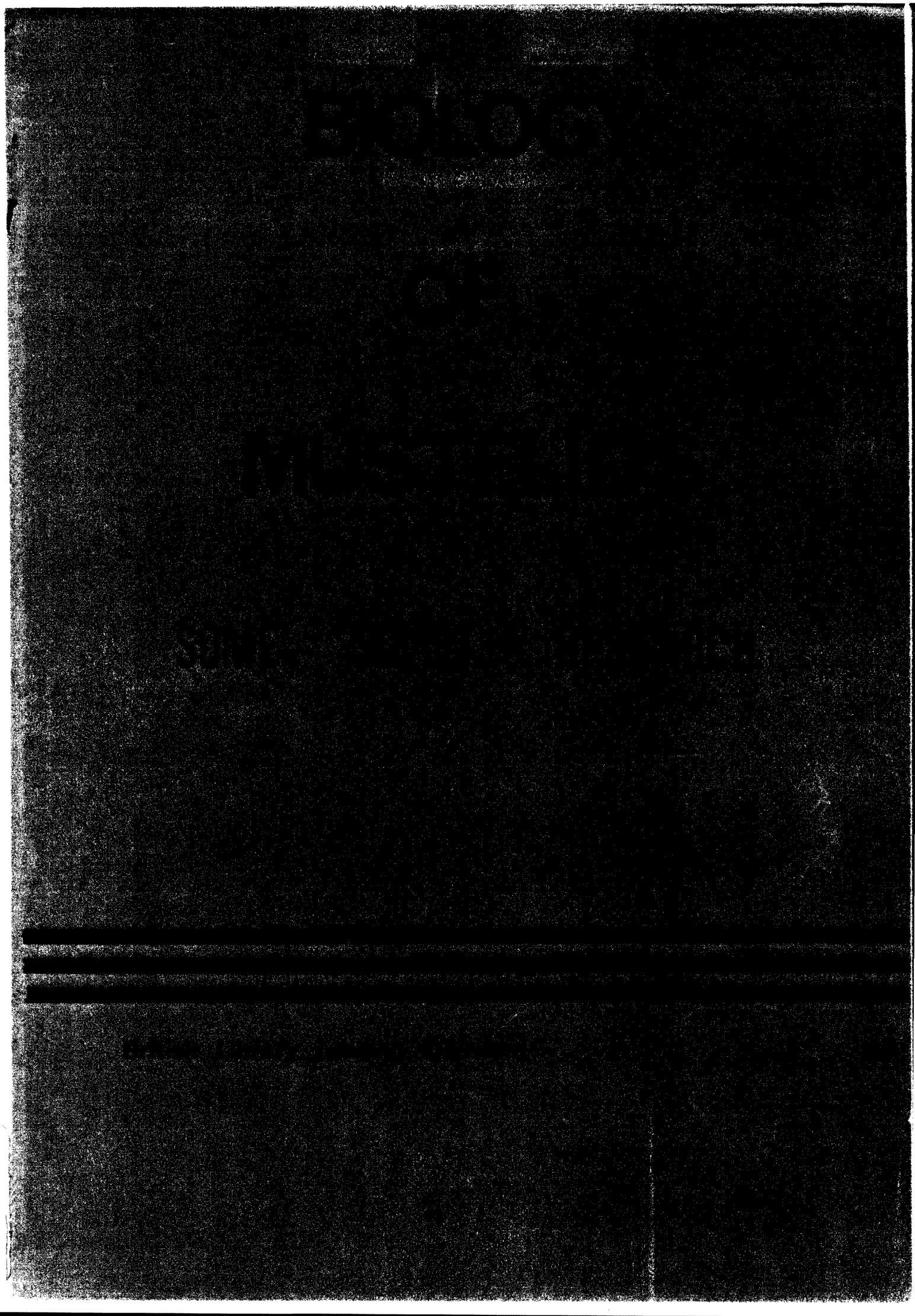

BIOLOGY OF MUSTELIDS

SOME SOVIET RESEARCH

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This book consists of translations of the following papers:

1. L.G. Morozova-Turova: Географическая изменчивость ласок Советского Союза. Geograficheskaya izmenchivost' lasok Sovetskogo Soyuza:- Okhotnich'e-promyslovye zveri: Biologiya i khozyaistvennoe ispol'zovanie. Ed. D.P. Dement'ev et al. Moscow 1965 (1): 265-79.

2. O.V. Petrov: О применимости "правила бергмана" при исследовании внутривидового разнообразия горностая. O primenimosti pravila Bergmana pri issledovanii vnutrividovogo raznoobraziya gornostaya: Vestnik Leningradskogo Universiteta, Biol. Ser., 1962 9 (2): 144-148.

3. P.B. Yurgenson: Об изменчивости черепа горностая (Mustela erminea L.). Ob izmenchivosti cherepa gornostaya Mustela erminea L:- Zoologicheskii Zhurnal 1933 12 (1): 60-68.

4. O.V. Petrov: О половом диморфизме черепа горностая (Mustela erminea L.). O polovom dimorfizme cherepa gornostaya (Mustela erminea L.):- Vestnik Leningradskogo Universiteta, 1956 (15) [Seriya Biologii (3)] 41-56.

5. P.B. Yurgenson: О половом диморфизме в питании как экологической адаптации вида. O polovom dimorfizme v pitanii kak ekologicheskoi adaptatsii vida:- Byulleten' Moskovskogo Obshchestva Ispytatelei Prirody-Otdel Biol, 1947 52 (6): 33-35.

6. V.Ya. Parovshchikov: Экология Mustela nivalis Linnaeus, 1766 Архангельского севера: Ekologiya Mustela nivalis Linnaeus, 1766 Arkhangel'skogo severa:- Vestnik Ceskoslovenske spolecnosti zoologicke 1963 27 (4) 335-344.

7. V.P. Teplov: К вопросу о соотношении полов у горностая: K voprosu o sootnoshenii polov u gornostaya:- Zoologicheskii Zhurnal, 1948 27 (6) 567-70.

8. V.A. Kraft: О влиянии температуры на подвижность горностая зимой. O vliyanii temperatury na podvizhnost' gornostaya zimoi:- Zoologicheskii Zhurnal, 1966 45 (1): 148-150.

9. Yu. N. Klimov: Материалы по биологии горностая. Materialy po biologii gornostaya:- Trudy Biologicheskogo Instituta, 1940 7: 80-88.

10. E.S. Nyholm: Karpasta ja lumikosta ja nuden talvisista elinpiireista:-Suomen Riista,1959 13: 106-116.

11. S.A. Mal'dzhyunaite: Определение возраста лесных куниц и их возрастное соотношение в Литовской ССР.. Opredelenie vozrasta lesnykh kunits i ikh vozrastnoe sootnoshenie v Litovskoi SSR:- Trudy Akad. nauk Litovskii SSR, seriya B. 1957 (3): 169-177.

12. L.S. Ryabov: Некоторые возрастные особенности морфологии кавказских лесных и каменных куниц. Nekotorye vozrastnye osobennosti morfologii kavkazskikh lesnykh i kamennykh kunits:- Zoologicheskii Zhurnal, 1962 41 (11): 1731-1738.

13. K.I. Kopein: Анализ возрастной структуры популяции горностая. Analiz vozrastnoi struktury populyatsii gornostaya:- Trudy Mosk. Obshch. Ispyt. Prirody, 1967 25: 33-39.

14. N.P. Lavrov: Роль глистных инвазий и инфекционных заболеваний в динамике численности горностая (Mustela erminea L.). Rol' glistnykh invazii i infektsionnykh zabolevanii v dinamike chislennosti gornostaya (Mustela erminea L.):- Trudy tsentral'noi Laboratorii Biologii i Okhotnichego Prom. Mark. SSSR, 1944 6 151-163.

15. N.P. Lavrov: Особенности и причины длительной депрессии численности горностая в лесостепной и степной зонах СССР. Osobennosti i prichiny dlitel'noi depressii chislennosti gornostaya v lesostepnoi i stepnoi zonakh SSSR:- Trudy Vses. n-i-Inst. Okhotnichego Prom. 1956. 16:89-107.

16. E.Z. Kogteva and V.F. Morozov. О зараженности лесной куницы (Martes martes) нематодами родов Filaroides и Skr abingylus на северо-западе РСФСР. O zarazhennosti lesnoi kunitsy (Martes martes) nematodami rodov Filaroides i Skrjabingylus na severo-zapade RSFSR:- Zoologicheskii Zhurnal, 1970 49 (1): 131-136.

17. A.M. Petrov and V.G. Gagarin. Изучение цикла развития возбудителей легочных гельминтов пушных зверей (филяроидоза и скрябингилеза). Izuchenie tsikla razvitiya vozbuditelei legochnykh gel'mintov pushnykh zverei (filyaroidoza i skryabingileza):- Doklady Vses. Akad. S-Kh. nauk im. V.I. Lenina, 1937 5 (8): 291-294.

18. A.A. Dubnitskii. Изучение цикла развития нематоды Skrjabingylus nasicola- паразита лобных пазух пушных зверей семейства куных. Izuchenie tsikla razvitiya nematody Skrjabingylus nasicola- parazita lobnykh pazukh pushnykh zverei semeistva kunykh:- Karakulevodstvo i zverovodstvo 1956, 1: 59-61.

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Editor's Preface

The papers collected in this volume were translated by the Russian Translation Service of the British Library Lending Division, then known as the National Lending Library, during 1970-71.

The selection of papers for translation reflects the editor's own research interests, since it was made before the idea of publication came up: it is not comprehensive, and unfortunately some of the interesting titles quoted, in the references to those which have been done, are difficult to obtain.

The additions of maps showing most of the places mentioned in the papers, and of indices, should assist the general reader. A bibliography of further translations available in this field may be useful to the specialist.

Cranial terminology has been standardised as much as possible. Readers unfamiliar with it should consult a standard anatomical text : I used Gilbert (1968), in which the skull of a carnivore (the cat) is very clearly described and illustrated. See also The Handbook of British Mammals, edited by H.N. Southern (1964 : new edition in prep.).

The two common names, "stoat" and "ermine" are used interchangeably for Mustela erminea. "Ermine" usually (but not necessarily) refers to the animal when in white winter dress, and the word may be singular or plural (some writers add an "s"). "Weasel" refers to Mustela nivalis.

Russian custom is to list Soviet and foreign references separately, and in the Soviet lists, the papers appear in order of the cyrillic alphabet, not of the arabic of the translation. References to Western literature which were obviously wrong or incomplete have been corrected where possible, although no systematic check against sources was made, nor have bibliographies been rigorously standardised.

Quotations in the text to a numbered reference given in an author's bibliography are shown thus : (1). Footnotes (inserted by author, translator, or editor) are shown thus : (a). Some photographs have been gently retouched for clearer reproduction.

The paper by E.S. Nyholm (1959) is not Russian, but Finnish : it is included here because it is widely known and often quoted but, so far as I know, there is no translation readily available.

The task of preparing these papers for publication was undertaken whilst I was employed by the Ecology Division, Department of Scientific and Industrial Research in New Zealand. The work was undertaken with the permission of the Director, Dr J.A. Gibb. Mrs Melishkin, of the Translation Service, N.Z. Department of Internal Affairs, was very helpful in sorting out queries, and the whole book was skilfully and patiently retyped by Mrs J.E. Berney.

Carolyn M.King

Lower Hutt, New Zealand

October 1974

GEOGRAPHICAL VARIATION IN WEASELS IN THE SOVIET UNION

(Geograficheskaya izmenchivost' lasok Sovetskogo Soyuza)

by

L.G. Morozova-Turova

Okhotnich'e-promyslovye zveri: Biologiya i khozyaistvennoe ispol'zovanie. (Game and fur animals: their biology and commercial exploitation.) Ed. D.P. Dement'ev et al. Moscow 1965 (1) : 265-79.

Up to now, the question of the geographical differences between weasels in the USSR and Western Europe has not been fully answered. The first systematic review of weasels in the Soviet Union was carried out in 1935 by S.I. Ognev: in Western Europe, several taxonomists in different countries have studied the species.

One of the principal problems, which all foreign authors have tried to solve, is that of whether the weasels in Europe and Asia are one or two species. Very small weasels with small skulls are often found in the region populated by what is called the normal, quite large, weasel, i.e. in the central and southern parts of European Russia and Western Europe.

Many of them (Pomel 1853, J. Allen 1903, Zimmerman 1940, Kratochvil and Kostroň 1945, Kahmann 1951, Barn 1952, Frechkop 1953, and Bauer and Rokitansky 1953) have considered the small weasel as being a separate species (M. minuta Pomel, M. pygmaea J. Allen). They consider that the small weasel is descended from the form found frozen in glaciers, and that this form, owing to steady interbreeding with the larger present-day weasel, is gradually disappearing, remaining only in the form of isolated groups in

the regions inhabited by the normal weasel. A number of authors have classified it in the sub-species "nivalis" (Barret Hamilton 1900, Cavazza 1908, Miller 1912, Ognev 1928, Bauer 1956) or American "rixosa" (Kuroda 1921, G. Allen 1933).

To generalise the descriptions of the small weasel of Western Europe given by the different authors: male body length 156-243 mm, tail length 25-55 mm, condylo-basal length 30.6-35.8 mm, skull narrow with slight [(a)] zygomatic arches. In summer the colour is brown, and in winter it is white. All authors recognise the same area inhabited by the small weasel, with slight variations; it has been found near Paris, in the Alps, in the Carpathians, in Northern Germany, in Bavaria, in Czechoslovakia, in Hungary, in Norway, in the Belovezh Forest[(b)], and in the Caucasus.

Since collections in the Soviet Union include only a small number of weasels from Western Europe, the only specimens used in this study were from the USSR. We have attempted to give a picture of the geographical differences between weasels in different regions of the Soviet Union, and to explain why the populations of normal weasels include small specimens.

Altogether we examined 510 weasels in the collections at the Zoological Museum of the Moscow University, the Zoological Institutes of the USSR, the Georgian and Armenian Academies of Sciences, the scientific research institutes at Frunze and Tashkent, and several private collections. It must be noted that even this comparatively wide range of specimens was still, in many cases, insufficient to enable us fully to revise the details of the group concerned.

Since very few data were available on the females of some groups of weasels, most of the dimensions given are for males, and details are given for females only when the number available was more or less sufficient.

(a) Could mean either "slender" (the arch) or "narrow" (the space) - Ed.

(b) ? In Poland - Trans. The Times Gazeteer gives only a "Bělores" in Czechoslovakia - Ed.

Analysis of the differences in the dimensions, colouring and craniological particulars of weasels in the Soviet Union, with relation to geographical conditions, leads us to the following conclusions :

1. The amplitude of geographical differences is very great in the weasels of the USSR.

2. Within the USSR, the weasels can be subdivided into two well differentiated groups :

Group I: small, short-tailed weasels with a small skull, of the North American species Mustela rixosa. Weasels in this group are found throughout Siberia and Kazakhstan, except for its Southern desert regions, in the Far East and beyond[(a)] Lake Baikal; weasels in this group, but with a narrow end[(b)] to the skull, are found in the Northern regions of the European part of the Soviet Union, and from there into Finland and Northern Norway.

Group II: very large, long-tailed weasels with a large skull; these are found in the Southern parts of the Soviet Union; beyond the Caucasus, in Southern Kazakhstan, in Central Asia, and eastwards of Semirech'. This weasel is of the Southern European species M. n. boccamela.

3. The differences between these two groups of weasels are so great that they could be regarded as different species.

4. Group III: there is a wide zone, populated by weasels with extremely variable morphological characteristics, between the areas inhabited by the above two groups, i.e. in the central and Southern regions of the European part of the USSR. The species is extremely variable in this zone, and we regard this part of the USSR as a wide zone of transition from one to the other of the two extreme forms of weasel.

5. While the weasels of the European part of the USSR show great differences from North to South, there is a definite pattern governing the dimensions of the body and the length of the tail: the weasels become much

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(a) "Beyond" - a word used frequently in this paper in descriptions of geographical locations - presumably means the side distal from Moscow - Ed.

(b) Presumably the posterior end, i.e. the mastoid region - Ed.

larger and longer-tailed southwards from the Kursk and Voronezh Provinces, the weight and length of tail reaching their maxima beyond the Caucasus.

6. The small animals, of which there are isolated specimens within the populations of medium and large sized weasels of the central and Southern regions of European USSR, differ from the latter only in that they are smaller sized; otherwise their proportions are absolutely equivalent.

While the overall dimensions of the small North European weasels and the Siberian weasels are no different from the dimensions of those of the Central and Southern regions of the Soviet Union, the former(a) however have an absolutely and relatively longer tail, comprising about 26-28% of the length of the body; the equivalent length for the small Northern European and Siberian weasels is 13.9%, while it is 21.8-30.2% for the large Southern weasel.

7. There is geographical variation in the colour of weasels in the USSR, from relatively bright yellowish-reddish to dark brown.

8. The change to the pure white winter colouring depends on the geographical location of the population. This is particularly well defined among the Southern weasels, in which pure white, parti-white, or entirely brownish specimens (with, however, the fur appreciably lighter), may be found among winter samples. This applies both to large and to small weasels. The colouration of the fur in winter is not, therefore, a feature of Mustela minuta.

9. According to foreign authors, the small weasel inhabits principally the mountainous and afforested zone of Southern Europe (the Alps and Carpathians), and the Caucasus and Siberia. This point of view is not, however, confirmed by the fact that small specimens have been found in Germany and Poland, and within the USSR in the Moscow, Voronezh, Kursk and Poltava regions, i.e. in forests and flat afforested steppe. In the Caucasus

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(a) Presumably, weasels from the Central regions - Ed.

the small weasel is found on the lowlands, in the foothills, and high up in the mountains, together with the large weasel.

It is not therefore correct to consider the small weasel as being an ecological form of weasel particularly associated with mountains.

10. In my opinion the small weasel found in Siberia and the Northern European part of the Soviet Union is the well differentiated sub-species Mustela nivalis pygmaea J. Allen.

11. In my opinion, the small weasel specimens found in the central and Southern regions of the European part of the USSR is a small phenotype of the extremely variable form of weasel inhabiting this territory.

12. The weasels found within the Soviet Union are a single, but extremely widely varying polytypical species, including a number of sub-species.

SUB-SPECIES OF WEASEL IN THE USSR

GROUP I: "PYGMAEA" GROUP WEASELS

Small weasels with a very short tail and a small skull of infantile appearance. Distribution: the north of the European part of the USSR, all of Siberia, the Urals down to their southern end, Northern and Central Kazakhstan as far as Syr-Dar'ya and Semipalatinsk, the Altai, Sayan, the Far East, the region beyond Lake Baikal, and North-Eastern Mongolia.

Sub-species: 1. Mustela nivalis pygmaea J. Allen

2. Mustela nivalis punctata. Domanievski

I. 1. MUSTELA NIVALIS PYGMAEA J. ALLEN 1903(a)

The small weasel

Mustela nivalis, Nordguist, Osk., Anteckniger och studier Sibiriska Ishajskutens Däggdjurs fauna, p.90 1883.

Mustela vulgaris, Iokhel'son V.I. Ocherk zveropromyshlonnosti v kalymskom Krae (Review of the wild animal industry in Kolyma Province), 1898, pp.73-75.

(a) Some typographical confusion here; the headings have been rearranged in the style of the rest of the paper. - Ed.

Putorius (Arctogale) pygmaeus, Allen J., Report on the Mammals. Bull. Amer.Mus.Nat.Hist.Vol.XIX, p.176-178, 1903.

Mustela rixosa pygmaea. Allen G.M. The least weasel, a circumboreal species. Journal of Mammalogy vol.14, No.4, 1935.

Mustela nivalis pygmaea. Ognev, S.I. Zveri SSSR i Prilezhashchikh stran (Wildlife in the USSR and neighbouring countries.) 1935, vol.3, p.56.

Mustela minuta pygmaea, Zimmerman, K., Zur Kenntnis deutscher Maus - u. Zwergwiesel. Zeitschr.f. Säugetierkunde, 15 (3), 1940.

Terra typica: Gizhiga (Eastern Siberia)

Materials available 132 specimens: 65 from the Kol'skii Peninsula, Finland, Archangel Province, Komi Province, Western Siberia and Eastern Siberia, 19 from Bashkiria, 30 from Kazakhstan, 17 from the Altai and 1 from Sayan.

Diagnosis. This is a small weasel with a short tail, which is as long as or slightly longer than the back foot, and averages 13% of the length of the body. Male body length (n = 32) 133-172 mm (M.[a] 159.6), tail length 12-28 mm (M. 22.6), back foot length 16-25 mm (M. 21.0). The skull is small, with little-developed supra-orbital processes, a short and wide postorbital constriction, and little developed pectines, even in fully grown specimens. In the male, the condylo-basal length of the skull is 22.8-34.8 mm (M. 32.7), the mastoid width 11.0-16.8 mm (M. 15.2), the interorbital width 5.0-8.2 mm (M. 7.2), the postorbital width 7.0-8.5 mm (M. 8.0), the length of the postorbital constriction 0.5-2.8 mm (M. 1.5), zygomatic width 13.8-19.8 mm (M. 16.5).

In summer the dorsal fur is dark brown. There are very rare specimens of a brighter rust colour. In winter the coat is pure white. Hair length (on the rump) is 10.3 mm in summer and 14 mm in winter.

(a) Mean, $\bar{x}$

Geographical distribution. The small weasel is found throughout Siberia, in the Northern Urals, through Northern, Central and Eastern Kazakhstan to Syr-Dar'ya in the South, in the Altai and Sayan, in the Far East, and in Kamchatka. In European USSR it inhabits a narrow belt along the Far North to the Kol'skii Peninsula, Finland and Northern Norway, and in the South to the Kirov and Gor'kii Provinces.

Remarks on taxonomy. The small weasel occupies a wide area in the Asiatic part of the Soviet Union, occurring in the European part only in a narrow belt through the Northern Provinces. In 1935, S.I. Ognev gave it as his opinion that the weasels from the Bol'shezemel'sk tundra and in the Northern Province occupy as it were an intermediate position between M. n. nivalis and M. n. pygmaea. It is my opinion that all the animals in our collections from Bukhta Indiga, the Pechorsk game reserves (Komi ASSR), Archangel province, the Kol'ski Peninsula and Finland are definitely of the sub-species M. n. pygmaea. The small weasel thus spreads far to the West, to Norway. K. Zimmerman (1940) and I. Kratochvilsa (1945) stated that the Scandinavian countries are inhabited by the small weasel. Several geographical varieties can be isolated from such a widely distributed sub-species. It is possible, for instance, to note certain differences between the Tomsk, Novosibirsk and Altai weasels. Far Eastern groups can be distinguished. S.I. Ognev, in 1935, gave it as his opinion that there are no weasels on Sakhalin. This is incorrect: weasels were caught by A.I. Gizenko in Southern Sakhalin (Moscow State University Zoological Museum collection). These weasels are very small and short tailed, and are similar to the Siberian weasel. Possibly the weasel from Southern Sakhalin is close to the Kuril Islands weasel (M. n. namijei Kuroda). The weasel from the Kuril Islands (1 specimen in the Academy of Sciences ZIN collection) is also of the small, short-tailed group. The colour is brown or brownish, with brown spots on the stomach. The available data are scarce and incomplete, so at present we are unable to determine the status of

the weasels from these regions.

I. 2. MUSTELA NIVALIS PUNCTATA DAMANIEVSKI [Sic.] 1926

Weasel from beyond Lake Baikal

Mustela punctata Domanievski. Neue Säugetiere aus Nordasien. Anal.Zool.Mus.Polon.Hist.Nat. Vola. I. pp.55-56, 1926.

Darasun, Chita Province.

Mustela nivalis pygmaea Ognev, S.I. Fauna of the USSR and neighbouring countries, 1935, p.56.

Mustela nivalis kerulenica Bannikov, A.G. Data for identifying the mammals of Mongolia. VI. Kun'i. Byulleten' MOIP, vol.VII, (2), p.100. Mongolia, Undurkhan. Right bank of the river Kerulen, 1952.

Terra typica: Darasun, Chita province

Materials available. eight specimens from the region beyond Lake Baikal, 28 from Mongolia.

Diagnosis: Like pygmaea, the animal has a short tail as long as, or slightly longer than, the length of the back foot, comprising 13.9% of the length of the body; it differs from pygmaea in that its colouring is brighter.

The length of the body of the male (n = 8) is 150-185 mm (M.166.6) the length of the tail 11-28 mm (M.20.2), the length of the hind foot 12-23 mm (M. 18.2)[a].

The skull is small and narrow, with a short, very much narrower postorbital constriction in adult specimens. The condylo-basal length of the male skull (n = 6) is 31.0-35.0 mm (M. 32.4), the equivalent for the female (n = 8) being 27.5-32.0 mm (M. 30.4). The mastoid width in the male is 14.0-16.3 mm (M. 15.4); in the female it is 12.5-16.0 mm (M.14.3); the interorbital width is 6.6-8.5 mm (M. 7.2) in the male and 5.5-7.5 mm (M. 6.3) in the female; the postorbital width is 6.5-8.0 mm (M. 7.4) in the male and 6.2-8.0 mm (M. 6.9) in the female; the length of the postorbital

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(a) These are measurements for Mongolian weasels only, since the data from the region beyond Lake Baikal do not include measurements - Author.

constriction is 1.0–3.0 mm (M. 1.8) in the male and 0.5–2.0 mm (M.1.4) in the female.

Geographical distribution. Southern and South-Eastern parts of the region beyond Lake Baikal, North-Eastern Mongolia.

Remarks on taxonomy. The weasel from beyond Lake Baikal is identical with the Mongolian weasel. It has the same bright colouring, small dimensions and short tail. Its dimensions are very nearly the same as those of Mustela nivalis pygmaea, the principal difference from that species being its colouring. There is a slight difference between the skulls. The skull of M. n. punctata is wider in the rostral region, with a more abrupt postorbital constriction, and the sexual dimorphism is less well defined. In winter the weasel from beyond Lake Baikal turns white. The coats of the two winter weasels from Mongolia and the region beyond Lake Baikal (in the Academy of Sciences ZIN collection and the Moscow State University Zoological Museum collection) were pure white. A specimen (S–43828) from Mongolia had a very narrow band of bright brownish fur along the spine and head, and a broad white area stretching up to the sides and spine (March). The animal was obviously changing from its winter white coat to its bright brownish summer coat.(a) The September and October specimens had bright brownish or pale brownish coats with no trace of change of coat colour.

GROUP II: "BOCCAMELA" GROUP WEASELS

Very large weasels with a long tail and a large skull.

Distribution: the region beyond the Caucasus, the flat plains of Western Kazakhstan and Central Asia from the Caspian Sea to Semirech'e.

(a) The weasel follows the same moult pattern as the stoat, which is well illustrated by van Soest and van Bree (1969). – Ed.

Sub-species: 1. Mustela nivalis boccamela Bechstein.

2. Mustela nivalis heptneri L. Turova

II. 1. MUSTELA NIVALIS BOCCAMELA BECHSTEIN, 1800

Weasel from beyond the Caucasus

Mustela boccamela, Bechstein. Pennati, Übers, vierf. Tiere, 2 : 395,1800.

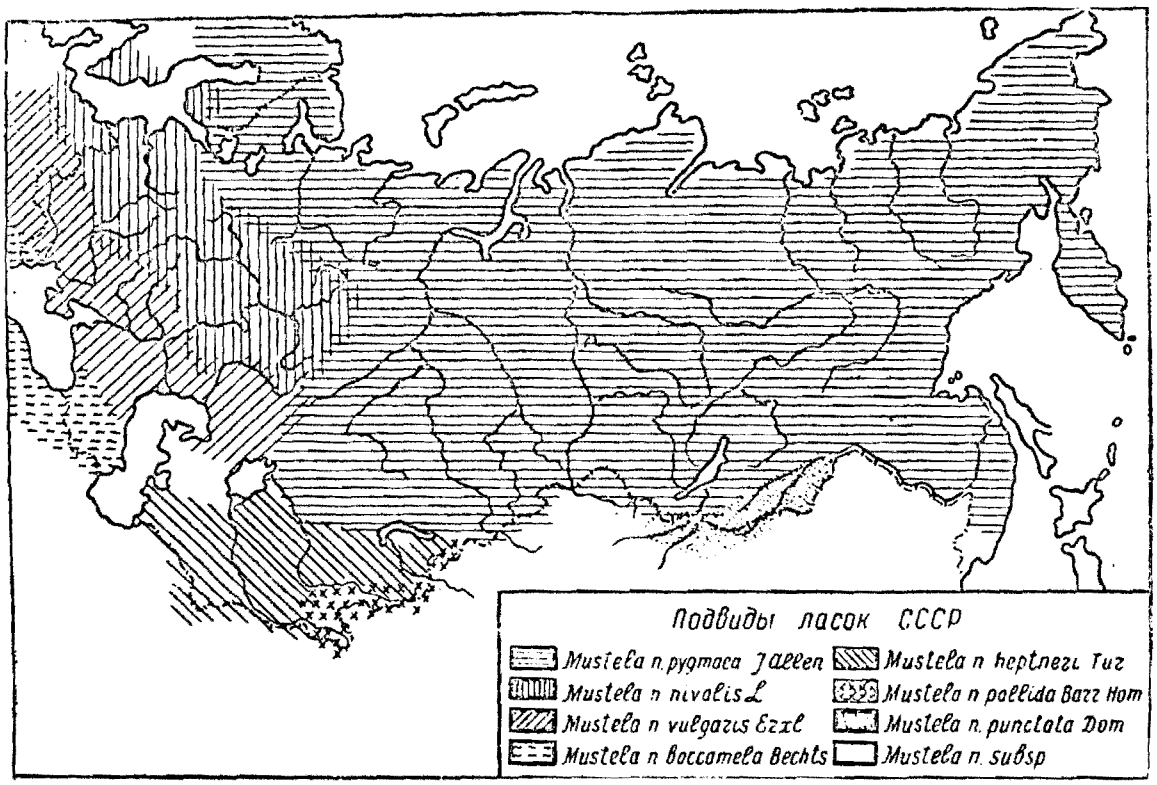
Putorius nivalis caucasicus, Barret-Hamilton, G.E. Note on the Weasel. Ann. and Mag.Nat.Hist.Ser.7, vol.V., p.48, 1900.

Ictis boccamela caucasicus Satunin, K.A. Classification of the genus Mustelidae. Izvestiya Kavkazskogo muzeya, 1911, vol.V.

Mustela rixosa caucasica, Allen G.M. The least Weasel, a circumboreal species. Journal of Mammalogy Vol.14, no.4, p.319, 1933.

Mustela nivalis dinniki, Ognev, S.I. Fauna of the USSR and neighbouring countries, 1935, vol.III, p.60.

Terra typica: Sardinia



SUBSPECIES OF THE WEASEL IN USSR

Fig.1

Material available: 48 specimens from the region beyond the Caucasus (Armenia, Georgia, Azerbaidzhan).

Diagnosis. The weasels of this group are very large, with a long tail, comprising about 30% of the length of the body and being almost double the length of the hind foot. In males the length of the body (n = 20) is 209-260 mm (M. 226.5), the length of the tail 55-85 mm (M.72.3), and the length of the hind foot 22-42 mm (M.35.9).

The skull is very large, with a pronounced postorbital constriction, wide zygomatic arches and well developed supra-orbital processes. The condylo-basal length of the skull is 41.0-46.2 mm (M.42.1) in the male,(a) and 29.8-36.0 mm (M. 31.2) in the female (n = 6); the mastoid width is 20.0-22.4 mm (M. 20.2) in the male and 14.0-16.8 mm (M. 15.1) in the female; the interorbital width is 8.5-10.0 mm (M. 9.5) in the male and 6.2-7.5 mm (M. 7.1) in the female; the postorbital width is 6.8-8.0 mm (M.7.4) in the male and 6.0-8.0 mm (M. 7.1) in the female; the length of the postorbital constriction is 3.5-6.0 mm (M. 5.3) in the male, and 0.5-2.5 mm (M. 2.2) in the female; the width of the zygomatic arches is 21.5-24.0 mm (M. 22.6)(b).

In summer the coat is bright brownish or chestnut with a yellowish or rusty tint. The under-side is white, with brownish spots at the corners of the mouth in some specimens. In winter the coat does not become such a pure white as in the more Northern weasel. The winter coats of some specimens are mottled, being a dirty white with brown markings; probably a proportion of specimens do not turn white at all.

Geographical distribution. In the USSR: the region beyond the Caucasus. Outside the USSR: Southern Europe.

Remarks on taxonomy. Zoologists have expressed different opinions regarding the taxonomic position of the weasels inhabiting regions beyond

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(a) No. of measurements of males not given - Ed.

(b) Sex not given - Ed.

the Caucasus. In 1911, Satunin expressed the opinion that the weasel from that area belonged to the Central Black Sea species Mustela boccamela Bechstein, and considered that the weasels from the steppes and foothill regions of the Northern Caucasus (the type from Stavropol) were the special sub-species Mustela nivalis dinniki. In 1935, S.I. Ognev thought that the weasels from the Northern Caucasus and from beyond the Caucasus were identical, and that they both belonged to the sub-species Mustela nivalis dinniki.

The relative wealth of material (48 specimens) available of the weasel from beyond the Caucasus convinced me that these weasels differ from those on the Northern slopes of the main range and from the neighbourhood of the Caucasus. The weasels from beyond the Caucasus differ from the latter type, and have longer tails. In the cranium they differ less in size (though the skulls of weasels from beyond the Caucasus are slightly larger) than from the point of view of structure. The postorbital constriction is much greater in the case of the weasel from beyond the Caucasus (M. 19.1% of the condylo-basal length) than in the case of the weasels from the Northern slopes of the Caucasus (M. 22.1%); in the mastoid region the width is much greater in the skull of the Northern Caucasus weasel (48.2%, as against 43.3% for the weasel from beyond the Caucasus). As to its morphological particulars, the weasel from beyond the Caucasus is very similar to the South European Mustela nivalis boccamela, and the weasels from Asia Minor are evidently also of that species.

The description of the South European weasel given by Miller in 1914 agrees entirely with our data on the weasel from beyond the Caucasus. Animals from Malta and Sardinia (S-2227, 2228 and 13030 in the Moscow State University Zoological Museum collection and no.8790 in the Academy of Sciences ZIN collection) were very similar to the weasels found beyond the Caucasus. The only actual difference between them lies in the brownish spots on the chest and stomach of the Mediterranean specimens, these spots

being found only very rarely on the weasels from beyond the Caucasus. Owing to the absence of sufficient comparative data on the European weasel, we cannot say sufficiently confidently that the weasels from beyond the Caucasus and from the Mediterranean (South European) region are absolutely identical, but one can still be certain that they are very similar and that the weasel from beyond the Caucasus belongs to the group of large Southern weasels of the boccamela type.

II. 2. MUSTELA NIVALIS HEPTNERI L. TUROVA, 1953

Turkmen weasel

Putorius stoliczkanus, Radde und Walter. Zöol. Jahrbücher, syst. IV, p.1023, 1889.

Ictis stoliczkanus, Satunin, K.A. Classification of the genus Mustelidae. Izd. Kavkazskogo museya, vol.V, p.255, 1911.

Mustela nivalis pallida, Ognev, S.I. Fauna of the USSR and neighbouring countries. Vol.III, p.63, 1935.

Mustela nivalis heptneri, Morozova-Turova, L.G. Zoologicheskii zhurnal, Vol. XXXVII, no.6, p.1267. S. Turmeniya, Badkhyz, R. Egri-Chek, 1953.

Terra typica: S. Turkmeniya, Badkhyz, River Egri-Chek.

Materials available: 18 specimens: 4 from Badkhyz, in Southern Turkmeniya, 2 from Gassan-Kuli, 1 from Murgab, 1 from Repetek, 2 from Uzbekistan, 1 from near Chimkent, 5 from Semirech'e, 2 from the Vakhsh valley.

Diagnosis. Very large weasels with a long tail comprising 25-30% of the length of the body and more than twice as long as a hind foot. In dimensions these weasels are similar to boccamela, differing from it and from all other varieties of the species in being a very bright sandy colour. The length of the body of the male (n = 7) is 230-242 mm (M.234.1), the length of the tail 55-87 mm (M.68.2), the length of the hind foot 27-35 mm (M. 33.2). The skull is large and massive, with wide zygomatic arches. The condylo-basal length of the skull in males is 40.5-45.5 mm (M. 43.1), the mastoid width 21.0-22.0 mm (M. 21.3), the interorbital width 9.8-10.8 mm

(M.10.3), the postorbital width 7.8-9.0 mm (M. 8.3), the length of the postorbital constriction 3.2-5.0 mm (m. 4.0), the width of the zygomatic arches 23.4-26.0 mm (M. 24.4). In summer the top of the coat is very bright straw-yellowish. The coat is short and stiff, and does not fully whiten in winter. In summer the length of the coat on the rump is 5 mm, and in winter it is 7 mm.

Geographical distribution. The level steppes and deserts of Southern Kazakhstan and Central Asia from the Eastern shore of the Caspian to Semirech'e.

Notes on taxonomy. M. n. heptneri differs greatly from all other weasels in the Soviet Union in that its coat is brightly coloured and short, the hairs being few and stiff. It belongs to the group of large Southern weasels of the M. n. boccamela type. M. n. heptneri is distinguishable from the M. n. boccamela found in the region beyond the Caucasus in that it is brightly coloured and the structure of the skull is slightly different. The zygomatic arches are wider apart, the post-orbital constriction is shorter and more abrupt, the skull is wider at the rostrum, and it is also wider in the mastoid region and between the m^1. [upper first molar teeth. - Ed.] The bullae are longer.

The heptneri weasel is closest of all to Mustela nivalis stoliczkanus both in size and colouring. Since we have no comparative data from Central Asia, the relationship between these two forms is still not clear.

The Turkmen weasel differs from Mustela nivalis pallida in that it is much larger and its colouring brighter.

GROUP III: "NIVALIS" GROUP WEASELS

Medium-sized weasels with an average length tail and skull, but greatly variable in dimensions. They occupy a position intermediate between groups I and II of small and large weasels. Distribution: the central and Southern regions of the European part of the USSR, the Crimea,

the region north of the Caucasus, and the northern slopes of the High Caucasus, Western Kazakhstan, and mountainous regions of Central Asia (except for the Kopet-Dag mountains).

Sub-species: 1. Mustela nivalis nivalis L.

2. Mustela nivalis vulgaris Erxl.

3. Mustela nivalis pallida Barr.-Ham.

III. 1. MUSTELA NIVALIS NIVALIS L., 1766

Central Russian weasel

Mustela nivalis Linnaeus C., Systema Naturae, 12th edition, p.69, 1766.

Mustela gale Pallas, P., Zoographia Rosso - Asiatica 1, 1820, p.94.

Ictis nivalis, Satunin, K.A. Classification of Russian Mustelidae. Izvestiya Kavkazskogo muzeya, vol.V, 1911.

Mustela nivalis nivalis, Ognev, S.I. Fauna of the USSR and neighbouring countries, vol.III, p.56, 1935.

Terra typica: Vasterbotten Province, Sweden.

Materials available: 84 specimens: 4 from the Baltic republics, 20 from the Belorussian SSR, 44 from the central provinces of European USSR, 16 from Denmark.

Diagnosis. The weasels in this group are medium sized, and the tail is medium length, about 1.5 times the length of a hind foot. The length of the body of the male (n = 14) is 162-213 mm (M. 186), that of the female (n = 9) 145-185 mm (M. 165). The length of the tail is 28-66 mm (M. 40.5) in the male and 20-42 mm (M. 33.6) in the female; the length of the hind foot is 22-30 mm (M. 27.3) in the male and 19-25 mm in the female (M. 22.1). The size of the skull is average for subspecies in the group. The condylo-basal length of the skull is 30.5-40.2 (M. 35.9) in the male (n = 13) and 23.0-36.8 (M. 32.0) in the female (n = 13); the mastoid width is 15.0-19.6 mm (m. 17.3) in the male and 12.8-18.5 mm (M. 15.0) in the female; the inter-orbital width is 6.0-8.5 mm (M. 7.7) in the male and 5.0-7.0 mm (M. 6.9) in the female; the width of the supraorbital processes is 5.0-9.3 mm (M. 8.2) in the male and 5.3-9.0 mm (M. 7.1) in the female; the length of the post-

orbital constriction is 1.5–7.8 mm (M. 3.6) in the male and 0.5–7.8 mm (M. 2.6) in the female; the zygomatic width is 11.0–22.0 mm (M. 17.9) in the male and 15.3–18.5 mm (M. 16.2) in the female. In summer the coat on the dorsal surface is dark brown or chestnut, but specimens coloured a brighter yellowish brown are found. In winter the coat is pure white. In summer the length of the hairs on the rump is 9.5 mm, and winter it is 2.5 mm [sic].(a)

Geographical distribution. This weasel inhabits the central belt of the European part of the USSR, approximately from the south of Leningrad and Kalinin provinces southwards to the Kursk and Voronezh provinces, and from the Baltic republics and Poland eastwards to the Central and Southern Urals. There is a weasel similar to M. n. nivalis in Western Kazakhstan and Chkalov Province. The Bashkirian weasel occupies a position intermediate between M. n. nivalis and M. n. pygmaea. The weasels found in the Belovezhsk Forest are slightly larger than the Central Russian weasel.

Notes on taxonomy. No-one has yet established what is the true Swedish weasel. S.I. Ognev (1935) considered that the Central Russian weasel was identical with the true Swedish weasel, and that the weasels from Central Europe andfrom the Southern regions of the USSR were the species Mustela nivalis vulgaris.Erxl. The facts that we have no details from Sweden, and that the available diagnoses of the true Swedish weasel are not clear, mean that we cannot establish sufficiently accurately its relationship to the Central Russian weasel. I tend towards the opinion held by S.I. Ognev, and classify the latter as M. n. nivalis L., but this is only conditional.

III. 2. MUSTELA NIVALIS VULGARIS ERXL, 1777

Central European weasel

Mustela vulgaris Erxleben, Systema Regni Animal, 1, p.471; Liepzig region, 1777.

(a) ? misprint for 12.5 mm - Ed.

Mustela nivalis nikolskii, Semenov, A. Certain considerations as to the past flora and fauna of the Crimea. Zap.Imper.Akademii nauk, series VIII, vol.VIII, no.6, p.14. Simferopol region, Crimea, 1899.

Putorius nivalis dinniki, Satunin, K.A. Mammals of the North-Eastern Caucasus. Izvestiya Kavkazskogo museya, vol.III, pp.105-110: Stavropol region, 1907.

Ictis boccamela dinniki, Satunin, K.A. Classification of the genus Mustelidae. Izvestiya Kavkazskogo museya, vol.V, 1911.

Mustela nivalis vulgaris, Ognev, S.I. Fauna of the USSR and neighbouring countries, vol.III, p.53, 1935.

Mustela nivalis dinniki, Ognev, S.I. Fauna of the USSR and neighbouring countries, p.60, 1935.

Mustela nivalis caucasica, Ognev, S.I. Fauna of the USSR and neighbouring countries, p.60, 1935.

Terra typica: Leipzig region.

Materials available: 92 specimens: 17 from the Voronezh and Kursk Provinces, 20 from the Ukraine, 2 from Saratov Province, 4 from the Crimea, 58 from the steppe and foothill regions of the Northern Caucasus and from the Northern slopes of the Great Caucasus.

Diagnosis. Within the limits of its group this is a large weasel with a relatively long tail comprising 27% of the length of the body and twice the length of a hind foot.

The length of the body of the male (n = 26) is 173-343 mm (M. 212.6) that of the female (n = 6) 155-211.8 mm (M. 181.3); the length of the tail is 45-75.5 mm (M. 57.9) in the male and 45-63.7 mm (M. 54.1) in the female; the length of a hind foot is 21-38 mm (M.30.8) in the male and 29-31 mm (M. 25 [sic.]) in the female. The skull is relatively large, with the zygomatic arches wide apart. The condylo-basal length of the skull is 31.5-43.0 mm (M. 38.8) in the male and 25.8-36.0 (M. 33.2) in the female (n = 6); the mastoid width is 13.5-20.5 mm (M. 18.4) in the male and

14.0–16.8 mm (M. 15.1) in the female. The interorbital width is 6.5–10.2 mm (M. 8.5) in the male and 6.2–7.5 mm (M. 7.0) in the female; the postorbital width is 5.0–10.2 mm (M. 8.4) in the male and 6.0–8.0 mm (M. 7.1) in the female; the length of the postorbital constriction is 2.0–7.0 mm (M. 4.1) in the male and 0.5–2.6 mm (M. 2.2) in the female; the zygomatic width is 17.0–22.0 mm (M. 20.0).

In summer the colour of the upper coat is between bright brownish and dark chestnut, while in winter the coats of most specimens are pure white. The length of the hairs on the rump is 7.5–8.5 mm in summer and 10.5–13.5 mm in winter.

Geographical distribution. From the South of the Kursk and Voronezh provinces throughout the entire afforested steppe and steppe zone of the Ukraine and the Northern Caucasus to the Northern slopes of the Great Caucasus; eastwards to the Volga. As yet we do not know how far into the region beyond the Volga this species is found.

Notes on taxonomy. The Southern Russian weasel is very similar to the Central European weasel. The descriptions of the European weasel given by Miller (1912) and other authors agree well with our data. The Crimean weasel is so closely similar to the weasels in the Southern regions of the USSR that there are no grounds for considering it to be a separate sub-species. In its dimensions and relative tail length it is identical with M. n. vulgaris, though it is slightly brighter, its colouring being ochreish-brownish. In 1891, however, A.M. Nikol'skii classified the Crimean weasel as being darker than the Southern Russian weasel.

In 1907, K.A. Satunin classified the weasel from the steppe, foothill and mountain regions of the Northern Caucasus as the sub-species dinniki. He compared it only with the Central Russian weasel (M. n. nivalis), and based his description of the new sub-species on its differences from the Central Russian weasel. To judge by our data, it is impossible to distinguish between the Northern Caucasus weasel and the

weasel from the afforested steppe and steppe regions of the Soviet Union (designated M. n. vulgaris), by either dimensions or colouring.

There are not therefore sufficient grounds for retaining the sub-species dinniki. Slight mean differences in the length of the tail and the proportions of the skull may be explained by the presence of individual specimens of the large M. n. boccamela in Northern Caucasus weasel population, which have reached the Northern slopes of the Great Caucasus from the regions beyond the Caucasus. It should be noted that the weasel from the Southern Russian afforested and open steppes (M. n. vulgaris), tends to decrease in size northwards. This tendency is most obvious in the far South. Thus, whether or not M. n. boccamela is present, the weasels on the northern slopes of the Great Caucasus are in some ways a form transitional between M. n. vulgaris and M. n. boccamela.

III. 3. MUSTELA NIVALIS PALLIDA BARR.-HAM., 1900

Turkestan Weasel

Putorius nivalis pallidus, G.E. Barret-Hamilton. Note on the weasel. Ann.and Mag.Nat.Hist. ser.7, vol.V, p.48, 1900.

Ictis nivalis pallidus, Satunin, K.A. Classification of genera: Mustelidae. Izvestiya Kavkazskogo muzeya, vol.V, p.255, 1911.

Mustela nivalis pallida Ognev, S.I. Fauna of the USSR and neighbouring countries, vol.III, p.63, 1935.

Terra typica: Fergana valley, Kokand.

Materials available: 15 specimens: 6 from the vicinity of Tashkent, 5 from various points in Tien Shan, 2 from Fergana, 1 from the Dzhungarskii Alatau mountains, and 1 from the Northern slope of the Gissarskii mountains.

Diagnosis. This weasel is (within its group) of average size, with a relatively long tail comprising about ¼ of the length of its body (24%). The length of the body of the male (n = 17) [(a)][sic.] is 180-215 mm (M. 192),

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(a) We must suspect n = 17, since only 15 specimens were available.

the length of the tail 37-60 mm (M. 47), the length of the hind foot 25-31 mm (M. 27). The skull is of average size and relatively narrow in the mastoid region; the postorbital constriction is short, and the skull here is relatively narrow. The condylo-basal length of the skull of the male is 31.8-10.0 mm [sic.] (a) (M. 35.4). The mastoid width is 15.0-19.0 mm (M. 16.6), the interorbital width 6.5-8.4 mm (M. 7.7), the postorbital width 6.5-8.5 mm (M. 7.5), the length of the postorbital constriction 1.5-2.5 mm (M. 2.5) [sic.] (b), the width of the zygomatic arches 18.0-22.0 mm (M. 19.7).

The colouring of the summer coat on the dorsal side is bright brownish. In winter the coat turns pure white.

Geographical distribution. The Turkestan weasel is found in the Tien Shan, Pamir and Altai mountain ranges.

Notes on taxonomy. The colouring of the Turkestan weasel is not consistent. The specimen from the Dzhungarskii Alatau mountains had by far the brightest coat of the entire group, being close in colouring to the Southern Turkmen weasel; the hairs in its fur were relatively long and soft.

