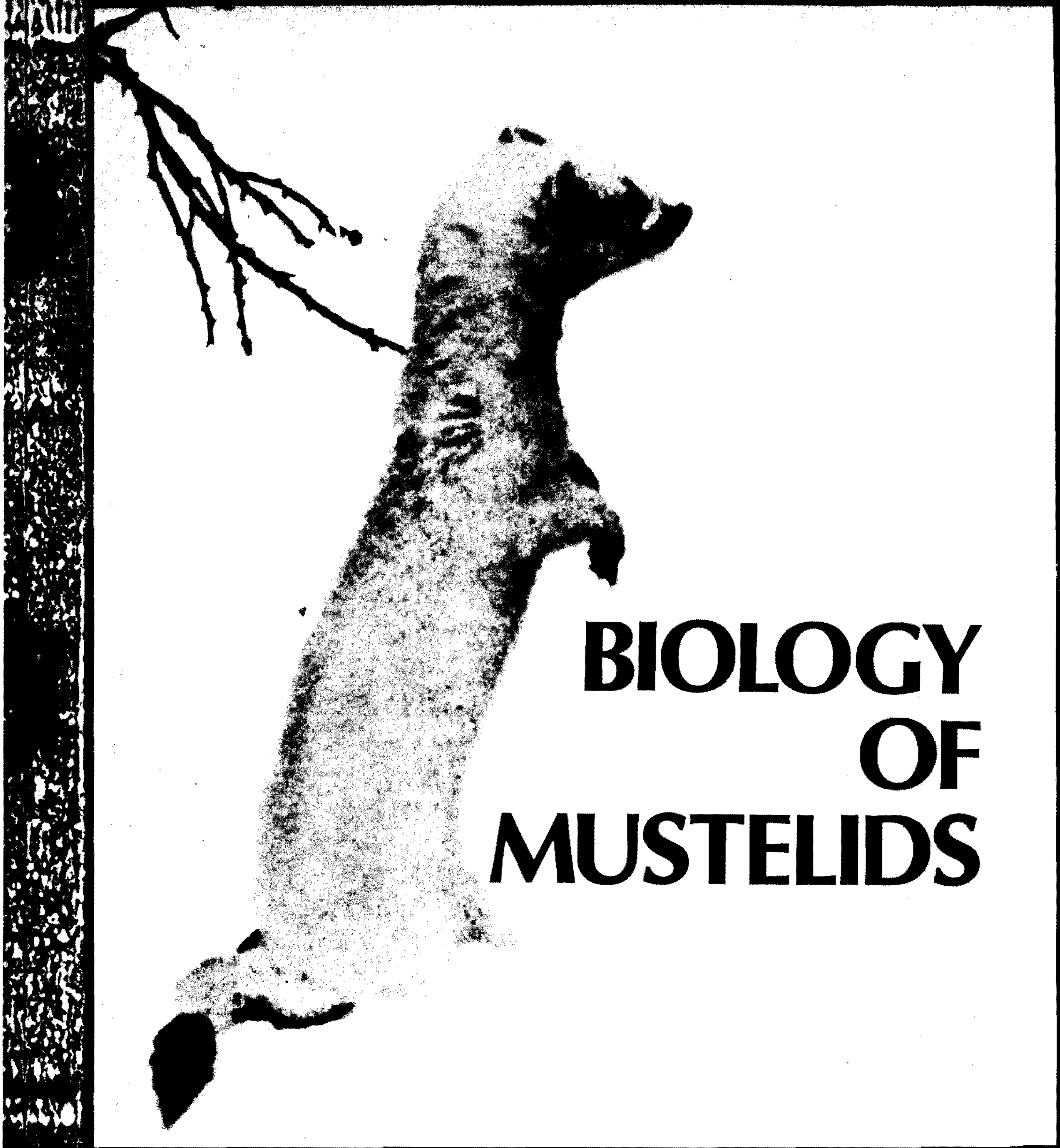
DSIR BULLETIN 227



BIOLOGY OF MUSTELIDS

SOME SOVIET RESEARCH Volume 2

NEW ZEALAND DEPARTMENT OF SCIENTIFIC AND INDUSTRIAL RESEARCH

DSIR Bulletin 227

BIOLOGY OF MUSTELIDS

SOME SOVIET RESEARCH

Volume 2

Translations by: Translation Service
Department of Internal Affairs
Wellington, New Zealand

Edited by: Dr C. M. King

Published by: Science Information Division
Department of Scientific and Industrial
Research, P.O. Box 9741, Wellington
New Zealand

BIOLOGY of mustelids : some Soviet research
: volume 2 / translations by Translation
Service, Department of Internal Affairs ;
edited by C.M. King. - Wellington : DSIR
Science Information Division, c1980
(DSIR bulletin, ISSN 0077-961X ; 227)
Vol. 1 published: Boston Spa : British
Library Lending Division, 1975. ISBN 0-85350
-126-2
ISBN 0-477-06659-3

*FRONT COVER: The ermine motif is reproduced, with permission,
from an original photograph by Fred and Dora Burris*

СОДЕРЖАНИЕ

15. ПОЛОВАЯ СТРУКТУРА, ПРОМЫСЕЛ И ЧИСЛЕННОСТЬ ГОРНОСТАЯ 160
К.И. Копеин
Продуктивность Биогеоценозов Субарктики (Материалы симпозиума по изучению, рациональному использованию и охране вопроизводимых ресурсов Крайнего Севера СССР) Академия Наук СССР, Уральский Филиал,Свердловск, 1970. Печатается по постановлению Редакционно-издательского совета Уральского филиала АН СССР. Ответственные редакторы: В.П. Фирсова, С.Г. Шмятов, Л.Н. Добринский.

16. ЧИСЛЕННОСТЬ ПОПУЛЯЦИЙ И НОРМИРОВАНИЕ ДОБЫЧИ СОБОЛЯ В СССР 162
Н.Н. Бакеев, Г.И. Монахов
Труды IX Международного Конгресса Биологов-Охотоведов, Москва, 1970

17. ИЗБИРАТЕЛЬНОСТЬ ПРОМЫСЛА СОБОЛЕЙ 167
В.К. Мельников
Бюллетень М. О-ва Исп. Природы, Отд. Биологич., т. LXXX(6), 1975

18. КОЛИЧЕСТВЕННЫЙ УЧЕТ ВЫДРЫ, СОБОЛЯ,КУНИЦЫ И МЕЛКИХ ПРЕДСТАВИТЕЛЕЙ СЕМЕЙСТВА КУНЬИХ 173
В.П. Теплов
см. ссылку в переводе

19. ПОЛОВЫЕ РАЗЛИЧИЯ В РАЗВИТИИ, РАЗМЕРАХ И ПРОПОРЦИЯХ ЧЕРЕПА ЛЕСНОЙ КУНИЦЫ MARTES MARTES L. (MAMMALIA, MUSTELIDAE) 180
О.Л. Россолимо, И.Я. Павлинов
Бюллетень М. О-ва Исп. Природы, Отд. Биологии, т. LXXIX (6), 1974

20. ВОЗРАСТНЫЕ И СЕЗОННЫЕ ИЗМЕНЕНИЯ НЕКОТОРЫХ ФИЗИОЛОГИЧЕСКИХ ПОКАЗАТЕЛЕЙ У ЛАСКИ И ГОРНОСТАЯ 192
И.Л. Туманов, В.Г. Левин
Вестник Зоологии , 1974, № 2

CONTENTS

Part 5. Morphology and physiology

Part 6. Maps and indexes

EDITOR'S PREFACE

The papers collected in this volume were translated by the Translation Service of the Department of Internal Affairs of H.M. New Zealand Government, Wellington, at various times between 1972 and 1978. The appearance of another substantial collection so soon after the first (King 1975) is possible because the Russian literature on mustelids is relatively rich, and also because my own research interests in the field continue unabated. This volume is another step towards making some of this extensive Russian work available to western biologists.

The papers vary greatly in type, quality and statistical rigor. Inclusion of an article does not imply endorsement of it; some contain occasional statements with which I disagree or which have been disproved by later work, and some describe techniques (for example, snow-tracking) of limited use in milder climates. But all are interesting, and the few serious errors I have detected are either obvious or are identified in footnotes.

As before, I have interpreted the idea of a "translation" in rather broad terms; the original texts are rendered from Russian not only into English but also into more or less the style and terminology of contemporary English scientific writing, so far as was possible without entirely rewriting each paper. This has often involved some simplification of language or insertion of clarifying words (in square brackets) and headings. The result is less faithful to the author's own words than the translator's version was, but more readable.

Great care has been taken to ensure accurate transcription of all roman letters and arabic numerals from the published text, and peculiarities which the reader might dismiss as typing errors are noted. Very obvious misprints are corrected without comment; others are pointed out.

Bibliographies are translated literally and are not standardised or checked further than to the text. Different translators may give slightly different transliterations of proper names, which accounts for some variation in spelling in the bibliographic and geographic sections. Russian authors always list Soviet and foreign references separately, and the Soviet papers appear in order of the cyrillic alphabet, not that of the translation.

Illustrations are reproduced directly from the published texts, and they vary greatly in quality. We have chosen to maximise the number of translations that can be included, at the expense of improving the accompanying illustrations. Readers requiring better detail than is possible to give here are recommended to seek out the original papers.

