed species of forest fauna that may dwell in various parts of the forest zone. The frequency of encountering subfossil remains in excavations of the Neolithic stations is not, for the most part determined by the relative profusion of individual species in nature but by a series of circumstances—the adaptation of the stations to the shores of the rivers and the lakes, the relative accessibility of these or other species of animals and birds to the Neolithic hunters of a given level of hunting technique, the absence of a fur trade, the better preservation of the bones of large animals, etc.

In addition to the forest marten and sable, the most significant animals are the ungulates. We must also note the complete absence of the forest cat (wild cat), found simultaneously in the Scandinavian Neolithic and Epipaleolithic. A.N. Formozov, 1946, has shown that in winter the forest cat can obtain its food only when the height of the snow is 10—20 cm. From this we may affirm that such conditions were not present in the Neolithic north region of the Oka River Valley.

The wild boar was considerably more widespread. Its remains are found in the fauna of 15 stations to 60° N. lat. In the Onega Krai, the northern limit of its Neolithic range inclined considerably to the north, even further north than the contemporary average isotherm for a 50 cm deep snow cover. A. N. Formozov considered the limiting level for boar at only 30—40 cm. We may explain this by the aridity of the climate, since the amount of winter precipitation in the northwest in the Neolithic period was less than at present, and we should also take into consideration the deep northern penetration of such species as the oak, hazel, and others, which provided the boar with winter food which is not available at present even considerably to the south. The presence of winter food enabled the boar to exist when the height of the snow reached 50 cm or more, especially when there was no intensive persecution by man.

The roe deer is rarely encountered in the Neolithic fauna and only in the remains of four stations: the Baltic vicinity (the city of Pyarnu), Lake Ladoga, at Modlona pile settlement, and at Shigirskaya Station in the central Urals. In the last case, we are probably not dealing with the European but with the Siberian species. The Modlona Station is located north of the contemporary boundaries of the roe's range. The roe deer was encountered in the fauna of the Epipaleolithic and Neolithic periods in Scandinavia considerably more often, being one of the leading species in the region. It is apparent that, as now, the forest zone of the European USSR was not highly favorable for this animal. The roe is an animal of the forest clearings, the small forest hill, and the forest coppice, and definitely not of the large forest massif.

The frequency of remains of European deer is characteristic. The deer was found in fauna of three stations: the Oka River Valley (Volosovskaya, Panfilovskaya, Kropotovskaya), in the fauna of the L'yalovskaya Station on the Klyaz'ma River (above the railway station at Skhodnya of the October Railway), and in the Baltic area (city of Pyarnu). The last site is dated from the sixth to seventh millenium and the L'yalovskaya site from the middle of the third millenium B.C. The European deer is an animal typical of small broadleaf forests and the forest steppe. Its northward distribution undoubtedly was limited not only by the snow cover, which was 40—50 cm (according to A.N. Formozov), but also by the food resources;—in summer, the grazing stretches, meadows, and small valleys and in winter and fall, the acorns of the oak. According to data of the Voronezh Preserve, oak acorns are of great importance in the nutrition of the European deer in winter. In the extremely snowy winter of 1950/51, there was a considerable loss of bucks, which, according to data by P.A. Merts, was caused by the absence of acorns. Deer which were exhausted from sexual running were unable to reestablish their normal winter fat reserves. It is of interest that the boar, which is less tolerant of the depth of the snow, penetrated considerably farther north than the European deer during the Neolithic period. This indicates that the snow was not the decisive factor in the distribution of the animal. In the limits of the contemporary Oblast's of Voronezh and Kursk, the European deer survived for long periods and only disappeared because they were exterminated by man. In the Voronezh Oblast', the remains of the European deer and the boar were found in the fauna of the ancient city of "Kuznetsova Dacha" near the city of Voronezh (tenth to eleventh centuries, excavations by P.P. Efimenko) and in the ancient city of Borshchev (eighth to tenth century excavation by P.P. Efimenko). In Kursk Oblast' (E.S. Ptushenko, 1937), the European deer sustained itself up to the fifteenth and the boar up to the eighteenth century.

The remains of wild bulls, the aurochs (Bos primigenius, B. latifrons), were encountered in the Baltic area (Kunda, in the region of Lake Ladoga, in the fauna of the Bologoe and Kolomtsy lake sites, and in the valley of the Oka. It is highly probable that I.G. Pidoplichko (1951) is correct in connecting the distribution of the aurochs with the growth of the tall grasses along the shores of the forest pools.

However, the auroch was never encountered north of the Oka River. The data on the frequency of elks added nothing to the ecological characterization of the fauna. To this day they inhabit the entire forest zone.

The data on the reindeer are undoubtedly of interest. It was encountered in the fauna of nine sites. The southern boundaries of its range in the Neolithic period closely coincided with that of the sable. We may say with certainty that it was present in the same pine forests, then as today, in the small white lichen forest, the lichened marsh and among the spruce with a profuse development of tree lichens on the shores of rivers and lakes. Along general lines, the southern boundary of the reindeer in the Neolithic period did not differ greatly from the southern boundary of the animal in the various regions inhabited by it during the second half of the past century. We may assert that any alteration of the boundaries of the range of this animal after the Neolithic period was determined directly or indirectly by the activities of man alone: by direct extermination, the eradication of Iceland moss vegetation, repeated forest fires, alteration of the type of forest as a result of the felling of trees, etc.

The data on the frequency of the badger is of interest. It was encountered in the fauna of nine Neolithic sites, five of which are located in the valley of the Oka River. Two finds were connected with the cemeteries of the Fat'yanovskaya culture (the end of the second millenium B.C.). A badger was also found in the fauna of the L'yalovskaya site and the Modlona pile dwellings. The badger is an animal of the forest fringes, of low hills in the forest and of forest coppices, as is the roe deer. This fact makes it easy to understand its gravitation toward the

valley of the Oka River. The Fat'yanovo man was a cattle breeder. In the fauna of their cemeteries we also find the hamster, as we do in the old cities of the Anan'in culture. Thus, in the places where they lived, there were undoubtedly some open spaces. Thus the badger also found an ecological environment peculiar to it. However, the fauna of the Modlon settlement indicates that, as today, the badger penetrated deep into the dense forest massifs of the north.

Discoveries of the forest polecat (Putorius putorius L.) have been made in the Yazykovskaya, Ladoga, and Vladychenskaya sites and in the Vaulovskii cemetery. The forest polecat is also uncommon in dense forests and, when dwelling there, lives near the abode of man. The same was probably true in the neolithic period.

The fauna of the ancient cities of the Anan'in culture, situated mainly in the Kama River Valley and its tributaries, as well as along the Vetluga River, is poorer than the fauna of the Neolithic period. This is explained by its territorial limitations, the later historical epoch, and the fact that this culture existed a short time (only five centuries). Finally, it is of importance that the population of these ancient cities consisted to a considerable degree of cattle breeders, for them, as for the Fat'yanovi, hunting did not have the exclusive importance it had for the coastal settlements of Neolithic hunters and fishermen who possessed no domestic animal except the dog.

The fauna of the ancient cities of the so-called "Dyakov" type of the third century B.C., to the fourth to sixth centuries A.D., was of a still poorer type. Here (V.I. Bibikova, 1950, and others), remains of domestic animals already predominated in the osteological material of the ancient city, and wild fauna constituted no more than 30—37%. For this period we chiefly find the remains of the forest marten in the fauna of these ancient cities.

Individual cases of finds of the kidas occurred further eastward. Special interest is attached to the reports of the entry of the Arctic fox in the region of Kimry Raion of Kalinin Oblast' (Pekunovskoe—ancient city, data by V.I. Bibikova).

Concluding, we see that in the Quarternary period, in the territory of the East European Plain, conditions for sable habitation were less favorable as a result of the distribution of the Siberian cedar, than in the postglacial period. The wide Neolithic distribution of broadleaf trees and the presence of needle and broadleaf forests, similar to those of today, permit us to consider them as more densely inhabited by Muridae rodents than the needle forests of the taiga type. This was as favorable for the sable as for the forest marten. Thus, while we encountered them at the outset of the Neolithic period in the region indicated already, they maintained their position almost up to the start of our era. The disappearance of the oak and other broadleaf species from the needle forests brought in its train the depletion of small mammal fauna and, accordingly of the food of the sable. The forest marten ate squirrels which were unattainable to the sable, thus found itself in a better position and enabled it to displace the sable. However, the principal role was played by man, since the last sable disappeared from the European USSR, except for the Urals, only in the middle of the nineteenth century.

In 1869, Academician A.F. Middendorf, as did a number of other zoologists up until B.M. Zhitkov (1937), probably greatly doubted the reports from a number of ancient sources on the previously wide distribution of the sable in the European USSR. He considered it possible that the sable was confused with the forest marten and that in a number of cases the importation of furs was meant instead of furs of local capture.

He wrote: "The problem of whether it sometimes reached Lithuania up to our Ostzee Region and the north of the Scandinavian Peninsula will remain unsolved until we discover undoubted proof of this in ancient documents. Thus, I draw special attention to this lacuna. Zoology must draw numerous deductions from historical documents" (1869).

As we have seen, the osteological material from archeological excavations and the newest data on the distribution of a number of species of the taiga fauna completely confirm the accuracy of the sources presented by us, while the data of Vinekhold, Paul Novia, Goesner, Stuckenberg, Mueller, Gackstenhausen, which aroused the doubts of A. F. Middendorf, are much more convincing than new archive documents.

We see that while the truth may sometimes be combined with fantasy in ancient sources, this constitutes no basis for condemning the data of the source in its entirety.

In addition, there was a Lithuanian Statute (sixteenth century) which fixed a tax for each sable killed. It is completely impossible to believe that a juridical document named an animal which was absent from Lithuania (as it was formerly constituted).

From all the previous data we may assume that the ancient southwestern boundary of the sable range did not begin on the east coast of the Bay of Riga but much further to the southwest, possibly including the entire contemporary belt of the broadleaf spruce forests.

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Morphological Adaptations in Martens and Sables

Geographical variability of body size

The ultimate body dimensions are not less characteristic of the organism than its other features. The various body dimensions in a species result from evolution and complex reactions between the organism and the environment in consecutive stages; given the same hereditary characteristics, the size of the body may change according to the influence of the external environment (conditions of nutrition and temperature which determine and accelerate the processes of differentiation and final maturation). Growth processes are closely linked with all physiological processes. There are no changes in the organism which fail to manifest themselves in one way or another as a limitation upon the growth process. It is pertinent to mention here the data of R. Hesse (1927) established that the area of the absorptive surface of the intestine determines the upper limit of possible growth, since in the growth of an organism its requirements for food materials increase proportionally to its mass, while satisfying these needs is proportional to the intestinal surface, i.e., it lags behind the requirements. This is one of the links in the long chain of relationships between the total size of the body and its organization. This factor must be taken into account no less than the dependence of the amount of heat loss on the ratio of body size to external surface area.

The maintenance of the energy balance of the organism is the paramount problem to the solution of which all the adaptive properties of the organism are exercised (N.I. Kalabukhov, 1946). It is effected by all the measures at the disposal of the organism, very often in complex combinations, and it is completely unnecessary for the body size to be named the principal factor. The physiologist K. Bergman in 1847 enunciated the law which later became widely known, to the effect that: "If two species of animals differ only in body size, the geographical distribution of each will be determined by its dimensions, the smaller requiring a warmer and the larger a colder climate" (E. I. Lukin, 1940). As was stated by K. Bergman, the smaller the animal the more sensitive it is to cold. However, he himself exercized caution in his pronouncements, stating that in addition to body size there exist other no less influential adaptations which lead to similar ends, i.e., the provision of normal thermoregulation under varying climatic conditions. E.I. Lukin (1940) has devoted considerable place in his studies to the K. Bergman law and researches connected with it.

We will now proceed directly to the objectives of the present study. We note that the K. Bergman law should be considered effective only within the limits of a single species or group of closely related species. The species of the marten genus are divided into a number of geographical races which considerably differ precisely in their dimensions. As is known, the condylobasal length of the skull has the closest correlative relationship to the total dimensions of the body, from which it follows that when a sufficient number of direct measurements of the body length are lacking, we may possibly consider it legitimate for our purposes to employ serial measurements of the condylobasal length of the cranium of the forest martens and sables of the various geographical races. We took our figures from the work of B.A. Kuznetsov (1941), with some of our own data (Table III).

The data presented in the table on the geographical races of sables do not reflect the characteristics of all varieties, but for our purposes this is unnecessary. Nor shall we dwell greatly on a meticulous comparison of one fact with another

with regard to latitudes and longitudes, January isotherms, and so on, since the chief elements are visible even without such data. By selecting individual races, we are able to present here an apparently not unsatisfactory illustration of K. Bergman's law; for example, living in the north, is the large Kamchatka race and in the south the considerably smaller Sakhalin race. However, we may make this assertion only if our treatment is to be formalistic and superficial. Let us note that the climate of the Tugur-Uda coast and the Shantar Islands is harsher than that of Kamchatka, although they lie further south. Let us note further that the large sables of the nominal race (basin of the Konda and Sosva Rivers) are replaced south of the range by the Altai race which are no smaller in size (upper reaches of the Katun' River); that is, from the lower reaches of the Ob' River to the Chinese boundery, despite the differences in climate, the size of the the sable remains unchanged. Finally let us mention that one of the smallest sables, the Zhigansk sable inhabits the region with the coldest and most severe climate of any region inhabited by sables at the present time.

A conclusion may be drawn that the law of K. Bergman does not apply to the geographical races of the sable and thus neither does its interpretation of the adaptive significance of geographical variability on the dimensions of the body. Material on the geographical races of the forest marten is also presented in Table III. It would ostensibly seem that here too we could speak of the applicability of the K. Bergman law: the largest forest martens of western Europe live in Scandinavia, and the smallest on the Island of Sardinia in the Mediterranean. However, very large races inhabit the southern Urals, the Caucasus, and Central Europe. The martens in Spain are also large. The middle and northeastern European forest belts are inhabited by smaller races. Both large and small races occupy ranges varying greatly in climate, winter temperatures, etc. Bearing in mind the contemporary ranges, the K. Bergman law is as inapplicable to the geographical races of the forest marten as it is to the sable.

The latitude range of the stone marten is of no particular interest. The data on the American sable presented by E. Thompson-Seton (1926) indicate that here too the situation differs from the conditions that D. Allen wished to demonstrate (E.I. Lukin, 1940). The large acutosa race lives on the Alaska Peninsula together with the smaller kenaiensis race. Further, while small sizes are typical of the California race (caurina), the same could also be said of a number of more northerly island races, the brumalis of Newfoundland and the nesophila of Queen Charlotte Islands. The contemporary climate does not explain the features of geographical variability in the body sizes of a number of species of the genus Martes.

Examining the representatives of the genus Mustela the ermine and weasel, produces a very significant picture. Like the sable, the large (Tobol'sk) ermine race in Western Siberia ranges from the Arctic Sea to the steppes of northern Kazakhstan, whereas Yakutia (including the Pole of Cold) is inhabited by a smaller race. The ermine of the European USSR also does not visibly fluctuate in size over the entire region from the Barents Sea to the Volga-Dnieper Delta areas. The considerable differences in size between the Kamchatka and Karaginskii Island ermine and Shantar Isle and mainland ermine are explained by the insularity of the island (P.B. Yurgenson, 1936).

A good illustration of the geographical variability in body size governed by law completely contradictory to that of K. Bergman, is also observed in the weasel. The entire north and central belts of the European USSR are inhabited by the small nominal race. To the south, the chernozem-steppe belt is inhabited by a larger and long-tailed Central European race, the vulgaris. South of this, in the Caucasus, we find the even larger Dinnik weasel and, in the Transcaucasus, the very large Mediterranean race (M. bocamella). The Central Asiatic race (pallida) is also

larger than the small weasel inhabiting the country north of it. The order is disturbed only by the presence in the Caucasus of a smaller light race — the caucasica, in addition to the large Dinnik race.

Table III

Geographical variability of the condylobasal length of skull in the sable and forest marten

Species and race	Males		Females		Remarks
	No	Mean	No	Mean	
Martes zibellina kamtschadalica	93	88.49 ± 0.18	76	80.81 ± 0.21	Kamchatka
M.z. zibellina	11	85.8	10	79.12	Tumen' Oblast'
M.z. altaica	2	85.6 ± 86.5	3	78.1 ± 80.2	Upper reaches of Katun' River
M.z. tungussensis	26	83.0 ± 0.47	19	77.0 ± 0.38	Lower and Stony Tunguska
M.z. sajanensis	5	81.40	4	74.5	Eastern Sayans
M.z. princeps	11	81.0 ± 0.73	10	73.8 ± 0.34	Baikal area
M.z. jenisensis	67	80.3 ± 0.33	29	73.9 ± 0.40	Krasnoyarsk Taiga
M.z. sachalinensis	22	79.77 ± 0.39	18	73.52 ± 0.34	Maritime Territory
M. martes martes	25	87.95	—	—	Kola Peninsula
M.m. uralensis	5	83.57 ± 0.72	—	—	Central and Southern Ural, Bashkir ASSR
M.m. lorenzi	20	83.57 ± 0.72	—	—	Northern Caucasus
Central-European Race	22	84.53 ± 0.48	—	—	Western Europe, western regions of USSR
M.m. ruthena	32	82.04	—	—	North and central belt of USSR
M.m. sabaneevi	23	82.1	—	—	Northern Ural, upper reaches of Pechora River
M.m. latinorum	3	86.0 ± 88.0	—	—	North Italy (Miller)
" "	1	80.6	—	—	Sardinia Island (terra typica)

A highly important factor for the entire marten family is the presence of a distinctly expressed sexual dimorphism as regards total size. The difference here is so great that to recognize the adaptive thermoregulatory importance of body size would mean also recognizing that one of the sexes is better adapted and the other more poorly adapted, which is, of course, impossible. Sexual dimorphism is deeply inherent in the nature of the species in question, and thus it considerably hinders

natural selection in this direction. Sexual dimorphism is excellently expressed in the sable (Table I): for instance, the difference between the sexes, is larger in the nominal race than the difference between the latter and the Barguzin race. According to our data in the forest marten of the Central Russian race — ruthena there is no overlap at all between the varying total dimensions of the skull of the male and female: the maximal skull size of females is less than the minimal in the males of the same race.

In addition to sexual dimorphism, R. Genzel (1881) established the presence of a considerable range of individual variability of body size in a number of families of the marten with all possible stages, from examples of gigantism to dwarfism. This is characteristic of polecats, minks, Siberian minks, ermines, weasels, and other species, and may be abundantly illustrated by examples. Considerable individual and sexual variability of overall body size indicates that this feature has no decisive significance for the survival of the species of the marten family. Under equal environmental conditions small and large individuals possess equal vitality. However, the majority of geographical races of martens and sables differ from one another in size. It may be mentioned in passing that the species ranges of fluctuation in the dimensions of the sable and the forest marten are very similar.

What is the origin and cause of this geographical variability in body size, in as much as we have rejected the K. Bergman law?

We must not fail to scrutinize the prime importance of nutrition and the problems of environment as determining factors in species body size. It is generally known that the absence of available food and the lack of ability to obtain it under snow-cover conditions is precisely that which compels migratory birds to leave their nesting places and not the direct influence of the low temperatures. We imagine that very often the variability of the total body size is determined not by temperature conditions but by the amount and quality of the food obtained.

The largest race of elks possessing the most powerful antlers, inhabits the northeastern Siberian areas and the Alaska peninsula; the smallest, with less developed antlers, lives in the mountains of the Maritime Territory. Does the law of K. Bergman operate here? No. The study of elk ecology has shown that the degree of development of the antlers is above all an indication of the adiposity and general condition of the animal. In the Kaliningrad Oblast', where the largest elk with powerfully developed antlers are found, the main foods are the highly nutritious shoots of various willows (P.B. Yurgenson, 1935). The same willows are the chief food of elks of the Kolyma and Anadyr Rivers and Alaska Peninsula. The crux of the matter is that despite the severity of the climate the feeding conditions there are more favorable than those in the mountainous dark-needled taiga of the Sikhote Alin. (P.B. Yurgenson, 1935, L.G. Kaplanov, 1948). At the same time, the large, heavy, and widely-branched antlers are not a hindrance to the elk under the conditions of the sparse near-Polar forests and brushes. On the other hand, in the mountainous taiga they are completely unfavorable, like a massive body size. A smaller and lighter animal with small light antlers is more mobile in the mountanous taiga. This is particularly important since elk are not mountain animals by nature,

Thus, facts which apparently correspond to the rule of Bergman acquire a different and ecologically broader basis : the smaller the mammal, the higher the heat loss, the more active the total metabolism, and thus the more food required for the replacement of energy expenditures.

The weasel is a typical monophage, eating Muridae rodents almost exclusively.

Arctic tundras, where the smallest weasels live, are rich in voles and lemmings, which are the weasel's food, and, in order to capture them successfully here, small body size is incomparable more profitable than large size. A small size gives the weasel access to the subsnow and underground burrows and dens of the lemmings and voles in which they pass the winter. It is impossible to doubt that the large Mediterranean weasel, which is no smaller than the ermine in size and can penetrate into the burrows of the water rat only, is less well adapted than the smaller weasel, despite the smaller weasels heat losses. High heat loss is reduced by the subsnow life habits of the weasel, which is provided with food and the possibility of warm shelter in the nests of rodents. The ecological advantages of small size exceed the physiological advantage of larger size in the thermoregulatory processes.

Which factors are associated with the occurrence of geographical variability in the overall dimensions of the sable and forest pine marten? Our studies on the ecology of the species permit us to underline the following factors: degree of food availability: under equal conditions more food is needed by the larger animal of the same species in order for it to maintain its energy balance; when food is lacking the potential limiting growth cannot be provided for; size of prey: during the investigation of sexual dimorphism in the nutrition of the Pechora forest marten (P.B. Yurgenson, 1947), we established a very marked difference between the sexes; we found in the food of the male, which is stronger and larger, the wood grouse, black grouse, and white hare, which are apparently difficult for the female to obtain predominate, while in the food of the female, voles, small birds, and hazel grouse predominate. The squirrel is eaten equally often by both sexes.

In the forest food of the large forest marten of the Kola Peninsula (A.A. Nasimovich, 1948), which belongs to the Scandinavian race, we discovered a higher percentage of large prey than among the smaller Pechora race. In the former case the wood grouse constitutes 35 % of the diet in winter and the white hare 7 %; in the latter case, the wood grouse constitutes only 3.4% and the white hare 0.4 %.

Academician A. F. Middendorf identified larger and lighter plain (Urman) sables and smaller and darker mountain— taiga sables. L.P. Sabaneev (1875) agreed with this opinion. This formulation is generally correct and is explained by the fact that the plain Urman sable is better provided with food. The highest density figures known today were found among sables in the more favorable Urman regions in the former Konda-Sosva Preserve (marshy, dark-needled Urman forests along the shores of rivers). In 1869, A.F. Middendorf wrote that animals in mountainous regions are smaller than those living in the plains. He considered that the small forms of animals encountered on high mountain ridges, except for the pure alpine forms, apparently correspond to the recent generations in the deep north. A. F. Middendorf observed in this connection that even if the animals survive they have no time to attain their full natural height. The autumn molting begins before the animal has had time to grow sufficiently. He also believed that sharp temperature changes and rough autumn foods influence the not yet fully developed organism, accelerating the onset of maturity and cessation of growth. Normal sizes were also not attained by the recent generation of the red-backed forest voles— Clethrionomys - in the northeastern Altai (P.B. Yurgenson, 1938). A. F. Middendorf was also convinced that a decisive role in the variability of the overall body size is played by the amount and quality of the food. He wrote: "The quantity and quality of the food became a most important instrument in the hands of man by means of which, in the breeding of animals, extraordinary results in the area of dimensional increases were obtained." Nor is it coincidental that the potential fertility being equal, the large west Siberian and Kamchatka sables are in fact more fertile than the mountain-taiga sables of the Barguzin race. Thus, according to data by

V. L. Zaliker (1953), the average number of corpora lutea of the ovaries in the Kamchatka sable was 3.2, and in the sables of the Tyumen' Oblast' 3.4, while in the Barguzin sables during the 1951-52 season, according to the data of Yu. B. Baevskii, it was 2.7 (13 specimens). It is noticeable that in the season of the year 1952/53 when the food was better, the corpus luteum figure was 3 (32 specimens). Thus, in the final analysis, the fertility is the result of the availability of food.

We present in percentages the chief nutritional components of the Barguzin race (830 specimens), according to V. K. Timofeev (1948) (analyzed by the author of this paper), and of the Konda-Sosva sables (V. V. Raevskii, 1947).

Barguzin sable		Konda-Sosva sable	
Sorbus berries	37	Voles	56.6
Cedar seeds	33	Cedar seeds	51.5
Voles	28	Birds	25
Cedar fronds	21	including black grouse	10.8
Squirrels	0.36	Bilberries	11
Hazel grouse	1.4	Shrews	11
		Squirrels	6.6

Black grouse and wood grouse are completely absent from the food of the Barguzin sable. The plain Konda-Sosva sable is better provided with food. The percentage of animal food eaten by the Konda-Sosva sable, which belongs to the large race, is higher than in the Barguzin sables. We must particularly note a higher frequency of relatively large prey. Black grouse 10.8% as compared to 1.4%, squirrels 6.6% as compared to 0.36%. We may indicate here that according to a number of features of the masticatory apparatus the carnivorousness of the Konda-Sosva sable is considerably more marked than that of the Barguzin sable (including the degree of development of the cranial ridges).

The large Kamchatka sable may also be considered to be well supplied with foods. Its special combination of foods includes voles, berries, seeds of the Libocedrus, cedars, and also a considerable percentage of willow ptarmigans and, during the spawning period, transient fish. The comparatively small dimensions of the Zhigansk sable are undoubtedly explained by the scarcity of the food resources on the left bank of the Lena River.

From the previous data one may conclude that the sable or marten can only attain large sizes when fully provided with food. Comparatively the large size makes relatively large prey available to them, thus increasing their food supply. Thus, in the forest marten and sable the overall body size is most intimately related to their nutritional ecology.

Relative Dimensions and Proportions of the Skeleton

The deepest qualitative difference between the forest marten, the semiarboreal forms and the ground form, and the sable consists in the fact that the first is able to obtain its food in the tops of trees. It was this very ability that enabled the marten to broaden its original range, the broadleaf forest of the Western European type, and, adopting squirrels for food, to inhabit the needle forests of the East European Plain, thus entering into successful competition with the sable.

The semiarboreal mode of life could not help being reflected in the characteristics of the marten. In studying the features of the forest marten and its differences

from the sable and stone marten, we were able to discover a number of species characteristic in the relative dimensions and proportions of its vertebral column and limbs. We studied over 100 complete skeletons in order to make a comparison between the forest and stone martens, sables, and kidas (Table IV).

Table IV

Relative proportions of bones of forelimbs

Species and race	Relative scapula length	Relative scapula width	Relative humerus length	Relative radius length	Humerus radius index	Sums of relative lengths of anterior limbs
Martes martes lorenzi	8.9	8.4	15.9	11.8	1.34	36.6
M. M. sabaneevi	8.9	8.3	15.4	12.5	1.23	36.8
M. zibellina zibellina	8.6	7.9	14.8	12.1	1.22	35.5
M. foina nehringi	9.0	8.1	13.9	11.7	1.10	34.6
Range of average sizes	0.4	0.5	2.0	0.8	0.24	2.2

All figures are given in percentages relative to the length of the skeleton.

The interspecies differences in the relative dimensions and proportions of the bones of the anterior limbs are quite significant, and undoubtedly assume importance in the ability of the animals to climb. The narrowest scapula is possessed by sables, followed by stone martens and kidas. The forest marten has the widest scapula. A wide scapula is closely associated with the powerful musculatory development of the proximal portion of the forelimbs, which in turn is an adaptation to climbing in the semiarboreal mode of existence. However, a narrow scapula is characteristic of the good runners among Mammalia (I. Krumbigel, 1930). According to our observations, the forest marten is distinctly inferior to the sable in its speed of motion over the surface of the ground or snow.

The sable and the stone marten, which are entirely ground forms, also have shown a relatively shorter humerus than the forest marten (Table IV). The shortening of the humerus is also observed in forms leading a semisubterranean mode of life. Thus, in the least weasel, the humerus equals 11.8% of the body length (5 measurements), and in the Russian wild hare it is 60% of the length of the humerus.

The climbing mechanism in mammals has not been studied sufficiently to provide a basis for the significance of the differences found among both species of martens and the sable. The total relative lengths of the scapula, humerus, and radial bones in the ground forms of the marten and sable (34.6-35.5%), is also less than in the forest martens (36.6-36.8%). The differences demonstrated are supplemented by differences in proportions. In the ground forms, in connection with the shortening of the humerus, the index of the proportions of the humerus to the radial bones is less than that found in the forest marten. The proportions of sables and stone martens are close to the following: the least weasel 1.09, Brandt vole 1.05 and Dawrian gopher 1.03. We found the smallest figures among the jumping rodents: Mongolian jerboa and Russian hare 0.81, and wild rabbit 0.92. A similar picture is provided by the index of the ratios by the scapula and the humerus: sables and stone martens 1.4 and 1.5; both races of pine marten 1.7. The tubular or long bones of the anterior limbs in the forest marten, in association with the more powerful musculatory development also proved to be somewhat more massive than those of the sable. The massivity index (ratio of greatest diameters to length of the humerus)

in the pine marten is 0.66, and in the sable 0.63; for the radius, the corresponding figures are 0.063 and 0.064.

To turn to the skeleton of the hind limbs (Table V), it is found that in both races of the pine marten the tibia is 0.4% longer than in the stone marten and 1% longer than in the sable. In the pine marten the bones of the foot (tarsals and metarsals) were also longer. They were somewhat shorter in individuals of the Pechora race in comparison to those of the Caucasian race. They are even shorter in the ground forms, the sable and the stone marten.

Table V

Relative dimensions and proportions of skeleton (%) of hind limbs

Species and race	Femur		Tibia		Tarsal and metatarsal		Index of hind limbs	Sum of relative lengths
	To body length	To total length	To body length	To total length	To body length	To total length		
Martes foina nehringi	17.2	40.2	18.4	43.0	7.1	16.8	0.93	42.7
M. zibellina zibellina	18.7	39.7	17.8	42.5	7.5	17.8	0.95	42.1
M. martes sabaneevi	17.8	40.0	18.8	42.3	7.8	18.6	0.94	44.4
M. M. lorenzii	16.8	35.9	18.8	44.7	8.6	19.4	0.85	44.2

The relative dimensions of the femur provide a less distinct picture. This bone is shortest in the pine or forest marten of the Caucasian race and longest in the sable, but in the stone marten it is shorter than in the forest marten of the Pechora race.

The total length of the above bones turned out to be, as had been already noted in the case of the anterior limbs, shorter for the ground forms than for both races of the forest marten.

The index of the posterior limb (the ratio of the femur to tibia) has shown that in the forest marten of the Caucasian race the traits of the typical tree climber are well marked (0.85%). Rodents which climb and jump skillfully, the squirrel and pocket mouse, have indexes of 0.82 and 0.71 and the Mongolian jerboa (3 measurements) 0.70. In the Russian hare the index is 0.81, as compared to 0.92 in the wild rabbit, and 0.94 in the forest marten of the Pechora race. In this case characteristics are observed that seem transitional between the forest marten and the sable (0.95) which we associate with the origin of the race as the result of a lengthy process of hybridization on the boundary of the range of the two species (P. B. Yurgenson, 1948). These characteristics are thus reflected in a large number of indexes and not merely the dimensions of the shorter tail. This is also confirmed by the fact that in the arboreal marten of the Zhiguli, the index of the posterior limb equals 0.87.

The massivity indexes of the long hind limb bones of the marten, as in the anterior extremities, indicate that they are more massive than in the sable (the difference is 0.001). So that the proportions of the bones of the hind limbs may be more obviously marked, the corresponding measurements were once again calculated as a percentage of their total relative length taken as 100. It became even clearer

(Table V) that in the proportions of hind limbs the Pechora race occupies an intermediate position between the forest marten and the sable, as is especially clearly marked in the relative sizes of the femur and the tibia, while in the relative dimensions of the posterior foot bones the species specificity of the forest marten makes itself apparent: the differences between the races of martens is 0.8%, while between the Pechora and sable it is 1.2%.

In the Caucasian race we see the maximum shortening of the femur (35.9%). whereas the tibia and the bones of the hind leg are longer in this race.

Thus, the features of the tree-climber are strongly expressed here.

It is known that among mammals the swift runners and good jumpers are distinguished by a low anterior and high posterior, which is sometimes very strongly marked. Among the ungulates, a well-marked high posterior is clearly seen in the musk deer and chamois. Among the races of domestic dog this is very well marked in the borzoi; among rodents, the jerboa possesses this characteristic; while in the small Dauri hamster, the length of the hind limb is in a 1.40:1 ratio to the fore limb; in the Mongolian jerboa the ratio is 3.09:1. The height of the posterior portions especially during movement, is also obvious in all predators, including species of the genus of martens. In this the index fluctuates from 1.18 to 1.27. It appears once again that the index of the forest martens of the Pechora race (1.20) it is nearer to that of the sable (1.18) than to that of the Caucasian race (1.27).

Thus, we find confirmation of the fact that in tree climbers which execute long leaps from tree to tree a high posterior is more strongly marked than in small ground predators. The index of the sable is nearer to that of the least weasel (1.16) In the stone marten it is closer to that of the forest marten or the Caucasian race than to that of the sable.

We could only compare dimensions and proportions of the pelvic bones of the forest and stone martens of the Caucasian preserve (6 and 9 specimens). It proved that the pelvis of the forest marten is considerably smaller than that of the stone marten in absolute dimensions as well as in ratio to the overall body length. The total length of the innominate bone in the forest marten is smaller by 0.5%, the length of the ilium by 0.4%, the diameter of the aperture of the pelvis by 0.34%. Considerable differences also exist in the sum length of the different regions of the vertebral column. In the forest marten, the distinguishing features are the shortness of the cervical region (14.03% as compared to 14.42%) and of the thoracic (30.27% as compared with 31.94%). In the regions of the vertebral column the sum of the relative lengths of the lumbar and sacral regions in the forest marten is 35.7% as compared with 32.6% in the ground marten, i.e., these regions in the forest marten grow at the expense of a shortening in the length of the cervical and thoracic regions.

Observations by B. B. Dubinin (1949) confirm that in all climbing, jumping forms and in those which leap or glide from tree limb to limb, the relative length of the cervical vertebral region is shortened as compared to the precaudal length of the vertebral column (lynx, marten, squirrel, howler monkey, orangutan, and others). This is not only true of the Caucasian forest martens. In martens of the Pechora race the sum of the lengths of the lumbar and sacral vertebrae (8 specimens) also equals 35.2%. In all species of the genus of martens the usual manner of locomotion is jumping (fore and hind limbs act in concert). An important role in this process is played by the flexing and unflexing of the vertebral column under the pull of the very powerful back muscles, but the elasticity of the vertebral column is intimately associated with the length of its lumbar regions and with the length of the back muscles, including especially that of the sacrospinalis muscle. The shortening of the cervical region in the forest marten occurs to the extent of 0.39%, chiefly at the expense of the third and sixth vertebrae.

The tail of mammals (an organ which enables it easily to maintain equilibrium while in motion) is of particular importance in rapid pacing, jumping, and turning.

The tail is also of great importance in gliding jumps from tree to tree and in tree to earth jumps. An indirect pooof of the fact that the forest marten, according to our observations and the observations of Pechora hunters, actively uses its tail when jumping is that in jumping from trees to the snow it leaves no tail prints. Thus, it is curved upward at this time, is somewhat lifted, and participates actively in the mechanics of jumping. The sable and kida, when jumping on the snow, leave an imprint of the tail, and it is thus inert in these animals at this time.

In connection with this, an important adaptive value is attached to the relative length of the tail and the number of tail vertebrae and their dimensions, which determine the length of the tail (Table VI).

Table VI

Number of tail vertebrae and their variability

Species and race	No of specimens	Range	Average
Martes zibellina zibellina	4	15-17	16.00
M. m. sabaneevi (male)	17	18-22	18.66
M. m. sabaneevi (female)	31	17-20	18.63
M. m. lorenzi	5	18-21	19.40
M. foina nehringi	9	20-22	21.20
Kidas (male)	13	16-20	17.53
Kidas (female)	6	16-18	17.00

From the data it may be seen that the number of tail vertebrae is an inconstant figure with the species and races. We see also that the smaller figures are characteristic of the sable, followed by the kida--the hybrid between the sable and the forest marten, followed by the forest and the stone martens.

As is seen from Table VII, there are distinct differences in the average value of the relative length of the tail among species and races of sables and martens.

Table VII

Relative length of tail (in comparison to body length)

Species and race	No of specimens	Range	Average
Martes zibellina zibellina	16	24.4-42.0	31.1
" " jeniseensis	93	--	36.4*
" " sajanensis	22	--	35.2*
" " sachalinensis	22	--	30.0*
" " kamtschadalica	4	--	34.1*
Martes martes sabaneevi	67	37.0-54.0	45.2
" " ruthena	18	46.3-54.6	50.8
" " lorenzi	17	42.0-52.1	47.2
" foina nehringi	5	--	53.0

Note: All data refer to males.

However, it possesses a considerable individual variability, which is of an overlapping character. As a result of this, the relative length of the tail cannot constitute a distinct diagnostic feature, neither as to race, nor as to species. Nevertheless we see that the greatest relative tail length is characteristic of the ground marten (53%), followed by the forest marten (45.2%-50.8%), and finally the sable (30-36.4%).

It is quite clear that the optimal relative sizes of the tail are adaptations to the semiarboreal mode of life and are distributed in the range of 45-51%, while the average relative length of the tail of the ground marten is exceeded in single individuals of the forest marten, reaching 54.6%. From this, the shortening of the tail length in the sable should be considered as an adaptation to a ground and subsnow mode of life with a simultanous loss of ability to use the tail actively when jumping (gliding is also not characteristic of the sable). The tail of the stone marten should be considered too long for these purposes. Probably this was the size of the tail of presable forebears.

The data of the table also indicate that the species of the genus Martes are not subject to the "Allen law" which asserts that the tail length in kindred forms decreases from south to north. The tail of the Kamchatka sable is longer than that of Sakhalin race, while among forest martens it is shorter in the Caucasian race than in the middle Russian race. Simultaneously with the process of tail shortening a reduction in the number of tail vertebrae and a lessening of the length of the centrum occurs among some of the species. In comparing individuals of various species, differences in the length of the centrum are present in all tail vertebrae, while within a species the differences are observed only from the ninth vertebrae, being most varied in the distal portion of the tail.

In the forest martens of the races studied, the length of the centrum of individual vertebrae gradually increases from the first to the ninth vertebrae inclusively and later evenly decreases. In the stone martens and kidas the increase in the length of the body terminates at the seventh centrum and rudimentary forms begin from the twentieth. In the forest marten of the Caucasian race, the reduction of vertebral size to 3.5-6.0 mm also begins from the twentieth vertebra, in martens of the Pechora race from the eighteenth and in the kidas from the fifteenth to the sixteenth.

In summary we may say that during the process of adaptive evolution in the sable there occurred a reduction in the number of tail vertebrae, as well as a change in the size of some of them, while in the forest marten only a reduction in number occurred.

Osseous Auditory Tympanum (bullae osseae)

Max Weber considered the function of the auditory tympanums to be the amplification of sound. They are especially well developed in desert mammals. R. Pocock (1921) established the presence of two types according to the internal structure of the auditory tympanums in the marten family, one characteristic of the stone marten and the yellow-throated marten, and the other, more primitive, typifying the forest [pine] marten, glutton, and badger.

To carry out an objective evaluation of the external dimensions and their variability we multiplied the bullae osseae by their maximum width (in two cases in percentages of the condylobasal cranial length). We have only individual measurements on several races and thus these figures require more precision(Table VIII).

We should also note that among the stone martens the smaller indexes characterized the central Asiatic and Crimean races, in the forest marten the Caucasian, and among the sables the Far Eastern (Sakhalin). The figures obtained show considerable

interspecies variability with overlapping in the variability of the sizes of the bullae osseae. For the stone marten, the interspecies range is 188.16-217.56; for the forest marten, 212.5-246.8; for the sable, 213.0-280.0. The average index for four races of the stone marten equals 201.8; for five races of the forest marten, 231.4; for six races of sable 248.3.

Table VIII

Indexes of bullae osseae

Species and race	Number	Mean
Martes foina intermedia	8	188.2
" " nehringi	10	204.4
" " rosanovi	--	197.1
" " foina	15	217.6
Martes martes lorenzi	20	212.5
" " sabaneevi	23	224.0
" " lafinorum	1	226.6
" " ruthena	21	244.0
" " martes	15	246.9
Martes zibellina sachalinensis	1	213.0
" " kamtschadalica	1	240.3
" " allaica	5	246.8
" " zibellina	11	256.6
" " princeps	1	280.0
" " tungussensis	1	257.8
" paleosinensis (fossil)	3	222.6

Thus, the largest bullae osseae characterize the sable; this data coincides fully with reports of experienced hunters of the Komi ASSR (for example, I.I. Mezentsev) who claim that the sable possesses more acute hearing than the forest marten. In fact, in the northern Urals, the index of the sable is 251.77 and of the forest marten only 244. This is quite natural because of the terrestrial mode of life of the sable which is undoubtedly less safe than the semiarboreal mode of life of the forest marten.

Examining the indexes of the geographical races of the forest marten, we see that the maximum size (246.9) belongs to the martens of the Scandinavian (nominal) race on the range of the Kolo Peninsula. This is natural, since in this region the marten leads the same strictly terrestrial mode of life as the sable. Furthermore its carnivorousness is here maximally manifested, and, in order to acquire large prey, acuteness of hearing is absolutely essential. The relatively high figure for the Central Russian race (244) is explainable by the fact that martens of this race from time immemorial have been subjected to the maximum degree of persecution by hunters and, at the same time possessed less favorable ecological conditions than, for example, in the Caucasus, where they were faced with a fiercer struggle for existence. Acute hearing is required for successfully capturing prey and for defence.

As a whole, we consider the stone marten the most primitive and ancient species, which deviated less than the others of the Pliocene marten ancestors. The maximum index (217.5), which is distinctly different from that of the other races (188.2-204.4) is shown by the Western European (nominal) race (our species from the Ukrainian SSR). This may also be interpreted as a secondary adaptation to close contact with man in an area which we also consider to be secondary in nature. Habitation by wild animals in populated areas and even around cities understandably requires more acute external sensory receptors.

What has been said concerning Central Russian forest martens is also completely applicable to the Barguzin race of martens, in which the figure (280) considerably exceeds the index of other races (213.0-251.8).

The markedly different index (213) of the Sakhalin race, i. e., the sables of the Far East, also commands attention. This may be connected with the slight snow cover there, since obtaining food beneath the snow undoubtedly demands more acute hearing.

Masticatory Apparatus

Two factors are of interest in the masticatory apparatus of martens, these being the degree of carnivorousness and, on the other hand, the degree of omnivorousness. The best indication of the degree of carnivorousness may be the extent of development of the upper PM^4 (carnassial) tooth. One of the objective features expressible in figures for this tooth could be the height of its shearing crowns in relation to its relative length (Table IX). In each of the three species we deal with the mean size obtained in measuring series (10 skulls of adult males from 4-6 geographical races of each species). We present the range of variation of the mean sizes according to the species and the overall mean. The higher the shearing crests, the smaller the value.

Table IX

Tooth data

Species	Height of PM^4		Width of M^2	
	Limit	Mean	Limit	Mean
Forest marten	1.53-1.64	1.58	1.30-1.39	1.35
Sable	1.50-1.59	1.56	1.35-1.39	1.36
Stone marten	1.44-1.64	1.54	1.53-1.60	1.56

As seen in the table, overlapping sizes are found, but it is quite clear that the most developed shearing crests belong to the stone marten, followed by the sable, and are most strongly developed in the forest martens. In complete correspondence to this, the characteristic feature of the stone marten is the narrow, poorly developed talonids of the upper molar teeth, the only food-triturating surface in the dental system of species of the genus Martes. The next position, on the basis of this feature, is occupied by the sable, followed by the forest marten. The small difference existing among the latter is determined by the Caucasian race of the forest marten, with an average index of 1.30. In fact, in the food of this marten, vegetable food and insects are presented in greater quantities (P. B. Yurgenson, 1951), whereas large (relatively) warm-blooded animals are absent. For the forest marten we have already had occasion to show (P. B. Yurgenson, 1951) a distinct relationship between the degree of carnivorousness in food and the structure of the masticatory apparatus. This also plays a role in the differences between the most carnivorous sables, which capture large prey and which are mostly of the plain races, and the more omnivorous and herbivorous mountain-taiga sables. In fact, in the mountain-taiga sables of the Barguzin race, the index of the height of the PM^4 is 1.57*, while in the plain sables of the nominal race it is 1.39.

Table IX shows the indexes as differing sharply from the contemporary food habits of the stone marten, which eats more herbivorous food than the other two

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* The ratio of length of this tooth to the height of the middle crest.

species. This can be explained by the sharply expressed conservatism of the heredity of of the given species and the more primitive type of its structure. The nutritional changes resulting therefrom found no reflection in the morphology.

External Integument of the Body

After considering the significance of the sizes of the tympanic bulla in the degree of development of acuity of hearing, there is room for some remarks on the role of the dimensions of the helix of the ear. According to data by R. Pokock(1921), the highest type of development of the external ear in the family of the martens is found in the species of the genus Martes (martens) and the genus Lamprogale (yellow-throated marten). This author (1914) himself indicated that the ears of the forest marten are longer and wider than those of the stone marten and that the species significance of these differences are not to be doubted. In the forest marten the height of the ear is 41 mm and the width 37 mm. In the stone marten the corresponding figures are 37 and 31 mm.

Academician I. F. Brandt (1855) wrote that the ear of the sable is larger and more peripherally angular than that of the forest marten, in which the ear is shorter, rounded, and covered by short sparse hairs (in the specimen of the nominal race, the height of the ear is 53 mm in males and 48 mm in females, constituting 8.7% of the length of the body). Thus, the sizes of the external ear constitute a valid series extending from the stone marten through the forest marten to the sable. This must be associated with the extreme acuity of hearing which all sable hunters and naturalists studying the sable have noted in the animal in question. Thus, the size of the internal ear is an adaptive feature connected with the direct function of the hearing organ, while the direct task of the external ear is to help collect and magnify sounds.

Glover Allen, in his work on the geographical variability of the mammals and birds of America, first established that the sizes of the peripheral parts of the body—limbs, ears, tail in many mammals, and birds— obey a law of increase moving southward. Glover Allen associated this with a climatic factor—temperature.

Consequently, this increase proved to be in inverse ratio to the geographical changes in the body size determined by the "law" of K. Bergman, and was related to the thermoregulation of the organism. Allen's data were later confirmed by research made by R. Hesse and B. Rensh (E. L. Lukin, 1941), and which were termed the "Allen law".

R. Hesse emphasized the significance of the helix of the ear of mammals in thermal regulation, whereas B. Rensh (data by Anthony) has shown that for American mammals the "Allen law" was confirmed in 13 cases and unconfirmed in three cases. Thus, the material for checking was limited.

Our data on the genus of martens are completely in conflict with "Allen's Law". The stone marten is distinguished by a smaller ear size and its entire range lies to the south of the sable range, whose ear, on the contrary, is very large. The forest marten, on the other hand, occupies an intermediate position.

From this we may conclude that the adaptive significance of the size of the external ear which is correlatively associated with the sizes of the bullae osseae is directly connected with the direct function of the organ of hearing. This direct function undoubtedly is of greater significance than thermoregulation for species of the marten genus. This is compensated by the fact that the larger ear of the sable living in the colder regions is well protected by a dense hair cover which protects it from the cold. Within the species, no geographical variability in size of the

external ear is observed. In the Central Russian race, as in the case of the Caucasian race of the forest marten, its relative size is mainly 11.1-11.6% of the total body length.

The vibrissae as tactile organs are of considerable importance in the life of mammals, increasingly so in animals conducting a dusk or nocturnal mode of life. In predatory animals which carry on a semiarboreal way of life, Academician L.F. Brandt (1855) was the first to draw attention to the interspecies differences in the vibrissae. The vibrissae of the sable, in his studies were thinner and shorter than those of the forest marten. They are long in the latter, extending posteriorly and protruding somewhat behind the ear, whereas in the sable (vibrissae of the upper lip) they do not reach the upper edge of the ear.

R. Pocock (1921) has noted that in predatory animals with an active terrestrial mode of life—the genera Martes and Mustela—the tactile vibrissae are longer and more abundant than in animals conducting a suberranean mode of existence—the badger, Meles, the honeyeaters [honey badgers] Mellivora, and the skunks, Mephitis. The corporal vibrissae are also more strongly developed in the active terrestrial forms. The vibrissae are also weakly developed in the aquatic forms. According to G.A. Novikov (1939), in the European mink there are only two short vibrissae near the nose, two supraocular ones, two angular ones, and two on the chin, all of them short. In the species of the genus of martens, seven groups of vibrissae exist, each containing large and small vibrissae.

The number of vibrissae of the various groups is shown in Table X (material: forest martens 2, kidas 2, sables 5, stone martens 3).

Table X

Species	Vibrissae					
	Upper lip		Lower lip		Chin	
	Limit	Mean	Limit	Mean	Limit	Mean
Forest [pine] martens	20-20	20.0	8-8	8.0	3.3	3.0
Kidas	15-16	20.5	16-20	18.0	3.3	3.0
Sables	14-23	18.8	6-10	18.0	1.3	2.0
Stone martens	14-18	16.3	6-8	7.3	2.3	2.3

Vibrissae

Angular		Supraocular		Nasal		Corporal	
Limit	Mean	Limit	Mean	Limit	Mean	Limit	Mean
4-4	4.0	4-4	4.0	2-2	2.0	3-4	3.5
4-4	4.0	3-5	4.0	2-3	2.5	2-3	3.0
0-4	2.4	3-5	4.2	1-3	2.2	2-3	2.5
3-4	3.6	6-7	6.7	2-5	3.3	3-3	3.0

The counting was carried out on one side, the total number of vibrissae in the forest marten on the average equalling 44.5, in the stone martens 40.5, in the kidas 37, and in sables 36.6. Thus, the forest marten has the greatest number of vibrissae.

The maximal length of the vibrissae of the upper lip proved to be: kidas, 75.0-90.0 (mean 82.5); forest martens, 59.8-60.8 (mean 60.3); sables, 54.1-76.2 (mean 68.5), and stone martens 43.8-72.0 (mean 57.2).

These data are not contradictory to the reports of Academician I. F. Brandt, since the greater absolute length of the vibrissae in the sable is connected with its larger over-all size. The abundance and length of vibrissae, as well as the distinctly expressed bristle quality of the fur in kidas, should be considered as one of the manifestations of heterosis in the hybrid.

The most characteristic trait of the forest marten is the number of its corporal and chin vibrissae, which must be considered as an adaptation to the semi-arboreal mode of life. The sable occupies the last position in the number of corporal, angular, and chin vibrissae. In the stone marten, the number of near-nasal and supraocular vibrissae draws attention. All species have large and small vibrissae in equal number on their upper lip. Small vibrissae predominate on the lower lip.

The dimensions of the postocular aperture of the cranium are closely connected with the development of the function of the tactile cranial vibrissae, because it is precisely through this that the nerve innervating the vibrissa passes.

The nerve completely fills this aperture; thus, the area of its section is equal to the area of the aperture. The degree of development of the nerve in question and the dimensions of the postocular aperture are in complete agreement.

What is clear is that the relative diameter of this aperture in the kidas equals 5.8% of the condylobasal length of the skull; in the forest martens of various races, 4.7-5.2; in sables of various races, 5.4-5.5; in stone martens of various races, 4.1-4.9%. In the forest marten of the Pechora race, to which we ascribe hybrid origin, the diameter of the postocular aperture is the same as that in the sable (5.4%). Thus, the development of the postocular aperture and the postocular nerve are adequate.

The forepaws of the sable have the thickest fur trim, especially in the winter; those with the least amount belong to the stone marten. On this basis the surface calluses of the sole of the stone marten are well developed. The significance of fur-trimming on the foot is twofold: for heat insulation and to increase the surface area of the paw, which promotes locomotion on snowy surfaces. These features of single species undoubtedly possess permanent hereditary value, since in our observations they are maintained in the northern Urals even when the sable and the forest marten live together within the range of the same mountain valley. The same is also true in the northern Caucasus in regard to the forest and stone martens. There is no room for doubt that the relative size of the surface area of the paws is an adaptation which assists in the locomotion of the animal on the snow. According to data obtained by us from animals taken simultaneously in the valley of the Uk-Yu River (northern Urals), 9.55 g of body weight in the sable rest on one cm^2 of the sole of the paw; in forest martens, 11.90 g and in the kidas 13 g.

One must remember that in the white hare and the willow ptarmigan, which are more adapted to locomotion on the surface of the snow, the weight load is 8.4-11.8 g and 15-17 g (O.I. Semenov-Tyan'shanskii, 1939; A.N. Formozov, 1946). In the Tolai hare [Lepus tolai] and in the European hare [Lepus europeans], it rises as high as 19 and 22-24 g.

Thus, the sable, forest marten, and kidas are animals which are well adapted to locomotion on the ice, but the sable is better adapted than the forest marten and the kida.

The features of the claw structure are of great significance. The differences between the species here may even be seen by the naked eye. However, up to this time, the systematists and morphologists have not given sufficient attention to these features. The claws of the forest marten are shorter than those of the sable,

but they are bent at a more acute angle and are more prehensile. The claws of the stone marten are relatively small, but substantial. It is necessary to translate this into quantitative language: taking into account the method of Ulrich Duerst (1926), we made the following measurements for the claws of the fore limbs: 1) the length of the greater curvature of the claw; 2) the length of the lesser curvature; 3) the length of the base of the claw (measured in a straight line); 4) the height of the base of the claw; 5) the width of the base of the claw; 6) the height of a perpendicular lowered from the highest point of the lesser (internal) curvature of the claw to the middle of the straight line which constitutes its chief length; 7) the oblique length of the claw.

Using these measurements we obtained four ratios: the relative length of the claw, (the ratio of the length of the greater curvature to the length of the body), the index of the curvature (the ratio between the third and sixth measurement above), the index of massivity (the ratio of the height of the base to the oblique length), and the relative height of the base (ratio of this measurement to the body length). Five sables of the nominal race (northern Urals) were used for measurements, as well as two forest martens of the Pechora race, one kida, and three stone martens. The data of these indexes are presented in Table XI.

Table XI

Indexes of the claws of the fore limbs

Species	Index of relative length		Index of massivity		Curvature index		Relative height of base	
	Limit	M	Limit	M	Limit	M	Limit	M
Forest marten	6.8-8.3	7.4	0.29-0.31	0.30	0.31-0.39	0.35	7.9-8.3	8.1
Kida	8.6	--	0.37	--	0.33	--	9.3	--
Sable	9.8-10.1	9.4	0.26-0.31	0.29	0.26-0.35	0.29	10.2-13.5	11.6
Stone marten	10.4-10.8	10.6	0.28-0.38	0.32	0.20-0.29	0.24	11.2-13.5	12.6

Note: M = mean

Muscular System

There is no doubt that the weight of any muscle or group of muscles may serve as an index of the degree of muscle development. It is therefore permissible in ascertaining this, to use the relative weight of the muscle (in pro mille of the weight of the skeleton muscular system of the given individual). In order to evaluate the development of the masticatory musculature, the temporal, masseter, and the biventer muscles of the mandible were measured.

The relative weights of the muscularis pectoralis major were also demonstrated and examined, as well as those of the anterior and posterior extremities as a whole. Fifteen forest sables of the Pechora race served as material for the study, as well as two kidas, 19 Trans-Baikal steppe polecats, six ermine from the upper reaches of the Pechora River, one glutton, and nine least weasels from the Trans-Baikal. Herbert Schutze (1936) also investigated 12 stone martens and forest polecats by these methods. We had no opportunity to study the musculature of the sables by this method.

Table XII presents the appropriate quantitative data of the relative sizes of the musculature. Table XIII presents data on sexual dimorphism in the development of the musculature. From Table XIII we see a well-expressed sexual dimorphism in the muscular development of the forest sable and stone marten (although

the latter is denied by H. Schutze) and its absence in the steppe polecat. It will be more distinctly expressed in absolute weight because the total weight of the skeletomuscular system in females is considerably lower than that of males (769.0 and 1,021.2 g for stone martens).

Table XII

Relative development of musculature

	Number of data	Temporal muscle	Masseter muscle	Biventer muscle	Index of temporal-masseter muscle	Musculus pectoralis major	Fore limb	Hind limb	Difference between limbs, %	Index of hind limb
Forest marten	15	8.3	3.0	2.0	0.36	14.5	71.3	103.7	32.4	1.46
Stone marten	12	11.1	2.5	2.3	0.26	13.0	49.0	99.0	50.0	2.02
Steppe polecat	19	13.6	3.5	3.8	0.25	14.3	55.6	66.1	10.5	1.18
Forest polecat	-	-	-	-	—	-	41.0	71.0	30.0	1.73
Ermine	6	9.6	2.4	1.7	0.25	17.0	55.6	85.9	30.9	1.54
Small weasel	9	14.4	5.8	-	0.40	17.2	48.2	58.7	10.5	1.21
Glutton	1	15.8	4.1	2.4	0.25	12.7	127.0	110.0	17.0	0.85

In pro mille of the weight of the skeletomuscular system, in percentage of weight of skeletomuscular system.

Table XIII

Sexual dimorphism in the development of the musculature

Species	Number	Temporal	Masseter	Biventer	Fore limb	Hind limb
Forest marten (males)	7	9.4	3.2	2.4	73.4	111.1
" " (females)	8	7.5	2.8	2.0	69.5	97.3
Stone marten (males)	8	12.5	2.6	1.8	50.0	97.0
" " (females)	4	9.7	2.3	2.2	48.0	101.0
Steppe polecat (males)	11	13.0	3.4	3.7	54.3	66.2
" " (females)	8	14.0	3.6	3.9	57.5	68.1

The problem of the significance of the sexual dimorphism in martens and the causes of its absence in steppe polecats was studied by us elsewhere (P. B. Yurgenson, 1947).