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(a) ? 31.8-40.0 (mean 35.4) ? - Ed.
(b) ? 1.5-2.5 (mean 2-5) ? - Trans.

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(a) Ref. incomplete

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THE VALIDITY OF BERGMAN'S RULE AS APPLIED TO INTRASPECIFIC VARIATION IN THE ERMINE

(O primenimosti pravila Bergmana pri issledovanii vnutrividovogo raznoobraziya gornostaya)

by

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Vestn. Leningr. Univ., Biol. Ser., 9 (2) : 144-148. 1962.

It is known that the vitality of the ermine is greatly affected by the temperature of the surrounding environment. Populations of ermine living in the far north and south of the region in which they are distributed experience widely differing temperatures. In the north of Siberia, in winter, the difference in temperature between the body of the animal and the external environment may reach 80 or more ^{o}C. This severe temperature regime has been important in determining the adaptation of the ermine to life in an extreme climate (6, 15).

Apart from a direct action on the animal (reduction of the activity of the adults, increase in mortality rate of the young, etc.), temperature also has a marked indirect effect. According to the observations of V.I. Tikhvinskii (17) and D.I. Aspisov and V.A. Popov(1), the decrease in the number of ermine trapped in the Tartar ASSR, in years with a cold spring, is not due to the death of ermine from the low temperature, but to the decreased availability of Muridae for food. The cold inhibits the activity of rodents in spring, and it is markedly more difficult for the ermine, hunting outside their burrows, to obtain enough food when the rodents are less active. In addition, in years with a cold spring (according to the opinion of a number of workers) there is a decline in the rate of reproduction of the Muridae. This all leads to a decreased food supply and to starvation both of the adult and the newborn young stoats.

The ermine is widely distributed throughout the Soviet Union, and shows quite a marked variation in body size. It would be of interest to know if there is any relationship between the size of the animal and the temperature of the external environment, which, as has already been mentioned, is of great significance in the life of this predator. In ecology and zoogeography, the so-called "Bergmann's Rule" attempts to explain a possible relationship between the size of the animal and the temperature conditions under which it lives. According to this rule, forms (subspecies) of a given species of homothermic animals living in a colder climate have a large body size; in a warmer climate, forms with smaller body size are found.

Boetticher [20] has already examined the problem of the relationship between body size of the ermine and the temperature of its environment. This author, presenting examples which, according to his opinion, support "Bergmann's Rule", attempted to find a relationship between the variation in body length of the ermine and the mean January isotherm in different geographical regions.

According to Boetticher, the size of the European ermine varies in relation to the average January temperature, as follows (Table 1) :

Table 1. Variation in body length of European ermine in different geographical regions

Geographical distribution	Mean January temperature	Body length (mm)
Northern and Central Scandinavia	-10^{o} to $0^{o}C$	approx. 300
From Southern Sweden to the Alps and Pyrenees	-4^{o} to $+6^{o}C$	251-292
England, Scotland	$+2^{o}$ to $+6^{o}C$	254-280
South West Scotland	$+4^{o}$ to $+6^{o}C$	220-270
Ireland, Isle of Man	$+4^{o}$ to $+8^{o}C$	228-283

The data presented by Boetticher appear to support "Bergmann's Rule". Nevertheless, such a conclusion would be incorrect. Apart from

the error in attempting to find a law concerning the change in body size of an animal only by a simple comparison of the body length with the mean January temperatures, the following points should be considered :

1. Boetticher had no data of his own from which he formulated his conclusions, but used only references from the literature.

2. He does not present average values for body sizes of the groups of ermine examined by him. Also, the number of animals studied, and their sex, is not mentioned.

3. The data in the table were selected so that they include, not only mainland forms, but also island forms of the ermine. The larger individuals were found to be from the mainland, and the smaller ones were from the islands. This phenomenon is well known for a number of animals, although it has no direct relationship with "Bergmann's Rule".

4. A comparison of Boetticher's data with the literature enables one to establish that he made no attempt to present information from important references, but used only information concerning the size of individual examples of ermine from Miller's catalogue [21]. Further, certain figures were taken from the work of Miller without critical evaluation. For example, with reference to the form of ermine found from Sweden to the Alps and Pyrenees, Boetticher for some reason includes in his table only the extreme values for the body size of eight individuals obtained in Switzerland, and devotes no attention to references concerning body size of individuals from the other parts of this area.

Therefore, the conclusions concerning the patterns of variation in body size of the ermine, stated in the work of Boetticher, have no serious foundations. Moreover, the position of Lukin[8] is also untenable. In a study especially devoted to an analysis of geographical variation in size of organisms, he found that it was possible to present the data of Boetticher without serious discussion. In particular, Lukin, citing the work of Boetticher, refers to freshly examined material concerning the

ermine as an example supporting "Bergmann's Rule".

A criticism of "Bergmann's Rule", and an analysis of its application to homiothermic animals, was presented in the work of Terent'ev[16]. However, in later summaries of the ecology of animals[9] critical evaluation of this "rule" is ignored, and, as before, the ermine is used as a representative of the mammals in which the pattern of intraspecific variation in body size may be understood in terms of "Bergmann's Rule".

These facts caused us to re-examine the pattern of intraspecific variation in body size of the ermine from various regions in the USSR and to determine to what degree "Bergmann's Rule" is applicable to this pattern. Altogether, more than 250 individuals were studied (mainly from the stock of the Institute of Zoology, Academy of Sciences of the USSR).

As the animals at our disposal were from distinct geographical regions, it was possible to separate all the data into twelve groups, arranged from west to east in two separate series. The northern series represented Central Russian, Tobol'skii, Turukhanskii, Kolymskii, Karaginskii, and Kamchatskii ermine: the Southern series, Ferganskii, Semirechenskii, Altaiskii, Mongolian, Zabaikal'skii, and Shantarskii ermine. According to theor geographical distribution, these groups correspond to subspecies of ermine described in the works of Ognev[10] and Yurgenson[19].

By comparing the mean body lengths of the ermine from different regions, it is possible to establish a definite pattern in the variation in size, between different groups of one series and also between adjacent groups of the northern and southern series (Table 2).

Table 2. Intraspecific variation in body length (mm) of the ermine

Ermine	Males			Females		
	No.of individuals studied	Range	Mean (arithmetic)	No. of individuals studied	Range	Mean (arithmetic)
Central Russian	49	199-350	253.4	16	190-270	227.5
Tobol'skii	4	225-350	272.0	6	205-260	233.0
Turukhanskii	56	207-350	255.3	18	196-228	210.4
Kolymskii	22	203-250	230.4	4	176-221	201.0
Karaginskii	3	220-230	226.7	-	-	-
Kamchatskii	10	216-325	252.7	2	215-222	218.5
Ferganskii	8	187-300	224.9	3	162-195	177.0
Semirechenskii	7	218-260	241.9	3	170-224	205.0
Altaiskii	14	200-380	250.2	3	210-255	225.0
Mongolian	3	217-257	234.0	1	213	213
Zabaikal'skii	7	220-242	234.0	1	195	195
Shantarskii	5	205-226	219.6	1	186	186

The data in Table 2 indicate a rule in the variation in body length of the ermine from different regions of Soviet Union. Among the groups in the northern series examined by us, the Tobol'skii animals show the greatest body length . From here, both to the west, represented by Central Russian ermine, and also to the east, towards the Turukhanskii, Kolymskii, and Karaginskii districts, there is a decrease in body length. In this series the Karaginskii ermine have the smallest body length. The group of Kamchatka animals occupies a special position, as their body length is similar to those of Central Russia.

Among the groups of the southern series, the greatest body length is found in the Altaiskii ermine. From here it successively decreases both towards the west (Semirechinskii and Ferganskii groups) and towards the east (Mongolian, Zabaikal'skii, and Shantarskii groups). The Shantarskii animals have the smallest body length in this series.

Our data, concerning the intraspecific variation in body size of the ermine, correspond well with other information concerning the size of ermine skins from different mountain ridges [12, 7,11]. These studies found that the Tobol'skii and Northern Kazakhstan animals were the largest.

In analysis of this material, we took into consideration the fact that each geographical region, in which one of the groups of ermine lives, differs, not only in the details of each meteorological element, (temperature, moisture, etc.), but also in the climate in general. However, as our main task was to evaluate "Bergmann's Rule" as applied to intraspecific variation in the ermine, most attention was devoted to the temperature factor. Fairly accurate information was also collected on differences in the amount of precipitation in the geographical regions we examined. In the course of this work the data of Berg[2,3,4], Rikhter[13,14], Formozov[18] Borisov[5] and other workers were used.

A study of the annual range of temperature and precipitation in the [twelve] regions enable one to make the following preliminary conclusions :

(1) The largest groups of ermine (Central Russian, Tobol'skii, Altaiskii, and Kamchatskii) are found in regions with a moderately cold winter (average monthly temperature for December-January of -10 to -20°C), during which there is a large amount of snow (from 25-40 mm of precipitation received during the period November-March).

(2) Regions in which the small continental ermine are found (Kolymskii and Zabaikal'skii) have extremely low winter temperatures (average monthly temperature for December-January is -20 to -50°C), during which there is an insignificant amount of snow (from 0-10 mm of precipitation received during the period November-March).

(3) In the parts of Central Asia where the average monthly temperature for December-January is from 0 to -5°C, the small Ferganskii ermine is found. In winter (November-March) the monthly precipitation here is equivalent to 20-30 mm, and in summer (June-September) there is very little precipitation at all (1-5 mm per month). One should note that the boundaries of the distribution of this form of ermine have not yet been adequately determined, and so our data concerning the temperature and precipitation characteristic of the region of its distribution are provisional.

(4) In the desert regions of Central Asia, where in the period between June and September, the average monthly temperatures reach from +20 to +30°C and there is usually no precipitation, the ermine is not found at all.

Despite the fact that these approximate conclusions do not enable one to explain the precise relationships between body size of the ermine and the annual range of the temperature and precipitation, it is obvious that the largest forms of this species are usually found towards regions characterised by moderate frosts and a large amount of precipitation in the winter months: while small mainland forms, such as those of the Kolymskii and Zabaikal'skii groups, are found towards regions of extremely low temperatures and a very small amount of precipitation in the winter.

The ermine is a species for which snow free winters are not favourable. The fact that the large ermines are most often found towards regions with a deep snow cover can be understood from their ecology: under a thick layer of snow, a large number of Muridae (the staple food of the ermine at this time of the year) are active for the whole of the winter. Where the snow cover is lighter and the temperature severe, as in the Zabaikalii and Yakutiya districts, the rodents under the snow are less active.

Summer temperature and precipitation are apparently of no vital significance for the ermine colonising the northern and mild regions. But in contrast, in the southern regions they probably do play an important role. One should remember that climatic factors affect the ermine not only directly, but also, as has already been mentioned, indirectly, mainly in relation to the food supply.

Also, one must not forget that, in the course of their evolution, representatives of the marten family (Mustelidae), including the ermine, have developed extremely varied mechanisms for surviving unfavourable extremes of environmental temperature. A definite relationship between

heat production and heat emission in individuals from different geographical regions has been determined, not only in body size, but also in the intensity of the utilisation of the thermal energy of food[a] in the characteristics of the structure of the hair covering, and in the degree of attachment towards various dens and sanctuaries, etc.[b]

A study of the material at our disposal has shown that the pattern of intraspecific variation in body length of the ermine does not support "Bergmann's Rule". Variation in external characters, including the dimensions of the animal, is determined by the combined effect of many environmental factors. This is shown by study of the ermine, which is widely distributed and lives under greatly variable ecological conditions.

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(a) See Brown and Lasiewskii (1972) on the metabolism of weasels. - Ed.

(b) This could mean either the number of days on which an ermine returns to the same den, or the number of hours in a day it spends within it - Ed.

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SKULL VARIATION IN THE ERMINE (*Mustela erminea* L.)

(Ob izmenchivosti cherepa gornostaya *Mustela erminea* L.)

by

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INTRODUCTION

In the spring of 1929, S.I. Ognev suggested that I study an interesting series of skulls of ermine from the Shantar Islands, sent to him by G.D. Dul'keit who, together with E.V. Borisov, had collected them during the Shantar Expedition of 1925-1927. A number of the skulls from this series had been used by Ognev in order to describe the new ermine subspecies which he had identified - *Mustela erminea baturini* Ogn. (1929). It was because of these circumstances that I have only recently finished the preliminary stage of the study of this interesting series, which I undertook at that time.

The series which I investigated consists of 103 skulls of ermine (♂♂ and ♀♀) caught in ten different places on the island of Bol'shoi Shantar. It is in a good state of preservation and has been carefully labelled. The insular origin of the series, its high standard of labelling and its considerable size were great advantages to the study of individual, age and sexual variation, for the influence of geographical (a) variation could be eliminated in this case (owing to isolation on the island and the limited area involved). G.D. Dul'keit (1929) estimated from the results of the winter count in 1925 that, on 1100 km^2 of suitable habitat on Bol'shoi Shantar I., the approximate population of ermine was 2000, with a reserve

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(a) The translator's word was "group" as on p. 33, but this word now has quite different connotations in discussions of evolution, and I think that "regional" was the sense intended - Ed.

index Z_1 [a] equal to 18.1 per 10 km^2; the series investigated thus constitutes about 5% of the population living in that area. When beginning the investigation, my object was to shed some light on the problem of the degree of individual variation, to examine the character of sexual dimorphism and, finally, to establish the character and degree of age variation in the craniological features of the ermine. On the basis of the data for age variation it was hoped to discover whether a reliable and easy diagnosis of age groups in an extensive series of craniological material would be a practical possibility. A biometric analysis was undertaken to elucidate this problem.

The whole series ofskulls was measured with respect to a large number (over 30) of characteristics. The extreme variants and the mean values with standard errors were then determined, and the standard deviations of each series and the coefficients of variation with their standard errors were calculated. Graphs of the variance curves of each characteristic were also plotted, and a series of correlation tables drawn up. The measurements were chosen in order to give a sufficiently complete description of the contours of the skull from all the principal points of view (normae verticalis, lateralis, frontalis, occipitalis et basilaris). Of the total number of measurements usually adopted in craniometry, measurements of the nasal bones (nasale) and the greatest width of the hard palate were rejected, for the sutures bounding these bones unite relatively early and no differences whatever are found between adult (adultus) and senile (senex) individuals. To characterise the relationships between the bullae osseae, the shortest distance between them and the longest distance between the foramina lacera posteriora were taken. To characterise the skull from behind (norma occipitalis) the measurements taken were the greatest height and width of the foramen occipitale magnum,

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(a) No reference is given on how to calculate this interesting statistic - Ed.

the height from the superior edge of this foramen to the highest point of the occipital crest, and the width between the lowermost points of this crest.

SEXUAL DIMORPHISM

The series of 103 skulls includes 73♂♂ and 29♀♀ specimens. Most of the material therefore comprises male skulls, as is usual in large collections of mustelids. For this reason, the biometric analysis of the male skulls is more accurate than that of the female skulls.

Tables 1 and 2 show undoubted sexual dimorphism in the structure and size of the skull. With respect to skull size, the features studied fall into the following groups :

1. Variables whose ranges overlap considerably on comparison of the two sexes. Examples of this group are the size of the bullae osseae, the distances between them, the rostral height, the width between the ends of the supraorbital processes, and the height of the foramen magnum.

2. Variables whose ranges are slightly transgressive; most of the measurements (14 of the 30 compared) belong to this group.

3. Variables whose ranges are contiguous. These include facial length, zygomatic width, the mastoid width, height in the region of the hard palate, and the height of the mandible.(a)

4. Variables whose ranges are exclusive. Only three belong to this group: total length, basilar length, and condylo-basal length of the skull.

In the accompanying tables, all the measurements are arranged in order of the coefficient of variation, and it must be remembered that sometimes the very great differences between the mean values (from 42.96 to 2.89) mean that the coefficient of variation does not sufficiently accurately determine the order of the parameters in their degree of variation. However, it does not matter whether we take this coefficient

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(a) The height of the mandibular coronoid process - Ed.

or the standard deviation, for examination of the tables clearly shows that the analogous measurements in males and females have very different degrees of variation. The parameters do not rank in the same sequence in males and females, when arranged in order of degree of variation. For example, the total length of the skull: in males it scores the 4th place in its degree of variation with a coefficient of 1.64%; in females the same measurement scores 24th place with a coefficient of variation of 0.23%. This is clear enough from the tables. It is necessary to add only that, of the 32 measurements on the ♂♂ skulls, approximately one-third have a coefficient less than 0.50%; one-third a coefficient of between 0.50 and 1.00%; finally, one-third with a coefficient over 1%.

Meanwhile, of the 30 different measurements on the ♀♀ skulls, 16 (i.e. more than half) have a coefficient less than 0.50%, and only three (i.e. 10%) have a coefficient greater than 1%. It will be recalled that the figures express individual and age variation of the skull simultaneously. Consequently, sexual dimorphism is also expressed in the lower degree of age variation of the skull in females. This applies to the subadultus, adultus and senex stages. It applies also to structural features of the ♀♀ skulls in which the characteristics of the senex stage are less marked than in ♂♂ - they are almost confined to wearing down of the teeth (this refers only to the Shantar ermine).

AGE VARIATION

G.D. Dul'keit (loc.cit.) observed that the female ermine on Bol'shoi Shantar I. produces its young in April. The series of skulls under study was obtained between November and April inclusive. Consequently, they belong to animals aged 6 months or more. The ages of ermine under 1 year old can easily be determined from the information on the labels with an accuracy of not more than 2 weeks. The purpose of the investigation was therefore to look for signs of age distinguishing between the group under 1 year old and the group of adult and old animals over 1 year of age,

and to determine whether each age group can thus be identified. Bimodality and multi-modality of a variance curve indicates heterogeneity of a test material consisting of a mixture of two or more types. In our case the presence of bimodality and multimodality can be explained by mixing of the age groups in the material studied (ermine ♂♂ and ♀♀). Comparison of the variance curves for 32 parameters of the male skulls showed that in 11 cases the curves were unimodal, in 10 cases they were slightly bimodal or multimodal, and in 18 cases they were definitely bimodal or multimodal. These characteristics were : facial length, interorbital width, total length of the skull, basilar length, length of the hard palate, length of the upper row of teeth, length of the bullae osseae, the greatest distance between them, the width of the foramen magnum, and the height and width of the supraoccipitale. Correlation tables for the 12 pairs of most typical characteristics were then compiled. In most cases positive correlations were found, the degree varying from one case to another. Where a negative correlation between the characteristics would be expected (e.g. length of the cranial capsule and facial length), only absence of any correlation, either positive or negative, was found. The apparent reason is that the skull of some members of the Mustelidae family (for example, Mustela nivalis L., Putorius putorius L.), including the ermine, as Hensel[3] showed, may be of three types regardless of age: average (normal), small, and large. In our series of skulls, No.736, belonging to an old male, has a total length of 44.5 mm, while No.657, also from an old male, has a total length of 41.0 mm; since the amplitude of variation in this parameter (range 39.8 to 45.0) is small, this represents a very considerable difference in the measurements. This observation, of course, considerably reduces the possibility of detection of age variation in the dimensions of individual parameters, but it does not deprive the results of all value and meaning.

TABLE 1. Measurements of Male Skulls

Serial No.	Location of measurement	Number of measure-ments (n)
1	Greatest distance between bullae osseae	57
2	Height of upper canine teeth	59
3	Interorbital width	74
4	Total length of skull	73
5	Height of rostrum behind canine teeth	58
6	Greatest width of foramen infraorbitale	74
7	Condylo-basal length of skull	74
8	Height of supraoccipitale	23
9	Width of nasal orifice	71
10	Shortest distance between bullae osseae	53
11	Basilar length of skull	73
12	Height of skull in region of hard palate	58
13	Length of upper carnassial tooth	74
14	Length of upper row of teeth	74
15	Width of bullae osseae	74
16	Rostral width	73
17	Postorbital width	73
18	Height of nasal orifice	74
19	Width of middle part of ossa palatina	58
20	Height of foramen magnum (occipital foramen)	55
21	Width of supraoccipitale	24
22	Width between supraorbital processes	72
23	Length of bullae osseae	74
24	Length of cranial capsule	70
25	Height of skull in region of bullae osseae	73
26	Zygomatic width	72
27	Mastoid width	74
28	Width of foramen magnum	57
29	Width of skull between foramen infraorbitale	59
30	Facial length	74
31	Length of hard palate	74
32	Height of mandible [coronoid process]	59

Measurements of Male Skulls

Table 1 (continued)

	Range (pim)[a]	Mean value (M)	Standard error of mean (m)	Standard deviation of series (σ)	Coefficient of variation C (in %)	Mean error of coefficient (mc)
1	4.0- 9.0	7.13	±0.013	1.012	14.20	±1.330
2	4.9- 6.6	5.22	±0.018	0.122	2.34	±0.215
3	8.8-10.9	9.69	±0.022	0.190	1.94	±0.159
4	39.8-45.0	42.96	±0.083	0.716	1.64	±0.013
5	6.1- 8.1	7.14	±0.014	0.114	1.60	±0.148
6	2.6- 4.0	3.05	±0.000	0.004	1.31	±0.107
7	39.3-45.3	42.67	±0.064	0.548	1.28	±0.105
8	4.4- 7.3	5.22	±0.012	0.060	1.16	±0.171
9	3.7- 5.0	4.38	±0.005	0.046	1.07	±0.081
10	3.0- 4.9	3.55	±0.005	0.036	1.01	±0.092
11	35.5-41.4	37.37	±0.129	0.315	0.84	±0.069
12	10.0-12.2	10.90	±0.011	0.088	0.81	±0.077
13	4.0- 5.2	4.37	±0.040	0.346	0.79	±0.006
14	10.6-13.2	11.36	±0.009	0.084	0.74	±0.060
15	7.0- 9.6	8.19	±0.005	0.050	0.62	±0.050
16	7.3- 9.9	8.52	±0.005	0.051	0.60	±0.049
17	8.9-11.3	10.10	±0.006	0.058	0.57	±0.047
18	4.0- 5.1	4.65	±0.004	0.042	0.57	±0.047
19	4.5- 5.9	4.99	±0.003	0.028	0.56	±0.051
20	5.1- 7.0	5.91	±0.003	0.029	0.49	±0.046
21	14.4-16.9	15.59	±0.014	0.070	0.45	±0.065
22	10.6-12.9	11.70	±0.005	0.047	0.40	±0.033
23	13.0-15.9	14.39	±0.006	0.055	0.39	±0.062
24	25.5-30.5	28.14	±0.121	0.101	0.35	±0.029
25	14.2-16.9	15.54	±0.006	0.054	0.35	±0.028
26	21.0-24.4	22.40	±0.003	0.072	0.32	±0.108
27	19.1-21.6	20.21	±0.005	0.050	0.24	±0.019
28	6.9- 8.6	7.59	±0.001	0.015	0.19	±0.010
29	9.8-11.2	10.60	±0.002	0.017	0.16	±0.014
30	9.0-11.0	10.05	±0.001	0.013	0.13	±0.108
31	14.5-17.8	16.19	±0.001	0.042	0.07	±0.006
32	9.4-11.1	10.24	±0.006	0.045	0.40	±0.033

(a) derivation of this abbreviation not given – Ed.

TABLE 2. Measurements of Female Skulls

Serial No.	Location of measurement	Number of measure-ments (n)
1	Length of upper carnassial tooth	29
2	Height of skull in region of hard palate	29
3	Shortest width between bullae osseae	27
4	Greatest distance between bullae osseae	27
5	Height of rostrum behind canine teeth	28
6	Width of nasal orifice	27
7	Height of upper canine teeth	29
8	Width of middle part of ossa palatina	29
9	Greatest width of foramen infraorbitale	29
10	Height of skull in region of bullae osseae	29
11	Postorbital width	29
12	Interorbital width	29
13	Width of bullae osseae	28
14	Rostral width	29
15	Length of upper row of teeth	29
16	Height of nasal orifice	28
17	Width of foramen magnum	28
18	Height of mandible [coronoid process]	29
19	Facial length	29
20	Width of skull between foramen infraorbitale	29
21	Length of hard palate	29
22	Height of foramen magnum	27
23	Length of bullae osseae	29
24	Total length of skull	29
25	Condylo-basal length	28
26	Basilar length of skull	27
27	Length of cranial capsule	29
28	Mastoid width	29
29	Width between supraorbital processes	29
30	Zygomatic width	26

Measurements of Female Skulls — Table 2 (continued)

	Range (pim)[a]	Mean value (M)	Standard error of mean (m)	Standard deviation of series (σ)	Coefficient of variation C (in %)	Mean error of coefficient (mc)
1	3.4- 4.1	3.84	±0.018	0.061	1.60	±0.210
2	8.9-10.0	9.41	±0.022	0.120	1.27	±0.166
3	2.3- 3.8	3.00	±0.006	0.033	1.10	±0.075
4	5.0- 7.9	6.69	±0.011	0.062	0.93	±0.126
5	5.2- 7.0	6.06	±0.009	0.050	0.82	±0.110
6	3.1- 4.1	3.81	±0.005	0.028	0.76	±0.010
7	4.0- 5.1	4.56	±0.006	0.034	0.75	±0.098
8	3.7- 4.7	4.14	±0.005	0.028	0.68	±0.089
9	3.4- 3.1	2.83	±0.003	0.020	0.68	±0.089
10	12.7-14.5	13.41	±0.015	0.081	0.61	±0.080
11	8.2-10.0	9.17	±0.009	0.051	0.56	±0.073
12	7.4- 8.9	8.09	±0.007	0.043	0.53	±0.070
13	6.3- 7.8	7.14	±0.006	0.036	0.51	±0.069
14	6.5- 7.6	6.94	±0.006	0.036	0.51	±0.066
15	9.0-10.5	9.73	±0.007	0.042	0.44	±0.005
16	3.5- 4.2	3.93	±0.003	0.017	0.44	±0.058
17	6.2- 7.5	6.87	±0.005	0.030	0.43	±0.057
18	8.1- 9.4	8.76	±0.006	0.037	0.42	±0.055
19	7.7- 9.0	8.48	±0.016	0.034	0.41	±0.053
20	8.0- 9.4	8.95	±0.006	0.033	0.38	±0.049
21	13.0-15.0	13.68	±0.008	0.046	0.34	±0.044
22	4.8- 6.8	5.68	±0.003	0.016	0.28	±0.038
23	11.9-13.9	12.80	±0.005	0.030	0.23	±0.032
24	36.3-39.0	37.77	±0.076	0.090	0.23	±0.030
25	36.4-39.0	37.44	±0.015	0.083	0.22	±0.029
26	32.2-35.0	33.70	±0.012	0.077	0.22	±0.039
27	24.8-27.3	25.93	±0.009	0.051	0.20	±0.053
28	17.7-19.0	18.24	±0.005	0.025	0.19	±0.025
29	9.6-11.2	10.59	±0.002	0.012	0.12	±0.015
30	18.4-20.0	19.40	±0.002	0.013	0.06	±0.210

(a) derivation of this abbreviation not given – Ed.

The ermine and, in particular, its subspecies (such as the Shantar ermine, which forms the subject of this investigation) are distinguished by their small size, and in general they have no clearly defined age-related features in skull structure and moulding or, in particular, features characteristic of the senile stage, such as are found in the brown bear (Ursus arctos L.) and the badger (Meles meles L.), apart from those distinguishing the juvenis from the adultus stage. As has been said already, the cranial sutures unite early and they quickly lose their sharpness of outline and become difficult to distinguish. The crista sagittalis is generally very poorly developed in the ermine and, as it is most clearly identifiable in the occipital part of the skull, it often comes to resemble a slight ridge. The presence of a sagittal crest, of powerfully developed, concentric, wave-like prominences on the lateral surfaces of the cranial capsule, and of a firm, smooth and, sometimes, an apparently polished surface of the bones forming it are, considered together, reliable features distinguishing the skulls of the adultus and senex stages of the ermine from those of the subadultus (less than 1 year old) stage. In the latter group, because of incomplete ossification, the surface of the cranial capsule is rough and porous, and the concentric prominences are poorly developed. The postorbital constriction, taken by itself, is a less reliable characteristic of age because of its very small variation. Wearing down of the teeth, especially the upper canine teeth, is a feature of old age. The canines are commonly asymmetrical: one canine is much more worn than the other. This may be explained by the ermine's habit of tearing pieces of meat off its prey, biting into it not with its incisors (which are weak in the ermine), but with its carnassials,(a) as may be observed in ermine in captivity. Hence, both the relative asymmetry in size of the canines (e.g. 3.8 and 5.0) and the degree of wear reflect the age of the animal. With the aid of this group of characteristics it was possible to distinguish, among the total number of 74 male ermine skulls, a

(a) the implication seems to be that use of the carnassials on one side more than the other would also cause more wear on the canines of that side - Ed.

group of 20 (i.e. one-third of the total number caught) belonging to adult and old (adultus and senex) males.

This ratio between adultus and subadultus stages is typical of a collection of skulls obtained by commercial trapping methods. Approximately the same results were obtained for the Siberian polecat, Putorius eversmanni Les. in Nizhnevolzhskii krai (Lower Volga Territory) by Kozlov (1931, 14), namely, 5:2.

A diagram of the monthly distribution(a) of the male ermine caught revealed a definite predominance of animals aged from 7 to 9 months in the material studied; the curve was bimodal, with two distinct maxima at the ages of 7 and 9 months respectively. The same results, broken down for periods of 2 weeks, gave a multimodal curve with three principal maxima at the ages of 7.5, 8.5 and 9.5 months. These results, when compared with the variance curves for the selected characteristics, show that, despite the considerable individual variation observed in some cases, the structure of the variance curves does express the character and degree of age variation, although not clearly or accurately enough to allow a diagnosis to be made on statistical grounds. The fact that most of the curves are asymmetrical, and have a clearly defined single maximum, strengthens this conclusion. The sharp-pointed peak in the [variance] curves corresponds to the predominance of ermine aged 7-9 months in the material, with very small differences in their age characteristics. The coincidence between the peaks [of the variance curves] for some statistics (length of the upper carnassial, smallest width between the bullae osseae), and the unilateral asymmetry of these curves, also indicate a small degree of variation in the skull in general, as is clear from the results given in the tables.

Age variation is also seen in the relationships [ratios] between the dimensions of the individual craniological features. The method of comparing the measurements suggested recently by Paramonov (1932, 5), with slight modifications, was used for this purpose. The measurements taken for

(a) i.e. a frequency distribution histogram of age classes - Ed.

the formula were as follows :

I. Total length of the skull

II. Basilar length of the skull

III. Length of the hard palate

IV. Distance from anterior border of the foramen occipitale magnum to beginning of hard palate (i.e. difference between II and III).

V. Length of upper row of teeth

VI. Interorbital width

VII. Postorbital width

VIII. Zygomatic width

IX. Mastoid width

X. Height of skull in region of bullae osseae.

The total length [I] is taken as 100% and all the other characteristics calculated as percentages of it.

While it is recognised that Paramonov's suggestion, that the proportions of the skull be expressed as percentages of its total length, is very valuable, it was decided not to express these results as a special formula. The reasons for this decision are as follows: the formula, in the form in which it was suggested by Paramonov, does not make comparison of the data any easier, and the brackets and signs of mathematical manipulations, inserted by convention, simply obscure and complicate the true meaning. Our results are given in Table 3. The first group includes adultus and senex males of the Shantar ermine, the second group includes subadultus males of the same subspecies, and the third group consists of senex male ermine of other subspecies.

It can be seen from these results that, with age, the length of the hard palate increases, and there is a corresponding decrease in the difference between this value and the distance between the anterior border of the foramen occipitale magnum and the beginning of the hard palate. There

TABLE 3. Variation with age in the ratios of certain skull measurements (see text)

No. (a)	Subspecies	Sex and age of group	I (100%)	II	III	IV	V	VI	VII	VIII	IX	X	Difference between III and IV
657	*Mustela erminea baturini* Ogn.	♂ senex	41	92.6	37.8	52.3	27.4	22.5	22.2	52.4	46	36	14.7
726		♂ adultus	42.4	92.8	39.2	53.3	26.4	23.3	21.1	52.3	46.6	36.4	14.1
735		♂ adultus	43.5	90.9	39.5	51.3	27.9	23.4	23.2	53.2	49.5	35.1	11.8
736		♂ adultus	44.5	92.9	40.4	52.9	27.2	23.1	22.7	53.6	47.9	34.3	12.5
603		♂ subadultus (6 mths)	43	90.4	37.7	53	28	22	23.2	52.5	46.6	38.8	16.3
632		♂ subadultus (7 mths)	41.1	94.6	38.7	55.8	26.8	22.4	24.6	53.1	49.5	37	17.1
669		♂ subadultus (8 mths)	42.7	90.9	37.8	53	26.6	23.5	25.9	52.1	48	35.1	15.2
689		♂ subadultus (9 mths)	42.7	92.8	38	54.7	26.4	23	23.5	53.3	47.8	37.1	16.7
708		♂ subadultus (9 mths)	40.9	88.7	36.2	52.5	27.5	24.7	22.2	53	50.5	36.2	16.3
16	*M. erminea* Merriam (Kamchatka)	♂ senex	49	91.6	40.8	50.8	27.1	23.7	21.4	53.8	48.3	35.1	10.0
1	*M. erminea ognevi* Yurgenson (R. Maz)	♂ senex	49	90	40.6	48.9	26.8	24	20.2	57.1	49.7	37.1	8.3
2111	*M. erminea aestiva* Kerr. (Delta of R. Volga)	♂ senex	50.1	89.8	41	48.7	28	25.8	20.4	–	48.6	40	7.7

(a) Catalogue number See p.43. - Ed.

is also a small increase with age in the interorbital width, together with a decrease in the width of the postorbital constriction. However, these results are not strictly regular in character and they contain some deviations. This applies even more forcefully to the height of the skull in the region of the bullae osseae, which has a tendency to decrease with age. It is most probable that racial variation within the species has some influence on the differences in the skull proportions of the third group. Be that as it may, these features taken independently are of no diagnostic importance.

It must also be ascertained whether the proportions of the skull undergo analogous changes in the different subspecies. As a provisional estimate it could be taken that the differences between items III and IV of the formula in the subadultus stage of the Shantar ermine Mustela erminea baturini are greater than 15.0. For greater convenience in the practical application of the table, it can be reduced further in size by removing columns V, VIII and IX; column V of the table will be the difference between the results given in its columns III and IV.

CONCLUSIONS

To make possible a craniological analysis of a mass commercial catch of ermine, in most cases it is necessary to know the sex ratio of the material, and to determine the numerical proportions of the three chief age groups : under 1 year old (subadultus), adult (adultus) and old (senex). If the material is labelled (meaning material from the same district), the sex ratio is determined without difficulty. If not, by knowing the range of measurements of the principal variates (obtained on large series of skulls, of course) of a given subspecies, the material can be arranged in sexes (♂ and ♀) without serious error by classifying on characters which do not overlap, or do so only slightly, between the sexes. In doubtful cases the age characteristics of skull structure can be helpful, for the

dimensions of old females often coincide with those of subadult males. Then there remains only the risk of classifying a very small adult, or even old male skull, as a female.

Next, by using a combination of surface and structural features (the appearance of the surface of the bones, and development of the crests and prominences), the adultus and senex groups can be distinguished. In doubtful cases the shortened table will have to be used, especially if material, however small, for the particular subspecies is available for comparison. Senex skulls can easily be determined by the state of the teeth, especially the canines. Severe wearing down of the premolar and molar teeth indicates extreme old age in the ermine. Wearing down of only the canines indicates a younger animal, and its degree depends on age. Wearing down of the canines because of old age must be distinguished from injury to the teeth resulting from attempts to bite their way out of the trap, snare, cage, etc.

Finally, if the material is labelled and the dates of trapping are given, the age of the animals in the subadult group can be estimated with an accuracy of less than 1 month.

It can be concluded from this brief analysis of the material available for study, that the existing diagnoses of subspecies are very inaccurate, for even if they are based on large series of skulls, the age composition of the series is heterogeneous. True geographical variation can be established only in material homogeneous with respect to age, and diagnoses of each age group of the subspecies to be described must be given.

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SEXUAL DIMORPHISM IN THE SKULL OF *Mustela erminea* L.

(O polovom dimorfizme cherepa gornostaya (*Mustela erminea* L.))

by

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The stoat is one of the most important fur-bearing animals in the Soviet Union, and Soviet zoologists have accordingly paid great attention to it (N.M. Berger 1940, N.D. Grigor'ev 1938, I.V. Zharkov 1941, Yu. N. Klimov 1940, N.P. Lavrov 1939, 1941a, 1941b, 1943, 1944a, 1944b, A.A. Nasimovich 1948, 1949, S.I. Ognev 1928, 1929, 1935, V.A. Popov 1943a, 1943b, 1947, S.U. Stroganov 1937, V.P. Teplov 1948, V.I. Tikhvinskii 1937, 1939, N.I. Chertkov 1947, S.V. Shibanov 1935, P.B. Yurgenson 1931, 1932, 1933, 1936). However, despite so much research, no detailed analysis of intraspecific variation in the stoat is to be found in the literature.

A comprehensive study of the intraspecific variation of the stoat is essential for several practical reasons, e.g. to determine the age structure of stoat populations, and to establish methods to forecast future "yields" in different regions, and standards for pelts, etc., as well as being interesting for its own sake.

An analysis of intraspecific variation in a species is impossible without a survey of the morphological characteristics (body proportions, structure of the skeleton, dimensions of the claws, character of the coat and so on) in different parts of its range. To obtain reliable results, series of specimens from different districts must be compared. Unfortunately, investigation of the postcranial skeleton and of the soft parts is hampered by the absence of sufficient suitable material (skeletons and carcasses) in collections. But, as a rule, collections of skulls are much more numerous, although, in analysis of intraspecific variation in skulls,

differences due to sex and age must be taken into account.

A special investigation of the [variations in] dimensions and shape of the skull in male and female stoats was undertaken. In all, about 1,500 skulls of stoats were used, from different parts of the Soviet Union. In order to define and record the age and sex differences in the skulls, 33 measurements were taken from each one: 13 along the longitudinal, 13 along the transverse, and 7 along the vertical axis.

To study the sexual dimorphism in the skulls, extensive use had to be made of material from existing collections. Here it should be mentioned that in the opinion of some zoologists (for example, V.P. Teplov 1948), the percentage of males in collections of stoats made by trappers does not reflect the actual sex ratio in nature.(a) The problem of the sex ratio in stoats in their natural environment has not yet been completely solved.

Many specialists consider that the number of male and female stoats found in nature is about equal (D.I. Aspisov and V.A. Popov 1940; A.A. Nasimovich 1948; V.A. Popov 1947, V.P. Teplov 1948). M.D. Zverev (1931), who examined 1734 stoats from Western Siberia, reports 53% of males and 47% of females. Yu.N. Klimov (1940) found 56.1% males (43.9% females) among 506 stoats from the Novosibirsk region and the Altai Province, and 58.5% males (41.5% females) among 1603 pelts obtained from the Kuibyshev district (Novosibirsk region).

These investigators attribute the excess of males in collections obtained from commercial organisations to the fact that female stoats are more cautious and less active. According to V.E. Ushakov (1930), in winter sometimes whole groups, consisting of large males only, have been caught. Whereas fewer females than males are caught at the beginning of winter, by the end of the trapping season this situation is reversed : some writers therefore believe that the sex ratio largely reflects the degree of commercial exploitation of the stock. The percentage of females collected rises with increasing exploitation, and vice versa.

(a) See p. 98. - Ed.

Conversely, P.B. Yurgenson (1932) considers that the number of newborn males may exceed the number of females. S.I. Ognev (1935) states that only one female is born to about every three males. According to N.P. Lavrov (1944a), generally there is no difference between the sexes in activity; nor are males trapped in preference to females. Having examined more than 1600 carcasses of stoats from different parts of the Soviet Union, Lavrov concludes that males predominate everywhere. In his opinion, this disproportion is a "biologically advantageous characteristic acquired by the species in the course of evolution" (p.146), and as a result of it nearly all the females become fertilised despite the fact that more females than males take part in the rut.(a) The reason for this is that females become sexually mature a year sooner than males, and the proportion of stoats [both sexes] less than one year old at the time of the rut is about 60%.

Sometimes, more females are caught than males. Citing a statement by V.V. Bunak (1938), Lavrov tries to account for this by assuming that, when embryos are resorbed, during unfavourable conditions (e.g. periods of insufficient food), male embryos die first: hence, in subsequent years in that place, females will outnumber males.

There is no material to test Lavrov's (1944a) conclusion. However a special investigation has been described by V.P. Teplov (1948). From personal observations in natural surroundings, Teplov concludes that the higher percentage of males caught by commercial trappers does not reflect the actual ratio between the sexes, but it is the result of biological (including nutritional) differences between them. He observed that the two sexes do differ in their activity: in winter female stoats spend a large part of their time in burrows beneath the snow, while males forage on the surface of the snow. Consequently, according to observations at the beginning of the winter, the proportion of males is 55-60%, while when the snow is deep, it rises to 70-80%.

These striking differences in the biology of the two sexes are

(a) See p. 78

associated by Teplov with the feeding habits of the females; they eat many more small mammals, which rarely emerge on to the surface of the snow, than do the males. In the stomachs of the females, for instance, voles and shrews account for 98% of the species found: in those of males not more than 88%. Only in years when the supplies of food underneath the snow run low does the percentage of females caught by commercial trappers rise; then the sex ratio of the collections tend toward unity.

In my view, the statements made by Teplov (1948) merit attention. They also confirm my own observations that, in winter the claws of females, which more frequently enter the subnivean burrows of rodents, grow relatively longer than those of males. In summer the length of the claw on the middle digit of the female forelimb is 86.5% of the length of the claw in the male, while in winter this figure rises to 95%.

The sex ratio and number of skulls investigated are shown in Table 1.

TABLE 1. Skulls of stoats investigated

	Age group *												Total	
	I		II		III		IV		V		VI			
	n	%	n	%	n	%	n	%	n	%	n	%	n	%
Males	404	60.5	343	75.7	185	79.0	45	78.9	5	62.5	2	100	984	69.2
Females	264	39.5	110	24.3	49	21.0	12	21.1	3	37.5	-	-	438	30.8
Total	668	100	453	100	234	100	57	100	8	100	2	100	1422	100

* The following age groups are distinguished: (I) from 0.5 to 1 year; (II) from 1 to 2 years; (III) from 2 to 3 years; (IV) from 3 to 4 years; (V) from 4 to 5 years; (VI) from 5 to 6 years- Author

It must be emphasised that the skulls examined were collected from widely separated districts, and that in different parts of the range of the stoat, the sex ratio varies considerably. The obvious nonhomogeneity of

the material prevented a more detailed examination of the sex ratio of different age groups.

The two sexes differ in the structure of the body and skeleton, and also in the size of the skull. Parallel curves(a) were drawn to compare the skulls of each in respect of each variate : see, for example, that for the condylobasal length (Fig.1). However, the analysis of such curves contributed very little to understanding the sexual dimorphism of the skull, for, in every variate measured, the extreme maximal values in the females exceeded the extreme minimal values of the corresponding measure-

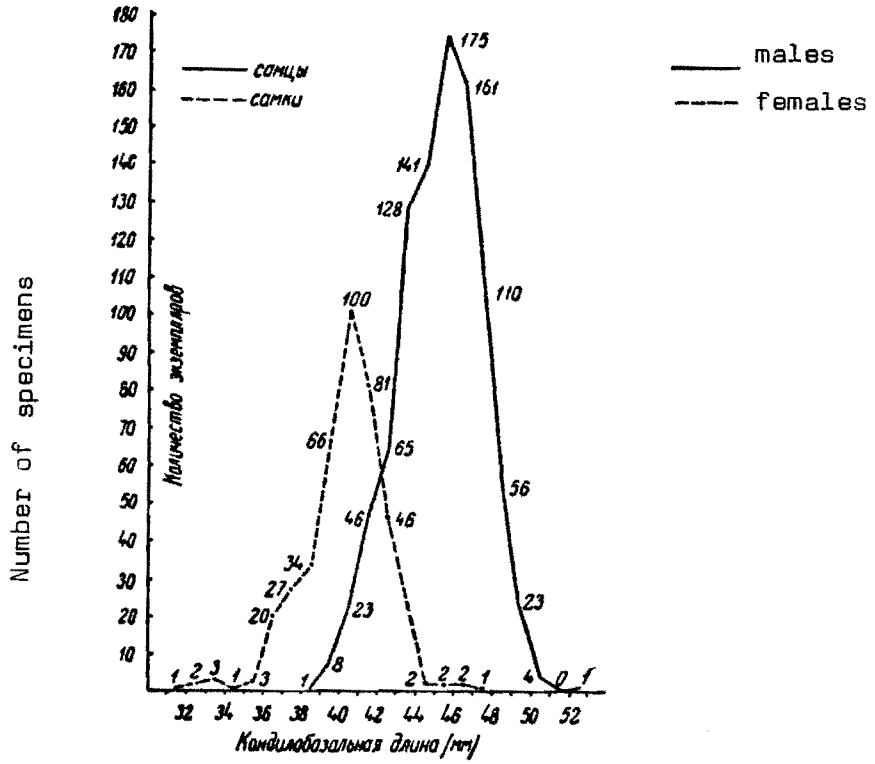


Fig.1. Differences between condylobasal length of skulls of male and female stoats

ment in the males. This will easily be seen if the range of measurements of each feature in the two sexes in Tables 2 and 3 are compared. Clearly, it is not possible, by analysis of collections obtained from different areas, to specify craniological measurements whose limits would not be

(a) Presumably frequency distribution curves - Ed.

transgressed by one sex or the other.

P.B. Yurgenson (1933), who examined the sexual dimorphism of the Shantar stoat, found, however, that the male skull can be distinguished from the female skull in several features, either non-transgressive (total, basal and condylobasal length) or contiguous (facial length, zygomatic width, mastoid width, height of the skull in the region of the hard palate, and so on).(a) Most measurements of the skull (14 of 30) in the series which he investigated had a slight tendency towards transgression, and only a few (length of the tympanic bullae, the distance between them, height of the skull behind the canine teeth, width between the supraorbital processes, and height of the foramen magnum) showed considerable overlap of the extreme values.

It is possible that, in the stoat, there is regional variation in the degree of sexual dimorphism of the absolute dimensions of the skull. However, in order to discover why Yurgenson (1933) reached different conclusions from my own, it is necessary to analyse differences between the craniological features of males and females in collections from different parts of the Soviet Union.

To begin with, following Yurgenson I repeated the investigation of specimens of the Shantar stoat, and proved to my satisfaction that in this series there definitely is a very clearly marked sexual dimorphism of the absolute dimensions of the skull (Table 4). However, a more careful study suggested that the extent of the sexual dimorphism in the Shantar collection is influenced by the nature of the sample.