Despite the most careful precautions there still remain some inconsistencies in style and ambiguities in meaning. The latter were all rechecked with the translators: those that remain are mostly errors attributable to the author - especially in references or cross-references - some of which are remarked on and some obvious. The number of serious mistakes I found convinced me that translations produced by even so careful a service as ours should not be used without line-by-line checking.

As before, I have added maps showing the principal places mentioned in the text and geographical, subject, and species indices.

It is a pleasure to acknowledge the excellent work of the team of translators at D.I.A., under Mr S. Aldridge, especially Mrs Melishkin, who again dealt with repeated lists of queries. At the Science Information Division of the Department of Scientific & Industrial Research, David Zwartz and Cleveland Duval supervised the editing, and Bernice Fowler, Betty Huss, and Collette McDouall typed and corrected the manuscript from my appallingly muddled draft.

I gratefully acknowledge the permission of the Russian copyright authorities to print translations of seven papers published after 1973.

References cited in the editor's footnotes are:

Corbet, G. B. & H. N. Southern (eds) (1977). The Handbook of British Mammals, 2nd edition. Blackwell Scientific Publications, Oxford.

Hall, E. R. (1951). American Weasels. Univ. Kansas Publ. Mus. Nat. His. 4: 1-466.

Heptner, V. G., N. P. Naumov, P. B. Yurgenson, A. A. Sludskii, A. F. Chirkova, & A. G. Bannikov (1967). Mammals of the Soviet Union, Vol. 2.

King, C. M. (ed.) (1975). Biology of mustelids: some Soviet research. British Library Lending Division, Boston Spa, Wetherby, Yorks LS23 7BQ. U.K. pp. 1-266. ISBN 0.85350 126 2.

Müller, H. (1970). Beiträge zur Biologie des Hermelins, *Mustela erminea* Linne 1758. Saug. Mitt 18: 293-380.

Carolyn M. King
3 Waerenga Road
Eastbourne
New Zealand

October 1979

ECOLOGY OF THE ERMINE IN THE COLD SEASON IN THE EUROPEAN NORTH

by

M. A. Vaisfeld

Graphical Institute, USSR Academy of Sciences, Moscow

[From: Zool. Zhurn. 51: 1705-14, 1972.]

Material and methods

The ecology of the ermine (*Mustela erminea* L.) was studied in the Kirov Province in January and February 1970, and in the Archangel Province in February, March, September, and October 1971. Field studies were carried out in areas of unfarmed land in the Nenets District, which included some flood-plains, some forest, and some forest tundra.

The basic method of investigation was by tracking in the snow. In addition, an assessment of the food resources available in these areas was carried out, and information on the ermine trapping industry collected, etc.

Distance covered in a 24-hour period

A total of 70 km was covered in following the trails of ermine (Table 1): 27 individual trails were followed.

The length of the trail made in a 24-hour period was established in 22 cases (Table 2). To assess the amount of food available to the ermine, we estimated the numbers of small rodents from standard traplines and from snow-tracking. As can be seen from Table 2, the distance covered by ermine in 24 hours varies greatly - from 0.45 to 8.8 km - and this is because a number of different factors, in particular the amount of food available and its accessibility, [influence the hunting behaviour of ermine].

By far the shortest distances covered by ermine in search of food were observed on the flood-plain of the Northern Dvina River, where voles (*Microtus* sp.) were numerous during the period of our investigations. The supplies of potential prey in the other areas were lower than on the flood-plain of the Dvina, and there the ermine covered considerably longer distances in their search for food.

By far the greatest distances covered by ermine were in the Kirov Province, and in the areas of forest tundra in the Nenets District where very few small mammals were observed. (In the Nenets District in 1971 a lack of food caused local extinctions of the arctic fox and a sharp reduction in the number of snowy owls.)

TABLE 1: Distribution of ermine trails by regions and habitats

	Number of trails followed (A) and their lengths in km (B)													
	Flood-plains of the rivers										Forest edges		Total	
	Northern Dvina		Uftyuga		Pechora		Oma		Cheptsa					
	A	B	A	B	A	B	A	B	A	B	A	B	A	B
Kirov	-	-	-	-	-	-	-	-	2	6.3	5	17.1	7	23.4
Archangel	11	9.7	3	7.7	1	3	3	19.3	-	-	2	6.9	20	46.6
Total	-	-	-	-	-	-	-	-	-	-	-	-	27	70.0

TABLE 2: Length of ermine trails over a 24 h period in various regions and habitats

Province	District	No.	Length of 24 h trail (km)	Air temp. (°C)	Sex	Food supply	Period of observation
Kirov	Mixed forest	1	5.2	-32	F	Very bad	Jan. 1970
	"	2	3.5	-46	F	"	"
Archangel	Flood-plain of Nthn. Dvina River at Cherevkovo Village	3	1.3	-3	M	Very good	Up to thaw, 1971
	"	4	0.45	-3	F	"	"
	"	5	0.7	-3	M	"	"
	"	6	0.6	-3	F	"	"
	"	7	0.7	-3	M	"	"
	"	8	0.8	-3	F	"	"
	"	9	0.9	-3	M	"	"
	"	10	0.56	-3	F	"	"
	"	11	1.2	-10	M	"	After thaw Jan. 1971
	"	12	1.3	-10	M	"	"
	"	13	1.2	-10	M	"	"
	Flood-plain of Uftyuga River at Verhnyaya Uftyuga Village	14	2.7	-22	M	Average	After thaw Feb. 1971
	"	15	2.4	-20	M	"	"
	"	16	2.6	-15	M	"	"
	Flood-plain in the Pechora Delta	17	3.0	-10	F	Very bad	Oct. 1971
	Flood-plain of Oma River in the strip of forest tundra 5 km Sth of Oma Village	18	6.2	-6	M	"	Sept. 1971
	"	19	8.8	-3	M	"	"
	"	20	4.3	-11	M	"	"
	Clearing in spruce and fir forest	21	3.6	-18	M	Bad	March 1971
	"	22	3.3	-17	M	"	"

It is interesting to note that even during the severe frosts that occurred in the Kirov Province at the time of our visit there, ermine were still actively searching for prey, travelling far afield. It is our impression that in general, air temperature does not affect the length of the ermine's hunting trails to any great extent, but rather, that the latter are closely related to the structure, density and depth of snow cover. Whereas loose snow makes hunting under the surface of the snow easier for the ermine, a frozen snow crust prevents them from penetrating into the hollow subnivean spaces, and obliges the predator to travel more widely across the surface. On the flood-plain of the Northern Dvina, several trails were followed (Table 2, Nos. 11-13) after prolonged thaws interspersed with frosts that led to the formation of a structured snow cover composed of several alternating layers of buried crusts and fissured strata of varying granularity. Under these conditions the ermine began moving about more widely. Traces of their prey, i.e., voles (*Microtus* sp.), were also found more often.

At the beginning of winter when the snow is not deep, ermine usually travel far afield. If the area where the ermine live is poor in food resources, they will travel considerable distances (Table 2, Nos. 18-20). With an increase in the depth of snow, the distance travelled becomes shorter, and sometimes at this time of year, when there is [still] plenty of food about, ermine may not be seen on the surface of the snow for more than 24 hours, as observed on the flood-plain of the Northern Dvina.

Differences in hunting behaviour between habitats also indicate how food supplies affect the distance the ermine travel. When living in a forest the ermine have to traverse foodless areas, and spend time only in places where food is plentiful (clearings, glades beside streams, etc.), hunting their prey.

In the Kirov Province (Table 2, Nos. 1-2) small rodents were scarce in clearings and almost completely absent in large blocks of forest. Here, the ermine visited a number of clearings, traversing areas of uncut woodland poor in food in the course of one hunting foray. The length of trails under such conditions is naturally greater than if the ermine had not gone outside one clearing, as we observed in a clearing in a spruce-fir wood in the Archangel region (Table 2, Nos. 21-22).

On the flood-plains the ermine hunted mostly in scrub, which provided the main source of food and hiding places. In such habitats, only very small areas were covered by the ermine in their hunting excursions. The trails were extremely winding, and almost 4/5 of them consisted of loops made in the course of hunting, which could not always be traced completely. In the forest the ermine trails were tortuous only in places where the animals had been hunting. It is difficult to determine the degree of tortuosity of an ermine's path by any kind of coefficient.

To record the characteristics of the tortuosity of the path of the pine marten, Yazan (1970) suggested relating its length to the distance between its starting and finishing points. This method cannot be used in studying the ermine, however, because having once come out of its den, the animal frequently travels in a circle, disappearing under the snow either into the same retreat as before, or into another in the immediate vicinity.

Obviously, the coefficient of tortuosity could be [unrealistically] high in this case, although it could reflect the animal's true path along a more widespread hunt with a greater number of loops.

The route taken in a 24 hour period can be influenced by many other ecological factors not considered in the present paper, for example, the density of prey, the presence of neighbouring resident ermine, the number and periods of activity of enemies and competitors, the characteristics of the prey, the hunting methods of the ermine, etc.

The home range

The home range of the ermine was determined in full 13 times and in part twice. This was done by tracking a particular animal several days running and plotting the data obtained on a map of the area. Another method was also used, which will be dealt with later. Before describing our results, something should be said about existing terminology and methods of determining the limits of the areas described.

Referring to the sable, Dulkeit (1929), and Nadeyev and Timofeyev (1955) define the hunting range as the area on which the animal hunts for several days. Rayevski (1947) considers the hunting range of the sable to be the area on which the animal permanently lives and hunts. In another paper Dulkeit (1957) suggests taking as the hunting range of the sable "the area traversed by the animal in 24 hours". Gusyev (1966) takes a similar point of view, but defines "the area on which the sable permanently lives and hunts" as the hunting region. Yazan (1970) subscribes to Gusyev's opinion when considering in his own paper the hunting ranges (but not regions) of the sable, marten and kidas.