The simple scissorlike up and down movements of the lower jaw provide for the shearing function of the dentition and are chiefly made by means of three muscles, the temporal, masseter, and biventer. The first two raise the lower jaw superiad and the third lowers it (a passive movement) together with the action of the gravitation of the jaw.

As is known, the temporal muscle is very strongly developed in predators

and the masseter considerably less, whereas in rodents the situation is the opposite. The movements of the lower mandible anteriorly and posteriorly and its limited lateral movements are made by the masseter, together with an increased function by the temporal. These functions, as shown by Yu. A. Orlov (1947), are caused by the various layers of the masseter. In connection with the passive function, the biventer muscle is equally developed in the majority of species, the only exceptions being the forest and steppe polecats. We see that the temporal muscle is most weakly developed in the forest marten (8.30%), followed by the ermine, and only then by the stone marten (11%). The muscle of the glutton is most strongly developed, since this animal eats the carcasses of large animals (15.7%). The strong development of the muscle in the least weasel, the smallest predator of our fauna, probably compensates for its insignificant absolute size (14.4). It could not otherwise kill its victims by severing their occipitum. The masseter muscle in the stone marten (2.35), is, on the contrary, more poorly developed than that of the forest marten (2.23). The relative development of this muscle is also reflected in the index of their ratios. The most highly developed masseter muscle in relation to the temporal is that of the least weasel (0.40), followed by the forest marten (0.36) and the stone marten (0.26). The indexes of the glutton, ermine and steppe polecat are equal in magnitude (0.25).

The degree of development of the masticatory musculature is chiefly reflected in the development of the cranial osseous pectens, in the width of the zygomatic arches, which is closely connected with the development of the masticatory muscles, and in the relative width of the postorbital narrowing, which in turn is connected with the development of the temporal muscle. While the development of the osseous pectens in small predators is difficult to describe in figures, it is not difficult to express by two other indexes. The appropiate measurements can be implemented on skulls in almost any scheme.

This permits us to study more widely the variability of development of the masticatory muscles also including that of the interspecies type.

It is known that the more strongly developed the masseter, the wider apart are the zygomatic arches of the skull. This may be seen not only in herbivorous forms but also in predators in which the powerful development of this muscle sometimes takes place at the expense of those layers of it which increase the strength of the temporal muscle, i.e., the seizing and shearing function of the jaws and the dentition. The same situation is seen in cats, lynx, etc.

In other cases, when the dentition possesses triturating surfaces and the animal eats various foods (including fruits, berries, and invertebrates) a larger separation and a widening of the zygomatic arches is associated with an increase in the size of the other layers of the masseter muscles and in a reduction of carnivorousness. The latter is particularly true of the sable.

The geographical races of the sable may be divided into three groups on the basis of relative zygomatic arch width: 1) nominal and Tungus races; 2) Kamchatka Far Eastern, and Yenisey races; 3) Sayan, Altai, and Barguzin races. The zygomatic arches in the third group are placed most widely apart—in the mountain taiga sables.

The first group differs from the second by 0.6% in this respect, and the second from the third by 1.3%. The amplitude and range of variability in the first group is 0.2, in the second 0.4, and in the third 0.5%. Thus, these groups are not artificially separated. In addition, each group possesses a common group range. These data once again confirmed our conclusion that the mountain taiga Barguzin type of sable is less carnivorous than the nominal West Siberian type which inhabits the plain taiga. Besides the peculiarities of the dentition and the disposition of the

zygomatic arches, we find a reflection of the latter in the weakly developed osseous pectens of the skull (the weaker development of the temporal muscle) and in the proportions of the lower jaw.

In the Barguzin race the relative width of the zygomatic arches is 2.5% higher than in the nominal. Their wide separation in the Altai race (58.1%) is very close to the Barguzin type and confirms the differences between the mountainous and plain sables which were already correctly assumed by Academician A. F. Middendorf on the basis of nutrition. It may be mentioned here that according to Academician A. F. Middendorf (1869), the interspecies differences in sizes depend primarily on the varied food supply, particularly during the period of the organism's growth. The Sayan race of sable, included in the third group, is also a mountainous taiga group. The sables of the second group are transitions between the mountain-taiga and plain sables.

The dependence of interspecies differences in the development of the musculature of the masticatory apparatus on the type of food and the degree of carnivorousness in forest martens has already been shown by us (P. B. Yurgenson, 1951).

Yu. A. Orlov (1947) remarked justifiably that the limited mobility of the lower jaw of predatory animals also limits the possibility of anterior, posterior, and lateral movements, which produce the wide separation of the zygomatic arches and the strong development of the masticatory muscles, which, in turn, should chiefly increase the action of the temporal muscle. In a number of cases this is actually so, but not in the sable and marten, in which increase of the masticatory muscles parallels the weakening of the temporal muscle and the decrease in the development of the osseous ridges of the cranium.

It is well known that in predatory birds, along with the development of the temporal muscles, the width of the posterior ocular narrowing of the cranium is considerably decreased. The same is seen in the process of ontogenetic development among individuals: together with the age increase in the power of this muscle, the postocular narrowing decreases and the osseous ridge parallelly increases in size. In various races of the forest marten the average figures for the relative size of this narrowing vary from 22% to 23.6% (mean 22.64%); in the stone marten of various races from 22.3 to 22.6% (mean 22.62%); in the races of the sable from 17.9-22.5% (mean 19.98%). The species average values for forest and stone martens are identical. In martens the range of the interspecies variability is 3-4.6%, in the sable more than 4.6%. In all cases the postocular narrowing is less in the sable than in the two species of martens. Thus the temporal muscle is more strongly developed in sables and carnivorousness is more markedly manifest. It should be noted that only fully mature individuals were compared in all cases.

The postocular narrowing was least marked in the Sakhalin race of sable (22.5%) and most strongly expressed in the Kamchatka race (17.9%).

The type of development of the musculus pectoralis major in species which are studied in Table X and the role of this muscle in the mechanics of the movement of the fore limbs indicates its special significance for animals which climb in trees (the forest marten) and for rodents, which often also move subterraneously for long periods.

The forest marten occupies the second position in development of the skeletomuscular system of the fore limb in the marten family, being second only to the massive muscular glutton, in which the fore limbs are even more strongly developed than the hind; in the stone marten the skeletomuscular system of the fore limbs is considerably more weakly developed than in the forest marten. In this we should

undoubtedly recognize the adaptive character of the stronger development of the muscular system of the forest marten in accordance with its semiarboreal mode of life (function of climbing in trees). The musculature of the fore limbs is most weakly developed in the forest polecat.

In the majority of cases the skeletomuscular system of the hind limb in species of the marten family is more strongly developed than that at the fore limb. This is associated with the jumps which are its most frequently employed methods of locomotion (compare the particularly powerful development of the hind limbs in jerboas, hares, and borzoi). The single exception is the glutton, the typical gait of which is the lope; on the other hand, the powerful development of the musculature of the fore limb in the glutton is associated with the capture of large ungulates and the tearing apart of carrion, which in winter may even be frozen.

The forest marten is in second position after the glutton (103.7%), whereas the stone marten occupies third place (99%). The index of the posterior extremity (the ratio of the relative weight of the fore and hind limbs) indicates that in the stone marten it is more strongly developed than in the anterior extremity. The lesser index of the forest marten is connected with the more powerful musculature of the fore limb. The powerful (103.7%) musculature of the hind limbs provides it with jumping ability for moving from tree to tree, while for crawling it is provided with the musculature (71.3) of the fore limbs. Probably the development of the musculature in the sable and stone marten is similar.

Internal Organs

The relative weight of a number of internal organs of wild animals possesses a distinctly marked individual variability. Thus the relative weight of the liver of the pine [forest] martens of the Pechora race ranges between 14.3 to 46.7 pro mille (53 measurements). The index of the relative length of the intestine varies from 3.7 to 5.2. In the Dzhungara hamsters the relative weight of the heart ranges between 11.8 to 24, of the kidney from 8.8 to 22.1, of the spleen from 4.4 to 13.3, and so on.

Thus, the race and interspecies variability of the relative sizes of the internal organs is of a distinctly overlapping character. In viewing the internal organs we should also consider changes due to age (for the heart), as a result of the exercise of the organ in life.

Table XIV compiles all data in our possession on the relative heart weight (pro mille) in relation to the total weight of the animal's body. The method of treating the organ was the same as that used by S. N. Bogolyubskii (1941). The range of the relative heart weight within the marten family is very great, extending from 4.60 in the massive sluggish skunks up to 16.80 in the most minute predator, the least weasel. According to our incomplete data, the relative weight of the heart fluctuates from 7.40 to 9.62 in the sable. Among sables bred on farms in cramped quarters, the relative weight of the heart is, of course, less. The forest marten is represented by four races. The smaller heart size—7.41—is found in the southern race of large size animals (Caucasian). The heart of the large Central European race is similar in size—7.66. In the smallest (north-central Russian) race, the heart is already considerably larger—9.83. It is relatively larger in forest martens of the Pechora race, which are undistinguishable in size from the previously mentioned animals but which dwell considerably farther north—11.52.

Thus, the range of the geographical variability of martens equals 4.11, confirming the observations of R. Hesse with the corrections of B. Rensh.

Unfortunately, there are no data on the forest marten of the Kola Peninsula, which is the most northern type. Kidas occupy intermediate positions between the sable and forest marten (10.66); we then see that the heart of the Pechora ermine is considerably larger than that of the central European variety. The heart of the steppe polecat of the southeastern Trans-Baikal is twice as large as that of the German forest region. That of the European wild mink is also larger than that of the American mink, which is also confined in cages on farms. A very considerable relative heart size in the smallest predators is closely connected with their small size and northern origin, which results in an intensive metabolism. In the large, sluggish, deliberate glutton the size of the heart is considerably larger than that in skunks (4.60 and 9.62). This is linked to its greater distribution in the north, as well as its extreme endurance. It may be noted from all the previous data that the relative dimensions of the heart depend on the load imposed on it, which is chiefly determined by the intensity of the metabolism and the manner of life. The connection with the geographical location and the body size is a derived effect determined by the intensity of metabolism. It should be noted that the relative dimensions of the heart in the forest marten (7.41-11.52) are considerably larger than those of its prey, the squirrel (5.0-5.90), which undoubtedly is of help to the marten when hunting. However, the examples of the squirrel and lynx (lynx--4.35, according to V. G. Geptner and L. G. Turova) demonstrate that brief muscular efforts cannot influence the relative dimensions of the heart. These animals are unable to perform intensive work with their heart muscle (Table XIV).

Table XIV

Relative weight of heart

Species and race	Number	Mean
Skunks (Bogolyubskii)	10	4.60
American mink (farm; Bogolyubskii)	15	6.38
Forest polecat (Krumbiegel)	-	6.37
Sable (farm; Bogolyubskii)	14	7.40
Caucasian forest marten (Bogolyubskii)	33	7.41
Forest marten (Central Europe; Krumbiegel)	-	7.66
Stone marten (Central Europe; Schuetze	15	7.50
European mink (Moscow Region)	7	9.52
Sable (nominal race of North Urals)	4	9.62
Glutton (Pechora)	8	9.62
Forest marten (Moscow Region)	7	9.83
Kidas (Pechora)	10	10.66
Ermine (Central Europe; Krumbiegel)	-	11.02
Forest marten (Pechora race)	63	11.52
Steppe polecat (Daurian steppes)	20	12.34
Ermine (Pechora)	5	13.54
Least weasel (Daurian steppe)	9	16.80

Changes in the relative weight of the liver are undoubtedly adaptive, being closely connected with the quantitative changes in the function of this organ and the reaction the organism to the change of the environment of the habitat, which is reflected in the diet, metabolism, and thermoregulation. We have already noted the high variability in the relative liver weight of the forest marten. In the Trans-Baikal steppe polecat it also fluctuates from 50.1-101.7, in the least weasel (Trans-Baikal) from 84.9 to 144, and so on. Despite this, the curve of the variability in forest martens of different races has a sharp peak, which permits us to consider the average values obtained from a series of weighings to be sufficiently reliable.

Table XV

Relative weights of internal organs

Species and race	Number	Liver	Kidney	Spleen
Forest polecat (Germany)	44	79.7	5.7	6.6
Steppe polecat (southeastern part of Trans-Baikal)	20	74.6	6.0	8.1
Ermine (Pechora)	5	58.5	6.0	-
Least weasel (Trans-Baikal)	9	57.6	7.6	14.6
Skunk	10	54.9	4.2	3.1
American mink	15	46.1	4.2	3.2
Forest marten (Caucasian race)	33	41.3	3.8	2.8
Glutton (Pechora)	8	39.6	4.6	-
Sable (farm, Bogolyubskii)	14	37.6	3.7	2.0
Stone marten (nominal race)	15	36.8	3.5	2.6
Forest marten (Pechora race)	63	33.8	4.2	-
Sable (nominal race)	4	33.4	4.0	-

The function of the liver has considerable significance in carbohydrate and fat metabolism. Its role in protein metabolism is not very important. It would thus seem that the heaviest liver should be found in omniverous predators, which is apparently confirmed by the figures for skunks (54.9) and the Caucasian race of forest martens, in which the liver is heavier than in the more carnivorous Pechora race (41.3 and 38.8). However, while in the purely carnivorous ermine and least weasel the large sizes of the liver (53.5 and 57.6) are connected with their small sizes and consequently their heightened metabolism, the maximum figures are demonstrated in the purely carnivorous species of larger sizes (the forest and steppe polecat). Unfortunately nothing is known of the relative intensity of the fat metabolism in all these species of predators. Thus, the only certainty is that interspecies and intraspecies differences in the average relative weights of the liver do exist.

There is no complete parallelism in the relative development of the kidney and liver. Nevertheless, the larger relative dimensions of the kidneys are observed in precisely those species with the heaviest (relatively) livers. This permits the assumption that the size of these organs is governed to a large degree by the intensity of the overall metabolism and, as a result, the type of constitution, as noted by S. N. Bogolyubskii (1941). The smallest predators (the least weasel) possess the relatively largest heart, liver, and kidneys (14.6). The kidneys of the northern forms of the north Ural sable and the Pechora forest marten are also larger than those of the southern Caucasian race. In martens and sables the spleen is moderately developed, but is considerably larger in both species of polecats, particularly in the least weasel, whose weight (14.6) is seven times heavier than that of sables raised on farms, relative of course to the ratio of the body weight of the respective species.

The general conclusion is that the degree of development of individual internal organs shows the same kind of environmental adaptation as is shown in other structural features. Intra- and interspecies variability is as characteristic of internal organs as it is of those diagnostic features firmly rooted in the systematics.

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* Translator's note – The spelling of this author's name varies in the Russian original (spelling such as Schulz and Schutze also occur but it seems that the same author is meant in all cases).

G. N. Likhachev

SOME ECOLOGICAL TRAITS OF THE BADGER OF THE TULA ABATIS* BROADLEAF FORESTS

(Nekotorye cherty ekologii barsuka v shirokolistvennom lesu tul'skikh zasek)

Oka-Terrace Preserve

Our observations were carried out in the center of the southwestern part of the forest massif of the Tula abatis (Krapivna and Odoeva Raions, Tula Oblast') in 1936-1939 and, to some extent, in subsequent years (1940-1950).

The Upa River crosses the territory studied, which is 7,300 hectares wide, and forms a rather broad valley. All other forest rivulets and brooks are very small with valleys which are not wide. The forest-covered area is characterized by clearly marked erosion surfaces. The trees of the Tula abatis are oak, linden, maple, elm, and ash. More than 80% of the territory in the region of our study is covered by forests which are between 20 and 120 years old, with individual regions of aged forests more than 200 years old. The forest areas younger than 20 years of age are small and hidden among older forest areas. The narrow strip of the Tula abatis is 2-6 km wide, surrounded on the north and south by agricultural land, and is the most important habitation area for badger in the entire region examined by us.

The badger of the Tula abatis only rarely leaves its den in November, mainly in the evening for a short time. Morning excursions are rare. At the end of November and beginning of December it enters into total hibernation. In cold winters a short warm period does not cause the badger to emerge from its den. In warm winters when some of the badgers apparently do not hibernate at all, they have been observed to emerge from their dens in January and February (Table I). The dates of the spring mass emergence of the badger from its burrow depend on the type of spring (Figure 1). In the majority of cases the badger leaves its burrow after several days of warmth. The average date of the spring emergence is 13-14 March, with ranges from 3-23 March.

We studied the nutrition of badgers (1936-1939) by analyzing their stomach contents and the food remains in their excrement (Table II). The latter were collected on the paths near the burrows occupied by the badger since in the Tula abatis the badgers do not dig "badger latrines".

The badger eats many different kinds of food (Table III). However, during the analysis of the contents of individual stomachs, it was possible to note that very often during a night the badger ate one or several kinds of food (Table IV).

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* Translator's note—An abatis is a clearing in a forest. It may also be an area among dense tree growth where trees are sparse. The Russian word is "zaseka".

Table I

Emergence of badger from burrow in winter

Year	Sum of median daily temperatures		Description of emergence
	December	January-February	
1942/43	251.5	680.2	Badger began hibernation and remained in burrow all winter
1943/44	97.6	284.3	Emergence of badger from burrow was noted throughout winter
1944/45	300.1	657.1	All three winters without emergence of badger observed
1945/46	303.2	475.6	
1946/47	260.0	696.0	
1947/48	89.8	524.7	Entire December without beginning hibernation; in this winter, without much snow, despite cold, some badgers emerged from burrows in January and February
1948/49	176.2	345.8	Badger began hibernation toward end of November, but single individuals also occasionally emerged in December
1949/50	129.8	729.6	Separate emergences of badger from burrows noted throughout December, later ceasing
1950/51	218.3	763.1	Badger began hibernation in November and did not emerge from burrow entire winter

Table II

Amount of material studied for badger nutrition

	Time of collection							
	May	June	July	Aug	Sep	Oct	Nov	Total
Excrement	10	30	53	20	12	1	0	126
Stomach	2	1	1	4	1	9	1	19

In a single stomach the presence of 81 voles, 152 earthworms, 362 bumblebee larvae, etc, indicate that the badger requires a large amount of food.

Among the mammals, the badger primarily exterminates the common and red vole; it hunts all the other species of rodents and also insectivores considerably more rarely, even incidentally (Table V).

In the Tula abatis it is a rare phenomenon for the badger to eat insectivores; apparently the hedgehog is the most frequent victim of the badger. In the stomach of a badger obtained on 18 August 1938, almost the whole carcass of a hedgehog

was discovered (four paws, head, much flesh, bones, and viscera), including the skin and five vertebrae. When eating a hedgehog, the badger concisely devours the entire underside of the small beast, leaving only the armor intact. We have found such completely cleaned-out spiny integuments of hedgehogs on numerous occasions near burrows occupied by badgers.

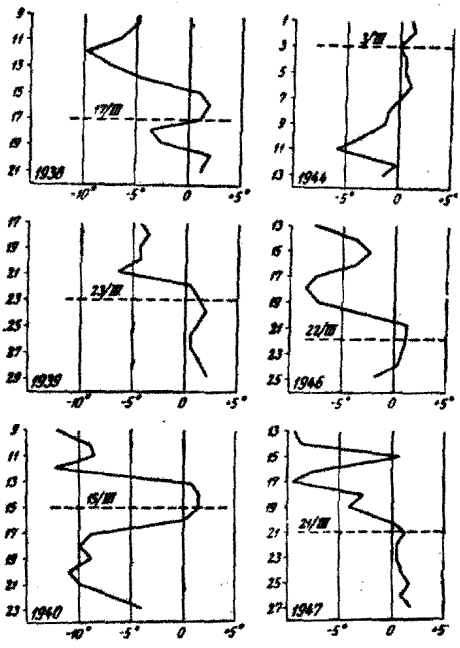

Figure 1. Dates of mass emergence of badger from burrows depending upon temperature conditions. (Curve indicates average daily temperatures in March)

Table III

Composition of the food of the badger in the Tula abatis

Amount of Material	Stomach		Excrement	
	19		126	
Food	Number of occurrences	% of occurrences	Number of occurrences	% of occurrences
Vertebrates	13	68.4	106	84.1
Mammals	6	31.6	89	70.6
Carrion (large animals)	—	—	1	0.8
Rodents	4	21.0	87	69.0
Insectivores	3	15.8	5	4.0
Birds	5	26.3	34	27.0
Reptiles	1	5.3	5	4.0
Amphibians	5	26.3	—	—
Fish	—	—	1	0.8
Invertebrates	18	94.7	121	96.0
Earthworms	12	63.1	—	—
Insects	12	63.1	121	96.0
Fruit	6	31.6	30	23.8

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Table IV

Analysis of contents of stomach of badger

Date of dissection / Food	31/V	20/VI	5/VIII	18/VIII	20/VIII	22/VIII	29/VIII	2/X	10/X
Voles	2*	–	–	–	–	–	81	–	–
Hedgehogs	–	–	–	1	–	–	–	–	–
Fledgling birds	2	–	–	1	–	–	–	–	–
Frogs	–	–	–	–	2	1	–	–	1
Toads	–	–	–	–	2	2	–	–	–
Earthworms	–	–	–	–	3	152	–	104	89
Beetles	–	–	–	22	10	2	1	–	3
Wasps	–	–	15	–	51	–	–	–	–
Wasp larvae	–	–	–	–	42	–	–	–	–
Bumblebees	–	–	10	–	–	–	–	–	–
Bumblebee larvae	–	–	362	many	–	–	–	–	–
Maybug larvae	97	–	–	–	–	–	–	–	–
Oak longicorn beetle larvae	–	146	–	–	–	–	–	–	–
Caterpillars	–	–	–	9	–	–	–	–	–

Table V

Mammal food of badger

Food	Stomach		Excrement	
	Number of occurrences	% of occurrences	Number of occurrences	% of occurrences
Mouse-like (undetermined species)	-	-	31	29.5
Common vole	83	86.4	35	33.4
Red vole	10	10.4	22	21.0
Water rat	-	-	1	1.0
Mice (unidentified species)	-	-	3	2.9
Yellow-necked mouse	-	-	2	1.5
Field mouse	-	-	1	1.0
House mouse	-	-	1	1.0
Russian hare	-	-	3	2.9
Squirrel	-	-	1	1.0
Hedgehog	1	1.1	1	1.0
Mole	1	1.1	-	-
Common shrew	1	1.1	4	3.8

The role of birds in the badger diet is not great. In the majority of cases the badger catches the nonflying fledglings, since in its excrement single bird feathers are encountered only in the spring and summer, chiefly in June at the peak of the nestling period (Table VI).

At the same time the shells of eggs were found in the excrement. The role of birds in the food of the badgers increases in years when the number of voles in its range is small.

Thus in the Tula abatis, when in 1938 there was an unusual number of red voles and a plentiful number of common voles, the remains of birds were found in only

* The figures indicate the number of specimens of individual species.

9% of the excrements but in 1939, when voles almost disappeared in summer, bird remains appeared in 67% of the excrements.

Table VI

Frequency of occurrences of bird remains in badger excrement during the summer months

	Months					
	May	June	July	August	September	October
Number of excrements including remains of birds	10	30	53	20	12	1
	3	16	11	4	0	0
% of occurrences	30.0	53.3	20.7	20.0	0	0

Badgers in the Tula abatis rarely eat reptiles--lizards and snakes. We cannot confirm the prevalent opinion that the badger eats snakes "with especial avidity" and is immune to their venom. Amphibians (toads and frogs) are among the important spring foods of badgers. Their remains are, as a rule, absent from the excrement but are found in the stomach. In three stomachs (August to September) five common toads were found, and in four (August-November) six grass frogs were discovered. As we had no badger stomachs at our disposal, for April, we had no opportunity to demonstrate the character of the amphibian food of the badger during the early spring However, just at this time, when the number of voles are still low and when fledgling birds are absent from the region, the eating of amphibians should be maximal.

In analyzing the excrement composition, the amount of earthworms which the badger eats was not determined. However, to judge from finds in the stomach, the worm is one of the badger's chief foods for the entire second half of the summer (Table VII), especially during wet, rainy years.

Table VII

Number of earthworms found in badger stomachs

Date	Number of worms in stomach	Date	Number of worms in stomach	Date	Number of worms in stomach
20/VIII 1937	3	10/X 1938	89	19/X 1938	52
22/VIII 1937	152	11/X 1938	35	20/X 1936	10
28/IX 1937	63	13/X 1938	37	20/X 1936	4
2/X 1937	104	16/X 1936	30	5/XI 1938	20

The typical food of the badger is the various species of insects which it eats each year during the entire summer. The species composition of insects eaten is diverse (Table VIII).

The species composition of the food is subject to annual and seasonal variability (Table IX). In analyzing the excrement of the badger, only the remains of adult insects were discovered while, in examining the stomach, a large number of larvae were found. Apparently, it is most typical for the badger to exterminate just the larvae and not adult insects, which are not so easy to obtain in large numbers. We found insects (63.1%) in 12 out of the 19 stomachs examined, predominantly single specimens of beetles; in species composition they were similar to those in the excrement, while in stomachs examined from 31 May, 97 larvae of the maybug and on 20 June, 146 larvae of the longicorn beetle (Cerambyx cerdo) were found.

Table VIII

Insect nutrition of badger (analysis of excrement)

Species of insects	Number of occurrences	% of occurrences
Beetles, without further identification	9	3.77
Dung beetles, Geotrupes stercorarius	46	19.25
Dung beetles, Copris lunaris	15	6.28
Dung beetles, Onthophagus sp.	1	0.42
Cockchafer, Melolontha hippocastnis	10	4.18
Cockchafer, Amphimellon solstitialis	24	10.00
Chafer, Oryctes nasicornis	5	2.09
Rose chafer, Cetonia aurata	1	0.42
Chafer, Cetonia sp.	1	0.42
Ground beetle, without further identification	13	5.44
Ground beetle, Carabus granulatus	14	5.86
Ground beetle, Carabus coriaceus	23	9.62
Ground beetle, C. concellatus	7	2.93
Carab beetle, Calosoma inquisitor	7	2.93
Beetle, Harpadus [Harpalus] ruficornis	1	0.42
Beetle, Pterostictus sp.	14	5.86
Beetle, Platysma [Platysoma] nigrum	1	0.42
Carrion beetle, Silpha carinata	1	0.42
Carrion beetle, S. obscura	1	0.42
Carrion beetle, Hylodrepa quadripunctata	1	0.42
Carrion beetle, Oxceoptoma thoracica	1	0.42
Sawyer, Pirionus coriaceus	33	13.81
Capricorn beetle, Phaquium inquisitor	2	0.83
Weevil, Phillobius sp.	1	0.42
Seven-spot ladybird, Coccinella septempunctata	1	0.42
Grasshopper, Decticus verrucivorus	1	0.42
Mole cricket, Gryllotalpa vulgaris	1	0.42
Caterpillars, without further identification	3	1.26
Pupae of butterflies	1	0.42

Table IX

Occurrences of beetles in food of badgers in various years (Analysis of contents of excrements)

Year	1936		1937		1938		1940	
Name of beetle	No. of occurrences	% of occurrences	No. of occurrences	% of occurrences	No. of occurrences	% of occurrences	No. of occurrences	% of occurrences
Geotrupes stercorarius	26	60.5	7	35.0	6	8.0	7	41.1
Pirionus coriaceus	5	11.6	3	15.0	23	30.6	2	11.8
Amphimellon solstitialis	4	9.3	3	15.0	15	20.0	2	11.8
Carabus coriaceus	4	9.3	5	25.0	14	18.7	0	—
Corpis lunaris	0	—	2	10.0	8	10.7	5	29.4
Carabus granulatus	4	9.3	0	—	9	12.0	1	5.9

The larvae of bumblebees and wasps have a seasonal character in the nutrition of badgers and are eaten during the second half of the summer. Very often along badger paths, especially in young forests, very deep wasp and bumblebee burrows, similar to funnels, are found. Judging from the number of such excavations, these types of food are very common at the end of summer. In examining the contents of the stomach of an animal obtained on 20 August we found 51 adult wasps and 42 larvae (Vespa vulgaris). In the stomach of an animal obtained on 8 August, in addition to other food, there were several bumblebee honeycomb pieces of not less than 50 cells (Bombus terrestis). Especially interesting was the discovery in 362 honeycomb

cells in the stomach of a badger obtained on 5 July. The cells contained young bees ready to fly out and a certain number of adult Bombus, as well as 15 wasps.

Vegetable food plays a very considerable role in the badger's diet only during the second half of summer, near autumn, when the berries, fruits, acorns, and cereal crops become ripe. Of the fruits discovered in 30 or 23.3% of the excrements (July-November), the following were found: acorns, apples, pears, shadbush fruit, strawberries, and roseberries; of the cereals, wheat, rye, and barley were found. In dissecting stomachs vegetable remains were found six times (3.6% of all stomachs) but each time in very small amounts.

The data presented on the nutrition of the badger in the Tula abatis show that it possesses an extremely large choice of foods. It is able to change easily from one kind of food to another regardless of the time of year (seasonal changes); when any object of food disappears from its range, it immediately replaces it with another food of equal value. The food regimes of the badger in various regions of its range (the Crimea, Volga-Kama Krai, Buzuluk Forest) have much in common, but in each region they are specific, depending on the presence in the range of one or another kind of food substance. The omniverousness of the badger is a characteristic trait of its feeding habits.

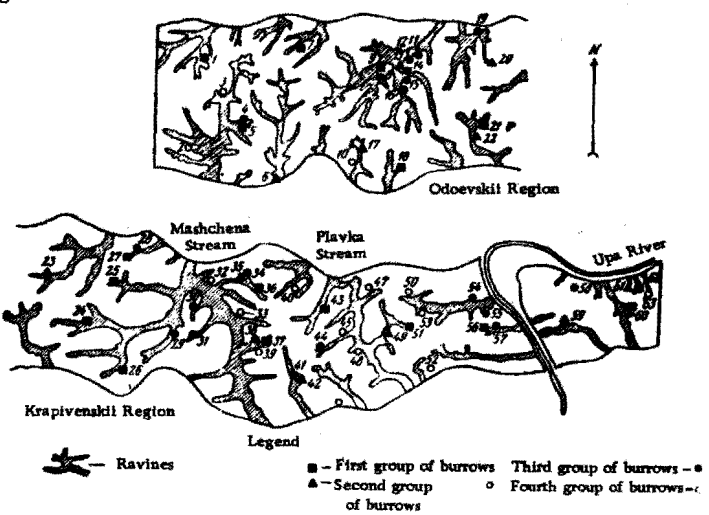

Figure 2. Schematic plan of counting area (Odoevo and Krapivna areas of the Tula abatis).

Within the limits of the part of the Tula abatis investigated by the author, 63 burrows were found during the period of our work, only five of them being new. We divided all of the burrows into four groups (Figure 2):

Burrows in which a family and litter of badgers were discovered, 17 (27.0%);

Burrows which were systematically frequented and kept in state of repair by the badger, 11 (17.5%); (Burrows only rarely frequnted and slightly dug up by badgers, 21- 33.7%);

Burrows never occupied by badgers or only visited by them one or two times during the period of observation (1935–1952), 14 (22.2%). To describe the structure of the burrows, three burrows of the second group and one of the fourth group were completely excavated. Burrow No 61 was located on the tongue of land formed by the

confluence of two small ravines, which then became one large ravine. The grade of the land on the shore of this "cape" fluctuated between 45° and 60°. The area occupied by the burrows was 53.5 sq. meters, and the total length of all passages amounted to 39 meters. They had two exits and three living chambers–"caldrons". The depth of the dens below ground (to the ceiling of the "caldron") was 1.3 m for the first and second "caldrons" and 1.85 m for the third. The interden passages lay at a depth of 1.3–1.5 m. The entire burrow thus lay in almost a single plane. Differences in the depth of individual lairs did not exceed 20 cm. The dimensions of the first "caldron" were 65 × 80 cm, with a height of 32 cm; 85 × 70 × 37 were the dimensions of the second, and 75 × 87 × 31 cm for the third. The distance from the entrance hole to the "caldrons" (in a straight line) was 5.5 m to No 1, 1.6 m to No 2, and 8 m to No 3. The width of the passages was from 25 to 64 cm, with a height of 20-29 cm; on the average, the dimensions were 33 × 25. The total volume of the burrow and thus the earth removed therefrom was approximately 9.5 cubic meters.

The soil subsoil profile near the first den gave the following data: A_1: 0-10 cm. Light gray fresh loam. A_2: 10-30 cm. Brownish-gray loam. B_1: 30-85 cm. Sepia-brown, thick loam. B_2: 85-130 cm. Yellow-sepia-brown, uniform, heavy fresh loam. The last two layers were not highly permeable to water. C: 130 cm and lower. The parent material was sand of a yellow color.

All passages and "caldrons" were dug by the badger in the upper layer of the sand immediately under horizon B_2. The arches in the burrow were formed by solid and waterproof layers of loams, the floor being pure sand. The entrances into the burrow were made at points where the sand on the banks of the ravine was only slightly covered with loam, expecially the main entrance No 2.

Burrow No 20 was arranged in the upper reaches of the "cape" formed where a small ravine entered the main ravine. This burrow had four entrances. The grade of the slope of the cape near entrance No 1 was in excess of 50°. At entrance No 2 it decreased to 30°. The total length of the passages of the burrow was 35 m, and the surface area occupied thereby was 45.5 sq. meters. There were no living chambers ("caldrons") in the burrow. The depth of the burrow passages fluctuated between 1 and 1.65 m. The widest point of the burrow lay at bifurcation No 1, its size being 73 × 68 cm and 54 cm in height. The width of the passages varied from 23 to 63, the height from 15-32, averaging 35 × 20 cm. The total volume of the burrow was 8.3 m^3.

At entry No 4, situated higher than the others, at the point where the bank of the ravine almost merged with the slope, the burrow descended precipitously, and at a distance of 1.5 m from the entrance was already more than 1 m deep. At a distance of 3.5 m from the entrance, at a depth of 1.4 m, bifurcation No 1 was located, lying below an old stump. At a distance of approximately 2 m from entrance No 4, the first soil measurement was taken, giving the following figures: A_1: 0-10 cm. Light gray, rather dry, dusty loam of an indefinite powdery structure. A_2: 10-50cm. White-gray, dusty crumbly loam. B_1: 50-110 cm. Yellow-sepia-brown fresh loam, rather dense. B_2: 110-140 cm. Yellow-sepia-brown fresh loam, dense, fused together, gradually merging into the subsequent horizon. C: 140-190 cm. Yellow-sepia-brown dusty fresh loam, dense, of average cohesion. The soil cross section No 1 describes the soil-subsoil conditions of the entire central part of the burrow, including bifurcation No 1. At this point the passages of the burrow lie at a depth of between 1-1.4 m, i. e., in the yellow-sepia-brown loam of the lower layers of horizons B_1, B_2, and partially in the upper part of horizon C.

The second soil section was made in the western part of the burrow, where the soil conditions differed:

A_1:0-15 cm. Gray dusty, fresh loam with indefinite powdery structure, somewhat sodded.

A_2: 15-30 cm. Light gray, dusty, fresh loam, rather friable and porous.

B_1:30-100 cm. Sepia-brown, fresh loam, with indefinite powdery structure, compacted.

B_2:100-125 cm. Yellow-sepia-brown, compact, fresh loam, which merges clearly with following horizon.

C: 125-200 cm. Soil of alluvial origin, forming a bed, complex in character and with alternation of layers of loam, sand, gray clay, etc. Below is a sand layer at a depth of 2 meters, turning into a light loam. At this point the passages of the burrow lay at a depth of 1.25-1.45 m, in the type of layered soil as in horizon C. However, despite the presence of sand, which is convenient for digging, a living chamber was absent.

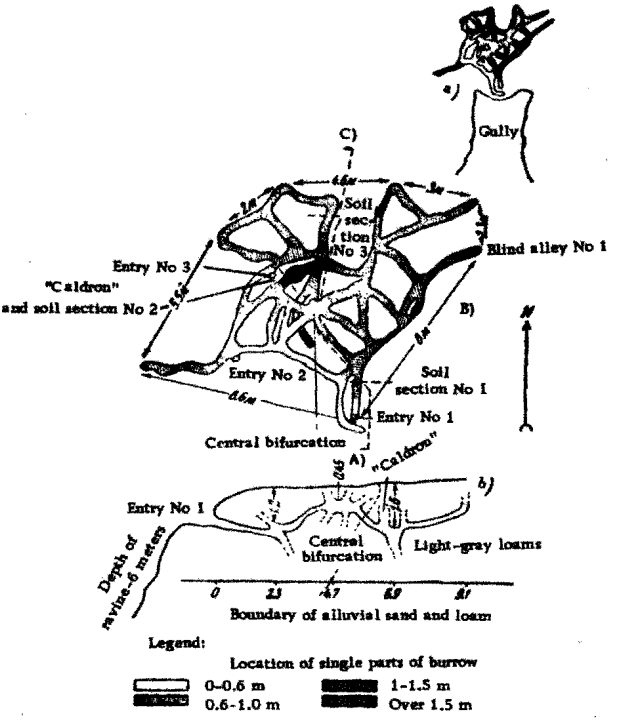

Figure 3. Plan and section of Burrow No 59
a— location of burrow in ravine; b—plan of burrow; c—section of burrow along line AB.

The soil at the northern part of the burrow was characterized by soil section No 3.

A_1:0-25 cm. Light gray, rather dry loam with a very small amount of humus and almost complete absence of soils.

A_2: 25-50 cm. Yellow-sepia-brown, rather dry sandy loam, somewhat porous, with a small amount of roots of trees, passing sharply into the subsequent horizon.

B_1: 50-85 cm. Brownish light-gray fresh loam, rather dry, of average density.

B_2: 85-115 cm. Yellow, rather loose, porous fresh sand with single roots of woody vegetation.

B_3: 115-170 cm. Light gray, rather dense, fresh loam.

C: 170-220 cm. Yellow, loose porous fresh sand. Here the passages of the burrow lay at a depth of 1.4-1.65 m in the lower part of horizon B_3, loam; the sand of horizon C formed a bed at the bottom of the burrow.

In addition to the burrow just described, we discovered above it, at a depth of 20-30 cm, a second burrow, only one branch descended deeper in the direction of bifurcation No 1 but did not connect with it. This was a very narrow and not deep burrow with one entry terminating in a "caldron" in the roots of a stump lying above bifurcation No 1 of the main burrow. The size of the "caldron" was 55 × 40 × 35 cm, the total length being 7.7 m.

Burrow No 59, in contrast to the first two, was not dug on the tongue of land but on the southern bank of the ravine in the upper reaches of a small gully (Figure 3a), the steepness of the bank being approximately 50°. The burrow possessed three entrances, from which abundant sand and loam had been excavated. The overall length of the burrow was 81 meters, the surface area 87.4 sq. m. This was the largest of all the burrows opened by us. Nevertheless, only one "caldron" was in it (Figures 3b and 3c). The depth of the passages of the burrow varied, ranging between 0.4 to 1.65 m. The width of the passages changed from 22 to 63 cm, the height from 14 to 32 cm, and, on the average, its dimensions were 35×20 cm. The dimensions of the living chamber were 73 × 68 × 54 cm, the distance from the entrance to the 'caldron' was 6.5 m, and the total volume of the burrow was 19.2 m^3.

The structure of the burrow was highly complicated. From entrance No 1, lying almost at the edge of the ravine, the burrow descended steeply, and already at a distance of 2 meters from the entry, at a depth of 1.2 meters, fork No 1 was encountered from which four passages emerged. The soil at this point happened to be alluvial (Soil section No 1):

A_1: 0-10 cm. Light yellow, fresh, rather loose loam.

A_2: 10-25 cm. Grayish-yellow, loose, slightly humus loam.

B. 25-75 cm. Yellow, rather loose, fresh loam, with light strata.

C. 75-140 cm. Light yellow, fresh, loose sand, with layers of light loam. In this region of the burrow, the passages were 1.0-1.3 m, i.e., in horizon C.

A part of the burrow extended from bifurcation No 1 toward the northeast and another to the northwest, and a third passage extended almost parallel to the entrance passage to the south, terminating in blind alley No 1. The northwestern part of the burrow extended through the sand or the loam situated above it (Section No 1). This part of the burrow was characterized by very slight depth, from 0.45 (the central bifurcation) to one meter, and a great number of passages sometimes rather wide (36 × 22), sometimes sharply narrowing (26 × 61). From the central bifurcation, lying completely in the sand (the dimensions of the bifurcations were

42 × 32), passages extended in different directions and steeply downward. The passage which pointed northward was less deep and had an extension to the south, which passed almost above the bifurcation and terminated in a blind alley No 2, at a depth of 1.65 m. This was the only place in the burrow where two stories were present.

The passage which pointed northward became deep quickly and rapidly reached a depth exceeding 1.5 m. Where it turned westward, a living chamber of the burrow was discovered under the roots of the trees (Figure 3b). The soil section lying near the "caldron" presented the following picture:

A_0: 0-20 cm. Sepia-brownish-yellow with gray tones, light, dusty, fresh loam of an alluvial nature.

A_1: 20-30 cm. A deep brownish gray, fresh, rather loose loam.

A_2: 35-55 cm. Brownish, fresh, rather loose loam with roots of trees; gradually changing into an alluvial horizon.

B_1: 55-90 cm. Sepia-brown, dense, fresh loam, with large amount of tree roots.

B_2: 90-155 cm. Light brown, very compact, rather dry alluvial loam, riddled with the roots of trees and cemented together (difficult to dig), turning below into a lighter looser loam.

C_1: 155-185 cm. Light, fresh, dusty yellow loam, changing at a depth of 185 cm into a uniform minute light yellow sand.

C_2: 185-210 cm. Sand the main type of soil, the "caldron" at a depth of 1.6 m, in the lower part of horizon C_1 and in the upper part of C_2. The ceiling of the "caldron" was a compact water-impermeable layer of soil, and sand constituted the bedding.

The northern and northeastern parts of the burrow, which were quite long, were distinguished by a relative linearity in their passages, passing from a depth of 0.65 to 1.3 m, and only near blind alley No 3 was a depth of 1.65 m encountered. The dimensions of the passages were almost equal everywhere, averaging 31 × 17 cm. The soil conditions of these parts of the burrow were uniform. Soil section No 3 was as follows:

A_1: 0-10 cm. A gray rather loose fresh loam, slightly humus.

A_2: 10-30 cm. Brownish-gray, rather loose fresh loam.

B: 30-100 cm. Sepia-brown, compact loam, somewhat drier than the overlying horizon. The site of the soil section, the passage of the burrow was at a depth of 0.9 meters in the lower part of horizon B. The other passages also extended under approximately the same conditions. We did not discover sand even in blind alley No 3 at a depth of over 2 meters.

Summing up all the data on the three burrows of the second group excavated, the following may be noted. The badger made the living quarters of the burrow, the "caldron", at a depth of 1.3-1.6, on an average of 1.4 m from the surface of the earth, at the junction of the compact water-impermeable (alluvial) layer of soil (loam) with the predominant type (sand). In passages dug entirely in loam, the badger did not build living quarters. The "caldrons" lay (along a straight line) at a distance of 5-8 m, averaging 6.5 m, from the entrance holes into the burrow. The average dimensions of the "caldron" were 74.5 × 76.2 × 38.5 cm.

The dryness of the living chamber or "caldron" is the chief requirement of the badger. The presence of a layer of more than a meter of a water-impermeable soil, forming the ceiling of the "caldron", guaranteed it against ground water penetration. However, some penetration of water through the alluvial layer of soil covering the living quarters is not dangerous to the badger, since on entering the sand which forms the bed of the "caldron", this moisture passes through its rapidly. Thus, the water-impermeable layer of soil above the living chamber and thorough drainage by the sand which formed the bed of the "caldron" insured the constant dryness of the badger dens in the field of our observations. Because of the long and complex system of passages separating the den from the entrance, the "caldron" could not be flooded by water through the entrance aperture.

The temperature conditions of the burrow are also important for the badger. A relatively constant temperature is provided by the depth of the living quarters (over one meter from the surface of the earth) and their distance from the entrance apertures, while the sand which beds the "caldron" with a lower thermoconductivity than loam, creates a favorable temperature for the badger during its winter hibernation.

The badger can only survive its hibernation in the burrow if the freezing of the soil does not reach the "caldron". The dens in excavated burrows lie at a depth of 1.3-1.6 m from the surface of the earth. Usually the freezing of the earth in the abatis forest does not exceed 10-30 cm. The maximum freezing (only 16 years of observations) was noted during the winter of 1938/39, when it reached 102 cm in the open reaches of the forest. However, this extraordinarily intense freezing was not dangerous for the badger, which hibernates at a depth greater than one meter.

The strength of the burrow, which is so necessary for a den used by badgers for many years, was assured in all the burrows excavated by the presence above the "caldron" of a thick, hard, waterproof layer highly unlikely to collapse.

In burrows excavated by us, the most favorable conditions of habitation for badgers were found in Burrow No 61. This was almost entirely situated on one level in typical local sand with a hard water-impermeable layer of soil a meter thick lying above it. Owing to such a successful combination of soil and ground conditions, three "caldrons" were created by the badger in this relatively small burrow.

The soil conditions of Burrow No 20 differed. It occupied a cave consisting of an alluvial stratified type of loam mixed with sand. In the southwestern part of the burrow, the badger found the sand it needed, but it was mixed with loam and no "caldron" was established here. Advancing, it encountered different soil conditions. In blind alley No 1, sand lay at a depth of 1.7 meters as bedding material. However, it was not covered by a layer of water-impermeable soil (Soil section No 3). At this point, the badger waited to make a "caldron" (spurs of the blind alley) but apparently it abandoned this attempt.

The soil conditions of Burrow No 59 were rather interesting. The edge of the ravine was formed by an alluvial form of loam (Section No 1) mixed with sand; in this part of the burrow, the badger, searching for a place to build its den, created a series of shallow passages, but the upper compact clayey layer was abandoned here. After a cluster of passages, they seemd to separate into two portions: in the northwestern portion the badger found adequate conditions for a den in a small area at a depth of 1.6 meters. Here the "caldron" lay within the limits of the fresh light loam; over it a solid layer of soil (Horizon B_1 and B_2) and sand served as a bedding (Section No 2). However, the layer impermeable to water lying over the "caldron" was heavily pierced by roots of woody vegetation, which enabled the water to

percolate through to horizon C where the den lay. We may conclude from this that the site of the 'caldron' in this burrow was not completely favorable, since water could enter. In search of better living conditions, the badger continued to burrow further and excavated some dozens of meters more, but not finding appropriate conditions (Section No 3), even at a depth of 2 meters; (Blind alley No 3), where sand was also lacking it did not make a den and all this portion of the burrow, despite its size, turned out to be useless. The described soil-ground conditions of the burrows excavated by us were apparently characteristic of the majority of burrows lying in the Tula abatis, but here different conditions were also possible.

Litters of badgers were often encountered in Burrow No 7. An extremely large amount of clean sand was thrown out of this burrow. In the autumn of 1949, a part of the burrow collapsed and its passages were laid open. This proved that the whole tongue of land in which the burrow lay consisted of compacted sand. The alluvial layer of soil was absent here, which had caused the collapse. The passages of the burrow from the surface of the earth itself were laid down in pure sand, at times reaching depths of over 3,5 meters. However, at this depth we also failed to find signs of a "caldron". The passages descended deeper and the den was situated even lower, at a depth of over 4 meters. We did not succeed in making a complete excavation of this burrow.

Besides these large burrows inhabited by the badger, we also had the opportunity to open another burrow of the fourth groups (Burrow No 47), It was constructed on a cape in a small ravine and possessed a single exit situated in the roots of an old oak. Only one passage, approximately 4 meters long, lay in the burrow, which terminated in a spacious den (diameter approximately 75 cm). The depth of the den was only 50 cm below the surface. The entire burrow and "caldron" were dug out in loam, sand being completely absent. Above the "caldron" there was almost no solid layer of earth, and this was riddled with the roots of trees. Of course the badger was unable to hibernate in such a burrow. Even in summer the "caldron" proved to be damp. In this burrow we once found a fox litter, and the next year a wolf litter. The badger did not frequent this burrow every year, and came only during the second half of summer. In all probability this burrow was built by a fox.

In constructing its burrow the badger penetrates deep into the earth, and the question of air supply for the burrow arises. Are there special ventilating shafts? We did not find any on digging into the burrow. The air entered the tunnel through the main entrance, and through chance fissures in shallow portions of the tunnels formed by the collapsing of the ground, through crevices of the earth, and so on. We doubt that there are any special ventilation shafts made by the animal itself, at any rate near the den, since not only would air thereby enter the burrow, but also cold and, especially, water. Furthermore, it would be very difficult for the badger to make such apertures in the depths of the tunnels where they are particularly needed. To do it so it would have to dig through a meter layer of solid earth, their arrangement near the entrance would be without significance, since there is plenty of air there anyway. In most of the burrows there are several entrances through which air penetrates into the passages. However, the fact that the badger does not use several entrances during a given year does not permit us to regard them to any degree as special ventilation shafts.

Do badger burrows consist of many levels? Taking into consideration the soil conditions in which the badger constantly makes its burrows, we are inclined to think that the portion of the burrows are not as a rule of many levels. Passages on several levels are encountered (Burrow No 59) but as an exception, over short distances, and not in those places where the "caldron" is built.

It has been noted that the badger makes the entry apertures under stones or under the roots of trees, in order to protect itself from the collapse of the roofs of the entries,

i.e., it strives to exploit all natural vaultings in order to reinforce the entrance into the burrow. In the Tula abatis the great majority of badger burrow entrances were dug directly into the earth. Only individual burrows, and only some of their entrances were dug under the roots of trees (7 burrows) or under slabs of sandstone (2 burrows). One of the characteristics of a burrow which has been inhabited for a long time is the number of entries. Thus, in 56.2 % of the burrows in the first group, there were four or more entries. The same percentage also existed in burrows of the second category (45.5 %), of the third (23.3), and the fourth (14.2).

We find the most interesting data concerning the type and depth of badger burrows in the Moscow Oblast' in the work of A. M. Kolosov (1935). It is true that this author did not fully excavate the burrows, but for the determination of the soil and subsoil conditions he used pits dug by hunters for the rooting out of the badger from its burrow. Such casual excavations also at times hit on a "caldron" and on the passages of the burrows, and as a result it is difficult to judge the positioning of the den in the burrow. However, the description of the badger burrows made by A. M. Kolosov was much in common with the burrows excavated in the Tula abatis.

Quite different conditions for the disposition of badger burrows are described by N. A. Skorodumov (1930), without, however, indicating the region of his observations. He writes: "The burrows themselves are usually deep, since the badger constructs them under a thick layer of sand in a harder stratum of clay or another subsoil. The proximity of subsoil waters does not allow the badger to penetrate deeper, and thus the burrows are smaller in damp areas. We may say as a rule that the denser and harder the ground and the higher the level of subsoil waters the smaller the burrows, and vice versa. The burrows are deeper in places with light subsoil and deep subsoil water." From these words of N. A. Skorodumov, it follows that the soil water apparently pushes the burrows of the badger nearer to the surface of the earth, but we have observed the contrary. When constructing the burrow, the badger penetrated into the sand under a solid layer impermeable to water, striving to construct the burrow so that the underground (ground) waters pass above the burrow and not under it. Over a large range of badger distribution, depending on the soil-subsoil conditions and the climate, the arrangement and distribution of the burrow may in all probability be rather variegated, but the correctness of the description of the burrows presented by N. A. Skorodumov raises doubts.

In order to construct a permanently inhabited burrow, it is necessary for the badger to have a combination of a water-impermeable layer of soil one meter thick, and sand as a bedding under this layer. In which places and under which concrete circumstances of the Tula abatis can the badger encounter such soil and ground conditions?

The overall territory investigated by us may be divided into the following parts: the western region (Odoevo raion), which lies along the water divided between the Upa River and its tributary, the Bol'shaya Kolodnya River, and is the highest portion of the territory studied, with a maximum elevation of 270.3 m above sea level; the Mashchena forest river basin, and still further east of the Plavka stream and the right bank of the Upa River where an uninterrupted descent of water-dividing elevations extend from west to east, as well as the entire locality toward the Upa River (from 270 to 135 meters); the last portion in the left bank of the Upa, within the limits of the so-called Suprutskaya Bow, the maximal height of this region being only 180 m.

The distribution of burrows at various levels above sea level gives a varied picture. Under the actual conditions of the territory studied, depending on the height of the area, sand deposits hidden by covering loams are encountered within the limits of hypsometric readings from 150 to 235 meters. In the great majority of cases the burrows occupied heights the boundaries of which coincide with the boundaries of

the upper horizons of sand in nature. Exceptions to this rule in the burrows of the first two groups are rare, but are often noted in the burrows of the last two 4 groups which are less suitable for the badger. Thus, the majority of badger burrows in the Tula abatis are situated in the moderately high elevations of the region. The badger did not dig burrows in the highest and lowest parts of the territory.

In the highest spots of the territory (areas lying near the water-dividing stretches) the sand required by the badger is covered by a layer of many meters of compact loam which it cannot penetrate because a poorly developed ravine (hydrographic) net is present. Somewhat lower, where more developed ravine networks intersect the covering loams, the badger can dig into the sand by making use of the banks. This is the chief reason that under the conditions of the regions of our study 95.3 % of all burrows were formed in ravines. It should be noted that of the three burrows constructed outside the ravines, one was situated in the frontier branch and two in moats of old earth fortresses (Table X).

Table X

Distribution of burrows in the limits of ravine area

Group of burrows	Upper reaches of ravine		Middle parts		Lower reaches		Outside ravine	
	Number	%	Number	%	Number	%	Number	%
I	13	76.5	4	23.5	0	-	0	-
II	7	63.6	1	9.1	3	27.3	0	-
III	8	38.1	7	33.3	4	19.0	2	9.6
IV	4	23.5	7	50.0	2	14.3	1	7.2

At the sources of ravines (in the hollows) we found no badger burrows. Here the sand along the gently sloping banks is covered by an over-thick layer of surface loams. Nor are there many burrows in the lower reaches of the ravine network (dry watercourse) and valleys. The basic material (sand) here is on the contrary, too close to the surface and the water impermeable layer of loams so necessary to overlay the burrow are almost absent along the steep banks except for their very uppermost portion. The upper stretches of ravines and, to a certain degree, the middle parts are the most suitable places for the construction of badger burrows. These points of land occupy medium or higher-than-medium elevations in the region, i.e., those traversed by the upper horizons of sand deposits. By burrowing here, the badger easily reaches the sand only slightly covered with alluvial soil, along the shore, above which a thick water-impermeable layer of solid loams is situated within the limits of the slope. As a result we discovered 80.9 % of all burrows and 100 % of the burrows of the first group along the banks of the upper reaches, or more rarely in the middle stretches of the ravines (Table X).

The pressure of ground water increases in proportion to the advance down the ravine to the river. The small amount of ground water in the upper reaches of the ravine as compared to the lower portions is one of the reasons the badger utilizes precisely these parts of the terrain for its den. In the upper reaches of the ravines, the badger usually constructs its burrows on the sharp capes which are formed through the confluence of two originally small ravines or the blunter capes formed by a ravine entering at right angles. At such points, the drainage capacities of the small ravines forming the capes are so great that subsoil waters are almost absent here, except for the temporary perched waters.

In the Tula abatis the majority of burrows were encountered on water-divided slopes with sunny exposures and on steep insolated banks in the upper reaches of ravines (74% of the first and second and 49% of the third and fourth groups of burrows).

The badger prefers banks bathed in sunlight. This is explained by the fact that such sites are warmer, dry more rapidly, have quicker snow thaws in spring, and have shorter and less intense morning frosts in the autumn, all of which permits the badgers to emerge from their burrows earlier in the spring and begin hibernation later in the fall. However, in the Tula abitis, where the ravine (hydrographic) net is the result of ancient glacial erosion (A. S. Kozmenko, 1938), the native soil (sand) lies bare on the steep isolated banks of the valleys or is covered by a small layer of quaternary deposits. Only in such places is the sand accessible to the badger on the gently sloping sunny banks, the layer of covering loams is so deep that digging through it is a difficult task for the badger. Thus, the fact that in the locality studied by us the badger constructed better burrows on the insolated sunny shores of the ravines can be explained by two factors: the climate and the nature of the soil structures.

If we divide the bank of the ravine into upper and lower portions, it becomes clear that the entrances in the majority of burrows (85 %) were of the first two groups situated in the upper part of the bank, while those of the burrows of the last two groups were distributed rather evenly along the entire shore. The contact between sand and a water-impermeable layer of soil which is so necessary for the construction of a permanent burrow is always found in the upper stretches of the bank. When digging in the low stretches of the ravine bank, the badger would have to dig through a great layer of sand before reaching a sound roof for the burrow; for this reason the entrances into inhabited burrows were found in the upper portions of the ravine's banks.

The badger very rarely digs burrows in sliding soil, which occur in abundance along the banks of all ravines. Here, despite the profusion of sand, the badger does not construct burrows, owing to their possible collapse, due of course to the presence of a large number of irruptions of ground waters.

Usually the connection between a burrow and the nearest brook is emphasized when describing the sites where burrows are located. Such a connection is of no importance. The badger is a mobile animal, and roams many kilometers from its burrow for food; thus it is not necessary for water to be located near the burrow. Usually the presence of a stream not far from the burrow is explained by the fact that the animal is compelled to construct its burrow in ravines because of the prevailing soil conditions and here, streams flow in any case in the spring and autumn.

The great attachment of the badger to a once inhabited burrow is widely known. (A. N. Formozov, 1947), emphasizes that this animal stubbornly clings to places it once selected. In confirmation of this we may note that after the opening or, in fact, the complete destruction of Burrow No 61, which was of great benefit to the badger by virtue of its position, it returned there, lived two summers in the excavated burrow, and then built a new burrow directly adjacent to it. This attachment of the badger to its old burrow is caused by the fact that there are not very many places in nature where permanently habitable burrows can be made. If the badger finds the necessary conditions for a burrow it leaves such a site only after extreme and prolonged harassment, and always strives to return to its old excavations.