In the first place, the series is relatively small (103 skulls in Yurgenson's study and 109 in mine), and if it were enlarged, the range of measurements for some variates might widen. Secondly, differences in the age ratios of the two sexes are very noticeable: whereas 31 of the 71 male skulls belonged to animals more than a year old, 35 of the 38 female skulls belonged to semi-adult specimens. In other words, in my material

(a) See p.39

TABLE 2. Skull dimensions of male stoats

No.	Dimensions	Age in years	Number of specimens	Range	Arithmetic mean
1	Basilar length	(0.5–1	384	34.7–45.5	39.81
		(1 –6	548	35.5–47.4	41.39
2	Condylobasal length	(0.5–1	385	38.6–50.0	44.31
		(1 –6	557	39.5–52.5	45.91
3	Length of hard palate	(0.5–1	397	14.4–20.8	17.33
		(1 –6	569	15.1–21.7	18.16
4	Length of interpterygoid fossa	(0.5–1	361	5.2– 8.0	6.44
		(1 –6	510	5.5– 8.6	6.69
5	Length from foramen magnum to hard palate	(0.5–1	382	19.5–25.2	22.51
		(1 –6	549	20.1–25.9	23.18
6	Length of tympanic bulla	(0.5–1	394	12.4–16.1	14.34
		(1 –6	575	12.5–16.6	14.71
7	Length of upper row of teeth	(0.5–1	404	9.5–15.1	11.90
		(1 –6	580	10.4–14.1	12.37
8	Length of lower row of teeth	(0.5–1	373	11.8–17.4	14.96
		(1 –6	552	12.8–17.8	15.61
9	Length of upper canine tooth	(0.5–1	404	3.6– 5.5	4.41
		(1 –6	581	3.6– 5.8	4.56
10	Length of upper molar tooth	(0.5–1	401	1.1– 2.5	1.70
		(1 –6	577	1.1– 2.5	1.76
11	Length of lower canine tooth	(0.5–1	391	4.0– 6.2	5.07
		(1 –6	569	4.1– 6.3	5.25
12	Rostral width	(0.5–1	405	6.7–10.9	8.86
		(1 –6	580	7.2–11.2	9.37
13	Interorbital width	(0.5–1	401	8.4–12.8	10.53
		(1 –6	574	8.3–13.0	11.10
14	Width between ends of supraorbital processes	(0.5–1	393	10.2–15.7	12.72
		(1 –6	562	10.8–16.2	13.37
15	Postorbital width	(0.5–1	395	8.8–12.8	10.59
		(1 –6	570	7.8–12.7	10.59
16	Zygomatic width	(0.5–1	337	20.2–28.4	24.37
		(1 –6	504	20.0–30.2	25.60
17	Mastoid width	(0.5–1	389	17.5–25.0	21.40
		(1 –6	558	18.4–26.4	22.28
18	Auricular width	(0.5–1	388	18.4–23.7	20.79
		(1 –6	557	18.2–23.0	20.96
19	Width of hard palate	(0.5–1	399	10.7–15.7	13.45
		(1 –6	577	11.5–16.9	13.98
20	Width of tympanic bullae	(0.5–1	395	6.2– 9.9	7.78
		(1 –6	574	6.4– 9.4	8.02
21	Width of nasal aperture	(0.5–1	390	3.8– 5.8	4.63
		(1 –6	561	4.0–6.1	4.84

Table 2 (continued)

No.	Dimensions	Age in years	Number of specimens	Range	Arithmetic mean
22	Width of foramen magnum	(0.5-1	375	6.4- 9.2	7.86
		(1 -6	553	6.7- 9.5	8.04
23	Width of infraorbital foramen	(0.5-1	394	1.7- 4.1	2.95
		(1 -6	565	2.0- 4.1	3.02
24	Greatest width of upper molar tooth	(0.5-1	401	2.7- 4.7	3.48
		(1 -6	579	2.7- 4.5	3.61
25	Diameter of upper canine tooth	(0.5-1	376	1.0- 2.5	1.80
		(1 -6	550	1.2- 2.7	1.89
26	Diameter of lower canine tooth	(0.5-1	385	1.3- 3.1	2.16
		(1 -6	556	1.3- 3.3	2.27
27	Facial height of skull [at rostrum?]	(0.5-1	399	9.5-14.0	11.83
		(1 -6	575	9.8-14.9	12.25
28	Height of skull in region of tympanic chambers	(0.5-1	387	14.2-20.3	17.09
		(1 -6	554	14.0-20.4	17.41
29	Occipital height	(0.5-1	377	9.6-13.2	11.31
		(1 -6	549	8.8-13.8	11.64
30	Height of nasal aperture	(0.5-1	389	4.7- 7.3	5.99
		(1 -6	557	5.0- 7.6	6.30
31	Height of foramen magnum	(0.5-1	376	5.2- 7.2	6.14
		(1 -6	544	5.1- 7.4	6.21
32	Height of upper canine tooth	(0.5-1	357	3.9- 7.4	5.60
		(1 -6	383	3.8- 7.8	5.80
33	Height of lower canine tooth	(0.5-1	373	3.1- 6.3	4.90
		(1 -6	441	3.1- 6.8	5.00

TABLE 3. Skull dimensions of female stoats

No.	Dimensions	Age in years	Number of specimens	Range	Arithmetic mean
1	Basilar length	(0.5-1	247	29.0-41.0	35.84
		(1 -5	165	33.0-42.3	36.97
2	Condylobasal length	(0.5- 1	249	32.0-44.9	39.81
		(1 -5	166	36.7-47.4	41.18
3	Length of hard palate	(0.5-1	257	11.6-17.8	15.26
		(1 -5	173	13.0-19.0	15.91
4	Length of interpterygoid fossa	(0.5-1	231	5.0- 7.1	5.88
		(1 -5	154	5.3- 7.4	6.05
5	Length from foramen magnum to hard palate	(0.5-1	246	17.2-23.2	20.56
		(1 -5	165	19.0-24.0	21.09

Table 3 (continued)

No.	Dimensions	Age in years	Number of specimens	Range	Arithmetic mean
6	Length of tympanic bulla	(0.5–1	263	11.5–14.6	13.02
		(1 –5	170	11.5–15.2	13.38
7	Length of upper row of teeth	(0.5–1	264	7.7–13.3	10.57
		(1 –5	174	9.2–13.1	10.97
8	Length of lower row of teeth	(0.5–1	242	11.0–15.4	13.23
		(1 –5	162	11.1–16.6	13.79
9	Length of upper canine tooth	(0.5–1	263	3.0– 4.8	3.94
		(1 –5	174	3.1– 5.0	4.08
10	Length of upper molar tooth	(0.5–1	263	0.9– 1.9	1.39
		(1 –5	174	1.0– 2.2	1.45
11	Length of lower canine tooth	(0.5–1	256	3.5– 5.7	4.53
		(1 –5	170	3.8– 5.8	4.71
12	Rostral width	(0.5–1	565	5.9– 9.1	7.64
		(1 –5	171	6.2–10.4	7.98
13	Interorbital width	(0.5–1	262	6.5–11.0	9.14
		(1 –5	171	7.4–11.8	9.61
14	Width between ends of supraorbital processes	(0.5–1	258	7.5–13.8	11.22
		(1 –5	168	8.9–14.2	11.64
15	Postorbital width	(0.5–1	258	6.8–11.9	9.96
		(1 –5	169	7.6–12.5	9.80
16	Zygomatic width	(0.5–1	201	15.4–25.2	21.45
		(1 –5	136	18.8–26.9	22.39
17	Mastoid width	(0.5–1	248	14.7–22.2	19.11
		(1 –5	164	17.0–22.9	19.73
18	Auricular width	(0.5–1	248	14.6–21.8	19.04
		(1 –5	165	16.5–21.8	19.17
19	Width of hard palate	(0.5–1	259	9.2–14.0	11.93
		(1 –5	174	10.0–15.1	12.40
20	Width of tympanic bulla	(0.5–1	259	5.1– 8.2	6.87
		(1 –5	170	5.9– 8.5	7.12
21	Width of nasal aperture	(0.5–1	254	2.9– 4.9	3.96
		(1 –5	166	3.5– 5.3	4.16
22	Width of foramen magnum	(0.5–1	249	5.7– 8.4	7.10
		(1 –5	163	6.2– 8.8	7.25
23	Width of infraorbital foramen	(0.5–1	260	2.0– 3.6	2.72
		(1 –5	170	1.7– 3.6	2.77
24	Greatest width of upper molar tooth	(0.5–1	261	2.4– 3.8	3.04
		(1 –5	174	2.3– 4.0	3.15
25	Diameter of upper canine tooth	(0.5–1	244	1.1– 2.0	1.46
		(1 –5	155	1.1– 2.1	1.54
26	Diameter of lower canine tooth	(0.5–1	243	1.2– 2.7	1.83
		(1 –5	161	1.3– 3.1	1.91

Table 3 (continued)

No.	Dimensions	Age in years	Number of specimens	Range	Arithmetic mean
27	Facial height of skull [at rostrum?]	(0.5–1	261	7.8–12.7	10.61
		(1 –5	174	8.4–13.3	10.84
28	Height of skull in region of tympanic chambers	(0.5–1	250	11.3–19.8	15.16
		(1 –5	161	12.0–18.9	15.31
29	Occipital height	(0.5–1	248	7.5–12.7	10.23
		(1 –5	164	7.8–12.5	10.42
30	Height of nasal aperture	(0.5–1	252	3.8– 6.4	5.26
		(1 –5	166	4.5– 6.7	5.47
31	Height of foramen magnum	(0.5–1	246	4.0 – 7.0	5.60
		(1 –5	161	4.9– 7.0	5.74
32	Height of upper canine tooth	(0.5–1	237	3.5– 6.4	4.64
		(1 –5	113	2.6– 6.9	4.73
33	Height of lower canine tooth	(0.5–1	238	3.1– 5.9	4.02
		(1 –5	139	2.8– 5.7	4.08

skulls of relatively young females and of adult males were more numerous. Hence, variation due to sex and age were superimposed, exaggerating the difference in the absolute skull sizes in the two sexes. V.A. Popov (1947), who investigated a collection from the Volga-Kama district which was only slightly more numerous, although more homogeneous in its age composition, could find only three good indices (condylobasal length, mastoid width, and length of the upper row of teeth) on which to distinguish the sexes: but even in these, the ranges overlapped.

To test my hypotheses regarding the importance of age structure and sample size in the study of sexual dimorphism, I investigated large collections of the Turukhan stoat (785 specimens from the right bank of the Tazovskaya Guba, Gydanskii Peninsula, the banks of the Enisei River, and the left bank of the Khatanga River). This analysis showed that the ranges of all the skull measurements in males and females were transgressive. There were no features which were not transgressive, variable, or even slightly transgressive (Table 5).

TABLE 4. Differences between measurements of skulls of male and female Shantar stoats (*M. erminea baturini* Ogn.)

No.	Dimensions	Males (71 skulls)		Females (38 skulls)	
		range	mean	range	mean
1	Basilar length	35.0–40.2	37.75	31.2–34.6	33.22
2	Condylobasal length	39.2–44.6	42.12	35.0–39.0	37.05
3	Length of hard palate	14.5–17.5	15.88	12.5–14.6	13.58
4	Length of interpterygoid fossa	5.2– 7.3	6.37	5.1– 6.8	5.65
5	Length from foramen magnum to hard palate	20.1–23.5	22.0	18.7–21.0	19.63
6	Length of tympanic bulla	12.8–15.3	14.06	11.9–13.2	12.48
7	Length of upper row of teeth	10.2–12.0	11.10	8.9–10.2	9.47
8	Length of lower row of teeth	12.8–14.9	13.81	11.0–12.2	11.71
9	Length of upper canine tooth	3.9– 4.7	3.94	3.0– 3.8	3.41
10	Length of upper molar tooth	1.1– 1.8	1.52	1.0– 1.4	1.20
11	Length of lower canine tooth	4.0– 5.1	4.62	3.7– 4.5	4.00
12	Rostral width	7.2– 8.9	7.90	6.0– 7.2	6.59
13	Interorbital width	8.3–10.0	9.30	7.1– 8.8	7.90
14	Width between ends of supra-orbital processes	10.2–12.7	11.37	8.8–10.8	9.85
15	Postorbital width	8.6–11.2	9.84	7.9–10.0	8.98
16	Zygomatic width	20.6–23.8	21.98	18.2–19.7	18.87
17	Mastoid width	18.0–21.0	19.63	16.0–18.1	17.07
18	Auricular width	18.2–2–.7	19.59	16.4–18.3	17.54
19	Width of hard palate	11.2–13.3	12.29	10.0–11.6	10.72
20	Width of tympanic bulla	6.2– 8.2	7.12	5.5– 6.6	6.10
21	Width of nasal aperture	3.9– 4.8	4.20	2.9– 3.8	3.52
22	Width of foramen magnum	7.1– 8.9	7.71	6.3– 7.4	6.87
23	Width of infraoribtal foramen	2.3– 3.7	2.94	2.3– 3.1	2.67
24	Greatest width of upper molar tooth	2.7– 3.5	3.11	2.4– 3.1	2.69
25	Diameter of upper canine tooth	1.1– 2.0	1.64	1.1– 1.5	1.26
26	Diameter of lower canine tooth	1.5– 2.2	1.89	1.2– 1.9	1.53
27	Facial [rostral?] height of skull	9.6–11.5	10.69	8.7–10.1	9.38
28	Height of skull in region of tympanic bullae	14.0–17.0	15.19	12.0–14.1	13.06
29	Occipital height	8.8–11.1	10.20	7.8–10.1	9.12
30	Height of nasal aperture	5.1– 6.2	5.57	4.3– 5.8	4.76
31	Height of foramen magnum	5.2– 6.5	5.84	4.8– 6.3	5.31
32	Height of upper canine tooth	4.6– 6.3	5.24	3.9– 4.7	4.15
33	Height of lower canine tooth	3.9– 5.6	4.40	2.9– 4.2	3.52

The next step was to compare data on sexual dimorphism of the skull in stoats from different districts of the Soviet Union (Table 6). The results obtained also indicate that the presence or absence of exclusive indices distinguishing males and females is dependent to some extent on the number of specimens examined. Nevertheless, on the whole, sexual dimorphism of the

TABLE 5. Differences between measurements of skulls of male and female Turukhan stoats (M. erminea ognevi Yurg.) (specimens from the right bank of Tazovskaya Guba, Gydanskii Peninsula, the banks of the Enisei River and the left bank of the Khatanga River)

No.	Dimensions	Males (533 skulls)		Females (252 skulls)	
		range	mean	range	mean
1	Basilar length	34.7-45.3	41.04	33.4-42.3	36.73
2	Condylobasal length	38.6-49.8	45.64	37.8-46.7	40.82
3	Length of hard palate	14.6-20.8	18.00	14.0-18.3	15.78
4	Length of interpterygoid fossa	5.3- 8.2	6.57	5.2-7.2	5.89
5	Length from foramen magnum to hard palate	20.1-25.9	23.08	19.3-24.0	20.96
6	Length of tympanic bulla	13.0-16.5	14.67	11.5-15.2	13.34
7	Length of upper row of teeth	10.3-13.8	12.30	9.7-12.2	10.87
8	Length of lower row of teeth	11.8-17.4	15.52	12.1-15.9	13.60
9	Length of upper canine tooth	3.6- 5.3	4.50	3.4- 4.9	4.03
10	Length of upper molar tooth	1.1- 2.5	1.76	0.9- 1.8	1.43
11	Length of lower fanina tooth	4.1- 6.2	5.18	4.0- 5.5	4.61
12	Rostral width	7.3-10.9	9.39	7.0-10.0	7.97
13	Interorbital width	9.1-12.8	11.05	8.3-11.8	9.55
14	Width between ends of supra-orbital processes	11.0-16.1	13.28	9.5-14.2	11.61
15	Postorbital width	8.9-12.5	10.63	8.5-11.7	9.99
16	Zygomatic width	20.0-29.2	25.54	19.4-26.9	22.13
17	Mastoid width	17.5-24.9	22.20	18.0-22.9	19.66
18	Auricular width	18.6-23.7	21.10	17.4-21.8	19.34
19	Width of hard palate	11.5-15.8	13.97	10.8-14.8	12.26
20	Width of tympanic bulla	6.7- 9.4	8.01	6.1- 8.5	7.05
21	Width of nasal aperture	4.0- 5.6	4.79	3.4- 5.2	4.07
22	Width of foramen magnum	6.5- 8.9	7.98	6.5- 8.5	7.39
23	Width of infraorbital foramen	1.7- 4.1	2.96	1.7- 2.6	2.73
24	Greatest width of upper molar tooth	2.7- 4.5	3.60	2.8- 3.8	3.11
25	Diameter of upper canine tooth	1.4- 2.5	1.88	1.1- 2.0	1.50
26	Diameter of lower canine tooth	1.3- 3.0	2.20	1.3- 2.7	1.83
27	Facial [rostral?] height of skull	9.5-14.1	12.26	8.9-12.9	10.89
28	Height of skull in region of tympanic bullae	14.6-20.4	17.61	12.1-18.9	15.51
29	Occipital height	9.6-13.8	11.69	8.6-12.5	10.45
30	Height of nasal aperture	5.0- 7.3	6.21	3.7- 6.7	5.37
31	Height of foramen magnum	5.1- 7.2	6.17	4.8- 6.6	5.65
32	Height of upper canine tooth	3.8- 7.5	5.66	3.5- 6.8	4.61
33	Height of lower canine tooth	3.1- 6.3	4.89	2.8- 5.7	3.96

skull certainly occurs. From all the structural features taken together it is possible to identify the sex of a given specimen. Incidentally, the considerable difference in weight of the skull must be mentioned. According to V.A. Popov (1947), it is on the average 65% heavier in the male than in the female stoat.

With the material at my disposal I attempted to work out the extent of sexual differentiation in the stoat skull, and the structural details of its development in the course of postembryonic development. It was first necessary to calculate the percentage ratio of all the skull variates in females to the corresponding values for the males (Table 7); then the indices obtained for measurements along the longitudinal, transverse, and vertical axes of the skull were set out as diagrams (Figs. 2, 3 and 4).

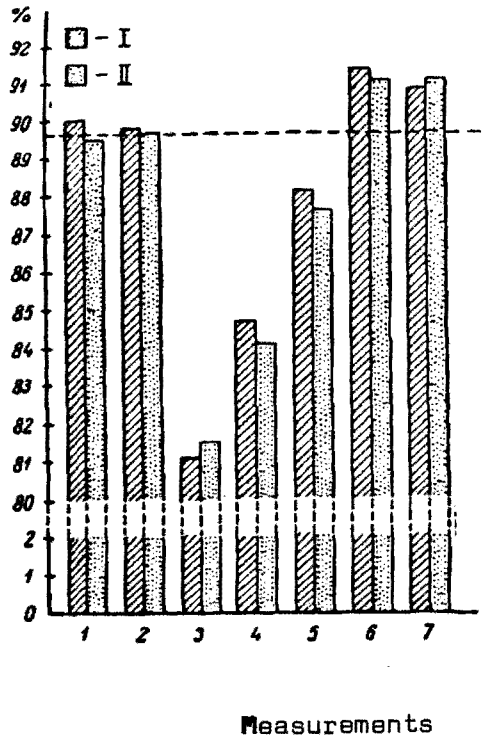


Fig.2 Sexual dimorphism of absolute dimensions along the longitudinal axis of the skull. (I) Ratio of skull dimensions in semi-adult females to those of semi-adult males (in %); (II) the same for adult females and adult males. Measurements: (1) Basilar-length; (2) condylobasal length; (3) diameter of upper canine tooth; (4) diameter of lower canine tooth; (5) length of hard palate; (6) length from foramen magnum to hard palate; (7) length of tympanic bulla. The horizontal broken line shows that the condylobasal length of the female skull is 89.7-89.8% of its length in the male skull.

The table and figures show that the female skull is not just a reduced copy of the male skull, for the ratios between corresponding dimensions are very different in the two sexes. The condylobasal length of the skull in semi-adult females is 89.8% of its length in males. In adults this ratio is 89.7%.

All the remaining features can be divided into two large groups: (a) those in the facial, and (b) those in the cerebral part of the skull. The cerebral part of the skull in the female is only slightly different in its absolute measurements from the cerebral part of the male skull, whereas the differences in the facial region are much more noticeable.

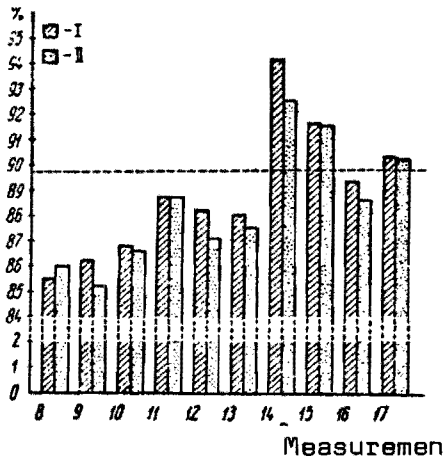


Fig.3. Sexual dimorphism of absolute dimensions along the transverse axis of the skull. (I) Ratio of skull dimensions in semi-adult females to those of semi-adult males (in %); (II) the same for adult females and adult males. Measurements: (8) width of nasal aperture; (9) rostral width; (10) interorbital width; (11) width of hard palate; (12) width between ends of supraorbital processes; (13) zygomatic width; (14) postorbital width; (15) auricular width; (16)mastoid width; (17) width of foramen magnum. The horizontal broken line shows that the condylobasal length of the female skull is 89.7-89.8% of its length in the male skull.

At the same time, these diagrams show that the facial part of the female skull is relatively smaller than that of the male, while the cerebral part is relatively larger. A noteworthy feature in the female is the

particularly small size of the canine teeth, and the length and width of the hard palate, i.e. features associated with the masticatory apparatus.

TABLE 6. Significance of differences between males and females in absolute dimensions of the skull

No.	Groups[(a)]	Number of specimens investigated			Number of measurements whose ranges in males and females :		
		males	females	total	do not transgress	transgress weakly or are only osculatory	transgress strongly
1	Turukhan stoat	533	252	785	-	-	33
2	Kolyma stoat	126	38	164	-	2	31
3	Central Russian stoat	78	36	114	-	-	33
4	Shantar stoat	71	88	109	5	18	10
5	Tobol'sk stoat	40	30	70	1	15	17
6	Kamchatka stoat	33	5	38	5	24	4
7	Karaginskii stoat	30	7	37	10	17	6
8	Transbaikal stoat	22	6	28	-	22	11
9	Altai stoat	12	6	18	2	23	8
10	Fergana stoat	10	2	12	23	10	-
11	Mongolian stoat	5	4	9	12	15	6
12	Semirechinskii stoat	5	2	7	25	8	-
	Total	965	426	1391	-	-	-

(a) In their geographical distribution they correspond to the subspecies listed for the stoat by S.I. Ognev (1935) and P.B. Yurgenson (1936) - Author.

A no less interesting discovery is that the structural features distinguishing the skulls of the male and female different in their post-embryonic development. Consequently, in young females, some measurements (rostral width, the width between the ends of the supraorbital processes, the zygomatic width, height of the nasal aperture, facial [rostral?] height of the skull, height of the skull in the region of the tympanic bullae, etc.) apparently lag behind those of males while others (length of the tympanic

bullae, height of the foramen ovale), on the other hand, are well developed at an early age.

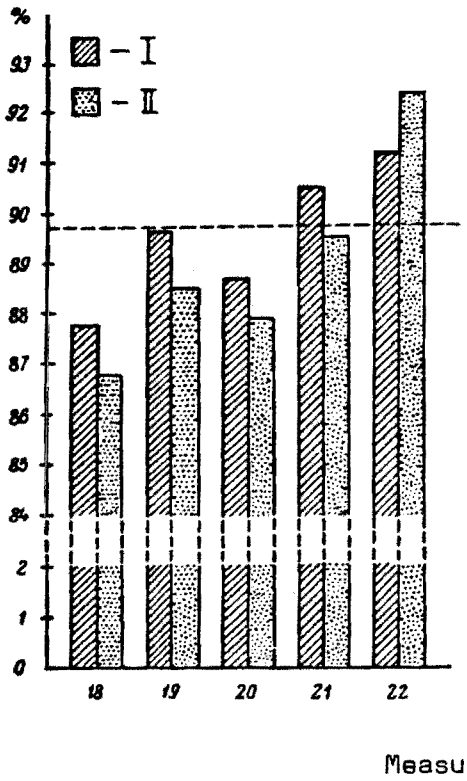
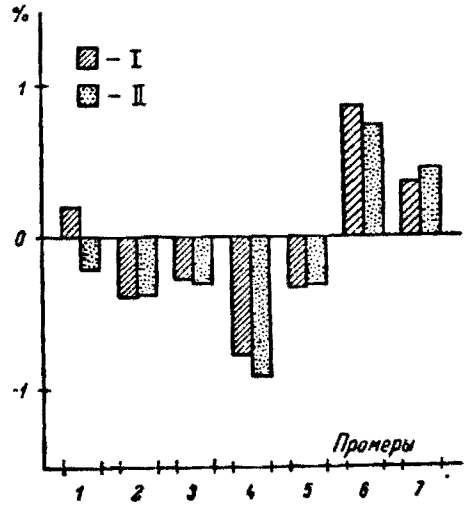


Fig.4. Sexual dimorphism of absolute dimensions along the vertical axis of the skull. (I) ratio of skull dimensions in semi-adult females to those of semi-adult males (in %); (II) the same for adult females and adult males. Measurements: (18) height of nasal aperture; (19) facial [rostral] height of skull; (20) height of skull in region of tympanic bullae; (21) occipital height; (22) height of foramen magnum. The horizontal broken line shows that the condylobasal length of the female skull is 89.7–89.8% of its length in the male skull.

In the skull as a whole, during the transition from semi-adult to adult, the ratios between the longitudinal dimensions in males and females show only small changes, but the ratios along the transverse and vertical axes decrease considerably. In adult females, therefore, the skull becomes comparatively narrower and flatter.



Measurements

Fig.5. Differences in longitudinal proportions in the skulls of males and females. (I) Differences between means (in % of condylobasal length of skull in semi-adult males and corresponding values in semi-adult females); (II) the same for adult males and females. Measurements: (1) basilar length, (2) diameter of upper canine tooth, (3) length of lower canine tooth, (4) length of hard palate, (5) length of upper row of teeth, (6) length from foramen magnum to hard palate, (7) length of tympanic bulla.

After examining the sexual dimorphism of the absolute dimensions of the skull, I next studied differences in skull proportions in males and females. To begin with, the principal measurements along the longitudinal, transverse and vertical axes of the skull in animals of both sexes were expressed as percentages of the condylobasal length, The differences between the relative values of the corresponding features in each sex were then calculated. These data were worked out both for semi-adult and for adult stoats (Table 8). Graphs were also plotted to show differences in the proportions of the skull in males and females (Figs.5,6 and 7).

It can be concluded the female skull differs quite considerable in its relative dimensions from the male skull: it is (1) shorter,

TABLE 7. Sexual dimorphism of absolute dimensions of the skull

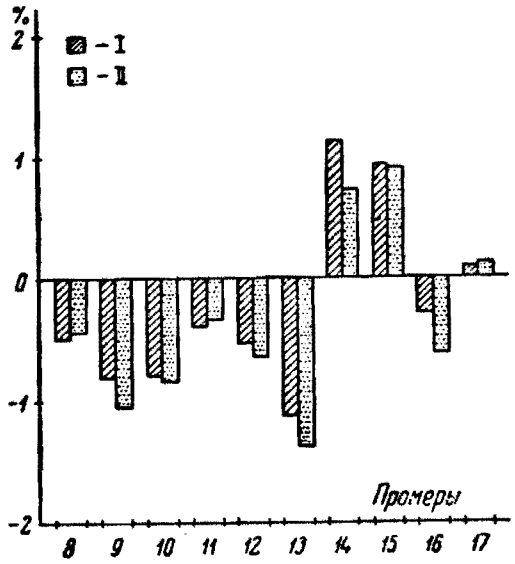
No.	Measurements	Semi-adult stoats			Adult stoats		
		arithmetical means			arithmetical means		
		males Ma	females Mb	Ratio Mb/Ma in %	males Ma	females Mb	Ratio Mb/Ma in %
	A. Measurements along longitudinal axis of skull						
1	Basilar length	39.81	35.84	90.0	41.31	36.97	89.5
2	Condylobasal length	44.31	39.81	89.8	45.91	41.18	89.7
3	Diameter of upper canine	1.80	1.46	81.1	1.89	1.54	81.5
4	" lower "	2.16	1.83	84.7	2.27	1.91	84.1
5	Length of hard palate	17.33	15.26	88.1	18.16	15.91	87.6
6	Length from foramen magnum to hard palate	22.51	20.56	91.3	23.18	21.09	91.0
7	Length of tympanic bulla	14.34	13.02	90.8	14.71	13.38	91.0
	B. Measurements along transverse axis of skull						
8	Width of nasal aperture	4.63	3.96	85.5	4.84	4.16	86.0
9	Rostral width	8.86	7.64	86.2	9.37	7.98	85.2
10	Interorbital width	10.53	9.14	86.8	11.10	9.61	86.6
11	Width of hard palate	13.45	11.93	88.7	13.98	12.40	88.7
12	Width between ends of supraorbital processes	12.72	11.22	88.2	13.37	11.64	87.1
13	Zygomatic width	24.37	21.45	88.0	25.60	22.39	87.5
14	Postorbital width	10.59	9.96	94.1	10.59	9.80	92.5
15	Auricular width	20.79	19.04	91.6	20.96	19.17	91.5
16	Mastoid width	21.40	19.11	89.3	22.28	19.73	88.6
17	Width of foramen magnum	7.86	7.10	90.3	8.04	7.25	90.2
	C. Measurements along vertical axis of skull						
18	Height of nasal aperture	5.99	5.26	87.8	6.30	5.47	86.8
19	Facial [rostral] height of skull	11.83	10.61	89.7	12.25	10.84	88.5
20	Height of skull in region of tympanic bullae	17,09	15.16	88.7	17.41	15.31	87.9
21	Occipital height	11.31	10.23	90.5	11.64	10.42	89.5
22	Height of foramen magnum	6.14	5.60	91.2	6.21	5.74	92.4

TABLE 8. Sexual dimorphism of proportions of the skull

No.	Measurements	Semi-adult stoats: arithmetical means males	Semi-adult stoats: arithmetical means females	Semi-adult stoats: Difference between sexes, in %	Adult stoats: arithmetical means males	Adult stoats: arithmetical means females	Adult stoats: Difference between sexes, in %
	A. Measurements along longitudinal axis of skull						
1	Basilar length	89.84	90.03	+0.19	89.98	89.78	-0.20
2	Diameter of upper canine	4.06	3.67	-0.39	4.12	3.74	-0.38
3	Diameter of lower canine	4.87	4.60	-0.27	4.94	4.64	-0.30
4	Length of hard palate	39.11	38.33	-0.78	39.56	38.64	-0.92
5	Length of upper row of teeth	26.86	26.55	-0.31	26.94	26.64	-0.30
6	Length from foramen magnum to hard palate	50.80	51.65	+0.85	50.49	51.21	+0.72
7	Length of tympanic bulla	32.36	32.71	+0.35	32.04	32.49	+0.45
	B. Measurements along transverse axis of skull						
8	Width of nasal aperture	10.45	9.95	-0.50	10.54	10.10	-
9	Rostral width	20.00	19.19	-0.81	20.41	19.38	-
10	Interorbital width	23.76	22.96	-0.80	24.18	23.34	-
11	Width of hard palate	30.35	29.97	-0.38	30.45	30.11	-
12	Width between ends of supra-orbital processes	28.71	28.18	-0.53	28.90	28.27	-0 (a)
13	Zygomatic width	55.00	53.88	-1.12	55.76	54.37	-1 (a)
14	Postorbital width	23.90	25.02	+1.12	23.07	23.80	+0.7
15	Auricular width	46.92	47.83	+0.91	45.65	46.55	+0.9
16	Mastoid width	48.30	48.00	-0.30	48.53	47.91	-0.62
17	Width of foramen magnum	17.74	17.83	+0.09	17.51	17.61	+0.10
	C. Measurements along vertical axis of skull						
18	Height of nasal aperture	13.52	13.21	-0.31	13.72	13.28	-0.44
19	Facial [rostral] height of skull	26.70	26.65	-0.05	26.68	26.32	-0.36
20	Height of skull in region of tympanic bullae	38.57	38.08	-0.49	37.92	37.18	-0.74
21	Occipital height	25.52	25.70	+0.18	25.35	25.30	-0.05
22	Height of foramen magnum	13.86	14.07	+0.21	13.53	13.94	+0.41

(a) ? misprints - Ed.

narrower and lower in the facial part, and longer, wider and higher in the cranial part; (2) not so wide in the interorbital, supraorbital and mastoid

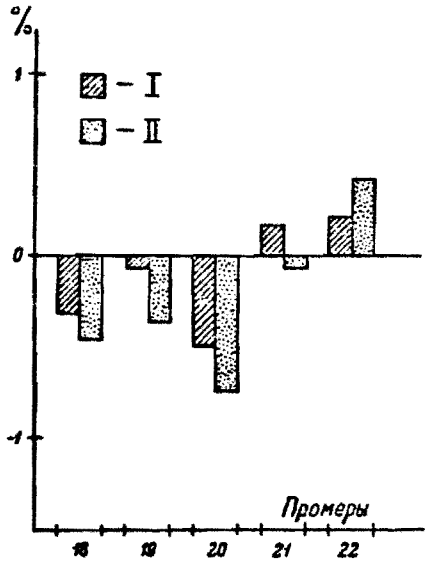


Measurements

Fig.6 Differences in transverse proportions of the male and female skull. (I) Difference between arithmetical means (in % of condylobasal length of the skull in semi-adult males, and the corresponding values in semi-adult females); (II) the same for adult males and females. Measurements: (8) width of nasal aperture, (9) rostral width, (10) interoribtal width, (11) width of hard palate, (12) width between ends of supraorbital processes, (13) zygomatic width,(14) postorbital width, (15) auricular width, (16) mastoid width, (17) width of foramen magnum.

regions; (3) characterised by a narrower span of the zygomatic arches; and (4) has a smaller occipital height.

With age the female skull becomes comparatively shorter still (see the change in length of the hard palate and the distance from it to the foramen magnum in Fig.5). In addition the rostral width, the zygomatic width, the postorbital width, the mastoid width, the facial height, the height in the region of the tympanic bullae, and so on, are [relatively] reduced.



Measurements

Fig.7. Differences in vertical proportions of the male and female skull. (I) Difference between arithmetical means (in % of condylo-basal length of the skull in semi-adult males, and the corresponding values in semi-adult females); (II) the same for adult males and females. Measurements: (18) height of nasal aperture, (19) facial [rostral] height of skull, (20) height of skull in region of tympanic bullae, (21) occipital height, (22) height of foramen magnum.

These observations can be summed up in the statement that sexual dimorphism in the proportions of craniometric features of semi-adult stoats are less clearly defined, so that at this stage the structure of the skull in both males and females is definitely "intermediate" in character. Later in life the sexual dimorphism of the relative dimensions of the skull becomes more distinct. The postembryonic development of the female skull terminates sooner, so that it retains more of the characteristics of young stoats: males pass through a much longer series of age changes and their skull gradually acquires a different shape.

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Note re p. 57

If the real sex ratio is 1.1, and 1st year stoats comprise 60% of the population, in every hundred stoats there will be 30 young males, 30 young females, 20 adult males and 20 adult females. Young males are the only animals which do not take part in the rut immediately after the breeding season : therefore the relative proportions of breeding animals will be males 20, females 50 - Ed.

SEXUAL DIMORPHISM IN FEEDING AS AN ECOLOGICAL ADAPTATION OF A SPECIES

(O polovom dimorfizme v pitanii kak ekologicheskoi adaptatsii vida.)

by

P.B. Yurgenson

Byull. Mosk. Obshch. Isp. Prirody (Otd. Biol.) 1947 52 (6) : 33-35.

It is generally known that most species of the Mustelidae exhibit significant sexual dimorphism in body dimensions and therefore in the absolute development of the musculature. The total body weight of males of the Trans-Baikal Siberian polecat Putorius eversmani michnoi Katsch. ranges from 550 to 1150 g (mean 811.7) and of females from 405 to 745 (mean 584.9): in a series of 10 specimens of each sex examined, the weight of the skeletal-muscular system in males averages 694.1 g (442-752) and in females 393.1 (286-510), i.e. 1.73 g per 1 cm of body length in males and 1.08 g in females.

The development of the musculature of the girdle of the fore-limbs, neck and [head], especially the temporal muscle (musculus temporalis) and to a lesser extent the masseter muscle (m. masseter - which is better developed in rodents), is of great importance in the catching, killing, dissecting and eating of prey by small predators.

Table 1 shows data on the relative weight of these muscles and groups of muscles, calculated as thousandths of the weight of the skeletal-muscular system.(a)

(a) Presumably the author is still talking about Siberian polecats - Ed.

Table 1

	Males	$\bar{x}$	Females	$\bar{x}$
Relative weight of fore limbs	39.9–58.0	54.73	47.9–61.9	57.50
Relative weight of thorax	8.6–18.7	12.66	7.6–21.6	15.08
Relative weight of musculus temporalis	8.0–12.3	11.11	9.6–25.2	14.46
Relative weight of musculus masseter	2.8– 4.0	3.43	2.7–11.2	3.58

We see clearly that the muscles having the above-mentioned functions are relatively more strongly developed in the females (which are smaller and lighter) than in the males.

Doubtless we have here an example of compensatory adaptation. Feeding in the steppes of S.E. Trans-Baikalia, mainly on conies, susliks and young bobac marmots, the females must compensate for their smaller size by relatively more powerful development which is necessary to get the food which determines the ecological niche of this species.

To support this conclusion, I can also point to the example of the weasel (Mustela nivalis pygmea G. Allen). In this very small Palaearctic predator the relative dimensions of the temporal muscle (9 specimens examined) were inferior only to those of the glutton (mean 14.40 versus mean 15.78), and the masseter was even more strongly developed (mean 5.80 versus 4.06). The main pectoral muscle in the weasel (mean 17.20) and stoat (mean 16.98) is also developed relatively more strongly than in martens, polecats and gluttons. This is quite understandable if we compare the dimensions of the weasel and its main prey - voles. It must compensate for its small body size by the relatively more powerful development of the musculature. There can be no other explanation for these species, as their range of food is similar.

As long ago as 1939[(1)] I noted that, in pine martens, the only individuals [behaviourally] specialised for catching the blue hare

(Lepus timidus) are males. This made me investigate sexual dimorphism in the feeding of martens. Accordingly I investigated 43 stomachs and intestines of males and 21 stomachs and intestines of females taken in the 1938/39 winter season in the region of the Pechora State Reserve (Table 2).

We see at once that only the males catch the big Galliformes (capercaillie, black grouse, willow grouse). Later on I found in five years there was only one instance of a female pine marten catching a hen capercaillie (winter 1941/42). On the other hand, the percentage of hazel hens found was much higher in the females than in the males (19.0 verses 4.6%). The females also take more voles (33.3 versus 13.9%), small birds (14.3 versus 0%), birds eggs (9.5 versus 0%), wasps (23.8 versus 4.6%), and Pinus sibirica 'nuts' (28.6 versus 4.6%). In catching one of the main winter foods, i.e. squirrels, no sexual dimorphism is observed. Thus the absence of such large prey as capercaillie, black grouse and willow grouse in the food of the females is compensated for by the higher percentages of foods that are more easily available to them. The sexual dimorphism in the feeding of the pine marten is obvious.

Table 2

No.	Food	Males		Females	
		no. of finds	%	no. of finds	%
1	Squirrels	21	48.8	11	54.2
2	Voles	6	13.9	7	33.3
3	Shrews	2	4.6	1	4.7
4	Birds (total)	13	30.2	12	54.7
5	Galliformes	5	11.6	4	19.0
6	Capercaillie	2	4.6	-	-
7	Black grouse	5	11.6	-	-
8	Willow grouse	1	2.3	-	-
9	Hazel hen	2	4.6	4	19.0
10	Small birds	-	-	3	14.3
11	Birds' eggs	-	-	2	9.5
12	Wasps	2	4.6	5	23.8
13	Pine 'Nuts' (Pinus sibirica)	2	4.6	6	28.6

The relative weight of the musculature and the sexual dimorphism in it were investigated in 15 pine martens from the region of the Pechora State Reserve, and I compared the results with data for 12 stone martens given by Schutze [2]. The results of this investigation, shown in Table 3, reveal that, in both species of Martes, not only is compensatory adaptation completely absent in the relative development of the musculature, but that the latter was weaker in the females. This applied not only to the absolute figures, but also relative to the males.

It should be noted that in the relative (not absolute) development of the dental system in pine marten there is also a definite though less pronounced trend in the same direction as for the musculature.

Table 3

Species and sex	n	Musculus temporalis	Musculus masseter	Musculus digastricus	Fore limb as a whole	Note
1. Pine marten ♂	7	9.40	3.20	2.42	73.40	
2. Pine marten ♀	8	7.50	2.80	2.02	69.50	Data calculated in % of skeletal muscular system
1. Stone marten ♂	8	12.50	2.64	1.82	50.00	
2. Stone marten ♀	4	9.70	2.30	2.25	48.00	

In the pine marten we have a distinct type of predator - a polyphage with an extensive and varied food range, within which [behavioural] sexual dimorphism [in feeding] has good scope of development. We do not see this in the Siberian polecat, a purely carnivorous animal with a restricted food range, and even less in a stenophage like the weasel. In the first case, evolution was towards ecological adaptation, which is shown as differences between the sexes in hunting behaviour. In the second case there was morphological adaptation, as within the food range there was not enough suitable and abundant food with a stable population for behavioural differentiation in hunting.

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A CONTRIBUTION TO THE ECOLOGY OF MUSTELA NIVALIS LINNAEUS, 1766 OF THE ARKHANGEL'SK NORTH

(Ekologiya Mustela nivalis Linnaeus, 1766 Arkhangel'skogo severa)

by

V. Ya. Parovshchikov

Věstník Československé společnosti zoologické 1963 27 (4) 335-344.

Little is known of the ecology of the weasel, Mustela nivalis L. Its reproduction and pronounced geographical variation have been studied very little. During 30 years of work at Arkhangel'sk, I was fortunate to be able to investigate personally many of these obscure questions, over the whole of the north of the European part of the Soviet Union, in the Arkhangel'sk North, including the Vologodsk and Arkhangel'sk regions, the Nenets national district (Malozemel'sk and Bol'shezemel'sk tundras) and the Komi ASSR.

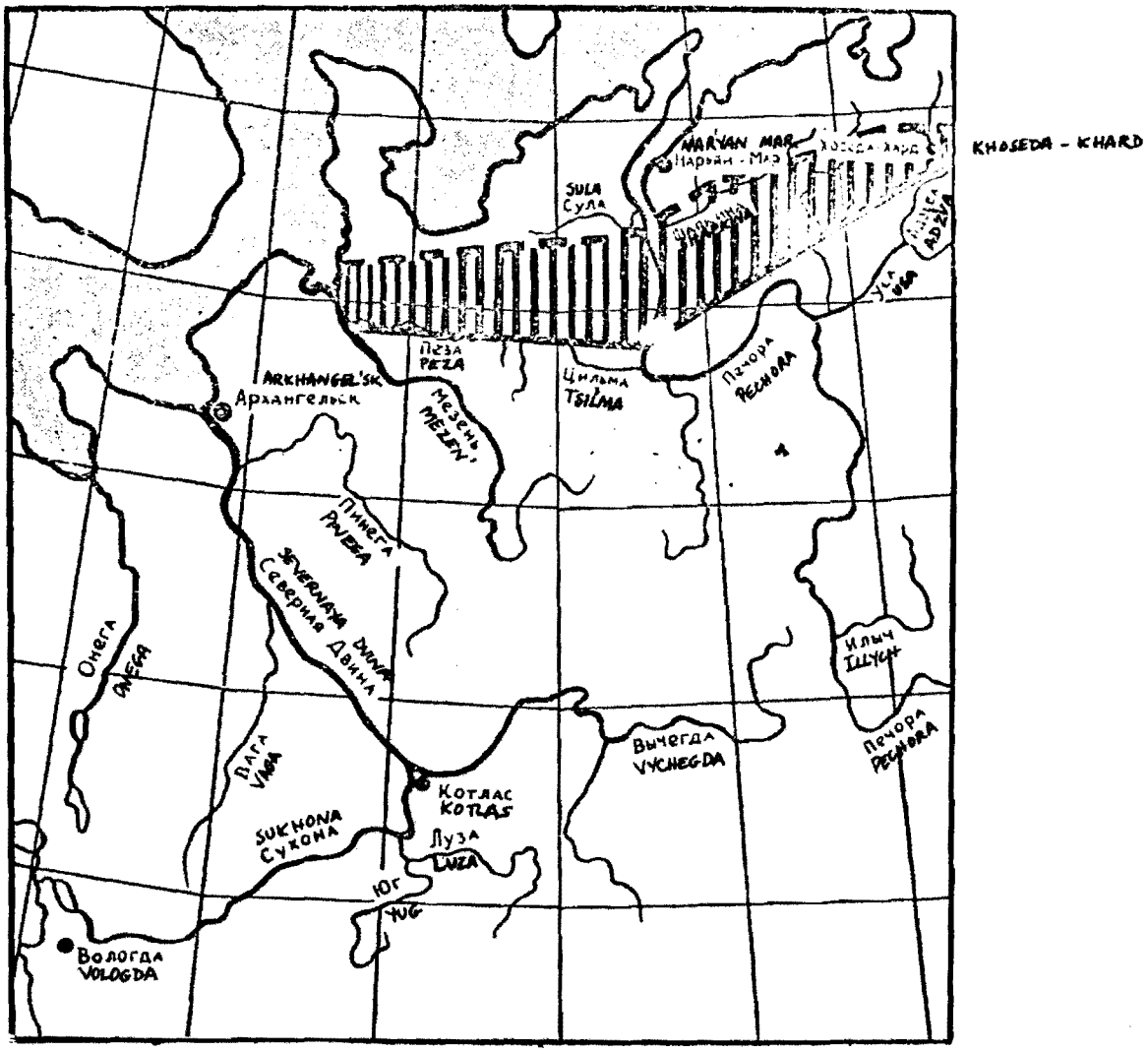
Distribution

Examination of 85 specimens indicates that two subspecies of weasel live in the territory of the Arkhangel'sk North. The northern or snow weasel, Mustela nivalis nivalis, is not similar to the Siberian, tundra or little weasel (short-tailed), Mustela nivalis pygmaea, which lives in the tundras.

The typical Mustela nivalis nivalis Linnaeus, 1766 described from Northern Switzerland, lives in the northern and central areas of the European part of the USSR. The northern boundary reaches to the southern edge of the Malozemel'sk and Bol'shezemel'sk tundras. Specimens of this subspecies were caught at the mouth of the River Mezen', along the River Peza, between the rivers Sula and Tsil'ma, further to the north-east along the River Shapkina, and some specimens from neighbouring Khoseda-Khard (River Adz'va, 67° north). The centre of the distribution is the southern

taiga zone: the basins of the rivers Kubina, Sukhona, Yug and Luza, and the southern watershed areas.

The tundra or little (Siberian, short-tailed) weasel, Mustela nivalis pygmaea J. A. Allen, 1903, is distributed throughout the tundra zone of the north of the European part of the USSR as far as the sea coast, but rarely east of Nar'yan-Mar (mouth of the River Pechora). It is absent from the islands of the Barents Sea. The southern boundary of distribution is the northern limits of the taiga and the forest tundras. Weasels transitional from the typical northern to the tundra form are found in the forest tundra, judging from the collections of material and skins examined in state museums.



Southern limits of distribution of Mustela nivalis pygmaea Allen

Northern limits of distribution of Mustela nivalis nivalis Linnaeus

Hybrids (crossing forms)

Fig.1. Geographical distribution of Mustela nivalis in the Archangelsk Region of the U.S.S.R.

Diagnosis

The winter coats of both subspecies are snowy white. The summer coat of M. n. nivalis is very dark-brown to brown on top and pure white underneath. The summer coat on the head and back of M. n. pygmaea is pale brownish with a rusty hue. In the series, the difference in the colour of the dorsal fur is sharply distinguished. The dark dorsal fur of both subspecies is sharply delineated from the light colour of the abdomen. The under-fur of M. n. pygmaea is lighter than in the nominal form.

M. n. pygmaea is smaller: it weighs 39-60 g, while M. n. nivalis weighs 40-75 g. The tail is a clear distinguishing feature: in M. n. pygmaea it is shorter, and is covered in winter by relatively long and shaggy hairs (in summer the hairs do not differ).

Table 1 shows the body dimensions of both subspecies in mm (M. n. nivalis, 63 specimens, M. n. pygmaea, 22 specimens). The skull of M. n. pygmaea is smaller. In M. n. nivalis the condylobasal length ♂♂ 31.2-38; ♀♀ 31-32.3; zygomatic width ♂♂ 17-19.5, ♀♀ 15-18; mastoid width ♂♂ 14.5-17.8, ♀♀ 13.5-17.5. In M.n. pygmaea, condylobasal length is ♂♂ 32-34.5, ♀♀ 30.2-33; zygomatic width ♂♂ 16.6-17.5, ♀♀ 14.6-17.2; mastoid width ♂♂ 15.3-16.1, ♀♀ 14.6-15.6 mm. The length of upper row of teeth in M. n. nivalis ♂♂ M 9.3 mm, ♀♀ M 8.8 mm; in M. n. pygmaea ♂♂ M 8.8 mm, ♀♀ M 8.4mm. The skulls of the females of both subspecies are smaller and flatter on top and the zygomatic arches are thinner than in the males.

TABLE 1. Measurements of weasels from Archangel'sk [data from present study]

	Length of head + body		Length of tail (without tuft)		Length of hind foot (without claws)	
	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀
Mustela nivalis nivalis (n = 63)	138-204	121-188	23-26	19-36.8	21.2-27	16-26.3
Mustela nivalis pygmaea (n = 22)	137-172	116-163	17-28	16.5-21.5	17-21.2	15.8-21

S.I. Ognev (1955) used skulls from some of the weasels I obtained from the Arkhangel'sk area in his monograph, so that those skulls have been measured. Generally, the results are all practically identical, and the differences [between the two sets of measurements] are insignificant. (See Table 2.) His data are as follows : the condylobasal length in M. n. nivalis ♂♂ 31.7–37.1, ♀♀ 30–34.7; zygomatic width ♂♂ 15.1–about 20, ♀♀ 14.2–17.8; mastoid width ♂♂ 14.1–17.6, ♀♀ 13–16.2 mm. In M. n. pygmaea the condylobasal length ♂♂ 33.4, ♀♀ 31–32.6; zygomatic width ♂♂ 17.3, ♀♀15–17; mastoid width ♂♂ 15.8, ♀♀ 14.1–15 mm. The length of upper row of teeth in M. n. nivalis ♂♂ 8.2–10 (M 9.1), ♀♀ 7.8–9.7 (M. 8.2): in M. n. pygmaea ♂♂ 9, ♀♀ 7.9–8.1 mm.