Some confusion can thus be noted among these authors' definitions, especially in differentiating between the two concepts of hunting "range" and hunting "region".

As far as the ermine is concerned it would seem to us not only simpler but also more correct to call the animal's hunting region its home range, and the area over which it hunts, its range of daily activity. This seems all the more feasible in view of the fact that in practice those parts of the area familiar to the animal but on which it does not hunt come into the home range, as it visits these places fairly regularly, travelling from one part of the range where food is found to another. Thus for example, an uninterrupted stretch of forest traversed by an ermine on its way from one clearing to another does not appear to be in the animal's hunting area, but falls into its home range.

For this reason the area of daily activity does not fully correspond to the hunting area, and so cannot strictly be called the hunting range. It should be added that although the range of daily activity varies from day to day within very wide limits, the home range of the ermine is remarkably stable at times, and usually has fairly well defined boundaries[1].

The [definition of the] boundaries of the home range also needs clarification. We do not completely agree with Yazan (1970) that the "hunting range" of the sable, marten and kidas (and, by analogy, of the ermine too - M.V.) is that area which falls within a rectangle, the sides of which are drawn enclosing the path of the animal and parallel to an imaginary line joining the beginning and end of the trail[2]. The other two sides of the rectangle are drawn perpendicular to the first, and also enclosing the trail.

In any given case, an area delineated in this way will include some parts that the animal never visits (the corners of the rectangle) and which do not therefore enter into the home range. These corners can be occupied by other individuals, which substantially alters the picture. In this case, especially if we describe the ranges of neighbouring animals by the same method, we can obtain the semblance of a considerable overlap of ranges which does not, in fact, exist.

---

[1] Strictly speaking, the stability of the boundaries of the home range cannot be unequivocally decided (see below). However, in comparison with the range of daily activity, the home range may be taken as constant without unduly straining the interpretation—Author.

[2] This [criticism] does not, however, exclude the application of this method to some other wild animals, for example, otters—Author.

Following on from this to an assessment of the boundaries and a description of the home range, we must proceed with caution, especially in those cases where several animals have adjacent home ranges.

An outline of the ermine's home range can be very curious indeed (Figures 1-3). It is ultimately defined by transferring onto a map of the area the details of the resident's daily travels that have been obtained by following its trail each day. According to our observations, the ermine usually makes a complete round of its range in 3-4 days, thus fixing its boundaries. Two of the ermine studied had not gone round their range in this time (Table 3, Nos 14, 15).

TABLE 3: Areas of the home ranges of stoats (hectares)

		Method of determining size of range					
		By means of a circuitous route	By means of tracking				
		Archangel Province					Kirov Province
		Flood-plains of the rivers				Forest Clearing	Forest
No.	Sex	Nthn. Dvina	Nthn. Dvina	Uftyuga	Oma		
1	Males	42	-	-	-	-	-
2	"	39	-	-	-	--	-
3	"	36	-	-	-	-	-
4	"	27	-	-	-	-	-
5	"	21	-	-	-	-	-
6	"	-	17	-	-	-	-
7	"	-	-	117	-	-	-
8	Females	-	-	-	-	124	-
9	"	69	-	-	-	-	-
10	"	29	-	-	-	-	-
11	"	26	-	-	-	-	-
12	"	-	13	-	-	-	-
13	"	-	11	-	-	-	-
X 14	"	-	-	-		-	120
X 15	Males	-	-	-	160	-	-

X Range only partly determined.

Apart from tracking, the ermine's home range can be determined by the "circuitous route" method. When the length of time it takes an ermine to cover its territory completely has been established by following individual trails, approximate estimates can be made - without following individual trails - for ermine living in similar conditions and in the direct vicinity of the home range of the first ermine. For this method it is sufficient that a circuitous route is made, enclosing all traces of the ermine, provided the observer walks close beside[1] the animal's tracks. If, while the ermine made his rounds of the range there was no newly fallen snow, the extent of the range can be determined

---

[1] Literally, "provided the observer will be going in the immediate neighbourhood of the animal's tracks"—Ed.

by [measuring the area enclosed by] one circuit. The shape of the range is shown by the outline of the circuit. If there is freshly fallen snow, similar circuits are made each day for the period of time taken by the ermine to cover its whole range once (which is determined beforehand, as mentioned above). An outline of the range in this case is determined by recording on a map all circuits taken. In our investigations, 8 out of 15 ranges were determined by this method (Table 3).

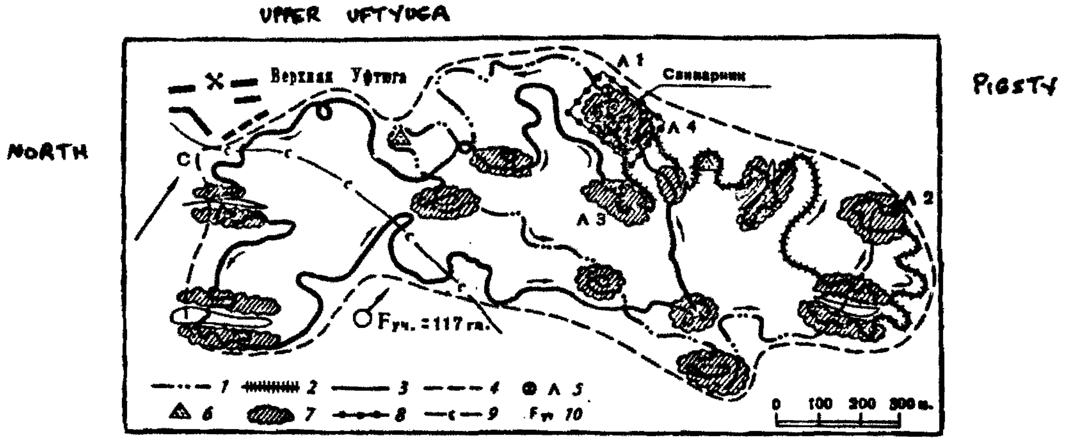


FIGURE 1: 24-hour trails and home ranges of an ermine on the flood-plain of the Uftyuga River (1971)

1. Path of ermine on 13 February	2. Same, 14 February
3. Same, 15 February	4. Boundary of home range
5. Spring-floodwater ditch	6. Haystack
7. Scrub	8. Pig-sty enclosure
9. Tractor sledge road	10. Area of home range (ha)

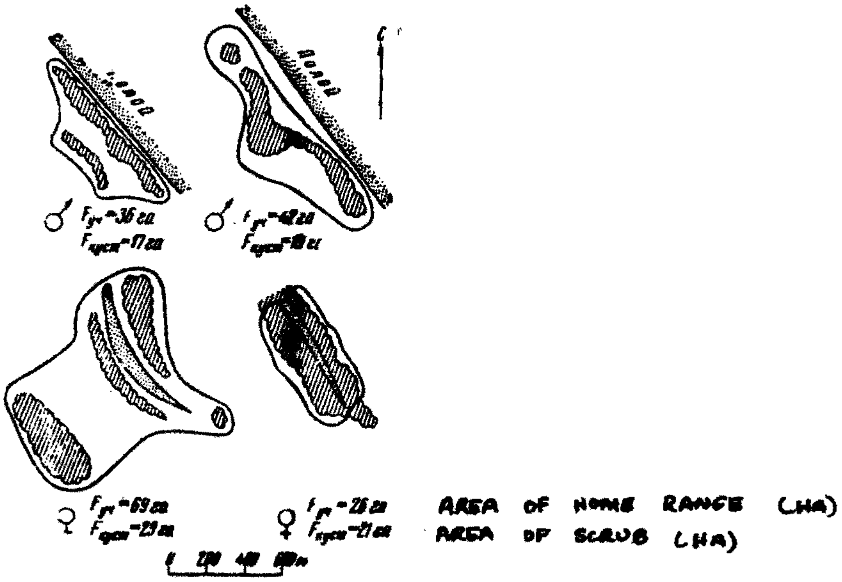


FIGURE 2: Home ranges of ermine on the flood-plain of the Northern Dvina (January 1971)

Symbols as in fig. 1.

The extent of the ermine's 24-hour activity shows that the area of its home range is closely related to the food supplies of the district where it lives.

In the flood-plain districts of the Northern Dvina, which are rich in voles, the home ranges of the ermine are all rather similar (Table 3). The various flood-plain areas were not especially varied in form, and 8 (Table 3, Nos. 1-5 and 9-11) of the 11 ermine whose home ranges were determined here lived in habitats which included flood-plain scrub. In each range, scrub occupied no less than 40% of the total area (Figure 2). As noted above, all hunting places were concentrated in the low growth around bushes. Consequently, some percentage of scrub on the home range of the ermine can, it seems, be considered as a necessary requirement for normal living conditions.

In most cases, male ermine living on the flood-plains of the Northern Dvina occupied larger ranges than the females. The home range of one female, however, (Table 3, No. 9) here reached the maximum of 69 ha. This was probably because the scrub adjacent to the lake did not provide sufficient food for her, so she was obliged to extend her sphere of activity to include the nearest group of bushes (Figure 2), which was separated from the main part of the range by a meadow offering her no food at all.