The life of the badger is linked with the forest to a marked degree. However, we were unsuccessful in finding any definite relationship between the character or even type of forest and the distribution of burrows throughout the area. A. M. Kolosov (1935) correctly indicates that such a relationship would be only "secondary" when an appropriate terrain is present, badger burrows may be found in the most varied forms of forest. The opinion to the effect that the food qualities of the region influence the distribution of the badger in the forest is rather groundless. The badger is omnivorous and undertakes considerable expeditions in search of food, sometimes emerging beyond the forest limits.

In a censused tract, 18.8% of the burrows of the first group, i. e. those most important for the badger, were in forests younger than 20 years of age. They were undoubtedly dug by the badgers long before the forest was lumbered. We have observed that uninterrupted heavy felling over a considerable area for many years compels the badger to abandon these areas temporarily. At the same time, the act of abandonment was a consequence of the systematic molestation of the badger in its burrows by persons conducting lumbering operations. However, the changes in living conditions as a consequence of all-out lumbering operations constitute a factor which does not so much have an effect on the departure of the badger as on the time of its return to its old haunts. Usually badger burrows in forests less than 10 years old are empty and have an appearance of disrepair. However, toward the end of this time, the badger occasionally begins to re-enter such burrows, and its litters have already been found in burrows in young 12-year-old forests. Short-term felling which does not greatly affect living conditions does not intimidate the badger. According to our observations it may only cause a brief absence for a maximum of one year.

The report that the badger inhabits the most remote and solitary regions of the forest is incorrect. We noted that one burrow systematically occupied by the animal was situated at a distance of only five meters from a well frequented daily by humans. In the badger, as in any animal, "fear and caution develop in direct proportion to persecution" (S. I. Ognev, 1931). In burrowing the badger always strives to dig a fully habitable burrow, but sometimes, not finding suitable conditions, it is compelled to halt a project once begun. Apparently not all animals build new burrows, but only repair and widen existing and inhabited burrows. Very frequently fresh burrows are dug by young individuals not far from old badger "settlements". Burrows started by young badgers are often not completely finished before they are abandoned, or sometimes they are refrequented by the animal in the summer. Some burrows of the third group should be classified as this type. However, it is possible that some of these "summer burrows", occasionally frequented by the badger were begun and built not by badgers but by foxes.

In characterizing burrows we selected 14 burrows of the fourth group, which badgers either did not enter or were only occasionally frequented over the sixteen-year period of our observations. These small burrows, usually lying in casual sites, were in all probability dug by foxes. Thus, in the area of the forest checked by us, the only burrows which should be considered as true badger burrows are those of the first, second, and partially the third group, the total being 49.

The average density of burrows throughout the 1,000 hectare area studied, of the thick Tula abatis forest had a value of 8.63 (Table XI) per 1,000 hectares. However, burrows of Group I, i. e., those in which the badger had reproduced numbered only 2.33. A. F. Chirkova (1947), not distinguishing between the burrows of the badger and fox, presents a value of 12 burrows per 1,000 hectares for the forest region of the Serpukhov and Vysokovsk Raions, in the Moscow Oblast'. For the Losino-Ostrovskii lumber concern near Moscow, V. G. Stakhrovskii presents a figure of 3.5 (A. F. Chirkova, 1947). Thus the density shown by us in the Tula abatis is rather high.

The highest density of burrows was noted in the Krapivna Region (Moshchena Stream, Plavka Stream, and Upa River) of the section of the Tula abatis investigated; in the Odoevo Region there were less (Table XI). However, if burrows of Group IV and fox burrows are excluded, another picture emerges. The badger burrows (Groups I, II, and III) were rather uniformly distributed in the forest. However, burrows of Groups I and II, particularly those of Group I, which is the most important group for the badger, were definitely encountered in the largest numbers in the western portion of the section of forest studied, where the ravine network was most highly developed and many ravines occurred. In the western, most elevated part of the forest the density of Group I burrows amounted to 2.12 and 3.68. Proportionately

to the decrease in the elevation of the area toward the Upa, this value dropped to 1.46 and 1.67 (Table XI and Figure 2).

Table XI

Density of burrows on 1,000 hectares of the broadleaf forests of the Tula abatis under study

Region	Odoevo	Moshchena Stream	Plavka Stream	Right and left banks of Upa River	Total
Area	2,835	1,900	1,365	1,200	7,300
Total and burrows per 1,000 hectares	22 / 7.76	17 / 8.95	12 / 8.79	12 / 10.0	63 / 8.63
Total and burrows of Groups I-III per 1,000 hectares	19 / 6.70	14 / 7.37	7 / 5.13	9 / 7.50	49 / 6.71
Total and burrows of Groups I-II per 1,000 hectares	11 / 3.88	9 / 4.74	4 / 2.93	4 / 3.34	28 / 3.97
Total and burrows of Group I per 1,000 hectares	6 / 2.12	7 / 3.68	2 / 1.46	2 / 1.67	17 / 2.33

Both the badger and fox inhabit burrows, but for the latter they are of considerably less importance. The badger passes most of its life in its burrow, in which it bears and raises its young, hibernates, and seeks shelter in summer. Thus, the badger is demanding in its form of domicile. The fox occupies its burrow in an unbroken stretch only during the period of training the young. The rest of the time devoted to rest and night sleep is spent in various shelters not only in the burrow. The fox occupies a ready-made burrow, and when reconstructing one anew, disregards many features absolutely indispensable for the badger when building a permanent burrow. Thus, for the fox the burrow is a place of temporary abode, for the badger a permanent lodging.

Burrows constructed by the fox are characterized by a haphazard selection of site, smaller size, fewer entrances, and more frequently have only one entrance. Such burrows are usually used for only one season, are not kept in repair, and are situated in chance locations, often with unfavorable soil and subsoil conditions, and quickly fall into complete disrepair.

Over 15 years (1936-1950) we found in the area observed 97 fox litters, 63% of which were found in large old badger burrows and only 37% in small casual burrows almost unfrequented by the badger. We did not discover fox litters of small pups outside the burrows. Thus, the fox, not being highly discriminating in its choice of burrow, may whelp in burrows of any quality, but most often occupies good badger burrows for whelping. The badger litters found were always discovered in the oldest and largest burrows of the area covered. The badger possesses the burrow, but the fox uses it merely to the extent that the badger is not disturbed thereby. It is reported that the fox drives the badger from its abode by virtue of its uncleanliness, which was justifiably doubted by S. I. Ognev. We did not have the opportunity of observing such an occurrence.

It may be noted that many entrances into badger burrows frequented in winter

by foxes give off a powerful odor of fox urine in the spring. However, by April some of these entrances have been cleaned by the badger. In early spring, the fox occupies free badger burrows in order to whelp, but if the badger wants to return, the fox, physically weaker, cannot resist. In 1938 we observed a male badger destroying two fox litters. On 29 May in an old large burrow (No 1), a fox litter was discovered with no appearance of badger footprints at the entrance of the burrow. Two days later, near one of the entries to this burrow, four large fox cubs with toothmarks in the neck region were found piled in a heap, and in another entry quite fresh traces of digging by the badger. An analogous picture was noted some days previously in Burrow No 7, not far from Burrow No 1, in which three fox cubs lay dead. Similar cases were also observed in other years, always in old burrows. M. A. Mamkin, who worked 20 years as a hunter in the Pershinskaya hunt, informed this author that he had often found and dug up dead fox litters after a burrow had become frequented by a badger. According to him, the cubs were always piled in one heap near one of the entrances or in a lateral passage inside the burrow.

The fox litter leaves the burrow in June, and we have often seen that almost immediately thereafter the badger occupies the burrow, digging out and cleaning just those branches of the burrow which the fox cubs had occupied.

There are reports that badger and fox litters may live together in a single burrow. The large badger "cities" possess numerous exits, some of them completely unused by the badger. These free exits are inhabited by the foxes. Here there may be room for simultaneous habitation by badger and fox litters in a single burrow, but separate external exits must be present. It is more correct in such cases to speak of the fox and badger as living together in two adjacent burrows. The underground part of such a burrow is so large that the badger and fox do not come into contact underground. It is also possible that the portion occupied by the fox is separated from the badger burrow by an earthen partition, the creation of which constitutes no difficulty at all for either fox or badger. However, such cohabitation in the same burrow is a rather rare phenomenon; we found such a case only once, in the summer of 1937.

In 1938-1941, in the region of our study, we noted a decrease in the number of badgers. In these years fox litters were found mainly in large old badger burrows. From 1942, the number of badgers in the region again increased and, in the period from 1942 to 1950 the great majority of fox litters were found in small burrows. The increasing occupation of the burrows by the badger compelled the fox to live in poorer shelters.

In constructing a burrow, the badger, while throwing out an enormous amount of earth—sand and loams—does not leave it near the exit but, flinging it beneath its body with its forepaws and walking backwards, drags the soil a rather great distance away. Thus, down the center of the excavated pile a narrow trench is formed from the exit toward the ravine. The more the badger works the longer and deeper this becomes. The greatest trench we had the opportunity of seeing was five meters long and 20-22 cm deep. The fox when throwing earth from a burrow, piles it near the exit and never makes a "trench". Thus, near the branches of the burrow occupied by the fox, a fanshaped rounded mound of thrown out sand or loam is formed. It is true that such a mound will sooner or later also develop near a badger burrow, as part of the sand must remain at the beginning of the trench, but it is invariably traversed by the trenchlike passage in all burrows and especially in freshly dug burrows.

In the spring, when the earth is just beginning to dry, the badger begins to rehabilitate its abode. At this time the sand thrown out from burrows where badgers had hibernated is mixed with dry foliage.

When excavating burrows we discovered that the badger prepares bedding for

the winter, consisting chiefly of dry leaves of the oak, linden, and hazel, and partly of dry grasses; such a bed was discovered in the "caldron" of a burrow excavated by us (No 59). The weight of the bed exceeded 5 kg, and it was difficult to stuff it into a large rucksack. Another burrow had less bedding, consisting of leaves, twigs, and branches (28 species of woody plants and grasses). In the spring the unneeded bedding is thrown out by the badger while it cleans its burrow.

It is reported that the badger seals the entrances to the burrows in which it hibernates. This has not been observed by the author. On the contrary, the burrows occupied by the badger for hibernation purposes were very often frequented in winter by the fox and their external entrances were not sealed. In all probability, if the badger does seal himself in, it is only near the "caldron"; to seal the passages near the "caldron", old bedding consisting of leaves may sometimes be used (Burrow No 59).

Since a fox litter leaves a burrow as soon as it grows somewhat older and the badger litter remains in its burrow throughout the summer, there are no feeding paths near the burrows occupied by the fox. Near burrows with a badger litter such paths are clearly manifested, and toward fall lead into the forest for over 100 meters from the burrow.

Near entrances of burrows occupied by a fox litter excrement and food remains in the form of partly eaten carcasses of voles and birds, bird feathers, etc., may be seen. Such remains were never found near burrows inhabited by the badger. Near burrows occupied by fox litters, excavations by the young foxes are observed, consisting of individual shallow holes and underpasses below the roots of trees, whereas different types of excavations and considerably more of them are found near burrows occupied by badger litters. Holes dug near stumps in the search for insect larvae are always found; the stumps are surrounded by these holes. Very often narrow surface ribbons of upturned forest floor are observed. The young and adult badgers when digging here do not move forward but backward, pushing the leaves under them. Digging by the cubs is observed near the burrow and also far away along the food paths, mostly in the middle of summer. Toward fall less and less fresh digging is encountered. Around this time the litter which has developed somewhat moves a considerable distance from the burrows into the forest to find food.

A census of badger litters was carried out annually by the method of repeatedly examining all burrows present in the census area during the spring and summer. With familiarity with the census area, new burrows were found which had been missed in previous years.

During the war none of the territory of the forest under study (Odoevo part of the logged forests) was included in the census. To judge the correctness of the census of the badger litters, we indicated the number of burrows of the first two categories per year, i. e., burrows where litters could be found while under observation (Table XII). The more badgers there are in the forest the more burrows are present which have been dug by them. Thus, the percentage of burrows dug (frequented) during the summer in Groups I, II, and III is an index of the number of badgers.

The numbers of badgers in the region of our survey were not constant. There were many badgers in 1936-37, but from 1938 to 1940 the number clearly decreased. In 1941-1943, the number of badgers increased again and remained considerable for all subsequent years (1944-1950, the years of our study) (Table XII).

It must be noted that during the years with large numbers of badgers they did not inhabit all the burrows, not even those of Group I. Apparently this is one of the reasons why we did not observe the building of new large burrows during our period

of study. This fact, however, permits us to emphasise that in the area of forest we examined there was no shortage of burrows in which the badger could procreate.

One of the causes of the decreased numbers of badgers was over-extensive hunting with hunting hounds. However, the increase in numbers noted was due partly to the ban on such hunting imposed in 1940. The complete cessation of badger hunting in 1941-45 also promoted an increase in their number.

Table XII

Count of number of badger litters

Year	Percentage of burrows dug		Number of burrows of Groups I and II	Number of badger litters	Year	Percentage of burrows dug		Number of burrows of Groups I and II	Number of badger litters
	Groups I; I-III					Groups I; I-III			
1936	100	57	20	4	1944	80	45	17	5
1937	62	35	23	2	1945	75	42	17	4
1938	43	23	24	0	1946	94	51	25	7
1939	58	29	26	1	1947	75	40	26	4
1940	62	30	26	0	1948	75	62	26	5
1941	80	43	25	3	1949	80	53	26	5
1942	75	40	15	3	1950	75	50	26	5
1943	80	45	15	3	-	-	-	-	-

The badger is omnivorous and readily changes to such food as is available in the range. Thus, the food factor should not greatly influence the dynamics of the population. However, it should be noted that the smaller numbers of litters coincided with years of extremely unfavorable climatic conditions, i. e., 1938-1940, which very markedly changed the qualitative and quantitative composition of the food supply. In the droughts of 1938-1939, the number of amphibians greatly diminished, the species complement of insects changed markedly and the number of earthworms decreased. Following the extraordinarily intense and extremely prolonged freeze of 1938 and the extremely severe icing of the earth in forests and fields in the winter of 1938-1939, mass extermination of all species of voles, as well as of hedgehogs, moles, shrews, amphibians, and reptiles, was observed. They were of negligible numbers in 1939-1940. After the intense cold of January 1940, oak, hazel, and apple trees bore no fruit for a number of years. Such a drastic deterioration in food conditions for three years in succession created a situation in which the badger, despite its omnivorousness, could not fail to be affected.

The decrease in badgers and the drop in their reproduction rate from 1937 to 1940 noted by us were a result of the simultaneous effect of intensive hunting (1936-1939) and the extremely unfavorable food conditions in 1938-1940, curtailing reproduction. The absence of these natural factors after 1940 provided the badger with the opportunity of gradually reestablishing its former numbers.

The maximum number of badger litters, 15 per thousand hectares, was found in the western part of the forest studied. There were considerably fewer badgers in other parts of the forest area (Table XIII).

The western part of the area studied in the broadleaf forests of the Tula abatis (Odoevo Region) which also include the upper reaches of the rivulets and streams entering the Kolodiya River, the upper reaches of the smaller tributaries

of the Upa River, and the Mashchena Stream Basin, totaling 4,735 hectares, is situated in the most elevated part of the census area. Here the ravine network is most highly developed as regards both length and rugged topography, as well as the number of ravine heads present. Thus, the badger is able to find many places here suitable for the construction of good burrows. This part of the forest contains the maximum number of Group I burrows (12 or 71%), the total number of burrows of the first three groups being 33, or 67%. The average density of burrows per 1,000 hectares was as follows: Group I 2.54; sum of first three groups 6.99. Thus in this portion of the forest, for the 15 years of the census, we really discovered 38, or 74.5% of all badger litters. The average for the year was 2.53, which gives 0.53 litters per thousand hectares, i.e., more than the average value for the entire area examined, which was 0.46.

Table XIII

Number of badger litters per 1,000 hectares

Region	Western	Eastern	Meadows of Upa River	Total
Total litters	38	10	3	51
Litters per year, average	2.53	0.66	0.20	3.4
Litters per 1,000 hectares, average	0.53	0.35	0.30	0.46

The other two regions (Krapivna part of the abatis, Table XII), the right tributaries of the Upa River (eastern) and the delta of the Upa, with a total area of 2,565 hectares are situated on the terraces of the Upa River in the lowest portion of the forest. There are relatively few ravines here but rather plentiful burrows (totaling 24), but their quality is low, only eight of them being of the first two categories. In this portion of the forest we found only 13 badger litters in 15 years. The total habitation in the two eastern regions of the section of forest studied were considerably less than in the western portion an average of only 0.34 litters per 1,000 hectares (according to finds in two areas).

Thus, over 15 years of observations, the chief site of badger habitation in the section of the broadleaf Tula forest studied was the highest western portion where the ravine network was most highly developed both in length and topographical shape.

The distinct preference of the badger for dwelling sites in definite regions of the forest instead of throughout the area is well illustrated by the count of burrows in which several litters were discovered during the 15 years study.

Only 5 burrows containing 5-7 litters were found (Table XIV). Twenty-nine litters were found in these, or 56.9% of all badger litters found during our entire study.

Thus, more than half of all cases of badger reproduction took place at only five points of the forest, the remaining 22 litters (43.1%) occupying 12 different burrows.

The badger not only lives in definite sites of the forest but is highly conservative in selecting a site for reproduction. Year after year it occupies the preferred burrows for bearing young. Litters in casual burrows are rarely found.

Table XIV

Number of badger litters found in a single burrow

Number of litters	7	6	5	4	3	2	1
Number of burrows examined	1	2	2	1	3	1	7
Total litters	-	29	-	13	-	9	-
Per cent of total number of litters	-	56.9	-	25.5	-	17.6	-
Litters per burrow	-	5.8	-	3.2	-	1.2	-

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M. N. Borodina

RESULTS AND PROSPECTS OF DISTRIBUTION OF THE RIVER BEAVER IN THE OKA RIVER BASIN

(OKA STATE PRESERVE)

(Rezul'taty i perspektivy rasseleniya rechnogo bobra v basseine reki Oki).

At present the center of the European part of the Union is very densely inhabited by beavers. Territorially this region almost coincides with the boundaries of the basin of the largest river of the Russian plain—the Oka. Approximately 30% of the rehabilitated beavers of the European part of the Union live within these boundaries. The large number of these animals in the Oka River Basin is explained by the fact that beavers were set free here at many points, most of which had favorable conditions for their reproduction and distribution. At those points where the first groups of beavers were released (in the 1936–1940 period), a beaver population of considerable numbers has made an appearance—the Meshchera, Mordov, and Klyaz'ma groups.

The variations in the natural conditions of the vast Oka River Basin, together with the rather high density of beavers inhabiting it and the possibility of using station observations carried out over many years, favor the selection of this region for the first summary of results of the distribution of the river beaver in the central belt of the Union. The work we carried out also had practical objectives, i. e., a determination of the prospects for economic use of beavers in the Oka River Basin.

The materials for the present study were observations on beavers carried out by the author in the station in the area of the Oka Preserve and other areas of the Meshchera lowland from 1937 to 1953, and investigations by expeditions in other beaver habitation areas in the Oka River Basin carried out in the period from 1951 to 1953.

The region of the lower reaches of the Moksha Basin in the Mordov Preserve, the middle reaches of the Oka River in the Oka Terrace Preserve, the flood plain of the lower reaches of the Klyaz'ma River (in the former Klyaz'ma Preserve), the upper reaches of the Moskva River in the former Upper Moskva River Preserve, and the middle reaches of the Tsna and Sh'ya Rivers on the western boundary of the Meshchera lowlands were included in the area studied. To study these regions and the habitats of the beaver in the Tesha and Serezha River Basins which the author was unable to visit, the data in literature and in manuscripts were used.

The author extends sincere acknowledgments to Professor V. G. Geptner and the Director of the Scientific Division of the Oka Preserve, V. P. Teplov, for valuable advice and assistance in her work and also thanks the persons who provided her with the recorded material required.

Natural Conditions of the Oka Basin

The Oka Basin, which is 239,300 km^2 in area, occupies the central part of the Russian plain, bounded on the north and east by the Volga Basin, on the west by the Dnieper Basin and on the south by the Don Basin. The territory of the Don Basin penetrates into the Oka between two protrusions of the latter—the western, which extends along the upper reaches of the Oka and the eastern, which extends along the paths of the Tsna and Moksha Rivers.

According to geomorphological descriptions of the Eastern European Plain (I. P. Gerasimov, 1939; B. F. Dobrynin, 1948), the surface of the Oka Basin everywhere bears a heavy covering of Quaternary deposits and signs of the direct or indirect influence of heavy glaciations on primary preglacial forms of relief. The topography, despite its general plainlike character, is not of a uniform nature and on the territory of the basin we encounter various geomorphological landscapes.

According to B. F. Dobrynin, the structure of the surface of the Oka Basin is of the following type: the northwestern part of the basin along the Ivanovo—Vladimir—Moscow—Kolomna—Kaluga line belongs to the moraine type of landscape, in which the ancient relief continues to play a considerable role. This part of the basin, which the author mentioned, relates to the central moraine region, occupies an elevated position, the highest zones being the Smolensk—Moscow and the Klin—Dmitrov Ridges, which extend in an east—west direction. The southern part of the basin, with a clearly marked erosional terrain is partly related to the elevated region of the Central Russian Plateau and partly to the plain bearing the name of the Oka—Don lowland. The rest of the basin consists of a lowered area bounded on the east by the northwestern slopes of the Volga heights. This area, bearing the name of the Oka-Klyaz'ma lowlands, belongs to the group of sandy lowland border zones of Quaternary glaciation, and the meridionally extending Oka—Tsna Ridge is divided into two sections—western and eastern. In the western part the lowest site lies in the Meshchera lowlands, in the eastern part in the Moksha and Balakhna lowlands.

The features of the geomorphological structure of individual regions of the basin also determine their characteristic hydrographical traits. The Oka—Klyazma lowland is marked by a great profusion of ponds. Its hydrographical network consists of natural bodies of water appearing as a result of the activities of man. The rivers of the middle and lower reaches of the Oka Basin belong to the first of these types, the numerous old meanders and oxbow lakes of the former riverbeds of the Oka, the oxbows and old beds of its largest tributaries, and the lakes lying outside its flood plain, scattered among the vast stretches of marsh. The second category includes the small land amelioration drainage canals crossing the marshes, the peat fields filled with water after the removal of the peat, and the ponds made by damming the rivers or dug specially without taking into account the enormous artificially created water reservoir of the Moscow "Sea". In the remainder of the basin the hydrographical network consists chiefly of rivers.

The climate of the Oka Basin, situated in the center of the European USSR, is rather severe, with continental characteristics expressed in the considerable ranges of average temperatures (up to 31.7°) and extremes of temperature (up to 75.1°). The climate becomes colder in the Oka Basin on moving from southwest to northeast and there is a change toward greater humidity on moving from southeast to northwest. This is illustrated by meteorological data (Table I) presented by S. I. Nebol'sin (1922).

The time of formation of the snow cover changes according to the changes of the atmospheric temperatures, as do also the dates of the disappearance of the snow, the freezing of the rivers, and the reopening of the rivers. In the southwestern part of the basin, the snow cover is usually established by 27 November, and it disappears by 10 April. The freezing of the rivers is observed between 27 November and

5 December. In the northeastern part the first snowfall occurs from 15 November to 22 November, and the snow melts by 15 April. The rivers freeze between 18 and 24 November. According to the data of S. I. Nebol'sin, the snow cover on the basin lasts 140–150 days; its height is generally 45–55 cm, and only in the region of the Meshchera lowland does it attain 55-65 cm in height.

Turning to the characteristics of the vegetation of the Oka Basin it should be noted that the boundary between two landscape zones of the European part of the Union crosses its territory, the forest and the forest-steppe. On the basis of data of the distribution of the gray podsolized soils and typical chernozems (black earth), soil scientists and geographers (I. V. Tyurin, 1939; F. N. Mil'kov, 1950) fix the northern boundary of the forest-steppe zone along the line of the unbroken distribution of gray podsolized soils of the forest-steppe with patches and tongues of leached and degraded chernozems. The geographical boundary between these zones on the territory of the basin is determined by the points Karachev–Tula–Kashira and then along the valley of the Oka to the mouth of the Moksha River. Along the valleys of this river and its tributary, the Tsna River, this boundary inclines southward, where the belt of the coniferous–broadleaf forest descends in a broad tongue toward the steppe zone. Geobotanists (E. M. Lavrenko and A. V. Prozorovskii, 1939; V. V. Alekhin, 1947) include almost the entire right bank of the Oka Basin in the broadleaf forest subzone and thus shift the boundary of the forest zone considerably southward. Without entering into a discussion of this fundamental divergence of opinion on the location of the northern boundary of the forest steppe, it must nevertheless be pointed out that the inclusion of the entire right bank of the basin in the forest zone has the effect of restoring the vegetation existing formerly and does not reflect the contemporary state of affairs. The forest was preserved south of the Oka River only as occasional coppices.

An almost complete absence of forest is characteristic of the right bank of the Oka Basin. All investigators visiting this region have noted this. The left-bank part of the basin in the region of the upper Oka toward the north to the line Karachev–Tula has a similar appearance. The remaining part of the basin, which is greater in surface area and has varied vegetation conditions, is still characterized by considerable forest growth. The northwestern corner of the basin belongs to the subzone of spruce forests with a mixture of broadleaf species (V. V. Alekhin, 1947). For individual administrative regions, as indicated by V. V. Alekhin, the percentage of forest fluctuates from 7 to 60 %. The northeastern corner of the basin also belongs to the subzone of spruce forests. Forests in this region, which includes considerable unforested area of the Vladimir fields are also nonuniform. The principal part, as stated by N. Dubenskii (1856), was "already without forests 700 years ago, almost from the time of the foundation of the Russian Kingdom. The Grand Duke of Suzdal, Yuri Vladimirovich Dolgorukii, who erected the city of Yuriev in 1152 in this area, called it "Yuriev–Pol'skii!" because of the absence of forests and the wide fields which surrounded it, while to Pereslavl, also erected at the same time, he gave the name Zalesskii (Forests) because of the forest remains which, to this day, surround it on three sides."

It is necessary, however, to point out that in a special study of the vegetation of the Vladimir fields conducted by L. I. Krasovskii (1949) it was established that when man first inhabited this region, it was covered by broadleaf forests constituting a unique region of natural history with its own peculiar complex of natural conditions.

In the western part of the basin, moving southward, we may trace the order of vegetal changes "caused chiefly by climatic influences" (V. V. Alekhin, 1947). A subzone of spruce–broadleaf–forests is situated adjacent to the subzone of the spruce, which in turn is bounded on the south by the region of the broadleaf forests. The zone of the spruce–broadleaf forests covers a considerable area. The average

Table I

	Average yearly temperature	Absolute minimum temperature	Absolute maximum temperature	Average amount of precipitation (mm)
Town of Kaluga Southwestern part of basin	4.5	−37.9	34.5	606
Village of Gulynka Southern part of basin	4.2	−37.9	34.5	479
Town of Gorkii Northeastern part of basin	3.8	−40.6	35.7	542

percentage of its forestation, according to data by V. V. Alekhin, is 38%. This author includes in the subzone of broadleaf forests a small region lying south of Moscow and a region in the western corner of the right bank part of the basin separated from the south and west by the Likhvin–Tula and Tula–Serpukhov lines. Narrow–leaf aspen and birch forests dominate the former region at present. The region is up to 40% forested. The remains of former forests are still preserved in the latter region. The forest of the famous Tula abatis is included in these, stretching in a narrow belt from Tula to the town of Chekalin. The percentage of forested area in this region is small–approximately 15%.

The eastern half of the basin in the northern corner, which is covered by spruce forests, lies adjacent to a large sandy lowered area–the Oka-Klyazma lowland, which V.V. Alekhin regards as a special intrazonal pine–tree marsh region. This author indicates that the vegetation conditions of the region are determined by the composition of the soils, mainly the sandy ones, and by the widespread development of marshlands. He mentions three subregions in this vast region: 1) Klyaz'ma vicinity, 2) Meshchera region, and 3) Tsna–Moksha area. According to V. V. Alekhin, the Klyaz'ma vicinity occupies the north of the Oka–Klyaz'ma lowland and is characterized by a predominance of pine–narrow–leaf forests, with the occurrence of pinespruce forests and highland marshes.

In the Meshchera subregion, which occupies the central part of the Oka-Klyaz'ma lowland, pine forests and lowland marshes predominate. In the Tsna–Moksha region, pine trees predominate. However, oak and oak–spruce forests are also present. This region differs markedly from the Meschera due to the presence of the latter forests, the dry stretches of which project southward, far advanced in the process of turning to a steppe. The afforestation of the entire pine-marshy region, as indicated by V. V. Alekhin, is considerable, amounting to 50% on the average, and in individual administrative sections rising to 75%.

The various vegetal conditions in the Oka Basin also determine the characteristic traits of its fauna. Among the mammals and birds living in the basin are types typical of the taiga, those characteristic of the broadleaf forests, and those living in open spaces. Two faunistic evolutionary complexes are encountered in the basin territory, the forest and the forest–steppe types of animal respectively.

At the boundary between the forest and the forest–steppe, i. e., the Oka River, we may note the penetration of single species far beyond the zone characteristic to

them into regions with conditions favorable to them. A study of the fauna of that part of the Oka Preserve which lies at the boundary of the forest zone revealed the penetration along the Oka Valley to the north of such southern forms as the jerboa, the white polecat, the bee eater, and the steppe pratincole. At the present time, the river beaver is representative of the forest fauna in the area of the basin. Its penetration into the forest part of the basin has, up to now, taken place in isolated instances.

In concluding this review of the natural conditions of the Oka Basin we should touch on the question of the degree of human activity in the area. An acquaintance with this problem indicates that the settlement and intensity of economic utilization of the land in various sections of the basin are not equal. According to the intensity of the use of the land the entire basin may be subdivided schematically into three types of regions:

a) Densely populated regions, where the landscape is of a cultured type and areas intensively used by man predominate, such as plowed areas, etc.

b) Moderately populated regions, where areas used intensively for economic purposes alternate with less extensively used areas (forests, meadows).

c) Sparsely populated regions, where most of the territory is occupied by areas with moderately used land--large stretches of forests and marshes.

The entire forest--steppe part of the basin, the intensely inhabited lands around, industrial centers and the large areas of the Vladimir--Suzdal fields belong to the first category.

The extensive forest--marsh stretches of the Meshchera--Balakhna and the Moksha lowlands belong to the third category.

The remainder of the basin may be referred to as moderately populated regions.

Review of Past Distribution of River Beaver on Oka River Basin Lands

Numerous references to beavers in historical documents of the fourteenth to eighteenth centuries grant deeds, petitions, and various ukases--are a clear sign of the great importance of the river beaver in old Russia. These documents as well as the reports of foreigners visiting Russia enabled later historians to reconstruct the picture of the former distribution of the river beaver when it was already on the verge of complete disappearance. In the extensive works of F. Keppen (1902), G. L. Grave (1927), A. V. Fedyushin (1935), and V. N. Skalon (1952) devoted to the beaver, the former range of the animal is described quite fully.

The information collected by us for the Oka Basin, detailing information from the reports of the above--mentioned authors, shows that even in the sixteenth century beavers were widespread throughout the area. Their distribution in the part of the basin which today is unforested, becomes comprehensible only by considering the former natural conditions. The presence of an extensive forest stretch north of the forest--steppe lying completely within the limits of the Oka Basin testifies to the existence of the abatis characteristics in the Moscow State in the sixteenth and seventeenth centuries in the region of the cities of Ryazhsk, Ryazan', Kashira, Veneva, Tula, Odoevo, Chekalin, Peremyshl', Belev and Kozel'sk (A. I. Yakovlev, 1916), i. e., in places where forests are now either absent or have survived in the form of coppices. According to L. F. Turganovich (1950), a region of dark forests (linden trees) existed in the basin of the Upper Oka and along the right bank of the Oka to the Don in this period (i. e., in the sixteenth century). "The data of V. P. Semenov (1902) on the

former distribution of forests in the Russian chernozem region distinguished by him, to which the entire steppe parts of the basin belongs, also correspond with this."

It is quite natural that the forest in those times occupying the most moist sections of the forest-steppe, should be widely distributed in river valleys. In notes by S. Gerbershtein (1908) referring to the seventeenth century, we may find mention of the fact that the "Oka River is surrounded by forests on both sides." L. F. Turganovich (1950) writes that A. Olearius, who visited Russia in the fifteenth century, noted vast forest areas in the region of the Oka below its confluence with the Moskva River, as well as forest on both shores of the Oka below the city of Kasimov. It is logical to assume that the valleys of the right tributaries of the Oka were forested to the same extent, starting at the very south of the basin.

F. N. Mil'kov (1950) characterizes the forest-steppe of the Russian plain as a region of ancient agriculture, the development of which was assisted by the fertility of the soils, the climate, and the presence of natural unforested areas. "The assimilation of forest-steppe zones", according to this author, "started north of the central Middle-Russian forest-steppe and became especially intensive during the sixteenth and seventeenth centuries. According to data of Lyashchenko, presented by F. N. Mil'kov (1950), in the seventeenth century after liberation from Tatar oppression the central forest-steppe already began to supply Moscow with bread, and toward the eighteenth century became an integral part in the over-all national economy of the Russian state, as the "productive south".

F. N. Mil'kov reported the time of particularly intensive felling of forests was to be the nineteenth century, in the middle of which the cultivated landscape became predominant. Using material accumulated by M. Palimpsestov and P. I. Lyashchenko, he writes that in the 100 years from 1774 to 1874 the forest area decreased by 20-35% and in some places by 50%, while plowland in the chernozem and nonsteppe belts amounted to 60.6% of the total surface area of land.

Turning to a study of the left bank of the basin which today is still considered to be forested, we find, in the writings of L. F. Turganovich, indications concerning its solid forestation in the sixteenth century. This author attributes the onset of the large-scale extinction of forests to the seventeenth century. In subsequent years forested areas decreased continuously. In the eighteenth century sparsely forested areas began to appear. Among them, L. F. Turganovich (1950) reports the southern part of the former Kolomna County (district), the locality between the Oka, Moksha, and Sura Rivers, and the area around the city of Murom. According to reports by E. Zyablovskii (1810), around this time, there was also a noticeable decline of forests along the Tsna and Moksha Rivers and along the tributaries of the latter, the Bad and Vysha-the center of potash production of those times.

According to data by V.P. Semenov (1902), during the previous century from the time of the total land division of the year 1777 (including almost the entire left bank of the basin) the forested areas in the Moscow industrial province dwindled by an average of one-third of the former area. For the former Vladimir Province N. Dubenskii (1856) indicates a 50% decrease of forest area during the same period.

The above-indicated change in vegetation in the basin took place parallel to changes in the quantitative and qualitative depletion of its fauna. In the wake of the elimination of forests the numbers of typical forest animal species were considerably reduced; today some of them are no longer encountered in the forest-steppe part of the basin, as for example, the bear, while others have become rare (pine marten and others). Some species disappeared completely from the territory of the basin. A similar fate also befell the river beaver. However, as may be concluded from the review presented earlier on the changes in the nature of the basin during the past century, the ruthless extermination of this valuable animal was carried out well

before the elimination of the minimum conditions necessary for its existence. Judging from the data of old documents and literary sources, the beavers in the basin had been almost completely exterminated by the seventeenth century, apparently a very small number of them surviving until the end of the eighteenth century.

In the fourteenth, fifteenth and sixteenth centuries, the beaver runs were still widespread. We could not examine documents of an earlier period, but turning to the investigation of V. N. Skalon (1951) we find convincing proof of the high economic value of the river beaver in Russia in ancient times. It should be noted that information to transmit the location of the beaver runs (i.e., the areas covered in obtaining beaver) refer to relatively few places, chiefly monastery estates. Some refer to regions which have changed in nature beyond recognition in recent centuries. This leads one to assume that the former range of the river beaver in the basin was unbroken and that its apparent patchiness was due to the incompleteness of the historical data in our possession. The organization of facts indicates beaver habitations in the following sections of the river basin: in the southern section beaver runs were indicated on the right shore tributaries of the Oka, the Pronya River (1403, 1456), the Pavlovka and Pletenaya Rivers (1597), the Osetr River (1505, 1595) and, in addition, the former Ryazan County where beaver runs were given to the Olga Monastery (1355, 1390). From articles by V. N. Il'inskii (1928) and M. V. Babkin (1929), it is learned that beavers were distributed in the former Skopin County in the fourteenth to sixteenth centuries and in the former Mikhailova Subdistrict in the fourteenth century. Today all these regions of the basin are almost unforested. The next part of the basin for which indications concerning the presence of beaver runs remain is the Meshchera lowlands. In this region beavers were also included in the Oka tributaries, the large ancient beds of the Oka River flood plain, and the marshy massifs of the Meshchera. Of the Oka tributaries the Solodka and Kishma Rivers (regions near the city of Ryazan) are mentioned. The latter apparently no longer exist today. It is of interest that despite its apparently small size it was a beaver domain and was known as such for centuries. We know of the presence of beaver runs in this river in 1380 from the grant of the Great Duke of Ryazan' Oleg Ivanovich. Some 200 years later the right to trap beavers in half of this river was bestowed on the Bogoslovskii Monastery (records of Bogoslovskii Monastery lands in the Okologoryadniyi and Ponisskii registries of 1553). Beaver runs in the old river beds are indicated near the mouth of the Solodcha River (1390), in the region of the hamlet of Sanskoe, the then existing Voingkii County (1380), and in the region of the village of Izhevskoe. Here beavers were hunted on the Shteka River, flowing from the marshes west of the village of Izhevskoe and entering Lake Izhevskoe. Our review of the erstwhile distribution of beavers on the territory of the former Meshchera lowland given earlier (M. N. Borodina, 1949) reveals that the Shteka River flows along a field which today still bears the name of Ostrov (island), as according to a veteran of the village of Malyshevo, I. E. Sigachev, it was formerly included between two rivers, the Shteka and another which has now disappeared. The shores of the Shteka River are devoid of trees; the regions were completely levelled even within the memory of elderly natives of the region. However, in ancient times forests providing the richest hunting regions were apparently present here. On a grant given in 1390 by the Duke of Ryazan', Oleg Ivanovich, to the Metropolitan Theognost, the "Island and the River Shteka are granted for the hunting of valuable animals, including beavers." In an article by Cheslav Chekhovich (1901), devoted to the history of the Ryazan' fauna, a report is given of the existence of beaver runs near Erakhtur Village (an extract from the personal registries of the village of Erakhtur for the year 1627 stating, ..."beaver runs in the said Lake Rumka and its streams").

Indications concerning the capture of beavers in the swamps have been found in one of the documents giving the Solodchinskii Monastery title to the land (1597). The following was written "... and from the Solodcha River to the right along the Pra River to the Uruzhskii Tract, 15 versts [3,500 feet] across, renowned as the Znvalovskaya border land, possessing fertile soil and beavers. "We then come to the Klyaz'ma Basin, whose many tributaries were once famous for their abundance

of beavers. In order to characterize the beaver supply of these places, there is great interest in the grant given by the Tsar and Grand Duke Ivan Vasilevich of Vladimir to beaver traders in 1537, announcing "These beaver traders in the service of my Grand Duchy are to be in charge of beaver hunting, and will take beavers in the Klyazma River from Orzhavka River to the Sudogda River, the entire Sudogda River and the entire Koloksha River; whatever beavers they catch shall be brought with their fur into my treasury." Besides these rivers, the Uvod' River was also mentioned as a beaver domain. A grant to hunt beavers given to the Vladimir District peasants by the Tsar and Grand Duke Ivan Vasilevich states:- "When our friend Suvorko comes to you with our grant papers, you will set out on a beaver hunt in our service and catch beavers for me and the Grand Duke in the Uvod' River, down the Uvod' River and in the Uvod' flood plain to the Klyazma and the mouth of the Uvod', and submit whatever is taken to our treasury." N. Dubenskii reports the capture of beavers in the seventeenth century along the Teza and Koloksha Rivers. It is known from the document of grant of Dmitri Donskoi to the Sergiev Troitsa (Trinity) First Order Monastery that on the Vora River (a tributary of the headwaters of the Klyazma River), "It is permissible to bag otters, beavers, and any other animal" (1360). Attention should be given to the fact that this small river retained its importance as a beaver region until 1423, when a new document of grant appeared, issued by the Duke Peter Dmitrovich to the Troitsa Sergiev Monastery to bag beavers in the section bordered by the Talitsa and Lepetnya Rivers. According to the text of this grant, Duke of Dmitrov bestowed on the monastery sections of the Vora River formerly in his use and known to contain beavers: "We, the Grand Duke Peter Dmitrovich, are pleased to issue grant to the Igumen (Friar) Nikon of the Holy Troitsa Sergiev Monastery and any other friar of his brotherhood: we grant of our possessions, on the Vora River and the Teremenevskii Pool for catching fish and capturing beaver. We also hereby grant him permission to catch fish and trap beaver along the Vora River and along monastery lands from the Talitsa River to the Lepetnya River, while my fishermen and beaverwomen will not catch fish or beavers for me ...." (4 August 1423). Direct proof of the richness of the Klyazma Basin in beavers is contained in the report by A. P. Shchapov presented in the book of V. N. Skalon (1951) to the effect that on the Klyazma River and its tributaries, even before the sixteenth century up to 24 villages and one small beavering* village were inhabited by beavermen who founded the "Ilmekhotskii Beaver Station".

East of the Klyazma and its tributaries we found indications of past habitation by beavers within the limits of the basin on the Tesha River only (data by F. Keppen, 1902, which he presented from the works of Stukenberg, who wrote a survey of the rivers of the Russian State). We found little data on the former distribution of beavers westward from the basin of the Klyazma River. They are limited to reports on the environs of Moscow and the region near the towns of Dimitrov and Malyi Yaroslavets. An address by K. Rule made on 16 July 1845, at a festive convention of the Moscow Imperial University, indicated that beavers lived near Moscow. Kotoshikhin, describing the reign of Aleksei Mikhailovich, clearly stated that beaver runs existed below the village of Izmailov. Pavel Oderbern, who visited Moscow at the time of Ioann Vasil'evich, described the way to capture beavers with "borzoi" hounds. Later K. P. Rul'e mentions the existence of a sunken meadow (the floors of stagnant pools) near the village of Rostokino which the old inhabitants used to call the "beaver place".

With regard to the region near Malyi Yaroslavets, we obtained information referring to the year 1649 and containing an order to the local village headman, Savva Mikulin, to effect the most exact inventory ("executing a head-by-head search") of all possible sources of income in certain uninhabited areas in the Zimnitskaya territory in the Medinskii County, ordering that "he himself register carefully how much of this uninhabited area was earth which is plowed and unplowed, as well as

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* Translator's note—The dwelling place of those who engage in the hunting of beavers or the processing of their skins.

the border forests, recorded in versts and desyatins [2.7 acres], and indications of the rivers, lakes, fish-catching sites, beaver runs, animal flushing places, animal crossings, border lands, and all other lands".

The contents of this document testify that it was possible to find beaver runs among other sources of income of this "empty area", i.e., places inhabited by beaver. The lack of knowledge of their presence in these relatively later times would not seem to be an indication of the full habitation of these places but rather a proof of their becoming poorer in beaver. It is characteristic that to obtain information from the village mentioned previously it was suggested that inquiries be addressed not to persons well acquainted with nature but to the local priesthood ("...and where the forest is large and it is difficult to measure it in desyatins, thou shalt write to ask of the local and neighboring priests and friars in the monasteries administering there, etc"), i.e., the kinds of persons knowing more fully than others the history of the use of the land, particularly with reference to unused and forgotten beaver runs.

A decrease in the number of beavers in the seventeenth century is also mentioned in the notes of Cheslav Chekhovich (1901), who wrote on the last appearance of beavers in the Ryazan' Province. Even in the year 1627 he ascribed the survival of beaver runs near the village of Erakhtur to the rational curtailment of beaver trading by the Dukes of Kasimov. He writes, "Since the Mongols were concerned with the protection of useful game, undoubtedly both Kasim Khan himself and his descendants, on finding beavers in the Kasimov Kingdom, put them under legal protection." This permits us to explain how, in the seventeenth century, when beaver trapping places were no longer mentioned in the written archives referring to the western part of the Ryazan' Territory, they were still plentiful in the eastern section of the Kasimov District. Nothing is known concerning the time of disappearance of the last beavers from Lake Rumka near the village of Erakhtur. However, as Ch. Chekhovich writes, "It may readily be supposed that the last Ryazan' beavers were found in the tributary of the Pra River and the nonfreezing Kad' River. On the boundaries of the Kasimov and Spasskii Counties, where there is a forest to this day and there are no settlements except for forest huts for a 30 verst radius, the last beaver died not long ago, at any rate in the last years of the eighteenth and perhaps the beginning of the nineteenth century." Confirming these words, he presents the tales of old inhabitants of Erakhtur who retained memories of the beaver trade. "Approximately 20 years ago, in the village of Erakhtur, recalling the Rumka River, I inquired whether the local old-timers knew any legends or tales about the beaver. A 70-year-old man thereupon told me the following: 'We hunt a great deal in these parts, but there is never any report of anyone killing a valuable animal. The marten is the most precious, and it seems that no more than 3 rubles are being paid even for that. My uncle Filatka (who died during the Battle of Sevastopol at the age of 70 or 80) boasted more than once, as I remember clearly, that they used to enter the Bel'skii Forest (north of the village of Bel'skoe) in search of animals along the rivers, and if they killed even one they could pay all taxes, with some left over.' Another old man, almost 100 years of age, Tit Seregin, who died approximately 15 years ago, also told me that when he was a lad, that is about 1800, while traveling through the forest to Urzha (also near the Kad' River), he saw in the inn a strange dead animal the size of a hare, but round like a ball, dark in color, and with a furless tail like that of a snake, but wider. "Apparently, concluded this author, the "precious animal with which all taxes could be paid was the beaver, which the Erakhtur people exterminated in their area in the Rumka, and being acquainted with the methods of hunting it, later went out to look for it in the Bel'skoe forests on the Kad' River. They entered the Pra River north of Bel'skoe, and here dealt the final blow to the beavers, which have now disappeared from the Ryazan' Province."

The staff of the former Klyaz'ma Preserve, on the basis of sources which

remain unknown to us, considered the disappearance of the last beaver in the Klyazma Basin to have taken place during the first half of the eighteenth century.

Contemporary Distribution and Numbers of River Beaver in the Oka Basin

The first experiments in the rehabilitation of the river beaver among the fauna of the Oka River Basin were carried out in 1936 and 1937. In these years beavers were released in two sections of the basin—in the Moksha Valley in the remote south of the Oka-Klyaz'ma lowland (area of the Mordov State Preserve, 1936), and in the Pra Valley (area of the Oka State Preserve, 1937) in the southeastern region of the remote Meshchera lowlands. The importation of animals in this section continued in subsequent years and came to an end in 1940. In all, 34 beavers were released in the Mordov Preserve and 23 in the Oka Preserve. In 1940, two more small groups of beavers were released at different points of the basin, 8 in the middle reaches of the Klyaz'ma River, in the area of the then-existant Klyaz'ma State Preserve, and 6 in the middle reaches of the Serezha on a lake of the Pustyn system (Biostation of the Gorki University).

Further work on the importation of beaver was interrupted by the war, and was continued only in postwar years.

In 1946, 26 beavers were released in the lower reaches of the Sh'ya River in the southwestern part of the Meshchera lowland. In 1948, 9 were released in the upper reaches of the Moskva River and 4 in the Tadenka River, which flows into the Oka not far from the town of Serpukhov. In 1949, 4 beavers were released into Lake Glubokoe on the territory of the former Glubokoe-Istra Preserve. In 1950, 17 beavers were released into the Tsna River which extends in the southwestern part of the Meshchera lowland. In 1952, 7 beavers (4 adults and 3 yearlings) were released into the Polya River, a tributary of the Klyaz'ma, which flows through the region of the Shatura marshes.

At present the range of the beaver in the Oka Basin is divided into separate sections (see map). Each of them belongs to the single group formed at the place of release. The size of the groups or, as they are usually called in referring to beavers, the "colonies", varies at present. In some the number of individuals amounts to a few or to dozens and in others to hundreds. In all, six beaver colonies may be counted on the territory of the basin, the Meshchera, Klyaz'ma, Mordov, Middle Oka, Upper Moskva-River, and Pustyn' Colonies; their description is presented below.

Meshchera Colony

The Meshchera beaver colony is today the largest on the Oka River. Approximately 400 head of beaver live there (according to the 1951 count). The area of this colony is approximately 7,000 km^2. The colony began when 23 beavers were released in the southeastern corner of the Meshchera lowland on the land of the Oka Preserve between 1937 and 1940. The beavers were released in two separate regions. In 1937, 7 beavers were released into Lake Ukhanskoe, a large lake outside the flood plain, lying in a dense stretch of marshes in the northern section of the preserve. In 1939 and 1940, 16 beavers were released in the western part of the preserve, in the ancient bed of the Pra Lakes (Sundritsa and Tolpega Lakes and Zakotetskaya Creek), and two bodies of water outside the flood plain (Lakes Svyatoe and Bel'skoe), which are connected with the flood plain in periods of high water. In the majority of cases only one pair took possession of a site on their release. The rest of the animals migrated along the flood plain and took over other bodies of water. Single migrating individuals were encountered up to 1942, creating

the impression that a growing young population was present, although this in fact began to be true only in 1943. The beavers released in the Pra flood plain and adjacent sections settled in the Pra Basin and penetrated into the basin of the adjacent Gus' River, the Oka Valley, and then its right bank tributaries. The beavers released in Lake Ukhanskoe, outside the flood plain gave rise to a beaver population in the wide marshland area of the part of the eastern province of the Meshchera lowlands near the Oka. In 1946, the number of the Meshchera beavers was increased by the release of new inhabitants. Twenty-six beavers were released by the Moscow Hunting Society into one of the lakelike expansions and a section of the channelized flow of the small Sh'ya River in the western section of lowland. The region of the release was declared a beaver sanctuary by decision of the appropiate authorities. The distribution of beavers took place along the Sh'ya River, its old bed, and its channelized sections. In 1950, 17 more beavers were released into the Tsna River, which is the natural boundary of the Meshchera marshes and which flows almost parallel to the Sh'ya River which is not far away (8-15 km). The importation of beavers was carried out by the Moscow Regional Office of the "Bureau for the Preparation and Provision of Live Natural Resources". The slight growth in the number of colonies noted here in 1952 apparently explained by the partial emigration of the animals into the Sh'ya River Basin, which was easily carried out as the marshes surrounding this river are united in the flood periods and communicate with one another in the lower reaches through the so-called Darovatevskii Canal. Thus, in the western part of the lowland, mainly in the Sh'ya Basin, a new focus of beaver distribution appeared, a rather important one, despite its recent formation. The settlement of the Sh'ya Basin took place in an eastward direction, and in 1952 the boundaries of the two focuses of settlement (eastern and western) grew so close together (the distance between the extreme settlements was 20 kilometers in 1952) and the interexchange of individuals became so obvious that a unified Meshchera Colony of beavers could be spoken of.

Conditions for the distribution of beavers on the territory of the Meshchera lowland are very favorable during flood periods, i.e., in the second half of April and at the beginning of May. Enormous areas of marsh and river valleys become covered with water. Numerous canals draining the marsh waters into the river valleys become filled with water. The large bodies of water outside the flood plain no longer remain separate. The beavers find abundant possibilities for underwater movement. In view of this it is of interest to follow their distribution in various areas by years. The spread of beavers in the eastern focus of distribution, where the beaver habitations are highly variegated because of the natural features of the environment, took the form shown in Table II.

The data presented in the table clearly reflect the process of beaver colonization in the water of the Meshchera lowland. In the first years the settlement of the ancient beds of the Pra took place. In subsequent years, the percentage of other types of bodies of water inhabited by beavers began to increase, primarily small rivulets and drainage canals. The gradual lowering of population density in the old river beds is explained on the one hand by their almost complete colonization in 1951 of the entire reach of the Pra River and on the other by the successful distribution of groups of beaver inhabiting the marshes in the vicinity of the Oka lowland, where they settled on the lakes outside the flood plains, small rivers, and ameliorative drainage canals.

In this connection we shall dwell on the direction of the beaver movements in taking over new territory and the distance covered while doing so.

In the Pra Basin, during the first years after release, when it was still possible to determine the origin of newly arisen colonies, these were noted predominantly in those sections of the basin situated higher along the Pra River than the territory of the preserve. Thus in 1943, for instance, 3 out of 4 settlements were

formed a considerable distance from the western boundary of the preserve. In order to do this the beavers had to cover a distance of 20-70 km along the valley of the Pra. In 1944 two new settlements were discovered a distance of 80-100 km in the upper reaches of the Pra Basin. In 1945, one of the new settlements in the Pra Basin was at the boundary of the preserve, a second in one of the canals of the marsh stretches, situated considerably higher along the Pra River (at a distance of 70 km from the western boundary of the preserve).

Table II

Distribution of beaver colonies on various types of bodies of water in the southwestern part of the Meshchera lowland according to years

	1942		1943		1944		1945		1947		1949		1951	
	No	%	No	%	No	%	No	%	No	%	No	%	No	%
Old beds of the Pra River	9	60	13	59	17	65	19	58	25	50	30	50	33	40
Pra River bed	1	7	1	5	-	-	2	6	2	4	4	7	6	7
Small river beds of the Meshchera lowland	-	-	1	5	1	4	3	9	9	18	11	18	14	17
Beds of drainage canals	-	-	1	5	1	4	3	9	6	12	7	12	11	14
Lakes outside flood plains	4	26	6	26	7	27	6	18	7	14	8	13	10	12.4
Intermarsh hollows	-	-	-	-	-	-	-	-	-	-	-	-	2	2.4
Old beds of Oka River	1	7	-	-	-	-	-	-	1	2	-	-	3	3.6
Oka right-bank tributaries	-	-	-	-	-	-	-	-	-	-	-	-	3	3.6
Total	15	100	22	100	26	100	33	100	50	100	60	100	82	100

In 1947, a total of 10 new settlements were noted in parts of the basin situated in higher sections. In 1948, 9 out of 13 new settlements appearing in the Pra Basin were noted in these sections. It is quite clear that not all could have been formed through former beaver settlement.

It was difficult to map out similar rules of settlement in the Meshchera lowland. However, it must be noted that penetrating into the small rivers (Chernaya River, which enters Lake Tatarskoe and the Siz—a tributary of the Kursha River) the beavers first inhabited their upper stretches. When beavers distributed themselves throughout the Oka and Sh'ya River Basins, a tendency to move upstream was clearly noted.

In addition to the information presented above on the Meshchera Colony, it has been said that a small party of beavers, 4 adults and 3 yearlings, were released into the Pol' River, a tributary of the Klyaz'ma. This project was organized by the Moscow Hunting Directorate. The beavers were exported from Belorussia (the only case in the territory of the Oka Basin). Notwithstanding the unfavorable time of release (13 November), a certain number of beavers managed to survive (their tracks were found in the spring of 1953 at two different points of the bed of the Pol' River). Thus, the basis was laid for a new focus of distribution of river beaver on the area of the Meshchera lowland—in its northwestern section.

Klyaz'ma Colony

The origin of the Klyaz'ma Colony took place on the release of ten beavers in June 1949 in the ancient bed of the middle stream of the Klyaz'ma River in the section of its valley lying between the mouths of the Uvod' and Teza Rivers on the land of the Klyaz'ma Preserve. The beavers were imported from the Voronezh Preserve, 10 in all. Two died on release. In 1942, 2 others died. Thus, the initial number of animals consisted of only 6 adult individuals, of which 4 paired off to dwell in Lake Sorokin, in the eastern portion of the preserve. One adult with 2 young, born in 1941, settled on the Shizhegda River, in the center of the preserve, and 1 adult female went to Lake Peskro in the western part of the preserve. In the first years following their release, the beavers colonized the old beds of the Klyaz'ma within the range of the preserve. Beginning from 1949 (to judge from data by A. P. Razorenova, 1951), their distribution extended beyond the limits of preserve territory. Judging from their settlement sites, the beavers moved up the valley of the Klyaz'ma River and its tributaries. Unfortunately almost all information regarding beaver habitation in the Klyaz'ma River are the result of collecting data by means of interrogations. Only in 1953 did the author of this paper succeed in revisiting the region of the lower flow of the Teza to inspect its beaver-inhabited old beds and peat fields. Supplementing the conclusions of the examination and survey of the old beds of the Klyaz'ma in the former preserve by interrogations*, we present the data obtained in Table III, where we compare them with the data of our census of 1951.

It is seen from the table that outside the territory of the former preserve, where the beaver dwell almost exclusively in the old Klyaz'ma beds, settlement took place in the rivers of the Klyaz'ma Basin and the old beds of its largest tributary, the Teza. It should be noted that most of the beavers were distributed along the upper reaches of the Klyaz'ma in Vladimir Oblast'.

The second factor which strikes us on examining the table is the lack of increase in numbers of beaver in the colonies. However, unless a detailed study is made of the regions adjacent to the focuses of distribution, this may be too hasty a conclusion. The fact that settling beavers were entering territory a distance of 50-60 kilometers from the boundaries of the preserve was already known in 1950, and thus the separation of the settlements which have arisen is very possible. However,

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* This information was obtained by us from the forest ranger protecting beavers in the sanctuary created within the former preserve, N. M. Potemkin, and from the buoykeeper of the river port (8 February on the Klyaz'ma River), G. T. Konovalenko, the hunting expert of the Ivanovo Hunting Directorate, I. G. Pankratov, and the hunting expert of the Vladimir Hunting Directorate, A. A. Dmitriev.

the slow growth* of new settlements in the region of the former preserve and nearby points shown by the data of examinations carried out between 1951 and 1953 is clearly not normal. The threat to the beavers by poachers is indicated by five demonstrated cases of beaver losses in 1951 to 1955. Protection of beavers on the territory of the sanctuary organized in the former preserve was not actually enforced.