TABLE 2. Measurements of weasels given by Ognev (1955).

	Length of head + body		Length of tail (without tuft)		Length of hind foot (without claws)	
	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀
M. n. nivalis	130.6–208	114–162	21–40	18–35.2	20–26.7	17.1–23.5
M. n. pygmaea	142–162.2	124–153	16.2–20	13–17.5	19.5–21.9	17.5–21

The structure of the baculum is similar in the two subspecies; in both there is a hamate flexure at the [distal] end, but there is a slight difference in dimensions. In M. n. nivalis (12 specimens) the maximum length is 12.6–20.8 mm the width at the base 0.7–1.2 mm, the height at the base 1.2–2.4 mm. In M. n. pygmaea (six specimens) the maximum length is 12.4–20.2 mm, the width at the base 0.7–1.1 mm, the height at the base 1.2–2.2 mm.

S.I. Ognev recognised two subspecies of weasels in European USSR, based on variations in the colour of the coat and the dimensions of the body (particularly the tail) and the skull; our material confirmed this distinction, and the distribution of the two groups was determined (see map, p 85).

Numbers

Trappers can not make a living from weasels, but catch them incidentally when trapping for ermine and moles (in the latter case in summer, in the absence of jerboas). Weasels are caught most frequently in the south-west of the province, in the Vologodsk region. The harvest varies from 6,000 to 7,200 [per year]. The total population, calculated from its density and distribution, is estimated, as a guide, to be between 15,000 and 25,000 (P.P. Smolin 1934). There are very few weasels in the open tundra, but they are found in the forest tundra, and in greater numbers in the Arkhangel'sk taiga (entire taiga zone). In the winters of 1938-1939, 1944-1945 and 1958-1959, one to three tracks of weasels were found per 100 km route in the Malozemel'sk tundra; there were 2 to 4.7 tracks [per 100 km] in the forest-tundra zone in 1938-1939 and 1944-1945; in the Arkhangel'sk taiga (on the Arkhangel'sk latitude and 250-300 km further south) there were 0.5-2.3 tracks [per 100 km] in different years; in the south-western areas, on the latitude of the town of Vologda, there were 12.3-23.8 tracks per 100 km.

We used methods of V.P. Teplov and E.N. Teplova (1947) to determine the number of Mustela nivalis in the area of the Pechorsk-Ilychak reserve. This is an area of more than one million hectares in the Pripechorsk lowland lying between the rivers Pechora and Ilych, and bounded on the east by the western slopes of the Ural mountain range (centre 62° north, 58° east). The weasel Mustela nivalis is found, in comparatively small numbers, throughout this area. Its distribution coincides generally with that of the ermine, Mustela erminea, but the weasel is rarer. In the winter of 1937-1938 in the Yakshch district there was no more than one track of Mustela nivalis for ten tracks of Mustela erminea (calculated after the first snow, before either species had settled into their winter routines). In this year (1937-38) there was a population increase in Mustela erminea, and 50 to 60 ermine per trapper were caught in the season. The number of Mustela nivalis in this area is apparently similar to that in Arkhangel'sk; there will be one to two tracks per 100 km route.

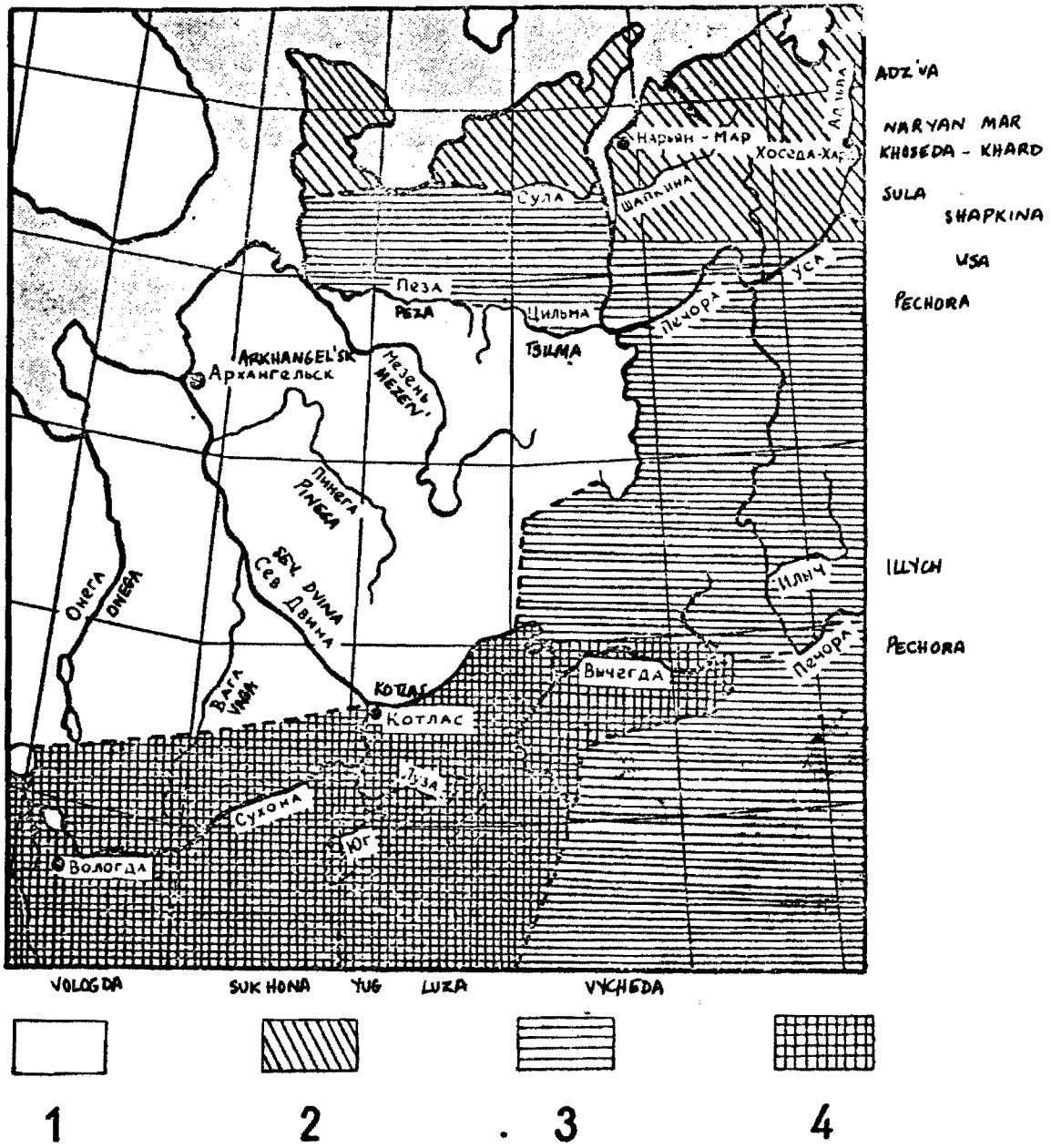


Рис. 2. Встречаемость *Mustela nivalis* по Архангельскому северу на 100-километровых маршрутах. 1 = очень мало (0.5—2.3 следа), 2 = мало (1 —3 следа), 3 = средне (2—4.7 следа), 4 = много (12.3—23.8 следа).
Fig. 2. Average numbers of footprints of *Mustela nivalis* found during the 100 km travels: 1 = 0.5—2.3; 2 = 1—3; 3 = 2—4.7; 4 = 12.3—23.8.

Variations in the numbers of predators are related to their food supplies, i.e. on the abundance of rodents. Unfortunately, although we know the years in which lemmings were abundant, we have no data on the harvests [of skins] of M. n. pygmaea, so we do not know if their numbers

show this relationship : but replies to enquiries of local trappers show that they do. However, the distribution, density and harvest of M. n. nivalis have evidently always been correlated with years of abundance of small rodents, and vice versa. For example, there were many weasels in the winters of 1934-35, 1937-39; 1947-49 (for three years running); 1952-54 (two years running) and the winter of 1955-56. Throughout the Arkhangel'sk taiga and forest tundra the number of weasels is always low every seventh year. Cold and snowy springs, relatively wet summer months, heavy winter rains, and severe floods in spring and autumn are unfavourable factors for rodents and therefore also for weasels. The south-western regions are more favourable, and the numbers of weasels are almost stable.

The species composition of the small rodent community changes from year to year. For example, in 1937, 1939, 1954 and, particularly, 1955, weasels fed mainly on the northern bank vole (Clethrionomys glareolus suecicus). In 1948-49 it fed mainly on the European red-backed summer vole (Clethrionomys rutilus rossicus). In 1933-34, 1938, 1952-53 and 1956-57, its main diet was the North-European root vole (Microtus oeconomus ratticeps); and in 1934, 1951 and, particularly 1956, it was the water vole (Arvicola terrestris). During and after a population peak of small rodents, the number of Mustela nivalis greatly increased.

An interesting opinion expressed recently suggests that where the number of weasels greatly exceeds the number of ermine, the ermine are at a competitive disadvantage. The idea needs to be more closely investigated.

Moulting

Judging by the skins examined, the spring moult of M. n. pygmaea begins in mid-May and ends in mid-June. The autumn moult begins at the end of August and ends at the end of September.

The spring moult of M. n. nivalis begins in the second half of April (mainly from about the 10th onwards), and is complete by the end of

May. The autumn moult begins between the 10th and 17th of September and ends in the second half of October; in years with dry, warm autumns it may be delayed until the end of November. Near Vologda, individuals of this subspecies begin to moult in March, and by the first ten days of May all of them have their summer coats; the period of autumn moulting is much later, beginning in October and ending in the first ten days of December (or sometimes a month earlier).

Food

In the diet of Arkhangel'sk weasels, the most important items are small rodents, chiefly voles and lemmings; other prey include mice, water voles, Insectivora, birds, Amphibia and reptiles, insects and plant residues.

Of 45 stomachs examined, 39 contained earth and twigs. Weasel hairs were found in 12 stomachs. Residues of birds' eggs were found in five stomachs (apparently shells from eggs of the willow grouse). In two stomachs, remains of the limbs of other weasels were found(a).

It was interesting that in several stomachs there were hairs of larger mammals : the mountain hare (Lepus timidus) in four and, in winter, the Siberian chipmunk (Eutamias sibiricus) in two, and elk (Alces alces) in four. In the latter case the weasels must have fed on the remains of elks caught by huntsmen. Two stomachs were crammed with flesh, bones and hair of the Red squirrel (Sciurus vulgaris).

An accurate determination of the diet of the weasel, particularly from scat analysis, is very difficult owing to the great comminution of the remains. Over 30 years we investigated 45 stomachs and 213 scats of weasels; the results illustrate the general diet of this species. The following were found :

(a) Weasels often swallow their own hairs whilst grooming : and in traps, may chew off their own feet in attempts to escape. - Ed.

	Percent. (a)
Voles (Clethrionomys, Microtus)	52
Mice (Muridae)	18
Water vole (Arvicola terrestris)	7
Insectivora	6.2
Mountain hare (Lepus timidus)	1.6
Red Squirrel (Sciurus vulgaris)	0.8
Chipmunk (Eutamias sibiricus)	0.8
Elk (Alces alces)	1.6
Birds (Aves)	5.3
Amphibia	4.3
Insecta	1.6
Plant residues	0.8

It is interesting to compare the food of weasels from different regions of the USSR. The diet of 57 Kazan weasels (N.D. Grigor'ev, V.P. Teplov and V.I. Tikhvinskii, 1931) included 75% of voles and mice in 1928-29, and 69.6% in 1929-30; 20 and 21.7% of Insectivora, 0 and 8.7% of water voles, and 5 and 0% of birds. Later, in 1952, the occurrence of small rodents (chiefly Microtus arvalis) in winter increased to 77%, and, during the snowless period of the year, to 92%. The percentages for Insectivora were 17 and 16%, those for water voles 3 and 8%, those for birds 1 and 8%, those for Amphibia 1 and 5%, those for Insecta 0 and 5%, and those for plant residues 0 and 16%. The main groups of foods in the diets of weasels from western Siberia (M.D. Zverev, 1931) in the winter of 1931 was as follows : small rodents (mainly voles) 72%, water voles 2%, and fish 2%. The diet of weasels in Mongolia (A.G. Bannikov, 1954) consists mainly of Brandt's vole (Microtus brandti Radde). In the Kol'sk peninsula adjoining the Arkhangel'sk North, the weasel feeds exclusively on lemmings and voles (our observations in the summers of 1944 and 1945).

(a) Unfortunately, Parovshchikov does not state whether these figures are percentages of items identified, or of stomachs containing each species - Ed.

Weasels may make caches, or larders, containing large stores of rodents and other prey, when there is a surplus of food. The following records, of caches found, give examples: 18 September 1934, 69 carcases: 1 October 1934, 34 carcases; 13 September 1956, 40 specimens of Microtus oeconomus ratticeps: 23 August 1948, 22 carcases: 17 September 1949, 37 specimens of Clethrionomys rutilus rossicus and 4 specimens of Microtus (=Stenocranius) gregalis tundrae: 17 August 1934, 13 carcases: 10 September 1956, 18 carcases: 17 June 1957, 12 specimens of Arvicola terrestris, 11 specimens of Sorex araneus araneus and two specimens of Talpa europaea europaea.

Besides rodents and Insectivores, the weasel stores frogs and lizards. On 2 May 1937, for example, at Lake Musino, 60 km south of Arkhangel'sk, we found 47 specimens of Rana temporaria in one cache, and in another on 27 May 1962, at the Severnsk lakes, we found 23 specimens of Rana temporaria and 19 specimens of Lacerta vivipara.

In the Crimea, on the spurs of Mount Chernaya, I found a cache of Mustela nivalis nikolskii on 30 April 1935, containing 34 specimens of the sand lizard (Lacerta agilis exigua), and 21 specimens on 17 May 1935[a]. At the River Mologa in the Kalininsk region, on 17 August 1941, a cache contained 18 specimens of the garden dormouse (Eliomys quercinus superans), and one on 15 September 1941, seven specimens of the striped field-mouse (Apodemus agrarius septentrionalis) and 12 specimens of house mice (Mus musculus).

In the winter of 1929-32 on the estate of the Timiryazevak Agricultural Academy near Moscow, we often found caches of weasels in the form of a collection of dead goldcrests (Regulus regulus) buried in the snow, with their brains eaten out. This happened in a forest after a heavy snowstorm, which forced the birds to come down to spend the night on young

(a) In the same cache, or another, is not clear - Ed.

spruces, where they were vulnerable to weasels. Ten to 16 birds were counted in the cache (V. Ya. Parovshchikov, 1941).

The above records suggest that the weasel is distinguished by considerable bloodthirstiness and destroys a much larger number of animals than it can eat. On three occasions I kept them at home, but gave up each time, so much did they eat in one day (up to 12 voles and up to five specimens of Arvicola terrestris)(a).

In the Arkhangel'sk area, the weasel is active in summer during every hour of the day and night (light nights !)(b). In the dark period of the year, in autumn and winter it prefers to hunt in the twilight of the morning and, particularly, the evening, and also during the day : it is much less active at night then. In the tundra it is active both by day and night throughout the year.

Reproduction

The Arkhangel'sk weasel does not have a definite period of heat, but evidently most individuals breed in April and May. In the Arkhangel'sk area, pregnant animals have been found, with embryos at different stages of development, in May and June; one pregnant female caught on 18 July 1948 (six embryos). Nursing females, and young weighing 25-33 g and with a body length of 91-105 mm, were recorded from 13 June to 10 September. On 10 September 1946, a weasel's nest was discovered with four young each weighing 18-26 g and with a body length of 82-88 mm (two ♂♂, two ♀♀). Young weighing 34-40 g and with a body length of 133-140 mm were found at the end of June, in the second half of August and at the end of September. Litters may be produced very late in the year : on 18 December 1954, two young males weighing 50 and 56 g and with a body length of 125 mm, and on 6 December 1956, a male weighing 43 g and with a body length of 133 mm, were trapped. But four old females, caught on 29 and 30 June, 20 July and 14 August, were all barren.

(a) This is quite absurd. The mean daily requirement of food for weasels is less than 40 g/day. See Southern (1964). - Ed.
(b) Author's comment !

There is no doubt that the male takes some part (not necessarily active) in the rearing of the young. The young remain with their parents for a long time. We often observed in late autumn, in September and October, old weasels hunting with full grown young.

Summary

The author described two different subspecies of weasel which occur in the Archangelsk Region of USSR: Mustela nivalis nivalis Linnaeus, 1766, and Mustela nivalis pygmaea J.A. Allen, 1903. The external characters of these subspecies are established, and their geographical distribution (see Fig.1) and their densities (Fig.2).

For the external measurements of both subspecies see Table 1. For comparison the external measurements of weasels according to Ognev (1935) are shown in Table 2.

Skull measurements in mm are as follows :

Mustela nivalis nivalis (n = 63): Condylobasal length ♂♂ 31.2-38.0, ♀♀ 31.0-32.8; zygomatic width ♂♂ 17.0-19.5, ♀♀ 15.0-18.0; mastoid width ♂♂ 14.5-17.8, ♀♀ 13.5-17.5; length of upper tooth row ♂♂ 9.3, ♀♀ 8.8 mm.

Mustela nivalis pygmaea (n = 22): Condylobasal length ♂♂ 32.0-34.5, ♀♀ 30.2-33.0; zygomatic width ♂♂ 16.6-17.5, ♀♀ 14.6-17.2; mastoid width ♂♂ 15.3-16.1, ♀♀ 14.6-15.6; length of upper tooth row ♂♂ 8.8, ♀♀ 8.4 mm.

The author also studied,over 30 years, some aspects of ecology and biology of the species in the Archangelsk Region. Many observations show that the number of weasels increases in direct correlation with the number of small rodents.

The author assumes that the ermine (Mustela erminea Linnaeus, 1758) probably does not do well in competition for food with Mustela nivalis, because in the areas where the weasels occur in a large number, the number of the ermine is relatively very small.

The weasel's diet consists mainly of voles and mice, occasionally including squirrels, small Insectivores, hares and birds. The data on the

diet of Mustela nivalis from other regions of USSR are discussed.

The spring moult of Mustela nivalis nivalis takes place from the second half of April to the end of May. The autumn moult starts in the middle of September, and it is completed by the end of October (in warmer years as late as by the end of November).

The spring moult of Mustela nivalis pygmaea starts in the middle of May and it is finished in the middle of June. The autumn moult begins at the end of August, and it is completed by the end of September.

The winter hair of both Mustela nivalis nivalis and Mustela nivalis pygmaea is white.

The weasels of Archangelsk Region may give birth to the young at almost any time of year, but the majority breed in April and May.

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THE PROBLEM OF SEX RATIO IN ERMINE

(K voprosu o sootnoshenii polov u gornostaya)

by

V.P. Teplov

Zoologicheskii Zhurnal, 1948 27 (6) 567-70.

All zoologists studying a series of commercial ermine corpses have observed a preponderance of males over females. The most widely accepted explanation for this was that the females of this species are shyer and less active than the males, and that therefore they were caught less frequently in traps. N.P. Lavrov(5), who published in 1944 a series of extremely interesting papers on the biology of propagation of ermine, regarded the sex ratio in ermine obtained by hunters as that existing in nature. He considered the preponderance of males over females to be "a biologically useful characteristic acquired by the species during the process of evolution".

As a result of my participation in a study of the biology of ermine, carried out by the Volga-Kama commercial biostation from 1928 to 1935, and of my collecting material on the ecology of this animal in the Pechorsk state game reserve from 1937 to 1947, a series of data on the characteristics of the two sexes in ermine is available to me.

The problem of the occurrence of polygamy in ermine is far from resolved. Observations made by E. Bekshtrem(1) and D.N. Grigor'ev(3) as well as several other authors, and my own experiment made while catching ermine for the Kazansk zoo park, showed that male ermine were frequently found together with the young, protecting them and apparently helping to obtain food for them. This type of behaviour in males does not at all accord with the concept of polygamous reproduction.

There is also no doubt that females differ from males as regards mobility and activity, which is denied by N.P. Lavrov. I.V. Zharkov(4),

who has studied in detail the ecology of ermine in winter, found that the daily area of activity is three times smaller in females than in males.

While studying, together with E.N. Teplova, the significance of the snow cover in the ecology of animals and birds in the Pechorsk game reserve(7), I found that during the deep snow period, the female ermine live mainly under the snow, while the males frequently move about on the surface. The percentage of males in the population, determined by foot-prints, in the period of first snowfalls was 55-60%, but when the snow became deep, it increased to 70-80%. I.V. Zharkov, when counting ermine in the Kamsk flood plain, where the depth of snow is considerably less than in the Pechorsk game reserve, determined that the males comprised 58% of the population.

This subnivean tendency of female ermine is apparently related to their smaller size compared with males, which on the one hand makes them less able to withstand low temperatures than males, and to use more frequently the warming properties of snow, and on the other hand determines the specificity of their feeding, which is based mainly on small mammals, voles and shrews in subnivean habitats. Larger males far more frequently hunt game birds, squirrels and hares, and therefore live mainly above the snow. Among mammals found in the stomachs of male ermine, subnivean forms (voles and shrews) comprise 88%, and in the stomachs of females, up to 98%.

During the period of deepest snows the female ermine very rarely show themselves on the surface. Among ermine obtained by hunters in March, when the snow cover in our region reaches a depth of 1 m or more, the females comprise only 12%. The comparable value for ermine obtained in October, when the depth of snow does not usually exceed 20 cm, is 27%.

Using the material published by N.P. Lavrov, and data obtained by the author for 270 ermine, the following figures were obtained for the average percentage of male ermine caught in different regions (for calculation the author used only regions for which data were available for not less than 3

commercial seasons): (1) Aktuybinsk region 51%; (2) North Kazakhstan 60%; (3) Tartar ASSR 63%; (4) Vologodsk region 64%; (5) Kirov region 62%; (6) Komi ASSR (region of Pechorsk game reserve) 72%; (7) Krasnoyarsk region (Achinsk area) 56%. It can be seen that the values for the various geographical regions are quite close in some cases and differ greatly in others.

In view of the fact that the percentage of males among ermine obtained in the region of the Pechorsk game reserve increases with increasing depth of snow cover, the author compared the percentage of male ermine in the yield, and the characteristics of the snow regime, in a number of districts (the height of snow cover was determined according to Rikhter[6] and using the Great Soviet World Atlas).

Figure 1 shows that the percentage of male ermine obtained changes directly in proportion to the depth of the snow cover. Apparently the relationship between depth of snow cover and number of male ermine obtained, observed in Pechora, is also valid in other regions.

Does the nature of the food supply also have an influence on the sex ratio of the ermine investigated ?

In Fig.2 are plotted the changes in the percentage of male ermine obtained in different winters in the Pechorsk game reserve, together with data on the number of voles caught in traps at night. It can be seen that during the winters 1939-40, 1940-41 and 1943-44, when a sudden decrease in the number of voles was observed, the percentage of male ermine caught also decreased. Apparently this was due to more frequent hunting forays by females on the surface of the snow, because in these years there was insufficient food for them under the snow.

N.P. Lavrov reported that in the winter 1937-38, an increased percentage of female ermine was observed nearly everywhere, and he believed that this was a result of [differential] resorption of embryos, due to scarcity of rodents. The assumption of N.P. Lavrov is supported by Prof.

Bunak[2], who believes that male embryos are preferentially resorbed. In my opinion, the increased percentage of females in the catch can be explained in this case by the same reasons as for the Pechorsk game reserve, i.e. insufficient food supply for the females under the snow cover.

Thus the dominance of male ermine obtained by hunters is explained not only by their greater number in natural conditions but also by their biological characteristics and particularly by the local supply of food.

N.P. Lavrov presents data on the sex ratio of 15 young ermine from two litters, and ten embryos, among which the males comprised 64%. At first glance this small amount of material suggests that males must outnumber females in the population.

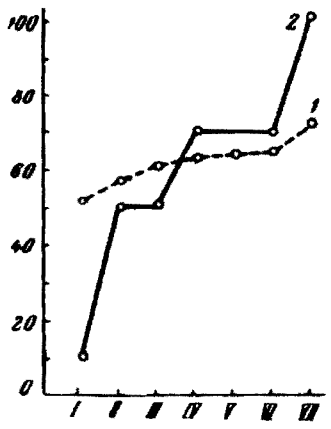

Fig.1. Comparison of sex ratio in ermine from regions with different depths of snow cover
I.- Aktyubinsk region; II. - Krasnoyarsk area (Achinsk district); III. - North Kazakhstan region; IV. - Kirov region; V. - Tartar ASSR; VI. - Vologodsk region; VII. - Komi ASSR (region of Pechorsk game reserve), 1-percentage of males among ermine obtained; 2 - depth of snow cover in cm.

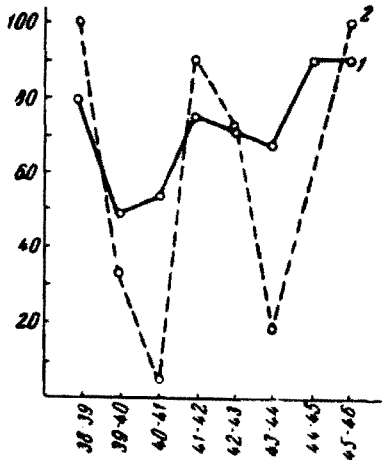

Fig.2. Comparison of changes in percentage of male ermine obtained in different years with changes in abundance of voles, in the region of Pechorsk game reserve
1 - Percentage of male ermine
2 - Abundance of voles (calculated from night trapping records; figures expressed as a percentage of the highest value [1939-39])

The excess of males over females in litters of mammals has frequently been observed by zoologists, in several species, but in the majority of cases subsequent observations showed that in later life, by the process of natural selection the mortality rate in males is higher than in females, and so the sex ratio of the adults is about even.(a)

Conclusions

1. The excess of males in collections of ermine obtained by hunters is due to the different biology and feeding habits of the two sexes, and therefore such material cannot be used for determination of the sex ratio in the population.

2. In years when the supply of small subnivean mammals is low, more female ermine are caught by hunters than usual, up to almost equal numbers with males. The same applies in regions where the snow cover is negligible.

3. A better conclusion on the sex ratio of ermine could be reached from a sufficiently wide collection of material made in the snow-free period of the year (but not in the breeding season), when the influence of snow cover on the biology and behaviour of males and females may be eliminated.

4. The occurrence of polygamy in ermine could be demonstrated only by observation in natural conditions.

5. The observed preponderance of males among embryos and litters of ermine requires confirmation from further material.

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(a) But see Leigh (1970). - Ed.

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INFLUENCE OF TEMPERATURE ON THE ACTIVITY OF THE ERMINE IN WINTER

By

V.A. Kraft

Zool. zhurnal 1966, 45 (1) : 148-150.

The material for this work was collected in the flood-plain of the River Ishim, near the town of Tselinograd, over four winters (1959-63, from 11 November to February). We used the method of counting the intersections between tracks of the predator [and the route of the observer] (Novikov 1953). The standard transect was 7 km (3 hrs) and the counts were made 2-7 days after a fall of new snow. The results of the counts are shown in Table 1.

As can be seen, the ermines spend most of their time under the snow; on average, they were active on the surface on 13% of the census days. When on the surface of the snow, each ermine keeps to a specific hunting area, which rarely overlap. In the winters of 1959-61, seven ermine lived on one plot[(a)], and in 1962-63, six.

According to the records of the Tselinograd Observatory, the climatic conditions in these four seasons differed. There was a rise in the average winter temperatures over these years; the snow cover was deepest in 1959-60 and in 1961-62, and considerably less in 1960-61.

From comparison between the data on (a) temperature and the numbers of water voles in the four winters and (b) the percentage of days on which the ermine were active on the snow surface (see Fig.1), it is clear that in the seasons with reduced temperatures, the percentage of active

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(a) The word could refer to length or area, but in this context probably means the number of resident ermine along the standard transect. - Ed.

TABLE 1. Activity of ermine above the snow, as % of census days on which tracks were observed.

Years	Total no. of census days	No. of census days when tracks observed	Percentage of census days when tracks observed
1959-60	37	4	10.8
1960-61	35	4	11.4
1961-62	44	6	13.6
1962-63	45	7	15.5
Total	161	21	13.0

days falls, while with rise in the temperature, it increases. The sharp fluctuations in the average annual numbers of water voles in the four winters, (which are the staple diet of the ermine, according to Novikov) were not related to the steadily increasing activity of the ermine.

(a) % trapping of watervoles

(b) Average monthly temperature °C

(c) % of days when ermine tracks observed

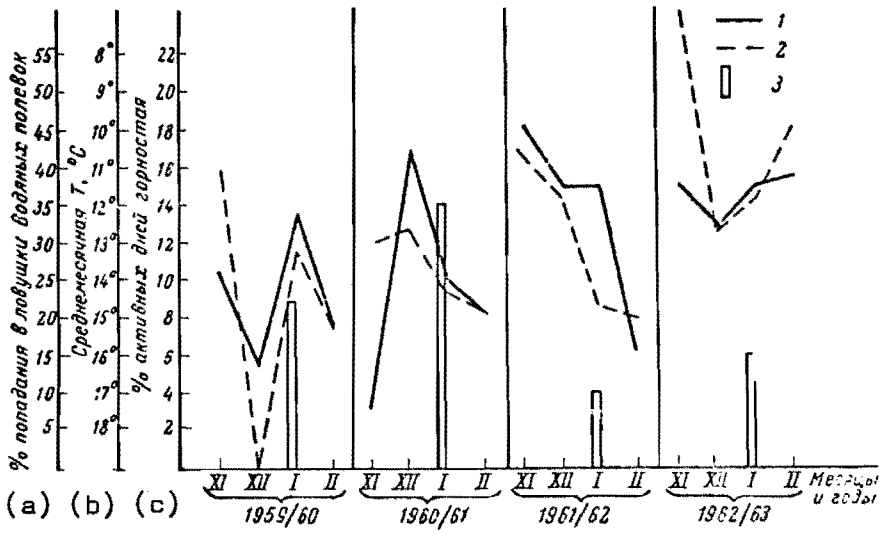

Fig.1. Relationship between temperature and activity of ermine on the snow surface. 1, activity of the ermine (% of days tracks observed); 2, average monthly temperature; 3, autumn-spring trapping of water voles as percentage. [Percentage of what is not stated . - Ed.]

Observations of ermine trails established a direct relation between the length of the foraging excursions of this predator and the average daily temperature (Table 2).

At high temperatures (about freezing point) the foraging trail of the ermine was 4040 m, while when the temperature fell to $-10^{o}C$, the trail was reduced to 368-585 m. On the days when the temperature fell to $-13^{o}C$ and lower, the ermine did not emerge from under the snow at all. We observed three individuals, which, in a period of low temperatures (below -13^{o}), stayed under the snow from 6 to 9.5 days.

Consequently, longer periods spent by the ermine under the snow may be related to colder weather. When the temperature rose above $-13^{o}C$, the ermine left their shelters and began to forage on the snow surface. Analysis of 208 excreta and 31 stomachs of the ermine collected after a stay of 6-8 days under the snow, established (Table 3) that the composition and amount of the food available to them there essentially depend on the presence of certain prey animals. Thus, in the winter of 1960-61 the number of water voles and other rodents were much higher than in the winters of 1959-60, 1961-62 and 1962-63. It follows that the percentage of filled stomachs found in the winter of 1950-61 was highest and that their contents consisted of residues of water voles and other rodents. When the numbers of subniveal rodents are low, the ermine feeds on shrews and plants, e.g. eglantine fruit (Table 3).

TABLE 2. Relationship between length of foraging trail of ermine and average daily temperatures

Dates of observation	Average daily temperature °C	Length of foraging trail of ermine in m	Dates of observation	Average daily temperature °C	Length of foraging trail of ermine in m
2 Dec. 1960	-10.0	585	26 Nov. 1961	-12.6	0.0
4 Dec. 1960	- 4.5	3500	14 Nov. 1962	-13.0	0.0
28 Dec. 1960	- 7.3	1150	15 Nov. 1962	-10.0	368
18 Nov. 1961	- 5.3	2800	16 Nov. 1962	- 7.0	3930
19 Nov. 1961	- 7.3	3100	18 Nov. 1962	- 7.0	3100
21 Nov. 1961	- 7.3	3050	21 Nov. 1962	-10.0	1288
24 Nov. 1961	- 2.0	4040			

TABLE 3. Contents of stomachs and excreta of ermine after a period of 6-8 days under the snow

Years of observation	Indices	No. analysed	Percentage of stomachs with contents	Percentage with residues of				
				Water vole	House mouse	Tundra vole	Shrews	Plant foods
1959-60	Stomachs	9	53.0	63.4	0.0	12.3	3.8	1.3
	Excreta	63	-	51.1	39.1	18.4	2.3	0.0
1960-61	Stomachs	8	75.0	100	33.3	16.6	0.0	0.0
	Excreta	56	-	100	50.0	0.0	0.0	0.0
1961-62	Stomachs	7	42.8	33.3	0.0	0.0	66.6	100
	Excreta	43	-	0.0	0.0	4.6	46.5	65.1
1962-63	Stomachs	7	28.5	0.0	0.0	0.0	57.1	100
	Excreta	46	-	0.0	4.3	0.0	43.4	100

Since the activity of the ermine on the surface of the snow depends on variations in the temperature, in warm winters with temperatures often above -13°C, trapping for ermine may be more successful, while in cold winters, fewer ermine will be caught.

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DATA ON THE BIOLOGY OF THE ERMINE[a]

(Materialy po biologii gornostaya)

By

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Trudy Biologicheskogo Instituta. 1940. 7 : 80-88.

The Biological Station for [research on] the hunting and trapping trade collected material for a study of the biology of the ermine between March 1936 and June 1938. Material for this article was available to the author at the station. Data were taken from day-books of the various out-stations, and from collected skins and carcases from ermine and certain other animals. Rough calculations made by workers at the station were also used.

All field observations, and most of the material, were collected in the Chlymsk, Kargat, Ubin and Vengerov districts of the Novosibirsk province by M.M. Varyshev. Particular attention was paid to studying the food and reproduction of ermine.

I. Food

The typical feeding habits of the ermine during winter were determined by examination of the gut contents of ermine collected by M.M. Varyshev, from hunters in the Chlymsk and Kargat districts, during the winter seasons of 1936-37 and 1937-38. Analysis of the gut contents was done by N.D. Chirkov, using both macro- and microscopic techniques. The latter were used where the stomach or intestines contained only hair and there were no bones or teeth present. In such specimens identification was made from the microscopic structural features of the residue of hair. A very large number of stomachs (75.2%) were empty. This may be because of the trapping

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(a) This old paper has some errors, but is interesting in that it illustrates the difficulties which writers encountered in interpreting field observations, before they tumbled to the fact of delayed implantation. See also Deanesly 1935) - Ed.

methods used : the trapped animal often remained alive for more than 24 hours, and during this time the contents of the stomach became digested and the intestines voided. Results of the analysis of food remains are given in Table 1.

The main food of the ermine during winter was the water rat,[a] which was found in 54% of guts examined in 1936-37 and in 76% of those in 1937-38. The large proportion of water rats found in 1937-38 may be correlated with the great abundance of water rats in these districts during the autumn of 1938, when water rats caused considerable damage to agricultural crops there. The worst losses were in plantations in the Northern districts where, on some collective farms, the harvest was reduced by some 30 to 40% because of water rats. (This estimate was made by the Novosibirsk station for plant protection (Stavzra), which investigated the damage done to crops by water rats in October 1938).

The second most important foods of the ermine,(occurring in 41% and 24% of the guts in 1936-37 and 1937-38), are the small mouse-like rodents which include various voles and field mice.

In four specimens, the remains of birds eggs were found in the ermine guts examined. These were probably the deserted eggs of partridges and other birds, which were commonly found by predators in the following winter.

In approximately 4% of the guts, the legs of the ermine itself were found, which it had chewed off after falling into the trap. Various plant residues occurred intermittently. In one or two instances, remains of chewed-up weasels were found near tracks made by ermine; of these, the ermine had eaten only the brain.

Information on the food of ermine in summer was provided by field observations of 'sign' of the creatures (scats, remnants of food, etc.). They suggest that the main food of the ermine during summer and autumn is still the water rat, which comprises 85% of the summer material, the remaining 15% consisting mainly of smaller rodents. Occasionally, amphibia,

(a) Arvicola terrestris (L). - Ed.

TABLE 1. Data on food of ermine

Date of Trapping	Material: No. of guts examined	Material: Empty	Material: Partly filled	Food remains identified: Water rats No.	Water rats %	Small mouse-like rodents No.	Small mouse-like rodents %	Jerboa No.	Jerboa %	Hamster No.	Hamster %
November 1936	130	106	24	11	45.8	13	54.2	–	–	–	–
December 1936	252	178	74	37	50.0	34	45.9	2	2.8	1	1.3
January 1937	293	260	33	22	66.0	7	21.2	2	6.1	2	6.1
February 1937	109	104	5	4	80.0	1	20.0	–	–	–	–
March 1937	14	11	3	1	33.4	2	66.5	–	–	–	–
Total for season	798	659	139	75	54.0	57	41.0	4	2.9	3	2.1
November 1937	179	124	55	42	76.3	13	23.7	–	–	–	–
December 1937	231	131	58	56	71.8	22	28.2	–	–	–	–
January 1938	201	133	71	58	81.7	13	18.3	–	–	–	–
February 1938	20	11	9	6	66.6	3	33.4	–	–	–	–
Total for season	631	419	212	161	76.0	51	24.0	–	–	–	–
Grand total	1429	1078	351	236	67.0	108	31.0	4	1.1	3	0.9

reptiles and insects occurred.

In the nests of the ermine containing young, only remains of water water rats were found.

The young ermine, when they reach independence, hunt mainly among reedy marsh plains, and, for the most part, catch water rats.

During summer, autumn, and winter, water rat is a very important prey of the ermine, despite the presence of other types of food. The so-called "concentrations" of ermine, which occur in Western Siberia during the second half of the winter, are observed in places where water rats are also concentrated. At this time, the ermine hunts actively under the snow, catching its prey by following their tracks and entering their burrows. The ermine, like other mustelid predators, kills many more prey than it actually needs for food. Surplus kills are dragged into burrows, under turf or brushwood and, frequently, a whole store is so formed. Sometimes it drags the carcase only a little distance away, and buries it in the snow. After the melt, in a season when small rodents are plentiful, such caches are found frequently, suggesting that the ermine frequently does not make use of its food reserves.

The prey of ermine is almost invariably caught under the snow during winter time. Kills on the surface are seen only very rarely.

In different regions of Western Siberia, the qualitative and quantitative composition of the food of the ermine may vary considerably, depending upon the distribution and abundance of different species of rodents. Zverev (1931), who analysed the gut contents of some 1600 ermine taken from the Southern part of the Omsk region during 1929, found that water rats accounted for 29.25% of the food of the ermine, whereas smaller rodents accounted for 64.7%. It should be mentioned that, in the Omsk region, the population density of the water rat is considerably less than in the districts [near Novosibirsk] which we have described.

II. Reproduction

Indications of rut or mating in ermine are: darkening of the sexual organs, increase in size of the testicles of males, and swelling of the milk glands and sexual organs in the females. These changes first appear during the month of February, and, at the same time, some increase in the activity of the males will be seen.

During the rut, the darkening of the sexual organs and elongation of the scrotum is clearly marked in the skins of males which are trapped. Examination of some hundreds of skins of ermine at the warehouses has shown that indications of the rut begin to appear in early March. During this period, few examples of paired tracks are observed in the field : occasionally, signs suggest that some ermine have mated in undersnow burrows. Mating activity is most frequently observed during the second half of March, and it continues right up until the end of April and is sometimes prolonged to the beginning of May. Direct field observations show that only one male mates with a female. Depending on the climatic conditions, the mating period of the ermine varies by about 10 days either way.

Pregnant female ermine are found towards the end of March, with embryos measuring 6 to 7 mm. The earliest births take place from 12 to 16 April, and the latest in the middle of May.

TABLE 2. Data on litters of young ermine

Period of birth	Date when discovered	Place where nest was located	No. of young	Age in days (a)
27.3- 1.4	16.4.36	In fissure in clayey soil	9	15-20
2.4- 5.4	17.4.38	In meadow in roots of willow shrub	9	12-15
10.4-11.4	12.4.38	In floodplain on hillock	6	1- 2
10.4-12.4	17.4.38	In floodplain on hillock	9	5- 7
8.4-18.4	8.5.38	On ridges in salt marsh, on dry mounds	12	20-30
8.4-18.4	8.5.37	On ridges in salt marsh, on dry mounds	6	20-30
14.4-15.4	17.4.38	On ridge in heap of hay	11	2- 3
14.4-16.4	21.4.38	In meadow on heap of straw	12	5- 7
18.4-19.4	20.4.37	In meadow on heap of straw	3	1- 2
25.4-28.4	10.5.35	In meadow, in hay rick	9	12-15
25.4- 5.5	25.5.37	In field of stubble in burrow	9	20-30
1.5- 2.5	3.5.37	In meadow in heap of rotted autumn sedge	11	2- 3
3.5- 5.5	10.5.35	In field in burrow	9	5- 7
4.5- 5.5	6.5.37	In floodplain on hillock	6	1- 2
5.5- 9.5	15.5.36	In heap of rotted birch-aspen wood	6	6-10
	27.3.37		12	Pregnant
	28.3.37		11	Pregnant
19.5-20.5	17.5.37		6	Pregnant

From the data given above it can be seen that births of young ermine occur between the beginning of April and the middle of May, and that the average number of young is 8, varying from 3 to 10-12. One female was found on 17.5.37 in the latter stages of pregnancy, which may indicate that the period of birth may be prolonged until the end of May.

The literature suggests that the gestation period for ermine is 74 days (Yurgenson 1930). According to our own data, young ermine are born in mid-April, and if we take the gestation period as 74 days, then this would place the occurrence of rut and mating in the period between the end of January and the beginning of February. In actual fact, the first signs of rut were observed only after the beginning of February, and most mating activity appeared to occur in March. Therefore, our estimate of the gestation period does not coincide with that given by Yurgenson (1930).

(a) Klimov's error, in estimation of the age at which kits open their eyes, may make these figures somewhat suspect - see p.114. - Ed.

Further, on 19.7.36, a male ermine was trapped which showed enlargement of the testicles (dimensions 7 by 16 mm): and between 10 and 20 November 1936, double or paired tracks were observed of "courting" male and female ermine, over a distance of 1.5 km (trampling down in some places, crawling on the belly, and other signs of mating behaviour similar to those observed in March).

In summary, these data on the periods of mating and birth, suggest that the breeding season of the ermine is very prolonged, and may possibly include some latent period, and that a false rut or mating occurs in March and April. N.D. Grigor'ev (1938) likewise concluded that there is a prolonged gestation, and that mating actually occurs during the autumn. If, however, mating does occur in spring, then the gestation period of female ermine must be only about one and one half months.

Observations of nests with young were made during the nesting period. The sites chosen by the ermine were often alike in different habitats (see Table 2). Marshy ground is no obstacle to nesting for ermine: earlier, M.M. Baryshev (1931-33) had twice found broods of ermine in covered nests among purple willow shrub in flood plains. If the nest is formed in a burrow, it is made as a circular chamber, having a diameter of about 30 cm. Apart from the principal burrow, the ermine also have a number of temporary refuges nearby. Dry leaves usually form the floor of the burrow, or wool or skin from prey animals. Sometimes reed-mace seeds, tow, or wool from domestic animals is used.

The young are born naked and blind and are about 5 to 5.5 cm long. Their eyes open in about 10 days,[a] and at the same time, their fur begins to grow. By the middle of August, the young males have reached the size of an average female, and by November they are almost full-grown. The young ermine leave the nest at the age of about two months, but the family stays in

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(a) Intensive observations on young born in captivity (Müller 1970 : 343) show that the eyes open at 34 days at the earliest, range 34-42 days. - Ed.

its vicinity until the beginning of September, making short excursions in search of food. From the second half of September and into October the families disperse, and ermine of all ages become more or less nomadic.

The female ermine is a very protective mother to her young. She is quite fearless if her nest is found by a man : she runs about, making a threatening "chirring" sound, and begins to carry away her offspring to a safer place from right under his hand. We happened to observe in 1937 how a female ermine successfully rescued her offspring from a forest fire. She carried the young some three hundred metres from a dry ridge, towards which the fire was running, into a hummocky marsh where there was water. In another case, in April, at a nest located in a stack of hay about to be inundated by flooding of the Kargat river, the mother swam through the flood carrying her kits to a dry ridge.

The female evidently commences to feed her young with animal food from a very early age, since in the nests observed, even those containing the youngest kits, freshly chewed water rats were always found.

There are few data on the participation of the male in the rearing of the young. Only on one occasion was a pair observed, when, on 30.5.36, a male and a female dragged something to a single burrow.

The female ermine apparently becomes sexually mature during the first year of life. A female was caught on 20.5.36 which was one year old and was feeding young.

The sex ratio of trapped ermine is shown in Table 3. The number of females caught at the beginning of the winter is typically much smaller than the number of males. At the end of the winter, the reverse is found, and females are more frequently captured. The reason for this is that the hunters prefer the male ermine which, being much bigger, are worth twice as much as the smaller female and, apart from this, the males are easier to catch than the more cautious females. However, when the supply of males begins to run out, the hunters begin to take the females.

TABLE 3. Sex ratio of ermines taken in the Kargat region, 1936-37 season

Time of take	Number of specimens examined	Sex ratio			
		males	%	females	%
November	124	90	72.5	24	27.5
December	408	259	61.7	149	38.3
January	148	64	43.2	84	56.8
February	43	15	34.8	28	65.2
Total	723	428	59.0	295	41.0

A batch of 506 ermine pelts, gathered at the Novosibirsk base from various districts in the Novosibirsk region and the Altai border, were examined in December 1936. Among these there were 284 males (56.1%) and 222 females (43.9%). A batch of 1603 pelts, gathered from the Kuibyshev district of the Novosibirsk region in December 1937 and January 1938, comprised 58.5% males and 41.5% females. Zverev (1931) found 53% males, and 47% females, among 1734 ermine caught during the winter in Western Siberia. These figures suggest that, under natural conditions, the sex ratio of the ermine is about 1:1.

Conclusions

The ermine is one of the main resources for winter industries in the woodland steppe zones of Western Siberia. The value of ermine pelts in warehouses in Novosibirsk is considerable, and is the second most important winter product (about 30% of total value) from this region. In view of the value of the pelts, and the highly developed techniques in the trade in them, the current depletion[a] of the reserves of ermine is very serious.

The intensity of the trade in ermine fur in the Novosibirsk region is certainly leading to over-exploitation of this valuable resource. This view is confirmed by the following figures(expressed as percentages of the total ermine catch from the Novosibirsk region during 1932):

(a) See Lavrov 1956, this volume - Ed.

TABLE 4. Catch of ermines in the Novosibirsk region

Year	1932	1933	1934	1935	1936	1937	1938
% in relation to 1932	100	117.1	77.6	70.0	58.4	69.3	63.2

It should be noted that the fall in numbers of pelts in the warehouses is most marked in the Western districts of the Novosibirsk region (to the West of the River Ob); where the ermine is the principal fur species: this has not so far happened in Northern and Eastern districts of the region. A different pattern is seen in the Narymsk province, where, in most places, the ermine are insufficiently exploited, because of the very low density of the [human] population.

Data on the diet of the ermine show that the value of these predators to agriculture is quite considerable; they consume many of the mouse-like rodents, which seriously damage farm crops. Among the rodents caught by ermine, the water rat is particularly important, as is the widely distributed farm pest, the narrow-skulled vole.(a) There is clearly a need to plan the organisation of the industry in the very near future, or to prohibit the taking of ermine for 2 to 3 years in the woodland-steppe of the Novosibirsk region, in order to conserve populations of ermine.

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(a) Microtus (=Stenocranius) gregalis. - Ed.

STOATS AND WEASELS AND THEIR WINTER HABITATS[a]

(Kärpästä ja lumikosta ja niiden talvisista elinpiireistä)

by

E.S. Nyholm

Suomen Riista, 1959. 13 : 106-116

Winter for many people is a dead time, without interest. Nature seems then as though in a state of rest, getting ready to prepare for another spring: most of the birds have migrated to southern wintering regions. Nevertheless, winter is actually the best season for the observer of mammals, for then their activities can be read by following trails of prints in the snow. It is possible to observe how they obtain their food in difficult conditions, and their shelter against cold weather and enemies. In the snow of early spring one can also see signs of the courting displays of many species.