Three ermine on the flood-plain had smaller home ranges than the rest (Table 3, Nos 6 and 12-13). The area they occupied had been disturbed by man, and its ecological capacity had increased appreciably as a result, being higher than that of lands in their natural state. Here meadows that were heavily overgrown by bushes had been treated with herbicides. When dried, the bushes were put by bulldozers into peculiarly shaped windrows up to 300 m long (Figure 3), and 1.8 m high. These offered optimal living conditions for the ermine. Voles abounded in the windrows, which also provided plenty of attractive shelter for the ermine. The defence and food potential of these places was so high that the ermine living there did not even go near a haystack during the whole of the period that they were under observation by us, although haystacks were within the boundaries of their home ranges, and in all other habitats haystacks were visited fairly frequently by ermine.

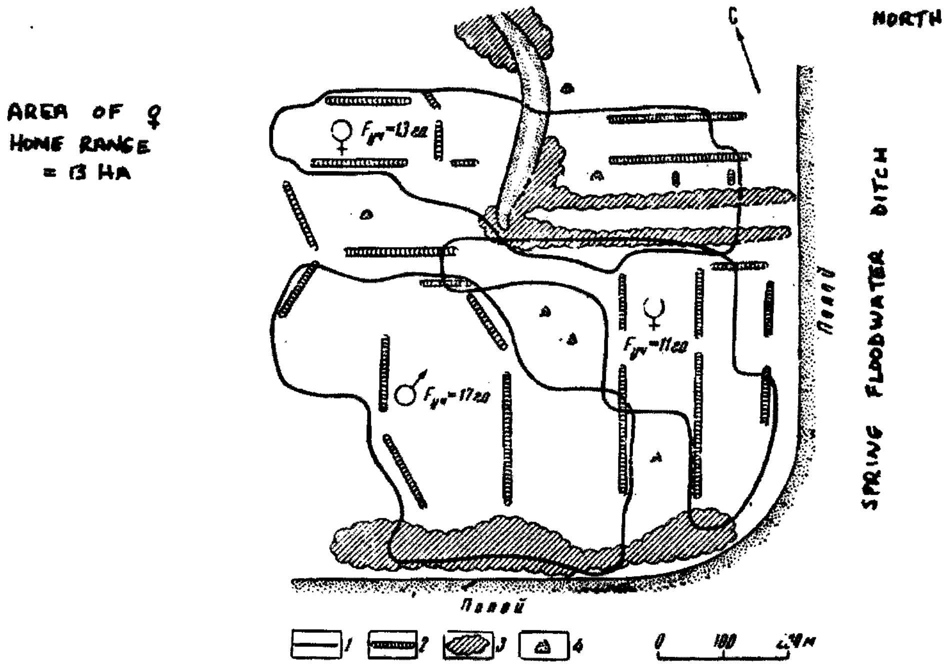


FIGURE 3: Home ranges of ermine on the flood-plain of the Northern Dvina in the district occupied by windrows of dead bushes (See text).

1. Boundary of home range
2. Windrows of felled scrub
3. Scrub
4. Haystack

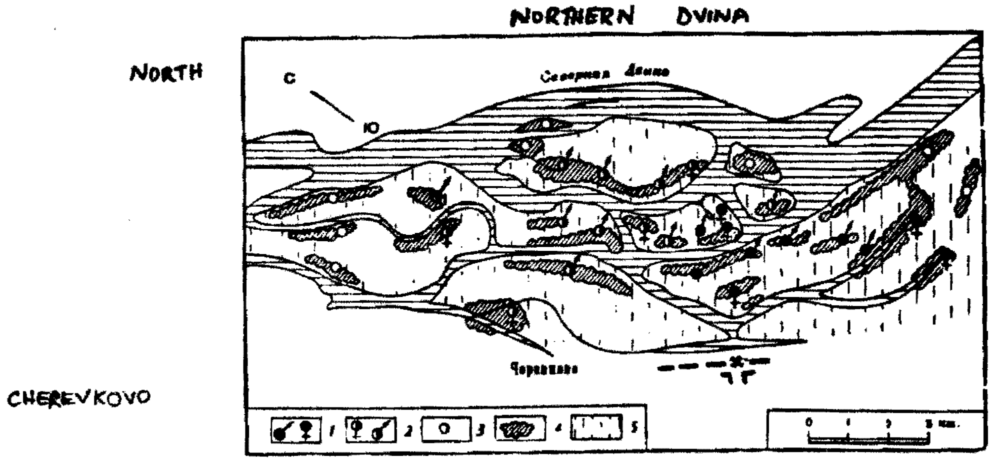


FIGURE 4: Distribution of ermine in relation to habitat on the flood-plain of the Northern Dvina (January 1971)

1. Sex of ermine and home range both determined
2. Sex only of the ermine determined
3. Sex unknown
4. Scrub
5. Flood-plain meadow

Eighteen ermine lived on an area of flood-plain not exceeding 80 ha on which there were windrows, at the beginning of the winter of 1970-71. At the beginning of our field work, 15 were caught by hunters, but the 3 that remained contented themselves with very small home ranges, distributed to correspond with the spacing of windrows (Figure 3).

The home ranges of the ermine in the other areas, (Tables 3, Nos 7-8, 14-15), were larger than those examined above, due mainly to a lack of food in these areas.

Those factors that were considered earlier to determine the daily excursions of the ermine, also affect the size of the home range. Apart from the number of potential prey in the district where the ermine live, the size of the range also depends on the severity of the winter, the structure of the snow cover, the type of ground and so on. In the first days of winter neither the position nor the extent of the ermine's home range can be determined, because it is not delineated until the snow reaches a certain depth (Zharkov 1941). An ermine on the flood-plain of the Oma River travelled over a territory of 160 ha in the course of 3 days' observations; however the boundaries of its range were not firmly fixed.

The 18 ermine living among the windrows mentioned above at the beginning of winter had no clearly demarcated ranges, judging by hunters' observations. The animals used defined pathways, and various individuals regularly visited certain spots; a number of ermine were caught in a trap laid on a runway, over an interval of time sometimes not exceeding 24 hours.

In the middle of winter the size of the range can change sharply with the weather and the subsequent reformation of the snow cover. The formation of a frozen snow crust, making access beneath the snow difficult, forces the ermine to go further afield in their hunt for food, and increases the size of the home range. Observations on the flood-plain of the Northern Dvina after the thaw showed that ermine tracks were found beyond the previously determined boundaries of the home range. This leads us to believe that the area of the ranges had increased, although we did not re-measure them.

The boundaries of the home ranges of the ermine do not, therefore, remain stable, but are influenced by various factors.

The stability of the home range changes noticeably with the approach of spring, when the ermine appear to experience false heat. As early as the beginning of March the animals travel considerably further afield, and their tracks are found in areas where they had definitely not been in the middle of winter. Male and female tracks are also frequently found together.

With the exception of 3 individuals, all stoats occupied isolated ranges. Only animals living among the windrows on the flood-plain exerted any pressure upon one another, but this overlapping was not serious (Figure 3). It is interesting to note that all cases of intrusion onto an occupied range occurred when the owner was in a remote part of his territory, and that the "trespasser" did not intrude further than 50 m over the boundary.

Distribution of ermine in relation to habitat

The various types of habitat in the districts investigated affected the distribution of ermine in them. In the dark coniferous forests of the upper reaches of the Uftyuga the tracks of 6 ermine were seen over a distance of 28 km. Four animals preferred clearings in the grassy stage of renewal, and two preferred the riparian spruce woods along the Yentol River, a right bank tributary of the Uftyuga. In the pine forests on the right bank of the Dvina no ermine tracks were found over distances totalling 26 km. None were found either in the pine forests of the Zuyevski district of Kirov Province. In this district the only stoat tracks that were found led toward the scrub of the flood-plains or toward clearings.

On the flood-plains of the Uftyuga, which we did not investigate fully, the tracks of only one ermine were found. The tracks of this animal showed that it was active mainly in the scrub of the flood-plain and in and around an abandoned pigsty (Figure 1).

On the flood-plain of the Oma, of which only one stretch of 20 km was investigated, the tracks of only one ermine were found. This animal lived in the scrub along the banks of the river and in the low growth around some dwarf birches. In the Pechora delta, another one was occupying a similar habitat.

On the hummocky marsh (tundra and riparian) country at the mouth of the Oma River no ermine tracks were found.

On the flood-plain areas of the Northern Dvina (Figure 4), all ermine studied lived either in the scrub or among the windrows as described above. They lived in the bushes along the banks of the river and beside the river and lakes on the flood-plain, never occupying areas where no bushes were growing.

From everything that has been said, the distribution of ermine can be seen to be closely related to the nature of the habitat. The animals frequent only those places which have potentially high food resources, and provide adequate shelter.

The sex ratio of the population

Data on the sex ratio of the ermine population were obtained on the flood-plain of the Northern Dvina. Thirty-one ermine were living in an area of 72 km^2. The home ranges of 3 of them were determined by following trails (in the area with the windrows) and the "circuitous route" method was used for 8 of them. In 12 others studied, the sex of the animals was determined by studying the signs of their activity, but the sizes of their home ranges were not established. Local hunters and fishermen informed the author of the presence of the remaining 8 [of the 31] animals. We also examined the bodies of 11 stoats picked up on the flood plain, 9 of which were males[1].

---

[1] This testifies to the great selectivity of the fur trade, in which males are trapped more readily than females. See also the work of Nasimovich (1948) in which similar but still more contrasting figures are quoted.—Author. The phrase "picked up" must therefore refer to ermine killed in traps, not found dead.—Ed.