Table III

Number and distribution of beaver of Klyazma Colony

	1951		1953	
	In territory of former preserve	Outside former preserve	In territory of former preserve	Outside former preserve
All beds of Klyazma River	22	5	19	2
Tributaries of Klyazma River	2	9	1	12
Ancient beds of Teza River	-	2	-	4
Peat fields	-	1	-	2
Artificial ponds	-	-	-	1
Total	24	17	20	21

Mordov Colony

Thirty-four beavers were brought into the territory of the Mordov Preserve from 1936 to 1940. This provided the nucleus for the colony. The number of beavers gradually increased, and in 1950 there were nearly 300. In 1950 the beavers inhabited an area of 3,000 km^2. The distribution of beavers spread along the Moksha Valley and its tributaries. As a result its ancient channels and tributaries became inhabited; in addition small rivulets and rivers of an average size were inhabited (Satis River). Gradually the beavers also penetrated into other bodies of water. Distribution of the beavers was also observed outside the preserve. According to data of 1950, the distribution of beavers on water reservoirs of various types can be seen in Table IV.

The number in this colony sharply decreased in 1952 because 100 specimens of the beaver were caught in the land of the preserve and adjacent regions. According to data of the zoologist L. D. Shcherbakov, who conducted a census in previous years, only 20 settlements (53 beavers) existed in 1952 on the territory of the preserve. One result of beaver trapping should be considered to be a sharp increase in small settlements and settlements of single beavers. In 1950, these constituted 30 % of the total number of settlements accounted for, in 1952, 70 %. It would be highly interesting to follow up their subsequent fate**.

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* Editor's note – and also a considerable mobility of beavers.

** In the fall of 1954, according to data by L. D. Shcherbakov, 28 settlements were accounted for, with a total number of 97-100 head of beavers. Their numbers did not increase considerably since 1953.

Table IV

Distribution of beavers of Mordov Colony in various types of bodies of water according to the study of the year 1950

	Number of colonies					
	In the territory of the preserve		Outside the preserve		Total	
	Number	%	Number	%	Number	%
Ancient beds of the Moksha River	17	42.5	17	53.0	34	47.0
Small tributaries of the Moksha River	14	35.0	13	41.0	27	38.0
Satis River	9	22.5	1	3.0	10	14.0
Artificial pond (dam on the Moksha River)	-	-	1	3.0	1	1.0
	40	100.0	32	100.0	72	100.0

Middle Oka Colony

The appearance of this small colony in the region of the middle reaches of the Oka near the city of Serpukhov took place relatively recently. Two pairs of beavers were released in 1948 on the land of the Oka Terrace Preserve, in the small Tadenka River—a tributary of the Oka. One pair descended the Tadenka River and covering approximately 40 km, settled on the small Golovlinka River (vicinity of the town of Stupino, Moscow Oblast'). Despite the not highly favorable living conditions along this river—it flows near inhabited areas, possesses only a limited supply of trees and bushy food, and is also a point where waste waters of thermoelectrical stations are discharged—the beavers stayed until 1951, after which they abandoned it, departing in an unknown direction. In the fall of 1952, a family with young was present in the Oka Terrace Preserve dwelling in the middle reaches of the Tadenka River, and the young beavers born in 1949 and 1950 settled at 3 different points on the Sushka and Rechma Rivers and in the lower reaches of the Tadenka River (according to data of the zoologist L. V. Zablotskaya). Their total number was 11 head. We should note that regions of release for beavers were almost exhausted.

Upper Moskva—River Colony

A second small colony of beavers appeared in the territory of the Oka Basin when 9 beavers were released in the upper reaches of the Moskva River on the territory of the former Upper Moskva-River Preserve. According to the data of the census of 1949-1950, conducted by the zoologist of the preserve, V. N. Ovidieva, the beavers lived at four points in the Moskva River.

In November 1952, Geltser established 6 points with fresh gnawing of trees by

beavers lying 300 m to 2.5 km apart on the territory of the former preserve and 1 region 4 km below its boundary, 2 km lower than the village of Novopokrov. This data may testify to the existence of 5-7 settlements. Beside this, Yu. Gel'tser reports finding beavers in the upper reaches of the Moskva River. In the spring of 1953, we found only 4 points in the former preserve which showed signs of beaver activity.

Pustyn' Colony

This colony appeared after 6 beavers were released in 1939 into one of the lakes of karst origin through which the channel of the Serezha River passes. The release was organized by the Biological Station of Gorkii University near the village Pustyn (Chernukhin Region, Arzamas Province). In 1948, according to data by I. A. Shilov (1950), approximately 30 beavers were counted in the colony, and their spread beyond the limits of the lake system had begun. According to a personal communication by V. I. Kozlov (lecturer of the Faculty of Zoology of Gor'kii University), which we received in the fall of 1953, no considerable increase in beaver numbers was noted there in subsequent years. According to him, encounters with beavers were also rare on the Serezha River, above and below the lake system.

Turning now to a review of the number of beavers in the Oka Preserve, it should be said that a reconstruction of the full picture of the change of beaver numbers in various years is impossible, as the data of the census in individual sections are rather inadequate.

From the table presented below, it is seen that a total of approximately 1,000 head were counted on the land of the Oka Basin (Table V).

Table V

Compilation of data on changes of beaver numbers in the Oka Basin

Year / Colony	1940	1941	1942	1945	1947	1949	1950	1951
Meshchera	27	35	39	132	200	240	-	400
Klyaz'ma	8	11			114			160
Mordov	81	107	111	160	202			300
Pustyn'	6				30			30
Middle Oka								10
Upper Moskva River								16
Total	122	153	150	292	546			916

Colonies of River Beaver in the Oka River Basin

Permanent colonies of beavers are encountered in all types of bodies of water in the Oka Basin. The lodges were noted* even on the streams of as large a river as the Moksha (this was apparently the temporary summer habitation of the beavers during the seasonal migrations). Beavers at the present time inhabit natural ponds,

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* At the time of investigating the water reservoirs preceding the trapping of 1952.

beds of rivers of moderate and small size, lakes outside the flood plain, temporary bodies of water among marshes, and bodies of water appearing as a result of human activities (drainage ditches, peat diggings, artificial ponds).

Comparative data on beaver colonization in various types of bodies of water reflect the characteristic traits of the hydrography of the regions where the individual colonies are distributed (Table VI).

Table VI

Comparative data on beaver colonies in various types of bodies of water (according to data from the census of 1950-1953)*

Type of body of water \ Colony	Number of settlements according to colonies					
	Meshchera	Klyazma	Mordov	Middle Oka	Upper Moskva River	Pustyn'
River beds — Average	6	-	10	-	-	-
River beds — Small	17	13	27	4	6	-
Ancient beds	36	25	34	-	-	-
Lakes outside flood plains	10	-	-	-	-	-
Temporary ponds in marshes	2	-	-	-	-	-
Drainage ditches	11	-	-	-	-	-
Peat fields	-	2	-	-	-	-
Artificial ponds	-	1	1	-	-	-
Karst lakes	-	-	-	-	-	7-8 (30) beaver

It is noteworthy that the heterogeneity of the structure of the surface, vegetation conditions, and degree of economic use in the Oka Basin produced a diversity of individual types of bodies of water in various sections. Thus, the ancient beds of the Pra, for instance, differ distinctly in soil and vegetation cover from the shores of the old channels of the Klyaz'ma and Moksha Rivers. The small rivers of the Meshchera lowland flowing along peat fields have little in common with such regions as the lower stretches of the Oka, whose valleys resemble ravinelike depressions and are bordered by high slopes of original shores.

The heterogeneity of the water reservoirs is further emphasized by the varying intensity of economical use. Thus, we use the hydrological classification of water bodies only to facilitate the placement of the material and do not identify it with the classification of beaver stations. As a basis for the description of the latter, we established the fundamental features which determine the degree of suitability for beaver habitation, namely: 1) soil structure of the shore; 2) hydrological regime; 3) abundance of trees and bushy food plants on the shores; 4) intensity of economic exploitation.

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* In the Mordov Colony the data given are for the census of 1950, in the Meshchera for 1951, in the Middle Oka and Upper Moskva River for 1952; in the Klyaz'ma for 1953; in Pustyn' as we had no other materials, the data is for the year 1948 (Shilov, 1950).

Beds of Rivers of Moderate Size

We include rivers 100-150 km long and 20-40 m wide in the group of rivers of moderate size. The number of such rivers in the basin which are inhabited by beavers has so far remained small. They include the Pra River on the territory of the Meshchera lowland, the Satis River in the Moksha Basin, the Teza River in the Klyaz'ma Basin, and the Serezha River in the eastern district of the region described here. Each of these rivers possesses a unique combination of feeding and protective conditions and represents a special type of beaver colonization site.

The Pra River has sandy banks and waterfalls alternating with wet sandy shallows. The dominant type of bank is the leafy forest. Along the shore, the river is fringed by bushy willow vegetation (Salix rossica L.). The herbage on the shore consists of grasses (Calamagrostis epigeus L., Molinia cerulea M.). The reed canary grass [Phalaris] (Dygraphis arundinaceus L.) and sedge (Carex gracilis) grow near the surface of the water. The river is 30-40 m wide. In summer the water rises 3.5 m. In years with abundant precipitation an autumn water rise of up to 2.5 m is observed. The current is rapid and the river forms many abandoned beds. Since rafting was stopped in 1950 the economic exploitation of the river has not been intensive. The banks of the river are mainly used for haymaking.

The beavers dwell in burrows. Their numbers are subject to seasonal fluctuations, increasing in summer, because the beavers migrate to the river channel from former beds. In winter, when the temporary inhabitants leave, the numbers decrease. Taking as the index of density the average length of the river bed for each beaver-inhabited section, in the western section of the preserve the index was 2 km for the summer of 1953 and 1.5 km for the winter of 1952. After the cessation of rafting down the river in 1950, the number of families dwelling permanently on the stream began to rise. In 1950 two beaver families hibernated within the bounds of the preserve on the bed (36 km long); in 1951, 3; in 1954, 4.

Satis River. The shore is similar to that of the Pra River. However, in contrast to that, the shore consists not only of sand but also of loam. As the Satis River flows past the Mordov Preserve meadows are the dominant landscape along the right shore, outside the preserve, and leafy forests along the left, inside the preserve. Both banks are bordered with willow stands. The grass cover of the shores consists of grasses, sedges and various herbs. The width of the river varies greatly, and in various sections of the middle reaches fluctuates from 1 to 30 m. Near the barrages of the hydroelectric stations it attains a width of 50 to 100 m. The spring rise of the water is 2.5 m. During repairs of the dams the surface of the water drops by 1.2 to 1.4 m. The current is swift. Former beds are not numerous. The right shore is used very intensively for economic purposes. Besides hay cutting, the meadows are used for cattle grazing and in some places are plowed for vegetable gardens. Two hydroelectric station barrages lie on the stream within the preserve. The beavers inhabit burrows. The numbers of their habitations are constant and rather high. In the fall of 1951, the presence of 9 colonies was established in the preserve along a 20-km stretch of the river. On this basis the beaver population density index equals 2.2 km per inhabited section.

Teza River. This river has precipitous clayey and loamy banks. The lower stretches of the river at one of the points at which traces of beaver were found is surrounded by meadows. The edge of the bank is fringed in some places by willows and alders. The width of the river is 30-40 m. The current is swift. The flood plain has numerous former channels. The seasonal fluctuation of the water level reaches 2 to 2.5 m. The beds and banks are intensively exploited for economic purposes. The river is navigable. Roads are built on the shores, connecting the villages situated along the river, and cattle are grazed there. The river contains locks. Traces of beaver habitation which have been discovered testify to their brief visits to the stream from the former beds.

Serezha River. The river has steep sandy banks mainly, and passes through dense fir, mainly pine forests, which also cover its shores. Meadow stretches are also present. Willow stands near the shore are not very strongly developed. The river current is sluggish. Economic exploitation of the shore areas is limited to hay raising. According to reports by lecturer V. I. Kozlov, the beavers live in burrows. Their settlements above and below the lake system through which the channel of the Serezha River passes, are rare and consist of individual beavers.

A comparison of the data on these rivers shows that the principal ecological conditions consist of an insufficiency of tree or bush food plants on the shores, economical exploitation, and poor shore soil composition. The first of these conditions determines the low density of beavers along the Serezha River, the second the Teza, the third the poor colonization of the bed of the Pra River. With regard to the latter, the beavers prefer the old channels, where the sandy shores characteristic for the Pra and the bodies of water of its flood plain are washed away to a lesser degree. Other conditions (hydrological conditions, velocity of the stream) exert a subordinate influence on the degree of habitation of the rivers.

Beds of Small Rivers

Small rivers of less than 50 km in length and 10-12 m in width are included in this category. In the basins enumerated, the number of such rivers inhabited by beavers is high and increases yearly. The majority are 3-7 m wide and 15-30 km long. The features of their natural conditions allow us to differentiate the following groups of beaver habitats:

1) Rivers which flow along peat deposits or marshy valleys, having the character of forested or bushy marshes.

2) Rivers which possess no greatly eroded valleys and which flow through forested nonmarshy plains.

3) Rivers with marshy valleys flowing on plains of an elevated type.

The first group includes the rivers of the lowlands--the Meshchera and Moksha lowland area (Rivers of the Pra Basin--Belaya, Urazh, etc; the basin of the Gus'-Kursha and Narma Rivers, etc, the rivers Chernaya, Lamsha, Sh'ya, Tsna, etc, of the near-Oka part of the lowland, the rivers of the Moksha River Basin--Chernaya, Pushta). The shores of these rivers contain peat, and are covered by alders, alder-birch, birch-alder, and brushy marshes with willows. The grass cover of these marshes consists of nettles, reeds, sedge, blue joint reed grass, reed canary grass, cinquefoil, and meadowsweet. Shore stands of willow develop in those sections where the river crosses either bushy marshes or meadow areas. The predominating species of willow is the gray willow. The spring rise of the waters in each of the rivers depends on the area drained and in larger rivers (such as the Sh'ya and Tsna) amounts to 2 m. Economic use of the fields near the river is not great and is restricted to haymaking. Beavers inhabit small lodges, more rarely burrows. They usually dam the river channels.

Rivers crossing plains covered with mixed forests belong to the second group of habitats. On the territory of the Meshchera they include the lower reaches of the Kad' River, in the Moksha Basin and the Vyaz'--Pushta Rivers and one of the streams in the western part of the basin, on the territory of the Oka Terrace Preserve. The hard nonmarshy banks of these rivers, composed of sands or loams,

are covered with forests, leafy species predominating. Shore willows are absent. The degree of fluctuation of the water level differs depending on the drainage areas of each river, but does not exceed 1.5 m. The beavers live in burrows. Lodges are constructed when the level of the water rises. The beavers dam the streams.

The third group of habitats include rivers flowing down the western half of the basin, of a higher altitude. These include the Moskva (upper reaches), Tadenka, and Sushka (flowing in the region where the Oka Terrace Preserve is located). All these rivers possess well-defined valleys where forest areas alternate with meadows. The flood plain forests consist of stands of gray alder (Moskva River) and black alder (Tadenka and Sushka Rivers), with a mixture of bird cherries and willow trees. The river channels are fringed for long distances by stands of bushy willows. The grassy vegetation of the shores consists of various herbs, the meadowsweet, angelica, chervil, etc. In some areas the river channels approach the original banks, overgrown with mixed forests consisting of birch, aspen and spruce trees. The banks are composed of clays and loams. The bottom is frequently stony. Economic use of the land along the shore is limited to hay cutting. Beavers live in burrows, sometimes lodgelike structures. They dam the river currents.

A study of the population density of all small rivers shows that this depends on two factors: the profusion of arboreal and bushy food plants along the banks, and the size of the rivers themselves. All small rivers up to 2 m in width and resembling brooks more than rivers have a very low beaver population density. In none, regardless of which group of habitats it belonged to, did we note the presence of more than one settlement. As an example we may present the list of all these small rivers in which one settlement of beavers is present per 4-5 km of river bed: Chernenkaya (first group of habitats), Vyaz'-Pushta (second group), Sushka (third group. The highest population density was encountered on rivers whose width reached 5-12 m, and which possessed sufficient stores of good beaver food, such as willows and aspens on their banks. An example is the Belaya River (first group of habitats) and the Moskva (third group), the population density index of which amounted to 2.0-2.5 km per settlement.

Old Channels

On the land of the basin away from the rivers, the beavers live in former channels of the Moksha, Oka, Pra, Klyazma, and the largest tributary of the latter, the Teza. The old channels reflecting the characteristics of the natural conditions of the rivers which created them, constitute a special type of beaver dwelling and merit special description.

Old Oka Beds Inhabited by Beavers

These are large oxbow lakes and lakes with a surface area of up to 9 hectares and clayey shores, the high regions of which alternate with gently sloping areas. The shore lands consist of meadows and forests composed chiefly of oak, with a mixture of aspen and birch. Along the water channel the lakes in certain places are aquatic fringed with willow stands. The marsh vegetation of the coastal zone is rather varied, consisting of cattails, reeds, rushes, manna grass, marshy flowering rush, arrowhead, bur reeds, spatterdocks, water lilies, and several species of pondweeds, etc. The spring water rise is very great--4.5-5 m. Intensive economic use is made of the land around the lakes for cattle grazing hay cutting, acorn gathering, and eglantine or sweetbriar fruit picking. The lakes are regularly frequented by hunters or fishermen. The beavers live in burrows. The colonization of the old beds of the Oka began fairly recently. Permanent beaver settlement on

individual lakes in the flood plains of the Oka River were first noted in the year 1950, before which only cases of wintering were observed, the beavers subsequently abandoning the lakes. Despite the large size of the lakes, the density of the beaver population is still very low. Only one beaver colony is noted on each inhabited lake.

Old Moksha River Beds Inhabited by Beavers

These are large lakes with an elongated form, 0.5-4 km long and 70-100 m wide. Some are situated between meadows, others among flood-plain forests, with old existing channels containing both meadows and forests. Steep shore regions alternate with gently sloping banks. The trees on the shores of the lakes consist of willows, the stands of which attain considerable density. The flood-plain forests covering the shores in the lowest regions of the old river beds consist of alder trees, and higher up of oaks, with a mixture of Russian elms. Shore willows are encountered only on a few old river channels. In periods without floods, the old beds are generally not connected with one another, an exception being a group of large old forested beds on the lands of the Mordov Preserve, through which the lowest reaches of the Pushta River flows. On the coastal fringes of the lakes the following are encountered: manna grass, reeds, spatterdock, water lilies, and cattail rushes. In the spring the water rises 2 to 2.5 m. Economic use of the shore areas is limited to hay cutting. The beavers inhabit burrows and lodges. The intensity of settlement on the old beds is not high. In the majority of cases one settlement was found per lake, an exception being a group of forest lakes connected to one another by the current of the Pushta River. On each lake of this group, according to data by I. D. Shcherbakov (1950), there were up to 3-4 settlements of beaver. These were from 0.6 to 2.2 km of coastal line per beaver settlement.

Old Klyaz'ma River Beds Inhabited by Beavers

These are large lakes of elongated form often connected by streams. The length of the lakes varies from 0.5 to 2.5 km, and the width is 30-80 m. These are typical forest lakes, separated from the adjacent meadows by a tongue of forest. Together with high shores composed of loams and covered with oak and aspen forests, with a mixture of birch, lower sections are present with loose peaty soils, covered with alder trees. The willows near the coast are spread chiefly along the lower parts of the shores, the grass cover of which is well developed and variegated. The herbage around the oak forests and aspens consists of meadowsweet, goutweed, cleavers, lilies of the valley, and footwort. Nettle predominates in the grass around the alders. The aquatic vegetation occurs on the low shores, consisting of groups of sedges, cattails, manna grass, reeds, water lilies, spatterdocks, etc. The water rises 2.5-3 m in the spring. Economic use of the shorelands and lakes is rather intensive, the former being used for hay cutting and cattle grazing. The lakes are regularly frequented by hunters and fishermen. The beavers live in burrows. As in the case of the flood plains of the Moksha one settlement of beavers generally inhabits a lake.

Old Pra River Channels Inhabited by Beavers

These are lakes of moderate size and elongated form, 150 m to 2 km long with a width of 20-40 m. They are not connected to one another except during high water. The lakes are fringed by forest-type vegetation. In some places meadows line the lakes. Steep high banks around the lakes alternate with those with gentle slopes. The soils of the shores are sandy. The elevated sections are covered with forests consisting of oaks and birch with a mixture of aspen, the lower parts are

covered with willow stands, chiefly the Russian and gray willow. The herbaceous cover of the shores is uniform and usually includes Molinia moor grass, reed bent, sedge, reed canary grass and cinquefoil. It also forms brushes in the shore zone of the lakes, promoting a cover on it. The aquatic zone contains spatterdock, water lilies and floating pondweed. In spring the water rises 3-3.5 m. The economic exploitation of the area is limited to hay cutting. Outside the preserve area, the lakes are visited by hunters and fishermen. The beavers inhabit burrows and semi-lodges, and in rare cases lodges. On each lake there is usually one permanent beaver settlement.

Old Teza River Beds Inhabited by Beavers

These are lakes of average size and elongated form, 0.5-2 km in length and 15-30 m wide, and are typical to forests. Meadow platforms line the banks and are separated from the water by a ridge of trees and bushy vegetation (alders, willows, etc). The higher regions have hard loamy soils and alternate with lower areas consisting of loose peaty soils. The woods in the elevated regions consist of oak, elm and linden, with a subforest of hazels, bird cherry trees, and sweetbrier, and a herbaceous cover consisting of goutweed, meadowsweet, and cleavers. Alder trees with a herbaceous cover of nettles and reeds are distributed on the lower platforms. In the coastal aquatic zone of the lake, manna grass, lesser reed mace, reeds, spatterdocks, and water lilies grow. The beavers live in burrows and lodges. In spring the water rises 2 m. Economic use of the land around is limited to hay cutting. The lakes are frequented regularly by hunters and fishermen. The presence of a single beaver colony was noted on each of the old river beds.

Considering the density of settlement of the old beds of the rivers, we should note that what is characteristic of the old beds of the Oka, Klyazma, Pra, and Teza is that one permanent* beaver settlement is situated on each old bed. Two settlements on one old bed constitute a rare event (noted in 1951 in Lake Sorokino in the flood plain of the Klyazma River and the old bed of the Chulimikha in the Pra flood plain). Such a type of beaver settlement distribution is encountered in the Moksha flood plain beyond the Mordov Preserve. The high population density in the forest lakes on the preserves may be ascribed to the flow of current which markedly distinguishes them from the old beds.

Lakes Outside the Flood Plain Area

Beavers inhabit lakes which are not on flood plains only in the region of the Meshchera Colony on the territory of the Meshchera lowland. These lakes are situated among marshes (bushy or woody) at extreme points in the area and are of a round form. The lake sizes are highly varied. The largest body of water inhabited by beavers is Lake Dubovoe, with an area of 120 hectares (the northern part of the Pra Basin). The smallest is Lake Semenki, the area of which is not in excess of 0.5 hectares (Oka Preserve). The regions of the bushy and woody marshes along the coast usually alternate, but colonized lakes are encountered which are surrounded only by forest marshes (Lake Veshcherki and Lake Mymrus in the Oka Preserve). The rows of trees of the bushy marshes consist of birch and several species of willow, among which gray willows and bay-leaf willows predominate. The trees of the

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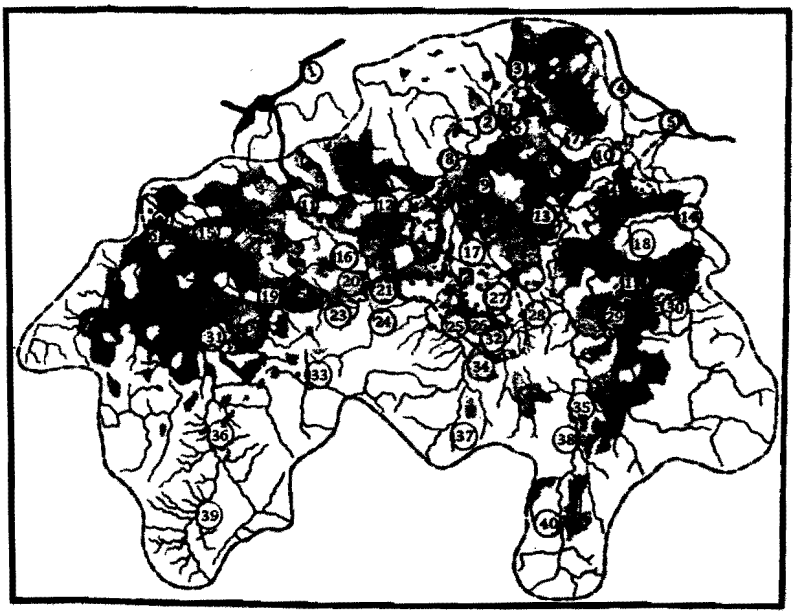
* We apply the term permanent to such settlements as are inhabited by adult beavers constantly living in the given body of water. The periodically appearing new settlements usually belong to matured young changing their dwelling, often passing the first winter of their independent existence not far from the parents and migrating only later.



1-Volga R
2-Suzdal'
3-Sinya
4-Volga R
5-Gor'kii
6-Kodrov
7-Klyaz'ma R
8-Vladimir
9-Sudogda
10-Oka R
11-Moscow
12-Klyaz'ma R
13-Murom
14-Arzamas
15-Mozhaisk
16-Moskva R
17-Tuma
18-Ardatov
19-Serpukhov
20-Kolomna
21-Oka R
22-Kasimov
23-Kashira
24-Zaraisk
25-Ryazan'
26-Pra R
27-Oka R
28-Erakhtur
29-Mok R
30-Temnikov
31-Kaluga
32-Shevkoe
33-Tula
34-Shilovo
35-Tusa R
36-Oka R
37-Ryazhsk
38-Marshansk
39-Orel
40-Tambov

Legend:
Oka Basin boundary
Approximate boundary
beaver colony distribution
Beaver colony
1- Mordov
2- Meshchera
3- Klyazma
4- Pustya'
5- Central Oka
6- Upper Moskva River

Figure 1. Map of the Oka River Basin indicating beaver lodges on the river in 1951-1952

forest marshes are mainly alder trees and birch, which are encountered in various proportions, and also stands of shore willows, which are found in the region of the bushy marshes. In the herbacous cover the usual vegetation consists of nettles, reeds, meadowsweet, sedge, lanceolate reed, bent cinquefoil, marsh cinquefoil, and water arum. The lakes outside the flood plains situated in the far parts of the marshes have elevated sections of bank covered by birches admixed with aspens, (Lake Svyatoe, Lake Ukhanskoe, etc). Close to the banks in the aquatic zone there are reeds, rushes, cattails, marsh horsetails, manna grass, greater reed mace, water lilies, etc. The banks rise over the water to a height of 30-50 cm. The soils are loose and peaty. The spring water rise does not exceed 0.8 m. The connection with surrounding marshes is effected through ditches and canals. The economic exploitation of the shore areas is limited to hay cutting in individual regions. The lakes situated outside the preserve are regularly visited by hunters and fishermen. The beaver live in burrows and huts. On each lake outside the flood plain on the land of preserve, regardless of its dimensions, one permanent beaver settlement is noted.

Temporary Bodies of Water in Marshes

All the beaver settlements on the temporary bodies of water in the marshes on the preserve are found only on the territory of the Meshchera lowland, which is the region most intensively inhabited by the beavers. Marshes where beaver settlements were discovered belong to the category of lowland marshes, since they are bushy and forest-covered.

The sites of beaver settlement in the marshes consisted of depressions filled with water, (apparently the remains of lakes in the last stages of becoming marshes) 100-500 m^2 in area, of an irregular form and 1.0-1.5 m deep. The water surface of these depressions is almost at the same level as the water-free marsh, and the beavers, unable to find shelter in burrows, construct lodges. In the event that high non-flooded regions are nearby, the beavers construct burrows there. The woody food of the beavers consist of willows and birches growing on the marshes. The fluctuation of the water-level is slight (0.5-0.8 m). These regions are not put to economic use. The settlement of beavers in such areas has been rare until now.

Ameliorative Drainage Ditches

Cases of beaver habitation in ditches are also specific for the Meshchera Colony. The ditches which are inhabited by beavers are part of the drainage network made in 1877 in the basin of the Pra and Gus' Rivers and part of the lowland near the Oka. The ditches traverse areas of forest and bushy marshes. Their channels are 1.0-1.5 m wide and are overgrown with aquatic and marsh vegetation — spatterdocks, cattails, and ditch reeds; they resemble natural bodies of water. Their shores, which are of artificial origin since they were poured there, rise above the surface of the surrounding marshes and the level of the water filling them. The height of the banks reaches 1-1.2 m. A characteristic of the vegetation is that it is xerophilic, which is not usual for the vegetation of the marshes which surround them (aspen). Willows are widespread near the water. The water level fluctuates between the limits of 0.5 m and 1.0 m. Economic use of the area is limited to hay cutting in individual regions of the marshes. The beavers inhabit lodges and burrows. The population density is 5-8 km of stream bed per settlement.

Peat Bogs

Beaver habitations in peat bogs which have become filled with water following the extraction of the peat occur in the region of settlement of the Klyazma Colony. Beaver settlements were discovered on the Yuzhskii peat bog (9 km from the eastern boundary of the former preserve). The economic exploitation of these bogs began in 1938 and the first sections of peat digging there becoming covered by a dense vegetation of trees and bushes. The peat bogs, where the beaver colonies are located, consist of a regular network of quadrangular bodies of water 0.5-1.0 m deep, 5-20 m long, and 5 m wide, separated from each other by low isthmuses (0.4-0.8 m high) covered by stands of birch, alder, arboraceous willows, and bushy, gray willows. The isthmuses are not wide—0.5-2.0 m. Groups of meadowsweet, nettle, reeds, and sedges are encountered in the herbaceous covers. Among the aquatic plants of the bog zone only duckweed has been noted. The realm of activities of the beaver family embraces an area of not less than 500 km^2, including a complete system of peat bogs. No economic use is made of the area. The beavers inhabit lodges and burrows. Beavers which settled on this marsh in 1950 already occupy several separate sections.

Data on the uninterruptedly increasing numbers of beavers in the Oka Basin indirectly demonstrate the normal course of their development. We have obtained direct data on the intensity of beaver reproduction through observations of the territory of the Oka Preserve and the adjacent sections. These were supplemented by data from other regions of the basin.

Information on the number of new families, the ratio of reproducing to non-reproducing families, and information on the number of young per litter and deaths per litter during the first months of life were taken as an indication of the intensity of beaver reproduction.

The data presented in Table VII indicates that there was a considerable percentage of newly formed settlements among the total number.

Table VII

Increase of numbers of settlements according to data of censuses taken in the years 1949–1952

Year	Total number of colonies	Newly formed settlements	
	Number	Number	% of total number of colonies
1949	27	2	7.3
1950	32	7	21.9
1951	36	8	22.2
1952	37	14	29.7

An average of 20% of all the settlements are new. It would be of interest to obtain similar data for the entire population. Data on the formation of new settlements on the territory of the former Klyazma Preserve in the 10 years following the release of the above beavers also testify to the high rate of reproduction of the beavers of the Klyazma.

Employing the data on beaver colonization of new water pools for the period from 1948 to 1950, we calculated that each newly inhabited body of water indicates the appearance of one settlement (with such an assumption errors were only possible by underestimating the number of newly formed settlements). The yearly figure for the increase of new settlements calculated from this was 26.3-43% (Table VIII).

The absence of new settlements in subsequent years on the lands of the former Klyazma Preserve apparently testifies not to a fall in the rate of reproduction but to the settlement of the animals beyond the limits of the preserve. Information on the presence of beaver settlements outside the territory of the preserve is rather limited. Data on the formation of new settlements are available for the Mordov Colony, where an increase in the beaver numbers was noted uninterruptedly up to 1952. We do not possess similar data for the former Klyazma Preserve.

Data on reproducing and nonreproducing families were obtained by us only for the territory of the Oka Preserve and the adjacent sections. According to our observations, in the period from 1950 to 1952, 12-18 families able to reproduce were present in this region. We assumed that families from the second year of formation were of this kind, while 6-14 families were newly formed, for which we could not

assume offspring. (In all, these consisted of 58-68% of all families inhabiting the area covered in our observations).

Table VIII

Number of bodies of water inhabited by beavers on the territory of former Klyazma Preserve from 1948 to 1950*

	1948		1949		1950	
	Number	%	Number	%	Number	%
Total number of bodies of water inhabited	14	100.0	19	100.0	27	100.0
Number of newly inhabited settlements.....	6	43.0	5	26.3	8	29.5

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* Translator's note—The rate of appearance of new settlements and the rate of settlement and remoteness of the sites of distribution often indicate unfavorable areas for beavers.

Data on the number of families with and without issue are presented in Table IX.

Table IX

Number of families with and without issue

Year	Number of families able to reproduce				Total number of families			
	Total families		Families with issue		Total families		Families with issue	
	Number	%	Number	%	Number	%	Number	%
1950	12	100.0	9	75.0	18	100.0	9	50.0
1951	16	100.0	12	75.0	24	100.0	12	50.0
1952	18	100.0	15	83.3	32	100.0	15	47.5

It is seen from the table that issue was produced on the average by 77% of the families able to reproduce or approximately 50% of all families (including new ones).

Families failing to procreate principally either belonged to settlements existing only for the second year (built by 3-year-old beavers) or had suffered changes in their composition and became weaker thereby. We possess data only for the Oka Terrace Preserve on the reproduction of beaver families inhabiting other regions of the Oka Basin. They testify to the high rate of reproduction of the pair of beavers which settled on the territory of the preserve after their release (on the Tadenka River, a tributary of the Oka). According to data by L. V. Zablotskaya, this pair produced offspring in the fourth year of life and reproduced uninterruptedly up to 1951. An adult female of this family killed by a poacher in 1952 proved to be pregnant.

We possess information concerning the number of young per litter from data collected on the territory of the Oka Preserve and results of observations by L. V. Zablotskaya (Oka Terrace Preserve).

For the Meshchera population we possess 12 records on the number of young per litter, compiled in 1950-1952. Of these 4 were compiled on the lake as a result of catching young beaver, 7 were drawn up from direct observations at the body of water, and one from the dissection of pregnant females.

On catching the animals it was possible to determine that in the 4 cases on the lake one-year-olds were involved (one litter) In 3 cases, 2 young were found in the litter. The average number per litter found when catching was 2.5. For each adult female caught, according to our data, there were also 2.5 young (4 females and 10 yearlings were caught). Similar figures are also obtained after analyzing the data of direct observations. In 2 cases there was one beaver cub per litter and in 4 cases there were 3 beaver cubs. One case indicating the presence of 4 beaver cubs originated from the beekeeper of a kolkhoz, an inhabitant of the village of Gorodnoe, V.I. Zakharkin, who chanced to see a female with 4 young in August 1951, on Lake Kholodnyi Klyuch. A pregnant female caught on 25 March 1952, on Lake Smolyanka, had 3 embryos. According to this data, the average number of young per litter is 2.55. Comparing this with the average of 2 (V.S. Poyarkov, 1953), established as the average yearly number of young under natural conditions, we must conclude that conditions for reproduction are rather favorable in the Oka Preserve region.

Information on the number of beaver cubs per litter for other sections of the basin is rather scarce. For the Mordov Colony we shall present the report of F.D Shaposhnikov who related a case of catching a female with 5 young, which is doubtlessly a very interesting exception.

L.V. Zablotskaya noted the following number of young in litters in the Oka Terrace Preserve: 13 young in 1949 and 2 in 1950. On dissecting a female killed in the spring of 1952, three embryos were discovered.

The death of young is highest during the first year of life. According to data of the Voronezh Preserve, the death rate amounts to 45% in natural conditions. We have no data at our disposal to calculate the mortality rate. Cases of discovery of beaver carcasses in nature are extremely rare, but single observations testify to the fact that deaths of young beavers do occur. We made observations in the spring of 1952 and 1953 on the composition of the beaver families. (Observations from the emergence of beavers for feeding before the thaws open the bodies of water and after floods attest to this). In these observations we were unable to note more than two one-year-old beavers on Lake Aleshina-Luka although in 1951 and 1952 we noted three young each year. There are also at hand direct observations on the death of one-year-old beavers. L.V. Zablotskaya reports a case of the death of a yearling in the middle of May 1950. The dissection and examination of this carcass showed that the animal was underdeveloped for its age and white tubercular formations were present in his lungs. In July 1952, according to data by the forester N.M. Potemkin, a carcass of a yearling was found on the territory of the former Klyazma Preserve, on Lake Purkhalovo. At the same place a yearling was found in death agony after fishermen ejected it from a Krylena* (information given by A.A. Dmitriev-scientist-hunter of the Vladimir Hunting Directorate.

The death of two-year-olds in fishermen's nets in the spring of 1952 was noted by L.V. Zablotskaya on the Rechma River, not far from the boundary of the Oka Terrace Preserve.

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* Translator's note-Krylena is a local name for a bottle-shaped weir.

We established the presence of young beavers on the Oka Preserve by listening to their calls near the burrows and lodges. Whining sounds coming from these or from under the ground indicated the presence of young beavers. We succeeded in discovering young beavers between 1 May and 14 June by listening for their sounds. The majority of these cases occurred in the period from 1 to 20 May (20 observations) and 21 May to 14 June (16 observations). On the basis of these data, we assume the time of appearance of most of the young to be the middle of May. However, the data from trapping introduced several corrections into our assumptions concerning the time of appearance of young beavers. Ten yearlings captured between 20 and 28 August 1952 weighed 4.3–6 kg, which, according to data of large-scale measurements on the Voronezh Preserve, corresponds to an age of 3.5–4 months (L. S. Lavrov, 1937). Thus, the time of birth of most of the cubs is the end of April to the beginning of May. This coincides with observations on the time the young beavers first swim from their burrows, which was noted on 17 May 1944, at Lake Sundritsa; 1 June 1940, at Lake Ukhanskoe, and 2 June 1942, at Lake Svyatoe.

It must be noted that during the summer the young stay very close to the adult beavers, or at least, to the females. Observations show that in June the adult beavers bring food to the young on Lake Svyatoe and Lake Ukhanskoe. We noted beavers swimming with leaves of spatterdocks between their teeth to the lodges containing the young.

All yearlings captured in August 1952 were taken in the same burrows as adult beavers. Manifestations of concern by the adults for the young were also noted in the early spring when they had already almost reached the age of yearlings. Observing the activity of the beaver for several hours (12 April 1952), we noted that young beavers stayed near the edge of the shore while one very large beaver went up the slope of the shore from time to time to obtain food (apparently a female). Strips of young birch bark brought by this beaver were immediately set upon and gnawed by the young beavers. The approach of the female with food for the young which were waiting near the water channel was accompanied by sounds, apparently a call and an answer.

Despite this there are indications that the younger beavers are to some extent already independent at the age of 3–4 months. Not infrequently they feed on the nearby aquatic vegetation somewhat distant from the adult beaver. We observed young beavers feeding on parts of reeds protruding above water in Lake Ukhanskoe (10 August 1942, Lake Ukhanskoe). On one of the old channels of the Pra, at Lake Krivoe on 11 August 1952 we kept watch for a long period on three young beavers feeding in the coastal growths of cinquefoil at a distance of 50–100 m from each other. Two young beavers which we watched on 31 August 1952 on the old bed of the Aleshina Lake also fed on shore growths of cinquefoil, but they stayed close together.

Diet

The species composition of plants eaten by beavers on the territory of the Oka Basin is highly varied. On the basis of our observations and those of other zoologists (L. V. Zablotskaya, V. N. Ovidieva, and D. D. Shcherbakova), we compiled a list of plants eaten by beavers which contains 20 species of tree or bush types and 49 herbaceous plants. This list is incomplete.

The list illustrates the wide range of the beaver in selecting his food. However, observations in all regions of the basin have shown that during its entire life at a settlement, each beaver family makes use of a comparatively small number of plants for feeding purposes, their composition being determined by their profusion in the region inhabited.

Especially important in the diet of beavers are the woody bushy foods which are the chief food in the fall, winter, and spring, and to some extent in the summer as well. The composition and abundance of these foods chiefly determine the well-being of the population. The observations presented have shown that for all sections of the basin of the Oka River which we examined, the most preferred arboraceous bushy peat plants were the aspen, several species of the very widely distributed willows—the Russian willow and the bushy willow which occupy the shaly parts of rivers, the gray willow, and the bushy willow which fringe the lower shores of the lakes, and the treelike bay-leaf willow, which grows in marshes.

When there is an insufficient supply of these plants in the shore belt, beavers eat considerable amounts of birch, oak, elm (mainly of a young age), birch, cherry, hazel, etc.

All settlements of beaver colonies now in existence on the basin of the Oka may be diagrammatically differentiated according to the nature of the fall, winter, and spring nutrition into four groups:

1. Settlements where beavers feed mainly on aspen or willow or both.

2. Settlements where beavers eat food of secondary value (birch, elm, oak, and alder, etc), in addition to willow and aspen.

3. Settlements where beavers mainly eat three species of food of secondary value (birch, elm, oak), aspen and willow playing the role of supplementary foods.

4. Settlements where beavers exist exclusively on three species of food of secondary value.

The bulk (70%) of the beaver population of the Oka Basin has a fall, winter, and spring food regime of full value, based on aspen and willow in various combinations. Beavers of the Klyaz'ma, Upper Moskva River, Central Oka colonies and the majority of the Mordov and Meshchera zones have such a fall-winter-spring diet. Those inhabiting the ancient beds of the Klyaz'ma eat chiefly aspens in the fall, winter, and spring. These are distributed over the shores. However, because of the maturity of the shore vegetation, where the aspen has an average diameter of 18-20 cm, their food value cannot be considered high. The combination which is most favorable for beavers is the diet provided by aspen and willow, which is characteristic for beavers inhabiting the majority of the old beds of the Pra and the Oka (in the region of the Oka's flow which bends around the Meshchera lowland), the small rivers of the region of the central flow of the Oka and the upper reaches of the Moskva River.

The willow is the chief food of the beavers in the old Moksha beds, which are meadowy in some old beds of the Pra, in the channels of drainage canals, and in the majority of the small rivers in the Meshchera lowland.

The willow and other species which have secondary food value (birch, oak, alder, etc), are the basis of the beaver diet on the surface of bodies of water of the Meshchera lowland, on the drainage cannals, on various bodies of water outside the lowlands, on small rivers, etc.

The birch is a principal food on several rivers of the Moksha River Basin (Pushta, Chernaya). The oak and the elm are of prime importance in the food of beavers on some Moksha channels once the supplies of willow are depleted. We should note that among the food plants which we grade as secondary fruits, the birch occupies a special position in the frequency of its consumption. A certain proportion of the total amount of food is made up by gnawings on this tree, even when there is plenty of aspen and willows. In this case it has the significance of a supplementary

food imparting variety to the beaver diet. Among other woody and bushy foods which are readily eaten, the mountain ash and the pine tree may be specified, when these are abundant on the shores of the bodies of water. The mountain ash may become a substitute for the chief food. The ash was important in this way outside the Lake Svyatoe–Poluninskoe flood plain (on the territory of the Oka Preserve). In the period 1942–1943 it was regularly gnawed by the beavers here until entirely destroyed.

The pines on the shores of bodies of water, which are eaten only rarely (such as the buckthorn among the leafy species) cannot be considered among the incidental foods. Our observations of Meshchera beavers convinced us of this.

The presence of pines among the leafy shore species on the shore of the Pra River and its old beds is a common phenomenon. Each year in several sections inhabited by beavers we may note that a small amount of pine bark is eaten. The beavers make a ring around the section of the trunk near the root where the diameter is 8–30 cm, or gnaw the bark of the trunk on one side of the tree (up to 80 cm in diameter). Small pines (8 cm in diameter) are gnawed through and removed. On small pines, gnawed branches of 3–4 cm thickness are found. In connection with this apparently unusual phenomenon, we conducted a count of the number of pines damaged in regions inhabited by beavers during several successive years. These regions were the shores of the old bed of the Chulimikha, where the beavers lived from 1949, and a region of the bed of the Pra River near the Samokhina Brook (Square 184) where beavers settled in 1951. The results of such counts are presented in Tables X and XI, and reveal that of the total number of pines (105) in the region of the shore of the old bed, which is 300 m long and 3 m wide, 39 showed damage (36.6%).

Table X

Counts of damaged and undamaged pine trees on a section of the bank of the old bed of Chulimikha

	Pine tree diameter (cm)											
	1-8		8-16		16-24		24-50		50-80		Total	
	No	%	No	%	No	%	No	%	No	%	No	%
Trunk ringed at height of 50–60 cm.....	-	-	5	38.0	7	21.9	3	33.3	-	-	15	14.3
Trunk gnawed on one side.....	-	-	2	16.0	8	25.0	1	11.2	4	13.8	15	14.3
Tree chewed up	7	30.8	-	-	-	-	-	-	-	-	7	6.0
Two or three branches of tree gnawed	2	9.1	-	-	-	-	-	-	-	-	2	2.0
Not damaged ..	13	59.1	6	46.0	17	53.1	5	55.5	25	86.2	66	63.4
Total.....	22	100	13	100	32	100	9	100	29	100	105	100

Table XI

Counts of damaged and undamaged pine trees on a section of the shore of the Pra River near the Samokhina Creek

	Pine tree diameter (cm)											
	1–8		8–16		16–24		24–50		50–80		Total	
	No	%	No	%	No	%	No	%	No	%	No	%
Trunk ringed at height of 50–60 cm...	1	8.0	5	9.7	4	50.0	–	–	–	–	10	13.1
Trunk gnawed on one side..	4	31.0	17	32.6	4	50.0	1	100	–	–	26	32.5
Tree chewed up	5	39.0	–	–	–	–	–	–	–	–	5	13.1
Two or three branches of tree gnawed	2	14.0	–	–	–	–	–	–	–	–	2	7.5
Not damaged	1	8.0	30	57.7	–	–	–	–	2	100	33	43.1
Total....	13	100	52	100	8	100	1	100	2	100	76	100

On a section of shore of the Pra River 150 m long and 5 m wide, 43 (56.9%) of a total of 76 pine trees were damaged.

On the basis of our observations we concluded that the beavers inhabiting the flood plain of the Pra River have a definite need to eat a small amount of pine bark. It is possible that this is connected with the general uniformity of the foods which are so characteristic for the Pra River Valley. On the Yuzhskoe peat bogs we noted one case of gnawing of a pine tree 7 cm in diameter. V. K. Khlebovich (1937) indicates a case of pine tree eating by beavers.

We turn now to a quantitative characterization of the fall-winter nutrition of beavers. We estimated the actual food requirements of beavers by considering the parts of trees gnawed by them. These were expressed in weight units of edible mass (we included tree bark, buds, and twigs). The quantity of edible mass of trees of various diameters and various species was determined experimentally. On comparing the data obtained with the data for the quantitative census of beavers on individual bodies of water, where the number of beavers was determined by means of observations from blinds, it appeared that the amount of edible mass taken by the beavers in the autumn amounted to a more or less constant value, fluctuating between 81 and 123 kg. At the same time, however, the total amount of damage and felling of trees per beaver varied very considerably. We should relate this to the considerable variation in the unused parts of the tree, consisting of (1) trees gnawed by beavers on the side or all around but left standing, (2) trees which hang on branches growing nearby and thus unattainable to the beavers and (3) unused remains of felled trees.

To compare trees with different degrees of use, we expressed this degree in units of volume of tree mass.

It proved that the used parts averaged 27.3% of the total arboreal mass of felled and damaged trees. For individual species this value varied from 15.5 to 50%. Observations have shown that the number of unused trees per beaver is not constant in different bodies of water and depends not only on the density of the vegetation on the banks (the increase in the number of unused trees being in direct proportion to the density) but also on their composition and age. Thus, in bodies of water with large numbers of aspens, the number of gnawed trees in the shore vegetation is considerably larger than in other aquatic bodies. Numerous examples of this are seen in the old beds of the Klyazma, where the aspen constitutes a considerable portion of the shore vegetation. When there is an ample supply of aspen, the beavers apparently ignore certain trees and clearly prefer others. In this connection, there are notable cases of the extreme persistence and the endeavors of beavers to fell trees which are severed from their stumps but remain suspended in the branches of adjacent aspens. We made an observation of this kind in 1944 on Lake Tolpega; in 1946 on Zakotetskaya Creek; in 1948 on the old bed of the Aleshina Luka (territory of Oka Preserve and adjacent area). Near such aspens, some of which are still standing, we have found billets from the lower part of the trunk gnawed by beavers, 3-4 in number, surrounded by a thick layer of chips, testifying to unsuccessful but persistent attempts to fell trees which, for some reason, attracted the beavers. A similar case was described by L. V. Shaposhnikov in the territory of the Mordov Preserve.

We shall note further that the younger the vegetation and the smaller its average diameter, the smaller the number of trees left partly cut by beavers and the higher the percentage of felled trees used. This also corresponds to the manner of using the bushes of the shore willows, the average diameter of which generally does not exceed 3-5 cm, when at the sites of beaver "cuttings"* no more than 5% of unused branches remain.

A count of the cuts carried out in the Oka Preserve has shown that on those bodies of water where beavers feed mainly on aspens of average age (14-20 cm in diameter), the number of aspens remaining cut up is approximately 10 times as high as the number of aspens found in bodies of water where beavers feed on young stands of aspen 8-12 cm in diameter. In the first instance, there is an average of 3.6-6.3 pieces or 0.526-1.103 cubic meters, in the second from 0.3-0.6 pieces, or 0.58-0.370 cubic meters. In bodies of water with feeding sections which correspond to the shore growths of birch on the banks, where the aspen is encountered only as an adjunct, the number of somewhat gnawed aspens is also not great (0.3-2.6 pieces), while they include the trees which are thickest (more than 24 cm in diameter). Thus, the data on the volume varying from 0.014-0.689 cubic meters are less indicative.

The total mass of trees and bushes gnawed and cut up per beaver in the fall period, to judge from the data on gnawing, varies from 0.19-2.9 m^3. It is highest in bodies of water surrounded by aspen groves without willows on the banks and less on lakes surrounded by willow growths with no forests in their vicinity.

We shall consider the nature of the succulent foods eaten by the beaver in the summer in greater detail later. The herbaceous foods start to predominate in the nutrition of beavers at the onset of growth. In areas flooded by spring waters growth is retarded and judging from observations in the Oka Preserve, beavers

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* Translator's note—The word "porubok" literally means the illegal felling of trees.

eat herbaceous plants regularly in June. In the flood plain of the Pra River, which is poor in various herbaceous shore plants, a special role is played by one-year-old willow shoots when the beaver changes to eating succulent foods. On the old Pra beds in June, the shoots, together with sedges, remain the principal food of the beaver (willow shoots encountered 100% of the time, and sedges 56%, on areas examined in the old beds of the Aleshina Luka, Popovo, and Krivoe, in June 1951 and 1953). Willow shoots are of similar importance in the diet of beavers on the bed of the Pra River, whose shores are particularly poor in herbaceous cover and bank and aquatic vegetation are almost absent. Here the importance of willow shoots has become particularly great as succulent food, making up for the insufficiency of herbaceous foods. In July and August of 1953, willow eating was noted in all places where beavers emerged on the Pra shores.

The herbaceous plants eaten by beavers of the Meshchera colony in the majority of cases are aquatic and marshland species. The chief food in the region of the Pra are sedges, whose parts near the roots are eaten with particular avidity at the beginning of summer (June, beginning of July), and the cinquefoil, together with other species of aquatic-marsh plants, such as great water plantain, water parsnip, manna grass, etc., which satisfy the requirements of beavers for green plants. The high food value of meadowsweet and dropwort for the beaver is widely known; it is eaten in small amounts in the Pra area, as it is extremely rare in the herbage on the banks. The dropwort is of great importance in the food of beavers which habitate ponds situated between marshes, lakes situated outside the flood plain areas, drainage ditches, and small streams, where apart from this plant an important nutritional role is also played by cattails, water arum and reeds. These plants are rarely encountered in the flood plain of the Pra River. We noticed that the roots of the spatterdock and water lilies were eaten in water reservoirs of all types.

In areas where the herbage on the banks is diverse and well developed, the herbaceous plants eaten by beavers in summer belong to a considerable degree to various species of shore grasses. In June 1952 L.V. Zablotskaya noted in 10 beaver feeding sites on the Tadenka River (Oka Terrace Preserve) that 18 species were eaten. These were distributed as follows according to the quantities consumed (percentages):

Meadowsweet	54.5
Horsetails (Equisetum hymale)	12.0
Small garden thistle	13.2
Nettles	3.5
River avens	3.5
Sedges	1.5
Forest reeds	2.0
Goutweed	1.4
Archangels	1.5
Angelica	2.5
Sweet cicely	1.3
Miscellaneous species: (Speedwell, St. John's wort, marsh marigold, Crepis chicories, horse sorrel, dead nettles, vervains)	0.25-0.8

The composition of the herbaceous foods in the flood plain of the Klyaz'ma River is apparently similar to this. We possess no factual data on the composition and frequency of consumption of species on the banks. In the period when the beavers lived in the flood plain of the Klyaz'ma in the fall we noticed that they ate only plants on the banks of the pools, i.e., water parsnip, manna grass, cattails, and cinquefoil.

Reflecting on the problem of restoring the tree vegetation destroyed by beavers, we should note that all data on the growth of seedling indicates that the development of the kinds of trees they destroyed en masse takes place rather rapidly in the central belt. An example is the rapid development of young aspen and birch groves on the shores of pools in the flood plain (Oka Preserve), which at the age of 18-20 years attained a height of 11-13 m and an average diameter of 9-12 cm.

However, in those places where there are beaver "cuttings" of aspen, we observed no vigorous or viable rehabilitation. The shoots from the roots of the aspen were low and thin, despite the considerable age they had reached, and a high percentage of the specimens had dry crowns. According to data from eight feeding platforms laid down in 1950 on the shores of the flood plain pools, the shoots were of an average height of 1.1 m and an average diameter of 0.5 (0.3-0.8) cm in cuttings 4-5 years old. Those with dry crowns amounted to 44%.

Shoots from stumps of birches gnawed by the beavers were in better condition. At the age of 4-5 years thay had an average height of 1.3 m (0.5-2 m) and an average diameter of 1.5 (0.5-20) cm on the shores of Lake Svyatoe-Poluninskoe which is outside the flood area. However, it appeared that the ability of birch stumps to produce shoots was not the same everywhere. On the plain pools, according to data of the 1950 census, only 29% of the stumps of old cuttings possessed shoots. The ability of the stumps to send out shoots is apparently very slight in marshy areas. In the marshy belt on the banks of Lake Svyatoe-Poluninskoe (northern part of the shore) only one (3.6%) of the stumps of a total of 27 (10-30 cm) possessed growing shoots. Those of three stumps (10.8%) proved to be dried up and the remaining 23 (85.6%) possessed no offshoots at all. These data indicate that following the destruction of birches and aspens by beavers, their rehabilitation proceeds in a very slow and unsatisfactory manner. The recovery of willows cut by the beavers follows a different course. The intensive shoot production of various species of willows is well known. Willow cutting by beavers, consisting of a peculiar straddling of the stump, is usually accompanied by the appearance of shoots. The formation of shoots depends on numerous factors, foremost among which is the age of the willow. In willow stands in the Lakes Kharlamovo, Popovo, and Sundritsa areas of the Oka Preserve of a considerable age (over 20 years), the number of small stumps sending out shoots fluctuated between 19 and 54.3% (1950 census). The development of processes indicates that when a second gnawing does not occur, the shoots of the Russian willow at the age of 5-7 years are 0.5-2.5 cm in diameter and 0.8-1.8 m in length (groves in the old Aleshina Luka bed and Alekseeva Creek). However, repeated gnawing of the shoots sharply depresses the shoot productivity of the willow.

Repeated gnawing of processes is usually observed in places where the willow does not form thick stands but grows in "curtains" (rows) adapted to one or another part of the bank. The consumption of willow in these places is accompanied by a progressive decrease in its numbers, finally culminating in its disappearance. Examples of this have been observed in various regions of the basin. In the territory of the Oka Preserve we may mention the lakes outside the flood plains, Lake Ukhanskoe and Svyatoe, where the rows of the willow near the shore were destroyed in the first years after the advent of the beaver. A scarcity of willow stands could be noted in a number of river flood plain pools which also had a distribution of rows along their shores (former beds of the Aleshina Luka and Lake Sundritsa, the ancient bed of the Chulimikha). The willow was completely destroyed by the beaver on several old channels of the Moksha in the Mordov Preserve. In regions where willows grow abundantly, their numbers are not observed to become depleted.

The fine prospects for beaver colonization where the willow grows profusely and constitutes the principal food are clear. Areas where aspen is the principal

source of nutrition have a limited period of use, first because of the aspens" rapid and progressive depletion in the shore zone, and secondly because of its loss of nutritive qualities in proportion with its growth and development to a mature age.

In concluding this review of the problems connected with the nutrition of beavers, we must dwell on the nature of the food trails and the factors influencing their extent and distribution. Observations in territories not put to economic use or destined for various kinds of use indicate that the length of the food trails of the beaver is determined by the distribution and abundance of the three food shrubs. Beavers inhabiting the immediate vicinity of human habitations, near roads but free from direct persecution, feed placidly at a distance of 15-20 m from the water. Observations carried out in the fall of 1953 on the Old Teza River, near Selishchi Village, showed that the beavers periodically moved a distance of 22 meters from the brink of the shore to gnaw on aspen 24 cm in diameter growing at a distance of 100 meters from the road to the village. Even more impressive was the discovery in 1950-1951 of paths and gnawings by beaver on the Satis River at a distance of only 40 meters from the buildings of a large sovkhoz (state farm). Even the bright electric lights and noises of motors did not frighten the beavers at night.

Building Activities of Beavers

In the Oka Basin, where beaver habitation conditions are highly varied, observations of their building activities show that the type of activity depends directly on the external environment.