Among the trails of predators, those of the stoat are most frequently found: sometimes, in the country, the stoat's trails are seen almost everywhere. It is easy to gain the impression that the stoat is particularly abundant in that area. Occasionally, very small "stoat prints" are also observed. All these trails appear to wander aimlessly here and there. In order to interpret these signs, an attempt must first be made to answer the following questions: what is the difference between the trails of stoats and of weasels ? and what is the difference between the foot prints of males and females ? In addition, there are other problems. For instance, how do stoats and weasels travel great distances at night time ? What kind of habitat do they live in, and how do they hunt in it ? How clearly defined are their living territories, and how do they behave towards each other ?

The best method of investigation into these questions is that of following their trails and making observations along them. This investigation, in which the above method has been used (making use of the relation between the stoat and the weasel, and also their habitats in winter), was carried out in 1952-58 in different parts of Finland. Observations were made in the following localities: Helsinki, Rautalampi, Joensuu, Kempele, Oulu, Oulojoki, Hailuoto, Ii and Kuusamo.

The best time for tracking, as with other mammals (Koskimies 1957), was 1-2 days after a fall of snow. I often had a dog to help me in following the trails.

The average length of the footprints was determined by measuring the lengths of 100 normal prints of both species in ordinary snow. I also measured the normal lengths of 100 strides between groups of prints of stoats and weasels. Then the tracks of males and females can be distinguished, and generally also the boundaries between the territories. I followed the trails on the map of the district's waterways, which I had enlarged from the regional topographical map. In the maps I used 2 scales, viz. 1:10,000 and 1:5,000. Gradually the areas of the territories, and their boundaries, became clear, and the sizes of the hunting areas within them(a). Moreover in trapping stoats previously my attention had been drawn to the questions of habitat and territory in stoats(b).

Stoats prefer a diverse habitat where fields, thickets and small ponds characterise the landscape. They hunt through haysheds and huts in clearings, and follow brookside coppices and the banks of lakes and rivers.

(a) In Nyholm's terminology, the "territory", the whole area known to the animal, comprises a number of "hunting areas" hunted in turn: see Fig.1 - Ed.

(b) Implying (?) that he had some earlier data for comparison with the present study - Ed.

The results show that each territory contains 1-5 dens, from which the stoats forage in different directions, although often in only one direction. By following these foraging trails, the positions and extent of the hunting areas may be worked out (Figs 1 and 2). The territory of a male stoat near Joensuu city (Fig.1) was observed. It covered 34 ha of very

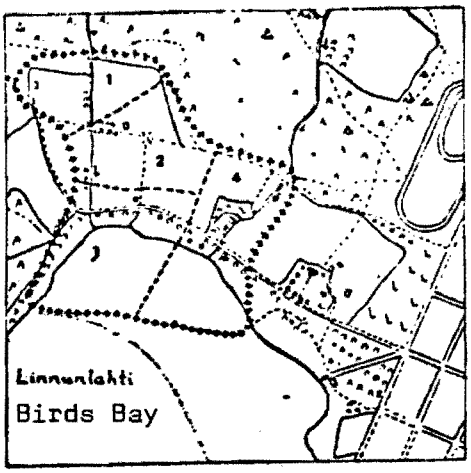

Fig.1 The territory of a male stoat near Joensuu, divided into four hunting areas (1,2,3 and 4). Theoutline of the territory is shown by a line of crosses, and of the hunting areas, by a broken line

variable terrain (see sketch map), comprising cultivated ground, ditches, haystacks, drains, thickets, undergrowth, brushwood heaps on the coast, and other places favoured by stoats. In Fig.2 are shown the movements of the owner of this territory, mapped for 17 different observation periods of 24 hours each, viz. on January 1,2,3,4,5,6,7,8,9,10,11,12,13,19,20,21 and 22 of the year 1957. The extent and size of the hunting areas in this territory - in which the stoat hunts one day, and then moves to another area - are clearly shown. The areas were 1 = 5.2 ha; 2 = 7.1 ha; 3 = 11.1 ha; and 4 = 10.8 ha. It is practically impossible to define the hunting areas very accurately: in this case the stoat had once hunted in more than one area in the same night, but broadly speaking the division is correct. It was of interest to observe that, on that night, the stoat used the same route as usual in moving between hunting areas. Likewise, when a new individual took possession of a territory after its former owner had been snared, the tracks made by the new owner were broadly the same as before.

These tracks ran between places which stoats obviously like.

I should also mention that the [Joensuu] stoat [of Fig.1] had two kinds of sleeping quarters in different places in its territory. Some of these were used permanently, some quite casually (Fig.2). Four of the permanent hiding places were found : two in barns, one in a pile of logs, and one under a fallen pine stump on a bank (Fig.3). The temporary sleeping quarters were mostly in ditches in hunting area No.4. Whenever the stoat transferred its activities from one hunting area to another, it generally slept in these regular hide-outs.

Voles and mice constitute the stoat's chief food, but along its trails I have found remains of other animals, e.g. rabbits, grouse, black-cock, partridge, thrush, duck and many small birds. I have observed a stoat as it examined a wagtail's nest, on a small rock in a lake to which it must have had to swim about 50 metres. Birds' eggs and young animals are eagerly hunted by the stoat and other mustelids. In making a kill, the stoat usually bites the back of the victim's neck or throat. Once I found a female black grouse, dead but apparently entirely unhurt, along the trail of a stoat. I discovered the cause of death only when skinning the bird. In the back of its neck, in the base of the skull, there were small tooth-marks.

The stoat usually hunts by lying in ambush for voles and mice, apparently in the following way (Fig.4). The stoat scents the prey(a), e.g. from beneath a stump or board, and then bolts it from the other side, by rustling and "jestingly thrusting at random with its front paw"(b) and growling. I have made many actual observations of this, both in the wild

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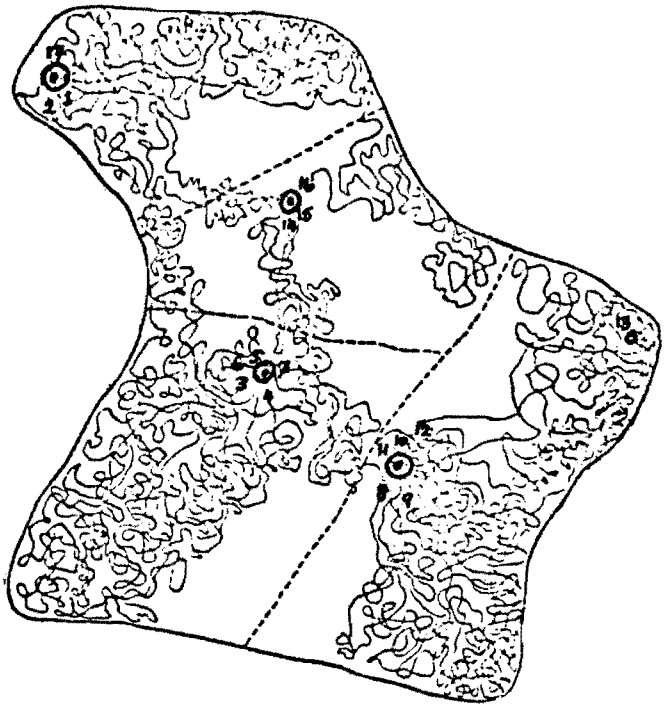
(a) or, locates a prey animal by scent and trails it to its hole - Ed.

(b) See footnote, p.122.



◎ Permanent sleeping quarters

∘ Temporary sleeping quarters

Fig. 2. Male stoat's territory (cf. Fig.1), scale 1:50,000, showing its movements during 17 different 24-hour observation periods. Its longest run on one night was 1850 metres: the average run was 520 metres.

and in captivity. When the small rodent begins to venture out onto the surface of the snow, the stoat gets round in front of it and grabs it with its paws, generally "just when the small creature prepares to steal off under the protection of the snow"(a).

The stoat is able to detect a rodent in a subnivean runway, and may then either dive through the snow, or else wait for the rodent to emerge and then pounce on it as it passes by. The galleries of the rodents run from one place of refuge to another, e.g. under a stump, or large rocks

(a) My attempts to translate the tone of these charming phrases into scientific language have entirely failed. One suggestion, regarding the first, is that the stoat makes a scratching noise, as of a dog at a rat hole. - Ed.

Fig.3. Part of a hayshed in the territory shown in Figs.1 & 2, the site of a stoat's nest. All photographs by E.S. Nyholm.

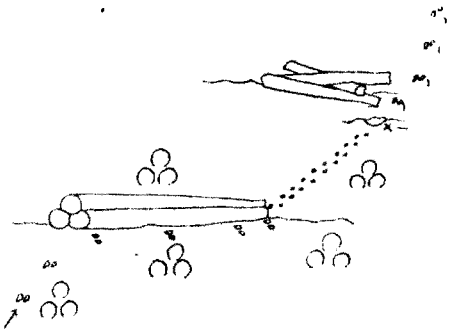


Fig.4 Usual hunting method of a stoat in a familiar territory. Key: stoat prints vole prints hedge stoat prints (vole in mouth) x site of kill

and so on. When hunting larger prey animals, the stoat usually makes use of surprise, either lying in wait for, or stalking up on them. White ptarmigans, partridges and other birds of that size are generally taken unawares from their sleeping quarters; similarly with grouse, blackcock and hares[a]. The stoat finds hares relatively difficult to catch, as they are active at the same time as itself, i.e. at night. For instance, stoats have not been recorded as killing a hare on the island of Krunni, although both hares and stoats are plentiful there.

Stoats hunt in fixed areas, but they will leave these areas if their food becomes scarce. Supplies of their kind of food can vary considerably in amount, and their territories therefore also vary in size. In these investigations, the territories of 63 stoats were examined; I measured the prints and trails, and determined species and sex in each instance. The size of the female stoat's territory varies from 3.7–16.8 ha; the average was 7.4 ha (n = 46). The territory of a male stoat varies from 28.6 to 40.3 ha; the average was 34.2 ha (n = 17). The difference in size of territories used by each sex is thus quite considerable.

(a) Translated as "hare" in one version, "rabbit" in the other - Ed.

It is interesting to compare these results with the figures obtained by Russian investigators. In 1934-45, I.V. Zharkov calculated the areas of the territories of stoats as follows :[a] those of females varied from 0.2-42.3 ha (average 7.1 ha : n = 28), while those of males were larger and varied from 4.2-49 ha (average 20.5 ha : n = 11). The difference was actually much greater than these figures suggest, for only one female's area exceeded 7.8 ha, and that was 42.3 ha: possibly she changed her territory that day.

The size of the stoat's territory can be estimated by two methods. One is to use parallel census lines, separated by the minimum width of the territory of a female : in this study this minimum width was 111 m, so 100 m would be appropriate. Measurements are made (see p.132) from every print encountered along each line. Another way to calculate distance between census lines is to add the average lengths of the territories of each sex, and divide by 2.[b] This method gives a greater distance between the lines which are therefore not only parallel, but also crosswise, or chequered. For example, to calibrate the chequer method from figures obtained in this investigation: the average width of the territory of a female stoat was 380 m, and of a male 900 m; the total is 1280 m, of which half - i.e., the distance between census lines - is 640 m. Calculations by the chequer method can be carried out quickly by 2 persons and the result is very satisfactory.

The shape of the stoats' territories varies noticeably as well as their aspect. Some territories are oblong, some a narrow strip (e.g. those along streams), and others were more or less circular (Figs.1 and 6).

(a) the original inserts an obscure phrase here, variously translated, which probably means "by the chequer method" (see below) - Ed.

(b) i.e. the mean of the 2 means - Ed.

Also, the size and shape of the territory is related to the chances of obtaining food within it. If food is plentiful in a district, the territory can be very small from year to year.

It is easy to become acquainted with stoats from their prints and also to distinguish each sex. The stoats in Figs.1 and 5 are good examples. The stoat in Fig.1 was male. The average length of 100 footprints was 4.2 cm, and the average stride length (for 100 strides) was 41.5 cm. In the larger territory shown in Fig. 6, the average length of footprint of the female stoat was 2.7 cm, with an average stride length of 22.9 cm. The owner of the smaller territory in Fig.6, also a female, had footprints averaging 2.5 cm and an average stride length of 26.3 cm. As a further example, a single male stoat from Rautalampi made prints measuring 4.3 on the average, and strides of 66.4 cm. In all the tracks examined the length of the prints of the female stoat varied from 2.5-3.9 cm (average 3.1 cm). Those of the males averaged 4.6 cm. The difference was therefore quite distinct. There was also a very marked difference between the length of the stride of each sex. In the female, it varied from 8-49 cm (average 30.2 cm): in the male, from 28-96 cm (average 56.3 cm). The sexes of the stoats tracked could therefore be distinguished; and in this investigation, the diagnosis for each individual was confirmed by trapping. Only one mistake occurred, involving a large female stoat. The going had been flocculent for some time and in the soft snow the print often became enlarged so that the measurement was not correct.

Many more females were encountered than males (46 to 17). This does not necessarily mean that the sex ratio would be this unbalanced in nature. The different movements of the male and female, or even sheer chance, could account for these results.

Stoats hunt principally at night, and, especially in moonlight,

they can run absolutely incredible distances in their own territories: once, I followed one almost 6 km. This stoat was clearly a transient, moving to another district. Such things happen very often; in some regions the stock of small prey animals may become exhausted. Or, stoats may suddenly move out of their territories for other reasons: I have caught them just leaving even places where there were plenty of small animals, e.g. field voles, wood voles, and harvest mice, especially in barns.

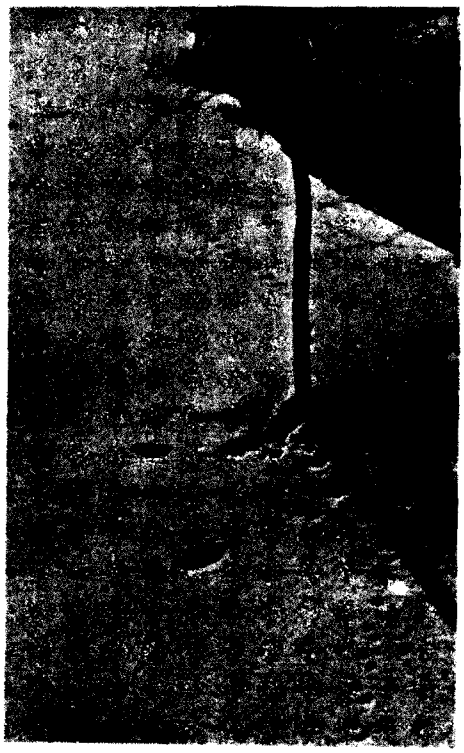
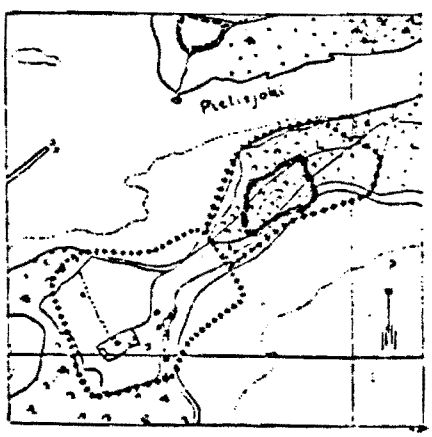


Fig.5. The stoat usually hunts his prey on the surface of the snow.



Pielis river

Fig.6. Territories of 2 female stoats and male weasels near Joensuu. The outline of the stoat territories is marked by a line of crosses, and that of the weasels by a broken line.

According to investigations in other countries, the rutting time of the stoat in Central Europe is summer, and if this is also true in Finland, would be difficult to detect.(a) In farmyards(b) I myself have seen indications of this kind on the 16 June; but also, at the beginning of February, I have confirmed stoat prints showing courting displays in the snow. It is difficult at present even to estimate at what time the stoats' rutting season occurs in Finland, but more recent investigations may be more informative. If conditions(c) in Finland are markedly different from those in Central Europe, the reproduction patterns of stoats could also be quite different.

The weasel preys on small animals e.g. voles and mice, but it eats insects and their larvae, and even worms. It steals the eggs and young of small birds and kills the mother too if it can. It has also been known to attack larger birds, such as grey partridges, partridges and white ptarmigans, by surprising them in their sleep at night, in the same way as does the stoat. It bites the throat, holds on and hangs there until life is extinguished. However, its methods of hunting small mammals are different from those of the stoat. Being small and supple, the weasel is well adapted to hunt along the voles' runways and can easily enter their holes. It seldom uses the stoat's "bolting" method: only once, in the early summer, have I actually observed this behaviour. Generally, the weasel pushes its way into a rodent's nest, kills the owner, and remains there for some time.

The weasel occurs wherever there are small mammals, but I do not know any part of our country where it is particularly common. In many places it follows [the movements of] small mammals: it can be encountered

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(a) i.e. Nyholm's snow tracking methods would not apply. - Ed.

(b) possibly meaning "in captivity" - Ed.

(c) presumably, climatic conditions. - Ed.

in the woods, in cultivated land, meadows, near lakes and rivers and similar places, and is often found in stacks of corn infested with mice and voles. Here when mice and voles are very abundant, it can romp like the devil, hoarding them in its den. The small weasel often uses a single such den for long periods. Once I followed a weasel up to where it disappeared in a snowdrift. The crust of the snow was hard, and I missed its tracks on a bare patch of earth. Then I strewed soft snow in a circle around the hole to which I had seen the weasel taking many voles. It hunted from this den for 5 days and nights. On opening the den, I found there 9 voles, 6 wood voles and 19 harvest mice: it appeared certain that this den had been used before. The dens of mustelids such as wolverines, martens, stoats and weasels, have a characteristic appearance. They are also able to find larger prey after 24 hours in the same place (Nyholm 1960).

The sleeping quarters of the weasel are found in various places. It may spend the day under a corn- and haystack or a shed. For a breeding den, it takes a nest of a vole or mouse, which may be in a brush pile, under a stump, on the ground, in moss or arable land.

This investigation comprises observations on only 6 female and 9 male weasels. The methods used were the same as with the stoat, but in the study of the weasel, determination of the size of the territory was much more difficult, as it moves about a great deal under the snow. The territories of females varied from 0.2-2.1 ha (mean of 6 observed was 1.2 ha). Those of males were 0.6-3.0 ha (mean of 9 observed was 1.7 ha). Because of the small number of observations, and the subnivean activity of the weasel, no further conclusions can be reached on the difference in size of the territories of each sex. However, the size and location of the territory is determined very largely by the distribution of small mammals. The territories of stoats and weasels can occupy the same ground (3 observations; Joensuu, Rautalampi and Kuusamo); there does not seem to be any rivalry between them (Fig.8).

In Finland, weasels are easily distinguished from stoats by their trails (Fig.8). On the other hand, the trails of male and female weasels cannot be distinguished by the length of the stride. The foot print of the weasel varies in length from 1.8–2.4 cm (average 2.05 cm : 15 examined). The length of the stride varied from 12–32 cm (average 19.6 cm). I checked my identifications by catching the weasels at the same time as the stoats, but the differences between the prints of male and female weasels were too small to be of use. The small number of observations added to the difficulty in making this distinction.

The weasel catches its prey at night like the stoat, but in moonlight I have occasionally seen a weasel continuing to hunt right into the morning.

Fig.7 The stoat and the weasel readily live in haysheds. In the figure we see the stoat in summer eagerly peering from his favourite haunt.

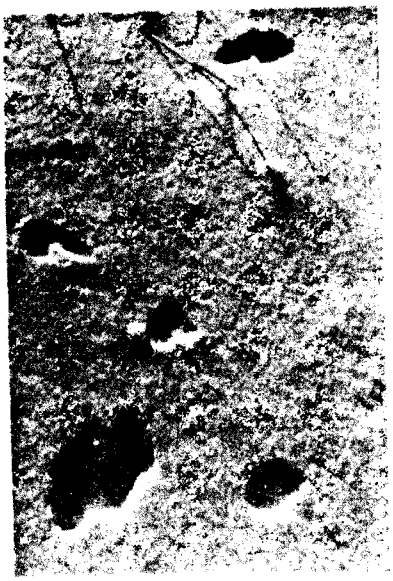

Fig.8 The prints of stoats and weasels, side by side in their common territory.

-Ed.

The stoat and weasel are closely related, but they can co-exist because of their different hunting methods: they are active on different levels. The stoat hunts principally on the surface of the snow, penetrating beneath it only occasionally (Fig.5). When it has scented a vole under the snow, it plunges through to catch it, or it awaits its opportunity, when the vole comes up to the surface to "breathe".(a) The weasel, slim as a snake, hunts chiefly below the snow surface, near or on the ground. It comes up only now and then, and before long is again waiting round about the voles' breathing holes(a) under the snow and in their network of tunnels. The hunting paths of these two predators meet infrequently, and I observed the common territories of stoats and weasels have been in use for many years. Apparently the two species benefit each other: the weasel drives the rodents up to the surface, and the stoat forces them back down again under the snow (Fig.9)(b).

(a) Figuratively speaking. There is usually sufficient oxygen in the subnivean runways. - Ed.

(b) A poor photograph, omitted. - Ed.

Fur trappers in the course of their work, may help to detect the stoats' territories, and so additional information can be made available to evaluate the populations of stoats by either the line or square method. Further investigation would clarify the effects of the stoat and weasel on the game industry. Agriculture does both species a great service in routing out small rodents.(a)

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(a) Many voles are displaced by harvesting and exposed to predation. - Ed.

AGE DETERMINATION AND AGE STRUCTURE OF PINE MARTENS IN LITHUANIA

(Opredelenie vozrasta lesnykh kunits i ikh vozrastnoe sootnoshenie v Litovskoi SSR)

by

S.A. Mal'dzhyunaite

Trud. Akad. Nauk. Litov. SSR Ser.B. 1957 (3) : 169-177.

Abstract: From craniological characters and the analysis of 16 measurements of the skull, pine martens from the territory of Lithuania have been subdivided into three age groups: under one year, one to three years and over three years. Data are presented on the age ratio of the pine marten in the Republic.

Investigations of the changes in the numbers and reproduction of furred animals, and study of their age distribution and sex ratio, make it possible to trace how hunting influences the numbers and age composition of each species and to standardise, and also to organise properly, the exploitation of these resources.

However, determination of the age of a dead animal presents no small difficulties. The weight and size of the body cannot serve as age indicators, since by the hunting season, young animals have already reached the size and weight of adults. For example, according to our findings, the average body length of female martens reaches 41.9 cm (from 39.5 to 44) within a year of birth, and the body weight on average 922 g (range 575-1250 g): the body length of adult [female] martens on average is 42.4 cm (40.5-45.5 cm) and body weight 940 g (740-1325 g).

The most characteristic features changing with growth of the animal are changes in the ratios of measurements of the skull, and the development of its various parts. The main changes in the skull result

from rapid development of the musculature, and also of the thickness of the skull. This has been noted by A.A. Paramonov[1] in Siberian polecats and by V.N. Nadeev and V.V. Timofeev[2] in sables.

The technique of age determination from craniological characters is dealt with by a number of authors. A.A. Paramonov[1] described the changes with age in the ratio of the various parts of the skull of polecats, and V.L. Zaleker[3] used craniological characters to subdivide wild-caught sables into two age groups. V.N. Nadeev and V.V. Timofeev[2] from analysis of 16 measurements of the skull, subdivided sables into four groups. P.B. Yurgenson[4], studying the skulls of martens caught in a hunt, subdivided them into four age groups.

To study the characteristic signs of age and establish the age groups of pine martens inhabiting the territory of the Lithuanian SSR, our basic material was provided by a series of 168 skulls and 206 carcasses of martens caught in the hunting seasons of 1952-1954. The reference material was provided by the skulls of martens of known age taken from the Zoological Farm of the Institute of Biology of the Academy of Sciences of the Lithuanian SSR. The skulls were treated according to the requirements of collection material.

Our investigations were based on 16 skull measurements :

(1) total length - from the most anterior point of the premaxilla (in front of the incisors) to the most posterior and highest junction of the occipital and sagittal crests;(a)

(2) the basilar length - from the posterior side of the incisors to the depression of the occipital bone;(b)

(a) In marten, the occipital crest of mature specimens protrudes posterior to the occipital condyles. - Ed.

(b) The posterior point for this measurement is usually the anterio-ventral margin of the foramen magnum, but from this text it is not clear whether the measurement could have been made to further back (it is the same measurement referred to (in stoats) on pp. 44,61ff). See also measurement no.4. - Ed.

(3) the condylobasal length - from the most anterior point of the premaxilla to the hindmost extentions of the occipital condyles;

(4) length of the ventral side of the cerebrum - from the palatine incisure [the posterior margin of the hard palate] to the "depression of the occipital bone"[a]

(5) length of hard palate - from the most anterior part of the premaxilla to the palatine incisure;

(6) the mastoid width - the greatest width of the skull in the region of the mastoid processes;

(7) the zygomatic width - measured across the posterior parts of the zygomatic arches furthest apart;

(8) the width of the skull capsule - in the mastoid region, the widest part of the cranium;

(9) the width of the rostrum (skull over the canine teeth) - the measurements were taken at the base of the canine teeth;

(10) the interorbital width - in the narrowest part of the skull in front of the supraorbital processes;[b]

(11) the postorbital width - in the narrowest constriction of the skull posterior to the supraorbital processes;

(12) the width between the apices of the supraorbital processes - at the most protruding points ;

(13) the height of the skull - in the region of the tympanic bulla ;

(14) length of upper row of molar teeth - from the anterior side of the canine[c] teeth to the posterior side of the last molar;

(15) length of upper row of teeth - from the anterior side of the upper canine tooth to the posterior side of the last molar;

(16) length of lower row of molar teeth - from the anterior side of the lower canine tooth to the posterior side of the last molar.

(a) See footnote re no. (2).
(b) The term "supraorbital process" is preferred to "postorbital process" (a common alternative) to avoid possible confusion with "postorbital constriction". - Ed.
(c) Nos. (15) & (14) appear to be the same unless in (14) the measurement was taken from the anterior side of the first premolar. - Ed.

We also studied the dimensions of the sagittal crest, namely: the width at the base, the width at mid-length, the width in the region of the postorbital constriction, the height of the sagittal crest and its length [from the occipital crest] up to the point of bifurcation.

In this way all the changes occurring during growth of the skull in length, width and height were covered.

On the basis of these measurements of the skull we subdivided the pine martens of the Republic into three age groups.

The first age group includes martens under one year (see Figs.1 (a) and 2 (a)). Absence of the occipital crest is characteristic of this age. At the age of two months, at the site of concrescence of the parietal bones and the superior occipital bone, there even forms an inward bend, which is later transformed into a wide ridge - the rudiment of the occipital crest. The left part of the occipital crest falls to meet the right part over a fairly long distance.

The individuals of the first age group have no sagittal crest. At this age, it is present only in the form of imperceptible ridges, the so-called temporal lines, along the parietal bones, starting from the occipital crest and ending in the supraorbital processes. The separation of the temporal lines at the base [i.e. posteriorly] is usually less than at the apices of the supraorbital processes.

A fairly wide postorbital narrowing is characteristic of the first age group. In young martens (two months old) the postorbital constriction is even wider than the interoribtal width of the skull. Later, the post-orbital constriction gradually diminishes, and at the age of 8-10 months, in the females its dimensions range from 16.5 to 21.0 mm (on average 18.7 mm), and in the males from 17.0 to 21.8 mm (on average 19.9 mm). It should be noted that the ratio of the width of the interorbital and postorbital constructions also changes with age. In the first age group, the width of the postorbital constriction is greater than the interorbital. For example,

the ratio of the interoribtal to the postorbital width in males is on average 1.02 (0.86-1.13) and in females 0.97 (0.74-1.10).

In martens of the first age group the total length of the skull, the basilar length, the condylobasal length and the zygomatic width of the skull are all shorter than in the other groups. With age there is also increase in the length of the cerebral part of the skull, the length of the hard palate, the greatest width of the skull and the width of the skull over the canine teeth. During the growth of martens the cerebral part of the skull decreases, namely, the width of the skull capsule, the postorbital width and also the height of the skull (see Tables 1 and 2).

In some individuals of the first age group the sutures of the skull bones are still visible. The sutures of the nasal bones are particularly clearly outlined even at the age of 8-10 months.

The second age group comprises adult martens under the age of three years (see Figs.1 (b) and 2 (b)). In the individuals of this age group, at the junction of the pareital bones and the superior occipital bone a rudimentary crest forms, the left part of which does not meet the right over a shorter distance than in the preceding group (see Table 3).

Appreciable changes are also observed in the development of the temporal lines, the width between which gradually narrows. This narrowing takes place over their entire length, and their union begins at the base [occipital end] of the skull. At the junction of the left and right parietal bones, an eminence forms - the rudiment of the future sagittal crest, the height of which, in the females reaches on average 1.1 mm, and in the males 1.4 mm.

The width of the postorbital constriction appreciably decreases, according to our findings, on average by more than 1 mm. Since the interorbital width and the width between the apices of the supraorbital processes increase, the postorbital constriction becomes more noticeable. The ratio of the interorbital to the postorbital width in males is on

average 1.09 (0.98–1.25) and in females 1.10 (1.00–1.23).

In martens of the second age group the nasal sutures are almost completely coalesced.

The third age group consists of martens over three years old (see Fig.1 (c) and 2 (c)). Because of the development of the muscles the occipital crest, in the martens of this group, becomes very pointed and stands out clearly. The left and right parts of the occipital crest unite through the sagittal crest. This particularly applies to males: in some females the distance between the right and left parts of the occipital crest is [still] quite considerable.

Drastic changes are observed in the development of the temporal lines. They converge forming the sagittal crest, which is higher at the base [posterior] of the skull, decreasing anteriorly. Sexual dimorphism is particularly manifested here : in the males the crest is always higher than in the females. The height of the sagittal crest at the base of the skull in males reaches on average 4.0 mm, and in females 2.1 mm. It should be noted that in females a well developed sagittal crest forms only at the base of the skull. The temporal lines diverge towards the anterior, forming the shape of a wedge. This bifurcation of the sagittal crest is observed in males only at the postorbital constriction of the skull, on average 38.5 mm from the base of the skull.

The changes in the postorbital constriction become particularly obvious if we compare its width in the individuals of the third and first age groups. According to our findings, the postorbital constriction decreases in width by almost 2 mm. The ratio of the interorbital to the postorbital width in males is on average 1.28 (1.02–1.64) and in females 1.17 (1.03–1.35). The sutures of the nasal bones grow together and become imperceptible.

Table 1. Measurements of skulls of male martens by age group (in mm)

	Age Group I		Age Group II		Age Group III	
	Range	Mean	Range	Mean	Range	Mean
1. Total length	80.6-90.8	86.84	81.0-90.8	87.37	77.8-90.2	87.60
2. Basilar length	70.5-84.8	77.80	74.7-87.8	78.76	71.7-81.8	78.13
3. Condylobasal length	76.8-88.8	83.51	73.8-87.2	84.30	78.6-89.3	84.54
4. Length of cerebral part	32.4-38.0	35.76	34.0-38.5	36.30	34.4-38.5	36.21
5. Length of hard palate	37.6-44.8	41.72	40.7-43.8	41.98	34.3-44.8	41.74
6. Mastoid width	36.3-49.2	39.55	34.7-41.5	39.41	36.2-42.4	40.03
7. Zygomatic width of skull	42.2-50.0	47.06	41.7-52.1	47.88	46.7-53.2	50.26
8. Width of skull capsule	34.3-38.4	36.51	33.5-39.0	36.15	32.8-37.9	35.72
9. Width of rostrum	15.0-18.6	16.80	15.0-18.0	16.65	16.0-18.6	17.27
10. Interorbital width	18.6-22.7	20.58	18.8-22.8	20.74	19.2-23.5	21.22
11. Width between apices of supra-orbital processes	21.2-25.7	23.93	21.7-27.2	24.01	23.0-28.6	25.55
12. Postorbital width	17.0-21.8	19.91	17.8-23.3	18.92	12.8-21.7	18.23
13. Height of skull (without sagittal crest	29.3-34.2	31.76	30.2-32.8	31.72	29.0-33.0	31.67
14. Length of upper row of molar teeth[a]	28.2-33.7	31.59	20.8-33.0	31.80	29.7-33.5	31.98
15. Length of upper row of teeth	32.0-38.0	35.73	32.6-37.2	35.90	33.2-37.3	36.09
16. Length of lower row of molar teeth	32.7-38.6	36.11	33.0-37.6	36.70	31.3-37.8	36.12

(a) See footnote (c) on p. 134

Table 2. Measurements of skulls of female martens by age groups (in mm)

	Age Group I		Age Group II		Age Group III	
	Range	Mean	Range	Mean	Range	Mean
1. Total length	67.3-82.3	79.70	77.6-82.9	81.00	76.5-88.9	81.67
2. Basilar length	58.0-82.0	71.35	70.0-77.4	72.01	67.1-78.0	72.62
3. Condylobasal length	63.0-80.0	73.45	77.0-84.3	77.11	74.5-89.4	79.36
4. Length of cerebral part	27.4-35.2	33.13	32.0-35.7	33.54	31.6-37.0	34.16
5. Length of hard palate	29.8-39.3	37.76	37.0-41.7	38.44	35.5-42.2	38.50
6. Mastoid width	33.5-37.0	36.39	35.2-37.8	37.10	35.3-39.5	37.23
7. Zygomatic width of skull	37.0-45.2	43.00	42.4-46.5	44.34	43.4-51.9	45.73
8. Width of skull capsule	35.5-41.6	35.07	32.2-36.0	34.26	31.0-37.7	33.34
9. Width of rostrum	13.2-16.2	14.92	14.1-16.2	15.37	15.1-17.8	15.89
10. Interorbital width	16.0-19.8	18.50	17.8-21.7	19.22	17.7-21.0	19.20
11. Width between apices of supra-orbital processes	20.7-23.5	21.73	21.2-25.0	22.57	21.0-24.8	22.62
12. Postorbital width	16.5-21.0	18.74	15.3-19.0	17.50	14.2-19.0	16.76
13. Height of skull (without sagittal crest)	29.0-31.2	30.02	27.0-31.5	29.38	26.6-31.4	31.66
14. Length of upper row of molar teeth[(a)]	19.3- 29.5	28.39	28.3-31.2	29.11	27.9-32.3	29.53
15. Length of upper row of teeth	21.3-38.2	32.14	31.4-35.6	32.80	30.8-36.0	33.03
16. Length of lower row of molar teeth	19.0-33.5	31.89	32.0-36.4	33.12	31.7-37.0	33.43

(a) See footnote (c) on p.134.

Table 3. Measurements of Sagittal crest of skulls of pine martens (in mm)

	Age Groups					
	I		II		III	
	Males	Females	Males	Females	Males	Females
Width at base	6.7	8.3	2.06	2.27	1.45	1.53
Width at mid-length	6.95	10.15	2.64	5.54	0.83	3.91
Width at postorbital constriction	11.38	13.09	8.59	9.72	4.55	8.51
Height at base	-	-	1.42	1.15	4.03	2.11
Distance between left and right parts of occipital crest	8.37	6.87	4.14	4.12	-	1.46
Start of bifurcation of sagittal crest	-	-	-	-	38.56	-

More exact determination of age, and division into age groups of the individuals over three years of age, present greater difficulties, since by this time the formation of the skull is complete. The technique of determining the age of martens over three is based on study of the process of wearing of the surface of the teeth (P.B. Yurgenson[4]). However, such determination is only relative, since the degree of wear on the teeth is not the same in all individuals. The intensity of abrasion of the dental enamel and dentine depends on the composition of the food.

In our investigations attention was also paid to change in the length of the upper and lower rows of teeth. We established that, with increase in the total length of the skull, the length of the toothrows also increases (see Tables 1 and 2).

The accuracy of determining the age of males from craniological characters was also checked against other osteological signs, namely the structure of the [baculum or] os penis. In the individuals of the first age group, the baculum has the shape of a straight thin rod-like small

bone, the posterior part of which is cartilaginous. The tip of the baculum is forked. Its length is on average 38.4 mm. In individuals of the second group the baculum becomes bony and thicker over its entire length. In the anterior part a closed ring forms. The length is now on average 40.6 mm. In adult martens (over 3 years) the baculum bends upwards in the terminal section, and at the very tip has a closed ring. The posterior part is rougher and more massive than the anterior. The total length is on average 42.6 mm.

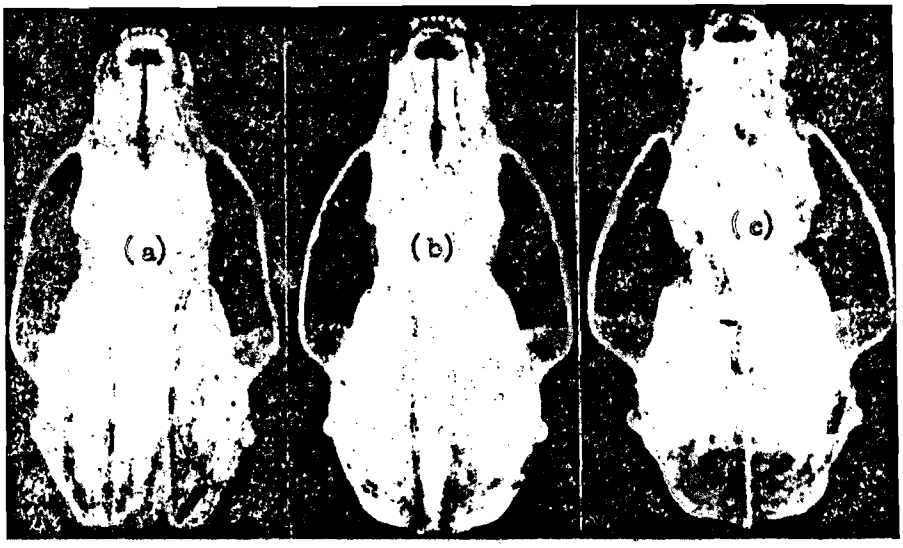

Fig.1. Skulls of pine martens (males). (a) first age group; (b) second; (c) third

Fig.2. Skulls of pine martens (females). (a) first age group; (b) second; (c) third.

Comparison of the results of these investigations on the age structure of the martens of the Republic, showed that the three age groups are unequally represented. Individuals of the first age group comprise the highest percentage (45.3%); second place is taken by the second group (28.6%) while martens of the third age group are in the minority (26.1%).

A somewhat different picture is offered by the structure of males and females separately. Among the females, young martens under a year form the highest proportion (48.4%), with fewer martens in the second age group (31.3%) and fewest of all in the third age group (20.3%). The age ratio in males is different: we observe males over three years most often (40.9%), with smaller numbers in the first age group (36.4%) and the smallest in the second (22.7%).

The structure of the total population of martens (by sex and age groups) was as follows : pride of place is taken by males of the third age group (25.8%), second place by males of the first age group (22.9%), third by females of the first age group (17.8%) and then come males of the second age group (14.4%), females of the second age group (11.6%) and, finally females of the third age group (7.5%).

It is important to note that in natural conditions there are almost half as many males again as females and their numbers in nature(a) considerably exceed the number of females. Of the 201 martens studied by us, 63.7 per cent were males.

Study of the causes of the predominance of individuals of one sex or age group is of great interest. V.P. Teplov(5), on the basis of study of extensive material, made some generalisations on the sex ratio in wild mammals. We do not have sufficient material at our disposal to show the causes of the pattern in the population structure of the martens of our Republic. However, there is no doubt that an important role is played

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(a) But see Teplov (1948), Kraft (1966) and Nyholm (1959), in this volume. - Ed.

here by the special features of the habitat of the martens, and also the time and methods of hunting.

Bearing in mind the fact that martens become sexually mature only in the second or even third year of life, and bear progeny only in the third or fourth year, it becomes obvious that only some 20 per cent of the females take part in the natural production of this valuable furred animal. It should also be noted that in natural conditions the number of progeny of martens is usually small, with on average two or three young per litter.

This possibly is one of the causes of the observed decline in the population of martens in the Republic, despite the increase in their stock each breeding season. Therefore, it appears necessary to modify the methods of hunting, and to capture martens alive, in order to release the females and also the males with the best fur qualities.

Summary

1. Martens inhabiting the Republic have been subdivided by craniological characters into three age groups: the first under one year, the second from one to three years and the third over three years.

2. The most characteristic signs reflecting the process of growth of martens are the changes in the structure of the occipital and sagittal crests, the changes in the relative ratio of the interorbital and postorbital constrictions, the changes in the length and width of the skull, the degree of coalescence of the nasal bones, and, to a lesser extent, the degree of wear on the teeth.

3. In determining the age of the males the development of the baculum is helpful.

4. In natural conditions in the Republic, martens of the first age group predominate (45.3%), second place is taken by individuals of the second age group (28.6%), the third age group being the smallest (26.1%).

5. In view of the reduction in the rate of natural reproduction of martens, it is recommended that they be caught alive and the breeding stock conserved.

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THE MORPHOLOGICAL DEVELOPMENT OF CAUCASIAN PINE MARTENS AND STONE MARTENS IN RELATION TO AGE DETERMINATION

(Nekotorye vozrastnye osobennosti morfologii kavkazskikh lesnykh i kamennykh kunits)

by

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A technique of age determination for the valuable fur-bearing animals would help to solve some important practical problems, e.g. in determining the optimum harvest, the annual population growth, the annual catch, etc., of a given species.

For several years (1952-1958) I studied the biology and hunting [statistics] of Caucasus pine martens (Martes martes lorenzi Ogn.) and stone martens (M. foina nehringi Sat.) in the Krasnodar region. On examination of a considerable amount of material (290 carcasses of pine martens and 54 of stone martens), some interesting data were obtained on the morphology of both species, some of which are given in this paper.

The Caucasian Pine Marten

Appearance and body dimensions. On 29 March 1955 we caught a pregnant female. In all probability it was about to give birth, as on dissection we observed embryos whose appearance and size conformed almost exactly to the description of new-born martens given by P.A. Manteifel (1934). The body length of the embryos, measured from nose tip to the root of the tail, was 9.8 cm, tail length 3.5 cm (Table 1). The embryos were covered with sparse whitish down, the vibrissae and claws were distinct, and the skin was light and devoid of pigmentation.

Observations in a zoo showed that young martens grow very quickly. Their eyes and external ears open on the 32-36th day of life, and the body

dimensions increase rapidly.

Young martens (aged about 2 months) trapped on 27 and 31 May 1954 had a body length of 37.0 and 37.5 cm, and a tail length of 17.0 and 16.0 cm. One taken on 2 June 1954 and about a week older than these was somewhat larger (body length 40.0 cm, tail 18 cm) (Table 1).

At age 3½–4 months the young martens are nearly the size of the adults. A marten taken on 22 July had a body length of 42.5 cm (in adults the body length is 44.0–50.0 cm) and a tail length of 20.4 cm (adults 24.0 cm). In appearance it differed little from adults. At age 4½–5 months the young are almost indistinguishable in size from adults (Table 1).

Martens 6–12 months old are the same size as older ones (18 months and older), which only have somewhat longer feet than yearlings (Table 1).

Table 1. Changes in the dimensions and weight of the Caucasian pine marten with age

Date taken	Approx. age	Sex	L[(a)]	C	P	A	Body wt with pelt, g
29.3.1955 *	–	Male & female	9.8	3.5	1.6	–	29
27.5.1954	57 days	Male	37.0	17.0	8.5	4.0	715
31.5.1954	55–57 days	Not determined	37.5	16.0	9.1	–	–
2.6.1954	62 days	Male	40.0	18.0	9.5	4.1	759
22.7.1954	3½ months	Male	42.5	20.4	8.5	4.4	957
23.8.1954	About 5 months	Female	43.0	22.5	8.5	4.0	769
24.8.1954	" "	"	43.0	–	–	4.0	816
Oct.–March **	6–12 months	Males	46.6	23.7	9.5	4.4	1280
1953–1955		Females	42.6	22.6	8.6	4.1	940
Oct.–March ***	18 months and over	Males	46.6	24.0	9.9	4.4	1360
1953–1955		Females	43.0	22.7	8.7	4.1	950

* Embryos taken from mother's uterus some days before birth

** 149 martens in all; average weight and dimensions given

*** 126 martens in all; average weight and dimensions given – Author

(a) L,C,P & A are abbreviations for the latin terms for the 4 standard measurements of length: Head and body Tail, Hind foot, Ear. – Ed.

Body weight. According to P.A. Manteifel (1934) the weight of new-born martens is 20 g. In the pregnant female we took on 29 March 1955 the weight of the embryos was 29 g (Table 1). The weight of the young at age 2 months is already close to the average weight of the adult female, though they are much smaller than the adults. A young one taken on 27 May 1954 weighed 715 g (without pelt 563 g). A young one taken on 2 June 1954 weighed 759 g (without pelt 635 g) (Table 1).[a]

Proportions and general dimensions of skull. In skull structure, martens aged 2 months exhibit some distinctly infantile features. The brain capsule is rounded, as if swollen; the jaws are shorter (face length 26.0 mm, in adults 35.9 mm); the postorbital width is greater than in adults (at this age it is 29.3% of the condylobasal length of the skull); and the width across the zygomatic arches narrow (greatest width 44.1 mm, in adults 49.6 mm). The whole skull is much shorter than that of the adult: total length 78.5 mm, in adults 87.5 mm.

In young martens aged 3½–4 months, the cranium is narrower and elongated. The face is longer, and so is the length of the upper and lower sets of teeth; the ratio of the postorbital width to the condylobasal length is increased. The total length of the skull of the female we examined at this age was 80.5 mm, the facial length 34.5 mm, and the zygomatic width 43.3 mm. The postorbital constriction was 24.6% of the condylobasal length of the skull.

By age 4½–5 months the skull dimensions approximate to those of martens aged 7–12 months, i.e. to those of yearlings caught in the winter hunting season (Table 2).

According to P.B. Yurgenson's description (1956), at age 7 months to 1 year the skulls have distinct sutures demarcating the nasal bones, rounded swellings directly behind the supraorbital processes, and a post-orbital constriction wider than in the adults. The skulls of the Caucasus

(a) Please turn to p.157.

pine martens exhibit all these features. Their dimensions are almost the same as those of skulls of adult martens (19 months and older). The basilar length of the skull in yearling males is 77.3 mm and in adult males 77.6 mm; females 70.9 mm and 71.3 mm respectively. The condylobasal length is 85.2 mm in yearling males and in adult males 85.3 mm; females 77.9 and 78.3 mm. The facial length is 35.5, 35.9, 32.8, and 32.8 mm respectively. The changes in the width across the supraorbital processes, and postorbital width, reflects the enlargement of the supraorbital processes, and the reduction in size of the postorbital constriction, occurring with age. In males aged 7-12 months the ratio of postorbital width to the condylobasal length of the skull is 23.8%, and in females 26.0%.

Table 2. Age changes in skull and os penis of Caucasian pine martens

Indices (dimensions in mm, weight in g)	Males 2 months	Males 3½ months	Males 7-12 months	Males 19-24 months	Males 2y7m and older	Females ca.5 months	Females 7-12 months	Females 19m and older
(n)	(3)	(1)	(104)	(35)	(18)	(2)	(45)	(73)
Total skull length	78.5	80.5	87.3	87.5	88.0	79.0	79.0	79.4
Basilar length	68.3	73.0	77.3	77.6	78.4	69.6	70.9	71.3
Condylobasal length	76.0	80.4	85.2	85.3	85.8	76.9	77.9	78.3
Rostral width (at posterior margine of canines)	19.2	16.4	17.0	17.6	17.9	15.5	15.6	16.8
Interorbital width	18.2	18.2	21.7	20.3	22.3	19.1	19.1	19.5
Width across supra-orbital processes	23.0	22.0	24.6	26.1	27.0	21.8	22.1	22.5
Width of postorbital constriction	21.8	21.0	20.5	19.0	19.0	20.1	19.2	18.7
Zygomatic width	44.1	43.3	47.0	49.6	50.9	42.6	43.0	43.7
Facial length	26.0	34.5	35.5	35.9	36.4	32.0	32.8	32.8
Mastoid width	38.8	37.4	36.6	35.9	36.1	36.5	34.7	35.0
Height of cranium at tympanic bullae	31.5	31.2	32.1	32.1	32.1	31.1	30.1	29.5
Length of upper row of teeth	21.0	29.4	29.7	29.9	30.1	27.0	27.1	27.3
Length of lower row of teeth	21.0	34.5	36.0	36.2	36.2	32.0	32.5	32.9
Length of baculum	26.5	35.4	40.3	45.4	44.6			
Weight of baculum	0.04	0.08	0.17	0.30	0.32			

At about 2 years of age, the sutures between the nasal bones fuse almost completely and become very inconspicuous. In lateral profile, the the contour of the frontal bones is higher than that of the brain capsule [parietal bones] while in the yearlings the reverse applies (the contour of the brain capsule is higher than or equal to that of the frontal bones). Directly behind the supraorbital processes there are round swellings (in some animals they are noticeable by the end of the first year). The post-orbital width is 22.3% of the condylobasal length of the skull in males, and 25.1% in females. In older martens (3 years and over) these values are 22.1% and 23.9% respectively. The zygomatic width also decreases significantly with age in the males (Fig.1).