On the flood-plain we obtained information on 42 ermine altogether (including the bodies we examined), of which 23 were males, 11 were females and 8 were not sexed. Therefore, of the total number of ermine whose sex we established, 67.6% were males. This concurs with Lavrov's data (1944), which gave the ratio of the sexes in ermine as nearly 1:1.7 in favour of males. Zverev (1931) says that males predominate slightly in Eastern Siberia (53%). Fog (1969), referred to in the bibliography, reports a higher percentage of males in the population (63%). These data do not agree with those of Teplov (1948)[1] according to whom the ratio of the sexes among ermine is near 1:1; [he believes that] the fact that the tracks of males are encountered more frequently is due to their greater activity.

SUMMARY

The length of the daily hunting route of *Mustela erminea* L. varies from 0.4 to 8.8 km and depends on the availability of food, type of habitat, height and structure of snow cover, weather, season and other factors. Home ranges consist of a series of periodically visited regions of daily activity. The size of the home range is determined by the same factors as the length of the daily hunt and varies from 11 to 160 hectares. The boundaries of the home ranges can change with time under the influence of weather and other factors. The ermine prefers habitats with a high number of resting-places and a high food potential near water. In the population under study the sex ratio was 67.6% males.

BIBLIOGRAPHY

Gusev, O. K. (1966): Ecology and stock-taking of the sable (Methods for determining the numbers of the sable and their ecological substantiation): 45-50 Izd-vo "Lesnaya promyshlennost", M.

Dulkeit, G. D. (1929): Materials on the study of the biology of the sable, and the sable farming of Bolshoi Shantar island. Izv. Tikhookeansk. n.-i. st./art./ 3,3: 30-35.

Dulkeit, G. D. (1957): Voprosy ekologii i kolichestvennogo ucheta sobolya: 32-42, M.

Zharkov, I. V. (1941): New methods for stock-taking of the ermine. Nauchno-met. zap. Izd. Gl. upr. po zapovedn. 8: 183-187.

Zverev, M. D. (1931): Materials on the biology and agricultural importance of the polecat and other small carnivores of the *Mustelidae* in Siberia. Tr. po zashch. rast. Sibiri 8: 5-46, Novosibirsk.

Lavrov, N. P. (1944): Biology of the reproduction of the ermine. Tr. Centr. h.-i. labor. biol. Narkomzaga SSSR 6: 143-147, M.

Nadeev, V. N. and Timofeev, V. V. (1955): The sable: 116-120, M.

Nasimovich, A. A. (1948): Essay on the ecology of the ermine in the Lapland Reserve. Tr. Laplandsk. zapovedn. 3: 3-37.

Raevski, V. V. (1947): The life of the Konda-Sosva sable: 37-49. Izd-vo Gl.upr. po zapovedn.

Teplov, V. P. (1948): The question of the ratio of sexes in the ermine. Zool. zh. 17: 567-570.

Yazan, Yu. P. (1970): The pine marten, sable and kidas in the northern Pre-Urals (winter observations). Byull. Mosk. o-va Ispyt. Prirody, Otd. Biol. 75: 16-27.

Fog, M. (1969): Studies on the weasel (*Mustela nivalis* L.) and the stoat (*Mustela erminea* L.) in Denmark. Danish Review of Game Biology 6: 1-14.

---

[1] Translated in King (1975)—Ed.

THE BIOLOGY AND TRAPPING OF THE ERMINE IN KAMCHATKA

by

A. A. Vershinin

[From: Byull. Mosk. o-va Ispyt.Prir. Otd. Biol. 77: 16-26, 1972.]

The material for the present paper was collected by us during the years 1941-1962 in various parts of Kamchatka.

Body size

The ermine is commonly trapped throughout the Kamchatka Region. The Koryak people and the Chukchi call it "imchachok", whereas the Eveni (the Lamuts) call it "gurnata". The fur trade classifies the Kamchatka ermine as one of a short stumpy kind - the "Yakut" (the length of the body is not more than 250 mm; Kuznetsov, 1952). Data on the size of the ermine have been contradictory, so we consider it helpful to publish our measurements of the animals obtained on the Kamchatka peninsula and in the valley of the River Penzhina during the years 1956-1961 (Table 1). For comparison there are the findings of L. G. Morozova-Turova (1961) relating to the eastern Siberian subspecies (*Mustela erminea kaneii* Baird), to which the Kamchatka ermine is attributed ("Mlekopitayushchie Sovetskogo Soyuza" Vol. 2).

The biggest ermine measured by us had a body length of 280 mm. The existence of the giants of 350 mm to which Morozova-Turova refers is doubtful, the more so in that they do not differ in skull size from those found by us.

The ermine of Karaginski Island are distinguished as a separate subspecies (*M. e. karanginensis* Yurgensoni). However, according to Yurgenson (1936), the condylo-basal length is 40.5-43.7 mm, i.e., they are indistinguishable from the Kamchatkan subspecies (Table 1). Probably the Kamchatka, Karaginski, and Penzhina ermine could be attributed to a single subspecies - namely, the eastern Siberian - once the maximum sizes of the animals have been precisely determined.

It is known that, from the sequence of developmental changes in the size, shape and proportions of the skulls of ermine, it is possible to use the skulls for age determination (Yurgenson, 1933[1]; Stroganov, 1937[2]; Popov, 1947). In the absence of standards for this determination, we made use of a combination of characteristics (Figure 1), which distinguish with sufficient clarity the skulls of the first-year animals from those of older ermine. Male ermine show clearer indications of age differences; the skulls of first-year specimens have a rounder shape, a relatively shorter face, a larger postorbital width, and incompletely joined parietal ridges. With age, the postorbital width becomes less, the parietal ridges grow together into the sagittal crest, and occipital ridges develop. The skulls of large females have the same distinguishing marks of age as the males. Skulls of small females, with fine transparent bones, evidently belong to first-year animals. The method of determining the age of ermine requires more accurate definition.

It is well known too that there is a very great individual variation in the sizes of ermine. Nevertheless, there is also an age-related difference in the sizes of the carcasses of trapped animals; the carcasses of first-year males at the age of 6-9 months (skinned) weigh on the average 10% less than the carcasses of older males. The maximum weight of first-year males is 180g, and of full-grown males is 230g; the average body length of the young male is 231 mm (24 specimens), whereas in full-grown males it is 238 mm (98 specimens).

---

[1] Translated in King (1975)—Ed.

[2] Translated in this volume—Ed.

TABLE 1: Measurements (in mm) of ermine of all ages caught in winter

Dimension	Our data			Data of L. G. Morozova-Turova (1961)		
	No. of Measurements taken	Range	Average	No. of Measurements taken	Range	Average
				Ermine in Kamchatka		
Males						
Head & Body length	89	200-280	237	27	201-350	260
Condylo-basal length of skull	105	40-49	45.9	110	42-49	45.6
Females						
Head & Body length	29	186-215	199	-	-	-
Condylo-basal length of skull	30	37.5-41	39.8	11	38.5-44	40.2
				Ermine in Penzhin		
Males						
Head & Body length	33	210-260	235	-	-	-
Condylo-basal length of skull	25	39.7-47	44.6	-	-	-

Accordingly, in Table 1 the individual variation in measurements of ermine should be considered to be somewhat overstated.

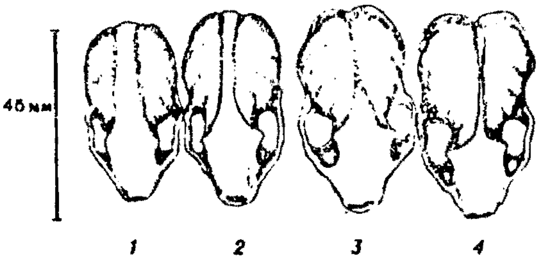


FIGURE 1: Age changes in the skull of the ermine.

1. first year animal, about 6 months;
2. first year animal, 8-9 months;
3. adult, about 1.5-2 years;
4. old animal.

The males weight from 100 to 230 g, on the average 160 g; females from 70 to 130 g (average 90 g). The pronounced sexual dimorphism in ermine indicates the existence of ecological separation in the behaviour and feeding of the two sexes which probably help to reduce intra- specific competition for food.

Habitat

Ermine are found in various habitats, from the sea coasts to the upper limits of forest and scrub vegetation. Yu. V. Averin (1948) found in the Kronotski reserve traces of summer and winter residence by these animals up to 1300 m above sea level. Evidently, this is the limit of their highest winter habitation in the southern half of the peninsula. In northern Kamchatka, ermine do not go so high in the hills in winter.

In the Kamchatka isthmus, in the valleys of the Rivers Lesnaya, Pankara (Ivashki), and Karag, the tracks of ermine are not encountered in winter any higher than 750 m. In summer, ermine climb higher. In the upper reaches of the river Apuka, A. A. Kishchinski observed them at a height of 1400 m. (Portenko *et al.*, 1963).

In comparative censuses of 10 km transects crossing various terrains, an average 0.8-1.0 tracks of ermine were found for each transect (Table 2). On a 356 km expeditionary survey, carried out in the first quarter of 1964 for the purposes of a biosurvey by the Masterhunters of the Russian Soviet Socialist Republic, on average 0.98 tracks per 10 km were recorded (Priklonski and Teplova, 1965), which is near the average found over many years, as shown in Table 2.