In bodies of water with high and frequently steep banks (the lakes in the flood plain of the Klyazma, Moksha, Pra, and Oka Rivers) and along rivers of medium and large size (Satis, Pra, and Moksha Rivers), the beaver shelters, both temporary and permanent, are burrows. The number of burrows in the area of each beaver settlement is always very large. In the course of time some of them collapse at the top and the beavers construct new ones in their place. The beavers readily utilize the collapsed stretches of burrows as exits to the surface in winter. The beavers of a settlement employ an abundance of burrows. Explorations and excavations of burrows in the former channels of the Pra (Oka Preserve) have shown that the number is very great. On the small Lake Sipnoe (120 m long), the gently sloping southern bank bearing willow shrubs possessed 8 burrows, the average distance between them being 15 m. The northern shore had 13 burrows; the average distance between them was 6.3 meters. On Lake Popovo, at a site higher and more convenient for burrow digging, along a portion of shore 250 m in length we discovered 12 burrows.

The temporary drop of the water level on the Satis River during the fall repairs of the dam of the Kolkhoz Hydroelectrical Station (19 October 1951), enabled us to discover 12 burrows in the slopes of the shore left bare in a region inhabited by one family (a family of average size as regards the number of members). The burrows showed signs of visitation by beavers before the water level fall. Among the burrows which we excavated on the Lake Sypnoe, on the former Siversk and Glushitsa beds, only a few burrows providing winter shelter for a whole group of animals possessed lateral branches consisting of tunnels 2-3 meters in length leading to the surface of the shore and terminating in small expansions. These were undoubtedly temporary (refuge) burrows. The winter burrows, in which the entire family gathers in the fall, are frequently constructed by the beavers on low stretches of the shore, very often under the roots of willows. When the water level in the ponds rises, the beavers are forced to reinforce the ceiling of such a burrow from the surface and it becomes transformed into a semi-lodge. Usually the construction of beaver burrows in low regions of the shore may be observed in years when there is a smaller amount of summer and fall precipitation.

The construction of spring lodges on the highest sections of the shore is a rather interesting beaver adaptation for surviving periods of spring high water in the Pra River flood plain. Although these lodges are inhabited by the beavers for a brief period only (the period of high water, which lasts from the middle of April to the beginning of May), they are repaired with great regularity. Thus, the summer lodge on Lake Popovo, for instance, has been inhabited yearly for 11 years; on Lake Tolpega, 7 years; on the former Aleshina Luka bed 6 years. Other lodges are used in the same way. As to the construction of their spring lodges, it should be pointed out that actually these are also semi-lodges, appearing as a reinforcement of the collapsed ceiling of the burrow. However, due to the high level of water in the lakes during the period of their construction and habitation, they assume rather impressive sizes. This occurs because beavers, endeavoring to raise their nest chamber above the surface of the earth, are compelled to construct a strong edifice above the surface of the ground. In shape these are typical lodges with a conical form attaining a height of 1.0-1.5 m, and a floor area of 15-20 m. To construct them the beavers use not only gnawed sticks and chiseled twigs, but also all kinds of arboreal debris and windfalls. The demands for building material during periods of high water stimulate the beaver to lift and lay on the roof of their lodges not only pieces of wood lying scattered about but even the forest litter itself. Thus, in the spring of 1953, for instance, the surface of the earth around the lodges near the Belyi Klyuch (White Spring) (square 186) and in Popovaya Creek was laid bare for a radius of 3 meters. This was characteristic of all lodges constructed during the short period of time in the fall of 1952 which was so unfavorable for beavers.

It should be noted that the construction of the spring lodges of the beaver colonies in the Pra flood plain were an interesting exception. In the period from 1943 to 1948, we noted the appearance of only 3 lodges, on Lake Popovo (1943), on Tolpega Lake (1947), and in the Aleshina Luka (1948). In subsequent years a considerable increase in the number of summer lodges took place in the old beds of the Pra. In the spring of 1952, nine settlements were already in existence, with lodges of the spring-shelter type. The autumn floods of the year 1952, which in the Pra flood plain reached the magnitude of spring floods and became a veritable natural catastrophe for the beavers (it began in the second half of October in the period when the beavers were making preparations for their winter hibernation), spurred the construction of lodges in almost all settlements where they were not yet in existence. In the fall of 1952 lodges made their appearance in 12 more settlements on the channel and former beds of the Pra River. Beavers hibernated everywhere on the Pra River in such lodges, spending the winter in 21 settlements. In the spring of 1953, all these lodges were inhabited with the exception of Lake "Sukhaya Reka" (Dry River), which the beavers abandoned. The appearance of cubs in the majority of the settlements of the Pra River testified to the successful survival of the beaver through the marked rise of the water before the formation of ice, which is thought to be very dangerous for them. The spring lodges constitute the lying-in chambers of the females giving birth. One of the signs of habitation by gravid females is a very thorough refurbishing of the edifice. It is not difficult to hear the young born in the huts.

We have not yet observed the construction of spring lodges in the flood plains of other rivers on the territory of the Oka Basin. As an exception, two beaver shelters of this kind were observed in the Kama Basin on the Timsher River and Belaya Kholunitsa River. The shores of both rivers are not flooded everywhere. In the flood plain pools and in river beds of average size, in addition to the burrows, semi-lodges and spring lodges which are the basic types of beaver buildings, we may note their dams, with which the beavers block the flow of water in the pools which they colonize. These dams are a supplementary type of beaver construction. They exist on all true water channels which connect the flood-plain bodies of water

with the bed of the Pra River. We observed the construction of dams in the Klyazma flood plain in a channel flowing from the enormous Lake Dolgoe.

In bodies of water with low, peaty shores, such as lakes outside the flood-plain area, ameliorative or drainage canals, and small streams flowing along peat fields or through marshy valleys, the beavers inhabit the lodges they build during the period when the family collects for hibernation and in the spring during the reproductive period. In summer, when the level of the water drops, the beavers inhabit burrows of rather simple construction. The fact that 11-35 burrows were discovered on both shores of ditches or small rivulets along a stretch of 150-200 meters in the region of the settlement area of one beaver family indicates how numerous the burrows may be.

We should note that burrows are the preferred type of shelter. In all places where the possibility of dwelling in burrows exists, beavers do not make lodges, as for example in the Chernaya River, the shores of which include stretches rising 1,2-1,5 meters above the water in some places. In two settlements where we carried out trapping on the Chernaya River, the permanent burrows were adapted to the most elevated parts of the shore, their existence making it unnecessary to construct lodges, which in fact we were unable to discover. Another example of the obvious preference for burrows over other types of shelter is the phenomenon of the substitution of burrows for semi-lodges (Lake Ukhanskoe) in the dry years 1938 and 1939, when the water level in the lake dropped considerably. A change of shelter was necessitated on Lake Svyatoe-Poluninskoe in the rainy fall of 1953, when the beavers left the burrows in which they had lived for many years to find shelter for themselves in lodges. They repaired all the lodges which had appeared at various times in different parts of the lake and inhabited them in the October of 1953. We discovered 5 such lodges inhabited by beavers. In this case, the lodges, which are the usual type of temporary shelters, replaced the site of daily habitation by the beavers, the burrows. We observed the same large number of lodges used simultaneously by beavers in settlements in lakes surrounded by a belt of vegetation rafts (Lakes Mymrus, Chernaya, and Erus), in the Oka Preserve. The construction of burrows was impossible in the raft and the beavers used the numerous hollows of fallen trees for the arrangement of shelters. The beavers camouflaged the surface of the stump with sticks, twigs, and mud. The passages from the nesting chamber situated inside this construction led directly into the water, its entire shape resembling a typical lodge.

On rivers and ditches with a small quantity of water, the beavers constructed dams, which are an indispensable adaptation for dwelling in such bodies of water. In a settlement 150 m to 3 km long on a ditch of a river bed, a complete system of dams is usually encountered. Each dam is diligently maintained in a state of repair even when the region in question is rarely frequented. On the shores of bodies of water with a loose peaty soil there are canals which are dug by the beavers into the stands of food plants preferred by them. On lakes situated outside the flood plain, (Lake Ukhanskoe, Oka Preserve), after the reserves of willows nearby were exhausted, the beaver excavated a complete network of canals in the area of the swamp adjacent to the lake which permitted them to leave the lake for a distance of 100 meters. The space traversed in various directions by beaver canals was approximately two hectares in area (observations of 1943-1945). In the fall of 1951 we observed numerous canals 10-20 m in length extending in all directions from the lake into the willow stands on a small vegetation-surrounded pond, the "Dubchiki", situated in a bushy marsh with brush willow in the ranks of trees (right-bank flood plain of the Pra River).

In concluding this review of the building methods of the beavers on the territory of the Oka Basin, it must be pointed out that the changes which they introduced in the land near the banks cannot conflict with the economic interests of the local

population. This refers primarily to the dams which create an artificial barrier to the current and are usually destroyed by the inhabitants of those places where the flooding of the meadows around sets in. We know of cases of the destruction of dams on the Moginskaya Canal, which connects Lake Linevo with the Pra River (according to the data of the study of 1947) and a channel connecting Lake Yukhra with Lake Berezovoe (in the flood plain of the Teza River, according to studies of 1953). In the first case, where the presence of the dam was a necessary condition for habitation by the beavers, they were observed to abandon the ditch when the dam was destroyed. This indicates that when distributing beavers on the territory of the Oka Basin account should be taken in each region of the possibility of combining an increase in beaver numbers with an increase in economic use of the land, primarily in the hay-cutting areas.

However, human economic activities do not always deny to the beaver the possibility of existence. The beavers adapt themselves to certain occurrences, even those which constitute an acute interference in their lives. The fact that beavers successfully survived the sharp fluctuations in the water level connected with the necessity of repairing the hydroelectric barrages speaks in support of this contention. We observed occurrences in October 1951 on the Satis River on the boundary of the Mordov Preserve. In one settlement 1.5 km from the Kolkhoz Hydroelectric Station, the beavers were compelled to abandon the burrows they occupied following the lowering of the water level caused by necessary repairing of the power dam. However, the region inhabited by the beavers was not abandoned, and one week after the water level dropped we noted beavers again inhabiting their winter burrows, near which they had prepared a reserve of willow branches.

In another settlement, at the time the man-made dam was repaired, the beavers also possessed a winter burrow, at the mouth of which they had begun laying in stores of willow twigs in the water. When the water level dropped by approximately 1.2 meters, the beavers did not leave this burrow, but continued their preparation of twigs in the water. They abandoned their former passageway which was clearly distinguishable under a portion of the stored twigs and had been laid bare. A new passage was built lower down, this also starting under twigs placed in the water.

Both cases may be regarded as experimental confirmation of the beavers' ability to adapt to living under variable hydrological conditions. As observations have shown, this experiment, made during the most critical period of the yearly cycles of the beaver (the period of preparing for winter) caused no serious crises in the beaver's life.

Competitors, Enemies, and Parasites of Beavers

In the Oka River Basin the beavers have no serious competitors for food or the use of the shoreland where they construct shelters. All animals using twigs or branches for food (elk, white hare) find them abundant in the areas away from the beaver colonies as well. The gnawing of beaver-felled aspen trees by elks and voles occurs mainly with trees untouched by the beavers for one reason or another. Water denizens (water vole and muskrat) cannot disturb such a large strong animal as the beaver. Nor does the otter compete with the beaver because of its considerable range per individual.*

The wolf and the lynx should be included among the enemies of the beaver in the basin. The lynx is rarely encountered and therefore represents no real danger to the beaver group. The destruction of beavers by wolves on dry land is more

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* Editor's note—and of its different types of food.

probable, particularly during the winter migrations, which are sometimes observed from one body of water to another. Cases of wolf attacks on beavers are also known to us from the region of the Tsna River, where two beavers became the prey of wolves after having been compelled to emerge frequently on the surface, through lack of food during the difficult period of their first wintering.

Material on helminthological infestation of Oka Basin beavers is so far not extensive, since it is based on data from dissections of individual animals and coprological analysis of fecal specimens taken from animals captured in the Mordov and Oka Preserves. A complete parasitological autopsy of three beavers obtained on the territory of the Oka Preserve has shown that all were infected by a trematode (Stichorchis subtriquetrus) localized (14-17 individuals) in the small and large intestines, particularly in the caecum. The dissection of two adult beavers (which died after being trapped in the Mordov Preserve) yielded the same results; both were infected by the same trematode. The coprological analysis of the feces of beavers trapped in the Oka Preserve area showed that of 20 beavers caught, only three were free of Stichorchis eggs.

We may assume from all this material that extensive infection by the above trematode exists in the beavers of the Meshchera and Mordov colonies. An indication of the existence of other infestations follows from the results of the parasitological dissection of one of the yearlings caught on the territory of the Mordov Preserve, in which a large number of minute forms of unidentified helminths was found in intestinal wall scrappings and in fecal masses.

A mite (Schizocarpus mindandi) which is localized on the hair is a widespread ectoparasite of beavers captured in the Oka Preserve area.

Perspectives of Distribution of River Beavers in the Oka Basin

Before turning to a study of the problem of the prospects of river beaver distribution in the Oka Basin, we will summarize the material presented above illustrating the past and present status of the beavers on Oka Basin territory and the characteristics typical of the beaver's life.

As the review of the former distribution of the river beaver shows, it was a normal representative of the fauna of the basin as early as the sixteenth century. A gradual change in the natural conditions of the basin as a result of human economic activities combined with incessant beaver hunting created such conditions that the reproduction of beaver herds no longer compensated for the losses caused by their destruction and the numbers of beavers began to decrease until they were completely exterminated toward the end of the eighteenth century.

The history of human colonization of the Oka Basin goes back to ancient times. Within its limits the first Grand Duchess of ancient Russia (Suzdal', Ryazan', Moscow, etc), and later also that of the Moscow State, were formed. Thus, the natural conditions of this regions are mixed with a high degree of domestication of all the natural resources by man. Nevertheless, because of the natural characteristics, individual regions still preserved the complex conditions enabling the existence of beaver populations, particularly the large depressions in the eastern part of the basin, the Oka-Klyaz'ma lowlands, in which areas of low economic value, such as forests and marshes predominate.

Works on the rehabilitation of the river beaver as a member of the fauna of the basin begun 17 years ago. The first experiments on their distribution were made in the eastern part of the basin in the Oka, Mordov, and Klyaz'ma areas. The experiments were successful and were repeated at new points. As a result six

beaver colonies appeared in the basin, the oldest and largest of which are distributed in its eastern half.

The number of beavers within the basin at the present time is close to 1,000 head.

Observations on beavers conducted in various points of the basin enable us to draw the following major conclusions characterizing the activity and status of the animals upon their contact with the new conditions of habitation:

1. The main direction of migration in the distribution of the beavers was an upstream movement from the focus of settlement along the main watercourse.

The beavers of the Klyaz'ma Colony, released on the eastern boundary of the preserve on the land of the Ivanovo Oblast', moved upstream in proportion to their increase in numbers along the Klyaz'ma River. Thus, at present most of the colony is located in regions situated higher upstream than the original site of release.

The beavers of the Meshchera Colony, released in the lower reaches of the Pra, distributed themselves mainly on its basin. The fact that the migrating animals moved over 70-80 km upstream is of great interest. This took place in the first year of the existence of the colony. Distribution along the Oka also proceeded chiefly upstream. All known beaver settlements in the Oka Valley and its tributaries are situated in regions which are higher upstream than the site of release and the settlement of the chief part of the colony. In the Mordov Colony, settlement took place upstream along the Moksha River and its tributaries.

2. Along the path of the distribution, the beavers settle permanently in the most varied types of bodies of water, and their density of settlement also varies, being determined by a number of factors. In the majority of cases a decisive influence is played by the economic use made of the water and the abundance of tree and shrub food plants on the shores. In flowing bodies of water, the density of beaver settlement is 2.2-2.5 km of river bed length per beaver settlement. We should note that in lakes in flood areas as well as in those outside the flood plains, regardless of size, only one beaver family makes its habitation per lake in the majority of cases.

3. The reproduction rate of the beavers on the basin is normal, the chief reproduction indexes (the number of young per family and the percentage of families reproducing) being rather high as shown by observations of the territory of the Oka and the Oka Terrace Preserve.

4. The range of foods selected by beavers on the territory of the basin is quite wide. In each release region the beavers utilize a group of foods characteristic of the area, the principal ones being tree and shrub food plants. The willow is particularly important in the beaver's diet, retaining its role as a food plant even during the summer.

5. The number of trees destroyed by beavers fluctuates rather considerably, depending on their age, composition, density of growth, etc. A satisfactory recovery of woodland vegetation destroyed by the beaver is noted only among the willows under conditions where they are abundant in places inhabited by the beaver. Areas where willow is the principal beaver food are thus more promising in terms of the duration of their utilization period.

6. The building activities of beavers are well adapted to habitation under the most variegated conditions of the external environments.

7. Further increase of beaver numbers is not inhibited by the presence of enemies or competitors for food and shelter. The principal inhibiting factor in the growth processes of the beavers is the economic activity of man, as well as direct persecution observed outside the preserve by man (poachers).

The material presented here provides a basis for stating that the beaver has favorable prospects as a commercial species on the territory of the Oka Basin.

The example of the existence of small beaver populations in the western part of the basin (in the middle Oka and the Upper Moskva River Colonies) allow us to assume that more of them are able to establish a large beaver population where the free interchange of individuals is possible. The distribution of beavers in this region, which is densely populated by man, would be characterized by the rise of single settlements or small groups in the upper reaches of the main water courses of the basin, where beavers would find the complex of conditions required for their existence and where their natural instinct to move upstream when settling would bring them.

A different situation prevails in the eastern half of the basin, where large beaver populations already exist which now contain hundreds of individuals. The spaces of this half of the basin, which are marshy and less occupied by man, are easily taken over by the beavers when inhabiting new water reservoirs. An example exists of several individual populations which appeared after the release of beavers in different parts of the Meshchera lowlands uniting into a single unit.

When looking at the map of the Oka Basin, the regions where large colonies are situated are the vanguards for the settlement of the remaining part of the eastern section of the basin. However, owing to the prolongation of the natural settlement processes in this area, cannot match our endeavors to create a beaver population of commercial importance in the region of the basin. The natural distribution must be accelerated by the release of several batches into separate regions with more promising conditions, particularly the area of the Balakhna lowland (northeastern part of the basin) which includes a large amount of lakeland among large marshy stretches and is drained by a rather large river, the Lukh, (left tributary of the Klyaz'ma), 200 km long. Preliminary information on the basin of this river enables us to assume that this area may become a region of beaver colonization numbering 200-300 individuals. It would later be necessary to extend the limits of habitation of existing colonies. Preliminarily we may indicate sites for the creation of new focuses of distribution on a number of rivers of the Meshchera lowland (Pol', Buzha, Kolp'), and on the ancient beds and tributaries of the Klyaz'ma (Nerl' and Sudogda Rivers), and when these become settled the boundaries of the regions of settlement of the Meshchera and Klyaz'ma Colonies will merge. To the north of the boundary of the Mordov colony, the settlement of single rivers of the large forest-marshy regions of the Moksha lowland is possible.

As a result of the work conducted, the region inhabited by beavers will have an area of 70,000 sq km, on which, according to approximate data, we would place not less than 1,500-2,000 beavers.

To reach this goal it is necessary to carry out a large number of operations, principally studies on the number and the protection of the existing beavers. Up to this time protective measures have practically not been implemented for beavers outside the preserve, no one bearing the responsibility for the safe existence of each beaver settlement (the value of which amounts to 6,000-10,000 rubles). The census of beavers was not exhaustive.

It is quite evident that a similar state of affairs in connection with the maintenance of such a valuable fur-bearing animal as the beaver can no longer be

tolerated. The beginning of the beaver trade has been postponed indefinitely, chiefly because of the absence of a protective service and census of the beaver herds. The organization of such a service is an indispensable measure in establishing a beaver trade and it should be centralized and carried out by specialists according to a well-integrated plant.

Concrete measures directed toward achieving economic density of the beaver herds are as follows:

Organization of a beaver census in all regions of the basin, to sum up the inventory of all beaver settlements.

The organization of the protection of the beaver and observations of changes in the numbers and strength of beaver settlement.

Organization of the prior investigation of sites designed for the release of beaver: 1)Lukha River; 2)a series of rivers on the territory of the Meshchera-Pol', Buzha, and Kolp' Rivers; 3) tributaries of the Klyazma River--the Nerl' and Sudoga Rivers; 4) old beds of the Klyazma River between the cities of Kovrov and Orekhovo-Zuevo; 5) Snoved' rivers and other rivers flowing in the northern part of the Mokhsha lowland, and the release of 4-5 groups of beavers taken from the Voronezh Preserve and numbering approximately 50 pairs in all on the territory of the basin.

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P. B. Yurgenson

METHODS OF COUNTING WHITE HARE

(K metodike kolichestvennogo ucheta zaitsa-belyaka)

The white hare is one of the principal and most common species sought by the hunting and fur trade of the USSR, although each individual pelt is of little value. This circumstance underlies the request of the hunting trade for a quantitative census of this species, and accordingly for a method of making the count.

Counting white hare cannot be done by counting each animal separately. This would be superfluous and would only complicate and raise the expenses of the work. The method of counting the species should be simple and cheap and should not involve too much labor. The problems confronting us consist of: counting the animals in extensive forest areas; correctly evaluating the number of the animals and their distribution in the area studied and according to types of hunting regions; and determining population trends by means of successive thorough counts.

An error in the determination of the population (density) of up to ± 10–15% may be quite readily allowed without loss to the practical objectives for which the count was carried out. Within these limits, however, the data obtained should be accurate and the method itself should be worked out on a scientific basis.

A Critical Survey of the Counting Method Now in Use

Interest in the problems of quantitative estimates of the numbers of white hare was first awakened 20–25 years ago during the period when the problems of the hunting trade began to receive wide publication in the press. We have in mind the experimental counts in the Volga area carried out by A. A. Pershakov and his students (1935) and the methodical studies of V. G. Stakhrovskii (1930, 1932).

The subsequent period brought nothing substantially new. The problem of the quantitative estimate of the white hare still remains practically unsolved or insufficiently worked out.

Since counting by heads is not applicable for the white hare all methods proposed may be divided into those of counting sample areas with subsequent extrapolation of the whole territory and those of relative census. As a result of his experiments, A. A. Pershakov (1935) proposed a method of counting sample areas. The size of the sample area recommended was 25 hectares, so that the census could be carried out by one or two counters in a single day. Simultaneously it was indicated that the size of the sample area should not be less than the area inhabited by one individual of the species under investigation. The census should consist of a count of entering and departing footprints and their recording, a sweep of the area by two or more census takers with dogs, and a repeat count of the footprints. Thus, in fact, this method is a method of the "traffic" in the area. The labor involved in this method may be set at 80 man-days for counting 1,000 hectares (10 km2)

The authors assumed that the sample area could be beltlike with a width of 1,000–2,000 meters. In order to preserve the characteristics of the belt, it should be 3–4 km long with a constant width and thus cover an area of 300–800 hectares.

V. G. Stakhrovskii has tried this census method in practice in an experimental sample area by counting the entering and departing footprints without investigating the interior of the sample area, and came to the conclusion that it was impractical. It appeared that when the population density was high and a large number of footprints was found, the census of the area (2 hectares) took up almost an entire winter day. In individual cases, when there were many footprints and paths, it proved to be impossible to count the number of hares.

We should say that generally the method of determining the number of animals by subtracting the number of entering and departing footprints is completely invalid, since it permits different interpretations of the same initial data.

V. G. Stakhrovskii (1930, 1932) proposed and tested counting white hare by the "beater" method in a tested sample area with a width of 300–500 m and elongated rectangular outlines. Censusing by this method consists of circumambulating the sample area while obliterating all entering and departing footprints, beating with beaters placed every 50 m (75 m for sparse vegetation) along the long axis of the sample area and a second circumambulation of the boundaries to count the fresh departing footprints, the number of which will be equal to the number of hares fleeing from the area covered. For this method 5–8 beaters are necessary in addition to the supervisor*.

According to V. G. Stakhrovskii, a count of 75 hectares may be made by this method in a single day (6 sample areas of 12.5 hectares each). In calculating 1,000 hectares this would constitute 117 man-days. Thus, this method is more laborious than A. A. Pershakov's method, but it is more exact.

It must be pointed out that one should use a sample area of 12.5–25.0 hectares only where the density of the white hare is high. When the density is not high (10–15 hares per thousand hectares), in mixed spruce–leafy forests, the dwelling area of each hare covers 45 hectares. In this case, the sample area cannot be less than 50 hectares, and their total number not less than 500 hectares. When determining the size of the sample areas it is also necessary to bear in mind that they should be evenly distributed along the region counted and should include the main types of the region's hunting areas.

In order that the density index and thus the count of hares in the territory be reliable, the sum of the sample areas must be a definite ratio to the size of the territory and constitute a known percentage of it.

In practice, in the census work of the antiepidemic institutions, it is customary for this sum to be not less than 0.5% of the area counted, i.e., 5 hectares per 1,000**. We have seen that the larger the area of the individual's habitation and the less the density, the larger the minimal dimensions of the sample area should be. If for the small ground squirrel the area equals 0.5 hectare, then for the white hare it should be 50 hectares. The more varied the conditions of life and the greater the fluctuations of density in the territory surveyed, the larger the number of sample areas should be.

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* D. Aspisov considered the area of census with 13 beaters to be up to 25 hectares, with 8 beaters up to 10 hectares (200 x 500 m).

** Up to 2% according to the instructions of the Ministry of Health now in force.

According to data by N. M. Semenov (1937), when the sum of the sample areas was 0.5%, the accuracy of the result for the small ground squirrel was not great but was sufficient for practical purposes. A two- or threefold increase in the size of the sample area increased the precision of the results by an insignificant 2–4%. In order to obtain more precise results the specific value of the sample areas should be raised to 5–8%, which is difficult to effect in practice.

It has been established that in order for the counting error in sample areas to remain less than 10%, the total area should not be less than 25% of the entire area surveyed.

According to our calculations for the white hare, the sample areas should total 2%, with approximately the same precision as 0.5% for the small ground squirrel. This will be 2,000 hectares per 100,000 hectares of area surveyed. To take a census with this sample-area plan would require 20–30 days for a counting team of eight or nine men. The data obtained from counting the central areas should be extrapolated for the whole area being surveyed. Two methods of extrapolation may be chosen: in the first case the average density based on all sample areas is calculated and is used to determine the density per unit area (for example, per 1,000 hectares) and on this basis, the number for the whole territory is determined (for an area of 100,000 hectares the value for 1,000 is multiplied by 100, etc).

In the second case the density is determined separately for each type of area. Of course, this is only possible (on the basis of data on forest conditions) when the areas are known. The density is then determined "per unified hectare" (after Yu. Rall', 1936), or the number of hares is determined for each type of area and then totaled.

For the relative census of the white hare, a number of methods have been proposed and applied.

In 1932, V. G. Stakhrovskii proposed a method of recording encounters with hares (and other animals) along the trail by means of special cards. This method was proposed in connection with the taxation of hunting areas.

For this purpose it was suggested that on every encounter with a small animal the habitation site be described in detail. S. P. Naumov (1947) also applied V. G. Stakhrovskii's method in the study of the ecology of white hare. The only merit of this method is that it permits a census to be made during snowy periods as well. Direct encounters with hares are rather rare and accidental, and consequently there is not even relative certainty of the reliability of the figures obtained. The frequency of encounters will also depend on the element of chance and the protective properties in each type of region for the hare.

Several relative census methods were proposed by D. I. Aspisov (1936). He proposed a method of evaluating the abundance of footprints on the paths counted by eye which is attractively simple but highly subjective. The judgment is expressed in grades and does not provide a numerical index. D. I. Aspisov also recommends making the count on the basis of the relative abundance of winter excrement at the beginning of spring before the vegetation cover is developed. Thus, it provides a retrospective picture of the number of hares and their distribution in the territory during the past winter. This method is more laborious than the winter census made according to the linear path of footprints and can be recommended only when the winter census periods were missed. The method consists in the fact that the excrement of the white hare is counted on a sample of 10–20 "stands" (one square meter) 25–30 meters apart from one another.

The stands are laid down by a diagonal line through the area under census. The results are totaled and the value calculated for one square meter for the region under survey. The method can only have a coadjuvating value.

D. I. Aspisov proposed a quarterly census of the entering and departing footprints (which is parallel to the method of the census taken by beaters). At the same time the sum of the footprints should be determined for one km, as well as the number of entering and departing footprints and the difference in number between them. The author notes that the said method is less laborious (4 or 5 times less laborious than the beating method). He considered it applicable for small areas in conjunction with the latter method. It is not applicable for large territories.

Of all the methods for making a relative census, the winter trail census of the number of footprints, as proposed by V. G. Stakhrovskii (1931–1932) should be considered the most successful (see G. A. Novikov, 1949). Its advantage lies in the fact that it permits a simultaneous relative census of the total number of species of commercial fauna. In addition this method clearly reflects the distribution of the numbers of each species according to the land and type of area and also enables temporal dynamics of the population numbers to be followed comparing them with the results of previous censuses.

We present several examples: in the region of the Upper Vychegda (Komi ASSR), in 1930 (V. G. Stakhrovskii, 1932, white hare footprints, found in seven types of hunting areas, fluctuated between 44.2 and 497.3 per 10 km (by a factor of 11); in the Zhiguli (1938–1939) they ranged from 42.5 to 1,361.6 (by a factor of 32); in the former Central Forest Preserve (Velikie Luki Province), from 0.4 to 65.1 (by a factor of 16)*, while in 12 out of 27 types of areas, the indexes were higher than the total index for the area (12.7). At the same time the average density per 10 km^2 was 13.5. Thus, this method fully permits us to demonstrate the differences in types of areas and the distribution of footprints encountered in them and accordingly in the region under survey.

The temporal dynamics and dimensions of these fluctuations are also clearly expressed. Thus, in the former Central Forest Preserve (for nine years, 1930/31–1940/41), the average number of encounters with the white hare fluctuated between 6.3 (1933–1934) and 75.6 (1939–1940) (by a factor of 12). The last figure was the highest value (1931–1951).

In the Zhiguli, in 1937/38, the average number of encounters totaled 111, while in the year 1938/39 it was 660.1, i. e., in one year the number increased sixfold. According to data of the relative census, it has been demonstrated that in the Pechora–Ilych Preserve, for 15 years the white hare numbers had hundredfold fluctuations (V. P. Teplov, 1951), and so on. Apparently the geographic variability of temporal and spatial fluctuations is also depicted.

The relative census count data according to the method of V. G. Stakhrovskii also permits us to demonstrate relationships between individual species. For instance, we succeeded in determining this law—the more footprints of the white hare are met, the more numerous are the traces of the lynx, but in this case, there are fewer footprints of the white hare than of the lynx than in the areas where the lynx is rarer. It has also been established that there is no correlation between the frequency of encounters of martens and white hares.

It is necessary to take the census on the same paths and the same time of the year when the weather conditions and the snow cover conditions are the same.

The use of symbols placed on a lineal sketch of trail also makes the method simple to use, even for semiliterate hunters. A per-time value was recommended for use in the original presentation of the method, but practice over many years

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* Translator's note–Apparently 162 is intended.

has shown that it is more convenient to count steps, accurately fixing the encounters with each footprint or group of them.

This enables us to determine not only the number of footprints per unit of range of walking (on 10 km) but also the number of individuals met. This also permits the application of the A. I. Formozov formula (1932), i. e., a transition from the linear census to an areal census in the survey belts.

These problems will be discussed below.

Basic Prerequisites for Carrying out Census Methods

As is known, the around-the-clock* activity of the majority of mammals takes place within their habitation ranges (microranges or hunting ranges, according to some authors).

In 24 hours, the animal covers only a portion of its range with footprints. Its range is called the area of around-the-clock activity. Thus, of the white hare, in one case, according to our observations in the Velikie Luki Province, the size of the habitation range was 45 hectares (leafy-spruce forests), and the areas of around-the-clock activity were 9.9 and 12.5 hectares (26 and 29 December). In the case in question we called the around-the-clock activity, which was reflected by the small chain of footprints of the animal the "footprint activity". The longer the chain of around-the-clock footprints the more frequently the footprint chain is crossed by the network of census-taking tours. Thus the frequency of encounters on the census tour is not only an index of the abundance of the given species but also an index of their footprint activity. This index permits us to demonstrate to what extent the frequency of crossing of footprint chains depends not on the number of individuals but on the environmental conditions.

The length of the around-the-clock track chain and the magnitude of the around-the-clock activity depends on the various environmental conditions, on the abundance and availability of food (the latter condition subject to seasonal variations), and in winter on the conditions of the snow cover and air temperature.

The last condition has not been sufficiently studied, but it is not doubted that at low temperatures (below minus 20°C) the mobility of the white hare, independently of its pasturing activity, increases considerably. For instance, if the length of the around-the-clock track chain in spruce-leafy forests in December and January at night atmospheric temperatures of minus 12°C is equal to 0.6-0.8 km, then when the temperature falls to minus 25° C under the same conditions, the length of the around-the-clock track chain should increase to 1.4 and even 2.8 km, i. e., it is doubled or tripled. In all cases the pasturing region with its confused networks of footprints was excluded. The feeding activities of the white hare do not reflect a great deal on the length of its around-the-clock track chain. When the area of the habitation range was 45 hectares, the pasturing areas in some regions were less than one hectare (i. e., approximately 8.5%). In other cases, other conditions being equal, when the size of the area of the around-the-clock activity was 18 hectares, the pasturing areas were 0.003 and 0.15 hectares, i. e., less than 1%.

The major part of the length of the around-the-clock track chain is made during the passage from resting places to pasturing places and back, and to movements within the limits of the daily activity area, which is accompanied by very slight pasturing activity.

When the snow cover is unfavorable for the movement of the white hare, the

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* Translator's note - 24 hour activity

footprints, as is known, are sharply curtailed. The hare remains within the limits of its small pasturing areas and runs chiefly on worn paths and forest trails, the latter usually during warmer periods. Under such conditions, a census taken over a net of census routes made over one kilometer or more can not fully ascertain the presence of hares.

We were able to establish from a large amount of material in the Zhiguli (1938–1939), that no differences existed between the average number of white-hare footprints along census routes over a light snow cover and those over a 60–70 cm high snow cover. The snow was loose in both cases. A difference existed only in that in the second case the footprint crossings were concentrated over very small pasturing areas and between them no footprints were encountered for a considerable distance, i. e., the areas of around-the-clock activity decreased. It is clear from this that in order to provide reliable and comparative data the census of the white hare should be conducted under similar weather and snow cover conditions. At the same time, these conditions should be sufficiently favorable for the footprint activity of this animal.

The data from a number of census tours in the former Central Forest Preserve indicates how the footprint activity of the white hare changes during the winter (Table I).

Table I

Dynamics of encounters with white hares in the winter of 1948/49 in the Central Forest Preserve

Total extent of routes (km)	Month	Value for 10 km
240.7	First half of January	2.70
155.7	February	7.25
174.4	March	9.83

The question of whether the frequency of footprints characterizes not only the intensity of activity but also the relative numbers of animals has been posed more than once. In our opinion this may be valid. In studying the commercial fauna of the Zhiguli in 1939, we reached this conclusion. This is correct if the figures obtained are taken with consideration for the conditions in the region which they represent.

We were able to determine that the frequency of wild hare footprints was positively correlated with the availability of food in the region and the number of white hares per unit area.

When there is a uniform sparse distribution of food throughout considerable areas of a similar nature and when there are numerous encounters with footprints, which do not correspond to the number of hares, a negative correlation is observed.

The application of the index of footprint activity also permits us to apply the indexes of footprint frequency to a relative evaluation of the number of animals.

The index of footprint activity is a figure indicating how many footprint crossings per single animal take place, on the average, on the census route. This index permits us to study the degree of around-the-clock activity under various environmental conditions and during various winter season periods. This index also permits the calculation of the number of individuals encountered on census tours

in those cases when the abundance of footprints in specific areas does not permit calculations on the spot and on the contour of the route. It is very important that in such cases the persons conducting the census refrain from calculating the number of individuals.

How should this be carried out in practice in taking a census? The number of footprints is counted over a considerable portion of the route (it is desirable to count over the whole route, subtracting regions with a profusion of footprints), and the number of species to which they belong is determined. From this it is easy to obtain the number of footprints per individual. The number of footprints in all regions with abundant footprints is then counted and the total is divided by the index of footprints obtained, giving as a result the number of hares in these regions.

Table II presents data on the footprint activity of the white hare for the spruce-leafy forests of the Velikie Luki Province (former Central Forest Preserve).

Table II

Date of census	Length of census route	No of white hare footprints	No of individuals	Index of footprint activity
14–29 December, 1933	154.1	122	49	2.8
18–31 December, 1949	35.9	136	49	2.7
26 December–9 January, 1949–50	26.7	233	33	7.0
9–31 January, 1949	57.8	100	50	2.0

It is clear from the above data that it is possible to determine the number of animals on a linear route under any conditions. On the basis of the data of the linear counting, we may proceed to zonal or areal computations. These provide the best prospect of working out easy methods of counting which may be carried out by means of a small force of counters covering considerable areas of the forest massifs.

The following conditions are necessary for this: the result of the linear count should be recorded on the sketch or map of the census route in the scale chosen and the distance from one crossing of footprints to the other should be determined by the method of counting pairs of footprints. Under these conditions it is also possible to determine the number of individuals from the data of the map, taking into account the direction of the footprints and the distance between them. A knowledge of the typical outlines and sizes of the regions of the around-the-clock activity of the white hare will help considerably.

The study of the around-the-clock activity of the white hare for the period from 26 December to 9 February 1949–50, in the Velikie Luki Province has shown that the area of the around-the-clock activity of the white hare takes the shape of something similar to a quadrangle with an approximate 3–1 ratio of sides (2.81) (Table III).

It is seen that in 12 cases the length of the range fluctuated from 450 to 900 meters, an average of 595 meters. The width ranged from 165 to 300 meters (average 220). The value or the ratio of the sides fluctuated between 1.66–4.50. At the same time the area of the around-the-clock range was 9–18 hectares (average 12.4). Thus, all values of this table fluctuate by a factor of two, the width of the region always being considerably smaller than the length (by at least

150 meters). On census routes we always cross the region along an axis with relatively small deviations. This is determined by the fact that most of the small clearings and the contacts between the growths of various kinds extended parallel to the cleared areas on which the study routes were laid down. Data on the extent of the sites of the around-the-clock activity areas may thus assist in ascertaining whether a group of crossed footprints belongs to a specific animal. For example, on 16 February, on a 14.5 km route, we counted 148 cross tracks of footprints belonging to 15 hares, the index of footprint activity was 9.86 (i.e., 10). Actually, in the range of one hare we encountered 3-16 footprint crosses.

Table III

Size of area of around-the-clock activity of white hare

Dimensions (m)		Ratio	Area of around-the-clock range (in ha)	Dimensions (m)		Ratio	Area of around-the-clock range (in ha)
Length	Width			Length	Width		
450	200	2.25	9.0	600	165	3.60	10.0
500	200	2.50	10.0	450	200	2.25	9.0
900	200	4.50	18.0	650	225	2.80	14.6
600	250	2.50	15.0	600	200	3.00	12.0
600	250	2.50	15.0	500	300	1.66	15.0
500	200	3.20	20.0	800	250	3.20	20.0

The length of the area of around-the-clock activity crossed by the tracks was from 300 to 700 meters, i.e., within the limits of variability which we demonstrated for the length of the around-the-clock range. This is quite natural, since very often such areas are found precisely along cleared and empty regions between stands of trees of various ages; this factor permits the verification of the validity of the hare census by this method.

In specific cases, the practical hunting trade may be completely satisfied by data on the number of hares which may be in one region of the forest massif or another, per unit length of route. It is more convenient to take 10 km as the unit of length, since this figure is closer to the around-the-clock circuit of the hunter than one or 100 km.

In order to organize his business successfully the hunter must know how many fresh hare prints may be encountered so that he may set snares or traps and know in what types of terrain to set them. How many hares can be flushed from the ground by the rabbit hound? The hunter deals not with areas but with trails through hunting regions. He is completely satisfied by data from linear calculations.

However, areas and the data from them are required in order to plan and prepare hunting operations on an oblast' or raion scale. Less accuracy is permissible here. It is not necessary to be confined to hunting ranges in the forest or to particular types of land.

It is undoubtedly more convenient to combine the elements which satisfy the various requirements. As a basis, we may take the calculation of the number of

hares along the routes in the forest regions and the forest coppices in the region associated with the particular type of area and forest terrain and then, on the basis of this data, also calculate the density of animals per unit area and the total number for the region.

What should be the standard length of the census routes? It is desirable that it should be one per 100 hectares (one km^2) or that the census routes be laid parallel over one kilometer, but this can rarely be done. If the census is limited to an area of 10,000–30,000 hectares a standard length of 5 km per 1,000 hectares (10 km^2) could be accepted. However, for considerable areas (in the region of 100,000 hectares) the standard should be lowered to 2 km per 1,000 hectares. The daily operation should cover 10–15 km, depending on local conditions, the abundance of footprints, and snow conditions. Thus, the daily output of one tracker should be 1,000–8,000 hectares.

A very successful solution of the problem of the daily linear census per unit area was proposed as early as 1932 by Professor A. I. Formozov. Unfortunately the formula which he proposed and discussed numerous times in the press has never been given an adequate trial or suffficiently comprehensive application. Single cases of application were based on limited factual material and lacked a well thought out analysis.

Special studies (S. Malyshev, 1936; S. D. Pereleshin, 1950) carried out independently and by different methods have shown that the formula was mathematically correct. The accuracy of the results obtained depends solely on the precision of the numerical data used in the formula.

The significance of the formula consists in the fact that the linear census route with its data may be converted into an areal one, the width of the belt being taken practically as the average length of the around-the-clock track of the animal in question at the time the census was carried out. Thus, the number of animals checked on the route is already referred to a definite sample area.

The formula itself is as follows:

$$z = \frac{s}{m \cdot d}$$

where z is the index of the foodstock per unit area, m the length of the census route, d the length of the around-the-clock footprint trail of the animal, and s the number of animals taken into account per route. In order to make the results more accurate, S. D. Pereleshin proposed introducing a coefficient of proportionality, $\frac{\pi}{2} = 1{,}57$ into the formula, after which it was as follows:

$$z = \frac{s}{m \cdot d} 1{,}57$$

This formula was based mainly on the assumption that the number of animals of a given type was directly proportional to the length of the route and inversely proportional to the length of the around-the-clock footprint trail. When the number of crossed footprints is equal in two different species over the same section of the route, the number of individuals will be inversely proportional to the length of their footprint trails.

Empirically, it is easy to establish that the accuracy of the numerical data for each of the terms in the formula variably influences the accuracy of the index obtained. Thus, in determining the length of the census route, the accuracy may be ten times less than when determining the length of the footprint trail, so that the index has deviations of equal size. An error in the calculation of the number of

individuals in one unit creates an error in the index which is less than when calculating the length of the footprints per unit. It is just here that the accuracy should be maximal.

To take the example already presented, 15 hares were counted on 14.5 km of route, the average length of the track of five paths being 0.9 km, from which it follows that $z = \frac{15}{14.5 \cdot (0.9)}$. As a result we obtain 17.88 per 10 km^2. If, in determining the length of the track, we have an error of 0.1 km, then the error in the index over the same 10 km^2 will be about one hare per 10 km^2. Otherwise an error in determining the average length of the footprint trail of 11.1% creates an error in the index of 5.5%. In our practice with lengths of route, the length of the footprint trails under similar external environmental conditions had no fluctuations within limits over 100–200 meters. In this case the fluctuation will be 22.2% and the differences in the indexes per 10 km^2 will be 6 units in round numbers, i.e., not by 5.5% but now by 33.3%. Apparently the permissible error in the determination of the length of the trail should not be greater than 10%.

We assume that in order to obtain the average length of the footprint trail under the conditions in which the census is carried out, that is when there are no sharp changes in the atmospheric temperature and in the condition of the snow cover, it is enough to carry out 20 tours for the footprints of the white hare. One counter per day can easily follow the daily footprints of two hares, i.e., the preparatory work will require not more than 10 man–days. Thus, a linear census with the application of the A. I. Formozov formula would require 30 man–days for an area of 100,000 hectares, while for 2 censuses 15 days would be required. Thus, the labor involved in obtaining results which are sufficient for practical purposes is perhaps a quarter or a fifth as great as that involved in performing the census of the sample areas by the beater method.

In the period from 10 January to 28 February 1955 an additional series of white–hare trails were covered under the supervision of Candidate of Biological Sciences, I. V. Aleksandrova in the Oka Terrace Preserve (Serpukhov Raion, Moscow Oblast').

According to results of 6 trails the length of the around–the–clock tracks from one resting area to another averaged 973 meters, fluctuating between 465–1,812 meters. However, we must point out that in 4 out of 6 cases the length of the track fluctuated within small limits, or from 922 to 990 m.

The atmospheric temperature during this period ranged within the limits of 1.6–15.7° C. These fluctuations had no important influence on the length of the daily circuit; at a temperature of 0 to + 1.6° C, fluctuations in this value ranged from 465 to 990 m, while at temperatures of minus 10.6° C, fluctuations of 987 to 1,812 m were observed.

The height of the snow cover fluctuated between 31 and 46 cm, but this also did not have a significant influence. However, the condition of the snow produced a different picture. The length of the track increased by a factor of 2 (from 987 to 1,812) as compared to the same temperature conditions when the height of the snow cover was connected with the formation of a crust.

The length of the 465 m journey was also determined under special circumstances (during heavy snowfall).

One may conclude from this data that in order to determine the length of the around–the–clock footprint trail for census purposes, it is necessary to make the census when there is a similar snow cover structure or when there is no snowfall (1 or 2 flurries daily).

It was shown above that a considerable decrease in the atmospheric temperature (to minus 25° C) causes a considerable increase in the nocturnal activity of the white hare.

The average lengths of the track were rather similar in our data (0.9 and 0.97 km), but several differences were discovered in the dimensions and configuration of the range in the data obtained in the spruce–leafy forests of the Velikie Luki Oblast' and the pine–broadleaf forests south of the Moscow Oblast' (Table IV).

Table IV

Sizes of around–the–clock activity area of the white hare in the Serpukhov Raion

Size of region (m)		Index	Area of around-the-clock activity (in ha)	Length of trail (m)
Length	Width			
224	140	1.60	3.9	946
259	168	1.54	4.3	987
399	252	1.58	10.0	990
266	252	1.06	6.6	465
420	336	1.25	16.1	922
420	238	1.26	9.3	1,812

As in our material, the predominating outlines are those of an elongated quadrangle and in only one case approach the shape of a square. However, the length of the meridional span is less clearly marked, while in our material, the ratio of the sizes was 1:2.8 (i. e., almost 1:3), in the material of the Oka Terrace Preserve, it was only 1:1.4, i. e., the difference in factors was one–half as large. The width of the ranges in our material ranged between 165 and 300 m, in the additional material (Table IV) from 140 to 336 m. Thus the differences are not very large here. The length of the regions is another matter: in our material it is 450–900 (mean 595 m), but from the data indicated in the table, 224–420 m (mean 328 m). There is not even overlapping between these two series of dimensions.

In our material there was no overlapping between the lengths and widths of the regions. The greater extension of the range along the long axis in our material could be explained by the location of the region on the boundary lines between spruces and leafy–tree stands which covered the old felled forest areas.

The new material convinces us that obtaining sufficiently reliable data for the calculation of the results of relative linear counting is entirely feasible and not excessively laborious. Nevertheless it is very desirable to compare the data obtained in this manner with data obtained by the method of beating in the same area.

CONCLUSIONS

In order to take a census of white hare over limited areas for game and commercial hunting we may recommend the beater method (V. G. Stakhrovskii).

For the same purposes, but for covering considerable areas (raion, oblast') we may recommend the route census of the footprint trails and the subsequent determination of the number of individuals. For this it is necessary to apply the index of footprint activity, plotting encounters with footprints on a map on a determined scale and including data on the sizes of the around-the-clock ranges of activity of the hares.

The possibility of calculating the linear census data of the area is given by the formula of A. I. Formozov with the correction [proportionality] coefficient. With this the length of the around-the-clock track may be determined by trackings of the around-the-clock footprints carried out when the census was conducted, and will encounter no practical difficulties.

The number of required trackings should be checked by the experimental method.

In order to check the methods recommended and the calculations made with a view to preparing instructions, it is necessary to carry out a trial census by means of both methods recommended in one of the preserves with an area of 3,000-4,000 hectares.

A practical check of the route census method with the determination of the number of individuals and the calculation of the data obtained per unit area on the basis of the A. I. Formozov formula and also verifying the results by the method of beater driving will permit extending this method, with appropriate corrections, for counts of other game animals. The white hare has a number of advantages as a subject of experimental work which make the work easier in practice, and thus have not only practical but also methodological influence.

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G. F. Bromley

ECOLOGY OF THE WILD SPOTTED DEER IN THE MARITIME TERRITORY

(Ekologiya dikogo pyatnistogo olenya v Primorskom Krae)

Many works have been devoted to the wild spotted deer. The majority of reports in the literature (K. G. Abramov, 1939, 1928; G. A. Menard, 1930; I. I. Mirolyubov and L. P. Ryashchenko, 1948) deal mainly with the problems of antlered deer breeding in the Far East; there is almost no information on the wild spotted deer.

A special study of the wild spotted deer was originally begun in the years 1936–1937 in the former Sudzukhe Preserve by the game specialist O. V. Vendland. This zoologist carried out a series of field trips in the preserve from the Gulf of Preobrazhenie to the mouth of the Taukhe River and one expedition into the depths of the continent along the Kanikheza River. Part of the expedition was carried out by O. V. Vendland together with the geobotanist B. P. Kolesnikov. As a result of this, O. V. Vendland published a work (1938) on the food plants of the spotted deer and also established the sex ratios among spotted deer, which are 1:3.

In 1939 K. G. Abramov first indicated that spotted deer are "stenotopic, i. e., maintain a definite and constant area of habitation, in the Maritime Territory. He explained the constancy of the deer in choosing their habitation site by the condition of the snow cover on slopes of a certain definite exposure.

A considerably greater number of studies have been published on "domesticated" [park deer] spotted deer, which are based on 60 years' experience in deer breeding. However, the data of these works could not always be applied to the wild deer. Even a superficial review shows differences in the ecology of the two; the park deer are constantly restricted in their choice of natural food and they become fat in the spring by gnawing on plants and by eating the monotonous food, the soya cakes and barley, which is given to the males only. In the parks the sexual running takes place abnormally over indefinitely extended periods, with the participation of hornless reproducers and sex ratio which is distorted from the normal one. Because of the protracted running period in parks, fawning extends over long periods and is shifted to late seasons. In a number of parks sterility is common, reaching more than 30%, but despite this it is customary not to provide additional rations to females and fawns in such establishments. Cases of disease and the deaths of weak deer are often registered in parks. The average height and weight of park deer is lower, and deer in captivity, so to speak, degenerate or "die out".

The life conditions of the wild spotted deer are completely different and the list of phenomena enumerated above in no way applies. Nevertheless, in the present work, we considered it possible to apply to wild deer certain results of observations in parks. We include among such results the duration of gestation for example, which in the wild forms is undoubtedly the same as in the park animals, i. e., 7.5 months. Apparently only the dates and the types of fawning places change; we shall refer to this later. We must presume that the sequence in molting does not change in captivity, as regards both the spring and the fall molt, but the speed and duration of molting undoubtedly vary. The same may be said of the shedding of antlers.

The study of spotted deer was continued after the work of O. V. Vendland in the Sudzukhe Preserve in the same places of deer distribution, along the ridges of Tachingchang. A series of expeditions was carried out starting in 1944 and continuing to 1948 (407 days) into the main deer habitation areas.

At the time of the new observations the number of deer had decreased, as compared with previous studies, which considerably complicated field work. Despite this during the above-indicated years, we succeeded in encountering deer more than 500 times in the most varied areas of the former Sudzukhe Preserve. Over 3 years eleven deer were shot especially for the study, while 19 specimens were discovered dead in the taiga from 1936 to 1948. Thus, the actual material consisted of 30 deer of both sexes, collected during the years shown below:

	1937	1938	1943	1944	1945	1946	Total
Male	1	1	2	5	4	1	14
Female . . .	1	3	–	3	5	4	16
Total .	2	4	2	8	9	5	30

Other information on deer ecology was obtained from observations in nature and sources in the literature.

Systematic Position of the Spotted Deer

The spotted deer of the Maritime (Primorsk) Territory belongs to the subspecies Cervus nippon hortulorum (Suinhoe, 1864), which lives in the southern Maritime Territory, Eastern Manchuria, North Korea, and North China. This subspecies differs from the Japanese spotted deer and the Formosan, Southern China, and Indian deer in its larger size, peculiar coloration and small white rump patch.

All attempts to determine any specific subdivisions of the Maritime Territory spotted deer (R. Maak, 1861; N. M. Prezhevalskii, 1867; K. G. Abramov, 1928; S. V. Baikov, 1915) turned out to be unconvincing and were rejected in the works of G. A. Menard, (1930) and I. I. Mirolyubov and L. P. Ryashchenko (1949); we cannot agree with the conclusions of these latter authors.

The stenotopic animals to which the spotted deer belong very frequently have varieties of size and coloration (the specialist may distinguish deer of the following parks: Sidemin, Gamov, Putyatin, and Askol'd). Externally the deer of each park have features which are peculiar to it alone, on the basis of which the veteran deer breeders could, according to the "dry antlers", determine the "species" of the deer. Undoubtedly all previous reports of finding different species of deer on the territory of the Soviet Union were related to the high individual variability encountered in the deer. On the basis of these properties hunters differentiated "mountain", "stony", "meadow", and "lowland" deer. As a result of a detailed examination of 30 deer in the former Sudzukhe Preserve, and of many encounters with them (over 500), we may assert with confidence that within the limits of their range, all forms may be encountered in all regions.

According to reports in the literature (K. G. Abramov, 1928; G. A. Menard, 1930; I. I. Mirolyubov, L. P. Ryashchenko, 1948), if the spotted deer and the red deer are found in the same place, as in the former Sudzukhe Preserve, they produce a hybrid which in Chinese is called "Chin-da-guiza". This hybrid is said to be

fertile but introduces negative features externally in the spotted deer, and also lowers the value of the antlers. In the former Sudzukhe Preserve, where both species have long inhabited the same area, we have never succeeded in finding such a hybrid. Undoubtedly under natural conditions it is a very rare occurrence, if not a complete "hunting fable", but with human intervention such a cross could readily be obtained in a number of breeding grounds.

Morphological Data

The spotted deer of the Maritime Territory subspecies are large. If we compare the spotted dear with a European group of deer we shall see that the females are equal in size to the deer of Corsica and Sardinia (V. G. Geptner and V. I. Tsalkin, 1948), and the males are equal in size to the Scottish specimens (weight 100 kg). All other subspecies of the group elaphus are considerably larger than the spotted deer.

The body form of the spotted deer, as has been successfully demonstrated by K. G. Abramov (1938), is "light and graceful". Undoubtedly it is more graceful than that of the fallow deer and other deer, but less so than that of the roe deer. According to A. I. Likhachev (1947), who studied Siberian deer, the spotted deer differ markedly from the specialized group in which the elk and reindeer are included.

In the proportions of the body parts the spotted deer most closely resemble the wapiti and are characterized by a long vertically positioned neck with a high-mounted head. In his work A. I. Likhachev indicates that in spotted deer the vertebral column and the metacarpal section are elongated, in connection with their highly mobile way of life and the predominance of the gallop in their gait. In connection with this, the joints of the legs are high, as they are in galloping animals.

The tail is longer in spotted deer than in all subspecies of elaphus and, as in the wapiti, at its root along the vertebral tendons and muscles a dark brown mass of fat and connective tissue forms. It is possible that this "gland" is a rudiment of the tail organ of fat accumulation which is found in forms of steppe origin living under water shortage conditions. Their organism is adapted to using water in the processes of breakdown of fat reserves which are accumulated for example, in the hump of the camel and zebu and the fat tail of sheep, and possibly in the rudimentary formation of the tail of the wapiti and the spotted deer. Thus, we may assume that spotted deer at one time inhabited water-scarce areas of the steppe and penetrated into the forest only later. Encountering new habitat conditions, they retained some traits alien to this environment, for example the large antlers which make locomotion in the forest difficult, fragile hair, which, when catching on the bushes falls out easily, excessive velocity in running, and fat deposits at the root of the tail.

It is possible that the attraction of spotted deer to burnt-out areas in the forest, open spaces and regions with a good view and which are convenient for galloping is explained by their steppe origin. It is also possible that the "fear" of extensive snow, which is not characteristic of sylvan species, is derived from this.

In the anterior corner of the eye of the spotted deer the lachrymal fossae are well marked, and secrete a substance with a peculiar odor. On the lateral side of the posterior limbs, 2-3 cm below the saltatory joint, there is a small oval region with long bristlelike hair, possibly a hoof vestige similar to that in the wapiti. The spotted deer also lacks the coarsened skin on the lips which the wapiti possesses. This is why they are unable to snap off large, thick twigs.

The color of the spotted deer changes markedly according to the season of the year, sex, age, and individual variability. In the summer the deer is typically

colored a primarily reddish tone which is from the bristle part of the hair. In the region of the nape ridge it is somewhat darker and toward the belly it changes to hues of clear ocher and dirty-white. The reddish color also spreads over the feet, where sometimes a pale-brown tone is present. The throat and chin in summer deer are pale-yellow or dirty-gray. In the region of the head, the hair is more often pale-brown. A dark-gray strip extends from the occiput and along the ridge of the neck; it is lost on the rump and reappears near the root of the tail, continuing down the surface of the tail to its tip. The lateral tail hairs are pale-yellow and the under part of the tail and the part near the anal aperture is totally devoid of hairy integument. In the spotted deer, below and to the sides of the root of the tail there is a "mirror" or rump patch of white hair lying in a triangle which points inferiorly and joins with the white hair of the belly in the groin. The hairs of the "mirror" or rump patch are long and when the deer is excited or frightened the hair "stands on end".

Clean white spots are distributed over the basic reddish color in both males and females. The spots are small on the back but gradually grow larger toward the belly. They have distinct outlines. On the sides of the body the edges of the spots are fused to one another and form wide elongated strips up to 10 cm long. The location of the spots varies in male and female newborn fawns and in yearlings, and apparently does not follow any definite laws, since in females of the same age various spot patterns appear. Nevertheless we may approximately distinguish two interrupted strips along each side of the ridge and one strip on each flank of the animal.