Fig.1. Skulls of male Caucasian pine martens

1 - age 2 months; 2 - age 3½-4 months; 3 - age 7-12 months; 4 - age 19-24 months; 5 - over 3 years.

Density and weight of skull. The mass of the skull increases with age, as a result of the bones becoming thicker and more massive. Therefore the total weight of the skull also increases, but the capacity of the brain capsule decreases.

In the skulls of 2-month-old martens, sutures are plainly visible. The bones are thin, light, freely separated, and their surface is rough (Fig.1, Table 2). The skull weight of 2 males averaged 13.880 g (13.380 g

and 14.380 g); density (i.e. the ratio of weight to condylobasal length) was 0.18 g/mm; brain capsule volume was 23.5 cc.

The skulls of martens 4½-5 months old were still somewhat rounded and rough in the occipital region, like young ones, but the surface of the bones already had characteristic concentric convexities. The bones of the ventral and facial regions had become so dense that their surface appeared glossy. Certain sutures between the bones were completely indistinguishable. At this age the weight of the skull of females is 14.310 g and its density 0.19 g/mm; the volume of the brain capsule is 21.0 cc.

From 7 months to 1 year, distinct sutures in the skulls remain only between the nasal bones. The bones become much denser. The weight of the skull of males aged 8-9 months is 19.550 g, and its density is 0.23 g/mm. The brain capsule volume decreases to 22.0 cc. In females the mean weight of the skull is 14.590 g, its density 0.19 g/mm, and brain capsule volume 19.5 cc.

At the age 2 years and older the weight of the skull in males increases on average to 22.645 g, and its density to 0.26 g/mm; the brain capsule volume is 22.5 cc. In females these values are 15.889 g, 0.20g/mm and 20.3 cc respectively.

Development of crests. The median or sagittal crest begins to develop in martens of both sexes from the end of the 1st year of life (it is not evident in animals 8-9 months old). At the age of about 2 years its greatest height (at the point where it joins the occipital crest) averages 2.5 mm in males (range 2.0 to 3.0 mm) (2.9% of the condylobasal length of the skull). In females the skull crests begin to form later and are less well developed than in the males. In 50% of female pine martens the sagittal crest was still absent at the age of 2 years. Its maximum height in the occipital part of the skull of some specimens was 1.0 mm (i.e. 1.3% of the condylo-

basal length).

The occipital crest begins to appear in female pine martens at about 4½–5 months. The height of the occipital crest in males 8–9 months old averages 1.7 mm (2.1% of the condylobasal length), and in females 0.8 mm (1.1%). In some females aged 9 months the occipital crest is scarcely noticeable. At age 2 years and older the mean height of the occipital crest in male pine martens is 2.6 mm (3.0% of the condylobasal length of the skull). The maximum height is 3.0 mm. In females the height of the occipital crest increases on average to 1.7 mm (2.1%), with a range of 1.3 to 2.0 mm.

Dental system.(a) In young martens the teeth (mainly the incisors) start to appear soon after the eyes and external ears open. At this time the young begin to take solid food.

The skulls of 2-month-old martens show both the milk teeth and the permanent teeth, which are already starting to form. The permanent incisors of the upper jaw are in the process of eruption. At this time both the middle and 2nd pair of incisors are full grown, and the 3rd pair has hardly appeared from the alveoli: in their position on the gums, there are only small bulges. The canines are small, needle-like and strongly curved; their width at the base is 3.2 mm, height 8.0 mm, and ratio of width to height 3.6. The same values for the permanent canines of adult male martens are 4.3 mm, 11.0 mm, and 2.5. The permanent canines in 2-month old martens are completely sunk in the alveoli, and on the gums are small openings through which their tips are visible.

In young martens taken on 27 and 31 May, growth of the permanent $\underline{pm}^1$ is observed on the upper jaw. In an animal taken on 2 June this tooth was completely formed. In all three martens the other two premolars and

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(a) In following this description of the development of the dentition, it may help to remember that the adult formula is $\frac{3.1.4.1}{3.1.4.2}$ - Ed.

one molar were still small milk teeth. The length of the carnassial tooth is 9.4 mm, the height 3.7 mm, the length of $\underline{m}^1$ is 3.9 mm, maximum width 3.0 mm. The length of the [upper] row of teeth is 21 mm.

The permanent incisors were formed on the lower jaw of a young marten taken on 2 June. In young taken earlier, the last pair was not fully developed. The permanent canines were completely sunk in the alveoli. The milk canines were 3.0 mm wide at the base, and 6.5 mm long. In a young one taken on 2 June the $\underline{pm}_1$ were almost formed, while in others they had only just appeared from the alveoli. The remaining three teeth present, two premolars and one molar (carnassial), are milk teeth. The permanent teeth are completely sunk in the alveoli, and their tips are visible through openings in the gums. The length of the row of teeth on the lower jaw is 21 mm.

In Caucasian pine martens the milk teeth are replaced at the age of 3-3½ months(a). In a young one taken on 22 July, the development of the permanent teeth was almost complete. A milk carnassial tooth was still retained in the upper jaw, lifted up by the growing $\underline{pm}^3$ and $\underline{pm}^4$. The permanent canines had already reached the size of the milk canines, though their growth had not completely ceased. The milk canines had not yet fallen out, and they were located behind the permanent ones and were completely displaced by them. In front of them was a space enabling the permanent canines to grow freely. Only after the permanent canines reach a size sufficient for them to carry out their function do they force out their predecessors.

In the lower jaw, the last premolar and the 1st molar (carnassial) [milk] teeth were retained on the left side and the 1st molar on the right. The remaining milk $\underline{pm}$ was pushed out by the permanent $\underline{pm}_3$ that had appeared from the alveoli. The $\underline{pm}_4$ which would replace the milk carnassial teeth were still not visible. The length of the row of teeth on the upper jaw was 29.4 mm, and on the lower jaw 34.5 mm.

(a) P.B. Yurgenson mentions the same timing for other martens, and P.A. Petryaev (1941) and others, for sables. – Author.

At the age from 7 months to 1 year, the milk teeth are all shed, and the permanent teeth have fully developed, but exposure of the dentine on them was not noticeable.

In the 2nd year of life in the pine marten the teeth as a rule do not show exposed dentine. However, at the end of the second year considerable wear of the enamel covering of the $\underline{pm}^4$ and $\underline{m}^1$ of the upper jaw and the $\underline{m}_1$ of the lower jaw may be observed (most often in the males).

The teeth in martens over 2 years old show exposed dentine, enlarging in area with age. Martens often have carious teeth, which in some specimens may be completely destroyed.

Dimensions of testicles and baculum. In a young one taken on 27 May 1954 (age 2 months) the testicles were small (4 x 2 mm) and undeveloped. In one taken on 2 June 1954 the testicles were 6 x 3 mm. In a young marten taken on 22 June (age $3\frac{1}{2}$–4 months) the testicles, 8.7 x 4.9 mm, were close in size to those of an adult male in the period of sexual quiescence (10.0 x 5.5 mm).

Adult martens can be easily distinguished from yearlings by the structure and size of the baculum (Popov 1943). In young animals this small bone does not have a thickened base, its length averages 40.3 mm (8.9% of body length), and its weight 0.17 g; in adults these values are 45.4 mm (9.9%) and 0.30 g (see Table 2).

The Caucasian Stone Marten

Proportions and general dimensions of skull. Table 3 shows the changes in the skull dimensions of stone martens with age. The table shows that the skulls of yearlings (6–12 months) differ little in size from those of adults. A male aged 6 months shows distinctly the outlines of the ossea praemaxillare, maxillare, nasale and jugale, and the sutures between the maxillare, nasale and frontale, parietale and occipitale (in the lower part), parietale, occipitale and petrosum, occipitale and basisphenoideum, and maxillare and

palatinum are also retained. In yearlings aged 9-12 months, only the sutures demarcating the nasal bones are still visible. In lateral profile, the contour of the frontal bones is clearly higher than that of the brain capsule; this is never the case in yearling pine martens. In contrast to pine martens, the postorbital width does not change significantly with age. In males aged 9-11 months it averages 23.1% of the condylobasal length of the skull, in adult males 21.3%; and in females [of this age] 24.0%, in adults 25.9%. The skulls of young animals differ from the adults in the lesser development of the supraorbital processes and in the absence of a sharp curve in the profile of the frontal part of the skull.

Compared to pine martens, on the whole the skulls of yearling stone martens exhibit less pronounced infantilism.

In the 2nd year of life in stone martens the sutures between the nasal bones are still sharply demarcated. The round swellings directly behind the post orbital processes are absent or scarcely noticeable. In lateral profile the contour of the frontal bones is considerably higher than that of the brain capsule.

Table 3. Age changes in the skull and baculum of Caucasian Stone Martens

Indices (dimensions in mm, weight in g) (n)	Males 6-12 months (15)	Males 2 yr and older (14)	Females 7-12 months (19)	Females 2 yr and older (6)
Total length	84.4	85.3	80.0	81.1
Basilar length	75.4	75.9	71.5	71.5
Condylobasal length	83.4	84.3	80.0	79.2
Rostral width	18.0	18.6	17.0	17.1
Interorbital width	21.7	22.7	20.9	21.3
Width across supraorbital processes	25.5	26.6	24.3	25.9
Width of postorbital constriction	18.1	18.0	18.3	20.5
Zygomatic width	48.6	51.0	45.7	44.9
Mastoid width	37.7	37.7	36.7	36.1
Height of cranium at tympanic bullae	31.0	31.7	29.5	28.9
Facial length	34.9	35.0	33.0	32.4
Length of upper row of teeth	28.8	29.2	27.4	27.7
Length of lower row of teeth	35.0	35.3	33.0	33.0
Length of baculum	54.8	60.0		
Weight of baculum	0.26	0.61		

Density and weight of skull. In male stone martens the weight of the skull at age 9-12 months averages 22.320 g, the density 0.27 g/mm, and the volume of the brain capsule 21.0 cc. In females, the skull weight is 18.520 g and the density 0.23 g/mm.

The weight of the skull of females is 22.573 g, density 0.27 g/mm; the volume of the brain capsule in females is 18.5 cc.(a)

Development of crests. In young stone martens the sagittal crest is formed by two distinct ridges, joined in the occipital region and gradually diverging towards the supraorbital processes. At the end of the first year they fuse (for about 1/7 of their length) in the occipital region into a crest which enlarges with age. Its maximum height at this age in males is 1.5 mm (1.8% of the condylobasal length of the skull), and in females 1.2 mm (1.5%). In pine martens the ridges forming the sagittal crest are almost parallel. They are indistinct and, at an early age, the whole crest appears like a wide band (Fig.2).

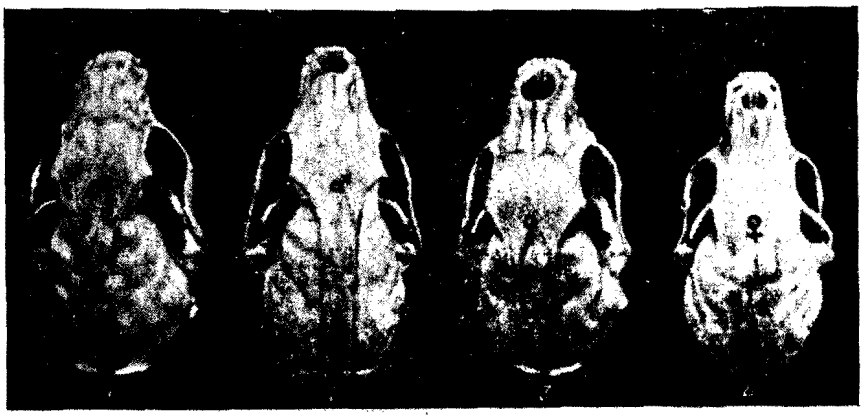

Fig.2. Skulls of yearling Caucasian martens

Stone martens (1 and 3); Pine martens (2 and 4)

In the second year of life the maximum height of the sagittal crest in males averages 3.4 mm (40% of the condylobasal length of the skull). The

(a) Ryabov has omitted to give the age to which these last 3 measurements refer - Ed.

range is 3.0 to 4.0 mm. The sagittal ridges fuse into the crest on average along about ¼ of their length. In females the sagittal crest is 1.2 mm (1.5%).

In male stone martens the height of the occipital crest at age 9-12 months reaches a maximum of 2.6 mm (3.1%) and in females 2.2 mm (2.9%). In the 2nd year of life the crest grows to 2.8 mm (3.4%) in males, and to 2.2 mm (2.8%) in females.

Dentition. In stone martens, by the age of 6 months the [milk] teeth are completely replaced by the permanent ones, but martens of this age may be distinguished from adults by the unbroken enamel surface, which shows no exposed dentine.

In the 2nd year the teeth retain the enamel almost completely. In some specimens there is slight wear of the enamel surface of $\underline{pm}^3$ and $\underline{pm}^4$ of the upper jaw and $\underline{m}_1$ of the lower jaw. Very rarely, exposure of dentine occurs in stone martens in the 2nd year of life.

Dimensions of the baculum. In male stone martens, like pine martens, the weight and size of the baculum is an additional characteristic of age. In young animals this bone is thin, without an enlarged base. Its weight is 0.22-0.32 g; length 50.6-58.2 mm (on average 11.8% of body length). In adults the baculum is longer (56.0-67.4 mm; 13.7% of body length) and more massive, with a fully developed basal knob. Its weight is much greater than in young martens (0.38-0.80 g). In pine martens the baculum is shorter and thinner than in stone martens (Fig.3).

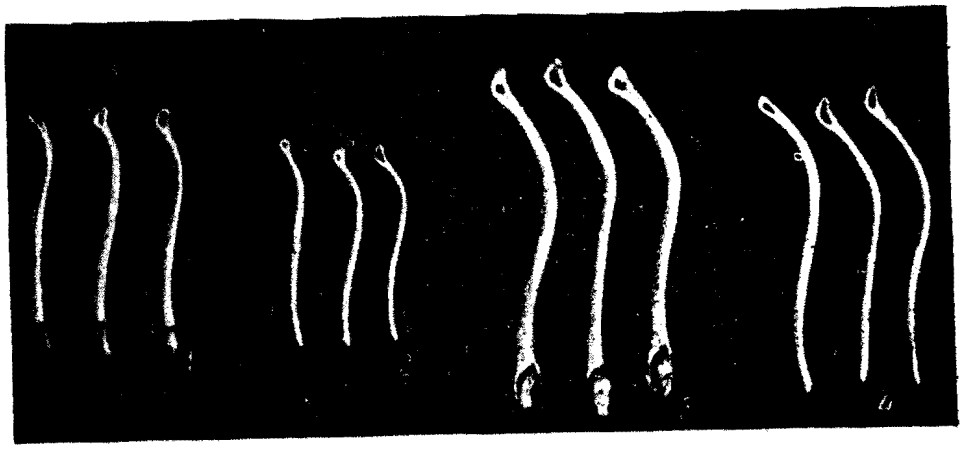

Fig.3. Baculum of Caucasian martens

1 - adult pine martens; 2 - yearling pine martens;

3 - adult stone martens; 4 - yearling stone martens

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During final checking the following paragraph was discovered to be missing from the translation. It follows after (a) on p.147 :

If we assume that the animals were born at the beginning of April and weighed about 30 g at birth, then the average gain for each of them was 12 g per day. P.A. Manteifel quotes the same figure for the young sables at the Moscow Zoo. Towards 4.5-5 months of age the weight and size of the young martens are close to those of adult martens (Table 1). The average weight of 6-12 month-old females differs only slightly from the average weight of animals aged 2 years and over. In males this difference is more substantial - 1280 g in the young of the year and 1360 g in animals aged 2 years and over.

ANALYSIS OF THE AGE STRUCTURE OF ERMINE POPULATIONS

(Analiz vozrastnoi struktury populyatsii gornostaya)

by

K.I. Kopein

Trudy Mosk. Obshch. Ispyt. Prirody, 1967. 25 : 33-39.

The principal characteristic of any population is its age structure, i.e. the relative proportions of each age group, and the variation in these proportions in different seasons and years. This characteristic is government by the mean lifespan of the individuals, and the rate at which the population turns over.

Practically nothing has been published on the age structure of ermine populations (Popov 1947, Petrov 1956, Kopein 1965). In this paper I shall attempt to use analysis of data from different regions in the USSR to deduce, and if possible explain, the population dynamics of the ermine. The basic requirement for such a study is that sufficient data should be available for reliable statistical analysis. It is also necessary to consider the region, the year and the season in which the specimens have been collected.

I used dead ermine from the north of Tyumen' province, which had been collected during the five commercial seasons of 1959-1964, in the autumn of 1964, also in the summers of 1959-61 and 1964; over 4000 ermine in all (4239 [?autumn and] winter specimens and 65 summer). In addition, we[(a)] used the skulls of ermine from different regions in the USSR kept in the Zoological Museum of the Moscow State University and at VNIIZhP (2236 specimens).

Age was determined by a slightly modified form of the procedure developed by V.S. Smirnov (1959) for polar fox. It is based on the

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(a) Kopein's use of personal pronouns is somewhat erratic. - Ed.

percentage ratio of the external width of the canines to the width of their pulp cavities, both measured at the root of the tooth. Statistical analysis of these measurements enabled us to subdivide all the specimens collected into three age groups :

(a) this year's brood (age up to 1 year), with a pulp cavity index of 100 (hollow tooth) to 20 for males, and 100 to 16.5 for females;

(b) adult (1.5-2.0 years), with a pulp cavity index of 19.5-10.5 for males, and 16.0-9.5 for females;

(c) old (2.5 years and over), with a pulp cavity index of less than 10.0 for males, and less than 9.0 for females. In addition, rings (layers) were to be seen in the tooth root cement in animals older than 2.5 years.

This method can distinguish the age groups with a reliability fluctuating between 98 and 99% for males and 96-98% for females: hence, the only errors possible are that a few specimens from the adult group could be classified as young, but not vice versa. When the procedure was checked on 26 captive ermine of known age, it was confirmed as reliable.

All the data which we analysed are given in Table 1. The age structures are similar in males and females from the different regions. For example, in Northern Kazakhstan, the young of the year comprised 64.2% of the males and 65.0% of the females; in North Tyumen' province the equivalent figures were 90.0 and 89.9%. The sex ratios for males and females are also similar in different years so we do not therefore subdivide the data by sex.

The young of the current year are always the largest class in the population (see Table 1). The adults comprise 25%, and the old ermine only 2.5% (i.e. 10 times less than the adults). One would expect from this that the proportion of ermine older than 3.5 years would not exceed 0.1%; in practice there may be none at all, even when quite large numbers are handled (up to a thousand specimens a year from one place).

When my data were analysed, using the equations of Martinson et al. 1961, I found that the mean lifespan of the ermine in the wild is 1-1.5 years, and that the population turn-over is complete in 3-5 years. By contrast, the mean lifespan of the weasel is 1.5-2.0 years[a] (Hill 1939), that of the forest marten 2 years (Grakov 1963), that of the sable 2.5 years (Zaleker 1962), and that of the fox 1.5 years (Schofield 1958).

This predominance of young is found both throughout the country as a whole, and also in each region from which specimens were taken (see Table 1). Even in northern Kazakhstan, where the percentage of young was lowest in comparison with the other regions, they still comprised two-thirds of the population. In Northern latitudes - the Pechora-Ilych game reserve, and in particular the north of Tyumen' province - the overwhelming majority of the population consisted of this year's brood.

The age composition varies in different latitudes. Taking four points with about the same longitude, the proportion of adult animals regularly increases from North to South, and that of the young decreases accordingly (Table 2). The reliability of these differences is 97-99%. Unfortunately we have insufficient data available from regions south of Northern Kazakhstan, but of eight skulls from Stavropol' region, five were from first year animals and three from adults, while of 21 skulls from the Northern Yakutsk region 20 were of first year animals and one adult. The pattern is similar in other regions (see Table 1).

Most of our data refer to the commercial (winter) seasons; for comparison, we collected a few samples in summer, in two regions (North Tyumen' province and Northern Kazakhstan), but these are sufficient for statistical analysis.

(a) It is not at all clear how Kopein extracted this unlikely figure from Hill's data. - Ed.

Table 1. Age structure of ermine populations in different regions of the USSR

Age groups	Statistics	North Tyumen' province (n = 4239)	Pechora-Ilych game reserve (n = 306)	Archangel and Vologda provinces (n = 128)	Krasnoyarsk region and Irkutsk province (n = 337)	Omsk province (n = 92)	Bashkir ASSR (n = 62)	Tatar ASSR (n = 126)	Northern Kazakhstan (n = 451)	Totals (n = 5741)
		Number of years of observation								
		6	9	5	9	2	2	7	3	
Young of the year	n	3815	254	90	241	66	43	92	291	4892
	% of n	90.0	83.0	70.3	71.5	71.7	69.3	73.0	64.5	73.1
	m %(a)	0.4	2.1	4.1	2.4	4.7	5.8	3.9	2.2	
Adult (1.5-2.0 years)	n	387	49	32	80	25	19	34	132	768
	% of n	9.1	16.0	25.0	23.7	27.2	30.7	27.0	29.3	24.5
	m %	0.4	2.1	3.7	2.3	4.6	5.8	3.9	2.1	
Old (2.5 years or over)	n	37	3	6	16	1	-	-	28	81
	% of n	0.9	1.0	4.7	4.8	1.0	-	-	6.2	2.4
	m %	0.1	0.9	2.0	1.2	1.0	-	-	1.1	

(a) The standard error of the proportion, ($SE_{(p)} = \sqrt{\frac{P\,(100-P)}{n}}$). - Ed.

In winter there is a substantial difference between the age structures of northern and southern populations, but there is no such difference in summer. The proportion of first year ermine in the summer collection (June to September) from the north of Tyumen' province (n = 65) was 66.6 ± 5.7%, and the equivalent figures for Northern Kazakhstan (n = 126)(a) were 64.2 ± 4.2%.

There was no seasonal variation in age structure in the ermine populations of Northern Kazakhstan (adult and old: 35.8% in summer, 35.5% in winter), but there were great variations in the north of Tyumen' province (adult and old: 33.5% in summer, 10.0% in winter). In the north, the ratio of adults to first year animals is 1:2 in summer and 1:9 in winter.

The age structure also varies from year to year. The percentage of adults among specimens collected during nine seasons (1938-39–1946-47) in the Pechora-Ilych game reserve were: 9.8, 19.0, 13.9, 13.7, 13.4, 5.0, 12.5 and 9.1(b) i.e., ranging from 5–19%. Table 3 shows the annual variations in the age structure in North Tyumen'; these figures were compiled using more data, and so are more reliable. In 1959-60 and the autumn of 1964, the ratio of adults to young was 1:25; in 1960-61 it was 1:16, in 1963-64 it was 1:14, and in 1961-62 it was 1:3. A difference was also observed in the oldest age group: in 1960-61 the ratio of old to adult animals was 1:29, and in 1963-64 it was 1:4.

Table 2 Variation in the age structure of ermine populations with latitude.

Region	Latitude of region	Number of years of observations	Percentage of adults and m, % (P% ± SE(p)%	Ratio of ages (adult and old to young)
North of Tyumen' province	66-68°	6	10.0 ± 0.4	2:18
Pechora-Ilych game reserve	63-64°	9	17.0 ± 2.1	2:10
Povolzh'e (Tatar ASSR)	55-57°	3	27.0 ± 3.9	2: 6
Northern Kazakhstan	53-54°	3	35.5 ± 2.1	2: 4

(a) Kopein does not mention more than 65 specimens collected in summer on p. 158 - Ed.
(b) 8 sets of figures given, but there should be 9 - Trans.

Table 3. Annual variation in age structure of ermine populations (1959–64) in the North of Tyumen' province.

Age groups	Statistics	1959–60	1960–61	1961–62	1962–63	1963–64	1964 (autumn)	All years together
Totals	n	285	2046	953	38	784	133	4239
Young (first year)	n	274	1926	723	32	732	128	3815
	% of n	96.2	94.3	75.9	84.4	93.3	96.3	90.0
	m %	1.1	0.5	1.4	5.8	0.9	1.6	0.4
Adult (1.5–2.0 years)	n	11	116	207	6	42	5	387
	% of n	3.8	5.6	21.8	15.6	5.4	3.7	9.1
	m %	1.1	0.5	1.3	5.8	0.8	1.6	0.4
Old (2.5 years and over)	n	–	4	23	–	10	–	37
	% of n	–	0.1	2.3	–	1.3	–	0.9
	m %	–	0.07	0.3	–	0.1	–	0.1

Large variations in age ratios, such as have been described, are characteristic of Northern latitudes. The data from the southern part of Krasnoyarsk region and Northern Kazakhstan confirm that there are no such fluctuations there (although this may be because insufficient data are available).

In all the regions investigated, first year animals comprised the great majority of the ermine population. It follows from this that the total numbers of ermine are governed by the breeding rate. Intensive breeding will increase the total numbers, while any reduction in the breeding rate will abruptly reduce the numbers.

My conclusions on the age structure of the ermine population differ from the ideas expressed by other research workers (Popov 1947, Petrov 1956); this I stated earlier (Kopein 1965).

In recent years deeper studies of the ecology of rabbits, foxes and certain other animals have proved that the population turnover of these species is very rapid, and that the mean lifespan of any individual is accordingly short (Boback 1957, Hill 1939, Wood 1958, Leichtleitner 1959). The youthful composition of the ermine populations which I showed, is therefore not of itself extraordinary.

According to Yu.N. Klimov (1940), in medium latitudes (Novosibirsk province) the fertility of the ermine averages 8-9 young per female. According to my observations, which it is true were not sufficient (5 litters), the fertility of the ermine in the north of Tyumen' province is 5-8. Therefore, the ratio of adults to first year animals [there] must, in theory be 1:4. But in the summer when the young have left the nest this ratio actually observed is 34% adults to 66% young [see p. 169]. The reduced proportion of young is probably due to their higher mortality rate compared with adult animals, and this is quite well known for many species. The age ratio in winter ermine populations is similar in most [southern] regions (see Table 1), but the picture is different in the north.

Even in the Pechora-Ilych game reserve the ratio of adult to young is 1:5, i.e. there are 10 first year animals to each pair of adult animals: in the north of Tyumen' province there are 18 first year animals per pair of adults. It is difficult to explain this age ratio from the fertility data known. My explanation was that it was due to increased mortality in the old age groups (Kopein 1965): data obtained in other regions have confimred my conclusions.

It may be suggested that the high proportion of first year animals in winter reflects selectivity in trapping. According to Smirnov (1964) and Grakov (1963), young animals are trapped more often than old ones. The age structure of trapped samples may therefore be biased. It is highly probable that trapping is a selective operation, particularly during the first half of the trapping season. But this factor must apply equally in all seasons and regions, since traps are used everywhere for catching ermine, yet the age ratios are still different. It follows therefore that there actually are seasonal and regional variations in the age structures of ermine populations, which are accurately reflected in these samples.

In the north of Tyumen' province,the age ratios vary between years, but the proportion of young is always high, in spite of abrupt population fluctuations. According to trapping results, over a six year period the numbers of ermine varied by almost 14:1 (40 500 pelts were treated in the 1960-61 season, 3 000 in 1962-63). Even a small reduction in the percentage of first year animals trapped (e.g. to 75.9%) therefore reduces the number of ermine by several times. Obviously, unfavourable conditions one year will mean that the breeding stock next year will be lower, and productivity will drop. Then, the number of first year animals in the coming commercial trapping season will be sharply reduced. Since the mean life of ermine in Northern latitudes is about 12-14 months, many of the adults i.e. those born the previous year, will die in the autumn, so the number of adults trapped will also be low. Although the ratio of first year to adult

animals changes little, the total population will abruptly decrease.

For example, in 1960-61 the ermine population was high owing to the good conditions in the previous season, and 40 500 were trapped. The true number of ermine in the population was much higher, and many more could have been trapped.(a)

The spring and summer of 1961 were poor for breeding, and the number of young, forming the basis of the winter population, was greatly reduced relative to the previous year. At the same time the adult animals, born the previous year, died. This caused an overall reduction in the number of ermine in the 1961-62 season, though to judge from the results of trapping the percentage of first year animals was still quite high. Since trapping continued at the usual, or even a slightly increased rate, the numbers trapped were only 75% less than the previous year (11 000 were trapped), but ermine population was decreased by far more than this.

The result of these factors (reduction in the breeding rate and continuing trapping) was that there were practically no ermine left by the 1962 breeding season. In spite of the better breeding conditions in that year, indicated by the high percentage of first year animals in 1962-63, the number of mother ermine was so small that the total numbers dropped still further (only 3000 were trapped in 1962-63). Only in the 1963-64 season did the population begin to increase (9 000 were trapped) though the optimum still had not been reached.

Annual variations in age structure are greater in animals such as the arctic fox, sable, and arctic hare than in ermine (Smirnov 1965, Zaleker 1962), but these variations (shown by the absence of first year animals trapped) need not be accompanied by great variations in the total

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(a) The intensity of trapping in the north of Tyumen' province is practically independent of the number of ermine in the population. The number of hunters, the number of traps set, the length of the trails, etc., scarcely alter. The result is that the rate of exploitation is about right in average years, but is low in good years and high in bad ones. - Author.

population, particularly in the arctic fox (Smirnov 1964). However, these are relatively long-lived species, and it is quite understandable that a single poor breeding season need not cause an abrupt reduction in their population numbers. In contrast, in species with an average life of 1-1.5 years, in which the young form the great majority of the population, after a poor breeding season the absence of young in the next commercial season will be serious.

CONCLUSIONS

1. First year animals comprise the basis (64-90%) of the ermine population of all the regions studied, i.e. the number of ermine is governed by the breeding rate.

2. The turn-over of the ermine population is rapid (3-5 years), and consequently the life of each animal is short (1-1.5 years). This is due to the high mortality rate of adults during the autumn and winter, when their environment is rapidly changing. Adult mortality is highest in Northern latitudes; southwards, the mean lifespan increases from 1 to 1.5 years, which raises the proportion of adults in the population [in winter] from 10.0 $\pm$ 0.43 to 35.5 $\pm$ 2.14%.

3. The rate of exploitation of the ermine is not related to the population level. Therefore: (a) when the population is high it is under-trapped, with the result that a large number of animals are not trapped, since they live to the following trapping season; (b) if the population is low there is over-trapping, resulting the next year in a population depression; the population is difficult to restore, and the numbers trapped remain at a low level for several years.

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(a) Given as Hill (1957), although with the correct volume number. - Ed.

EFFECT OF HELMINTH INVASIONS AND INFECTIOUS DISEASES ON VARIATIONS IN NUMBERS OF THE ERMINE (*Mustela erminea* L.)

(Rol'glistnykh invazii i infektsionnykh zabolevanii v dinamike chislennosti gornostaya (*Mustela erminea* L.)

by

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Trudy Tsentral. Laboratorii Biol. i Okhotnich'ego Prom. Nark. SSSR 1944 6 : 151-163.

There have been very few studies of the helminth and infectious diseases of game animals. The diseases of those animals which are more often kept in zoos or bred on hunting farms are rather better known, but the ermine does not belong to this category. The published information on this species is limited mainly to notes, recording carcasses found, and to lists of endoparasites.

We were interested in diseases from the standpoint of their influence on the variations in the numbers of ermine populations. For this purpose we undertook investigations, the results of which are summarised in the present paper.

In the Central Laboratory of Biology (V/O Zagotzhivsyre), 1717 ermines were dissected which had been caught between 1937 and 1941 in various regions of our country. They are divided by year and region as follows (Table 1):

Table 1

District	Total No. of ermines studied	No. of ermines examined in years				
		1937	1938	1939	1940	1941
Vologod Region	106	12	32	50	12	-
Kirov Region	116	22	62	32	-	-
Bashkir ASSR	99	17	44	16	17	5
North Kazakhstan Region	653	121	89	415	24	4
Aktyubinsk Region	74	38	10	26	-	-
Omsk Region (southern part)	236	-	98	6	93	39
Krasnoyarsk district (southern part)	433	68	87	141	82	55

The extent of the helminth invasion was relatively small : worms were found in 662 (38.5%) of 1717 ermine. The helminth fauna was poor in species, and usually, one individual was parasited by only a small number of worms. Table 2 shows the species of endoparasite found, and their position, the intensity of infection [number of worms per host] and the percentage of ermines invaded.

As well as these forms we encountered the following pseudo-parasites apparently entering in the food. In the stomach: Oxyurata gen.sp., Protospiruranucris and Syphacia obvelata. In the gut: Heligmosomatinae gen.sp., Spirurata gen.sp. and Trichostrongylidae gen.sp.

An ermine may be invaded simultaneously by three species of parasites belonging to different orders or classes. The proportion of the population infected by the various species changes with both year and region (Table 3).

Table 2. Species and distribution of endoparasites in ermine.

Species of parasite	Localisation	Maximum No. of parasites per ermine	Frequency of invasion as % of total number of ermines examined
Nematoda			
Capillaria putorii Rud.	Stomach and gut	200	8.0
Molineus patens Dujard	Stomach and gut	40	4.9
Strongyloides martis Petrow	Stomach and gut	42	10.5
Ascaris columnaris Ledy	Gut	3	0.3
Spirocerca arctica Petrow	Gut	15	Found in one ermine
Soboliphyme baturini Petrow	Gut	4	Found in one ermine
Skrjabingylus nasicola Leuc	Stomach	4	Found in one ermine
	Frontal sinuses and nasal turbinals	45	14
Cestoda			
Taenia tenuicollis Rud	Gut	47	1.1
Mesocestoides lineatus Goeze	Peritoneal cavity	5	0.1
Acanthocephala			
Acanthocephales gen.sp.	Gut	2	0.2

Table 3. Variations in the rate of infection by the 3 most widespread species of parasites.

District	Species of parasites / Years	Capillaria putorii		Molineus patens		Strongyloides martis	
		Max. no. of worms per ermine	% of ermine infected	Max.no. of worms per ermine	% of ermine infected	Max. No. of worms infected	% of ermine infected
Vologod Region	(1937	2	8.3	0	0	0	0
	(1938	6	3.1	2	9.4	11	9.4
	(1939	200	8	32	4	9	10
	(1940	4	8.3	0	0	1	9.1
North Kazakhstan Region	(1937	4	2.5	2	1.6	2	2.4
	(1938	5	40	2	9	5	10.1
	(1939	12	1.9	5	1	42	10.1
	(1940	0	0	0	0	0	0
Krasnoyarsk district	(1937	9	20.5	12	14.7	4	7.3
	(1938	24	13.8	10	11.5	22	5.7
	(1939	20	10	5	3.6	20	10.7
	(1940	22	21.4	15	9.5	42	16.6

The species composition of the helminth fauna in ermine differs between the regions and this is related to special features of the geographic distribution of the parasites (Table 4):

Table 4. Distribution of helminth parasites of ermine

Species of parasites	Vologod Region	Kirov Region	Bashkir ASSR	North Kazakhstan Region	Aktyubinsk Region	Omsk Region	Krasnoyarsk district
Capillaria putorii	+	+	+	+	+	+	+
Molineus patens	+	+	+	+	+	+	+
Skrjabingylus nasicola	+	+	+	-	-	+	+
Ascaris columnaris	-	-	-	+	-	+	+
Spirocerca sp.	-	-	-	+	-	-	-
Strongyloides martis	+	+	+	+	+	+	+
Soboliphyme baturini	-	-	-	-	-	-	+
Taenia tenuicollis	-	-	+	+	+	-	+
Mesocestoides lineatus	-	-	-	+	-	-	-
Acanthocephales gen.sp.	-	-	-	+	-	-	-

+ denotes the presence of a parasite in the ermines in the given region;

-, absence.

The richest helminth fauna was found in the ermines of North Kazakhstan and the Krasnoyarsk district. Three species of parasitic worms, Capillaria putorii, Molineus pateus and Strongyloides martis, were recorded in ermines of all regions. On the other hand, the distribution of Spirocerca sp., Soboliphyme baturini, Mesocestoides lineatus and Acanthocephales gen.sp. is much more limited. The range of the helminth species listed in the table is naturally not confined to the above mentioned regions: for example, Ascaris columnaris is found in ermines of the Gorkii Region(2).

The absence of Skrjabingylus nasicola in ermines inhabiting the North Kazakhstan and Aktyubinsk regions is particularly interesting. Of 727 carcasses inspected during four years, neither the nematodes, nor traces of their recent sojourn (swellings or holes in the frontal bones) were found. The reasons for this anomaly were given in our previous work,(1) and are summarised here. The chief and perhaps the only intermediate hosts of Skrjabingylus nasicola are certain species of ground molluscs. The latter are evidently not found in the northern part of Kazakhstan, or their numbers are so small that contact between ermine and molluscs is extremely rare. The absence or sparse distribution of these invertebrates in Kazakhstan is due to unfavourable ecological conditions. Ground molluscs require very wet habitats protected from direct sunlight. But in the northern part of Kazakhstan the rainfall, and the number of days with rainfall, are about three times less than, for example, in the central regions of the USSR. The dry period is longer and the nominal moisture balance is reduced; the soil and air temperatures in the summer, and also the number of hours of sunshine, are considerably higher. In winter there is relatively little snow, but it is cold and inhospitable there. Dark forests, thick bushes and overgrown ravines are absent - habitats which are particularly suitable for ground molluscs.

The proportion of the ermine population infected, and the infestation rate in individuals, were relatively low. In the lungs, heart, liver, kidneys and urinary bladder, parasites were not found at all. The preservation of the carcasses in formalin probably made the search for helminths more difficult. However, if the latter had been present in large numbers, they undoubtedly would have been found even in the preserved organs. In addition, no pathological changes in the organs as a result of invasion were noted.

The number of worms in the intestinal tract in one ermine never exceeded 200 specimens. Only in two of 1717 ermines, were more than 100 worms found. Usually, the number of helminths did not exceed twenty per ermine.

The pathogenic significance of the parasitic worms found in the stomach and gut of the ermine has not been established. Undoubtedly they weaken the host body to some extent and make it more susceptible to infections. Helminths disturb the integrity of the mucosa, producing an inflammatory process and bleeding. Possibly a heavy invasion may affect the fertility of the ermine to some extent, which is known in domestic and furred animals bred in captivity. Helminths of the intestinal tract, which are usually few, are probably not lethal save in exceptional cases. Therefore, the invasion by helminths localised in the stomach and gut cannot be the cause of the appreciable fall in the numbers of ermine [a].

The invasion by Skrjabingylus nasicola is of greater importance. The distribution of this parasite is extensive, and it is encountered considerably more often in the ermine than in other species[b]. In some years Skrjabingylus nasicola affects over 50 per cent of the population. The worms are nearly always located in the frontal sinuses, very near to the

(a) See Lavrov 1956, present volume - Ed.
(b) The rate of heavy (i.e. destructive) infection is generally in inverse proportion to body size in mustelids, so is greatest in the weasel: the reference here is probably a comparison with other (larger) furbearing mustelids. - Ed.

brain. In some individuals we encountered Skrjabingylus nasicola in the nasal turbinals. The weight of the infected animals decreases (Table 5).

Table 5. Mean weight of carcasses of ermine (skinned) caught in the hunting season of 1938-39 (a) (in grams)

District	Vologod Region	Kirov Region	Bashkir ASSR	Omsk Region	Krasnoyarsk District
Weight of infested males	135	158	145	167	138
Weight of non-infested males	145	164	171	177	150

The difference in weight is even more clearly marked in heavily infested animals. Thus, for example, in the Vologod Region in 1939-40 the number of worms per ermine ranged from 10 to 45 (average 6-8). The mean weight of 11 infested males was 121 g and of 13 healthy ones 193 g. When there is widespread invasion by Skrjabingylus nasicola, the numbers of ermine may go down (see Table 6).

The detrimental effect of infection by Skrjabingylus is unquestionable. However, the information now available does not allow an exact description of the pathogenic influence of worms on the ermine, or to predict the significance of different intensities of infestation.

There are two probable consequences of heavy infestation, which could contribute to a decline in the numbers of ermine. The first is diminished fertility, caused by the adverse effect of helminth toxins on the physiology of reproduction, which has been demonstrated in other mammals. Resorption of the embryos occurred in 93 percent of a group of female rats injected with excretion products of ascarids. In the control females the

(a) The mean weight is given only for 1938-39, because the greatest number of ermines was studied in this season. - Author.

percentage infertility ranged from 10 to 20. Death of the embryos may occur even in the last stage of their development(4). In fur animal breeding a reduction in the size of the litter, as a result of even weak helminth invasion, has often been observed(3). This is also well known in the breeding of [domestic] stock, and there is no reason to suppose that the ermine would be different.

Secondly, adult ermine may die as a result of the action of toxins or mechanical irritation, for example, pressure on the brain.

If this assumed pathogenic influence of Skrjabingylus nasicola does occur, then the result must be a reduction in the ermine stock, which must affect the pelt figures for the following year. This assumption may be supported by the following argument(a).

Infestation with Skrjabingylus occurs in the warmer months of the year and, taking into account the ecology of the intermediate hosts, and the duration of the development of the larvae of the parasite up to the invasive stage, does not take place earlier than late summer [in the first year]. The process of debilitation [by parasite toxins] proceeds relatively slowly. During the [first] autumn to winter season the great majority of invaded ermines do not show any sign of destruction of the skull bones. At this time of the year the disease, which has not reached the terminal stage, is clearly not a cause of mortality.

At the same season, solitary individuals may be observed, which are convalescing from skrjabingylosis; they have perforated apertures in the frontal bones but no worms in the frontal sinus on that side. This agrees with the conclusion on the life span of the parasite, that it lasts about a year.(b) Our observations show that the apertures in the frontal bones appear in the summer months. Therefore the perforation of the bones, which

(a) The following passages read logically only if we assume that Lavrov is describing the course of an outbreak of skrjabingylosis in a previously healthy population; a process which takes two years. Words inserted in square brackets assist in following his account . - Ed.

(b) Labrov gives no reference for this conclusion. Later work suggested that the parasite usually survives for the lifetime of the host (Hansson 1971) Sometimes the worms vacate the sinuses and lie in the nasal turbinals, giving the impression that the infection has been shaken off. - Ed.

is the final and evidently the most severe and dangerous stage of the disease for the ermine, does not occur before the [spring at the] end of the next hunting season after invasion by the larvae of Skrjabingylus nasicola [in the previous summer].

Ermines mate in the late spring or early summer, i.e. before the skrjabingylosis infestation, and pregnancy lasts about ten months. Consequently, if toxins from the parasitic worms influence the survival rate of the embryos, the reduction in the size of the litter (and hence in the numbers of the population as a whole) will also affect the pelt figures only in the year following a heavy invasion.

Comparison between the changes in the pelt returns and the extent of the invasion of the ermine in the hunting season shows that the fall in the yield of pelts, reflecting a decline in the numbers of the animals, does in fact occur in the year following a mass invasion of the population by Skrjabingylus nasicola (Table 6).

The table shows that a definite relation exists between the yield of pelts and the degree of infestation of the ermine population by Skrjabingylus nasicola [in the previous year]

The years 1939-40 and 1940-41 in the Krasnoyarsk district are exceptional. Here, in 1939-40, the pelt figures dropped despite the fact that the rate of skrjabingylosis infestation in the preceding year was almost halved[a]. In 1939-40 the percentage of invaded ermines sharply increased: a reduction in numbers might have been expected in the following year but this did not occur. The discrepancy is evidently due to the low infestation rate in the population in 1939-40 (on average 3.8 parasites per ermine), and to improvement in food supplies. According to correspondents the number of"mice"[b] and water rats increased in 1939.

(a) Presumably meaning, the rate for 1938-39 was half the rate for 1937-38, but it is not according to Table 6, unless the figure 22.0, given by the original text, was a misprint; or else Lavrov has made a logical error by confusing the 50% difference between 1938-39 and 1939-40 with that between 1938-39 and 1937-38. - Ed.

(b) Small mouse-like rodents, including voles. - Ed.

Table 6. Relation between pelt returns and infestation of the ermine by Skrjabingylus nasicola (figures for 1937-38 are taken as 100%)

District	Vologod Region		Kirov Region		Bashkir ASSR		Omsk Region		Krasnoyarsk Region	
Year	Yield of skins	% infestation	Yield of skins	% infestation	Yield of skins	% infestation	Yield of skins	% infestation	Yield of skins	% infestation
1937-38	100	12.5	100	27.6	100	22.7	100	54.5	100	22.0
1938-39	121	35.6	285	31.2	257	38.0	49	15.8	67	17.8
1939-40	32	52.5	50	-	86	42.8	96	-	70	34.0
1940-41	13.6	-	-	-	35.5	40.9	68	22	80.9	46.8
1941-42					29		31.1		38	

The numbers of "mice" in the fourth quarter of that year were rated by them as follows: extremely many - 33.3% of replies; many - 41.7%; average 16.7% and few 8.3%. When making comparison with the same period of the preceding year, replies stated: more - 53.8%, just as many - 36.5% and fewer 7.7%.

The fluctuations in the numbers of the ermine should be related not only to changes in the rate of infection by Skrjabingylus nasicola, but also to food supplies, which remain the chief regulating factor. Under certain circumstances skrjabingylosis may have a profound influence on the dynamics of the ermine stock, and in our view, this factor explains the situations sometimes observed, where, despite relatively favourable supplies of food, ermine numbers show a decline, instead of the expected small rise or stabilisation. In the lean years skrjabingylosis makes a bad situation even worse, such as happened, for example, in the Vologod Region in 1940. The catastrophic decline in the ermine stock at the time of the 1940-41 hunting season must be attributed to the simultaneous action on the population of two unfavourable factors: starvation, as a result of the almost total absence of small rodents in 1939-40, and heavy invasion by Skrjabingylus nasicola (on average 24 specimens per ermine).

Even less is known about the infectious diseases which from time to time take a heavy toll among the stock of game birds and animals. Study of epizootics of wild animals is important not only from the economic point of view, but also in the interests of national health, since certain of these diseases are also infectious to man, such as tularaemia. The reservoirs and main vectors of the tularaemia bacterium are murine rodents, so medical workers and biologists are concentrating on this group of mammals.

Yet the list of wild animals susceptible in various degrees to tularaemia is long and varied, including certain amphibians, reptiles, birds and many mammals belonging to different orders. The VIEM tularaemia

expedition of 1938, working in European USSR, cultured isolates of tularaemia bacteria from shrews, water-shrews, moles, weasels and polecats. A tularaemia epizootic was established[a] in a number of game animals, for example, susliks, squirrels, water rats, muskrats and hares. In 1938 and 1941 in the central regions of Russia, there were epidemics of this disease among domestic cats, coinciding with the outbreaks of tularaemia in murine rodents.

The hypothesis that the ermine is also sensitive to tularaemia, is suggested by these facts, and also by frequent reports of hunters and investigators who have found ermine carcasses, and the decline in ermine populations observed after an epidemic among rodents. There is plenty of opportunity for ermine to become infected. They have very close contact with the common vole and the water rat, which are extremely sensitive to tularaemia: they feed on these rodents and give them special preference. During hunting, ermine enter the burrows of water rats and often use them as living quarters; and they visit the nests (which may be full of ectoparasites) of small rodents living beneath the snow, in straw and other accessible spots. Hence, infection through eating diseased rodents, and through picking up their ticks, lice and fleas, which are carriers of the infection, is quite possible. The occurrence of certain ectoparasites on ermine has been demonstrated. Fleas collected by me in the winter of 1940-41 from ermines in north Kazakhstan proved to be Amphipsylla kuznetzovi Wagn. and Ctenopsyllus bidentatus Kol[b]. According to Dr Ioff these species usually parasite murine rodents, the first mainly on mountain voles (Microtinae) and the second on forest Muridae.

Because of its importance in understanding the causes of the variations in numbers of ermine, experimental work in the laboratory was

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(a) ? in the sense of "found"; but could be "induced". - Ed.
(b) The fleas were classified by Doctor of Biological Sciences I.G. Ioff. - Author

undertaken, to determine the susceptibility of the ermine to tularaemia and the survival rate of diseased individuals. In 1940-41 I organised the capture of live ermines in the Petropavlov district of the North Kazakhstan Region. The ermines were caught in small sacks(a). The animals were kept singly in small transport boxes. At the site of capture I fed them on sparrows, magpies and hare meat: they ate the latter very reluctantly. Instead of water I gave them snow. In all we caught 12 ermines, of which five soon died. One was apparently badly crushed by a hunter, but the cause of death of the others was not established. The ermines on the eve of death appeared quite healthy. In the morning on the day of death they refused to take food and barely reacted to the approach of man. Then convulsions set in: the animals hit their heads against the roof of the box and knocked the side with their hind legs, crying weakly. Soon the hind limbs became paralysed, and the sphincters of the anus and urinary canal relaxed. A few hours after the start of the convulsions the animal died. Autopsy revealed no pathological lesions of the internal organs.