The ermine may be considered a typical inhabitant of the forest edges, particularly the edges of flood-plain forests and scrub. It visits less frequently large areas of unbroken scrub, or open swamps, meadows, and tundra. In birch forests it keeps to open stands, forest edges, clearings and small streams. It inhabits both the mixed forest of central Kamchatka and the birch forest. It avoids the interior of forest areas composed solely of larch and spruce trees. The concentration of ermine at the edges of forest is apparently explained by the diverse habitats and the rich fauna of small rodents and birds found at the junction of the forest and scrub with open lands. In the forest tundra regions of the north, ermine are most common on flood plains. During January and February 1957 a periodic survey made every 10 km in the course of an expedition along the banks of the River Penzhina disclosed that in poplar-willow forests and scrub, on average 3.4 tracks were to be found which were not older than 24 hours, whereas in larch forests there were 1.9 such tracks. In parts of the tundra that are not protected from the wind, ermine are few, which is probably because of the difficulty of procuring food there under the deep snow.

TABLE 2: Population density of ermine in the various areas of Kamchatka peninsula (according to records from 1942-1958)

Habitat	Total distance of survey (km)	Tracks per 10 km
Flood-plain poplar, willow forests and scrub, meadows, overgrown with scrub, swamps and tundra.	444	1.3-1.5
Birch forests and open forests (*Betula ermanii* Cham. and *Betula alba*)	903	0.7-0.8
Mixed larch - spruce - birch forests	188	0.6
Larch forests	91	0.4
Spruce forests	27	very seldom
Thickets of cedar and alder scrub	46	very seldom
Open meadows, marshes, and tundra	321	0.04
Total	2020	0.8

Food habits

From examining the intestines of 135 males, 69, or about 50%, turned out to be empty, and roughly the same figure applies to females. A significant distinction in winter feeding between males and females is found, linked to the peculiarities of their morphology and behaviour (Table 3). The females, being almost half the size of males, hunt chiefly under the snow, and are easily able to enter into the narrow burrows of small mammals. Voles and shrews are found in 94% of the stomachs of females but in only 45% of males. Ermine swim and dive well. Fish play an important role in the winter diet of male ermine and are found in 47% of intestines (voles amount to 25.8%). In one ermine's hide-out we found a cache of 10 small fish. However, that does not mean that the ermine is necessarily detrimental to fish culture. Most of its catch consisted of small loach and salmon fry hiding in holes made by frozen rivulents and tiny streams.[1] We did not find any plant food in the winter diet of ermine. Apparently, the animals are satisfied with the plant food which they

---

[1] But note also that later Vershinin states that 75% of the ermine were caught in traps baited with fish—Ed.

take in with the viscera of rodents and birds. In the entrails of three large males (body length 235-250 mm) the remains of ermine were discovered: however it does not follow from this that cannibalism had developed among them, because they had probably eaten only dead ermine held in traps.

TABLE 3: The winter diet of ermine (in percentages of the total number of guts containing food)

Species of food	Males (66 specimens)		Females (17 specimens)		Total	
	Number	%	Number	%	Number	%
Mammals	30	45.0	16	94.0	46	55.4
Voles	17	25.8	7	41.2	24	29.0
shrews	10	15.2	5	29.4	15	18.0
other mammals	7	10.6	5	29.4	12	14.5
Birds	10	15.2	1	5.9	11	13.2
Willow ptarmigan	1	1.5	-	-	1	1.2
Passerines	6	9.1	1	5.9	7	8.4
other birds	3	4.5	-	-	3	3.6
Fish	31	47.0	3	17.7	34	41.0
Vegetation	-	-	-	-	1	1.2

The life of the ermine under the snow during hard frosts is known in northern Kazakhstan (Kraft, 1966).[1] Since Kamchatka has even heavier snow, the same will apply only more so. The female ermine live and hunt mainly under the snow and rarely encounter traps. This evidently explains the widely known predominance of males in bags of trapped ermine. As winter progresses the proportion of females caught increases and towards spring the catch of females equals the catch of males (Kukartsev, 1970). The spring activity of females is probably linked with the beginning of the development of embryos within them, together with the rise in temperature and the packing down of the snow, and the decrease in numbers of small rodents.

Of the 707 ermine caught and examined in Kamchatka and Penzhina, only 22.6% proved to be females. In the less snowy parts of the U.S.S.R. they constitute 35-37% of the yield (Kukartsev, 1970). Out of catches of 404 animals at the River Penzhina during November-February, females constituted 13.3%, whereas out of 122 caught in March there were 53%. In the central wooded parts of the valley of the River Penzhina, higher than Ayanka village, in December-February, in the presence of heavy frosts (sometimes lower than -50°) and with an average snow cover in the forest of 160 cm, only 2 of 24 ermine taken were females (9%).[2] Hence, the colder the temperature and the deeper the snow cover, the fewer the females caught. The depth of the snow cover influences the sex ratio of the catch, and consequently the composition of the ermine population after trapping.

According to the observations of several hunters, female ermine are seldom trapped for the further reason that in winter they remain in the mountains, near the upper limits of the forest and scrub vegetation, less visited by hunters. The males winter in the flood-plains where hunting goes on continuously, and only in the spring, in February-March, do they take to the

---

[1] Translated in King (1975)—Ed.

[2] On average 16 fresh tracks of sables, but only 1.8 tracks of ermine, were noted in a survey taken every 10 km of a 200 km expedition in these areas, which confirmed the reduced winter activity and appearance of the ermine above the snow—Author.

hills. It would be interesting to confirm these observations. Such features of the winter behaviour and feeding of the female ermine could have great significance for the species, as adaptations to the severe conditions of their habitat.

There is an essential distinction to be observed between the diet of ermine on the Kamchatka peninsula and in the valley of the River Penzhina (Table 4). Birds composed 9% of the identified items of the diet of the ermine in Kamchatka, and 35% in Penzhina. In the valley of this river there are more small wintering birds and willow ptarmigans. The ermine often picks up the remains of partridges killed by sables. With scanty numbers of voles this main diet is replaced by fish, more rarely by shrews and birds (Table 5).

TABLE 4: The diet of ermine in Kamchatka and in the valley of the river Penzhin (in percentages of food specimens).

Species of food	Kamchatka (1956-1960) 65 specimens	R. Penzhin (1956-1960) 20 specimens
Voles	24	40
Shrews	23	10
Birds	9	35
including		
Willow ptarmigan	-	15
passerines	8	20
Fish	43	30

TABLE 5: Annual variations in the diet of ermine in Kamchatka.

Trapping season	No. guts analysed	No. of guts containing food		% guts containing:			
		No.	%	Voles	Shrews	Birds	Fish
1955/56	22	13	59	31.0	38.3	15.4	23.0
1956/57	32	19	59	42.0	10.5	-	55.0
1958/59	24	11	46	54.0	27.2	0.1	9.1
1959/60	45	14	31	14.3	35.7	7.1	50.0

The species competing with the ermine for its staple food are the sable, otter, and (introduced on Kamchatka) the American mink; and to a lesser degree all other predators feeding on voles and fish. All large carnivores and raptors may be considered as enemies. Sables, and more rarely foxes and wolverines, chase after the nimble ermine, but for the most part without success, and the losses inflicted are evidently small. The remains of ermine were found in 0.5% of examined intestines of 1336 Kamchatka sables, and in only one of 30 fox excrements, collected by G. A. Belov on Karaginski Island in 1957. The biggest enemy of the ermine may be held to be the American mink released in 1960 in the valley of the River Kamchatka, and settled in the Milkovo, Ust-Kamchatsk and Elizovo districts.

Reproduction

We have the reports of hunters concerning 129 ermine litters. The earliest date on which a litter was encountered in Kamchatka was 2 April. One litter was observed, not yet dispersed, at the beginning of September. The litters numbered up to 12 kittens, on the average 5.2. Towards autumn the number of young observed in a single litter decreases to 3.8 (Table 6) which means a drop of 32%.

TABLE 6: Size of litters of Kamchatka ermine according to the communications of hunter correspondents, 1952-60.

Months	No. of litters encountered	Young in each litter	
		Range	Average
April-May	35	1-12	5.6
June	35	2-10	5.2
July	19	2-8	4.2
August-September	22	1-7	3.8

The observations of hunters are confirmed by laboratory results. Out of 25 females the ovaries of which were examined during 1956-1960, 18 (72%) revealed from 1 to 8 corpora lutea of pregnancy, on the average 5.4 for each pregnant female, whereas in a survey of all females examined irrespective of whether they were pregnant or not,[1] on the average there were 4.1 corpora lutea.

The fertility of ermine is significantly reduced in years where the numbers of voles are low. In the season 1956/7, when the numbers of voles were at their minimum, the potential fertility of ermine was at its lowest (Table 7). In the same season a reduction in fertility of sables in Kamchatka was also observed.

TABLE 7: The rate of reproduction of ermine in relation to the population density of voles.

Trapping season	Number of voles captured per 100 trap-nights in the previous summer	Females examined	Average no. of corpora lutea per female[1] examined
1955/56	22.0	6	3.0
1956/57	7.7	9	2.6
1957/58	11.8	-	-
1958/59	47.5	6	4.6
1959/60	16.5	4	5.0

A study of the skulls of ermine (131 specimens), collected during 6 trapping seasons (1955-1961) showed that 45% of them belonged to first year animals. Hence, the probable average increase, computed from the basic (winter) livestock, is 82%. These figures confirm other indicators of the composition of the population given above.