The summer pelage of the males is somewhat different from that of the females. Dark-gray hair covers the head, and the hairs on the neck and throat regions are long and of a brown color. On the other parts of the body the coloration is the same as that of the females.

Toward winter, the spotted deer molt and acquire a gray-brown coloration. At about this time the head of the female becomes covered by a uniform light, dirty-gray hair-bristle. The inside of the ear is covered with pale-gray hairs and along the spine a weakly marked black-brown strip is noted, widening toward the rump. At the base of the tail this strip forms a black-brown ridge which extends down the sides of the white "mirror". The tail remains dark-brown above and white on the sides. The feet in winter are covered by gray-brown hairs, darker anteriorly and lighter posteriorly. The groin region and the upper medial parts of the feet remain grayish-white; the lower parts of the chest are a dirty-brown color with individual white hairs.

In the winter white spots are very rare in the adult deer but in the young we may often distinguish large merging pale-gray spots on the sides of the body and down the back. These spots lie in a completely different arrangement from the summer ones and they are considerably fewer in number.

In winter the males, in contrast to females, have long dark hair on the neck and withers. The hair on the chest is much darker, as is that in the region of the emergence of the penis. In individual males we may observe a uniform reddening of all hairs and a darkening to dark-gray hues over the entire neck region.

The spotted deer examined in the former Sudzukhe Preserve showed different morphometric data (Table I). From Table I it is apparent that at the age of $3\frac{1}{2}$ years the females already reach almost the maximum size and weight, i.e., 168 cm in length, 98 cm in height and 75.5 kg in weight.

The growth of the young stags follows a somewhat different course. However, at the time their antlers possess only a single tine (spike) they differ little in size

The weight and dimensions of wild spotted deer in the former Sudzukhe Preserve

Table I

Weight and dimensions (cm, kg) of adult females

Date	8/II/37	11/VII/45	2/VII/45	3/I/44	21/III/46	4/IV/45	8/I/46	2/III/46	7/III/45	25/VIII/46	23/VI/44	28/I/46	Minimum, average, and maximum weight and dimensions for females 27 to 60 months old		
Age in months	33	39	38	44	46	47	44	Approx. 60	60	Over 60	60	62			
Weight	76	74.6	75.5	67	60	68.5	68.2	62	77.4	81.5	80.5	85.7	60	73.1	83.7
Muzzle-anus length	152	149	158	167	168	152	168	169	165	165	159	171	149	162.4	174
Tail length excluding hair	16.5	20	15	15	16	15	17	16	20	17	14	16	14	16.3	17
Ear length	17.4	16	16.5	17	17.5	17	16	17.5	17	18	17.7	17.5	16	17	18
Height at withers	-	92	90	97	96	87	93	98	89	96	95	95	87	93.9	98
Chest girth	-	99	96	100*	110*	112*	107*	106*	103*	99	105*	111*	96	104.6*	112*
Shoulder length	-	25	23	28	23	27	30	26.5	29	24	27	31	23	26.6	31
Preshoulder length [Antebrachium]	-	30	29	31	32	28	36	28	29	27	31	32	28	30.2	36
Metacarpal length	-	33	35	33	35	30	37	36	33	37	33	32	32	35.2	38
Flank length	-	26	33	33	25	29	-	30.5	28	33	30	28	25	29.5	33
Cannon bone length	-	40	41	40	37	38	42	38	42	38	36	43	36	39.6	47
Saltatory joint length	-	44	44	45	46	49	47	47	47	45	48	47	44	46	43

Weight and dimensions (cm, kg) of males

Date	8/II/44	15/V/45	12/XI/44	8/II/44	29/VI/38	8/II/37	12/XII/43	12/XII/43	8/II/46	21/XII/45	27/XII/44	Minimum, average, and maximum weight and dimensions of males 12–33 months old			Minimum, average, and maximum weight and dimensions of males 44 months old and older		
Age in months	21	24	30	33	36	33	44	44	48	48	60						
Weight	74	78.4	82	77	100	96	124	131	104	108	120	74	84	100	104	117.4	131
Muzzle-anus length	149	156	163	154	163.5	150	168	170	172	176	180	149	156	163.5	168	173.2	180
Tail length excluding hair	18	17	16.5	20	20.5	16.8	18	19	17	torn out	18	17	18.4	20.5	17	18	19
Ear length	19	17	18	19.5	18	17.4	20	19	19	18	17	17	18.1	19.5	17	18.6	20
Height at withers	95	86	106	108	110	101	111	112	106	112	104	86	101	110	104	109	112
Chest girth	102	98	115	108	118	116	124	122	122	130	114	98	109.5	118	114	122.4	130
Shoulder length	29	29	32	34	-	-	30	32	29	30	29	29	31	34	29	30	32
Preshoulder length [Antebrachium]	32	30	34	33	-	-	35	37	38	31	28	30	32.2	34	28	33.8	38
Metacarpal length	38	39	39	39	-	-	39	39	41	39	34	38	38.7	39	34	38.4	41
Flank length	32	29	31	31	-	-	32	31	30	31	30	29	31.2	32	30	31	32
Cannon bone length	40	39	40	40	-	-	45	46	39	43	39	31	30.8	40	39	42.4	46
Saltatory joint length	51	48	51	50	-	-	52	52	48	47	49	48	50	51	47	49.6	52
Type of antlers	-	-	Thin-branched awl-like			-	Thick and large			-	-	-	-	-	-	-	-

* Females with embryos–thus the girth of the chest is somewhat greater.

from females of 2½ years of age. Toward the age of 3 years, the young stags become heavier than the females. Their average weight and dimensions at this age are as follows: length 163 cm; height at the withers, 116 cm; weight 100 kg. From this time, and sometimes even earlier, they become sexually mature but continue to grow. Toward 3½ years of age, the males, which already possess strong thick antlers, stop growing when the average weight is 117 kg, the length of the body 173 cm, and the height at the withers 110 cm.

The maximum weight and dimensions (kg, cm) of spotted deer in the former Sudzukhe Preserve are as follows:

	Females		Males		
Weight	Total length	Height at withers	Weight	Total length	Height at withers
85.7	174	98	131	180	112

The weight of the spotted deer changes considerably during different seasons of the year. In the summer the deer have varied green foods, and because of this become heaviest toward the fall. By October some deer become so adipose that a layer of fat 0.7–1.2 cm thick forms over the sternum.

During the sexual running (October) almost all stags grow very thin and by November completely lose their fat reserves; their weight decreases by 20–25% at this time.

The females grow less emaciated during the running period and their loss of weight sets in somewhat later (from January to March) during the periods of heavy snowfall and the noticeable increase in the size of the fetus. Thus, in the spring, there is also no observable fat accumulation. Only from the first days of July, after the fawns go out to graze, does the female gradually begin to fatten up. The young females and fawns with spike antlers which do not participate in the sexual run maintain their fall fat reserves for a longer time, in individual cases even until April. We have succeeded in finding 0.5 cm of fat in the sternal region of young one–year–old deer.

Young fawns less than one year old almost always lack fat deposits even in the fall, before the "hungry" winter. Such fawns have the same weight toward the spring that they had in the fall.

Thus all spotted deer acquire their maximal weight by the beginning of October and their minimal weight toward March.

Antlers and "Panti"*

Only the male spotted deer possess antlers. They appear in the second year of life. As a rare exception, something similar to small tubercles, somewhat like small antlers, are formed on the cranium of old females; we succeeded in seeing such a phenomenon only once in the former Sudzukhe Preserve on the skull of a 10–year–old female.

In the tenth month of life, in young saika** or saendysh** males, small 3.5 cm long outgrowths appear in the region of the parietal bones which

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* Translator's note – Soft, young growing antlers before ossification.

** Translator's note – Names of varieties of deer.

are not easily distinguishable in the fall when there is long winter hair on the head. In April of the second year of life, at the place of the outgrowth, the first spike of the antler appears. It is not branched, but covered with velvet, and at the age of 1 year 4 months (in August), the young stags rub it against the trunks of trees, baring the bony base. The males at this age are called "shil'hiki" [awl-like] as their thin long antlers are reminiscent of an awl.

The length and width (cm) of the first pair of antlers are given in Table II.

Table II

Length of "socket"		Length of antlers		Width of "socket"		Width of crown		Width of tip of antlers		Width between tip of antlers	Width between base of antlers
Right	Left	Right	Left	Right	Left	Right	Left	Right	Left		
4.4	4.5	11.5	11.8	1.8	1.8	2.4	2.5	1.2	1.3	17.5	6
4	4	12	13	1.8	1.9	2.6	2.5	1.1	1.4	19.6	6.2
4.2	4.1	14.5	10.2	1.9	1.9	2.4	2.0	1.2	1.4	17-18	6.5

As is seen from the table, the length and width of the antlers are constant.

The average weight of a pair of awls or spikes (Figure 1a), is approximately 120-190 g. The antlers are often split at the ends and rarely remain symmetrical. Such small shed or cast-off antlers are not normally found; because of their size-it is difficult to find them in the grass. At the place where the young antlers join the cranium in the young "shil'niki" a wide crown is not formed and the "sockets" turn evenly into the antlers.

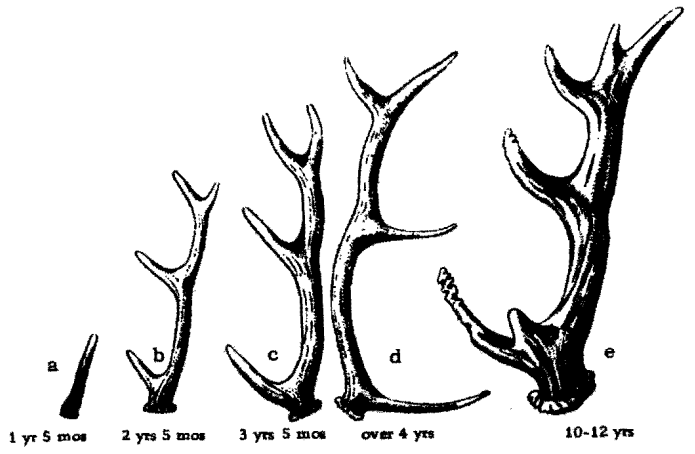

Figure 1. Antlers of spotted deer at various ages

The "shil'nik" or "awl-like" antlered deer retain their first antlers for the entire winter, shedding them considerably later than old stags, sometimes in May or even June. Second antlers grow in place of the first-shed antler in the two-year-old stags during the summer; these are small, but are now branched—young "panti". Toward the time of the fall running, in the weeks preceding October, at the age of 2 years and 4 months, the deer start to rub the velvet from their antlers (Figure 1b).

The weight and dimensions (g, mm) of the second pair of antlers of the spotted deer inhabiting the former Sudzukhe Preserve are presented in Table III.

Table III

Weight of one antler	Length	Width of crown	Width of neck of antler	Width of base of antler
307	452	47 x 48	29 x 40	23 x 27 left
235	205 (broken)	31 x 41	19 x 32	19 x 23 right
292	370	33 x 42	31 x 38	24 x 25 left
283	376	32 x 43	24 x 38	22 x 26 left
291	332	37 x 44	25 x 31	19 x 23 left

The first branched antlers of the young stag bear four tines: the first supra-orbital or brow antler, the second (bez antler), third (royal antler), and the terminal (crown antler).

Males at this age, judging from the broken off ends of the antlers, participate to a certain extent in the sexual running but of course cannot compete with the large, strong and more mature males.

Toward the end of two years, the young stag sheds his antlers somewhat earlier than the "awl-like" antlered stags—at the beginning of May; in their place, for the first time in his life, large, thick, true antlers begin to grow—the "panti". It is as difficult to find the shed antlers of stages younger than three years as it is to find the smaller "awl-like" antlers of the shil'niki. This is explained by the fact that each male possesses only one such pair during his lifetime, and thus it is difficult to find them in nature. In three-year-old stags (horned stags) the antlers grow rapidly and form bone branches for 120-150 days.

Unfortunately the exact rate of growth of such antlers has never been successfully determined by observations under natural conditions, and we may establish their condition only for individual dates. To clarify this, we present various stages in the antler growth of spotted deer compiled by I. I. Mirolyubov (1948) according to material from experimental breeding grounds in Table IV.

Stages in the development of the growing young antlers ("panti") are presented in Figure 2.

The processes or tines of the ossified antler of the adult stage have corresponding names: supraorbital (brow), second (bay or bez antler), third (royal antler), and the terminal (sur-royal or crown) which is the continuation of the main beam.

Table 1V

Stage of growth	Dates at which given stage was observed in Sudzukhe Preserve	State of growing antlers ("panti")	Number of days from time of loss of old antlers
1st	26/IV; 30/IV; 3/V	Skin envelops surface of socket—place of breakage of old antler	5–7
2nd	11/V	Swelling and buds develop at site of future "panti".	10_12
3rd	18/V–22/V	Fissure divides bud into two portions: the brow antler grows from anterior one.	20–25
4th	3/VI–8/VI	The brow antler separated from beam; stage of first division into two.	30–40
5th (Stage of cutting "panti" on the antler farm)	18/VI–20/VI	Thickening form at ends of beam—second buds . This is considered to be the optimal period for harvesting young antlers or "panti".	48–55
6th	28/VI–4/VII	Second buds grow into two tines, the posterior being continuation of beam and anterior the second tine (bez antler). Antlers at this stage lose their prime or first-class market condition.	60–65
7th	14/VII–18/VII	Third buds appear on ends of beams.	65–70
8th	22/VII– 3/VIII	Two tines form from third cones—third tine royal of the antlers and the continuation of beam.	75–85
9th	29/VIII–26/IX	Growth ends completely and antlers become ossified. Deer removes soft skin (velvet) from antlers by rubbing against tough tree trunks and baring raw bone antler core.	120–150

The time of shedding the old and the growth of the new antler depends entirely on the degree of fatness and the age of the males. Well-fattened stags—antlered specimens—shed them early, and new antlers regrow first in these animals. Somewhat later this process also occurs in the thin and young stags, occurring last in the "awl-like" or one-spiked stags. Thus, under natural conditions, the time of antler shedding does not occur simultaneously in all deer but takes place at various times. The numbers in Table IV illustrate the stages of antler growth for large stags only. It is interesting to note that the growth of antlers in wild spotted deer lags somewhat behind the growth in the park deer.

Panti-bearing deer (males with young antlers covered with delicate velvet) emerge almost daily toward dusk and go to the seashore to lick the foam. During the daylight hours they seek shelter near secluded springs, and later, as the growth of the antlers proceeds, they begin to go more and more often to open grazing grounds. From 29 August to 6 September (our observations) we already could find places in the preserve where the deer had scraped their antlers clean.

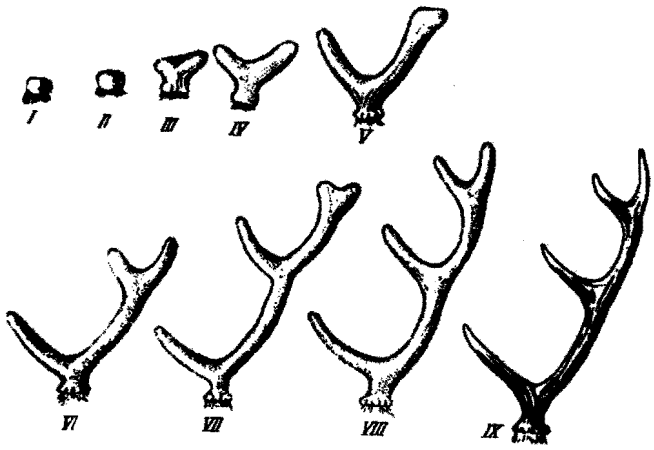

Figure 2. Nine stages of antler growth in spotted deer

The deer require the most valuable "panti" (Stage V) from 15-20 June. During this period the antlers are extremely distended, of a beautiful semitransparent blood-red hue and bear sparse, short surface hairs. Such antlers are of great value in medicine. In Stage V of their development the "panti" are delicate, soft and engorged with blood. The end of the supraorbital brow antler tine is blunted and the principal beam takes the form of a bud with a slight hollow at its tip. From the subsequent Stage VI, the hornification of the keratinous mass begins and thus the quality and value decrease.

Antlers of deer which have just become ossified are tuberculated and rough, with small particles of tree bark caught in the crevices of the antlers. Only the tips of the tines remain smooth and clear, and have the color of bleached bone.

The antlers of stags at the age of 3 years and 6 months have still not reached full size and continue to increase, retaining a constant number of tines. At this age the region of the antler—the crown—as in the majority of deer of the genus Cervus, has a tuberculated or annular surface from which longitudinal grooves extend along the beam, the site of the former blood vessels.

It is known from the practice of raising deer in preserves that by the age of 10-12 years the antlers reach their maximum size and weight. It is difficult to prove this from our scanty material, since we were unable to make detailed observations of males over six years old. At the end of April, when stags begin to shed their antlers, we succeeded in finding antlers of various sizes, weights, and shapes. Data on the weight and dimensions (g, cm, mm) of such antlers are presented in Tables V and VI.

It is interesting to note that shed antlers that lie about more than 3 or 4 months are usually gnawed by mice, field mice, and hares to various extents. Most frequently the tips of the antlers are gnawed, since these are more saturated with inorganic substances (Figure 1e).

Such differentiation in weight and size of antlers (Figures 1c, d, e) may be explained only by the age and the individual variability and different feeding of the stags during the growth periods of the antlers.

Table V

Weight	Length	Circumference of neck of antler	Weight	Length	Circumference of neck of antler
1,110	70	18.2	1,260	79	14.3
1,155	69	18.8	1,063	70	18.8
1,135	77	14.5	1,111	70	17.7
704	65	13.5	1,214	75	15

Table VI

Weight	Length	Width of crown	Width of neck of antler	Width of beam	Remarks
840	51.2	57 x 47	37 x 32	31 x 27	Left: broken
857	58	54 x 51	39 x 37	34 x 33	Right: eroded
1,176	68	62 x 58	46 x 36	38 x 36	Left: eroded
—	61	62 x 61	44 x 38	39 x 37	Left: complete
1,119	59	70 x 62	67 x 49	42 x 36	Left: eroded
1,255	58	73 x 67	62 x 50	49 x 35	Right: eroded
1,072	57	74 x 62	61 x 51	44 x 35	Right: eroded
1,041	69	68 x 61	58 x 38	41 x 38	Right: eroded
1,887	66	90 x 80	68 x 52	53 x 42	Right: six forks

The differences in the weight of antlers of adult deer as seen from the table are considerable, and together with antlers which weigh 840 g (Figure 1 c), we may find antlers which weigh 1,887 g and a pair weighing 3,774 g (Figure 1 e). The latter antlers even bear an extra terminal tine, as well as an extra tine in the angle between the brow antler and the beam. Judging by the dimensions of these antlers, it is clear that they belonged to a very large stag, about 10-12 years old, and in the prime of life. The antlers of younger stags, 5 to 6 years old do not attain such a weight but total 1,900-2,100 g and have four tines. We did not succeed in finding any other antlers in the preserve which were similar to the large ones indicated above. Judging from the white tips of the antlers, the crevices on their surface and the gnawed areas, these antlers have lain in the open since 1942, that is, five years.

It is rare to find deer antlers which have a distorted form. This is more often observed in wapiti and deer of the west, which have been well studied. During our entire observation period of deer, that is, from 1936 to 1949, we succeeded in finding only two such antlers (Figure 1 e).

Shedding

In March the winter hair of the deer begins to break off in the region of the shoulders and sides. This is particularly marked in pregnant females with fetus-swollen bellies.

From the first days of March, individual fallen hairs are already found on the snow, or caught in branches along the trails. This phenomenon increases toward the end of March. On several occasions—from 1-3 April—at stations in the Gulf of Ta-Ching-Kow near the base of the former preserve, we observed through field glasses grazing deer which had shed their winter hair in the head region, behind the ears, and in patches on the neck. No shedding was obvious in the young. In all other parts of the deer's body the winter hair had become very sparse and hung in tufts. On 12 April we observed deer with almost the same hair cover. By 20 April the head, chest, back,and neck of the deer became lightly reddened due to the development of new summer hair. Clusters of winter hair continued to cling only on the sides and near the rump patch. At the same time, toward the end of April, together with such deer, we observed some one-year-olds with the full winter pelage, which showed no signs of molting.

In the first third of May we still observed deer with winter wool on the sides, and only toward 20-22 May did healthy adults become completely free of the old hair and turn a dark color due to new hair, which had not yet reached full length. It is interesting to note that on 23 May, in one case, a female drowned in the sea, we even found completely naked patches on the neck, sides and shoulders and near the ears. Examining the carcass of this female carefully, we noted that due to the fact that the growth of the hair was retarded, the coloring was not completely of the summer type, and in many places the skin was visible through the hair, imparting to the hide a dirty hue even in places where the wool was white. In the one-spike antlered deer found at this time the molt occurred even later. In many sites on the body a small amount of winter hair remained, but naked places were also observed on the sides. In the station near the Ta-Ching-Kow biology depot we already succeeded in seeing female deer in vivid summer pelage on 24 May, and by 27 May all one-year old stags were found to have summer coats. By 13 June, all the deer of the former Sudzukhe Preserve, except the weak and the young, had acquired their summer coats. The molt of the one-spike antlered deer somewhat preceded the shedding of the antlers, and thus, in June, individual young stags went about in summer pelage, but with "dry" antlers. By 20 June there was no individual left among the young and the weak deer even with "dry" antlers, but the summer hair, which continued to grow, reached its full length only toward the beginning of July. As may be seen from this data, the spring shedding takes a long time not only in isolated individuals but in the group of spotted deer in general.

The summer pelage is sparse, almost devoid of an undercoat, and consists exclusively of the bristle or guard hairs, which are distributed irregularly over the body of the animal. The summer bristle is not as frail as the winter type, and appears through the microscope as a dense hair 0.07 mm thick, without an internal cavity, but with reddish pigment throughout its length and a dark-brown tip. The length of the summer hair differs in different parts of the body. We present data on the length of the summer hair as compared with that of the winter (mm) in Table VII.

The orange-red spotted summer pelage is worn by the deer for a brief period only, and the first appearance of the fresh winter hair may already be noted toward the end of August.

In the fall the change of the hair covering occurs less abruptly than the spring

change*, the new hair or "costume" of the pelage, the winter one, appears during the first 8 or 9 days of September, and the deer immediately acquire a new ocher-gray and black color. Toward the middle of September, as a rule, all the deer are already in possession of their winter habit, even in cases when the hair has not yet reached full length and the summer pelage lingers under it in certain places.

Table VII

Region of the body	Length of hair		
	Summer	Winter	
	Female	Female	Male
Behind mane	30	55	90
Withers	18	40	84
Shoulder blades	15	24	26
Middle of ridge	20	38	60
Rump	21	35	56
Side	20	28	30
Belly	33	47	59
Croup	16	32	44
Hind legs	8	12	13
Forelegs	6	10	12
Brush of tail	132	143	151
Length of hair on callus near saltatory joint	18	21	22

The winter hair differs markedly from the summer hair. It is arranged in whorls, and is considerably longer and thicker. It is very friable, hollow internally and has a white annulus near the tip. The winter coat, in addition to the guard hairs, is also made up of a fine, downy-hair undercoat. Simultaneously with the growth of the winter hair in the male, the antlers become ossified and the deer begin to scrape them clean in October, preparing themselves for the sexual run.

Distribution of Spotted Deer and Laws Governing it

According to earlier data, the subspecies of the spotted deer described, Cervus nippon hortulorum (Swinhoe, 1864), was once distributed in the Maritime Territory, Manchurian ridge of Changkwantsailing, Kentei Alin, Wanglungkow, Northeast China, and in the maritime portion of North Korea.

In the Maritime Territory the range of the spotted deer was small, and at the present time it cannot be exactly defined without special investigation of those parts of the taiga of the Maritime Territory still inhabited by deer in 1940.

The main features of the distribution of the spotted deer have been known

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* Translator's note–Sic in Russian text–the winter coat grows in about ½–1 month while the acquisition of the summer coat may take as long as 3 months.

from early times. The distribution is explained not by the uneconomical method of deer extermination in former times or by the appearance of the gray wolf in the Maritime Territory, but by causes of an ecological nature typical of a species at the limits of its range. Spotted deer, as a southern form, are located in the Maritime Territory at the northernmost limits of their range, and for this reason an insular, sparse type of distribution was observed. As a group, and in great density, the deer inhabited the southern part of Manchuria and the maritime areas of Korea. In the southernmost regions of distribution (Formosa Island, South China, and Japan) there are different species of spotted deer. Our spotted deer is the most northern subspecies; it had penetrated into the Maritime Territory from the south and adapted itself to the relatively severe climatic conditions.

In the northern limits of their range, our spotted deer inhabited only fixed regions which were appropriate for a sedentary life. It is interesting to follow the former distribution of the spotted deer in the Maritime Territory, which was considerably greater than at present. In 1860 R. Maak collected a number of facts about the distribution of the spotted deer in the Ussuri River Basin. He has written that the spotted deer, erroneously called elklike, were frequently encountered in the valley of the Sulfun River, from where the region of their range traversed the mountainous water divide toward the reaches of the Daubikhe and Mulyaikhe Rivers. R. Maak (1861) reports that, according to the accounts of local inhabitants, the deer were often encountered along the Daubikhe River itself, beginning from the point of confluence with the Ulakhe River; below the flow of the Ussuri River, deer were encountered more and more rarely in those days. R. Maak mentions the extreme rarity of the deer along the Ussuri River. He determined the limiting northern boundary below the mouth of the Iman River to be between the mouths of the Bikin and the Khor Rivers. M.I. Yankovskii (1882) indicated that spotted deer "inhabit only forests of the littoral belt from Korea to St. Olga Gulf and the Sikhote Alin Passes. They are already completely absent from the interior". Later he wrote that "even in the valley of the Lefu River and other rivers flowing into Lake Khanka, this species has been replaced by wapiti".

The old-timers of the Iman River area affirm that deer later inhabited the reaches of the Tatibe, Arma and Kulumbe Rivers (tributaries of the Iman), up to 1900. In this century spotted deer have been absent from these areas, which permitted G.A. Menard (1930) to reach the over-hasty and incorrect conclusion that "spotted deer are undoubtedly a dying species". G.A. Menard did not take into account the fact that since 1900 man has exterminated spotted deer en masse because of their valuable antlers.

Data on the distribution of spotted deer in 1928 are presented in detail in the book of K.G. Abramov, which includes an attached rather accurate detailed map, the first for the year in question, which was compiled from data of special observations of the entire Vladivostok District. In it, the distribution of deer is clearly indicated as consisting of isolated islands. From a study carried out in 1926, it became clear that the deer remained in the most southerly portion of the Khasan' Region, in the upper reaches of the Ryazanovaya, Adimi, Sidimi, Brus'ya, and Khedimi Rivers, and mainly in the Kedrovaya Pad' Preserve. In all places mentioned here there were few deer in the year in question, totaling 1-1.5 dozens (K.G. Abramov, 1928). Only in the protected region (the Kedrovaya Pad' Preserve) did their number increase from 90 head in 1924 to 200 head in 1928 (I.I. Mirolyubov, 1940), continuing to increase in subsequent years. When N.M. Przheval'skii (1867) was in the Maritime Territory, the Golds from the Ussuri River came especially to hunt the spotted deer during May and June in all the places mentioned above. In the Voroshilov Raion, in 1928, individual deer were also discovered along the Supitinka, Kedrovka, and Klepka Rivers, though there was no clear certainty that these were wild specimens and not specimens escaped from the deer-breeding locations.

In the Shkotovo Raion and near the city of Suchan, wild deer survived along the Maikhe, Steklyanukhe, Sitse, Baicha, and Popuga Rivers and the Mamontovaya Pad' in the Suvorovskaya Pad' slopes near the hamlet of Yastrebovka, on Joseph Mountain (apparently on its sunny slopes), in the upper reaches of the Suchan River, on the seashore of the Vostok Bay, near the Khualaza and Pidan Mountains and later in the upper tributaries of the Syao-Sudzukhe River, i.e., along the Tasinkow and Syaosinkow.

In the southern part of the Lazo Region where the Sudzukhe Preserve was situated, the deer were encountered in almost the same areas as they are today, but in larger herds. Here deer survived in the region of the Nizgou, Kwandagou, and Palengou Streams (Figure 3) and the Kanikheza Syao khinskaya; the Syaokhe, Ta-Chinkow, Syao-Chinkow, Ta-pikow, Syao-Pikow, and Khangan Rivers, the mouth of the Taukhe River, and the environs of the bays of Tasaval and Tikhaya.

At that time, groups of spotted deer inhabited western slopes of the Tachingchang, on the tribuaries of Sudzukhe-Sandakow, Ta-Pigou, and Elda-gou Rivers, along the tributaries of the Sandakow, Kanikheza River, along the tributaries of the Sudzukhe River and along the left tributary of the Wankow River, in the vicinity of the Gerasimov Stream and the Sikhote Alin passes.

More to the north of the Taukhe River, in the Olga Region, deer survived in small groups along the seacoast up to the mouth of the Phusun River; in the same area several deer were encountered in the region of Cape Nizmennyi, in the former Olga Game Preserve.

Still farther north deer were found in the Tetyukhinsk Raion along the reaches of the Tetyukhe and Akhobe Rivers, and in the Ternei Raion, along the Yodzykhe and Kema Rivers, near Nayna, along the Chashchevitaya, Yassi, and Momukcha Rivers, and along the Kolumbe River. We have no information of a more northern distribution of the deer.

In the map attached to the work of K.G. Abramov (1933), sites where deer were found have been indicated of which the text makes no mention. For instance, a small area is indicated on the left bank of the Tadusha River, north of the city of Bogopol'.

In 1938, Yu.A. Salmin reported the distribution of spotted deer in the former Sikhote-Alin Game Preserve in recent years. According to his data a small group of deer was constantly preserved in the Sikhote Alin Preserve along the Shanduiskii Spring and the Fata River (a tributary of the Tunsha River). There, far from the sea, the deer found the necessary combination of environmental conditions. Today, when certain conditions necessary for the survival of the deer are known to us, we must doubt the existence of the Shanduiskii group, particularly since no one has actually seen the deer and their presence was determined on the basis of their tracks in the summer. According to the data of Yu. A. Salmin (1938), in the same area in the Sikhote Alin Preserve, a small group of deer survived on the southern slopes of the Yodzykhe River, near the settlement of Kunalei.

O.V. Vendland (1938) mentions the most northern distribution of deer (in 1935). In his diaries he writes that he heard from the inhabitant of the upper reaches of the Kkhutsin River, that a small herd of deer dwelt at the mouth of this river. However, the local inhabitants themselves doubted whether these deer were wild. They were more inclined to consider them as escapees from local ranches. In any event, north of the Kkhutsin River there were no spotted deer, even those which had run wild. This was the most northern point of the Maritime Territory where deer had existed at all, for a certain time in 1935 and 1936.

The approximate range of the spotted deer in 1935-1936 may be visualized in the following manner: they occupied the southernmost limits of the Sikhote Alin Range and from there spread westward to the Manchurian boundary in the Khasan Region. From these special sites, which were almost completely inhabitated by deer, the boundary stretched northward, where occasionally islands of herd groups, of pairs, and even individual animals were distributed along the hills lining the Suifun and Daubikhe Rivers. The farthest island of deer on the western slopes of the Sikhote Alin was on the 44th parallel.

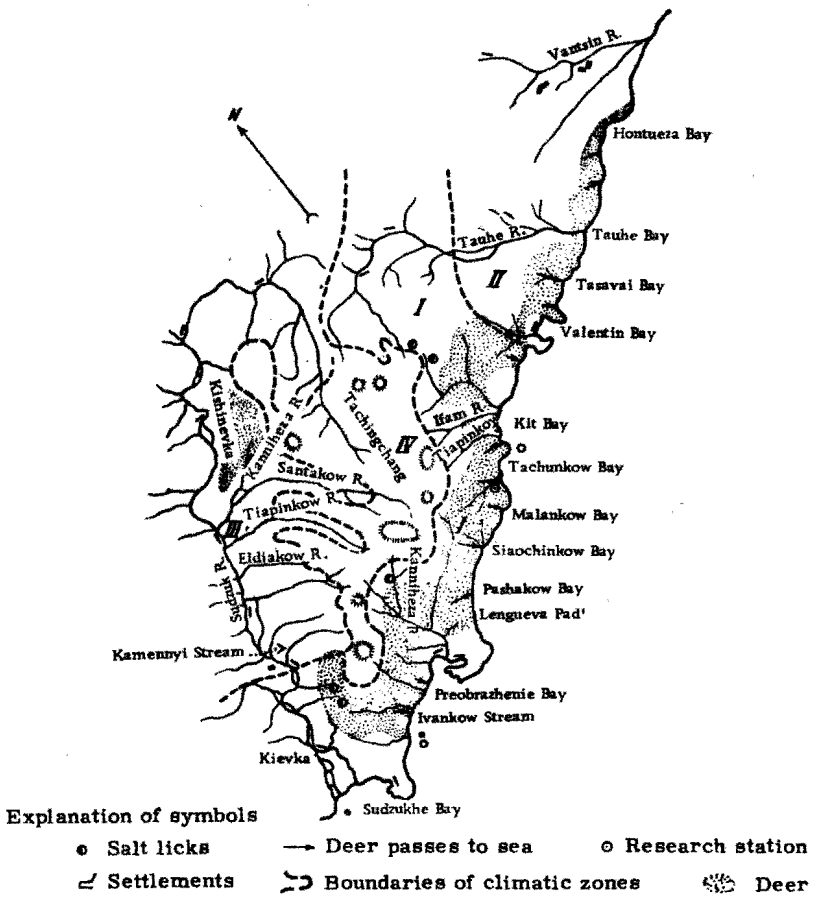


Figure 3. Map of distribution of wild spotted deer in the former Sudzukhe Preserve

The numbers of spotted deer on the eastern slopes of the Sikhote-Alin near the seacoast were higher than that in the Maritime Basin, and they possibly dwelt there as far north as 45° N. lat. This is the northernmost limit of encounters with deer in the past near the sea (in the Ternei Region).

Spotted deer have never lived on the heights of the Sikhote Alin, but they

skirted the entire mountain system to the south. Thus the herds of deer living on the seashore had not direct contact over the ridges with those living near the Ussuri River.

The above-mentioned 46° parallel [the 45th parallel is indicated above] is the ecological limit not only for deer but also for the following species: mole (Moger), raccoon dog, the Mikhno pika, wild Amur cat, pheasant, and others. None of these species even today cross in this "ecological barrier". In his work on snakes of the Far East, A.A. Emelyanov (1929) also indicates that 46° N. lat. is the approximate limit dividing the herpetofauna into northern and southern forms.

The distribution of spotted deer in former years was as follows:

A series of snow winters unfavorable for deer, as well as the appearance of a large number of wolves (gray) in the Maritime Territory and poaching, causes a radical change in the distribution of the animals and they disappeared from many places where they had previously been encountered. Examining the contemporary (1941-1948) distribution of deer along the seashore from north to south we may note that the herd that had been living near the Kkhutsin had been exterminated by illegal hunters as early as 1941.

A deer herd consisting of five head formed in 1936 near the village of Belimbe (emerging from their breeding grounds). They had increased to 18 by 1941 but they no longer exist today; they were exterminated by poachers.

The presence of deer in the region of Shanduiskii Spring, a tributary of the Tunsha River in the Ternei Raion, was not confirmed by investigations in subsequent years. The finding of deer in the jetlike Serebryanyi Spring and the Sitsa River in the Ternei Raion has also not been confirmed. In the Sikhote Alin Preserve deer only survived along the left tributaries of the Iodzykhe River, where, until 1946, they were preserved near the settlement of Kunalei, along the Iwankow, Khantakheza, and Kurmi Springs. Here the deer occupied the sunny slopes of the Kurumin Ridge on the "Verblyud" Peak, which sheltered them from northern winds. The existence of deer in these places has been established from tracks and traces of fur which were discovered in the excrement of wolves. In the regions along the Takema and Kolumbe Rivers, and also more to the south in the environs of Tetyukhe and Akhobe, there are absolutely no deer as a result of the poaching of recent years.

Deer survived near Cape Nizmennyi until 1944, but we were unable to obtain more recent data. Deer are found between the mouths of the Wanchin and the Taukhe Rivers even to this day, numbering several herds in the vicinity of the Khantueza Bay, on the littoral sun-warmed slopes. The principal reservoir of spotted deer of the former Sudzukhe Preserve, of which we shall speak somewhat later, starts somewhat to the south.

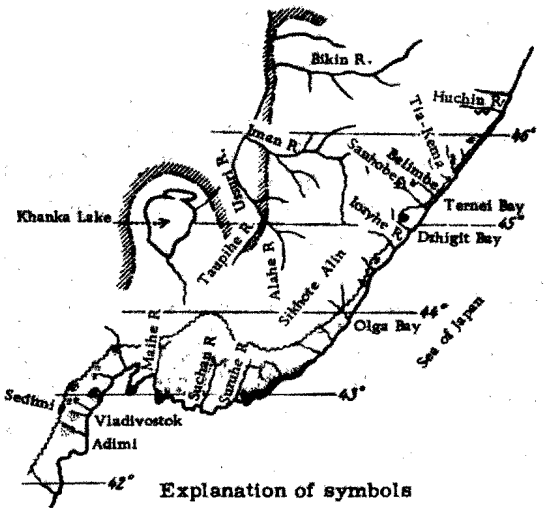
In the Lazo Raion, outside the former Sudzukhe Preserve, a small group of deer survived along the tributary of the Sudzukhe River, the lower Wankow (Syao-Sudzukhe), near the health resort there. They were observed here until 1947. How these groups succeeded in enduring the very snowy winter of 1947-1948 remains unknown.

Individual deer emerged in 1940 from the former Sudzukhe Preserve and occupied the declivitous slopes of the right bank of the Sudzukhe River, where they survived near the settlements of Kishinevka and Zvezdochka up to 1944. We do not possess more recent data on the fate of these deer.

There are no spotted deer in the Budennyi and Shkotovo Raions today. The last deer were killed from 1942 to 1946.

According to information by K.G. Abramov, almost no deer survived in the Voroshilov and Khasan Rayons, by 1946, even in the protected areas, and they almost disappeared in the Suputinka and "Kedrovaya Pad" (which belong to the Far Eastern Branch of the USSR Academy of Sciences) where approximately 500 head were counted in 1931.

Thus, in the Soviet Union, by 1948, only three regions remained where spotted deer had definitely been preserved: the Kedrovaya-Pad Preserve, the former Sudzukhe Preserve, and the Sikhote Alin Preserve (Figure 4).



Explanation of symbols

Places were spotted deer were found according to Maak, 1860.

Places where deer were found according to Abramov (1928)

\+ Places where deer were supposedly found according to Salmin's data, 1940

vv Data of Vendland, 1935

Places of habitation of wild spotted deer in 1948

Border, 1936

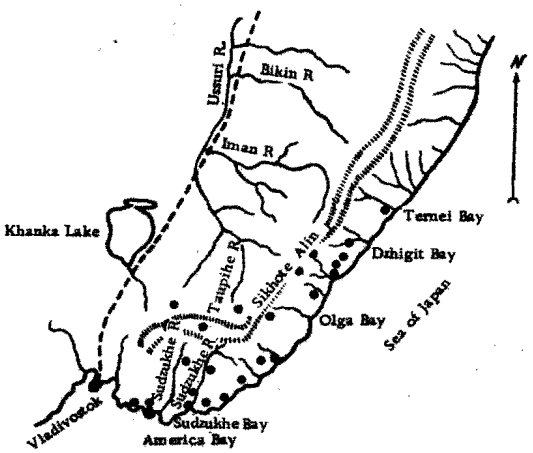
Figure 4. Distribution map of wild spotted deer in various years

The distribution of spotted deer in the former Sudzukhe Preserve did not change much by 1948 in comparison with former years and the description of K.G. Abramov (1928). The deer continued to survive along the Nizgou, Kwandagou and Palengou Spring to the extent of 3-4 herds which passed through the Torbaevskii Pass in the direction of the western slopes, toward the villages of Zvezdochka and Kievka. Two small separate herds were preserved in the upper reaches of the Nasaidenkov, Makarenkov, and Masloboinyi Springs. Deer also survived in small numbers along Kanikheza Spring (Syaukhinskaya) and the Syaukhe River.

Most of the deer survived in the vicinity of the maritime gulfs and springs. Of these we may name the Pashakow, Syao-Chingou, Malankow, Tachinkow, "Zarya", and "Kit" Gulfs. Deer also survived in regions farther from the sea along the Syao-tyapigou, Ifam, and Khapgan Rivers, and more to the north along

the maritime slopes near the Valentin-Taukhe, Tasavai, and Khontoueza Gulfs. (see Figure 3).

Thus, the coastal groups of spotted deer were distributed as shown in the figure and were composed of single herds, which made short migrations into the interior of the continent. In the northern part of the preserve the deer settled nearer to the seashore, and further they penetrated into the continent even to a distance of 20 km. Let us note in passing that the entire coastal strip occupied by spotted deer faced southwest and lay at the foot of the Tachingchang Ridge. In the portion that lay far from the sea, along the right slopes of the Kanikheza River (a tributary of the Sandakow River) and on the hills of the settlement of Kishinevka, two completely separate herds of deer which had no connection with the littoral individuals survived in the former preserve. Here the deer occupied the sunny slopes of the valleys of the Kanikheza and Sudzukhe Rivers, passing over the northwestern slopes in the summer.



• Remains of trapping pits

Figure 5. Map of former distribution of Chinese trapping pits

Almost no deer were found along the tributaries of the Sudzukhe River, the Sandakow River, the Tapikow, the Big and the Small Eldakow Rivers, and Sukhoi Spring, nor were they found along the upper reaches of the America River, where in the fall of 1944, we succeeded in seeing only one print of a young deer. There are also no deer in the Gerasimov River Valley (a tributary of the Verkhnyaya Wankow River), through which a traffic highway now passes.

In all the enumerated places in the former Sudzukhe Preserve, the spotted deer were unevenly distributed in various groups and herds of various sizes. The largest herds stayed on the bay seashore from the Pashakow Bay up to the Tachinkow Bay. These places were preferred by the deer, and they became very numerous here. The areas occupied by the deer along the seashore from the Tachinkow Gulf to the Tasavai Bay should be considered next in order as regards their numbers, and finally the smallest group of deer were encountered on the shore slopes of the Tsentralnaya Mountain and the Palengou, Kwandagou, and Nizgou Valleys, along the Masloboiny and Nasaidenkov Dprings and along the seashore from the mouth of the Taukhe River to the Khontueze Gulf. We should also include

the preserve territory near Kishinevka Village in the areas inhabited by deer along the Kanikheza Spring.

In examining the former area of distribution of spotted deer in the Maritime Territory, we note the following: during his travels, R. Maak (1861) proceeded along the Ussuri River, receiving information on the spotted deer from the hunters of the small tribes. He did not happen to visit the natural habitations of the live deer personally, and thus, we should consider his data with caution. Deer were undoubtedly very rare along the valleys of the Daubikhe and Iman Rivers and in other places in the northern limit of their range and it is possible that when he spoke with the hunters from the small tribes R. Maak may not have understood them well.

During the travels of R. Maak, the Maritime Territory was inhabited by Chinese animal hunters and traders, who used the pitfall method for catching spotted deer in "lu deu" (Chinese for "deer pit"). If we accept the data of V.K. Arsen'ev, (1947-1949), of N.M. Przhevalskii (1867), and of O.V. Vendland (1938), it would appear that spotted deer were never caught along the Ussuri and Iman Rivers by the pitfall method (Figure 5). For this it is necessary to have at least a minimal number of specimens of this species on the trails . This gives additional proof of the small numbers of spotted deer during the years of the expeditions of R. Maak in the places which he described.

The deer-catching pits were preserved until 1936 along the eastern slopes of the Sikhote Alin, in the former Sudzukhe Preserve in the nearby Olga, Shkotovo, and Budennyi Raions, and the near the town of Suchan. In some places they were even seen in 1944, which is the best proof of a considerable number of deer in these places 40-50 years ago. The places where remains of the pitfalls exist were also the regions preferred by the spotted deer, and the "lu deu" pits are a clear indication of the large numbers of deer in the past century in this area.

It seems to us that if deer were also numerous in the places which R. Maak visited along the Ussuri River, then the Chinese hunters would have dug their pitfalls here as well. For this method of trapping it is enough to have one path stamped out by a small herd of 5 or 6 head. All this compels us to suppose that there were so few spotted deer in the valley of the Iman and Ussuri Rivers that they did not even form herds.

Thus the range of the spotted deer in the recent past in the USSR extended from 42 to 45° N. lat., while their maximal numbers extended in a straight belt along the seashore between 42°30' and 44° N. lat., covered on the west by the Sikhote Alin Range. We should bear in mind that the spotted deer were distributed all along this range in individual groups which were sometimes very distant from one another.

Influence of Climate on the Distribution of Spotted Deer

The climate of the Maritime Territory is not uniform and cannot be considered as a unit and homogeneous. It is sufficient to indicate that the yearly precipitation near the Khingan is 350 mm, while in the Sikhote Alin precipitation may reach 1,000 mm.

The average yearly temperature also changes considerably and ranges from minus 8° in the northern part of the Amur Region up to plus 6° in the south of the Maritime Territory.

If we compare the range of the spotted deer with a series of climatic indexes of the territory, it appears that the deer select only definite types of climatic indexes and belts as determined by P.I. Koloskov.

Thermal Zones

1. The temperate zone (C) with total annual temperature of 2,000-2,500°.

2. The warm zone (B), with a total annual temperature of 2,500-3,000°.

3. Very warm zone (A), with a total annual temperature of 3,000°.

Precipitation Belts

1. The humid belt (IV) including regions with annual precipitation higher than 700 mm.

2. The subhumid belt (III), with annual precipitations of 500-700 mm.

Comparing the areas of the thermal zones and the precipitation belt with the former range of the spotted deer we become convinced that these regions spread north and west considerably farther than the limits of the distribution of the spotted deer. In other words, the deer inhabit only the southern regions of the thermal zones and the eastern parts of the humid belts, and their ranges do not extend completely over the areas to which these climatic indexes apply. Nor were the deer encountered in those parts of the continent where these climatic zones and belts were still clearly marked. Thus, the temperature and precipitation total are not the factors directly regulating the distribution of this species in the Maritime Territory.

Influence of Vegetation on the Distribution of Spotted Deer

Comparing the distribution of the deer and that of the plants which are indispensable to them as food in the wintertime, the reason for the limits of the range of the spotted deer is again not explained.

As an example, we present (in Table VIII) data on the range of the principal plants composing the winter food of the deer in Maritime Territory.

Table VIII

Plant	Northward and lateral limits of range	Time when used as food by deer
Mongolian oak	Up to Sovetskaya Harbor. Is found on Amur River. Grows on mountains to elevations of 700 m.	Almost the whole year round.
Aralia	Maritime Territory, Amur Oblast', Grows on mountains to elevations of 500 m.	"
Linden	Up to Sovetskaya Hr. Grows on mountains to elevations of 700 m.	"
Acanthopanax	Maritime Territory and eastern part of Amur Basin. Region toward southeast of Bureya River	All year round.
Bush (Japan) clover	Along entire Manchurian floristic region to elevations of 600 m.	Almost the whole year round
Vines-Actinidia and grapes	Southern Maritime Territory, Amur Oblast' to 50° N. lat., along the sea coast to Samarga River. Up to elevations of 400 m.	All year round

From this small table it is clear that the main winter food plants, not to mention other food plants which are not indicated, are distributed considerably more to the north than the spotted deer. Broadly speaking these plants are found up to 50° N. lat., whereas the range of the spotted deer formerly hardly reached 45° N. lat.

In addition, it has recently become known that spotted deer also lived freely in places where there is absolutely no Manchurian vegetation. Thus we may say with certaintly that the distribution of the deer in the Maritime Territory is not related to the food plants. The causes of the more southern and insular distribution are completely different, and statements concerning a relationship between the spotted deer and Manchurian flora are incorrect. Enormous areas of deciduous forests in the Far East were devoid of any traces of spotted deer habitation, even formerly. When this species is able to select its habitation sites, it occupied regions where the combined complex of conditions enabled it to survive the entire year for many years in succession, safely living through the winters, which are difficult for it. Weak deer, and sometimes whole groups of deer, are unable to survive the winter.

Influence of the Snow Cover on the Distribution of Spotted Deer

We must draw attention to one more factor—the snow cover which often constitutes a serious barrier for numerous species which radiated from the south while expanding their range.

The snow cover plays a highly important role both directly and indirectly. and in the southern Maritime Territory is subject to various changes according to the latitude, the terrain, the proximity of the sea, the prevailing winds, and the average cloud cover.

To trace the data of the first snowfall in the southern Maritime Territory according to M.M. Partanskii (1923), snow first appears in the northern part of the Sikhote Alin, above 45° N. lat. The curve connecting the dates of the first snowfall projects southward from the heights of the Sikhote Alin to the 44th parallel. The snowfalls occur later in the southern parts of the Maritime Territory. The line connecting the dates of the first snowfalls extends parallel to the shore, a slight distance from it, and curves around the southern end of the Sikhote Alin mountain. This line, which delimits the area of the first November snowfalls, is of the greatest interest, since here, from the seashore to the line, the majority of the spotted deer survived previously, and today as well. The maritime part of the Barabash Raion enters this area, as well as the Kedrovaya Pad' Preserve, the littoral regions near the sea of the Shkotovo, Budennyi, Lazo, and Olga Raions, and, retreating somewhat from the seashore at the 45th parallel, a portion of the Ternei Raion. It is clear that the date of the first snowfall is of great importance to the spotted deer, for the boundaries of their range coincide exactly with the definite isogram of the first snowfalls.

Comparing the range of the spotted deer during the winter, it appears that the curve describing total precipitation of 1,000 mm also surrounds the Sikhote Alin Range on the south, separating the littoral and Khanka lowland from the regions with low precipitation. A belt with a smaller amount of precipitation is situated more to the south and nearer to the sea, the precipitation being in the form of snow (800 mm per year). This belt extends along the litoral parts of the Khasan, Barabash, Shkotovo, Budennyi, and Lazo Raions. Comparing this belt along the sea with the range of the spotted deer, one may see that the deer occupied and occupy just those areas where the winter snow precipitation does not exceed 800-1,000 mm. Thus, the distribution of the deer is closely related to the snow distribution in the Maritime Territory. K.A. Abramov (1939, 1928)

was the first to establish this law and we now also observe its confirmation in analyzing the distribution of the deer in the preserve.

In the former Sudzukhe Preserve, the spotted deer occupy the seashore and repeat the laws governing distribution which are observed throughout the whole Maritime Territory. They remain in the environs of Khontueza and Tasavai Bays, and to the south in a single group near the Valentin Bay. After an unoccupied zone, they occupy the littoral parts of the "Kit" and "Zarya" Bays, not mixing with more southern herds from the shores of the gulfs of Tachinkow, Malankow, Syao-chinkow, and Pashagou. In short, the spotted deer turned out to be distributed according to the "snow rules", not evenly along the entire shore but in separate "islands". The cause of this distribution consists in the fact that deer, as stenotopic animals, select for themselves these areas which provide the necessary conditions for their normal existance throughout the entire year. In selecting these areas the snow cover has great significance.

The climate and the snow cover in the former Sudzukhe Preserve are very complex and require description.

B.P. Kolesnikov describes four different climatic regions in the maritime area where the preserve is situated (see Figure 3):

1. Coastal region, which extends along the shore to the 500 m contour line,

2. Olga region, which is more severe climatically, and often subject to cold summers and winters,

3. Continental region, occupying the western slopes of the Tachingchang Ridge up to 500 m elevation,

4. Mountain region, embracing the heights of the Tachingchang Ridge and the slopes higher than 500-600 m.

Spotted deer in the preserve chiefly occupy the coastal region somewhat less the Olga one, and only slightly the continental region. Deer have never been observed in the region of the mountain climate (see Figure 3).

The indexes which favor the distribution and numerical increase of the deer include the following:

a) 187-197 days of plant growth with 2,400-2,500° of annual temperature,

b) 90-140 days of snow cover, with the presence of single small regions devoid of constant snow,

c) Height of the snow cover from 0.3 to 24 cm in January and from 0.0 to 50 cm in March,

d) Absolute temperature minimum in January when there are strong winds not lower than minus 38°; average annual temperature higher than +3°.

However, a decrease in the number of days of plant growth from 170 and 150, a total annual temperature of 2,150°, 165 days with snow, 34-40 cm deep in January and 65 cm deep in March and violent mountain winds when January temperatures fall below minus 40° are unacceptable to the spotted deer even under the conditions of the Maritime Territory.

During the 1944 to 1949 period, a number of observations were carried out in the former Sudzukhe Preserve on the influence of snow on the way of life of the spotted deer. The results of these observations are presented below:

The first snow in the preserve falls toward the end of Ocotber or during the first days of November, but melts almost completely at the foot of the Taching-chang Ridge, persisting only higher than 600 meters in the region of the mountain climate. Permanent snow falls on the preserve later than the end of November, remaining unchanged in the northern-western slopes. With the appearance of snow, all the food lying on the ground on the northern slopes becomes covered and is not always accessible to the deer. On the southern seaside slopes, where there is almost no permanent snow cover during the entire winter, even snow 30 cm high melts 6 or 7 days after it falls in such amounts that in various places melted stretches are formed, which increase gradually until the next snowfall. On the north-western slopes of the ridge this phenomenon is not observed, and 10-15 km from the seashore even the sunny slopes are covered with snow for long periods. Later the repeated snowfalls usually add fresh layers of snow to the old layers and toward the end of winter it accumulated on the northwestern slopes to heights at least twice as great as in the southern areas. Thus, from the middle of winter the snow cover is unevenly distributed throughout the area of the preserve.

Strong March winds, which follow each snowfall, effect changes in the height of snow cover. They blow the snow from one place to another. On some peaks of even low hills, and on lee slopes, large snow"cornices" form as high as 3 m; and inversely, on the vindy side, part of the ground is completely bare of snow. These "cornices" or drifts, here called "blowings", form a barrier in the passes from one slope to another, blocking the deer's access to new feeding places. Such drifts are especially dangerous for those deer which did not manage to pass to slopes with little snow in the fall. In this case they are compelled to seek a passage through the snow, or if they remained on the northern slopes, to suffer from a lack of food.

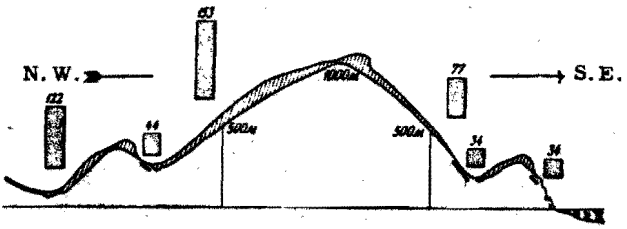
The varying height of the snow covering under the conditions of the preserve is caused by the rains. Very often heavy rains fall in the littoral regions of the preserve before and after snowfalls, and as a result a narrow belt along the sea-shore remains completely free of snow. At the same time, when there is no rain, a dry snow falls far inland, covering the summits and the western foothills of the mountain slopes. On the boundary of the regions covered by the rain, a very heavy ice crust usually forms. In short, under such climatic conditions, more snow accumulates a belt extending in a northeast-southwest direction, i.e., per-pendicular to the previaling winter winds. On the northern side, near the "cornices" regions appear which have little snow or are absolutely devoid of snow; apparently it is blown toward the "cornices" from these areas. Somewhat less snow is de-posited on the northwestern slopes of the mountain which are slightly warmed by the sun. Here the height of the snow gradually decreases in proportion to the descent of the rivers to the valleys. Finally, on the southeastern slopes which are strongly warmed by the sun the least snow of all remains. Here a thick ice crust forms from the winter rains.

To clarify this we present a cross section (Figure 6) of the Tachingchang Ridge, which shows the depth of the snow cover at different heights and slopes. The small columns in the scheme indicate the number of days in each region when deer are compelled to take their food from the trees instead of from the ground.

Spotted deer avoid regions with a 40 cm snow cover and stay in areas with a low snow cover for 34-44 days. In the former Sudzukhe Preserve these areas are situated only on the sunny slopes which face the sea and the southeastern

slopes of the mountains in the interior of the preserve. The height of the snow cover and the number of days it remains essentially determine the winter distribution of the spotted deer in the whole Maritime Territory. Those regions where a slight snow cover rests on the earth for a short time only are the best areas for deer habitats. However, where a high snow cover remains for a long period the deer cannot exist.

The dynamics of the snow in the former Sudzukhe Preserve is peculiar. By means of observations over a series of years we succeeded in determining that the first temporary snow at the end of October and the beginning of November does not greatly hinder the movement of deer in search of food. This snow remains until the end of February, gradually melting and evaporating (sublimating) in the dry air, with light snowfalls compensating for the losses. Thus, the normal snow conditions during the first half of the winter do not cause any shortages for the spotted deer.



Legend

Number of days in year when deer tear foliage from the trees

Height of snow cover

Places occupied by spotted deer

Figure 6. Schematic section of the Tachingchang Ridge, with indications of the snow cover, 15/III (section taken from the village of Kishinevka on Mount Goral)

From the end of February or the beginning of March the snow regime changes sharply. Frequent snowfalls occur associated with cold northeastern ("hunters") winds and the height of the snow cover sometimes increases for 2 or 3 days to 60-80 cm. The most difficult period of the deer's life begins at this time. Fortunately the March snowfalls coincide with the thaws, and because of this the fallen snow rapidly melts on the sun-warmed slopes, giving the deer wider and wider areas in which to locomote and search for food. We found that snow even higher than 80 cm falling after 15 March thaws so rapidly that as early as 5 or 6 days later no longer hinders the deer in their search for food. A snow covering which forms before 15 March is unfavorable for deer, since during this period there is still severe cold. At this time the snow thaws slowly even on the sunny slopes.

During most years the dynamics of the snow cover in the Maritime Territory is favorable for the deer. They successfully survive the severe winter period, which lasts approximately 30-40 days. In some winters, in 1948-1949 for instance, the snow-cover conditions were especially favorable, as the southern slopes were covered with snow only for 14 days.