While the ermine were being carried in the luggage compartment I fed them on freshly frozen sparrows, after first thawing them out. In Moscow the ermines were kept in the tularaemia laboratory of the VIEM, where they were fed on raw cattle meat. One animal died soon after arrival in Moscow in the same circumstances as described above. The experiments to test the susceptibility of the ermines to tularaemia infection were carried out under the direct supervision of the head of the laboratory Dr B.V. Voskresenskii. The results of the experimental work were documented. They were as follows :

(a) The Russian word is "rukavchik", which could be a misprint for "rukavitsa", meaning "gauntlet", but more likely to mean a "small sack" - Trans. A more easily imaginable alternative would be"with heavy gloves" : see p.202. - Ed.

Ermine No.1. On 10 January 1941 fed on white mouse No.1 injected subcutaneously the previous evening with a 48-hr culture of Bacterium tularense, strain No.15, with 1 000 000 000 bacterial cells per ml. On the next day fed on a second white mouse No.2 infected at the same time as the the first and with the same dose. The control mice died on 13 January, and the ermine on 23 January. The results of autopsy and bacteriological investigation were: size of spleen 3.5 x 1cm; liver with fatty degeneration, apices of lungs contained pneumonic nodules; precipitation reaction negative; B. tularense was not found in the smears of the organs; organ cultures sterile.

On the day of death of ermine No.1 a suspension of its internal organs was used to infect white mice Nos.5 and 6, which died on 28 January. In the smears of the organs of these mice B. tularense was found everywhere: the precipitation reaction was positive; a pure culture was isolated from the suspension(a).

Ermine No.2. Died on 27 January before infection. Autopsy showed inflammatory foci in the lungs. The suprarenals were solid with transparent nodules. In the heart muscle tissue, dense white nodules the size of millet. In the mesenterium the same miliary nodules. B. tularense was not found in the organ smears; precipitation reaction negative, cultures sterile. Subculture tests not run on white mice.

Ermine No.3. On 28 January fed on white mouse No.8 injected subcutaneously on the previous evening with a 48-hr culture of B. tularense strain No.15 with 10^9 bacterial cells per 0.5 ml. On the next day fed on a second white mouse No.10 infected at the same time as the first with the same dose. The control mice died on 28 and 29 and the ermine on 30 January.

(a) This corresponds to the procedure known as "Koch's postulates", used for identifying disease organisms. - Ed.

Autopsy and bacteriological examination gave the following results: spleen 2.5 x 0.6 cm; liver with continuous fatty degeneration; large pneumonic nodules in the lungs; precipitation reaction negative; B. tularense not found in the organ smears; all the cultures sterile.

On 30 January an organ suspension of ermine No.3 was used to infect two white mice Nos. 21 and 22 which died on 7 February. B. tularense found everywhere in the organ smears; pure culture isolated from the suspension.

Ermine No.4. On 29 January fed on two white mice Nos.11 and 12 injected subcutaneously on 28 January with a 48-hr culture B. tularense with 10^9 bacterial cells per ml. On 1 February fed on white mouse No.16 infected on 30 January with the same dose of B. tularense. The control mice died after 1-3 days. On 27 February fed on white mouse No.28 injected the night before with a 48-hr culture of a strain of B. tularense isolated from ermine No.3 with 10^9 bacterial cells per ml. The control mouse died on 27 February.

On 3 February the behaviour of the ermine changed: it lay down for long periods and ate with little relish. By 12 February it was worse; it lay practically all the time, lost weight and ate little. By 28 February it lay motionless and took food without getting up. Its condition sharply declined. In March it began to get better, ans was able to move; it jumped into the hay, and thereafter rarely came out. This secretive behaviour and slow improvement in the condition of the ermine continued up to 17 April (end of observations).

Ermine No.5. On 29 January fed on two white mice Nos.13 and 14 injected subcutaneously the previous evening with B. tularense strain No.15, 10^9 bacterial cells per ml. On 17 February fed on a third white mouse No.25 injected subcutaneously on 15 February with the same dose. The control mice died on 18 February. After 10 days, given a further two white mice Nos.29 and 30 infected on 26 February subcutaneously with a B. tularense

strain isolated from ermine No.3 with 10^9 bacterial cells per ml. The control mouse died on 27 February. On 8 March the ermine was injected subcutaneously with the B. tularense strain No.15 isolated from ermine No.1 with 10^9 bacterial cells per ml.

The behaviour of the ermine during this period sharply changed. After feeding on the first two mice the animal lay down almost the entire day. On 9 February it became more perky, and began to take food eagerly. On 24 February its condition again worsened, and it lay down for most of the day and ate with little enthusiasm. On 1 March there was a sharp improvement, it became more lively, and in the morning waited for food standing at the door of the cage. After the injection it again lost appetite and mobility, but by 19 March it was on the mend. In the first half of April it appeared and behaved as if healthy.

Ermine No.6. Not infected. On 30 January it began yawning and going into convulsions, and died after 15 min. Autopsy and bacteriological examination showed the following. The lungs felt solid, contained many small inflammatory foci and a small number of small necrotic nodules. Small necrotic millet-like nodules were found in the pericardium. B. tularense was not found in the organ smears. Under the microscope thin rods were found in the lungs resembling tuberculous forms. Precipitation reaction negative; cultures sterile. On the day of death of the ermine, a suspension of its organs was used to infect two white mice Nos.23 and 24 which were killed on 19 February. B. tularense was not found in the organ smears of the mice; all the cultures were sterile.

To summarise; four of the six test ermines died, and two of these four were infected with B. tularense. Bacteriological examination did not establish tularaemia in these two animals; the precipitation reaction was negative, B. tularense was not found in the organ smears, and the organ cultures were sterile. A pure culture was isolated [only] by the biotest.

In all four dead ermines autopsy revealed lesions in the lungs suggestive of tuberculosis. In all probability, death resulted from this disease, while the administration of a large dose of bacterial cells into the two animals only accelerated it. This assumption is confirmed by the presence of the same pathological changes in the lungs of the two uninfected ermines which, as it were, served as controls.

The last two ermines remained alive despite repeated infection with massive doses, by feeding them on diseased mice and by subcutaneous injection. One of these animals after each infection lost appetite and its customary activity, but then rapidly got better. In the second ermine the disease ran a more severe course: it lost much weight, and lay for some time motionless and ate without getting up.

These experiments, carried out with a small number of animals, do not allow final conclusions on the resistance of the ermine to tularaemia infection, but they do however suggest that the ermine is only weakly susceptible, possessing considerable resistance to tularaemia.

In natural conditions the contraction by ermines of tularaemia is quite possible, particularly where there is tularaemia among the murine rodents or water rats with which the predator has direct and close contact. It may indeed be fatal, but probably not frequently, so it is unlikely to be a serious mortality factor.

In conclusion it should be noted, that of 1717 ermine carcasses inspected, few of the organs of the chest and abdominal cavities bore outward signs of invasion by helminths or by infectious or protozoal diseases, which emphasises the general resistance of the ermine to various diseases.

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CHARACTERISTICS AND CAUSES OF THE PROLONGED DEPRESSION IN NUMBERS OF THE ERMINE IN FOREST-STEPPE AND STEPPE ZONES OF USSR

(Osobennosti i prichiny dlitel'noi depressii chislennosti gornostaya v lesostepnoi i stepnoi zonakh SSSR)

by

N.P. Lavrov

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A forecast of the yield of fur-bearing animals is important for the planning of skin deliveries to the fur trade, for the organisation and economy of the trapping industry, and for the conservation of fur-bearing animals, especially species whose numbers can vary rapidly and within wide limits.

The degree of accuracy of the yield forecast depends to a great extent on: 1, knowledge of the species, also of the causes of variation in its numbers and of their effect on the animals; 2, on obtaining full information on the qualitative and quantitative state of the breeding stock, and living conditions in the current and preceding years.

VNIO and its zonal laboratories are concerned with developing and improving forecasting procedures, and also with compiling such forecasts of the "crop" of the main species of fur-bearing animals. These forecasts are used by central and local planning and trading organisations.

The checking of "crop" forecasts [against subsequent observations] on many fur-bearing species, shows that the ecology of these animals is still not sufficiently studied, that little is known about the influence of man's many-sided economic activity on the ecology of wild animals, and that the causes of variation in numbers in any species are more complex [than we know] and the actual numerical fluctuations more varied [than we predict]. This can be illustrated by reference to the ermine(a).

(a) We started to compile a forecast of the ermine crop as from 1936. Author.

From examination of many data on the feeding of the ermine, research workers have concluded that the main factor influencing the numerical variations of this species is a change in the food supply. Years of high, or low, ermine numbers often coincide with good, or bad, years for its main prey, the mouse-like rodents and especially the common vole and the water rat. This is confirmed by the results of our investigations (Tables 1, 2 and 3)(a) and by information already published (Zverev 1931, Grigor'ev and Teplov 1939, Lavrov 1941, Nasimovich 1948).

On the causes of the instability in numbers of the ermine, for instance, Aspisov and Popov (1940) wrote: "The significance of this factor [state of supplies of water rat] in the Gor'kovsk and Kirovsk provinces, and the Tartar, Bashkir and Mariisk republics has been proved .... This factor can be used now to compile a forecast of ermine harvest [in the next year] from the pelt figures for the water rats in the second quarter of the current year".

In the opinion of Nasimovich (1948): "The fluctuation in numbers of ermine in the north is entirely determined by variations in the supplies of voles, since this predator, in the conditions of the Kolsk peninsula and of the greater part of the USSR (Formozov 1935a) is a typical myophage".

On the basis of our own research, literature sources, masses of information from correspondents, and the results of analysis of pelt harvests, we recommended (Lavrov 1941) that, when compiling a forecast of the ermine, the main consideration be given to the population density of small rodents and water rats in the past and current years. It was also mentioned that population increases or declines in ermine usually continue for 1-5 years; years with the highest yield recur every 5-9 years and the pelt harvest varies by a factor of 3-7 (Lavrov 1941).

As from 1941, disagreements between our forecasts and the actual

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(a) Identification of stomach and intestine contents of ermines was carried out by A.P. Rozarenova and myself. - Author

supplies of ermine became more frequent. Also, the recent unprecedented decline of the ermine stock in many provinces, and some new information on the ecology of the ermine, forced us to revise our conclusions on the population dynamics of the species.

A sharp drop in ermine numbers was recorded in some places as early as 1937 (the number of pelts harvested serves as an index, since it correctly reflects the numerical variations of wild commercial animals). Furthermore, particularly abrupt variations took place in the forest-steppe and steppe provinces of the Asiatic part of the USSR. Here the numbers of the species dropped so low, that in many regions the ermine became almost insignificant commercially where only recently it had played an important part in the trapping industry and the fur trade. In the same regions at the same time, the numbers of the polecat and Siberian weasel also fell. This gave rise to understandable anxiety in the trapping and trading organisations.

Let us examine the population dynamics of the ermine in individual regions. In the Kazakh SSR the yield of ermine pelts began to drop as from 1937. In the 1939-40 season, three times fewer pelts were delivered, compared with the "bumper"season of 1935-36. In the last 15 years the yield of ermine pelts has remained at a very low level; by 1953-54 it had been reduced by 36 times compared with 1935-36 (Fig.1). The importance of ermine in the fur trade throughout this region fell catastrophically; whereas, in 1929 the value of ermine pelts amount fo 11% of the value of the fur of all species, by 1938 this figure was 3.9%, by 1947, it was 0.7% and by 1953, it was 0.3%(a). One of the correspondents of VNIO wrote that in the 1943-44 season in North Kazakhstan province supplies of ermine, polecat and weasel were so small that the trappers could make do with 5-7 traps for catching them. Formerly they used to put out up to 40 traps for ermine alone.

(a) In working out the proportion of ermine in the fur harvest, the value of the pelts of wild acclimatised animals and the products of fur farms were not taken into account. - Author.

Table 1. Food of the ermine in North Kazakhstan province in winter.

Food	1937–38 146 guts[a]		1938–39 198 guts		1939–40 126 guts		Total for 3 seasons 470 guts	
	n	%	n	%	n	%	n	%
Mammals	110[b]	97.3	122	100.0	71	97.3	303	98.4
Muridae	103	91.1	118	96.7	67	91.8	288	93.5
Grey voles	35	30.9	64	52.4	38	52.0	137	44.7
Common vole	7	6.2	26	21.3	7	9.6	40	13.0
Narrow skulled vole	8	7.1	12	9.9	8	10.9	28	9.1
Root vole	5	4.4	3	2.4	5	6.8	13	4.2
Field vole	–	–	8	6.5	2	2.7	10	3.2
Other grey voles	15	13.3	15	12.3	16	21.9	46	14.9
Wood vole	7	6.2	4	3.3	2	2.7	13	4.2
Northern redbacked vole	5	4.4	1.	0.8	1	1.4	7	2.3
Other wood voles	2	1.8	3	2.4	1	1.4	6	1.9
Water vole	7	6.2	8	6.5	3	4.1	18	5.8
Steppe lemming	5	4.4	7	5.7	3	4.1	15	4.9
Common mole rat	6	5.3	2	1.6	–	–	8	2.6
Mice	13	11.5	8	6.5	4	5.5	25	8.1
Striped fieldmouse	3	2.6	6	4.9	1	1.4	10	3.2
Common field mouse	10	8.8	1	0.8	–	–	11	3.5
Harvest mouse	–	–	1	0.8	–	–	1	0.3
Other mice	–	–	–	–	3	4.1	3	1.0
Hamsters	12	10.6	5	4.1	1	1.4	18	5.8
Common hamster	8	7.1	–	–	–	–	8	2.6
Other hamsters	4	3.5	5	4.1	1	1.4	10	3.2
Other Muridae	18	15.9	20	16.4	16	21.9	54	17.5
Hares	1	0.9	–	–	4	5.5	5	1.6
Mountain hare	–	–	–	–	4	5.5	4	1.3
Brown hare	1	0.9	–	–	–	–	1	0.3
Susliks	6	5.3	–	–	–	–	6	1.9
Shrews	–	–	1	0.8	–	–	1	0.3
Carrion	–	–	–	–	1	1.4	1	0.3
Other mammals	–	–	3	2.4	2	2.7	5	1.6
Birds	9	8.0	–	–	3.	4.1	12	3.9
Fish	2	1.8	–	–	–	–	2	0.6
Insects	2	1.8	–	–	–	–	–	–
Empty guts	33	22.6	76	38.4	53	42.0	162	34.5

(a) Contents of stomachs and intestines were examined. – Author
(b) NB. – add only entries in one class, not whole column, e.g. 35 grey voles, 7 wood voles etc. Classes have been inset differently to aid distinction – Ed.

Table 2. Food of the ermine in North Kazakhstan in summer.

Food	1938 43 guts		1939, 186 scats and 100 guts										Total for 2 years: 186 scats & 143 guts	
			May 22 scats & 7 guts		June 34 scats & 29 guts		July 78 scats & 44 guts		August 52 scats & 20 guts		Total for summer 1939			
	n	%	n	%	n	%	n	%	n	%	n	%	n	%
Mammals	16	100.0	20	90.9	46	100.0	92	95.8	57	100.0	216	97.3	229	96.5
Muridae	15	93.7	19	86.4	44	95.6	89	92.7	53	93.0	205	92.7	220	92.8
Grey voles	6	37.5	9	40.9	15	32.6	29	30.2	22	38.6	75	33.9	81	34.2
Common vole	2	12.5	3	13.6	5	10.9	9	9.3	6	13.5	23	10.4	25	10.5
Narrow skulled vole	1	6.2	2	9.1	2	4.3	5	5.2	4	7.1	13	5.9	14	4.9
Other grey voles	3	18.8	4	18.2	8	17.4	15	15.6	12	21.0	39	17.6	42	17.7
Wood voles	–	–	–	–	4	4.3	9	9.3	–	–	13	5.9	13	5.5
Northern redbacked voles	–	–	–	–	–	–	1	1.4	–	–	1	0.4	1	0.4
Bank voles	–	–	–	–	4	4.3	8	8.4	–	–	12	5.4	12	5.0
Water vole	2	12.5	2	9.1	5	10.9	8	8.4	14	24.6	29	13.2	31	13.1
Steppe lemming	–	–	1	4.5	1	2.2	2	2.1	2	3.5	6	2.7	6	2.5
Common mole rat	–	–	1	4.5	4	4.3	3	3.1	2	3.5	10	4.1	10	4.2
Mice	1	6.2	2	9.1	–	–	5	5.2	–	–	7	3.2	8	3.4
Hamsters	–	–	–	–	3	6.5	4	4.1	–	–	7	3.2	7	3.0
Other murids	6	37.6	4	18.2	12	28.3	29	30.2	13	22.8	58	26.4	64	27.1
Suslik	1	6.2	–	–	–	–	–	–	–	–	–	–	1	0.4
Shrews	–	–	–	–	–	–	–	–	2	3.5	2	0.9	2	0.8
Carrion	–	–	–	–	–	–	–	–	3	5.3	3	1.3	3	1.3
Other mammals	–	–	1	4.5	2	4.3	3	3.1	–	–	6	2.7	6	2.5
Birds	2	12.5	–	–	1	2.2	1	1.0	2	3.5	4	1.8	6	2.5
Birds eggs	–	–	–	–	–	–	–	–	4	7.1	4	1.8	4	1.7
Insects	–	–	–	–	–	–	1	1.0	–	–	1	0.4	1	0.4
Empty guts	27	62.8	7	100.0	17	58.6	26	58.4	15	75.0	65	65.0	92	64.3

Table 3. Food of the ermine in the Achinsk district of the Krasnoyarsk region in winter and summer

	1937–38 63 guts		1938–39 85 guts		1939–40 100 guts		1940–41 108 guts		Total for 4 years = 358 guts		Summer seasons of 1939 & 1940 = 73 guts	
	n	%	n	%	n	%	n	%	n	%	n	%
Mammals .	26	96.3	35	97.2	30	81.1	24	100.0	115	82.7	10	100.0
Muridae	24	88.9	31	86.1	30	81.1	21	87.5	106	76.3	10	100.0
Grey voles	9	33.3	8	22.2	7	18.9	9	37.5	33	23.7	4	40.0
Common vole	2	7.4	2	5.5	2	5.4	2	8.3	8	5.8	1	10.0
Root vole	4	14.8	2	5.5	1	2.7	2	8.3	9	6.5	2	20.0
Other grey voles	3	11.1	4	11.0	4	10.8	5	20.8	16	11.5	1	10.0
Wood voles	2	7.4	1	2.8	1	2.7	–	–	4	2.9	3	30.0
Bank vole	2	7.4	–	—	–	–	–	–	2	1.4	3	30.0
Northern redbacked vole	–	–	1	2.8	1	2.7	–	–	2	1.4	–	–
Water vole	4	14.8	13	36.1	15	40.5	8	38.3	40	28.9	1	10.0
Mice	2	7.4	3	8.3	2	5.4	2	8.3	9	6.5	–	–
Striped field mouse	2	7.4	–	–	–	–	–	–	2	1.4	–	–
Hamsters	2	7.4	–	–	–	–	–	–	2	1.4	–	–
Other murids	5	18.5	6	16.6	5	13.5	2	8.3	18	12.9	2	20.0
Mountain hare	–	–	–	–	–	–	1	4.1	1	0.7	–	–
Long tailed Suslik	2	7.4	–	–	–	–	–	–	2	1.4	–	–
Shrews	–	—	1	2.8	–	–	1	4.1	2	1.4	–	–
Other mammals	–	–	3	16.6	–	–	1	4.1	4	2.9	—	–
Birds	3	11.1	2	5.5	–	–	–	–	5	3.6	–	–
Insects	1	3.7	–	–	–	–	–	–	1	0.7	–	–
Empty guts	38	58.5	49	57.6	63	63.0	84	77.8	219	61.2	63	86.3

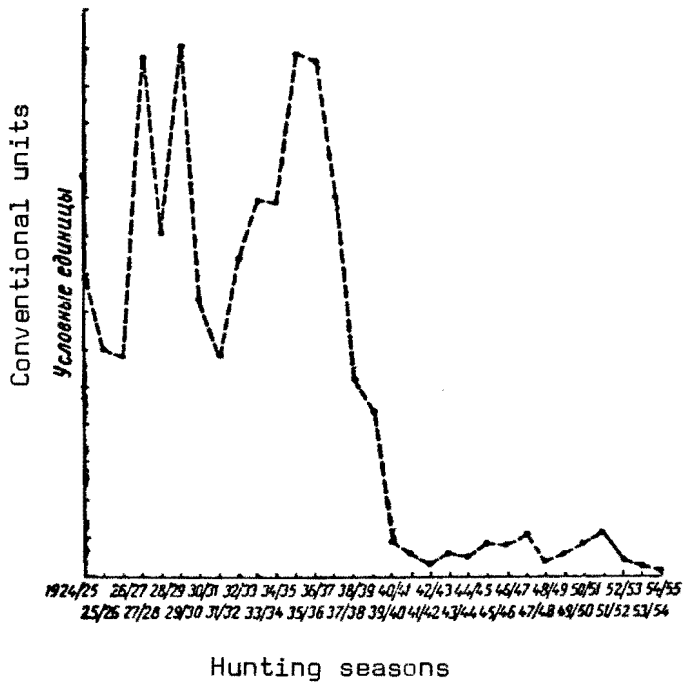

Fig.1. Dynamics of ermine pelt deliveries in Kazakh SSR

In some seasons of the post-war period, the North Kazakhstan province produced less than 500 ermine pelts, or approximately 100 times fewer than in the thirties. The following examples are, to some extent, evidence of the sudden decrease in the numbers of the species. As is known, it is very difficult to find and catch the ermine when there is no snow on the ground. In the summer of 1939, while working on our assignment in the vicinity of lake Chagla (frontier between Kokchetavsk and North Kazakhstan provinces), 5 trappers caught 121 animals. In the winter of 1940, when the numbers of ermine were already noticeably depressed, we counted ermine tracks along an 11.5 km trek, passing through various types of habitat, in the neighbourhood of Asanovo village (North Kazakhstan province): we

saw 7 on 11 December, and 5 on 16 December[a]. In recent years, according to reports from trapping correspondents in the same areas, ermine tracks are not even to be found on every day.

Roughly the same unfortunate situation developed in the forest-steppe of Western Siberia, where the ermine used to be the main commercial species. In Kurgansk and Chelyabinsk provinces (the first province was separated from the second in 1943) pelt deliveries of this animal in 1952-53 were down; in comparison with the "bumper" year 1935-36, by more than 27 times, and in the following season by 78 times. The drop in numbers began in the same year as in Kazakhstan. In the 1939-40 season a small increase in the numbers of ermine was recorded after a year's suspension of trapping; after this they remained at a very low level for 15 years. Of the total fur harvest in these provinces, the value of ermine pelts was: in 1940 - 7.2%, in 1942 - 1.5%, in 1953 - 0.3%.

In the thirties the yield of skins per 10 000 ha (all kinds of terrain) in Kurgan province reached 80 head, but in the best season of the last 12 years did not exceed 10 head.

From the data of K.A. Yastrebov, a scientific colleague of the Ural branch of VNIO, in the period 23 January to 5 February 1939 in the Makushink region (now Kurgansk province) tracks of 37 ermine were recorded on a 88 km trek. In the same district, on 29 January 1955 on a trek of 21 km, S.A. Abashkin, scientific co-worker of the Western Siberian zonal laboratory of VNIO, recorded the tracks of 4 ermine[b]. It should be pointed out that towards the end of the thirties ermine numbers were relatively low, so the provincial executive committee suspended ermine trapping for the 1938-39 season.

(a) In both cases the record was made after a fresh snowfall. - Author
(b) All counts were made after one day's snowfall. - Author.

In the fur harvest in Novosibirsk province, the ermine occupied second place (about 30% of the value of all fur); the decline began in 1934, evidently as a result of over-trapping (Klimov 1940). Some improvement was recorded in the seasons 1939-40, 1943-44, and 1949-50. The years 1952 to 1954 were particularly unfavourable; head trapper N.I. Blagoveshchenskii reports that the number of ermines was then at its lowest. In 1953-54 Novosibirsk province produced nearly 30 times fewer ermine pelts than in the pre-war year 1939-40, when numbers were already comparatively low. In 1954-55 ermine trapping was closed.

On the basis of his many years of observations, Yu.N. Klimov, scientific co-worker of the Western Siberian VNIO laboratory, considers that the prolonged depression in ermine numbers in Novosibirsk province is not due to their food supplies, but that the short fall in deliveries is due to the reduction in the number of trappers, or their lack of interest in catching this animal.

The same thing happened in the forest-steppe zone of the eastern part of the European territory of USSR. In the Tartar, Bashkir and Mordov ASSR, in Kuibyshev, Chkalov and some other provinces there was a bumper "harvest" of ermine in the 1927-28 season. In the following years the yield fluctuated generally with a downward tendency; there was an especially sudden decrease in the 1939-40 season.

In the Tartar ASSR, in years of high ermine numbers, the number of tracks on a 10 km route passing through flooded terrain reached 60, but in 1946 only 2 tracks were recorded (Popov 1947). In the Bashkir and Tartar ASSR, deliveries of ermine pelts during the 1953-54 season were down by nearly 44 times compared with 1927-28 (Fig.2). The value of ermine pelts as a proportion of the total fur harvest in Bashkir ASSR was 16% in 1927-28, 0.9 % in 1940, 0.1% in 1953; in Tartar ASSR, 7.4, 1.6 and 0.4%.

In the first years of the War, the numbers of many species of commercial animals (and consequently, of pelts harvested) went up noticeably,

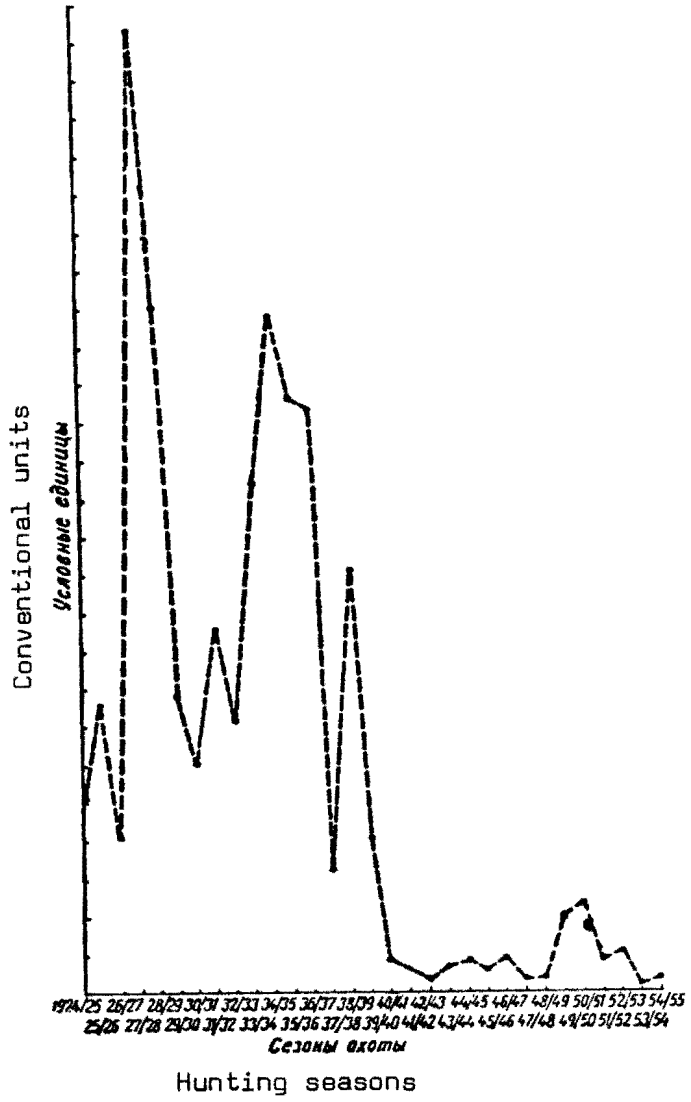

Fig.2. Dynamics of the yield of ermine pelts in the Bashkir, Tartar and Mordov ASSR and in Kuibyshev province.

particularly foxes, pine martens and sables: but supplies of ermine, even in this period, remained at a low level.

In the taiga and tundra zones the depression in ermine numbers was not so prolonged, or the range of fluctuations so wide. For instance, in the Yakutsk ASSR, between 1924 and 1954, relatively low numbers of the

species were recorded in 1930-31 and 1942-43; but these lower harvests, compared with those of the nearest "bumper" years, were down in the first case by only 4 times, and in the second by 7 times; even in these years the ermine was still important in the trapping industry and fur trade of the republic (Fig.3). In the Khabarovsk district and Irkutsk province ermine harvests varied in about the same way.

In the Khanty-Mansiisk national district the yield of ermine pelts in the last 24 years has varied little; the harvests in the "lean" year of 1948, and the "bumper" year of 1933, were in the ratio of 1 to 6.

In the northern part of the European territory of USSR (Komi ASSR, Arkhangelsk and Vologodsk provinces) harvests for the same period in the "leanest" trapping season 1951-52 and the "bumper" season of 1934-35, different by a factor of not more than 14. In recent years there were high numbers of ermine in 1949-50. The importance of the ermine in the fur harvest of, for example, Komi ASSR, has changed relatively little. For the years 1937-1954(a) the proportion of the total value of fur contributed by ermine skins fluctuated from 3.7% (1944) to 23.6% (1946); in the last three years it was 9-10%.

It is important to note the following circumstances. First: in many regions, the decline in ermine numbers, before the long depression, began at a time when food supplies were relatively favourable. Second: in the last 15 years, (the depression period) there were years when the populations of small rodents and water rats were very high in many forest-steppe and steppe provinces. But the ermine stock continued falling, or remained without noticeable change; in some places it even improved slightly, but was far from reaching the level of previous years. For example: in the Tartar ASSR, the numbers of small rodents were high in the years 1940-41; they were also plentiful in 1943. Meantime, the stock of ermine remained

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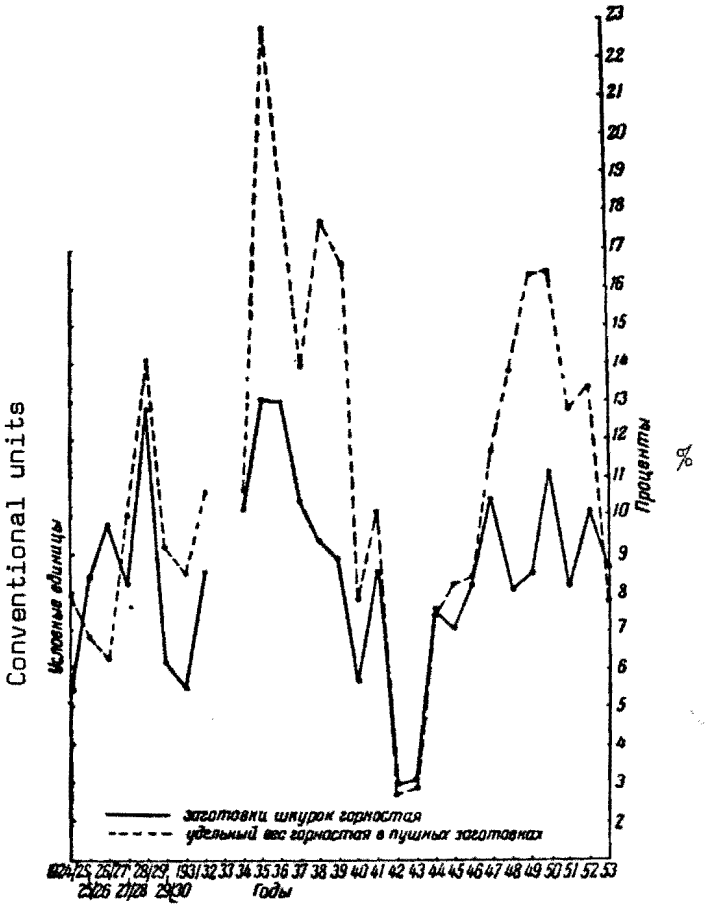
(a) Komi ASSR was formed at the end of 1936. - Author.



_____ deliveries of ermine pelts

– – – – – proportion of ermine in all fur

Fig.3. Dynamics of the yield of ermine pelts in Yakutsk ASSR and proportionate weight of this species in fur deliveries.

very low, as reflected in the harvest of pelts (Fig.1). An irruption of water rats was recorded in the years 1948-51. In the 1949-50 season pelt deliveries of water rats stood at an unprecedently high level, exceeding those of, for example, 1947-48, by 43 times. It is true that in the following trapping season (1950-51) the yield of ermine skins increased five times, but in absolute figures it fell far short of previous years and was approximately 10 times lower than in 1928-29. The same happened

in the Bashkir ASSR.

In Kazakhstan high ermine numbers were recorded in the years 1927-30 and in 1935-37; in the same years there was an outbreak of water rats. In 1937, i.e. when the food position was still favourable, ermine numbers started to decline: in North Kazakhstan province the yield of pelts for the 1937-38 season was down by about 32%. An increase in numbers of water rats in Kazakhstan in 1946-47 and 1950-51 evidently brought some increase in the numbers of ermine. Skin deliveries, as in former, food-rich years, were 2-3 times greater compared with preceding seasons, but in absolute terms they were below the figures for 1935-37 by about 10 times; the numbers of the species continued to remain at a very low level. In 1938-39, small rodents were plentiful in North Kazakhstan, during which time supplies of ermine and the yield of pelts continued to fall. Again, in some of the following years, there were completely adequate food supplies, but stocks of ermine increased only slightly, and skin deliveries fell far short of the level of even the worst seasons of the twenties and thirties.

In the territory of Novosibirsk province in recent years the numbers of small rodents were high nearly everywhere and there were very high populations of water rats in the years 1947-50. In the 1949-50 trapping season stocks of the ermine and pelt deliveries were slightly higher, but then again dropped to an unprecedently low level.

It must be mentioned that, in the Asiatic parts of regions we have discussed, the food of the ermine has become in recent years more varied and stable, because of the extending distribution and great increase in numbers of the muskrat[(a)] on which, as observations have shown, this predator readily feeds.

Analysis of this and other information suggests that the catastrophic diminution in stocks of the ermine, and the perennial depression

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(a) Ondatra zibethicus - a large American rodent: escapees from fur farms established feral populations in much of Europe and Russia. - Ed.

in its numbers, are due to many causes. Conclusions that, for example, in Kazakhstan (Sludskii 1953) the low numbers of the species are due to the poor food supplies, the periodic drying-up of lakes and the mortality of ermines due to flooding by melting snow-water, are inadequate. These causes, reported by many VNIO trapping correspondents, can undoubtedly have an adverse effect: however, in the relevant period, they were not the only ones and not, in every case, the principal ones, because, (as already mentioned) these were years with high numbers of small rodents and water rats. The lakes, after the last severe drought, recovered in the years 1941-43; for several consecutive years no widespread spring floods have been recorded.(a) Apart from this, the decline in ermine numbers has also occurred in regions where the ground is more broken and melt-waters are not dangerous for the ermine, and where lakes are few and the water level in them is relatively constant.

In some places diseases have played an important part in this decline. Mortality of ermine from diseases have been known for a long time. As long ago as in 1927 N.P. Sokol'nikov wrote as follows: "We have not seen any ermines behaving strangely, but we do sometimes find them dead from unknown causes". VNIO correspondents have often found dead ermines. Some of them point out the very severe emaciation of the dead animals, and also to the presence of mange in the skin, abscesses in the eyes, black spots on the flesh side of the skin (b) or slight cuts.

(a) In the conditions of Kazakhstan summer floods are apparently of little danger to the ermine. In North Kazakhstan province, after the heavy rains which fell in July 1940, a vast area was inundated; in places the water reached a depth of over 0.5 m. Escaping ermines were often seen in trees. In spite of this disaster ermines were still comparatively plentiful in the winter of 1940-41, and tracks were seen by us in every type of habitat; particulars of the count are given on pp.194-195. - Author.

(b) Caused by accumulation of melanin in the follicles, in preparation for the spring moult (Santisteban 1949): certainly not a pathological symptom. - Ed.

Of the parasitic diseases, skrjabingylosis is widespread among ermines. In some years in certain regions 50% of the population is infected with the nematode Skrjabingylus nasicola. During the recent depression, in some provinces a high rate of infection of the ermine was found. Investigations revealed the unfavourable effect of this invasion on the stock (Lavrov 1943, 1944b; Popov 1947).

Some apparently infectious diseases were also recorded; possibly these are still more important. The presence of a highly contagious disease was recorded in 1940 among ermines in North Kazakhstan province: about a half of the animals died soon after capture with identical symptoms.(a) The day before death the ermines were looking well and were eager for food (I used to feed them once a day, in the morning). The next morning they would refuse food, ignore observers, and their muzzles would be covered with a discharge from the nose. In the afternoon they would be found lying on the floor (healthy ermines usually buried themselves in the hay) with their fur fouled with excrement and urine. About every 20-30 minutes convulsions would start, the animals knocking their heads on the roof of the cage and their hind legs on the sides, uttering a faint cry; in some animals the hind limbs were paralysed. They would not react at all to the presence of man. In general the clinical symptoms were reminiscent of those exhibited by the sable when infected with bubonic plague (Sorina 1955).

The ermines were caught with gauntlets; the same day they were delivered to the base camp, where they were kept in the attic of a house in small travelling cages. They were fed on sparrows and occasionally given raw hare meat. Cats and dogs were denied access to the attic.

The report of VNIO correspondent, P.F. Shafranov (Kemerovsk province), is of interest, as in it he mentions finding 4 dead ermines on 5 May 1945 which had apparently died of diarrhoea. Evidently their fur was

(a) One ermine died in the laboratory of the All-Union Institute of Experimental Medicine (Moscow) about 2 weeks after capture. - Author. See p. 183. - Ed.

fouled with excrement, as in our animals which had died while being kept in captivity. It is possible that the nature of the disease and the cause of death of the ermines was the same in both cases.

Experiments in infecting the ermine with Bacterium tularense showed the low susceptibility, and high resistance to tularaemia, of the ermine under laboratory conditions (Lavrov 1944). But it does still suffer from tularaemia, and we can assume that, in the years when epizootics of this disease affected very many small rodents and water rats, ermines would be likely to pick it up. Many VNIO correspondents reported finding the dead bodies of ermines without visible signs of damage (they were sometimes ploughed up by tractors). Perhaps, the death of some of these animals was a result of tularaemia infection.

Yu.P. Klimov, who is well acquainted with the ecology of the ermine in Novosibirsk province, suggests that the fall in the numbers of this species during the last 25 years there was most probably caused by some disease.

There is yet another biotic factor which cannot be ignored, the importance of which, as it seems to me, is often underestimated: the influence of enemies and competitors. The fact of the displacement of the weasel by the sable is well known. As the population density of sables increases, so the number of weasels is reduced, and vice versa. V.V. Timofeev, scientific co-worker of the East Siberian VNIO zonal laboratory, who for many years studied the sable in the wild, has often found weasels killed or partially eaten by sables (Timofeev 1951). Cases of the almost complete extermination of the raccoon dog by the wolf have been recorded in a number of regions. On the interrelations of these species V.F. Morozov writes as follows: "In recent years the number of wolves has greatly increased, and this has become a factor substantially limiting the populations of the raccoon dog." And elsewhere: "In some regions the wolf greatly reduces the number of raccoons ... At many points the failure of the

raccoon to become acclimatised is due to the fact that wolves destroy them ..." (Morozov 1948, 1951). Latterly, it has been established that casualties to foxes are attributable to the wolf (Teplov 1954).

On Great Shantar island instances have been recorded of persecution of the ermine by the sable. In studying the feeding of the sable in two collections of scats (total about 110 samples) remains of ermine were found. Its tracks occur more often in places where there are no sables (Dul'keit 1929). Similar interrelations between these two predators were recorded in Sayany (Solov'ev 1921) and in Kamchatka (Bormantov 1933). In the autumn of 1933 the ermine was driven out of the Tarsk district by migrating weasels (Belyshev 1934).

Many VNIO correspondents in the forest-steppe and steppe regions of Western Siberia and Kazakhstan report on the relationship between the fox and the ermine. Foxes kill ermine, and leave the dead bodies lying around; as the foxes multiply, the numbers of ermine visibly decline.

To one of our special enquiries concerning the reasons for the low numbers of ermine from North Kazakhstan province, an answer was received from P.E. Tret'yak: "The question of the ermine has long worried us too. As from 1937, with the appearance of a large number of foxes in our province, the ermine has become scarcer. Thinking that there would not be enough support for my opinion, I read your letter to old and experienced trappers. We all came to the same conclusion - the fox had wiped out the ermine. None of us had observed wholesale mortality of ermine from disease, but we had all seen how the fox exterminates it. The fox can easily dig up ermine nests, and then eats the young. Furthermore, in winter the fox also kills fully grown ermines".

Head trapper N.A. Lavrenyuk, director of the Makushinskii muskrat farm, reports foxes frequently eating ermines that were caught in traps; he considers one of the chief reasons for the low numbers of ermines to be

due to the rapid increase of foxes.

We do not have the data to conclude that the activity of the fox is responsible for the decline in ermine numbers: but we can assume that, at a certain numerical ratio between them, the fox can partly restrain the population growth of ermine, either directly, or indirectly by influencing food supplies.

In some provinces the number of foxes has recently been at a very high level. For example, in the Bashkir and Tartar ASSR, before the War, ermine pelts were delivered in far greater numbers than those of foxes. In the post-war years the position was reversed. In Novosibirsk province before the war, the yield of ermine pelts exceeded that of fox pelts by many tens of times, in 1945-46 by less than three times; in 1951-52 the yield of skins of both species was about the same, but in 1953-54 the delivery of ermine skins was down to a half.

In North Kazakhstan (North Kazakhstan and Kokchetav provinces) according to old and experienced trappers questioned in 1939, the fox was formerly very seldom seen : results of track counts indicate the low population density of this species in pre-war years (Table 4). From 1932 to 1940 in these areas deliveries of ermine skins were many times greater than those of the fox; in 1935, for example, 500 times greater (see Table 5).

In the last 8 years the ratio has changed, and in the same North Kazakhstan and Kokchetav provinces up to 8 times as many fox skins are delivered. Formerly in these provinces one good trapper used to catch 1-4 foxes during the trapping season, but now more than 50. A further example: A.L. Malin, kolkhosnik of the Red Army region, together with a friend, after finishing his day's work as a fisherman, caught 10 foxes between 15 February and 1 March. Before the war this region produced only a few fox skins a year.

Before the War the fox was a rare animal in Kurgansk province

Table 4. Results of fox-track counts in parts of North Kazakhstan province

Locality	Approx. length in km	Date of census	No. of tracks counted		Observer
			Fox	Ermine	
Mamlyntka district	10	9 Dec. 1937	1	4	A. Bakhman
Petropavlovsk district	11.5	11 Dec. 1940	2	7	N.P. Lavrov
Petropavlovsk district	11.5	16 Dec. 1940	1	5	N.P. Lavrov
Bulayevo district	18.5	13 Mar. 1941	1	8	A.S. Pokrovski

Table 5. Numbers of fox and ermine pelts obtained, 1937–1940

District	1937		1938		1939		1940	
	Fox	Ermine	Fox	Ermine	Fox	Ermine	Fox	Ermine
Bulayevo	5	1747	8	807	25	1535	32	669
Mamlyutka	19	1580	65	843	21	1004	38	306
Petropavlovsk	65	1491	31	980	99	1230	56	139

(in particular in the Makushinsk region). Latterly its numbers have greatly increased, as can be seen from the following figures. In this region, fox pelts in 1944 numbered 16, in 1946 - 30, in 1948 - 95, in 1950 -130, in 1952 - 426 and in 1954 - 150 skins. Every year more fox skins than ermine skins are delivered here, for example, in 1951, 3.4 times as many. The numerical proportion of both species is indicated by the results of a count carried out by S.A. Abashkin on 29 January 1954 (in this year fox numbers were considerably down). On a 21 km trek the tracks of 4 ermines and 8 foxes were recorded.

The various activities of man have probably played an important and, in some regions, perhaps a decisive part in the prolonged depression in numbers of the ermine. In the northern forest provinces, these effects are probably beneficial. "In distinction from some other species", writes A.N. Formozov, "the ermine is not a typical forest animal and only benefits from the changes brought by human activity into the forests. There is no doubt that, with the passage of years, ermine numbers in the district [Gor'kovsk] are not falling, but rather on the increase".

However, the same factor, which has grown stronger in recent times, acts differently in forest-steppe and steppe. The draining of bogs and lakes, the clearance of undergrowth and deep ploughing of the steppe, the felling of woodlands in river floodplains, the chemical control of agricultural pests, the control of susliks and hamsters, (e.g. by flooding of the burrows with water) the burning of straw heaps in the fields, the starting of forest fires, and many other measures make living conditions worse for the ermine. Forest fires deserve special attention, recently they have been lit wholesale in forest-steppe and steppe provinces. Bogs, reed beds on lakes, areas of uncut grass and undergrowth are burned out. Here on these open spaces, fire spreads extremely rapidly, and in some places (e.g. in peat bogs) penetrates the top layer of soil. Forest fires can be a direct or indirect influence on the ermine population.

Adult and young ermines perish in the fire and smoke; eggs and nestlings of birds, small rodents and water rats are destroyed, leaving extremely unfavourable conditions for food and shelter for the surviving ermine. Ermine burned to death in fires were often reported in the press. The number of similar reports received from trapper-correspondents of VNIO has increased considerably recently. Some trappers find as many as 12 carcasses of ermine killed by fire every spring.

In conclusion we mention one more important factor - the fur trade, the value of which is impossible to underrate. The point is that with a few exceptions, ermine trapping has not been stopped throughout the whole period of the decline (a closed season was notified from 17 January 1938 to 15 October 1939 in Chelyabinsk province, in the 1940-41 season in Kazakhstan, in 1947 in the Altaisk district and Chkalovsk province)(a). So that in spite of the comparatively low stock, trapping has continued, and because it lives in the immediate vicinity of villages, trapping methods are not complicated and the value of the skins relatively high. The ermine are found in the same habitats as the muskrat, (bogs and localities adjacent to lakes) which are visited by muskrat-trappers almost daily. "And if an ermine", says head trapper Lavrenyuk, "did not get caught in a trap set for a muskrat, the trapper catches it without fail by setting a trap in the runway".

According to the mass of information from correspondents in the post-war years, the best trapper in the Tartar and Bashkir ASSR would catch up to 13 ermine per season, on average: in North Kazakhstan, up to 25 ermine, in the forest-steppe provinces of Western Siberia up to 100 ermine. In years when it was more plentiful, many more were caught: see, for example, the figures from Kurgansk province (Fig.4).

(a) Even in the season when trapping was closed ermine pelts were coming in. For example, in 1938-39 in Chelyabinsk province several thousand pelts were delivered. - Author.

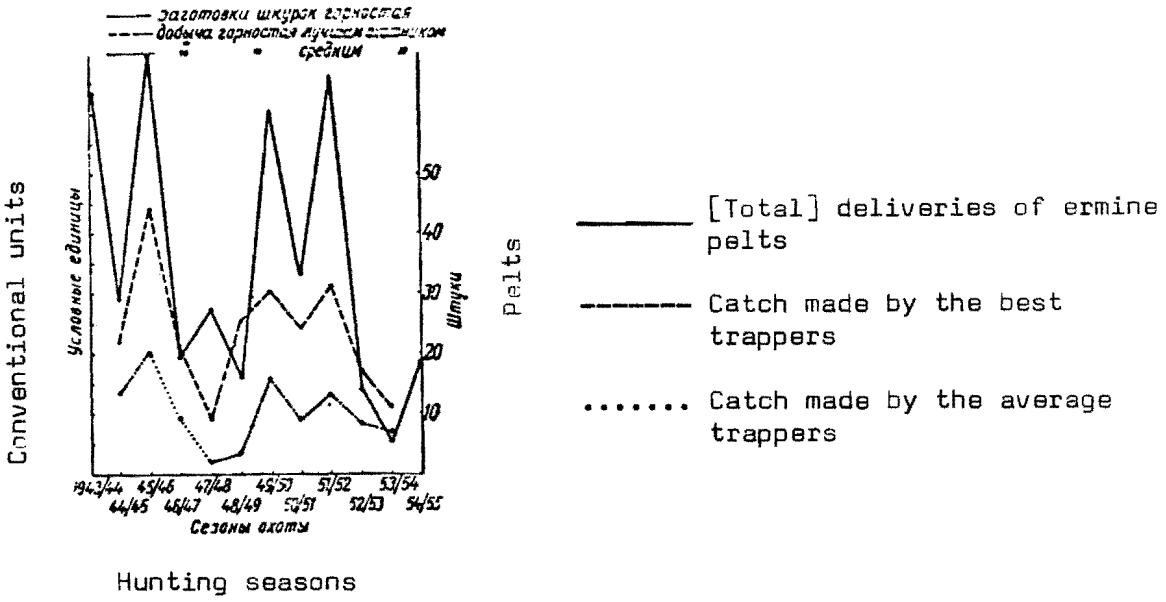

Fig.4. Variations in the yield of ermine pelts and average annual catch by the best trappers in Kurgansk province.