Parasites

Three species of fleas are found on Kamchatka ermine (Violovich, 1963). The ermine are severely infested with helminths. Out of 184 individuals subject to cursory helminthological analysis during the years 1955-1960, helminths were

---

[1] It is not clear whether Vershinin uses "pregnant" to mean only females with visible embryos or both these and females with unimplanted blastocysts. It may be worth noting here that the mean ovulation rate for this species elsewhere is about double the mean given here (King, in Corbet & Southern 1977, and unpubl.): either the Kamchatkan ermine are half as fertile as those in Britain and New Zealand, or else Vershinin is quoting the number of corpora lutea per ovary, not per female—Ed.

found in the guts of 35.4%, and in the respiratory system of 7.7%; 38% of the males were infected, and 23% of the females. On complete helminthological analysis more helminths were found, and the general infection of ermine in central Kamchatka in the winter of 1959-60 reached 74% (Kontrimavichus and Skryabina, 1963). According to the data of V. L. Kontrimavichus and E. S. Skryabina, and also our own, 6 species of helminths are encountered in Kamchatskan ermine. These are enumerated in Table 8; besides these, ascarides (*Ascaris columnaris*) are also found.

TABLE 8: Infestation of ermine with helminths

Species	No. of ermine examined (1955-1960)	% of sample infested	No. of helminths found per ermine	
			Range	Average
Skrjabingylus nasicola	50	62.0	1-32	11.3
Capillaria putorii	50	20.0	1-32	9.0
Molineus patens	50	20.0	1-7	2.0
Soboliphime baturini	149	5.4	1-3	2.1
Trichinella spiralis	50	2.0	-	-
Mesocestoides lineatus	149	2.3	-	-

To a very large degree ermine are affected by infestation with *Skrjabingylus nasicola* in the frontal sinuses (found in 69%[1] of animals examined). In the sinuses of one ermine, 32 of these helminths were found. Small nematodes (*C. putorii*, *M. patens*) were found in the guts of 20% of animals examined. In 5.4% of specimens, small numbers of *Soboliphime*, a common parasite of the sable, were found. In the diaphragm of two animals trichinosis was found, while three were infected with *Mesocestoides*. Ermine were infected with *Soboliphime* and *Mesocestoides* to a moderate extent compared with sables (50-70%), which suggests there is no very close contact between these species in places where they co-exist.

The large number of Kamchatka ermine infested with *Skrjabingylus nasicola* is evidently linked with the abundance of land molluscs, which are the intermediate hosts of the helminth. Mollusc species are comparatively few, but the number of individual molluscs per unit of area in central and southern Kamchatka is very high (Likharev, 1963).

Ermine which had died from unknown causes were encountered in the Anadyr basin (Sokolnikov, 1927), at the river Penzhina near the village of Ayanka (in 1958 and in February 1960), and further south (in 1955 near Kichiga on the eastern coast of the isthmus, and in the summer of 1959 in the neighbourhood of Ust-Hairyuzov on the eastern seacoast of Kamchatka). Hunters observed dying ermine in years of epidemics among foxes.

In the Sobolevo district N. A. Kravchenko reported that on 7 June 1959 he found 4 young ermine dead in a hollow tree which had been washed away by high floods. A reduction in the numbers of ermine after lengthy floods is not infrequently observed in the Kamchatka Valley (for example in 1960), and in other districts of the peninsula. High floods alter the distribution of the animals in different habitats, and this is reflected in the hunter's bag.

---

[1] but 62% in the table. Both figures correctly transcribed from the original—Ed.

Hunting statistics

The yield of ermine skins varies markedly according to the season, with a 3 to 4 yearly cycle (Figure 2). Over the whole region it fluctuates from 4000 to 12 000 [per year]. On the peninsula itself, according to the data for the last 30 years, the maximum season of productivity exceeded the minimum by 15 times; in the Tigil and Milkovo districts, by more than 50; in the Ust-Bolsheretsk by more than 30; and in the Bistrinsk and Ust-Kamchatsk by 20 times. The size of the catch of ermine is determined by the numbers of voles and usually coincides with the periodicity in the numbers of the Kamchatka sable.

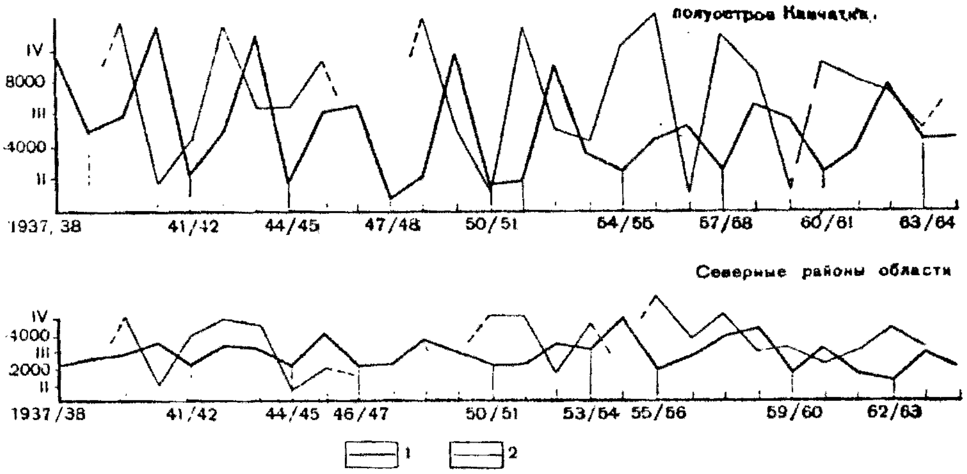


FIGURE 2: Variation in the yield of stoat pelts and the number of voles (in units from I to IV) in the Kamchatka region during the period from 1937 to 1964.

1. stoats caught (no. of pelts)
2. number of voles

First graph: Kamchatka peninsula;
Second graph: northern districts of Kamchatka.

The level of production of skins from one season or region to the next depends on the number and distribution of ermine present, which in turn is linked with the availability of food. V.P. Teplov (1952)[1] correctly noted that success in bagging ermine depends not only on the number of ermine available, but also on how hungry they are.

Most ermine are caught in flood-plains, near inhabitated areas. In a cold wet summer, as a result of repeated high floods, the voles in the flood-plains die or migrate to higher ground; the number of them on the lower areas diminishes, and at the same time the ermine also abandon the flood-plains, so that the hunter's bag drops sharply. In such years ermine are more often encountered in the depths of birch forests, along clearings, forest-fringes, and in the higher reaches of the forest belt below the tree-line.

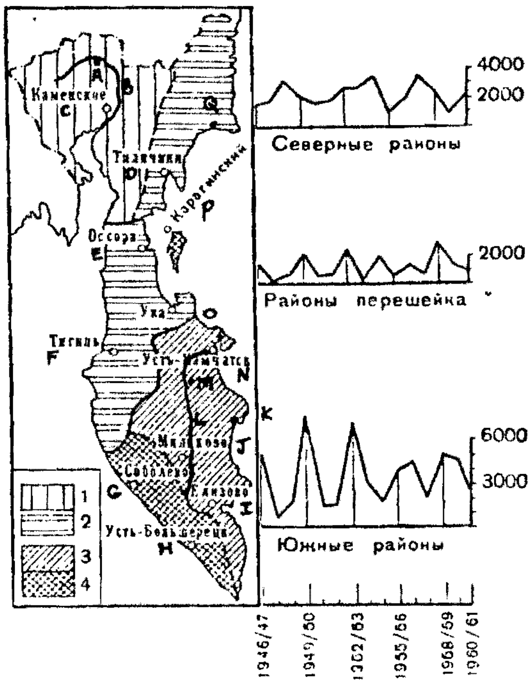
During a dry summer the grass quickly dries out in the light Kamchatska birch forests and on the hills, but fresh growth remains in the flood-plains, where the voles congregate, followed by the ermine, which hunts them with success.

An increase or decrease in the hunter's catch of ermine is usually experienced simultaneously over a large part of the peninsula, but not to the same extent throughout. A distinct three yearly periodicity is observed in

---

[1] Translated in this volume—Ed.

the southern and central districts (Figure 3). In the districts of the isthmus, in Tigil and particularly in Karaginski, this cycle is sometimes disturbed. In northern mainland districts, in Olyutorskoye and Penzhina, a periodicity is observed that does not coincide with that known for the peninsula. Fluctuations in the catch of ermine on Karaginski Island do not coincide with those on the nearby coast of the Kamchatka isthmus. The boundary lines of the zone of equal productivity of ermine for most years can be drawn along the northern narrowest part of the Kamchatka isthmus and in its southern part (Figure 3).



KEY TO NAMES

A	AYANKA
B	PENZHINA R.
C	KAMENSKOYE
D	TILICHIKI
E	OSSORA
F	TIGIL'
G	SOBOLEVO
H	UST-BOL'SHERETSK
I	YELIZOVO
J	MILKOVO
K	KRONOKA
L	KAMCHATKA R.
M	KOZYREVSK
N	UST-KAMCHATSK
O	UKA
P	KARAGINSKI Is.
Q	OLYUTORSKOYE

FIGURE 3: Seasonal and geographical variations in the yield of ermine (the regions of analogous fluctuations are delimited by a thick line)

1. 0.5 to 1.2 ermine per 100 km^2 of hunting ground;
2. 1.3 to 2.0;
3. 2.1 to 3.0;
4. over 3.1 ermine

The graphs show the number of skins procured each season.

The uppermost graph is for northern regions;
The middle graph is for regions of the isthmus;
The lowest graph is for southern regions.