In that winter the deer roamed extensively all over the slopes and did not suffer at all from the usual March shortages. The snow fell only toward the end of December and accumulated only on the northern slopes, in depths of more than 25 mm; the southern exposures remained almost entirely free of snow.

Quite different conditions were observed in the winter "snow catastrophe" of 1947-1948 which was like none other inthe litoral area for over 60 years. In November 1947 approximately 100 cm of snow fell on the northern and 70 cm on the southern slopes. Consequently a heavy layer of snow remained in all climatic regions throughout the winter. The snow layer (60 cm high) was maintained during this "catastrophe" up to the end of February even on the precipitous mountain slopes and increased in March to 75 cm. Only on 24 March for the first time since the snowfall, did the deer again find it possible to move freely in any direction and to select living food from the earth and the trees in new places. During this winter the deer did not have the usual 34-44 "tight"days, but as many as 122 such days. Sinking up to the chest in the deep snow, the deer tried the passes into the valleys of the streams and rivers and toward the seashore, where they were trapped in the unfrozen beds of the rivers, rivulets and the seashore, ordinarily convenient for locomotion. The branches of various kinds of trees which in other years remained almost entirely uneaten were completely devoured by the hungry animals in these places. Because of the lack of food and the low nutritive value of the diet, a proportion of the spotted deer died that winter; the first to die were the young born in 1947, followed by gravid females, and finally the antlered stags and the nonpregnant females.

Similar "snow catastrophes" are very rare in the Maritime Territory, however, deep snowfalls at the beginning of March during which some weakened deer die, recur each 6-14 years.

Thus, winters with a large amount of snow are a periodic cause of the reduction in the numbers of the spotted deer and are an obstacle to their successful expansions of their range northward.

The snow cover also brings about the peculiar insular distribution of deer in the Maritime Territory. It must be admitted that in places where the precipitation in the form of snow does not exceed 800 mm per winter and where there is the possibility of finding bare spots which are covered with snow only for 50 days during February and March, the deer can live without additional food. They are also able to survive even more severe conditions of very snowy winters, but in such cases their number will diminish to some extent. In days of thaw or rain, an icy covering may form on the snow surface, facilitating the hounding of the deer by wolves. Were it not for the ice crust and the wolf attacks associated with it, the number of spotted deer in the Far East would possibly increase swiftly. Proof of this is the increase in the total number of individuals in former years when there were no wolves. In Sidemi, N.I. Yankovskii was able to obtain 2,000 individuals from 15 deer in 30 years when the deer were permitted to roam freely and the region was kept under protection. The same was also observed in Askol'd Island, where the Vladivostok Society of Amateur Hunters simultaneously obtained 2,500 head from 15 deer, while in the year 1905 the Society already found an overpopulation of deer on the area of the island. A rapid increase in deer numbers was observed in the "Kedrovaya Pad'" Preserve and in the former Sudzukhe Preserve from 1936 to 1940. All this proves that merely protection measures make it possible to increase the population of this species.

Ravages by wolves among the deer start mainly when the snow cover increases to a depth of 20-30 cm. A 60 cm snow cover somewhat prevents the pursuit of the deer by the wolves, and they quickly fall behind as the deer bound ahead. Loose deep snow without an ice crust even helps the deer elude the wolves. Unfortunately

a crust forms each year on the southern slopes all through the winter, melting by day and freezing again at night. From mid-March crust formation starts over the entire slope country without exception, particularly during the night, This enables the wolves to move freely in the most interior regions of the taiga preserves. In certain years, the crust forms during the first snowfall and the deer are doomed throughout the winter to constant pursuit by the carnivores.

Another undesirable element for the deer is the formation of ice on the rivers and streams. Observation over several years have shown that its formation is in direct ratio to the type of snow cover; the stronger and more frequent the snowfall the weaker the formation of ice on the river. Thus, there was absolutely no ice on the river during the very snowy winters of 1947-1948, and the deer were able to move freely along the unfrozen beds of streams.

During infrequent and slight snowfalls, a heavier formation of ice occurs on the river. Ice of great thickness forms a layer upon layer for dozens of kilometers, not only in the beds of rivers and rivulets, but also in their valley. Wolves easily traverse such ice formations in the uppermost reaches of the rivulets and in any regions of deer habitation. Thus, the formation of an ice crust and thick ice formations are sometimes more unfavorable for the deer than loose deep snow.

Distribution Along Biotopes

In the Maritime Territory forest massif, the deer occupy the zone of deciduous oak forests covering the southern and southeastern slopes of the Tachingchang Range. In higher zones, with dark needled fir forests, they enter only the southern; regions of the Maritime Territory (Khasan Raion), where a considerable uniformity of the vegetation under the influence of the sea takes place. Thus, at the latitude of the former Sudzukhe Preserve deer do not go above 500 m.

All forests in the preserve which are occupied by deer are "new", i.e., have been re-established after systematic fires lit at various times. Among them the deer exercised particular preference for regions under the constant influence of cold streams of sea air and which formed underbrush thickets, glens, and overgrown groves which formed after repeated fires.

The fires changed the forest vegetation considerably. Cedars, for instance disappeared completely, although previously forming part of the deciduous oak forests, even near the seashore itself and later, the maple and other deciduous broadleaf species also disappeared. A mass of young thickets sprang up in place of the species that had been burnt, and large areas became overgrown with small groves of oak, Japanese clover, maple, hazel, Manchurian nut, and a number of vines.

The fires and resulting vegetation changes did not force the deer to change their habitat, but on the contrary, in the thickly tangled thickets in the groves they found good protection against persecution by wolves and plentiful leafy food. The deer, as observations have shown, are completely unafraid of fire and quietly leave a burning area, to return when the green vegetation begins to grow again. They particularly prefer to frequent burnt areas during the summer, when they begin to eat the young shoots of the trees and to lick the ashes remaining on various stumps.

In summer during prolonged rains, the spotted deer fan out over the burnt-over deciduous oak forests without showing preference for any particular slope and roam in groups down the valley of various streams.

There are usually regions which possess heavily shaded stretches of poplar, elm, Manchurian nut, ash, and secondary growths of bird cherry trees, alders, honeysuckle, and other vines.

After the formation of a 45-50 cm snow cover, the spotted deer strive to reach the sun-warmed southern slopes where there is less snow, but they never remain on sites clear of snow by the wind ("bald spots") on the northwestern slopes of the hills , as do the wapiti. In such areas, the entire foliage is blown away from the trees and earth in the wintertime and almost no important deer foods remain.

During the winter the deer remain on the southeastern slopes until the spring thaws. From these slopes, if the snow cover permits, they stamp a series of trails through the drifts in the passes toward the northern and northwestern slopes, where they gnaw at the choicest oak, linden, and maple leaves. As the snow covering increases, the passes along the mountain paths become more difficult, but the deer succeed in gnawing a considerable part of the leaves of the trees. In this case it is easier for large herds to maintain the trails for access to the feeding areas, and gregariousness becomes an important positive feature of the deer. Does and fawns which have strayed from their herds lack the ability to cross the deep snow into the necessary feeding grounds.

After heavy snowfalls when snow up to 70 cm high accumulates on the northern slopes and "cornices" to the height of three meters form in the passes, the deer almost completely stop passing and concentrate in the least snowy places on the southern slopes. The large snowdrifts are successfully crossed only very rarely. Thus in winter the deer more readily take positions along the open valleys and the slopes facing the southeast and in the upper levels which are protected from the northwestern winds of the ridges. In snowless periods of the year, the deer climb the field-covered southwestern slopes where vines Aralia and Acanthopanax grow. They never go onto the slopes covered with fir trees and face north and northwest.

In winter the spotted deer mainly remain in forests where the following species of trees prevail: oak, various maples, Kalopanax pictum, Amur cork tree, ash, rarely hornbeam, two species of hazel, Japanese clover, honeysuckle, wild pepper, and jasmine. The more low forms of such vegetation there are with leaves in good conditions, the more the deer prefer to remain among the bushes on the southern slopes.

Thus, during the year, the deer select the southernmost and most southeasterly slopes of the mountains lying near the shore and protected by the ridges from the cold winter winds, where the snow is less abundant and the weather is warmer, where the sunlight lasts longer and there are more decidous trees. At the same time, near these places there are fewer botflies, the salt licks are close, and the deer may easily save themselves from wolves by entering the sea.

To conclude this section on the laws governing the distribution of the spotted deer we present a number of characteristic phenological data registered in the older Sudzukhe Preserve in the region of the Tachinkow River Basin where a considerable proportion of the spotted deer are concentrated:

First frost: 1-6 October
First subzero ground temperature: 4-8 October
First snowfall: 24 October-12 November.
Formation of ice on the rivers: 20 December-4 February
Last snow near the sea: 2-20 April
Last snow in the mountains: 24 April-May 15.

Rhododendron blooms: 11 April
Young sedge appears: 27 April
Willow blooms: 1 April
Pear blooms: 7-15 May
Bird cherry blooms: 4-27 May
Apple blooms: 18-23 May
Oak turns green: 15-25 May
Grapevine leaves open: 16 May
Maackia leaves open: 1 July
Linden blooms: 11-19 July
Acorns drop: 3 August-5 September
Mass yellowing of leaves: 10-15 September
Leaves fall: 16-29 October

Numbers of Spotted Deer in Former Sudzukhe Preserve and Characteristics of Herds

In the last century the number of spotted deer in the former Sudzukhe Preserve were more widespread than now and were met in the large herds along almost the entire southern shore of the Maritime Territory. N.M. Przheval'skii (1867) colorfully described hunting spotted deer in the vicinity of Vladivostok. He writes: "We were not more than two versts away from the city before I sighted seven axis deer.... calmly roaming near the ravine". On the following day, he again went hunting and killed one of two deer. At the same time his companion came across a large herd and "killed two deer with one shot". Judging from the data of M.I. Yankovskii (1882), up to the year 1877 spotted deer were still numerous in the southern Maritime Territory and herds of them, 40-50 head each, were encountered around Vladivostok; in any case their meat was more easily obtainable than beef.

After a winter of plentiful snow (1877-1878) and irregular hunting, the deer disappeared from the vicinity of Vladivostok and venison almost disappeared from the market. During the entire spring of 1878, on the south of the Maritime Territory, to judge from the description of M.I. Yankovskii, dead deer were found without signs of violent killing. After the fall fires, the valley around the fresh-water lake near the Slavyanskii Peninsula was strewn with skeletons of spotted deer, wapiti, and roe deer, which perished during the "snow disaster" of that year. Spotted deer almost disappeared from the southern littoral forests.

The deer also became less abundant in the area of the former Sudzukhe Preserve, where they began to be hunted somewhat later, in the year 1907, from the time of the appearance in the valley of the Sudzukhe and Taukhe immigrants from China and the west. Andrei Dodo, an immigrant from Moldavia, reported that in 1909-1910 there were so many spotted deer that in addition to the left shore they occupied the entire right shore of the Sudzukhe River. From that time on deer were constantly hunted until 1932 when closed areas were established, followed in 1936 by the establishment of a game sanctuary. According to A. Dodo, in the years when people first appeared here deer often crossed the roads around the village of Kishinevka and the Sudzukhe River, while the dogs of the village always took to running them down by their tracks. The year 1914 was unfavorable for the spotted deer.

An old hunter, I. Gol'dberg, of the Preobrazhenie settlement, called it a year of "deer misery" and supplied a number of interesting facts. According to him, in 1914 the shores of the Preobrazhenie Gulf were not yet inhabited and only the village of Sokolovka was in existence. The arriving immigrants immediately started a year-round hunt of all animals; each tried to kill as many as possible to prevent his

neighbors from getting some. In the second half of 1914, a meter of snow fell, and it became possible to reach any spotted deer on skis. Taking advantage of this circumstance, the entire population launched a deer hunt despite the fact that a ban had been imposed on hunting.

The Forest Ranger force readily yielded, receiving a large bribe from the organizers of the deer hunt. Encouraged by the support of the kulaks [wealthy landowners], the entire population moved out to the mountains to kill the animals without fear. Three days later I. Gol'dberg left for a ski tour of the vicinity of the Gulf of Pashakow and Syao-Chinkow, on the territory of the former preserve, and was deeply shocked by what he found: in one place alone he saw 25–30 dead deer heaped in a pile, in other places he found 5 or more live deer already placed in cages; at the mouth of the Syao-Chinkow River he came across a whole mountain of deer skins already processed for export and packed for sea shipment.

Seeing such a shambles, I. Gol'dberg reported it to the director of the Forest Rangers, who evidently had also been bribed. Only after the next snowfall did the forest wardens leave for the poaching areas indicated by Gol'dberg, but it appeared that the facts regarding the capture and slaughter of deer were impossible to prove. I. Gol'dberg himself was accused of making false accusations. Many deer also perished from lack of food that year, and many old-timers thought that after 1914 only one-tenth remained.

Increased extermination of deer in the region of former preserve also continued during the years of the Civil War (1918–1920), when people returned from the front armed with rifles.

Many deer perished after snowfalls in the coastal areas of the Ta-Chin-Chtan Ridge (1926–1934), when the territory of the future preserve was already declared a closed area. However, despite all this, the number of spotted deer in the Ta-Chin-Chang Ridge gradually began to increase from the time of organization of the closed area in 1928, but in adjacent unprotected areas the deer continued to be slaughtered and consequently were almost completely exterminated.

During World War II, the number of deer gradually began to decrease due to the increased amount of poaching.

The first information on the number of spotted deer in the former Sudzukhe Preserve is presented by O. V. Vendland, in his diaries. According to his count (the method of which was not reported by him), 500 head of deer were alive in 1937–1938 In his reports L. G. Kaplanov writes on the number of deer in 1942, indicating 300 head as an approximate figure. This figure is undoubtedly exaggerated; it would be more realistic to consider the number of living deer as 400 in 1942.

A quantitative census of spotted deer by the linear method was also carried out during the 1944 winter season. But since the principal haunts of the deer were insufficiently known, the data were only approximate. Only 250 deer were counted in 1944, which undoubtedly is closer to reality than the figure given by L. G. Kaplanov. A more detailed count was carried out in 1945, with a preliminary examination of all the places inhabited by deer. We must bear in mind that the vast territory of the preserve with its dense thickets, its rugged terrain, and its winters with little snow, do not always permit an assessment to be made in complete accordance with standard methods. Thus, in practice we had to use combined assessment methods which were based on the peculiar characteristics of the deer's mode of life. Of these the following may be mentioned:

1. From the first days of April to the middle of May the axis deer readily go out out into open meadow spaces, into old wallows and burnt areas where they seek

young green sedges and leguminous grasses. In these open spaces it is easy to observe them through binoculars and to note the sex and even the age of the deer. There are four open spaces in the preserve which are frequented by deer in the spring; observations were conducted in three of them which were situated close to the research station.

2. After the mass appearance of ticks, and later, during the rainy periods of the summer, the deer very frequently go to the seashore at dusk to rest and chew seaweed. They prefer bays with a sandy shore where there is easy access to the water. In these areas, it was possible to determine exactly the numbers of deer which were closest to the seashore by the footprints in the sand. By an annual assessment of the footprints in the sandy bays, we could also determine quite accurately the relative gain and loss in the numbers of the herd in the area in question.

3. In the fall, before the beginning of the main deer calls, it is easy to determine the running sites near the place of assembly and the mud wallows. Here it is possible to record the number of roaring stags, thus determining their numbers in the deer regions. By multiplying the number of deer stags heard by the average number of females near one stag, we may estimate the total number of deer inhabiting the preserve. The ratio of females per male is determined from total number of deer encountered during the year.

The chief places occupied by the spotted deer in a given year may be determined by making use of the three indicated features of the deer's habits; the coming out to the sedge and grasses, the coming out to the beach, and the fall roaring. This helps in making a later, more exact count. The next count is carried out in March, during the period of the year when all the spotted deer are forced onto the lightly snow-covered coastal slopes by the heavy snows, and distribute themselves in separate herds which are no more than 3-4 km from each other. The count itself is carried out after a snowfall from the number of tracks crossing the assessor's path along the seashore. Tracks of this kind were made from the Lengueva Pad' to the mouth of the Taukhe River (see Figure 3).

As deer cling stubbornly to the same sites, the census in winter may also be carried out on successive days after a new snowfall. The heavier the March snows the closer the deer converge on sunny slopes and the easier it is to count them, but when there is little or no snow, such a census is impossible.

Employing all these possibilities 270 deer were counted in the former Sudzukhe Preserve up to May 1945. They were distributed in the following areas:

In the vicinity of the bays:

Taukhe	9
Tasavai	20
Valentin	12
Kit	16
Zarya	8
Ta-Chinkow	12
Malankow	16
Syao-Chinkow	24
Pashenkow	16

The total number in the environs of the bays was 133 deer (females). In the regions somewhat removed from the seashore, the count was as follows:

Ta-Chinkow River	22
Kamennyi Spring	8
Kanikheza Syaokhinskaya	8
Kanikheza River near Kishinevka	18
Ifam River and Malaya Tapikow River	11
Tsentralnaya Mountain	8
Vicinity of Sudzukhe Deer Preserve	8
Total	83 females

In 1945 we counted the deer which could be seen and determined that there was one male per four females. Thus there were 54 males for 216 females, or a total of 270 deer.

In 1946, using the same methods, we succeeded in establishing the following deer numbers in individual sections of the preserve:

In the vicinity of bays:

Taukhe	9
Tasavai	12
Valentin	11
Kit	21
Zarya	8
Tachinkow	23
Madenkow	16
Siao-Chinkow	28
Pashakow	18
Total in the vicinity of bays	146

In addition to the coastal part of the preserve, the census was also carried out in the basin of rivers and springs 3–4 km from the sea. The results of this census are presented below:

Tachinkow River	18
Kamennyi Spring	9
Kanikheza River below Kishinevka	12
Ifam and Taipikow Rivers	14
Tsentralnaya Mountain	6
Kanikheza River (Syaokhinskaya)	7
Total	66

According to rough estimates of the footprints on the new territory of the preserve which was added to it in 1946, approximately two herds were found each possessing 8–10 head, on the regions of the coastal slopes from the Taukhe Bay to Vanchin Bay, while more often the majority of the deer were located near the Khontueza Bay. Eighteen deer were counted in these places.

A total of 230 does were counted in the places mentioned. Considering that there is an average of four does to each buck, the total number of deer is 290–300. This figure is apparently somewhat less than the actual figure, and also includes deer of the new territory. In 1946–1947, when there was a profusion of acorn food, the spotted deer maintained well during the winter. Thus, by the above methods we succeeded in counting 320 deer of various ages and both sexes in the preserve.

The winter of 1947–1948 was extremely snowy. The snow (84 cm) lay on all mountain slopes from the end of November to the beginning of April. The deer lacked food on the ground from November and were restricted in their movements in search of food. Numerous deer could not survive the lack of food and began to die of exhaustion. Judging from the carcasses discovered in this region only, from the Siao-Chinkow Bay to the Valentin Bay, approximately 50 deer died that winter. The excessive March snows prevented us from conducting even an approximate count, but according to the visits of the deer down to the gulfs, to their stations and to their running sites, their numbers were halved, dropping to 150–160 head.

We should note that the deep snow cover of 1947 formed only near the seashore, and deer occupying the deep interior parts of the preserve near the village of Kishinevka did not suffer at all.

In December 1948 no census was carried out because of the complete absence of snow in the deer regions, and only during several days in January and March of the following year (1948), after the first snowfall, did it become possible to count them throughout the preserve. The data of the count are presented in Table IX.

Table IX

Deer sites near the	Females	Young	Males	Total
Gulf of Taukhe	3	2	–	5
" " Tasavai	4	3	2	9
" " Valentin	5	3	3	11
" " Kit	3	1	1	5
" " Zarya	4	1	2	7
" " Tachinkow	4	2	4	10
" " Malankow	4	1	1	6
" " Siaochinkow	4	2	2	8
" " Pashakow	3	2	2	7
Total	34	17	17	68
Tachingou River	2	–	1	3
Kanikheza on Imishinskaya Village	11	6	1	20
Ifam and Taipikow River	5	6	3	10
Tsentralnaya River	6	3	3	12
Kanikheza and Syaoukhe River	3	2	–	5
Khontueza Bay and Red Cliffs	5	3	1	9
Glazkovskii Pass	2	2	1	5
Total	34	19	11	64

In the preserve, including the additional portions, the following deer numbers were counted: 68 females, 36 fawns up to the age of one year, and 28 antlered stags which remained apart; a total of 132 deer. It is possible that single deer in places remote from the sea were not included. It would thus be more correct to say that there were 150-160 head.

The number of spotted deer in the former Sudzukhe Preserve in various years is indicated in Table X.

Table X

Year	Surface occupied by deer (hectares)	Number of individuals	Remarks
1936	36000	500	Data by O. V. Vendland (1938)
1937	36000	500	" " " "
1938–1941	–	–	No data
1942	36000	800	According to L. G. Kaplanov; the figure is not very accurate; 500 head is more exact
1943	36000	400	Data by L. G. Kaplanov
1944	36000	250	Our count
1945	36000	270	" "
1946	42000	300	Including deer of new territory
1947	42000	320	" " " "
1948	42000	150	" " " "
1949	42000	160	" " " "

The total number of white spotted deer in the Soviet Union in 1949, not including those acclimatized in new regions, was not higher than 300 head, including those in the former Sudzukhe Preserve (160), the Sikhote Alin Preserve (20), the Kedrovaya Pad' Preserve (30), and the Suputinskii Preserve (30), and deer roaming around the preserves in unprotected regions (60). Thus, the former Sudzukhe Preserve is now the largest preserve of wild spotted deer in the Soviet Union and possibly in the whole world.

The area occupied bythe spotted deer in the former Sudzukhe Preserve covers approximately 42, 000 hectares. On this basis, we may calculate that the deer density in the preserve in recent years has been 3.5–12 head per thousand hectares. A density of 12 deer per thousand hectares in areas where there is no supplementary food, should normally be considered near the maximum saturation point of the region as in winter the deer are grouped more closely together on the southern slopes. This is apparently the natural density, and in case of increase, the deer will begin to occupy nearby regions.

Structure of Herds

In the time of N. M. Przheval'skii (1867), deer herds of 60 head each were observed in the Maritime Territory. Old–timers who entered the Maritime Territory in 1905 affirm that deer herds with 20–30 head were extremely common phenomena in the old days, but at the present time such large herds are not observed; the largest herd seen in 1944 consisted of 14 head. After the snow disaster of 1948 in the Kanikheza River area, where the deer had survived fairly well, we succeeded in seeing 8-9 head of deer together in herds. Near the seashore of the preserved herds were even smaller, no more than 5 head. Apparently the number of deer in the herd depends directly on their total number, which is why a diminution of the herds was now observed.

The composition of the deer herd does not remain constant but changes with the seasons. The most numerous deer herds form toward the winter, particularly in years of large acorn crops. The winter herd usually consists of males, fawns born in the past year, and one–spike antlered deer. Stags with slender branching antlers $2\frac{1}{2}$–3 years of age rarely graze with the herds, but like the large stags, climbing to heights of 300–400 meters along the southern slopes of the mountain, where they remain the entire winter. The members of herds almost never climb

to such heights, but keep to the low foothill regions, where less snow accumulates. Toward the time of parturition in May, the females leave the herds for several months in the summer, and consequently in the spring the number of deer in the herd decreases considerably, only the one-tined yearlings and nonpregnant females remaining.

Toward the period of running, the spotted deer reassemble into herds, and remain in the enlarged herds until the time of deep snow. Only the large stage separate after the end of the running, and leave to pass the winter together with the young males. The old males are the most cautious members of the herd. Their cry (whistling) is a signal of the appearance of danger. The female usually leads the herd through paths and snowdrifts and thus we may regard the experienced old females of the leaders of the herd.

To judge from recorded data on observed deer, the sex ratio does not remain constant. The sex ratio of the deer is presented for various years in Table XI.

From this table one can see that age and sex ratios change, according to the number of males, from 0.8-1.5 for young and from 2.7-3.4 for females. It is obvious that these data are not absolutely exact.

Table XI

Year	Number of males	Number of females	Fawns (up to 1 year)	Ratio of males to females	Ratio of males to females and young	Remarks
1934	126	409	101	1:4	1:3, 3:0.8	Data of hunting trade
1935	20	64	-	1:3.2	1:3.2	After
1936	9	32	-	1:3.5	1:3.5	O. V. Vendland
1937	24	64	-	1:2.7	1:2.7	(1938)
1938	16	45	-	1:2.8	1:2.8	
1944	15	42	14	1:3.7	1:2, 9:1	
1945	22	64	30	1:4.5	1:3; 1.5	
1946	18	62	28	1:5	1:3, 4:1.5	
1948-1949	27	65	33	1:3.6	1:2, 4:1.5	
Total	277	847	206	1:3	1:3; 1	

Note: The totals in the table include ratios in which all three groups are presented.

Reproduction

Old-timers and hunters of the Maritime Territory say that running was clearly seen in spotted deer at the beginning of this century and took the same form as in some large park establishments, with frequent bugling and fights between stags. Apparently this information is not devoid of truth and where there were more deer we undoubtedly succeed in seeing and hearing them during the running periods.

When the deer numbers are what they are today, the signs of running become less apparent. We do not always succeed in observing the deer during the running

periods, since they lose almost none of their caution. Indications that timid males become uncautious during running and sometimes even dangerous refer apparently to specimens in parks. Under natural conditions the wild spotted deer are as difficult to approach during the running period as at other times.

During running periods usually silent males begin to produce a peculiar roaring sound which most commonly resembles a whistle with a coarse growling roar. It is easy to determine the start of the general running of all spotted deer from this cry. Under the conditions of the former Sudzukhe Preserve from 1944 to 1948 the beginning of the running period takes place at various times, as shown in Table XII.

From this table it is difficult to draw any conclusions about associations between running periods and individual natural phenomena, but undoubtedly a good, large acorn crop on which the spotted deer fatten well in the fall causes a vigorous running period. To some extent the running period is connected with the first appearance of frost.

In 1944, average running was recorded only in regions far from human habitation – in the vicinity of the Siao-Chinkow Bay where up to 3 roaring stags could be heard at once. On the slopes of the Ta-Chinkow and Kit Bays, where the buildings of the preserve administration were located, the roarings were weaker and heard not more than 2 or 3 times daily. This permits us to describe the running of 1944, presented in Table XII, as weak running. We succeeded in hearing the roaring of a total of 14 stags during the autumn of the year in question.

In 1944, the first stag called on 10 September, after which there was sporadic running until 5 October. Continuous roaring started after this, the temperatures being as follows: at 0800 hours the temperature was minus 1.2 to plus 4°; at 1300 hours the temperature range was 16°–21°, at 2000 the temperature was 5°. The weather was cloudless, without precipitation, and foggy on certain days. Among phenological data we may indicate the following: first frost 1 October; first cold (water frozen in stagnant pools to a depth of 5–8 mm), 9 October; by 15 October, all the leaves had fallen from the trees and bushes, except for the alder. In the daytime, mass swarming of bloodsucker gnats was observed.

The most powerful roaring in the year in question occurred in the period from 11-17 October, particularly in the Siachinkow Gulf area. The last stag was heard on 31 October. The running of 1944 was described by old-timers as late and slight, as in the opinion of local inhabitants the peak should have occured on 7-10 October, when the yellow leaves have not yet fallen from the trees. Apparaently this is erroneous, since in 1936, when a large number of deer was present in the preserve, O. V. Vendland determined the normal run as occurring in the 11–31 October period, the peak occurring on 23 October, while in 1936, running occurred in the vicinity of certain gulfs even at 1600 hours.

In 1945 there was a large accumulation of persons at exactly the places where spotted deer running usually occurred. That year all stags and does were compelled to move to unfamiliar areas, where they voiced no signs of running. In the entire fall of that year, the stags were heard roaring only twice. Nevertheless, despite the slight external manifestations of running, in the subsequent year no nonpregnant females were found. Pregnancy was universal.

In the fall of 1946, a large harvest of acorns was seen in the narrow half–kilometer–wide coastal belt of the preserve. All spotted deer concentrated in the oak forests on the northern slopes of the mountains from the first days of September, staying there almost throughout the snow–free period of the year. In 1946 running started early, on 29 September, and increases from October, the morning temperature being minus 1.5° and the daytime temperature plus 16°.

Table XII

Year	Roaring of deer			Type	First frost	First permanent cold	Mass yellowing of leaves	Mass leaf shed	Type of weather		Acorn crop	First snow	
	Start	Peak	End						Summer	Fall		Temporary	Permanent on northern slope
1936	11 X	23 X according to data by O. V. Vendland	31 X	–	–	–	–	–	–	–	–	–	–
1944	5 X	15 X	31 X	Weak *	1 X	15 X	10 X	15 X	Rainy, warm	Dry, warm	None	28 X	9 XI
1945	No roaring heard				5 X	9 X	8 X	20 X	Very rainy, cold	Cold, dry	"	18 X	8 XII
1946	28 IX	19 X	6 XI	Good *	23 IX	13 X	14 X	20 X	First cold, damp, later dry, warm	Damp, warm	Large crop	8–10 X	1 XII
1947	10 X	?	4 XI	Very weak*	6 X	12–11 X	10 11 X	?	Warm, dry	Warm, dry	None	7 XI	10 XI
1948	No roaring herd				14 X	23 X	8–12 X	24 X	" "	" "	"	20 XII	20 X

* Weak: 1 or 2 cries of stags heard in roaring area; average: 2–3 stag calls; good: 3–4 stag calls heard in roaring area.

There was neither wind nor precipitation throughout the period. The weather was clear by day and stars were visible at night. Among the climatological phenomena in nature, we may cite the beginning of extensive yellowing of grapevines, linden leaves, marigolds, etc. On 14 and 20 October almost all the leaves fell to the ground. On 28 September, at the very beginning of the roaring, gnats appeared, and on 17 October frosts began. With the formation of ice crusts in stagnant water pools from 15–19 October, the roaring was most intensive; on 6 November we heard the last whistling of the male. Old hunters described the 1946 running as late, delayed by 5 or 6 days.

In the fall of 1947 the roaring was poor, despite the fact that meteorological and phenological conditions were favorable; we could not determine the cause of the poor running. In the fall of 1948 almost no running occurred. With great difficulty we were able to discover single "wallows" of the stags in the preserve. The heavy snowfall of 1947-1948 considerably reduced the number of deer head and as a result running became imperceptible. In the period from 14 October the beginning of the first frost, to 31 October, we heard only two whistles in two quite different areas. After a very careful search we were unable to find even a single area where running occurred, or a single group of a stag with does. Apparently the deer were extremely scarce, forming small herds of 2–4 individuals, which was reflected in the nature of the running. Running takes a violent course only when a large number of deer is present.

The first roaring (29 September– 5, 10, 11 October), is preceded by the males' preparation for it. The stags, which remain aloof throughout the summer around shady streams and rarely come out into the open, bring their summer mode of existence to a halt from the moment their antlers ossify (23 August) and begin emerging farther and farther from their previous haunts, moving into the damp river valleys and coastal slopes. Thus, when the stags begin to clean their antlers (17 September), they are already close to the streams where the running will eventually take place.

From the middle of September near such streams we may often find trunks of cedars and maples with the bark stripped off, a sign that a stag had been there to prepare himself for running. Somewhat later the time of running may be ascertained from other signs, particularly the appearance of the ground, where an area 2 m in diameter is cleared to the bare earth. To make such platforms the deer select damp regions in the valley, where they tear up with their hoofs and fling aside the fallen bark and foliage; nearby the stag scrapes his antlers on the tough trunks of trees. At the time such platforms appear the females do not seem to participate in the running, but a number of parturition dates indicate that mating sometimes occurs even before such platforms are erected.

At various distances from the platform, depending on the type of ground water, the males search for one, or more rarely, two marshy tracts in which to form wallows — called urine-wallows and press plots–in which they periodically roll and smear themselves with filth and muddy urine.

The number of platforms which a stag possesses varies. If he is undisturbed during his seasons' run they may number 6 or 7 in a single stream or river valley, lying 15-18 m apart. Such a region of small platforms may cover a total of 4 km when the herd contains 4 or 5 deer. A larger herd numbering 14-16 head occupies an area of 8-9 square km usually with a path leading down to the seashore.

If the group of deer is frequently frightened, then the number of platforms constructed by the stag increases, and he may change them almost daily. By overfrequenting regions of running sites, one may drive the deer out completely to

new areas in different river valleys with the same kind of terrain. Together with the increase of running, the stags more often dig up the ground of the platform with their hoofs and frequent their mud baths. Males which are immaculate at other times of the year take on an odd appearance, wallowing in the mud to such a degree that their entire hairy coat becomes matted with a thick layer of dirt. Such excited stags may more often be found in the Sudzukhe Preserve from 15-20 October. Females in heat approach these platforms but do not change their appearance or behavior.

At the height of the running, at the time of maximum roaring, the stags seek out and persistently follow the nearest females by their tracks and try to drive them to their platform areas, where mating takes place. In several days one stag succeeds in driving to his platform some 2 or 3 does, which subsequently continue to loiter around the stag's running sites. Large harems are not formed by wild spotted deer in the preserve as they are in the parks. The stag guards and protects only his own small herd consisting of 3 or 4 does, not permitting them to depart from the valley selected.

We were not successful in observing battles or the encroachment of a strange male on any stag's running sites, and it is very possible that the males test their strength even before running, and later, recognizing each other by scent and call do not give battle to each other. The one-spiked fawns do not participate in the running and the adults constantly drive them off. Young females approaching the region of the platforms also fear the large excited stags.

Mating itself always takes place during the darker times of the day and thus it is not possible to present any exact data on the details of copulation; the behavior of the deer during mating can be deduced only from traces. Sometimes $2\frac{1}{2}$-year-old deer invade the platforms of the old stags where couplings have taken place. They urinate there, dig up the ground with their hoofs, and attempt to roar.

The best running sites for spotted deer in the former Sudzukhe Preserve are situated in the Syao chinkow-Valley and Gulf, encircled on all sides by mountains and rarely visited by humans. Here the roaring of the deer is undoubtedly natural (see Figure 3). In other places on the coastal slopes of the preserve near the Tasavai, Valentin, Ta-Chingou, and Pashagou Bays and also on the slopes, the running is less animated. In all these regions, the places selected for running are small taiga rivulets which flow into the Sea of Japan from northwest to southeast and are sheltered by a small ridge from the northwestern winds.

In the valleys stretching from northeast to southwest, along the northern and northwestern slopes of the precipitous water divides or in the zones of the dark needled fir forests 400-500 meters above sea level, deer do not engage in running, which almost always takes place in the deciduous oak forest zones, containing oak, linden, various maples, ash, Kalopenax pictum, Manchurian nut, and Amur cork trees, and in the undergrowth, Japanese clover, maple shrubs, and oak seedlings. Damp areas among such forest stands along river terraces with soft ground near the mouths of rivulets are the best regions for these platforms when the exposure is appropriate. It is of interest that after the running these same places are the best sites for the deer to winter on and when they are trapped by the heavy snows in such valleys the deer rarely stir from them. The snow here thaws quickly, leaving bare large areas of earth with leafy and grassy food.

Despite the fact that from 1944 to 1946 we succeeded in seeing herds of 8-14 head each in the preserves, these do not form during running. This is explained by the fact that at this time young individuals detach themselves from the herd and roam apart, not participating actively in the running.

During the running the females graze normally, roaming from one place to another in the vicinity of the stags. The stags eat very little, constantly listen to noises in the taiga, dig platforms, wallow in the mud, and rub their antlers against the hard trunks of trees. Strong stags from the age of 5 years start roaring somewhat earlier than the young deer, and leave the group of females only toward the end of the running period. The one-spiked fawns do not generally roar at all, while young males (2½ years), roar inexpertly and weakly, rarely mating with young females which wander away from the herd.

At the beginning of running the antlered stags bugle 2 or 3 times every evening. Toward the peak of running, staying with the group of females, they roar 30-40 times per evening and 10-15 times during the morning. Toward the end of the year (November), the roaring almost stops, and the antlered stags often give voice to only one final groaning call. At the end of the run, on 5-8 November, the stags become completely indifferent to females and gradually depart for the high coastal slopes, leaving the females with the fawns on the foot-hills of the mountains.

In the first days of January (3 January, 1944), after approximately 60 days of pregnancy, the fetus in the female deer reaches a weight of 6.3 g and a length of 52 mm. At this stage the embryo completely resembles the deer. Almost at this time (8 January, 1946), an embryo was discovered in the uterus of a female, weighing 51 g and measuring 112 mm, apparently at the age of 85 days. Around this time we may discover embryos of various shapes and sizes. This is explained by the fact that the running period in the deer fluctuates greatly. Toward the end of January (28 January, 1946), embryos reach a length of 250 mm, and a female uterus with the embryonic fluids weighs 2 kg. The January embryos are still completely naked and possess no pigment or tactile hairs on the body. All this appears in later months. The size of the embryo in the first half of March is considerably larger, and when its weight is 645 g the length of its body is 310 mm, length of tail 28 mm, length of ear 32, height at withers, 180 mm, and girth of chest 224 mm. The period of gestation of such an embryo has been determined as approximately 150 days. Another March embryo was obtained which was considerably larger, weighing 1,303 g and having the following dimensions: total length 390 mm, length of tail 35 mm, length of ear 44 mm, height at withers 230 mm, and girth of chest 210 mm. This large embryo, approximately 170 days old, was absolutely naked, but had small dark pigmented spots near the nostrils and long tactile hairs on the chin, upper lip and near the eye. The skull of this embryo was well ossified and could be well prepared. Its dimensions were as follows:

Maximum length	99.4 mm;
Condylobasal length	85.9 mm;
Width of supraocular bulge	48.9 mm;

Toward the end of March (21 March, 1946) a larger embryo was extracted from a 3 year-old female; it weighed 1,610 g and had the following dimensions: total length 440 mm, length of tail 34 mm, length of ear 52 mm, girth of chest 260 mm, and height at withers 280 mm. Such an embryo may be estimated as 180 days old; it already possessed long vibrissae on the facial parts and faint spots on the surface of the skin in the region of the vertebral ridge and rump.

In April almost all embryos have a spotted coat of hair, the longest hairs located on the edges of the "mirror" or rump patch or along the spine and in the tactile zone of the muzzle.

The dimensions and weight of the large April embryo (4 April, 1945) are as follows: weight 2,715 g; total length 510 mm, length of tail 45 mm, length of ear

65 mm, height at withers 380 mm, and weight of uterus and embryonic fluids 4,200 g. This fetus, apparently 190 days old, possessed a well-formed skull with developing milk molars and incisors beneath the gums. Its skull had the following dimensions:

Total length	125.3 mm;
Condylobasal length	108.8 mm;
Width of supraocular bulge	55.8 mm;

At the beginning of May, parturition commences in those females which mated first. In individual rare cases parturition also occurs before this. Thus, in 1944, as early as 28 April, we succeeded in seeing a female with a trotting fawn. More often the young appear from the beginning of May, when the tree, underbrush, and herbaceous vegetation begins to bloom profusely. We did not succeed in catching and measuring a newborn fawn, but judging from the material of the park husbandries (I.I. Mirolyubov, 1936) the young should have the following weight (Table XIII).

Table XIII

	Maximum (kg)	Average (kg)	Minimum (kg)
Weight of males (8 specimens)	6.95	5.55	4.75
Weight of females (6 specimens)	6.2	5.44	4.8

According to data from park husbandries the males are somewhat heavier than the females. Table XIV presents the sizes (cm) of newborn fawns.

Table XIV

	Males (4 specimens)			Females (5 specimens)		
	Minimum	Average	Maximum	Minimum	Average	Maximum
Muzzle	17.5	18	18.5	17	17.5	18
Ear	9.3	10.1	10.7	9.7	9.8	10.2
Body along vertebral column	54.0	57.5	61.0	54.2	56.7	59.0
Tail excluding hair	8	8.5	9.2	6.5	7.3	8.1
Chest girth	40	42.5	44	39.5	41.0	42.0
Height at withers	50	51	52,5	45	46	48.2

As is seen from this table there is little difference in the size of fawns of different sexes.

Spotted deer almost always give birth to one fawn only, but according to data in the old Sudzukhe Preserve a case was recorded of finding two embryos in one female (27 April, 1938).

The sex ratio among the embryos and newborn fawns, according to our materials (7 descriptions) was five males to two females. According to the data published by I.I. Mirolyubov (1936), the excess of males was found to be the same, with eight males per six females, i.e., 1⅓ times as many males as females.

Before fawning, the females leave the herd, abandoning their one-year old fawns and seek shaded spots in the taiga. According to careful observations at nine places of parturition discovered, these areas are stretches thickly overgrown with trees and bushes and situated along springs on the northern and northwestern slopes of the mountains with a good cover of high sedges. In such places on Mount Tumannaya, particularly in May, we succeeded in startling fawns. In all, on the slope of Mount Tumannaya, we encountered as many as 16 fawns of various ages, the fawns in the majority of cases permitted men to come right up to them, then suddenly leaped to their feet and scampered to their dams.

The selection of cool shady rivulets by the does is explained by the fact that in such places there are almost no gnats or flies. In addition, the fawn is concealed here from predatory birds and crows.

Newborn fawns lie quietly for a long time while the female prowls about at a distance of 20-40 m. After 10-20 days the fawns begin to graze independently and roam far from the mother. At this period, on the slopes of the mountain, we may often hear the mothers calling to their young at dawn. The female stays with the fawn at the place of birth until the fawn starts to graze on green fodder but does not lag behind nor lose the mother. At this time, approximately in the middle of June, on Mount Tumannaya, we succeeded in encountering fawns of large size, approximately 60-65 cm in height at the withers.

The female is very attached to her fawn and in the event of its loss continues to call in the region where it disappeared. It is very difficult to chase away the female from the area of the forest where her fawn is lying or grazing even with the help of dogs. When predators attempt to attack the fawn the female strives to divert the pursuer and lead it away from the fawn. In this event, in order to save herself, she often makes use of her ability to swim in the sea. The same is also true of females which have become heavy in the last months before parturition. As a result, in spring and summer, the majority of the deer which enter the sea, fleeing from wolves or stray dogs, are either pregnant or those nursing young, which have been temporarily left on the shore.

Toward the middle of June, the fawns have grown visibly in the withers (by 10-12 cm) and doubled their weight. Such a fawn was caught by chance in the former Sudzukhe Preserve on 16 June, 1944. We present below data on its weight and dimensions:

Total length	790 cm
Height at withers	620 cm
Length of tail	12 cm
Chest girth	530 cm
Length of ear	107 cm
Weight	12 kg
Sex	female

In the stomach of this fawn a curd of coagulated milk and a mass of unidentified sedge were discovered.

We did not succeed in obtaining data of the weight, dimensions, and stomach contents of older fawns, but to judge from the size of the udder of a female thrown up by the sea still warm in Kit Bay on 25 August, 1946 (the udder weight was 980 g), we may assume that the does still nurse their fawns at this time. Even later (in November) on an open field we observed, through binoculars, a fawn sucking its mother's udder. We may suppose that in rare individual cases the fawns suck the udder even at later dates, for on 3 January, 1944, a female was opened which possessed a nursing udder weighing 580 g (a non-nursing udder weighs 360 g).

Apparently such late nursing is a rare exception, and the majority of dissected fawns 7 months of age possessed no milk clots in the stomach. We may suppose that on the average the female deer nurses her fawn for 4-5 months.

In the summer, the wild fawns grow rapidly, feeding on the abundant green fodder and the fat milk of the female (according to I.I. Mirolyubov, 1936, the milk of the spotted deer has a 13% fat content after giving birth and 30% toward the end of lactation). Table XV shows the weight and sizes (kg, cm) of the deer at the age of 9-12 months:

Table XV

	Females			Males		
Age	9 months	10 months	11.5 months	8 months	12 months	12 months
Date	5.II.44	2.III.38	12.IV.38	8.I.45	12.V.38	1.V.45
Weight	48	49	55	54	59	49
Length of body	132	138	127	134	130	141
Length of tail	16	16	14	15	15	12
Length of ear	16	15.5	14.7	15	15.5	15
Height at withers	90	95	87	89	96	87
Girth of chest	90	92	87	89	86	79

To compare the weight of wild fawns with that of young of the same age from husbandries in parks (I.I. Mirolyubov, 1936), it becomes apparent that the latter are lighter (Table XVI).

Table XVI

Domestic Fawns			Wild Fawns	
♂	8.5 months	36 kg	8.5 months	54 kg
♀	9 "	41 "	9 "	48 "

The March fawns are lighter in the husbandries, weighing 36-46 kg, while wild fawns of the same age weigh 48 and even 59 kg. Such a difference in weight may be explained by the earlier parturition of females in the preserve, and by the abundance of natural foods.

In two summer seasons young fawns grow considerably and young females are mated in the first running at the age of 1 year and 4 months. At this time their weight reaches 65-70 kg. Male fawns at this age are somewhat heavier (70-75 kg).

After the fall change of the hairy coat in fawns, as in adult animals, the spotty pelage disappears and in its place grows a new one with a long fragile bristle and down which keeps them warm on cold nights.

Such a pelt does not protect the young fawns well from the strong winds, and

as a result they avoid the windy valleys in the winter and try to keep to slopes and valleys sheltered from northwesterly winds. To conclude this section, we should point out that running in the wild deer, as compared to park individuals, occurs earlier and continues for a shorter period. In turn this causes early parturition and as a result the young have time to attain a large size and weight by winter. Such wild fawns are more adapted to the snowy period of February and March and endure the cold winters better. Park fawns become weaker in winter. The periods of running, gestation, and parturition established in nature constitute a reproductive rhythm regulated by natural selection. We should strive to attain such a natural rhythm in the park husbandry.

Judging from the embryos and dates of parturition in wild forms, the maximum occurrence of roaring, running and other indications of sexual activity corresponds to the period of time when the females have already been mated. This is explained by the fact that the mating of females often occurs in the very first days of oestrus, sometimes on 3 October or even 10 October. Late matings occur more rarely, on 3 November. The maximum number of parturitions in nature occur on 15-16 May, the earliest occurring on 28 April and the latest on 18 June.

No sterility has been encountered among sexually mature wild deer. Of 16 females examined in the former Sudzukhe Preserve, 8 individuals examined in the winter had embryos, 4 summer specimens had nursing udders, and 4 were not sexually matured, not yet being 2 years old. In parks sterility reaches 70 %.

Diet of Wild Spotted Deer and Competition for Food

A work studying the wild foods of spotted deer has been published by G.I. Ryabova and A.P. Saverkin (1937), in which all the literature of the previous years is covered and a full list of the plants consumed by deer is given. Unfortunately, the work does not completely describe the feeding of the wild spotted deer of the Maritime Territory as it is based on the semiexperimental methods of park conditions. It is clear from the list of food plants presented in this work that many plants are consumed by the deer because they are compelled to do so but are not consumed by them in nature. Besides this the natural frequency of the consumption of the food is also changed.

The work of O.V. Vendland (1938) carried out by the method of field observations in the former Sudzukhe Preserve characterizes the feeding of wild deer more accurately. This zoologist, by means of meticulous determinations, classified 45 species of plants eaten by deer in various seasons of the year.

In studying the diet of deer, the places of grazing were investigated and all the stomachs of deer specially obtained for this work and of those found dead in the taiga were studied. There is no need to introduce any radical changes into the comparison of foods compiled by O.V. Vendland. We succeeded only in making the evaluation given for food plants more precise and in supplementing the list with new species.

It has been indicated that deer occupy the southern slopes, where there is little snow and where those deciduous trees grow which deer eat readily. Individual parts of woody shrubs and bushy species of trees constitute 70% if not more of the food of the spotted deer. Herbaceous food is consumed by them to a lesser extent and only during periods of growth. Of the food plants there is usually one leading type which is more readily eaten in large amounts but the deer usually also eat a group of secondary plants which they take in passing on the grazing ground. Although the deer are not so particular about natural foods, when there is not enough of the first choice food, they readily take second-grade food. For instance,

when there are no oak or sedge leaves, they eat leaves of other trees. It is very difficult to find regions where both first and second grade foods have been completely consumed by the deer in summertime. Individual herds spread out somewhat along the preserve, and a number of days must be spent in finding even one tree or bush whose edible parts have been completely consumed. In winter it is very easy to find the places where deer fed along the white trails and especially during periods of much snow when the herds are trapped on the southern slopes.

We present in Table XVII a general list of the food plants of spotted deer which we succeeded in compiling over many years of observation in the former Sudzukhe Preserve. The plants are grouped in the list according to the degree to which they compose the general nutritional balances of the deer.

Group I (preferred foods) includes the chief food species eaten almost daily by deer in season and sometimes out of season during the entire year. These constitute 70% of the total food volume in the winter. These species keep the deer close to their growth areas for most of the year.

Group II (second-grade foods) includes species of plants much eaten by deer, but to a lesser degree and during almost the entire year. These plants attract deer for a short period in definite regions but are not completely consumed.

Group III (third-grade foods) includes plants eaten in moderate amounts in various seasons and sometimes with intervals of up to 6 months during the year.

Group IV includes plants eaten more rarely and in individual cases only.

Group V includes plants eaten in small amounts as mineral foods.

Group VI includes plants rarely eaten by deer. The dates and volumes of their consumption remain unelucidated.

Group VII includes agricultural crops eaten by change. The "grading" in the table indicates the proportion which the plant constitutes in the total food intake of the deer during the given month. By the grades we understand the following:

Grade O. The plant is eaten accidentally, the deer rarely tear off the leaves without causing appreciable loss to the plant.

Grade I. The plant is eaten very rarely and thus has no great significance in the diet of deer.

Grade 2. The plant is eaten frequently but in small amounts. There are almost no places in which all the plants were eaten. Only leaves are torn from the plant.

Grade 3. The plant is eaten in moderate amounts. Grazed regions may be discovered with difficulty through small patches of eaten leaves.

Grade 4. The plant is widely eaten by the deer, but it is not the principal food in any single season. Grazed patches are observable but are not very close together. Very often only leaves and buds are consumed, the branches remaining untouched.

Grade 5. The plant is very extensively eaten by the deer and without discontinuity in certain regions. It constitutes the main bulk of the food in certain months. All parts of the plant are used down to the bark and branch 1.5-2 cm thick.

The climate of the Maritime Territory and its influence on the development of plants and the snow cover are highly variable. As a result, the deer have at their disposal variable amounts of natural foods.

Most favorable for the deer is a good crop of acorns, which recurs every 3-4 years. In certain cases, after a dry spring, the acorn crop may be so abundant that for 5-6 months, from September to March, they provide all spotted deer and their competitors with a nutritious diet.

Eating acorns, the deer rapidly fatten during the fall and so enter into the period of heavy snows in winter. Even after the first light snowfalls, the deer successfully continue to dig up acorns from under the snow, preferring them to all other natural foods. Only after a snow cover of more than 30 cm high has formed, which usually occurs toward the end of February and in March, do the deer become unable to pick up the acorns from the ground, when they begin to make short excursions into less snowy areas. Only in cases when heavy snowfalls alternate with rains, as a result of which a heavy ice crust forms, is access to the acorns denied to the deer for two or more months.

Another highly unfavorable extreme of feeding conditions is associated with the formation of an excessive and sometimes disastrous snow cover. The heavy snow compels the deer to remain near the channels of the nonfreezing rivulets and rivers and the belt of tidewater. In such cases, the principal and obligatory winter foods for deer "trapped" at the rivulets are species of trees and bushes which incline over the banks of the rivers and streams and are almost uneaten in ordinary winters. In such years the exhausted deer, moving with difficulty throughout the winter, completely gnaw up all branches accessible to them, even those on trees which are not eaten in normal years, for example, the willow, the birch cherry tree, and chozenia*. Toward the end of February and in March, when all food on branches along the beds of the flowing streams have been destroyed, the weakest individuals succumb. A great influence on the diet is also exerted by the winter "mountain gales" which start in the fall. They hurl the foliage of the trees to the ground, which, as a result, decays and loses its nutritive value. Thus, violent unseasonal "mountain gales" prematurely deprive the deer of important winter food.

Sometimes the cold winds start in the fall after the November rains, as a result of which heavy foliage and small branches encrusted with ice break off and fall to the ground. During one such windy night in 1945, the entire arboreal and bushy vegetation in the coastal part in the former Sudzukhe River was stripped 80% bare not only of foliage but also of small branches 3 mm thick. This occurrence, despite the favorable snow cover of the winter, caused a food shortage and the deer were compelled to weather the entire winter without leaves or buds, using much bark. There were no acorns in the year in question.

It is seen from the above that the deer diet is not constant but varies from year to year. They must often consume plants which in "full" years are never eaten by them. The degree of consumption of any plant for food also depends on the extent of its occurrence in nature. Many trees, e.g., apples and pears, would probably be eaten in greater quantities in May, but unfortunately there are not many of them in the coastal forests of the preserve.

A relationship also exists between the dates of the foliage shed from the trees and the times it is eaten by the deer. Thus, it is known that the foliage on the crown of the oak remains on the tree longer. This tree sheds its old foliage

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* Translator's note— The Russian name "chozenie" is given in the text. We have been unable to find any Latin name for this plant.

only after the buds open. Apparently this property is the cause of the low consumption of its foliage in winter not only by the deer but by most ungulates - wapiti, gorals, and roe deer.

The leaves of other trees and bushes are all shed and become covered by snow by the end of December. However, if the deer discover a fallen tree in the summer with the foliage still on its branches, they will unquestionably prefer it to the ubiquitous oak. In such cases they even prefer aspen and birch to any other winter food. For this reason the deer stamp out large plots near such fallen trees in winter, stripping their crowns naked not only of leaves but also of small twigs. In the summer the fresh vegetation of the birch and aspen is completely avoided by the deer.

From what has been said here it follows that the grades applied in the list of food plants cannot be associated with any given year, and to provide an invariant scale of food evaluation is apparently impossible. It must be noted that the deer eat the most varied parts of the trees. Shrubs are fully consumed, as are the foliage of trees and the buds, branches, bark and the spicy stems of Aralia.

At the beginning of October the first frosts occur and all grassy vegetation perishes, compelling the deer to change to winter foods—dry stems of bushes, buds of trees, small branches, and particularly the yellowing foliage of the trees. What remains green at this time is the foliage of alders and individual species of sedge (the latter retain their chlorophyll throughout the winter). All other vegetable foods become sere, coarse, and of little nutritive value.

In the middle of October after light frosts, the foliage of the trees finally becomes yellow and is shed. Thereafter the last green foliage of the alders is excluded from the food of the deer and from November until the heavy snowfalls they are compelled to feed on yellow leaves and the tops of dry herbage. At this time green food may be found by the deer only among the rough sedges not covered by snow.

During December and January the deer continue to eat leaves, buds, small branches of arboraceous species, dry herbage, protruding from the snow, and hibernating sedges in nonsnowy regions. February and March are the snowiest months of the year, and during this time more and more buds, twigs, and shoots are included in the deer's diet.

Toward the end of March, from the onset of the first warm days, if there is an insufficiency of other food, the deer begin to gnaw the bark of the linden ash, and Aralia on the sunny side of the tree where the sap first begins to flow. The bark of elms, which is rarely gnawed by the axis deer, as some think, is eaten readily only by the wapiti. More rarely the deer in March gnaw the lichens from the various fallen trees.

In the beginning of April, young sedges appear on the southern slopes near the seashore. Later in April grasses grow out as well as a number of other herbaceous plants which are readily eaten by the deer. Later, together with the growth of the grassy vegetation, deer leave for new grazing areas on the shady slopes, obtaining greater and greater amounts of new green foods. From the end of April the deer almost completely stop eating dry leaves and shoots, buds, and the remains of stems.

In May, after the buds open on the trees, the deer gradually change to green arboraceous leaves, first while continuing to use the young sedges and grasses on open fields and meadows.

Table XVII

Food plant	Season of year												Remarks
	Winter			Spring			Summer			Fall			
	XII	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	
I Principal food species (primary)													
Oak acorns	5	5	5	4	-	-	-	-	-	3	5	5	In heavy crop years
Oak	5	5	5	5	5	3	1	4	1	1	4	5	l, b, t, * rarely bk
Aralia	4	5	4	3	1	-	1	2	2	1	2	3	l,b,bk
Linden	4	5	4	5	1	-	1	2	1	2	2	3	l,b,bk
II Plants eaten often (secondary)													
Japanese clover	1	2	2	2	-	-	2	5	5	4	2	1	l, t
Smilax	-	-	-	-	-	-	4	5	5	3	2	1	l, s
Acanthopanax	1	1	3	3	1	1	1	4	1	1	1	1	l, t
Sedge	1	1	1	4	5	5	1	1	-	-	-	1	l, s
Elm	2	5	4	4	1	-	-	1	1	1	1	2	l, t, rarely
Manchurian pecan	3	3	2	2	-	-	-	-	1	1	2	3	l, t, shoots
Maple	3	2	1	1	-	-	1	1	2	2	1	3	l, t, small
"Akatnik"**	2	1	1	-	-	-	-	1	2	2	3	3	l, b, bk rarely
Dropwort	-	-	-	-	-	-	3	4	4	1	-	-	l, s,
Ash	2	2	4	-	-	-	-	2	2	-	2	3	l, t, b, bk, rarely
III Species of plants eaten in moderate amounts (tertiary)													
Elders	2	2	1	2	-	-	-	1	1	1	2	3	l, t,
Wild pepper	-	-	-	-	-	2	2	3	2	1	-	-	l
Hazel	1	2	4	2	1	-	-	2	2	-	1	2	l, t, b,
Actinidia vines	-	-	-	-	-	1	1	2	2	1	-	-	l

* l-leaves; bk-bark; s-stem; b-buds; t-twigs.

** Translator's note—Those plants for which we have been unable to find English equivalents have been left transliterated, some with appropriate notes.