[Summary]

From these data it can be seen that the observed depression in ermine numbers in the forest-steppe and steppe provinces of the USSR has gone on for an unusually long time - about 15 years - and the yield of pelts has been reduced by a higher factor than was the case in any one season during the period from 1924 to 1940. There were no such large variations in the quantity of skins coming into the Irbitsk market between 1883 and 1895 (Turkin and Satunin 1902).

In many provinces where, until quite recently, the ermine had been the main winter trapping species, it has been unimportant in the trapping industry and fur trade for many years now.

In the last 15 years the relationship between ermine populations and those of its prey has been disturbed: favourable food supplies are

not now always the deciding factor in the population dynamics of the ermine stock, nor are they a reliable index when compiling a forecast of the harvest of ermine skins. This changed situation, which we noted several years ago (Lavrov 1944b), was confirmed by subsequent events.

The reduction in the stock of ermine to an unusually low level, as well as the continued depression in numbers were due, in our opinion, to a complex combination of diverse causes. During the many years of depression unfavourable conditions must have kept in check any population increase in the ermine - a species which is by nature highly prolific. The high reproductive potential of ermine is shown by the following data: the females mature in the year of birth, but in the sable, for example, in the second or third year of life; average number of young in the ermine about 9, of the sable about 3; and the mountain hare and the common hare, which breed two or three times a year, do not produce more young in a season than the ermine (Saleker 1953, Lavrov 1944a, N.P. Naumov 1934, S.P. Naumov 1944).

Conservation of species of commercial importance, in particular the ermine, is difficult. In some cases, man cannot yet control certain natural phenomena (e.g. the drying-up of undrained lakes, flooding from rapid snow melting etc.), and in others, the elimination of unfavourable conditions caused by the activities of man (draining of bogs, control of weeds, ploughing-up of waste land etc.), is not economically justifiable. It is however within our powers to control one of the main factors, i.e. commercial trapping, which is carried on nearly everywhere. For example, in years of slight increase in ermine numbers, trapping is intensified, with the result that the remaining breeding stock could not provide for a growth in numbers for the next season.

In order to promote a more rapid reinstatement of stocks of the ermine to its former commercial importance, we recommend that the following measures be taken :

1. In provinces affected by the prolonged depression of ermine numbers, to suspend trapping for two or three years. The experiment of declaring a closed season for one year did not give the expected results, for the breeding stock at the conclusion of a short-term closure evidently is insufficient to allow increased reproduction of the species.

2. Simultaneously to ban trapping of the polecat and weasel. It has been shown in practice that by authorising the catching of these animals, the efficiency of the first measure is greatly reduced. Where there is a large number of polecats and weasels, trappers should be recommended to catch them by methods and equipment unlikely to catch ermine (for instance, setting the trap near a polecat den or a temporary hide-out).

3. To recommend trappers to trap water rats, susliks, hamsters and muskrats by methods least dangerous for the ermine.

The data presented in this article do not of course fully explain that complex phenomenon - the population dynamics of ermine and the prolonged depression in its numbers. These are questions of practical importance and theoretical interest, and merit the establishment of a special research project.

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INFECTION OF THE PINE MARTEN (MARTES MARTES) BY NEMATODES OF THE GENERA FILAROIDES AND SKRJABINGYLUS IN THE NORTH-WEST RSFSR

(O zarazhennosti lesnoi kunisy (Martes martes) nematodami rodov Filaroides i Skrjabingylus na Severo-Zapade RSFSR)

by

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Zool.Zhurn. 1970 49 (1) : 131-136.

Summary

In the North-West of the USSR, the rate of invasion of the pine marten (Martes martes L.) by the pulmonary nematode Filaroides ranged from 27.0 to 66.6% (mean 50.3%) in the period 1957-58 to 1967-68; in some regions it was 43.5-53.1% (maximum in Karelia). There was a sharp drop in invasion in years with a good harvest of Sorbus berries. On average, females were less infected than males. Young-of-the-year were infected more (61.0%) than adults (47.5%). Infection by Skrjabingylus ranged from 62.5 to 85.3% in the different regions (being higher in the north than in the south). 90.4% of the population were infected by the two species of helminths. The mean invasion by Skrjabingylus was from 5.4 to 13.2%; decreasing at the end of the year. Poorly fed martens were more heavily infected.

To date, 19 species of helminths have been recorded in the pine marten (Troitskaya 1967). The most frequent and numerous of these are the pulmonary nematodes Filaroides martis Werner (1782) and nematodes parasitic in the frontal and maxillary (Highmore)[a] sinuses, Skrjabingylus petrowi Bageanov (1936) and S. nasicola Leuckart (1842; Petrow 1927). These helminth species are distributed everywhere. The literature records

(a) Maxillary sinus, also known as antrum of Highmore, according to Webster's Dictionary. - Ed.

data on invasion of martens by helminths in the Archangel region (Leble 1951, Grakov 1962) and the Vologda region (Gribova 1959), and also in the Tartar, Mari and Bashkiria ASSR (Aspisov 1959, Troitskaya 1962, 1963, 1965). The stone marten (Martes foina Erxl.) is known to be infected by Filaroides and Skrjabingylus in North-West Russia (Kogteva and Morozov 1963, Shakhmatova 1964). This has encouraged us to publish these data on the infection dynamics of the helminths most pathogenic to the pine marten, which were obtained while studying other aspects of its ecology.

In order to determine infection of martens by Filaroides, macroscopic and microscopic investigations were made of the larynx, trachea, bronchi and lungs of 558 specimens during 11 autumn-winter seasons (1957-58-1967-68); in order to determine infection of martens by Skrjabingylus, the frontal and maxillary sinuses were examined in 155 specimens during two hunting seasons (1966-67-1967-68). The material was collected in the Karelian ASSR, and the Leningrad, Novgorod and Pskov regions.

Filaroides are long, very thin light-grey nematodes closely interwoven with the lung tissue and fine bronchi, and they form dense foci, often the size of a pea. It is not possible to extract the parasites undamaged, so it is difficult to determine their numbers and we characterised the degree of invasion by foci changes in the lungs.

Skrjabingylus are comparatively large bright-red nematodes parasitic in the frontal and maxillary sinuses. We did not differentiate them into species.

Martens are infected by Filaroides and Skrjabingylus by eating terrestrial molluscs (intermediate hosts) and small rodents (Muridae - reservoir hosts) invaded by larvae of the parasites (Lyubashenko and Petrov 1962). The development cycles of the pulmonary pathogen (Filaroides bronchialis) and of the frontal-sinus pathogen (Skrjabingylus petrowi) have been described by A.M. Petrov and V.G. Gagarin (1938).

There is no doubt that the helminths have a deleterious effect on

the physiology of the host, due both to their mechanical action on the tissue and also to their metabolic products. The pulmonary parasites have a specific effect on the tissue, as a result of which parts of the lungs lose their capacity for gas exchange (Fedorov 1963). Cases are known of sables dying due to Filaroides, and in stoats of Skrjabingylus causing skull bones to become thin and perforated, reducing the fertility, and reducing numbers due to intoxication(a) (Lavrov 1944, Lyubashenko and Petrov 1962).

In 1957-58-1967-68 in North-West Russia the infection rate in pine marten populations varied from 27.0 to 66.6%, averaging 50.3% (Table 1). There were three major invasions (1958-59, 1960-61, 1966-67) and two minor ones (1957-58, 1964-65).

The lowest infection was observed in years of low marten populations. After a heavy invasion of the population, the numbers of marten decreased somewhat in the following year. According to N.N. Grakov (1962), the populations of the marten in the Archangel region and the Komi ASSR fell in years of very extensive and intensive infection by helminths.

Table 1. Infection of pine marten by Filaroides in the North-West RSFSR in autumn-winter (Nov.-March), 1957-58 - 1967-68

Years	No. of martens examined	Infected		Years	No. of martens examined	Infected	
		no.	%			no.	%
1957-58	48	13	27.0	1963-64	10	5	50.0
1958-59	90	60	66.6	1964-65	68	24	35.3
1959-60	88	43	48.8	1965-66	27	12	44.4
1960-61	40	25	62.5	1966-67	87	55	63.2
1961-62	11	5	45.4	1967-68	72	32	44.4
1962-63	15	6	40.0				

(a) Russian word "intoksikatsii" - literally, poisoning by toxins. - Trans.

We observed a sharp reduction in Filaroides invasion in years of abundant fruiting of Sorbus, when these fruits were more important in the food of martens (63%, as opposed to 12.5% in normal years). In these periods the marten ate fewer small rodents (30%, as opposed to 50%), and so the opportunity for infection by helminths was reduced. A.A. Troitskaya (1962, 1963) also mentions this distinct correlation between the rate of infection of the marten population by Filaroides and the yield of Sorbus fruits. Apparently Sorbus has a dehelminthic effect, not only on intestinal parasites but also on parasites of the lungs and frontal sinuses.

In some regions the rate of invasion fluctuated from 43.5 to 53.1% (Table 2). Infection in martens tends to increase from southwest (Pskov region) to the north and north-east (Karelian ASSR). Possibly this is because the marten population in S. Karelia, where the research material was obtained, was higher than in the more southerly regions (e.g. in the Pskov region). A.A. Troitskaya (1962) thinks that invasion decreases from west to east, and suggests that this is due to the harsher climate of the Bashkirian Pre-Urals as compared with the Mari ASSR.

Table 2. Infection of Marten by Filaroides in the North-West RSFSR in 1957-58-1967-68

Place of investigation	No. of specimens studied	Infected	
		no.	%
Karelian ASSR	177	94	53.1
Leningrad region	256	129	50.4
Novgorod region	102	45	45.1
Pskov region	23	10	43.5
Total	558	278	49.8

According to our data the mean infection rate in males is 50.6%, and in females 48.0%. In four of the 11 years observed, females were much

less infected than males (by 12.6-27.6%); and in only one year, males were less infected (by 20%) than females (see Fig.1): in the other years the difference between infection of males and females was slight, ranging from 1.1 to 6.7%. According to Troitskaya (1965) the difference in infection rate of males and females from the Mari, Tatar and Bashkiria ASSR was also slight (1.5%), while in the Archangel region and the Komi ASSR it was 15% (Grakov 1962). Although there is no close relationship between infection with Filaroides and sex, in years when infection of martens is at an average level, the females are much less infected than the males, but in years of heavier invasion the infection of the females increases and reaches values similar to the males. The lower infection of the females can be explained not only by their physiology (Shikhobalova 1950) but also by their ecology. Females come down to the ground more rarely than males, and therefore have less contact with molluscs.

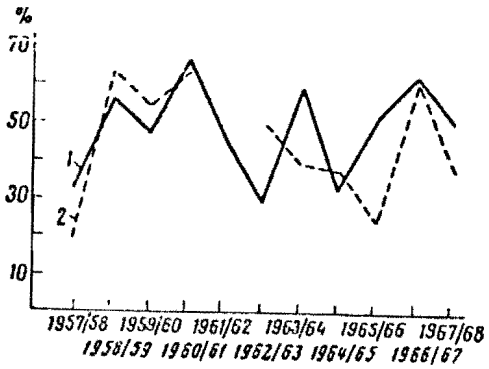

Fig.1. Infection of male and female martens by Filaroides in each hunting season, 1957-58-1967-68, in the North-West RSFSR

1 - males, 2 - females

We classified the intensity of Filaroides invasion by the number of foci containing helminths in the lungs. Out of 170 martens investigated, 71% had from 1 to 3 foci. The maximum number of foci was 7, which

was observed in 2.3% of the martens (in December and January). The average per infected animal was 2.7 foci. From December to February the number of martens with the maximum number of foci in the lungs increased almost two-fold (from 5.6 to 10.5%), while the number with one focus increased towards the end of the winter from 15.7 to 31%, and the number with 3 foci fell by more than half. The mean intensity and extent of invasion did not change significantly (Table 3).

Table 3. Infection of martens by Filaroides through the hunting season, 1957-58-1967-68 in the North-West RSFSR

Month	No. of martens studied	Infected		Mean no. of foci in lungs, per infected animal
		no.	%	
November	123	70	56.9	2.8
December	203	96	47.2	2.8
January	160	80	50.0	2.8
February-March	67	32	47.7	2.5
Total	553	278	50.3	2.7

The intensity and distribution of Filaroides invasion in the North-West RSFSR is lower than in the adjacent areas of the Archangel region and the Komi ASSR (Grakov 1962), and the Vologda region (Gribova 1959), but is higher than in the Mari, Tatar and Bashkirian ASSR (Troitskaya 1962).

In martens in the North-West RSFSR, there is a clear relation between Filaroides invasion and age (Table 4): yearlings are much more infected (61.0%) than adults (47.5%). The proportion infected gradually decreases in the older age groups, because immunity of the martens to helminths increases with age (Shikhobalova 1950, Dogel 1962).

Table 4. Filaroides infection in martens of different age groups in the North-West RSFSR in 1957-58-1967-68 (136 yearlings and 242 adults examined)

Age groups	No. of specimens	Infected	
		no.	%
7-11 months	136	84	61.0
19-22 months	152	87	57.2
31-34 months	63	24	38.1
Over 3 years	27	4	14.8

Skrjabingylus shows the same pattern (Table 5). This nematode is widespread in the North-West RSFSR. The same marten may harbour both Skrjabingylus and Filaroides, though the mean rate of infection by Skrjabingylus is much higher (79.6%) than by Filaroides (49.8%): 90.4% of the population were infected by one or other of these two species of helminths in 1966-67-1967-68. In some regions in the North-West, infection by Skrjabingylus ranged from 62.5 to 85.3%, and the intensity of invasion ranged from 5.4 o 13.2 helminths.(a) Here, as with Filaroides, the infection clearly increases in the northern regions (Table 6).

The rate and intensity of Skrjabingylus invasion varies from year to year. In 1967-68 it fell, compared with 1966-67, being 71.0% and 9.9(a) versus 87.4% and 12.6.(a) Simultaneously there was a reduction in Filaroides invasion. No significant differences were observed in the extent of Skrjabingylus infection of males (76.9%) and females (79.3%).

In the North-West RSFSR, on average there are 11.6 Skrjabingylus per marten, with a maximum of 53. The maximum number of Skrjabingylus in the Vologda region was 15 (Gribova 1959), and in the Archangel region 90 (Grakov 1962), worms in one marten.

(a) per host. - Ed.

Table 5. Infection by Skrjabingylus in 1966-67-1967-68 of martens of four age classes (114 martens examined)

Age class	No. of specimens	Infected	Rate of Invasion %	Intensity of Invasion
7-11 months	50	45	90.0	14.2
19-22 months	43	37	86.0	13.8
31-34 months	17	14	82.3	7.1
Over 3 years	4	2	50.0	1

Table 6. Infection of martens by Skrjabingylus in four regions in the North-West RSFSR in 1966-67-1967-68

Place of investigation	No. of specimens studied	Infected		Mean intensity of invasion
		no.	%	
Karelian ASSR	96	79	82.3	13.2
Leningrad region	34	29	85.3	11.3
Novgorod region	16	10	62.5	5.4
Pskov region	11	7	63.6	5.8

In cases of mixed invasion (when a marten is also infected by Filaroides), the intensity of infection by Skrjabingylus is almost twice as high (15.1 worms each) as when only Skrjabingylus is present (8.6 worms each). The mean intensity of infection by Skrjabingylus in males is 12.6, and in females 10.3 worms each. The frequency distribution in 1966-67-1967-68 was as follows :

Number of Skrjabingylus per marten	1-10	11-20	21-30	41-50	51-60
Number of martens infected	70	33	9	1	1
Number of martens infected, %	57.4	27.1	7.4	0.8	0.8

The rate of infection by Skrjabingylus decreases somewhat at the end of

winter; the mean intensity of invasion in autumn and winter remains at about the same level, although the maximum increases slightly (Table 7).

Table 7. Infection of martens by Skrjabingylus in different months of the hunting season 1966-67-1967-68 in the North-West RSFSR

Months	No. of martens studied	Infected		No. of Skrjabingylus	
		no.	%	range	mean
November	26	25	96.2	1-36	10.6
December	54	48	88.8	1-48	12.1
January-February	49	42	85.7	1-53	11.8

The infection rate of martens was related to their physical condition. Filaroides and Skrjabingylus were commoner in poorly fed martens (93.3%) than in well fed or average ones (88.6%). The intensity of Skrjabingylus invasion was also higher in poorly fed martens, [averaging] 19.7 versus 10.6 [worms per marten]. At the beginning of the hunting season (in November), half the martens (53.9%) in a sample were well fed, but by the end of winter this proportion was halved, and the number of those poorly fed or average increased. Intensity of Skrjabingylus invasion in poorly fed martens increased towards the end of winter (Table 8).

Table 8. Distribution of martens by condition and intensity of Skrjabingylus infection, in the months of autumn and winter in the North-West RSFSR (1966-67-1967-68)

Months	No. of martens studied	% martens per condition class			Mean no. of worms per condition class		
		good	average	poor	good	average	poor
November	26	53.9	42.3	3.8	9.9	11.8	3
December	54	35.2	53.7	11.1	12.4	10.7	18
January-February	49	26.5	57.2	16.3	6.1	11.1	21.3

Infected martens also weighed less. Among adult males, five non-infected weighed on average 861 g; 12 infected by Skrjabingylus (mean of 4 worms each) weighed on average 783 g; 14 infected by both parasites, with enhanced infection by Skrjabingylus (mean of 10.7 worms each) weighed on average 817 g. Among 9 yearling males, 9 badly infected by Skrjabingylus (mean of 29.3 worms each) weighed less (669 g) than 9 other slightly infected animals, 745 g (mean of 6.9 worms each). However, there were some very heavy and very well fed specimens (1000-1200 g) among badly infected martens. These were old males, which had usually fed on honey of wild bees.

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A STUDY OF THE DEVELOPMENT OF THE HELMINTHS OF FUR-BEARING ANIMALS (FILAROIDOSIS AND SKRJABINGYLOSIS)[a]

(Izuchenie tsikla razvitiya vozbuditelei legochnykh gel'mintov pushnykh zverei (filyaroidoza i skrjabingileza)

by

A.M. Petrov and V.G. Gagarin

Dokl.Vses.Akad.Sol'khoz.Nauk im.Lenina 1937 5 [8] : 291-294

Helminthoses of the respiratory tract of furred animals are widespread on fur breeding farms and take a heavy economic toll every year. The respiratory organs of sables, martens, minks, polecats and other mustelids are known to be parasited by specific helminths, but as their biology has so far not been studied, methods of controlling these helminthoses are still unknown.

The most frequent helminthoses of the respiratory tract of sables, martens, minks, polecats and mustelids, are filaroidosis of the lungs and skrjabingylosis of the frontal sinuses. This paper is concerned with study of the cycles of development of the agents of these diseases.

Experimental

The work was done at the Pushkin Fur Farm in the Moscow Region. We had established, from previous work in 1935-36 on the vital diagnosis of lung helminthoses of furred animals, that the usual parasites of the respiratory organs of sables and martens on the Pushkin fur farm are Filaroides bronchialis (Werner 1782) and Skrjabingylus petrowi (Bageanow 1936).

A. Study of the development cycle of Filaroides bronchialis (Werner 1782)

The agent of filaroidosis of the lungs of furred animals is the species Filaroides bronchialis (Werner 1782) localised in special pulmonary nodes (cysts) and closely intermeshing with the pulmonary tissue and small

(a) Preliminary communication. - Author.

bronchi. The posterior end of the female parasite communicates with the lumen of the bronchus into which the larvae are released.

We established that the larvae of F. bronchialis are released into the environment through the digestive tract, in the excreta of the infected animals.

The light grey larvae (first stage) freshly eliminated in the excreta reach a length of 0.295–0.334 mm and a maximum width of 0.018–0.020 mm. Their tail end is conically pointed and its tip is always curved to the dorsal side.

Attempts to cultivate freshly excreted larvae of F. bronchialis in 0.75% agar-agar in a thermostatic chamber at 25–26^{o} showed that these larvae, while remaining viable for a long time, do not grow or moult. This suggests that further development of the first stage larvae of F. bronchialis can occur only in the body of certain intermediate hosts.

Since various species of ground molluscs have been established as intermediate hosts for many parasites of the family Metastrongylidae, to which the species Filaroides bronchialis belongs, we experimentally infested molluscs with F. bronchialis larvae.

1. Experimental infestation of molluscs by the larvae of Filaroides bronchialis

The experiments with infestation of the experimental molluscs by the larvae of Filaroides bronchialis were carried out on the following three species of ground molluscs: Succinia putris, Zonitoides excavata and Arion intermedis.

The molluscs for the experiments were collected a long way from the fur farm. From each batch of molluscs collected, several specimens were opened up, and only batches not naturally carrying nematode larvae were used in the experiments.

Technique of infesting molluscs. We investigated the excreta of sables and martens, which had caught filaroidosis in the wild, by using German's method. The F. bronchialis larvae were collected and placed in the bottom of a Petri dish, with a cover on top and containing lettuce leaves. Then 10-15 molluscs were placed in these Petri dishes, where they were kept for 1-1.5 days; then they were transferred to large glass jars (serving as aquaria) measuring 30 x 20 x 22 cm. Cut sod with grass was placed in the bottom of these glass jars. The jars were covered on top with a fine wire mesh or gauze. Extra lettuce leaves or pieces of carrot were added as food for the molluscs. Each jar contained from 15 to 23 infested molluscs. To maintain humidity, the grass in the jars was sprinkled from time to time with water.

The experimentally infested molluscs were dissected at intervals. Invasive larvae of F. bronchialis could be seen in the pedicles. After entering the mollusc, the larvae began to grow, and 8-9 days after experimental infestation the first moult could be observed. Such larvae had already reached 0.424-0.436 mm in length and 0.033-0.045 mm in maximum width. Their tail end was conically pointed and its tip curved to the dorsal side.

On the 15th-16th days the F. bronchialis larvae underwent the second moult, and reached 0.452-0.553 mm in length and 0.042-0.050 mm maximum width.

These [third stage] larvae of F. bronchialis were invasive, since they could be used to infest the experimental polecat with filaroidosis: so the complete development of the larvae of F. bronchialis to the invasive stage in the body of the mollusc lasted 15-16 days.

2. Experiments with infestation of a polecat and a cat with filaroidosis

The definitive hosts for the parasite Filaroides bronchialis are sables, martens, minks, polecats, ermines, weasels and Siberian ferrets.

We tried experimental infestation with filaroidosis of a polecat and a cat.

Experimental infestation of the polecat. For the experiment we used a young polecat aged 2-2,5 months. Preliminary helmintholarvoscopy revealed no larvae in it.

It was kept in a small cage with a netted floor and a sliding metal bottom. Its housing conditions completely excluded any possibility of natural contact of the polecat with molluscs in the period of the experiment.

On 25 July 1936 the polecat was fed on seven molluscs of the species Succinia putris L. which on 7 July (i.e. 18 days before the experiment) had been experimentally infested with the larvae of Filaroides bronchialis This was followed by daily helminthloarvoscopic examination of the excreta of the polecat by Berman's method.

On 14 August 1936, i.e. 20 days after infestation, the larvae of Filaroides bronchialis were found for the first time in the excreta of the polecat. These larvae were detected through the next 16 days i.e. up to 30 August 1936, and then the polecat was killed for control autopsy. Several sexually mature specimens of Filaroides were found in its lungs.

The growth of the parasite F. bronchialis up to the sexually mature stage in the body of the definitive host (polecat) therefore took 20 days from the moment of feeding it with molluscs carrying larvae of Filaroides.

Experimental infestation of a cat. For the experiment we used one kitten aged 2 months. On 25 July 1936 this kitten was fed on five specimens of the same molluscs, Succinia putris, which on 7 July had been experimentally infested with the larvae of F. bronchialis. Subsequent examination of the excreta of the kitten for 25 days (up to 19 August) regularly gave negative results. On 19 August 1936, i.e. 25 days after infestation, the kitten was killed for control autopsy. Inspection of the lungs was based on the method of complete helminthological dissection. No F. bronchialis parasites were found.

This experiment indicates that the cat (unlike the polecat) is not susceptible to infestation with filaroidosis.

B. Study of the developmental cycle of Skrjabingylus petrowi (Bageanow 1936)

Skrjabingylosis of the frontal sinuses of sables, martens, minks, polecats and other mustelids is caused by the nematode species Skrjabingylus nasicola (Leuckart, 1842) and Skrjabingylus petrowi (Bageanow, 1936) located in the frontal sinuses. The developmental cycle of these parasites is still unknown. In the frontal sinuses in sables and martens at the Pushkin fur farm we found only the species Skrjabingylus petrowi, whose developmental cycle we subsequently studied.

We established that the larvae of S. petrowi are released into the environment through the digestive tract together with the excreta of the infested animals.

The light grey larvae of S. petrowi (first stage) eliminated in the excreta of sables and martens reach a length of 0.375–0.425 mm and a maximum width of 0.016–0.019 mm. The tail end is provided with a pointed awl-shaped appendage and an unpaired postanal papilla.

Attempts to cultivate the freshly excreted larvae of S. petrowi on 0.75% agar-agar in a thermoststic chamber at 25–26°C showed that these larvae, while remaining viable for a long time, do not grow or moult, which indicates that further development of S. petrowi larvae can occur only in the body of certain intermediate hosts.

S. petrowi, like F. bronchialis, is a metastrongylid, so we infested molluscs with the larvae of S. petrowi.

1. Experimental infestation of molluscs by the larvae of Skrjabingylus petrowi

The experiments were run only on molluscs of the species Succinia putris L. They were collected from a marsh 1.5 km from the fur farm. Before the experiments we dissected 60 specimens of Succinia putris L.

collected from the same marsh; none contained nematode larvae.

The technique of infesting the experimental molluscs, and the arrangements for keeping them were the same as in the experiments with the larvae of Filaroides bronchialis.

Dissection of the experimentally infested molluscs revealed larvae of S. petrowi penetrating into the pedicle. After entering the molluscs, larvae began to grow very quickly, and 8–9 days after infestation the first moult could be observed. The second stage larvae reached a length of 0.730–0.950 mm and a maximum width of 0.045–0.070 mm, and continued to grow rapidly: by the 15th–17th days they underwent the second moult and were transformed into the invasive third stage larvae. These reached a length of 1.070–1.120 mm and a maximum width of 0.076–0.082 mm, and were used to infest the experimental polecat with skrjabingylosis.

Therefore, the complete development of the larvae of S. petrowi to the invasive stage in the mollusc Succinia putris lasted 15–17 days.

2. Experimental infestation of a polecat, dog and cat with skrjabingylosis

So far only sables and martens have been established as the definitive hosts for the parasite S. petrowi. We were unable to carry out experiments with infection of expensive sables or martens in the summer, so we confined our experiments to the polecat, dog and cat.

Experimental infestation of the polecat. In the experiments we used a young polecat aged 2–2.5 months which had first been experimentally infested with filaroidosis. The housing conditions of this animal were described above.

On 12 August 1936, the polecat was fed on 10 molluscs Succinia putris which on 26 July (i.e. 17 days before the experiment) were experimentally infested with the larvae of S. petrowi. Then a daily helmintholarvoscopic examination of the excreta of the polecat was made by Berman's method. On 30 August 1936, i.e. 18 days after infestation, a large number

of S. petrowi larvae were found for the first time in the excreta of the polecat. On the same day the polecat was killed and in its frontal sinuses five sexually mature Skrjabingylus petrowi specimens were detected, including two males and three females. The growth of the parasite S. petrowi from the moment of feeding on molluscs invaded by the larvae of skrjabingylus organisms to the sexually mature stage in the polecat therefore lasted 18 days.

Experimental infestation of a dog and cat. For the experiments we used a puppy aged 2-2.5 months and a kitten aged 2 months. The dog was fed on 10 and the kitten on six Succinia putris molluscs, which, on 26 July (17 days before the experiment), had been artificially infested with S. petrowi larvae. The subsequent investigations of the excreta of the dog and kitten for 18 days (up to 30 August) consistently gave negative results.

On 30 August 1936, i.e. 18 days after infestation, the dog and kitten were killed for autopsy which revealed no parasites in the frontal sinuses. These experiments indicate that the dog and cat (unlike the polecat) are not susceptible to infestation with skrjabingylosis.

CONCLUSIONS

The present study suggests the following conclusions :

1. Filaroidosis and skrjabingylosis infestation of sables, martens, polecats and other furred an imals of the family Mustelidae is contracted from ground molluscs which have been invaded by the larvae of Filaroides bronchialis and Skrjabingylus petrowi.

2. The development of the larvae of Filaroides bronchialis and Skrjabingylus petrowi to the invasive stage in the body of molluscs takes 15-17 days.

3. The growth of the larvae of Filaroides bronchialis to the sexually mature stage in the polecat lasts 18 days.

4. The growth of the larvae of Skrjabingylus petrowi to the sexually

mature stage in the polecat lasts 18 days.

5. Since ground molluscs are the sources of infestation of sables, martens, polecats and other mustelids, [to control these diseases] it is necessary to destroy molluscs and to isolate the cages and farms from re-colonisation by them. This requires that :

(a) The cages of sable, marten and mink on farms be placed in dry positions, avoiding shade from small shrubs, since the molluscs find the most favourable conditions for their development in wet and shady spots.

(b) The farms must be cleared of refuse, brushwood, planks, stumps, logs, stones, old leaves and other extraneous objects under which molluscs usually live.

(c) The cages and housing must be carefully strewn with sand, which is an unfavourable substrate for molluscs.

(d) During the spring, summer and autumn careful inspection of the cages must be made daily (during cleansing) and molluscs present there be collected in special jars (but not in the buckets with the excreta). The molluscs within the cages and housing must be not squeezed, but must be destroyed in a solution of copper sulphate, creoline[(a)] etc.

(e) On furred animal breeding farms affected by filaroidosis and skrjabingylosis, chemical control measures against the molluscs must be applied not less often than twice a year - spring and autumn - by spraying the whole of the farm not occupied by the furred animals with a solution of copper sulphate (in a dilution of 1:1000 - 1:3000).

(f) In order to deter new molluscs from entering the farms, the outer wall of the enclosure should be coated with tar or resin to a height of 25-30 cm from the ground.

(a) ? creosote. - Ed.

A STUDY OF THE DEVELOPMENT OF THE NEMATODE SKRJABINGYLUS NASICOLA, A PARASITE OF THE FRONTAL SINUSES OF MUSTELIDS

(Izuchenie tsikla razvitiya nematody Skrjabingylus nasicola - parazita lobnykh pazukh pushnykh zverei semeistva kun'ikh)

by

A.A. Dubnitskii

Karakulevodstvo i zverovodstvo 1956 1 : 59-61.

The parasitic nematode Skrjabingylus nasicola (Leuckart, 1842) is very often found in the frontal sinuses in various mustelids. The hosts may recover, with difficulty, from a slight infection, but a heavy invasion is often lethal. V.A. Popov (1943) established an inverse correlation between the numbers of mustelids and the rate of their infection with skrjabingylosis. This accounts for the heavy economic damage inflicted by this disease on furred animal breeding. However, the life cycle of the parasite S. nasicola has still not been unravelled, so effective measures to combat and prevent it have not been developed.

In the present paper we outline the results of our study of the development of S. nasicola.

After helminthological examination of the total stock of martens in the Bakurnaskii furred animal breeding farm (Georgia), we diagnosed skrjabingylosis in 6.4 per cent. Complete helminthological autopsy of 51 polecats received from various regions of the European part of the Soviet Union showed that S. nasicola, from 11 to 41 worms per host, parasitised 6% of the total.

On the furred animal farm of the VNILZO we observed polecats which had been naturally infected with S. nasicola, and established that the female worms are viviparous. They release the larvae into the lumen

of the frontal sinuses. By active movements, and also in the nasal secretions, the larvae pass from the frontal sinuses into the nasal cavity, and are expelled to the outside when the host sneezes. However, a large number of the larvae pass with the nasal mucus from the nasal cavity through the choanae(a) into the throat and are swallowed. Then the larvae pass unharmed through the gastro-intestinal tract and are excreted with the faeces into the environment (Table 1).

Table 1. Localisation and number of S. nasicola larvae in polecats heavily attacked by skrjabingylosis

Polecat No.	Frontal sinuses	Nasal cavity	Nasal secretions	Throat	Oesophagus	Stomach	Gut	Faeces	Larynx	Trachea	Lung
325	Very many	Very many	Solitary larvae	10	5	Very many	Very many	Very many	1	Neg.	Neg.
621A	Many	Many	2	8	4	Many	Many	Many	Neg.	Neg.	Neg.

Note: The number of S. nasicola larvae in the frontal sinuses, nasal cavity, throat, larynx and trachea was determined by inspecting a scraping from the mucosa under the microscope; untreated smears from the nasal secretions were studied in the same way; the contents of the stomach and gut were placed on copper wire mesh with gauze in a funnel, and studied by the method of Berman; the same method was used to study the faeces and small pieces of the lung.

When freshly excreted in the host's faeces, the bright grey S. nasicola larvae have a length of 0.375–0.420 mm and a maximum width

(a) posterior nares, leading into the pharynx. – Ed.

of 0.016–0.019 mm; the tail end has a pointed awl-shaped appendage, and the non-paired postanal papilla are located near the anus (Fig.1). Our observations showed that in favourable environmental conditions these larvae remain viable for a long time, but do not grow or moult.

Since larvae of related nematodes often continue their development in the tissue of ground molluscs, we decided to try experimental infection of the ground molluscs Agriolimax reticulatus (M and II)[a] with freshly excreted S. nasicola larvae. These molluscs were collected in swamps in districts where there was no natural habitat for the mustelids.

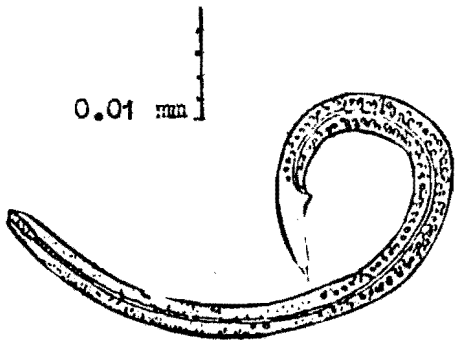

Fig.1. Freshly excreted larva of S. nasicola (one gradation 0.01 mm)

Before the experiments, we opened up some tens of molluscs, and found no larval nematodes in their tissues. Two control minks free of helminthosis were fed on 30 A. reticulatus molluscs immediately after they had been collected in the marsh. Subsequent investigations of the faeces of these minks by Berman's method for 50 days revealed no excretion of S. nasicola larvae. One of the minks was dissected, and in its frontal sinuses no S. nasicola nematodes were found. It was therefore established that the A. reticulatus molluscs collected by us were sterile (i.e. not spontaneously infected with skrjabingylosis).

(a) Meaning of these two latin letters quoted, as shown, in the original, not known. – Ed.

We used Berman's method to investigate the faeces of polecats naturally infected with S. nasicola. The larvae were placed in Petri dishes and also on the surface of dandelion leaves placed therein, then some tens of molluscs were placed in the dishes with them. After a few days the molluscs were transferred from the Petri dishes to 0.5 litre jars covered at the top with gauze. Dandelion leaves and carrot were used for food for the molluscs. To maintain humidity a small amount of water was added to the jars once a day.

Some of the test molluscs were dissected at various times after infection. All the dead molluscs were also dissected. It was established that the freshly excreted larvae of S. nasicola, in the first 24 hrs after contact with the molluscs, penetrate into the tissue of their pedicle, grow there and undergo their first moult after 7-8 days. The second moult occurs at 15-17 days. After the second moult the S. nasicola larvae cease to grow, coil up in the form of a helix, surrounded by a cyst, and become dormant. Their measurements are as follows : length 0.793-0.862 mm; width at the cephalic end, at the level of the excretory aperture, 0.032-0.037 mm; width at the level of the end of the oesophagus 0.042-0.045 mm; width in the region of the anal aperture 0.021-0.024 mm. The length of the oesophagus is 0.300-0.305 mm, and its maximum width 0.027-0.030 mm. The distance from the cephalic end to the excretory aperture is 0.115-0.127 mm. The cone-shaped tip of the tail is separated from the anal aperture by 0.044-0.047 mm (Fig.2).

We then attempted to infect mink (Lutreola vison) with skrjabingylosis by feeding them on the experimental molluscs. For the experiments we used young mink reared on the fur farm in cages on raised netted floors. Preliminary larvascopy revealed no nematode larvae in the test minks. During the experiments these mink were kept in cages with raised netted floors in conditions completely excluding the possibility of natural contact of the test animals with the molluscs. The experimental molluscs, first finely

cut up with scissors, were mixed with 10-15 g meat stuffing and fed to the mink as the morning meal, instead of the usual food. The mink usually immediately ate up the food offered. The results of the experiment are shown in Table 2.

Table 2 shows that the molluscs A. reticulatus were infected by skrjabingylosis, and when fed to the test mink, produced invasion by the nematode S. nasicola. Therefore we established that the ground molluscs Agriolimax reticulatus are intermediate hosts for the nematode S. nasicola. This nematode reaches sexual maturity in the body of the definitive host (Lutreola vison) in 18-25 days.

Judging from morphological signs in the mollusc tissues, S. nasicola larvae reach the invasive stage in 15-17 days. As a biological check to confirm this, we ran a series of experiments on farm mink and polecats which were free of nematodes. The molluscs A. reticulatus were fed to the mustelids after various periods since their contact with freshly excreted larvae of S. nasicola. These biological experiments confirmed that, in the tissue of the molluscs A. reticulatus, S. nasicola larvae reach the invasive stage within 17 days.

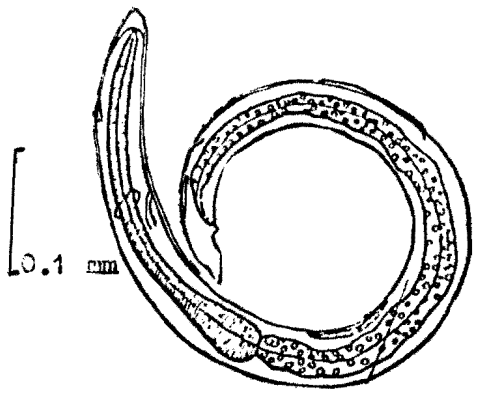

Fig.2. Invasive larvae of S. nasicola

Subsequent experiments established that other intermediate hosts for S. nasicola, apart from the slug mentioned, may include the molluscs Zenobiella rubiginosa (A.Schm) and Cochlicopa lubrica Mull.

Since mustelids are invaded by the nematode S. nasicola after eating ground molluscs (loricate and non-loricate), it is essential to wage a vigorous struggle against molluscs to protect valuable furred animals from infection with skrjabingylosis. On fur farms the molluscs must be destroyed by the methods devised by Prof. A.M. Petrov and V.G. Gagarin (1937)(a). On furred animal breeding farms and in zoological parks, mink, martens and other mustelids must be kept in cages inaccessible to molluscs which might enter and be eaten. A very useful method to achieve this, is to set the cages on a raised netted floor. Several hundreds of carcasses of farm mink and martens, which had been reared on fur farms in cages on raised netted floors, were dissected in the slaughter period of 1950-53; none contained the parasite S. nasicola in their frontal sinuses.

(a) Reference not given, but translation included in this volume. - Ed.

Table 2. Results of experimental infection of mink with the nematode *S. nasicola*

Mink No.	No. of molluscs supplied	No. of days after contact of larvae with molluscs	Results of helmintho-larvoscopic examination of mink after infection	Time of killing of minks since start of expt (days)	Results of dissection of frontal sinuses
609	2	45 days 35 days	Not studied	13	2 sexually immature nematodes found
1832/2	9	6-36 days 3-30 days	24 days after infection *S. nasicola* larvae appeared in faeces	83	8 nematodes found
2200/1			Ditto after 23 days	258	2 nematodes found
1832/1	19	30 days	Ditto after 18 days	235	1 nematode found
2200/2	8	30 days	Ditto after 25 days	167	6 nematodes found
1882/1	20	31 days	Ditto after 19 days	163	9 nematodes found

Summary

1. Mustelids are parasited by the nematode *Skrjabingylus nasicola*, transmitted by the ground molluscs (*Agriolimax reticulatus*, *Zenobiella rubiginosa* and *Cochlicopa lubrica*) which are infested with the larvae of this nematode. These species of molluscs are intermediate hosts for *S. nasicola*.

2. The development of the larvae of *S. nasicola* to the invasive stage in the body of these molluscs takes 17 days.

3. The growth of the nematode *S. nasicola* to the sexually mature stage in the body of mink (*Lutreola vison*) lasts from 18 to 32 days

4. To protect the animals from infection with the nematode *S. nasicola* they must be kept in cages on a raised netted floor.

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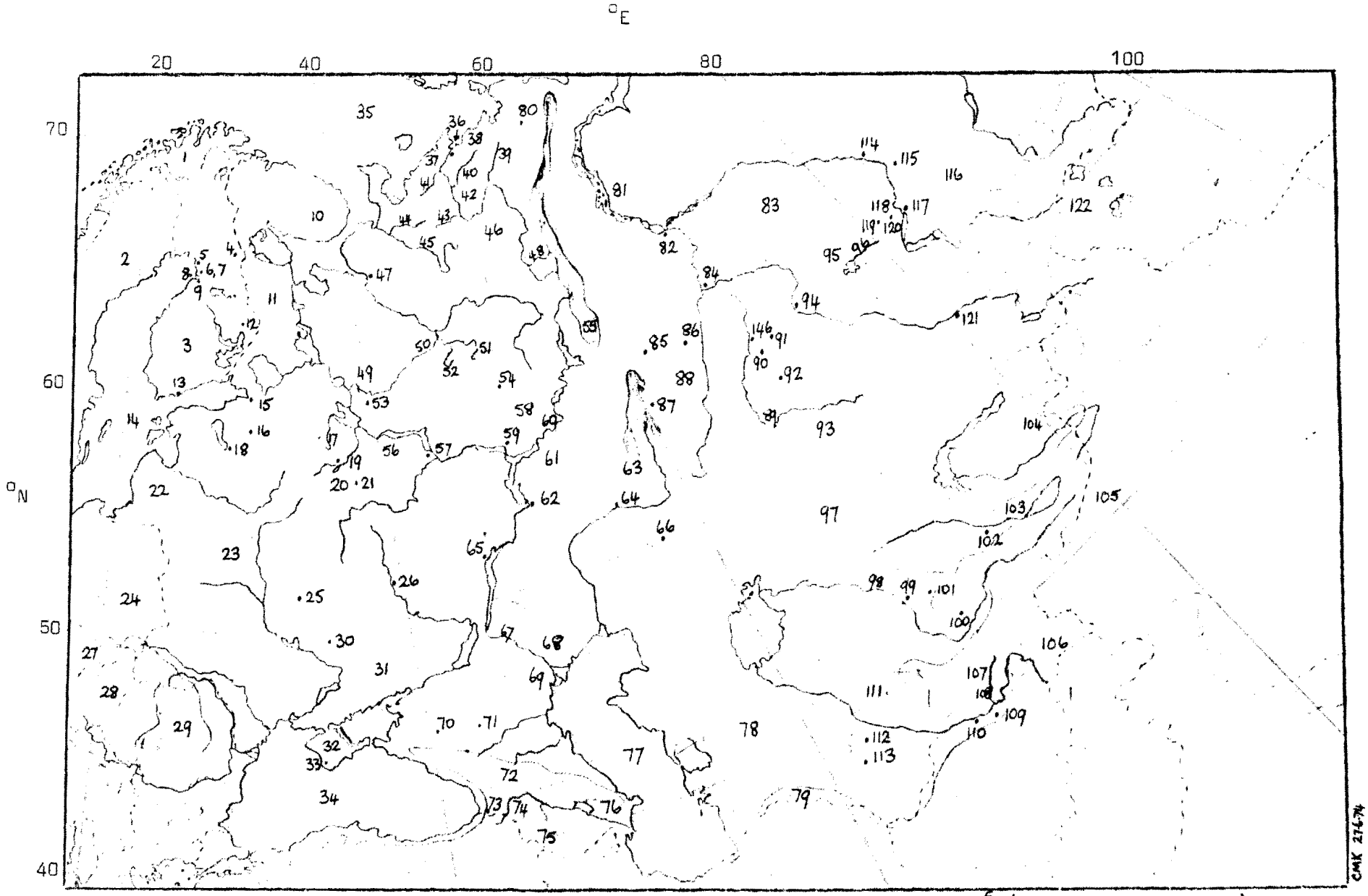

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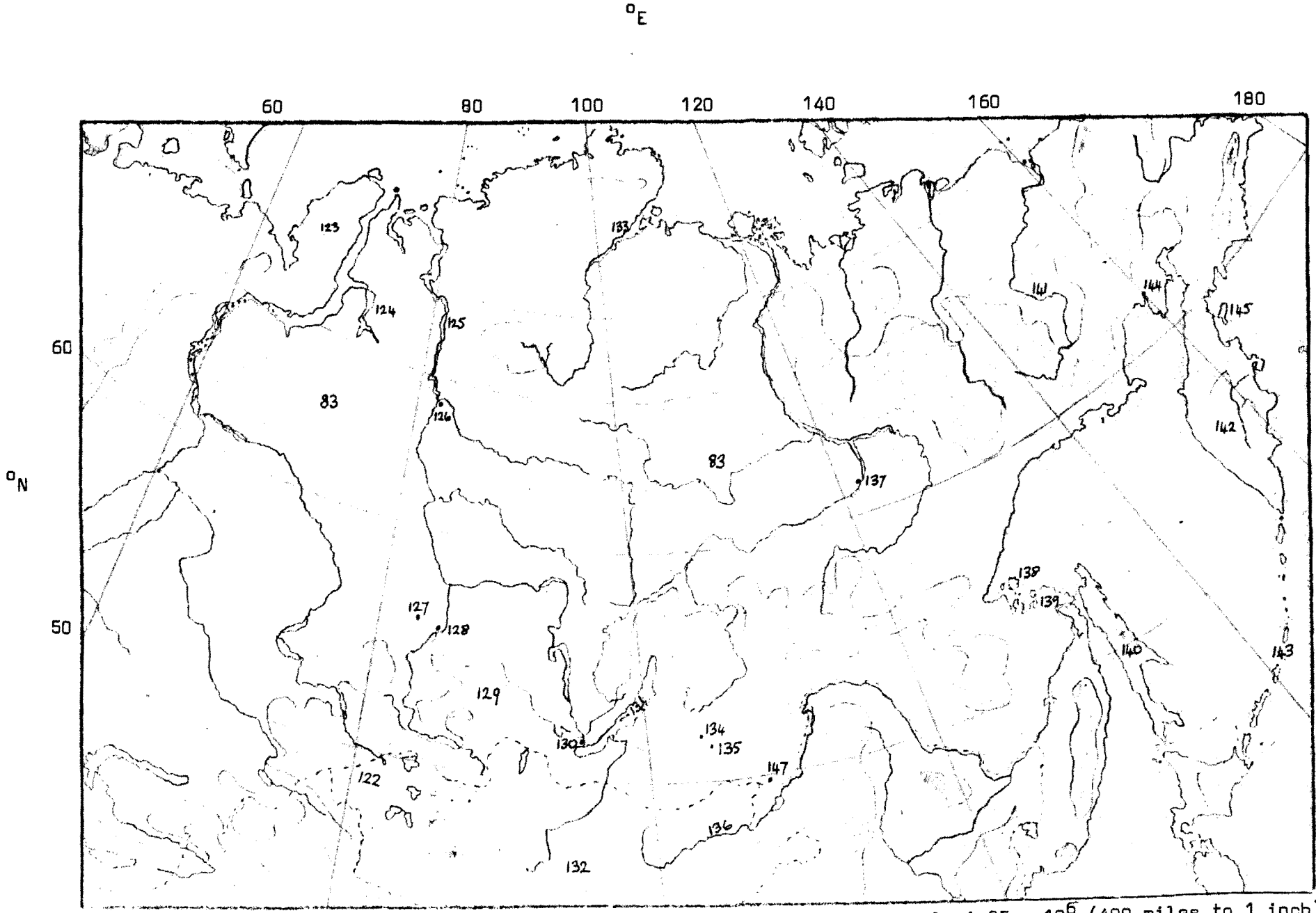

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Scale 1:25 x 10^6 (400 miles to 1 inch)

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