Table XVII (continued)

Food plant	III Species of plants eaten in moderate amounts (tertiary)												Remarks
	XII	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	
Bird cherry	-	-	-	-	4	2	2	1	-	-	-	-	1, b
Mulberry	-	-	-	-	1	1	2	4	3	2	1	1	1, s
Raspberry	1	2	2	1	-	1	2	1	-	-	-	1	1, s
Lily of the valley	-	-	-	-	-	1	2	4	2	-	-	-	1, s
Various Vicia	-	-	-	-	1	4	3	2	-	-	-	-	1, s
Jasmine	-	-	-	-	-	2	4	2	1	1	-	-	1, t
Hawthorn	1	-	-	-	1	2	1	1	1	1	-	-	1
Plectranthus	-	-	-	-	-	-	1	4	3	1	1	-	1
Honeysuckle	1	1	-	-	-	1	1	2	1	1	-	-	1
Ashberry leaves	-	1	-	-	-	2	1	-	-	-	1	-	1, t
Rose	-	1	1	-	-	1	1	2	1	1	-	-	1
Wormwood	1	1	-	1	1	-	1	1	1	-	1	1	1, s
Burnet bloodwort	-	-	-	-	-	-	1	2	1	-	-	-	1, s
Lilac	-	-	1	1	1	1	2	-	-	-	-	-	1
Cacalia plants	-	-	-	-	-	1	3	1	-	-	-	-	1,s
Apple	-	-	-	-	1	2	1	-	-	-	-	-	1
Pears	-	-	-	-	1	2	1	-	-	-	-	-	1
Speedwell	-	-	-	1	2	1	2	-	-	-	-	-	All
Alder	1	1	1	1	-	-	-	-	-	-	2	1	1
Red currant	-	-	-	-	-	1	2	-	-	-	-	-	1
Coltsfoot	1	1	1	-	-	-	-	-	-	-	-	-	s, beneath snow
Grasses	-	-	-	1	2	-	-	-	-	-	-	-	1, s
Lichens	-	1	1	1	-	-	-	-	-	-	-	-	s
"Syusyuraya"*	-	-	-	-	-	1	3	3	1	1	-	-	1
Reeds	-	-	-	-	1	4	1	-	-	-	-	-	1
Vines	1	-	1	-	-	2	2	1	1	1	1	1	1, b
Reedbent	-	-	-	1	2	3	1	-	-	-	-	-	1, b
Smooth angelica	-	-	-	-	-	1	2	1	1	-	-	-	s
Guelder-rose	-	-	-	-	-	2	3	1	-	-	-	-	1

* See note on page 204

Table XVII (continued)

III Species of plants eaten in moderate amounts (tertiary)

Food plant	XII	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	Remarks
David's grasspea	-	-	-	-	-	1	2	1	1	-	-	-	l
Tatarian aster	-	-	-	-	-	1	1	2	1	-	-	-	l, flowers
Saw wort	-	-	-	-	1	1	2	1	1	1	1	1	All
Cow wheat	-	-	-	-	-	-	2	3	2	1	-	-	l, s
Bellflower (Adenophora)	-	-	-	-	-	1	2	2	1	1	-	-	All
Balsam	-	-	-	-	-	-	1	2	2	2	-	-	l
Spindle tree	2	1	-	-	-	-	1	2	3	3	2	2	l
"Krasodev"*	-	-	-	-	-	4	3	-	-	-	-	-	Young plant
Ribwort	-	-	-	-	-	-	1	2	2	1	-	-	l
Willow	1	1	3	4	3	-	-	-	-	-	1	1	l, b, t
"	1	1	-	-	-	-	-	-	-	-	-	1	l, b, t
"Chozeniya"* willow	1	1	2	1	1	-	-	-	-	-	1	1	l, b, s
Corktree	4	2	3	2	-	-	1	1	-	-	1	3	l, t, s, b, bk
Cowparsnip	-	-	-	-	-	1	2	2	3	2	1	-	l, s
IV Plants eaten rarely													
"Black mustache" fern	-	-	-	-	-	-	-	-	-	-	-	1	Middle part
Osmunda (royal) ferns	1	-	-	-	-	-	-	-	-	-	-	1	Middle part
Chinese magnolia vine	-	-	-	-	-	-	1	1	-	-	-	-	l
Birch	-	-	1	-	-	-	-	-	-	-	-	-	l
European hornbeam	-	-	-	-	-	-	-	1	-	-	-	-	l
Barberries	-	-	-	-	-	-	-	1	-	-	-	-	l
Buckthorn	-	-	-	1	-	-	-	-	-	-	-	-	l
Reeds	-	1	1	-	-	1	1	-	-	-	-	-	l
Violet	-	-	-	-	1	1	-	-	-	-	-	-	All
Iris	-	-	-	-	-	1	-	-	-	-	-	-	l

* See note on page 204

Table XVII (continued)

Food plant	V Plants eaten for mineral content												Remarks
	XII	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	
Eelgrass (Zostera)	1	2	2	1	-	1	1	1	1	1	-	-	Masticated in summer, eaten in winter
Laminaria (Kelp)	1	2	2	1	-	1	1	1	-	-	-	-	" " " "

VI Plants eaten rarely by spotted deer
(Exact time of use could not be determined)

Fern; onion; Greek valerian; buttercup; false helleborne; geranium; bedstraw; flowering "diadrena"*; Siberian "spodiopogen"*; Bergenia; marsh marigold; Siberian speedwell; "prilipalo"* (adhesive); Dahurian lily; melilot; "lapchatka"* (shoe-like); cinquefoil; pinks; rhododendron; marshy meadow grass; cedar.

All plants listed are eaten in small amounts during the summer. It was impossible to ascertain the proportions of these plants eaten by the deer.

VII Agricultural plants

Corn	-	-	-	-	-	-	0	0	-	-	-	-	Young leaves
Oats	-	-	-	-	-	0	-	-	-	-	-	-	Young plant
Buckwheat	-	-	-	-	-	-	0	-	-	-	-	-	" "
Soybean	-	-	-	-	-	1	1	0	-	-	-	-	Leaves
Beans	-	-	-	-	-	1	1	0	-	-	-	-	"
Foxtail millet	-	-	-	-	-	1	0	-	-	-	-	-	Young plant
Bristle Echinochloa grass	-	-	-	-	-	1	0	-	-	-	-	-	Young plant

In the summer season, when almost the entire green vegetation has appeared the deer eat the most varied species, but as formerly they prefer the leaves of trees.

In certain months of winter and summer, the deer accurately select two genera eelgrass and kelp—Zostera and Laminaria. They eat them chiefly in the intervals between the long rains of June and July at dusk or during dense fogs. More often, as may be noted, the deer frequent for these purposes the Tasavai, Kit, Zarya, Ta-Chinkow; Siao-Chinkow, and Pashakow gulfs which are completely uninhabited, and with ready access to the seashore (Figure 3).

Judging by the seaweed remains the deer hardly eat them but only lick, suck, and chew them a little. The deer use seaweeds also in the winter, but to a lesser extent.

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* See note on page 204

In this season, Zostera and Laminaria are completely consumed. Thus, in winter these plants may be included among the food plants. If there are no salty algae, the deer satisfy their hunger for minerals by licking anything thrown up by the sea: holothurians, sea urchins, driftwood, pebbles with salt incrustations, and sea foam.

Groups of deer which inhabit the deep interior of the preserve frequent the warm mineral springs which are located in the taiga. Five such springs are known, but deer select only three of them, situated nearest to the chief points of their inhabitation.

Only rarely, from July to August, do we observe the deer to frequent the fields of oats, buckwheat, beans, "chumiza"*, and "paiza"*, where they penetrate to protect themselves from the gnats, and in passing tear off small amounts of leaves, which causes absolutely no damage to the crops. All previous communications concerning damage by deer apparently refer to those times when the Chinese inhabited fanza (Chinese houses) along the seashore and planted vegetable gardens in the taiga. The deer visited these planations after rains, trampling down the plants but not eating the crops.

The spotted deer particularly like to visit the sites of spring fires where, during the summer season, young vegetation grows up around each burnt out tree, with tender, soft stems, and large leaves. The leaves of such low-growing vegetation are very delicate and are so firmly attached to the stems that they seldom fall in strong winds, remaining in place during the entire winter. Because of this, these areas are preferred the first year after the spring burning not only by the axis deer but also by wapiti and roe deer.

The process by which the deer graze is of interest. They never fall on food with avidity or eat grassy, dendrous and woody parts all together, but instead they tear off individual leaves, the tips of racemes, and the finest branches and twigs, languidly, as if not interested, not touching the thickly wooded portions. Even when the delicate, tender parts are absent and when necessity compels them to eat the bark, they gnaw it without haste, frequently passing from one tree to another. After early disastrous November snowfall, the deer begin to gnaw on branches 1-2 cm thick from the beginning of winter, later changing over to the bark of trees.

By biting the small shoots and twigs of trees, they undoubtedly damage the crowns, inhabiting their growth (the Amur cork tree, linden, oak, Aralia and other species). If the trees are gnawed several years in succession they begin to grow in a deformed manner, never reaching full height. This phenomenon is particularly marked in the coastal deer sanctuaries. The gnawing of the trees is so rarely noticeable in the preserve that no damage worth mentioning is done to the forest.

The deer eating the tree bark seldom damage the trees, as they rarely gnaw off the bark over the entire circumference but restrict their gnawing to one or two longitudinal grooves.

The competitors of the wild spotted deer may be considered the wapiti, goral, roe deer, and, in years of abundant crops, all animals which feed on acorns. However, the territory of the former preserve is so large that all ungulates are provided with food for the greater part of the year.

In snowless periods of the year, there is no competition at all for the good food, as there is abundant vegetation. Even in the good acorn seasons so many fall that there are enough not only for ungulates but for other mammals and birds as well.

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* Translator's note–We have not been able to find English equivalents for these plants and present the transliteration–"Chumiza" = Setaria italica subsp. maxima, "piaza" = Echinochloa frumentacea.

Competition for food begins only with the reduction of the feeding areas (i.e., after frequent snowfalls). Proportionally to the increase in the snow cover the deer obtain their food with greater and greater difficulty on the northern slopes and they exert the effort to cross to the less snowy southern regions of the hills. These passages are carried out gradually during the first half of the winter, and by the first March snowfall they have already reached those places where the snow thaws systematically and no deep snows exist.

Individual wapiti emerge on these slopes at the height of the March snow, hastening the depletion of food over small areas. The competion becomes greater after "snowfall disaster" which compel the deer to inhabit common plots in less snowy regions and, as mentioned before, unfrozen streams of water, at a distance of 200-500 meters from each other. In these cases the close proximity of the two species may prove fatal for the spotted deer, as they are unable to find food after the long-legged wapiti consume all branches to a great height.

The roe deer usually select regions occupied by deer while there is still no snow, and only in the snowy period of the year, when there is insufficient food, do they enter into common areas with the spotted deer.

The gorals keep to different ranges when the snow is abundant, selecting declivitous cliffs where the snow cover slides from the steep slopes and leaves bare various patches of turfy sod. However, rare individual encounters on regions common to the spotted deer and goral also occur in the winter. It is of interest that in such encounters the spotted deer always drive the goral away from the feeding grounds, but in turn give ground before the wapiti. Spotted deer graze peacefully and without quarrels with roe deer, as a result of which inexperienced observers may frequently confuse the two.

Examining the species composition of plants eaten by spotted deer, wapiti, goral, and roe deer, we find several species which are common food to all, including acorns, small oak branches and leaves, Aralia, elm, several species of sedge, two species of wormwood, ash, Plectranthus, vines, and others. Some of these plants, as explained previously, consititute summer food and thus may be eaten by ungulates in any amount. We may say that there was almost no competition in the Maritime Territory in snowless seasons of the year in the case of the former density of ungulates prevalent in the preserve.

To conclude this section on the food of deer, we should mention the following: deer consume up to 129 species of food plants, of which they greatly prefer 14 of the first grade. If a shortage in the choice of food is experienced, they readily switch to other types. This flexibility concerning foods should be considered a positive quality for acclimitization in other parts of the Soviet Union. Thus the deer very readily switch over to strange forms in areas where they are newly released.

A definite food rhythm characterizes the diet of deer, which may be described briefly as follows: in the summer they eat the green portions of the herbs, leaves of bushes and trees, and mineral foods; in the fall they eat acorns, herbs which have turned yellow, and yellowing leaves of trees; in the winter they consume acorns, sedges, the tops of grass stems, branches, and buds; in spring they eat young sedges, buds, bark, branches, leaves, late green herbs, and leaves of various trees.

Indications of Activities and Habits of the Deer

Hearing, sight, and smell are keenly developed in the wild spotted deer to a higher degree than in the goral, musk deer, elk, and roe deer, but to a lower degree in the wapiti. It is difficult to approach the deer; usually recognizing a human

at a distance of 150 meters, the adult females give vent to a cautioning cry (whistle), after which the entire herd runs off at a gallop. Deer can hear human footsteps during the fall in good visibility periods of the year, at a distance of 300-350 meters, but they continue to graze, looking back continuously. At a distance of 200-250 meters, they stop grazing and uneasily look around for a direction in which to flee.

Sometimes they may successfully be approached to within a distance of 60-70 paces on loose soft snow if care is taken not to make a noise and provided that dense vegetation does not prevent this.

This applies to individuals of herds, and females with young.

The male of the spotted deer, which remains aloof and almost always alone, is considerably more cautious, particularly during the antler-growing period.

The footprints of the spotted deer are smaller than those of the wapiti but larger than those of the roe deer. The small hoofprint of one-year-old fawns is difficult to distinguish from the male roe deer. The track of the wapiti fawn one year of age is easy to confuse with that of the stag of the spotted deer, but it is always easy to determine whether the print belongs to the spotted deer or other ungulates from the track it makes among the bushes and trees.

Table XVIII presents the average dimensions of the hoofprints of spotted deer of various ages (cm).

Table XVIII

Anterior hoofs		Posterior hoofs		Sex and age of deer		Approximate wt (kg)
Length	Width	Length	Width			
3.2	4.8	3	4.5	Fawns, 1 year		47
3.9	5.4	3.5	5	2 years	Females	65
4.4	6.0	4.2	6	3 "		70
4.5	6.3	4.3	6.1	4 "		77
4.8	6.9	4.4	6.8	5 "		81
4.0	5.5	3.6	5.5	2 "	Males	74
4.8	6.0	4.7	6	3 "		86
5.2	7.6	5.0	6.5	4 "		110
6	8	5.6	8	5 "		130

We must bear in mind that various ratios may exist between the size of the hoof and the age, and the table is not absolutely exact.

Various load coefficients have been obtained for various ages of the spotted deer. According to our calculations, based on measurements of the compressed hoofs of 30 different deer, the following figures were obtained (Table XIX).

It is clearly seen from this table that the maximum coefficient is shown by the young up to the age of 2 years , later with an increase in age, it decreases, reaching a minimum at the age of 5 years. On the average the coefficient is 960, which is much greater than that of the wapiti, in which in the compressed hoof it is 440.

Table XIX

Sex and age		Wt (kg)	Area of fore hoof (cm^2)	Area of hind hoof (cm^2)	Total area (cm^2)	Load coeff. per cm^2 (g)
Fawns (1 yr)		47	11	10	42	1110
Males	2 years	74	18	14.5	65	1140
	3 "	86	22	20	84	1020
	4 "	110	30	28	116	950
	5 "	130	41	37	156	830
					Average	980
Females	2 years	64	17	13	60	1070
	3 "	70	20	18	76	920
	4 "	77	22	20	84	920
	5 "	81	25	23	96	840
					Average	940

The length of the stride of the spotted deer in calm movement is 45-65 cm, according to the age of the individual; usually the forepart of the hoof is somewhat twisted outwardly. When the deer moves at a trot, the stride increases somewhat up to 75-110 cm, and if the deer is highly excited its hoof is widely splayed when placed on the ground, and extended at the end as in the roe deer and the wapiti.

The deer run swiftly with an awkward gallop, making bounds 3-3.6 m in length and leaping over obstacles 1.2-1.3 m in height. When moving more rapidly they switch to a careering motion. In this case they fling their hind legs in front of their forelegs and execute bounds up to 6 m in length, easily clearing obstacles, ferns, windfallen trees and high bushes up to 1.7 m in height. The deer flash into a career only when greatly alarmed, sometimes crashing into dense bushy undergrowth and hewing a path through it with the chest. The young sometimes have no time to pass to the side when careering and smash themselves against tree trunks. Such a case was observed in the vicinity of Pashagou Gulf.

While crossing slippery frozen ice surfaces the deer move cautiously, placing their feet wide apart and hardly lifting them from the ice. They fear such crossings, and on the shore, on feeling not the slippery ice but hard ground under their feet they run off at a career. Deer traverse declivities of stream boulders poorly held together by lichens and mosses. However, they avoid large conglomerations of stones.

Deer make the passage from one feeding ground to another over fixed trails. They travel along streams, and always pass around the steep slopes of hills or cliffs at the same place. Thus, in areas which they inhabit, good trails are formed which are used for many years. Similar trails are stamped out by the deer in places of passage from southern to northern slopes, particularly at the exits to the sea gulfs. The deer paths are so permanent that they are preserved unchanged for 15-20 years in succession, and only extensive landslides or falling trees compel the deer to seek new paths.

From the time the acorns appear on the ground en masse, the deer discontinue their use of paths and commence roaming under the crowns of the oak in an orderly manner, one after the other.

They also use the paths less frequently in winter after heavy snows, and try to stay on less snowy slopes. The spotted deer swim well and can cross any river, even at high flood or when rapids are encountered. They also swim a long distance out to sea. It is known, for instance, that during the running period individual stags have swum to the mainland from the Askold Islands, a distance of 9 km.

The places where deer grazed in the summer are difficult to discover, and rarely may a crown of gnawed bush clover, Plectranthus, and sedge be seen. It is considerably easier to find the deer from the traces of their food in wintertime when they feed on branches, buds, and more rarely tree bark. In this case, we may always find broken branches of lindens and Aralia with stripped bark in their dwelling places, while the time lapse since eating may almost invariably be judged by the degree of freshness of the bark vestiges. The bark is removed from the trees differently by the spotted deer than by the wapiti. The spotted deer do not eat it completely or lay bare all or half of the circumference of the tree but make some small chiseled grooves, then pass over to the next tree.

In certain years when an abundance of acorns and leaves are strewn on the ground through the action of winds, deer seek their food from under the snow from the beginning of winter, partly helping themselves by their hoofs (they do this in regions where there are depleted natural foods). When searching for acorns they loosen the ice lying under the oaks with their feet over areas of several hectares. They also do this when they obtain the fallen foliage of the linden, oak, Aralia, willow, etc. Digging in the snow is sometimes so extensive that inexperienced persons confuse the signs with those made by boars.

The excrement of the spotted deer is of the same type as those of other species of deer, smaller than that of the wapiti but larger than that of the roe deer. In winter, when dry food is eaten, it is always dense, dark-olive or black-brown in color, composed of separate "nuts" of various sizes and shapes in males, females, and young. The largest excrement is that of the males. It is blunted at the end. The female excrement is narrower, more elongated and rounded at the edges. The excrement of the young is somewhat larger than that of an adult deer, and thus it is easy to confuse them. After 6-10 May, from the time that succulent green food appears, the excrement loses the form of separate nuts and fuses into a general mass of an olive color, somewhat divided into lobes on the surface. In the fall, when the deer transfer to dry food, the excrement again takes on the winter form, and when they eat acorns it turns black.

The nature of the resting sites of the spotted deer is varied. In snowless periods they lie down on green grass or leaves a small distance from each other, The deer never lie down close together. In periods when midges, gnats, and botflies appear, the stags of the spotted deer select places to lie down which are swept by the wind on the seashore or in the saddles of the passes. If small hazelnuts or oaks grow around the place and leaves are plentiful on the ground. the deer make the resting site permanent, not changing it for 10-15 days in succession. In the seasons of the mass swarming of gnats, the deer lie down in the shady regions near streams, where,in the air cooled by the water there are few insects pests. In the fall, when there are almost no ectoparasites, the deer lie down anywhere, selecting spots convenient for jumping up and running off in case of attack by predators. Such sites are usually found at the foot of the hills, on slopes overgrown with hazelnuts, or near steep declivities near these sites.

In hot times of the year, they sometimes paw up the earth and the foliage before lying down, throwing it off to the side to a distance of 2-3 meters. They also dig their resting sites after the first snows, when the snow covers the earth with a damp blanket and quickly thaws. Later, in cooler and frosty times of the winter, they lie down directly on the snow (which is 15-20 cm high), without any

preparatory work. If after heavy snow in March the layer of snow reaches 60-70 cm, they stamp out a bed, which is why it assumes the appearance of a hollow. On the sunny slopes devoid of snow, the deer lie down directly on the naked foliage.

On windy or frosty days all the deer begin seeking sites protected against the cool northwestern winds, the "hill winds". In such quiet places we sometimes succeed in finding several resting sites on which they had spent several days.

When the deer dispose themselves on their beds, they lie with their heads upwind and their rumps toward the entering footprints. They do not lie with their heads pointing upslope, but lie down the slope, trying to keep a dense bush behind their backs. All these rules are not invariable, and in windless regions of the valleys of the springs they lie down haphazardly.

In periods of tick onslought, the spotted deer scratch themselves vigorously against tree trunks (in the region of the shoulder blades and neck). Trunks of trees with deer wool on the bark may be seen in almost any park range, but under preserve conditions we have never observed this.

Female spotted deer make a loud whistling, abruptly interrupting it with a snort. Young males also whistle, but without adding the rough snort at the end. Stags usually do not emit any calls whatsoever and begin roaring only during the running periods, as mentioned earlier. Deer also emit rough largyneal coughing-rattling sounds when they are strangled by wolves. This cry, which is hoarse and raucous, is quite different from the ordinary call.

It is interesting that the deer are not at all startled by the falling of a large stone or the noise made by a tree trunk splitting asunder on cold days at the river's edge, but are extremely alert to the slightest alien noise in the taiga, even the soft footfalls of man bringing them immediately to the alert. Deer are extremely alarmed at the sound of rapidly running dogs on dry leaves (apparently also the sound of the wolves) and prepare themselves for immediate flight.

Parasites, Natural Mortality, and Enemies of the Spotted Deer

Ectoparasites. In examining 30 deer from the former Sudzukhe Preserve, ticks of the genera Dermacentor and Ixodes were found on 23 (90%). The ticks were not found only on individuals thrown into the sea which had laid for a long time in the frost up to the moment of the detailed examination. Deer obtained especially for detailed scientific work and examined while still warm all had the ticks of these genera or their larvae to various degrees.

In the winter, from the beginning of December to the middle of March, not many ticks are encountered on deer. Most often these are individuals of Dermacentor sylvarum, attached in groups to the helix of the ear. After thawing and the formation of large thawed areas on the earth, new ticks of the same species begin crawling on the deer.

In April, spotted deer, feeding on young sedges, often frequent spots devoid of trees and bushes. The ticks remain on them in the previous quantities. These parasites maintain themselves chiefly in woody regions with a dense lichenous forest, but there are considerably fewer of them in open areas.

In May, after the appearance of the young tree leaves, the deer remain longer in the forest, when a large number not only of Dermacentor sylvarum but also of Ixodes persulcatus crawl on them. At this time, the spring molting starts and the

deer lose their winter hair on the anterior rubbed parts of the body, and often toward the time of new hair growth, the skin becomes almost naked on the helixes, muzzle, neck and shoulders. Ticks attack primarily regions of the skin with sparse hair, and at the beginning of June we may discover 200-500 individual parasites on the head, neck, and helixes. In one case the accumulation of ticks in the region of the neck was so great that there were two per cm^2. In the places bitten, small swellings form, which the deer scratch vigorously. Because of this their skin becomes free of the shedding winter hair and easy access to new regions of the body is given to the ticks.

Individual deer, especially stags, which are greatly disturbed by ticks, begin to go to the sea at this time, often immersing themselves to the chest in sea water, while they throw water over the muzzle, neck, and ears.

Old inhabitants of the Maritime Territory affirm that tick bites affect the deer severely and some individuals even die from them. Such a fact has apparently been observed in the breeding sites near the village of Sokolovka in 1935. Loss of the deer has not been registered among the wild spotted deer of the former Sudzukhe Preserve, even when ticks densely covered the bodies of the deer. Only small local swellings were formed. Thus we may consider that wild deer tolerate bites of these parasites very well and do not suffer as much as park deer.

As said above, another tick, I. persulcatus, appears simultaneously with D. sylvarum in May. This species attacks the deer in even greater numbers. Both species also attack the young (from the moment of birth), some of them crawling from the belly of the mother, while later the young deer collect them as they graze in the bushes. Newborn fawns do not move about much, but lie down for a long time. Thus fewer ticks are found on them than on the adults. In June, considerably more ticks appear and therefore more attack the deer. Later, with the onset of the first warm days, from July to September, their number decreases, and only several dozens may be discovered on the deer, distributed sparsely on various parts of the body.

From the time of the first frost and beginning of winter, the ticks spread evenly over the body of the deer, and later in winter, from the end of February to March, they appear in groups around the ear helixes, chiefly D. sylvarum remaining on the body, whereas I. persulcatus almost disappears.

The tick Haemophisalis concinna is encountered rarely and in insignficant numbers on wild deer as compared to the previous species. Notwithstanding the profusion of ticks on wild deer in various seasons, diseases from piroplasms were not noted in them.

In March 1938, the scientific worker O. Vendland found malophages in the region of the ear helixes of a 2-year-old female deer, but did not succeed in determining the species. However, it was apparently the usual form of Allantotrichus cervi, which are found on deer kept under park conditions.

In the last days of May, gnats appear in the coastal stretches of the Sudzukhe Perserve, mainly in the "buffalo gnat" or "black fly", Simulium maculatum, and the midge Culicoides obsoletus. Later, in the rainy season of the year, in June and particularly July, the number of these ectoparasites increases considerably. Gnats and midges disturb the deer greatly. The deer stop their placid grazing and begin to approach the seashore or the cold beds of the streams, where there are almost no midges or gnats in the cold air. The large stags at this time go up to the passes in the heights of the mountains or emerge on the sea slopes strongly swept by the cold sea winds.

When attacked by gnats and flies the deer often shake their heads violently, flap their ears, and scratch their most accessible parts—the ears, lips, and around the eyes, with their hind hoofs.

The swarming of the gnats comes to a halt during the first half of August and all the scratched places on the deer heal up completely.

On dry, sultry July days, many botflies make their appearance, particularly along the open valleys leading from the sea. To avoid their bites the deer try to move in the cold streams of air from the sea or try to go into the shaded regions of the taiga, stopping to graze during the hot bright period of the day. The mass swarming of botflies continues for a brief time, and toward the end of July their numbers decrease perceptibly.

Single specimens of the bloodsucker Zipoptema cervi appear toward the end of August in places where there are more deer and where the most trails are stamped out by them. From the end of September to October, this swarming increases markedly and all deer examined at this time show numerous bloodsuckers in the region of the neck, chest, and groins. The mass swarming of bloodsuckers sometimes continues in the warm days of October until the beginning of the first frost. In November, when on the stagnant pools of water an ice crust 0.5-1.0 cm thick forms during the night, not many bloodsuckers fly about, but they can be found during the warm parts of the day on the southern slopes of the mountains. From 15 November, flying forms cannot be found. However, on all deer killed throughout the winter up to March, we succeeded in finding, deep in the hairy coat, a small number of bloodsuckers which had cast off their wings.

According to the data of investigations by A.I. Shpringolts-Shmidt (1937), the mass attack by bloodsuckers produces an intense cachexia in the deer. Observing wild deer in the former Sudzukhe Preserve and examining those killed, we did not succeed in noting this. In periods of the fall swarming of the bloodsuckers, all wild deer are plump and in winter the number of bloodsuckers on the body of the deer is so small that they cannot cause pathological phenomena.

In wild spotted deer of the former Sudzukhe Preserve, we also did not succeed in discovering the nasal botflies (Pharyngomia hicta) common in park specimens. Thus, the rare finds of this parasite in two "wild" deer from the former Sikhote Alin Preserve is highly interesting (Yu.A. Salmin and P.D. Shamykin). The finding of the nasal pharyngeal bot in wild deer appears so improbable to us that we are inclined to believe the afore-mentioned two deer have been not wild but specimens which escaped from the deer preserve of the village of Belimbe of the Ternei Raion. In the deer park in this village, on 26 June 1937, a swarm of bots was in fact observed, and on 3 June, in two sacrificed deer, bot larvae were found in the choanal apertures (K. Ya. Grunin, 1947) these possibly being the same two deer observed by Yu. A. Salmin and P.D. Shamykin, as these were the only two cases of dissection of spotted deer by scientific workers in the Ternei Raion.

Endoparasites. On dissecting 25 deer, they proved to be mainly affected by the liver distoma, Dicrocelium lanceolatum, which is parasitic in the large biliary ducts which take the place of the gall bladder (the latter is lacking in deer). Approximately 75 % of all adult deer on the preserve are infected by these distomes, and they are absent only in the young, at the age of 3-5 months—the "syandysh" [deer fawns]. The same species of distome has also been found in the roe deer and wapiti, and apparently the manner of infection of all these species is the same.

In certain deer we found nematodes of undetermined species in the abomasum and in the anterior portion of the intestine, and in one case, the bladder form—Cysticercus tenuicolus—and setaria in the abdominal cavity. In "wild" deer dissected in the Sikhote Alin Preserve (perhaps the same females mentioned by K. Ya. Grunin (1941),

i. e., the park specimens) cysticercosis of the liver was noted. In the experience of parks, the spotted deer have many more endoparasites.

In periods of running under the cramped park conditions, stags usually inflict blows and deep wounds on one another, causing diseases such as pleuritis and peritonitis. Under natural conditions, battle wounds were not discovered in the deer. A number of infectious diseases characteristic of park specimens were not noted in the wild animals.

Natural Mortality

After fires, against the background of black, charred grasses, bushes, and tree trunks, white bones are clearly seen through binoculars—the remains of deer which perished at various times. The age of the deer which had lived there may be determined from various parts of the well-preserved skull.

As a result of determinations on 38 collected remains, it transpired that they were of the following ages (Table XX):

Table XX

Age	Fawns	Females	Males	Total	
				Absolute	Per cent
Up to 1 year	12	—	—	12	31.6
1-2 years	—	4	5	9	23.7
2-3 years	—	3	2	5	13.5
3-5 years	—	4	3	7	18.2
5-10 years	—	2	1	3	7.9
Over 10 years . . .	—	2	—	2	5.1
	12 31.5 %	15 39.5 %	11 29 %	38 100 %	100 %

From this table it is clear that in nature the first to die of various causes are deer up to 2 year old (55 %); older individuals are more resistant.

We succeeded in finding few skulls of old deer—apparently these are very rarely found in nature. For the entire period of the study, 1944-1946, we succeeded in finding only two lower jaws from 11- and 14-year-old females, all teeth in the latter being triturated down to the gums.

Enemies of Spotted Deer

There are many enemies which prey on the spotted deer: they include the gray wolf, stray dogs, yellow-throated marten, lynx, wildcat, tiger, and leopard. However, not all predators mentioned destroy the deer to the same extent. Some predators do not touch the deer.

The gray wolf must be considered the chief enemy of the spotted deer. There are no red wolves in the regions now inhabited by deer. The numbers of wolves are gradually increasing throughout the Maritime Territory, despite all combat

measures and bounties. In 1904, the Chinese, Korean, and Russian inhabitants of the coast of the Sea of Japan encountered almost no gray wolves. They knew only the red wolves, which were rare at that time, and which were known locally as "shakalka". The first case of the death of a spotted deer caused by wolves was recorded in 1924, and from that year the losses of the ungulates from this predator continuously increased.

Wolves later began to make their homes near large villages, feeding on carcasses of fallen cattle, attacking poorly guarded herds, and more rarely seizing wild ungulates in the forest. In 1934, deer losses from wolves assumed a constantly recurring character, but because of the lack of a government bounty almost no one fought them. An insignificant number of wolves were destroyed only by workers on the former Sikhote Alin Preserve and its Sudzukhe branch.

Statistical material on deer losses from wolves in the former Sudzukhe Preserve was collected from March 1936 to June 1938 by the scientific worker O.V. Vendland (Table XXI).

Table XXI

Deer losses				
From wolves	From stray dogs	From poachers	Unknown causes	Total
15 60 %	4 16 %	5 20 %	1 4 %	25 100 %

As seen from the table, deer losses in 1938 were considerable. In subsequent years registration of deer deaths in the preserve was not carried out, but the struggle against wolves proceeded successfully.

The figures for later years (from 1944 to 1948 inclusive) indicate that the number of deer killed by wolves, as previously, remained high, despite the yearly work carried out in the preserve in combating this predator (Table XXII).

Table XXII

Deer losses				
From wolves	From stray dogs	From poachers	From lynx	Total
30 86.5 %	2 4.5 %	2 4.5 %	2 4.5 %	45 100 %

These figures do not include deer which perished in heavy snowfalls from 1947 to 1948. The data indicate that the percentage of losses from wolves is still high.

It is difficult to fight the wolves, as all the former territory of the preserve is surrounded by 19 inhabited points in which cattle breeding is considerably developed, which causes the wolves to collect around the settlements. Thus a wolf cordon formed along the settlements around the boundary of the former preserve where this predator constantly concentrated. Applying any combat measures (particularly poison) consequently ran the risk of poisoning a dog with the bait or catching a calf or sheep in the traps. The struggle against the predator on the preserve territory only is insufficiently effective, as in regions of the main stretches of unbroken taiga, which are devoid of open fields, there are not many wolves. In the preserve we usually observed the tracks of wolf movements on the roads,

frozen ice surfaces, and ice-crusted snow, i.e., along courses convenient for travel.

If all cases of death of spotted deer from wolves from 1936 to 1948 are distributed by months, it develops that they kill most deer in March and April (Table XXIII).

Table XXIII

	Months												Total
	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	1936-1948
Number	9	9	21	12	6	—	—	—	—	—	—	2	59
%	15.2	15.2	36.5	22.4	10.2	—	—	—	—	—	—	3.6	100

The great percentage of loss in March and April (58) is explained by the fact that deer exhausted during the winter find it difficult to elude tracking by wolves on the snow crusts. Besides, at this time of the year fetuses are growing in some of the females, thus hindering free movement. We must keep in mind that it is easy to discover signs of the pursuit of the deer and find their carcasses on the white paths, while a considerable portion of the deer killed during the snowless periods of the year remain undiscovered even according to the cries of the hovering ravens.

In late spring and summer, it is already difficult for the wolves to reach and seize the deer in the high grass, and in addition they are less hungry and do not pursue their victim so tenaciously. For this reason no loss of deer from wolves is observed in this period.

Wolves have several methods of catching the deer, and the deer have several methods of eluding the wolves. The wolves move along the trails on the ice or snow crust, attentively considering each rustle and smell. Perceiving their victim by scent or sound, without even stealing up on it, they charge or even gallop up to the deer and try to seize the exhausted victim as it halts at some obstacle. To do this, the wolves attempt to drive the deer into open areas in the river valley toward the gulf of the sea or the mouths of rivers and the declivitous sea cliffs. The most successful movement for the wolf and the most fatal for the deer comes when the deer slips and falls. If it does not succeed in rising quickly it is eaten on the spot, hot and half-alive. If it succeeds in leaping off wounded, streaming blood and losing strength, after 1-2 kilometers it again falls victim to the pursuing wolf. It should be noted that more usually 2-3 wolves pursue a deer, trying to cross its path, which considerably hastens the time of its death. From wolves' hunts recorded in the preserve from footprints from 1936 to 1948, the described method of pursuit by wolves (driving the deer on to the frozen river ice), constituted 46 %.

In other cases, the wolves seize the deer as they emerge from the sea where they had been swimming to save themselves from wolves, and 24 % of all victims are killed in this way. More rarely, the wolves drive the deer onto cliffs, compelling them to jump from the abrupt edge (2% of cases). More often, the wolves try to reach and catch the deer in the thick bushes when there is a crust on the snow (28 %).

Young deer perish from wolves more often, whereas the adults, which are stronger, avoid capture by the following methods:

Hiding in the thick underbrush, and jumping over the top of it;

Entering deep spots in rivers and springs;

Entering the sea and trying to leave the water at a different spot; entering human habitations where there are buildings, hurling themselves into the water from steep cliffs.

In the majority of cases the deer succeed in eluding pursuit and escaping the wolves by means of these methods.

Running into thick bushes is the most common method the deer have of eluding wolves; using this method, only 40 % of the pursued deer fall victim to the predators if there was no ice crust. When a crust forms, almost none of the deer succeed in escaping the wolves.

Old stags, which because of their large antlers cannot maintain the speed of careering through the thick bushes, more often adopt a different method. They stand in pools in deep streams. This method is employed in regions of the preserve far from the sea where they may enter the deep streams up to the chest. This method of eluding the wolf is very successful, and if the wolf does not watch closely, its victim always escapes alive. The number of losses in this case amounts to 3 %.

Deer which inhabit the sea slopes of mountains where there are almost no rivers or springs, run,in case of pursuit, to the gulfs and throw themselves into the sea. In the warm periods of the year, such a deer, swimming a distance of 400-1,000 meters in the sea in 30-40 minutes, reaches the shore at a different spot and is saved. In winter, when the temperature of the sea is below zero, and the air temperature minus 20°, a mobile ice shelf forms in the tidal belt. Deer frightened by the pursuit of the wolves throw themselves into stretches of open water in the ice and swim from the seashore to a point 150-300 meters away. Coming upon a floating ice floe they often perish from blows by the ice. However, even when ice is absent not all deer succeed in reaching firm ground again and some drown in the ice waters and gales of force 6. Of 12 cases recorded of deer swimming into the sea, three perished. Two females did not return to shore and one large stag was crushed by the coastal ice floes.

The Syao-Chingou Gulf is a natural trap for deer which throw themselves into the sea to save themselves from wolves. This gulf has an open shore 80-100 meters long composed of large smooth pebbles. The edges of the gulf terminate in the steep cliffs of Mount Goral and Mount Pashagou, which sweep down to the sea. All deer inhabiting the nearby mountains have but a single path to the sea in the Syao-Chingou Bay. They come here for the salt licks and also to bathe themselves and rest from the gnats pestering them. Individual deer also enter the gulf in flight from wolves, saving themselves by swimming into the sea. Returning, they search for a new spot to emerge from the water, and thus swim for a long time aimlessly along the precipitous cliffs of the above-mentioned mountains, until they drown from lack of strength. Usually after several hours their carcasses are brought by the tide back into the same gulf. On 12 February 1945, when observers visited this gulf "trap" in the belt of the seacost, 7 deer carcasses crushed by the ice were discovered. In other winters, as a rule, we succeeded in finding 2 or 3 crushed carcasses untouched by wolves.

In other gulfs, if no ice forms and there is no violent tossing of the sea, the tired deer safely emerge from the water. In April, 1945, we saw a female chased by a pack of wolves for one hour while it was in the water and after it emerged. It was so tired that it lifted itself with difficulty onto the gently sloping pebbly shore. It rested here for 20 minutes, trembling with cold, and permitted approach to within 20 meters.

Some local inhabitants and veterinary surgeons of the Sudzukhe deer Sovkhoz [collective farm] report that in winter, after emerging from the cold water,

deer often fall ill with chronic lung diseases which are fatal. According to them some pregnant females abort from the low temperature, shock, overfatigue, and blows by the ice. Apparently eluding the wolves does not always end successfully and in winter 25-30 % of the deer perish.

In places where deer systematically keep to human habitations, for instance in the former Sudzukhe Preserve, in the Kit and Tachingou Bays, they become accustomed to buildings and approach to within 100 m or closer.

The wolves have more fear and do not always resolutely approach unknown inhabited areas. Exploiting this fact, deer pursued by wolves sometimes purposely dash through courtyards of buildings to cut the course of the pursuing predators. In such cases 90 % of the deer remain alive. Large female deer and stags also sometimes attempt to throw off the wolves by jumping from steep cliffs. In these cases, individual deer, jumping unsuccessfully, are mutilated or break their legs and become the victims of wolves. The number of deer losses in this case equals 20 %.

Table XXIV shows the relationship between various methods of hunting wolves and the successful elusion of them (per cent of total number of recorded cases).

Table XXIV

Method of pursuit	Percentage of total pursuits	Method of elusion chosen	Percentage of deer throwing off pursuit
Driving onto ice	46	Departing from ice	10
		Entering bushes without icy crusts	60
Driving into bushes with ice cover	28	Flight into bushes without ice cover	5-6
		Staying in springs	97
Waiting for deer to emerge from sea	24	Swimming in the sea in winter	70-85
		Swimming in the sea in summer	90-95
		Flight through inhabited areas	90
Driving to cliff	2	Jumping from cliff	80
Total (47 observations)	100	(62 observations)	

From the table it is seen that the most perilous condition for the deer is the ice cover of rivers and crusts on the snow, for which reason appreciably more deer perish in winters when these form. The most successful method of eluding the wolves is that of standing in deep springs, but unfortunately these are very small on the eastern slopes of the Tachingchang Ridge and completely frozen in winter.

To this day stray dogs from the 19 settlements surrounding the former preserve are also the enemies of the spotted deer. The local inhabitants keep dogs not

to protect their yards but to hunt, and each tries to keep a hound able to reach a beast of prey and hold it at bay. Sated dogs do not enter the taiga on their own, but if they are not fed for several days in succession they, like the wolves, take the initiative in launching a hunt for animals, going out in packs of 2 or 3 to catch any game available. Coming across fresh deer tracks, they begin to run the deer down, but cannot catch it if there is no ice cover. The chief harm done by dogs consists of their driving the deer from the taiga to the sea, where some of the deer, as was previously mentioned, perish. When there is a thick ice cover, the dogs reach the deer without difficulty and feed off their carcasses for 2–3 days. According to the records of 1936–1938, the loss of deer through dogs was 15% of all cases (drowning in the sea 7%, torn to pieces on the ice cover 8%). From 1944 to 1948, only 2 deer perished from dogs, as the keeping of dogs decreased among the inhabitants.

Other predators are harmless in comparison with wolves. Lynxes rarely kill deer, and from 1944, to 1948 only two cases of their attacks on deer were recorded, in the first case a fawn which fled from the lynx into the small undergrowth where its head was broken by a tree trunk, in the second a young female which passed under a tree where a lynx ambushed it. Lynxes are rarely able to attack large males, and when they do, they attack them unwillingly. The leopard and tiger are very rare species in the former Sudzukhe Preserve and thus cannot be considered enemies of the deer. Since the preserve was established (1936 to 1948), not a single case was recorded of loss of deer from these predators.

Such predators as the wildcat, fox, and yellow-throated marten cannot take the adult deer, but strangle young fawns up to the age of 2 months. According to old inhabitants who bred deer, the small predators attacked only the newborn and one-month-old fawns, while the females was far from the hiding place of the fawn and could not hear its cries.

In the former Sudzukhe Preserve, no real attack of the above-mentioned predators on deer were registered from 1936 to 1948.

Live deer are not taken by the sea eagle and golden eagle because in the period of parturition the females enter river valleys thick with bushes, where the birds cannot locate the fawns. However, these birds are frequently driven off by man from carcasses of deer killed by wolves. Carrion crows often injure newborn fawns in parks. We succeeded several times in seeing how they peck with their beaks at the not yet dried umbilical cords after the females moved of 10–15 meters to graze. According to statements of veterinary surgeons of the Sudzukhe Deer Sovkhoz, the crows sometimes peck the umbilicus to such an extent that it begins to bleed and the fawn dies.

Occasionally deer perish at the hands of poachers, despite the severe penalty for killing them. The actual numbers of animals killed by poachers is very difficult to establish, as the crime is usually committed away from inhabited places and at the times of year when there is no snow. Poachers may succeed in removing their meat completely on hidden paths, without leaving any signs of the crime at the site, and it is not always possible to establish the place where the deer has been killed according to some shots heard in the mountains.

In 1936 and 1937, poaching was more highly developed and each year 5 or 6 slaughtered deer were found. After a series of protective measures and educational work in subsequent years among the inhabitants in the vicinity, poaching decreased somewhat.

The Role of Preserves in Protection of Wild Deer

The practice of recent years has shown that wild spotted deer cannot survive in the Maritime Territory without protective measures. Thus the role of the former Sudzukhe and other preserves in maintaining this important species is very great.

By the year 1948 only small numbers of wild spotted deer remained in the Maritime Territory and then only in preserves and adjacent areas. But even here a gradual decrease in their numbers occurred, especially in the preserve in the Far Eastern Branch of the USSR Academy of Sciences (Kedrovaya Pad') where 30 head out of 300 remained. To a lesser extent the number of deer also decreased in the large Sikhote Alin and the former Sudzukhe Preserve.

The chief causes limiting the number of head of wild spotted deer is the activity of wolves, poaching, and the effects of deep snow. Our chief work should be directed to combating these three factors if we wish to increase the number of deer.

The number of wolves in the Maritime Territory increases from year to year, but nevertheless the struggle against them is conducted very laxly. Up to the present no rational method has been worked out to destroy them under the conditions of the very rugged terrain of the country and the methods of hunting and ambushing, luring, and others. The wolf traps manufactured, which are almost impossible to find on sale, are usually not satisfactory for trapping wolves and need additional mechanical improvement before use. A practical fight against wolves is carried out unsystematically by individual hunters in casual encounters and the results are so negligible that the numbers of predators are not diminishing at all. At any rate the number of wolves shot is lower than the number of their yearly increase. In order to successfully preserve the number of spotted deer, it is necessary to wage a systematic struggle against wolves over the land.

The second factor—poaching—will apparently disappear in time in accordance with the elevation of the cultural level of the inhabitants.

The final factor in deer losses, the snowfall "disaster" is rarely observed in the Maritime Territory, and as a result, in a number of normal winters with a light snow cover the herds of deer have sufficient time to restore their numbers. In this case the best assistance to the deer is the complete elimination of wolves from their places of winter habitation and guarding against the entry of new wolves. If there were a guarantee of the complete destruction of this predator it would be possible to facilitate the winter survival of deer by preparing small stacks of salted forest hay in July. In the former Sudzukhe Preserve this measure was effected in the Pashagou, Syao-Chingou, Malangou, Ta-Chingou, Zarya Kit, and Tasava Gulfs. Such measures should only be applied in cases when there is complete certainty as to the absence of wolves, or else convenient hunting spots will appear for the predators around the feeding sites.

By making use of the ability of the deer to survive in completely new areas, we must continue the acclimatization work which was successfully begun. For setting deer free, it is necessary to select areas with highly varied leafy trees and bushes, not fearing the crossing of the spotted deer with the elaphus group. Cases of such hybridization have not been observed during the past ten years even in the Maritime Territory, where the spotted deer constantly occupy common ranges with the wapiti. Places with a rugged topography in the southern parts of the Soviet Union, where the snow rapidly thaws on the sunny slopes, would be appropriate for the deer.

The first acclimatization experiments with spotted deer in the Khoper, Oka, Mordov, former Kuibyshev, Il'men and Tiberda Preserves and in the Buzuluk

forests (V. A. Arsen'ev, 1948) have shown that deer tolerate frosts well when there is no wind (42°)*. In such temperatures as we succeeded in determining, only very weak individuals suffer. The limiting factor for deer in new places was snow over 30 cm in height, which did not allow them to root up acorns and compelled them to eat the hay and straw prepared for them.

Toward 1948, some of the deer of the Khoper, Oka, and former Kuibyshev Preserves went out beyond the limits of their boundaries and inhabited the adjacent areas.

Knowing the snowy regime of the Maritime Territory coast, it is difficult to visualize how deer could adapt themselves without the help of man to natural conditions in the European part of the Union. The nature of the western preserves differs greatly from the Maritime Territory, the birthplace of the spotted deer. Thus, we must assume that increases in the herds of spotted deer in new areas will take place gradually, and of course under conditions of constant assistance on the part of man. Before releasing deer into new areas it is absolutely necessary beforehand to carry out a complete annihilation of wolves, conduct veterinary examinations, sterilize the areas which are intended for release, and prepare good food with salt licks for the initial periods.

However, in the Maritime Territory, the best individual spots for the rehabilitation of spotted deer are the southeastern slopes of the seashore from the Sidemi Bay to the Olga Bay. The best sites for raising park deer are located in those areas where there is not much snow and not many ticks, midges, or gnats, but where there is always salted jetsam from the sea.

It is quite possible that in all cases of acclimatization the wild forms of deer which have not lived much in captivity will display more endurance under the conditions of the new environment than those of the parks. Thus the wild deer present in Maritime Territory Preserve should be particularly well protected as a prime resource of the Union.

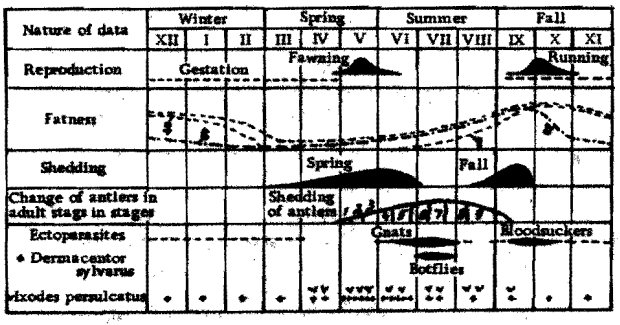

Figure 7. Phenological data on spotted deer

CONCLUSIONS

1. Spotted deer chiefly inhabit broadleaf forests in areas with a temperate climate. Wapiti go up high in the mountains, occupying even zones of the fir and silver-fir taiga and the "slanting forests", tolerating well the continental climate of the upper stretches of the mountains in winter. The spotted deer are less well

* Translator's note--Apparently minus 42°.

adapted to "disastrous" snow winters and in such winters up to 50% perish. In such cases wapiti inhabiting mountain ridges where they find bare surfaces cleared of snow by the winds pass the winter successfully. In profuse snow only the young succumb, and then only a few of them. Spotted deer are also inferior to wapiti with regard to motion over snow. Wapiti successfully cross snow 60-70 cm deep, whereas spotted deer in such cases sink to the belly in the snow, leaving behind a continous furrow.

Of natural food, deer chiefly eat leaves of trees and, to a lesser extent, herbaceous vegetation. Even light snow prevents their access to most of the food lying on the ground. Even when there are large amounts of tree leaves in winter, wapiti gnaw the bark of the elm, willow, linden, and other trees. Nevertheless, despite being so primitive in comparison with the elaphus group, the spotted deer should be considered a species with a high degree of vitality and a clearly marked tendency to further development.

The absence of sterility, the cases of giving birth to two fawns, the large species composition of plants eaten by them in their habitats and acclimatization areas, the absence of disease resulting from endo- and ectoparasites, the formation of varieties (which compels us to assume the existence of various systematic subdivisions)—all these factors indicate that the number of deer can be increased.

The initial protective steps in the Far East when gray wolves were absent have shown that the deer population quickly increases even with minimal protection, and greatly so when there is a resolute struggle against predators and poachers. The snow "disasters"with which the decrease in deer numbers is connected occur so infrequently that they cannot be a constant source of decreases in numbers in protected areas.

The disappearance of spotted deer from the majority of sites in their northern areas of distribution does not prove that deer are becoming extinct. Undoubtedly the spotted deer in the past were systematically destroyed by man as a highly valuable species, and now in the Maritime Territory they are being destroyed in increasing numbers by wolves in the protected areas. Provided that predators are absent, even with snow "disasters" and individual cases of poaching in all broad-leaf forests of the Maritime Territory, the deer may be rehabilitated.

In the "panti" antler concerns, methods have not yet been elaborated to prevent the gradual decrease in the size of the deer. The explanation of this occurrence should be sought in the incorrect feeding standards of the males only in the parks, in frequently spoiling the best producers by cutting off the antlers, in the constant inbreeding of deer within a single herd, and the lack of pedigree work. In parks all deer are placed under common environmental conditions, which is incorrect from the point of view of modern animal breeding. The dwarfing of deer in the parks has created a false impression concerning the deer extinction.

2. Males and females of wild spotted deer are larger than those in captivity. Fat specimens similar to individual fattened deer in the parks are not found in the wild forms. The maximum weight of the wild stag in the former Sudzukhe Preserve was 131 kg, the length 180 cm and the height 112 cm. The maximum weight of the female of this preserve was 85.7 kg, the length 174 cm and the height at the withers 98 cm. Wild spotted deer have no tendency to dwarf whatsoever.

3. Under natural conditions the change in antlers in adult stags begins on the average in the last days of April and continues up to the middle of September. The fifth stage of the growth of antlers begins from 18-20 June, the spring shedding, which begins in the first days of March, terminates on 1 July. The summer coat grows in completely by this time. The fall change of hair takes place more

quickly from 15 August to 25 September, the greatest pair of shed "dry" antlers found in the former Sudzukhe Preserve weighed 3.77 kg.

4. Spotted deer enlarging their range northward, in Manchuria and Maritime Territory, are at the edge of their northern limit of distribution and they they are distributed here in single isolated groups. This kind of distribution of spotted deer in the Maritime Territory was also known in the past century when they occupied the southeastern sea slopes in small herds, living on the broadleaf oak forests. Indications of the presence of spotted deer at the mouths of the Kkhutsin, Ta-Kema, and Belimbe Rivers and in the village of Sidatun' on the Iman River apparently belonged to species which had escaped from their breeding places.

Judging from the fact that Chinese hunters used no "lu-deu" pits along the Ussuri River and its tributaries, the Iman, Tatibe, and Armu, there were no deer, or only very few, in this area. The limit of the former northern distribution was here.

213 On the eastern sea slopes of the Sikhote Alin, the deer were distributed to the north up to the Yodzykhe River and their numbers near the sea always amounted to more than those on the western slopes of the Sikhote Alin.

At the present time, the distribution of the spotted deer has greatly decreased in range and become indeterminate. They have remained in quantity only in the preserves. In individual forests adjacent to the preserves, the wild deer roamed in uncounted groups of 2-4 individuals.

Spotted deer are exclusive stenotopes. They remain constantly in the same places, especially in the winter.

The spotted deer are inhabitants of the forest of the mountain foothills of the "Manchurian"type, which contain Mongolian oak, Amur linden, Kalopanax pictum , Amur cork, the Manchurian nut and a number of maple trees; in the undergrowth there is more often Japanese clover, hazel, wild pepper, and of the vines, grapes, Actinidia, and the Chinese magnolia vine. On the foothills the deer select fixed regions not higher than 500 m with a hilly relief and a network of streams 1.5-2 km long, the hillsides of a slope of up to 40° and facing the southeast. Such slopes are well heated by the sun in winter and are mostly free of snow.

The snow cover is the chief factor influencing the distribution of spotted deer. The character, time of appearance, thawing, and height of the snow determine the distribution of the spotted deer in the Maritime Territory. An indirect factor affecting the distribution of the deer is the relief and the northwest wind. Deep snow and wind often form high snow drifts on the passes which "imprison" the deer in small feeding stands on the sunny slopes. Deer avoid places with a permanent snow cover in winter.

The appearance of a thick ice cover is unfavorable to the spotted deer, as are numerous stationary ice formations on the rivers. Hunting is made easier for wolves by these.

5. The number of spotted deer in the former Sudzukhe Preserve was not constant and fluctuated for various reasons between 160-500 head. In the area indicated there were apparently never more than 500 spotted deer. This was the number that could be maintained in winter without food shortages in the places of their choice.

Almost 50% of the deer perished in the winter of 1947-1948 because of the "snow disaster".

The total number of wild spotted deer in the Maritime Territory in 1949 was approximately 300 head. The largest herd observed in the last decade in the former Sudzukhe Preserve numbered 14 head. The average ratio of the sexes among adults is as follows: three females and one young to one male (1:3:1).

6. Because of their low numbers, sexual running among wild deer takes place without battles and within a short period (25–35 days) on more or less fixed days of the year. The onset of the running starts approximately on 10 September; the peak is reached at the beginning of October and it terminates on 6 November. Mating with females occurs during the first days of running, when slight roaring of the stags is yet heard. Early parturition is noted near the end of April, the main period being in the middle of May and lasting until the middle of June. In 12 years only one case of 2 embryos has been noted. Sterile females are never observed.

7. Selected or choice foods are acorns, the leaves and buds of the Mongolian oak, and all parts of the linden, Aralia, Japanese clover, and a number of spring sedges. The species constitution of the plants eaten is very extensive and the deer readily exchange one species of food for another.

A definite seasonal rhythm is observed in the diet of the deer. Its features are as follows: in summer, green trees, leaves and foliage; in fall, yellow foliage, branches, buds; in winter, dry leaves, branches, sedges, buds, small twigs and bark; in spring, sedges, bark, buds, and later young green grass.

From May to September and from December to March, the deer readily lick and chew kelp thrown up by the sea. In years of good acorn crops, the deer eat them in large quantities from September to April if the snow cover allows.

8. Of the ectoparasites, two species of ticks, buffalo gnats, bots, blood-suckers and midges are found on wild spotted deer. Of the endoparasites numerous liver distomes are found. Loss through endoparasites or ectoparasites is not observed in nature. The death rate among deer from various causes is highest up to the age of 2 years.

The principal causes of the death of deer are attacks by gray wolves and periodic heavy snowfalls. In certain winters with heavy snows, 10–50% of the spotted deer may perish. Wolves in the Maritime Territory each year kill 5–30% of the deer. In frequently repeated snowfalls with wolves appearing en masse the protected herds of deer are liable to complete extermination. Loss of deer from stray dogs and poachers averages 4%. The role of other predators in the extermination of this species is negligible.

It was proven long ago that the tiger and wolf are two antagonists in the Maritime Territory. They are completely unable to live together on "common" hunting regions; thus the presence of a tiger in the deer region is highly desirable, one tiger causing less damage than even two pairs of wolves. For this reason we should prohibit the hunting of the tiger.

When the number of spotted deer in the former Sudzukhe Preserve (1948) is kept in mind, we may consider that there is no competition with other ungulates.

9. Dwarfing of deer is observed in the parks, and thus we should endeavor to maintain the remnants of the wild individuals by all means, striving to increase their numbers to the maximum limit: in the Sikhote Alin to 80, in the Sudzukhe to 500, and in the "Kedrovaya Pad" (cedar ravines) to 300.

Wild deer are a valuable natural resource for wide acclimatization in the appropriate parts of the Soviet Union and for reproduction in new areas.

It is possible to carry out these measures due to the great adaptability of the species in nature under conditions of protection by man.

We must keep in mind that the greatest natural sources of spotted deer are located in the frontier region. Thus spotted deer should be more widely acclimatized also in more interior regions of the Soviet Union.

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