In the typical forest tundra parts to the north of Karaginski, in the Olyutorskoye and Penzhin districts, the yield of ermine fluctuates to a lesser extent than in the peninsula (Figures 2 and 3). Here the periods of change in numbers sometimes take up to 6 years. This is because in the northern districts there is a lower diversity of habitats, and no forest belt; and hence, ermine are more sparsely distributed in these districts.

During shortages of food and in difficult hunting conditions (deep snow, ice-covered ground), the ermine migrate. In the valley of the Kamchatka and in Kronoka (Averin, 1948), ermine regularly move to the flood-plains when heavy snow falls early in the hills. This is also characteristic of sables. Usually the animals leave the hills in November-December, but later if the snow is sparse. In the north, in Olyutorskoye district, on the other hand, ermine migrate to the hills from the lowlands, which are snow-bound with deep dense snow blown from the heights by the prevailing strong north-easterly winds.

The catch of ermine per unit area regularly decreases towards the north with the impoverishment of the hunting grounds (Figure 3). In the south-west of the peninsula, in the Bolshevetsk and Sobolevo districts, unit areas of 100 km^2 produce an average of 3.1 to 5 ermine, in the central and eastern districts they yield 2.1-3; in the isthmus and in the Olyutorskoye district they yield 1.3-2; and in Penzhin district 0.5-1.2. The greatest yield on the Karaginski Island comprises up to 13 ermine from 100 km^2.

Localities which are frequented by hunters yield somewhat more. For example, in the Tigil district (1950-1953), where the average catch of ermine in the newly developed lands is 2.4, the flood-plains where the trapping of animals is intensive yielded 7-7.5 animals per 100 km^2. On the hunting grounds of correspondent hunters, which cover about 20% of the useful area of the land (44 700 km^2), on the average for the years 1957-1962 the yield was 2.5 ermine per 100 km^2. After 1230 specimens had been caught on these grounds there remained about 900 animals, that is to say, the yield was about 58% of the population.[1]

The ermine often takes up residence in settlements, under buildings or entering the huts and tents of hunters. With his own eyes the author, in August 1945, saw an ermine make off with a piece of butter, about half a kilogram in weight, out of a tent near which were woodcutters, and dropped its prize only when pursued.

In Kamchatka, ermine change to their winter coat on about 10-15 October, and from this time onwards they are hunted. With the concentration of ermine in the flood-plains, individual hunters specialise on them, earning their living not far from the villages. The highest yield known to us by a single hunter was in the rural settlement of Kozyrevsk (in the Kamchatka valley), and amounted to 75 ermine; this was in the season of 1940-41. In years when ermine are low in number they are caught incidentally in traps set for sables and foxes.

Ermine are obtained principally by traps Nos 0 and 1, with bait. About 75% of them are caught with fish bait (Table 9), of which number 32% are caught with a bait of fresh fish, for the most part loach (30%) and also navaga (6%), smelt, crucian carp, and herring. Less frequently used are fermented ("sour") and dried (sun-dried) fish - Siberian salmon, humpbacked and silver salmon, and loach. From time to time dried fish roe is used for bait, and - very rarely - salted fish. The meat of small mammals and birds is used by about 2/3rd of hunters, and this bait accounts for about 25% of ermine taken. About 36% of hunters use bait from the willow ptarmigan and 12% from wood grouse, catching about 20% of ermine. Less used is the flesh of hare. 27% of hunters use the meat and fat of large mammals - marine species, reindeer, snow rams, and even dogs. Towards the place where a trap is set a lure is made in the form of an odorous trail by dragging a carcass or the viscera of a bird or hare on the end of a string. The traps are set in holes in frozen streams where there are aggregations of loach and salmon fry. Otters, sables, and minks are also trapped there.

Throughout all districts of the Kamchatka region, the catching of ermine by cherkan snares is well known, but they are seldom used, only in the Penzhin and Bistrinsk districts, where hunting with the cherkan snare is one of the most widespread [methods] among the Eveni hunters. The best hunter in the Penzhin district, M. S. Ermachov, during 1947-1957, had 30 cherkan snares and 10 No. 0 traps, and caught in a season on the average about 30 ermine, and in the best season 58 ermine.

---

[1] Vershinin does not say how he calculated this interesting statistic—Ed.

TABLE 9: Baits for the ermine (according to 33 questionnaires sent in by hunters from 8 districts of the Kamchatka region for 1955-1956).

	Number of communications		Ermines caught	
	No.	%	No.	%
Meats	21	63	69	25
Baits	7	21	9	3
Mountain hare	1	3	-	-
Squirrel	4	12	6	2
Meat and fat of marine animals	5	15	1	-
Meat of other large mammals	12	36	36	13
Partridges, willow ptarmigan and tundra partridge	4	12	17	6
Wood grouse	1	3	-	-
Fish	30	91	206	75
Fish, fresh	12	36	87	32
sour	7	21	31	11
dried	4	-	-	-
loach	8	27	83	30
navaga	2	3	18	6
Total:			275	100

SUMMARY

The ermine, *Mustela erminea* L., is common in Kamchatka. Substantial differences in the size of males and females (Table 1) lead to differences in feeding habits (Table 3), thus lessening intraspecific competition. Only 27% of the trapped ermines are females. There are usually from 1 to 8 corpora lutea of pregnancy, with an average of 5.4. In 129 litters the number of young varied from 1 to 12 with an average of 5.2 (Table 6). Nearly one third of the young die during the summer. Cyclic fluctuations in abundance (3-4 years, in some localities up to 6 years) are marked. They are determined by periodic variations in the abundance of small rodents. Data are given on the habitats (Table 2), helminths (Table 8), and trapping (4-12 000 animals are captured yearly, Figures 2-3).

BIBLIOGRAPHY

Averin, Yu. V. (1948): Terrestrial vertebrates of East Kamchatka. "Tr. Kronotsk. zapovednika", 1, M., Izd-vo Glavn. upr. po zapovednikam.

Violovich, N. A. (1963): The flea fauna of Kamchatka peninsula. "Entomol. obozrenie" 42: (4).

Kontrimavichus, V. L. and Skryabina, E. S. (1963): The helminth fauna of the Kamchatkan sable and armine. Tr. Gelmintolog. laboratorii NN SSSR, 13.M.

Kraft, V. A. (1966): The effect of temperature on the modibilty of ermines in winter. Zool. zhurn. 45: (1).

Kuznetsov, B. A. (1952): Principles of commodity research into fur resources. M. Zagotizdat.

Kubartsev. V. A. (1970): On the question of the effect of hunting on the sex ratio of the ermine population. In the collection of articles "Okhota, pushnina i dich", No. 29, Kirov.

Likharev, I. M. (1963): The fauna of terrestial molluscs of the Kamchatka province. In the collection of articles "Fauna Kamchatskoi obl." M.-L., Izd-vo AN SSSR.

Morozova-Turova, L. G. (1961): Geographical variability in the ermine of the territory of the USSR. Sb. trudov Zool. muzeya MGU, No. 8, M.

Popov, V. A. (1947): Age structure, food reserves and helminths of the ermine as indicators of the fluctuations in the numbers of this species. Tr. O-va estestvoisp. pri Kazansk. un-te 57: (3-4).

Portenko, L. A., Kishchinski, A. A. and Chernyavski, F. B. (1963): Mammals of the Koryak range. M.-L., Izd-vo AN SSSR.

Priklonski, S. G. and Teplova, E. N. (1965): The first experiment in the All-Russian winter track-census of game animals. M., Izd-vo Byuro tekhn. informatsii Glavokhoty PSFSR.

Sokolnikov, N. P. (1927): The game and fur trade animals of the Anadyr country. Byull. Mosk. O-va Isyt. Priri., Otd. Biol. 36:(1-2)

Stroganov, S.U.(1937): Methods for age determination and an analysis of the age structure of ermine populations. Zool. zhurn. 16: (1).

Teplov, V. P. (1952): Taking a census of the otter, the sable, the marten and the small representatives of the Mustelidae family. In the Collection of articles "Metody ucheta chislennosti i geogr. raspredeleniya nasemn. pozvonochnykh", M., Isd-vo AN SSSR.

Yurgenson, P. B. (1933): Variability in the skull of the ermine. Zool. zhurn. 12: (1).

Yurgenson, P. B. (1936): Ermines of the Far East territory. Byull Mosk O-va Isyt. Prir., Otd. Biol. 45: (3).

THE ECOLOGY OF THE POLECAT, *MUSTELA PUTORIUS,* IN NORTH-WESTERN EUROPEAN RUSSIA

by

P. I. Danilov & O. S. Rusakov

[From: Zool. Zhurn. 48(9): 1385-95, 1969.]

Introduction

Though the polecat (*Mustela putorius*) is widespread in the European part of the USSR, only few papers have been written about it (Ljalin 1932; Yurgenson 1932; Lavrov, 1935; Grigoriev and Teplov, 1939; Rusakov, 1961, 1963; Danilov 1965; Ivanov, 1968). Ecological information is available in general mammal faunas (Ognev 1931; Novikov, 1956;[1] Gromov *et al.* 1963; Heptner *et al.* 1967), but on the whole the ecology of the polecat has been inadequately studied. This is true even in the North-West of the country, (in the Karelian ASSR and the districts of Leningrad, Novgorod and Pskov), where the polecat has for a long time been an important fur animal. Between 1957 and 1966 135 000 skins were harvested in this area, which represents more than 12% of the [total] number of polecats killed [in Russia]. In the last 5 years (1962 - 1966) this proportion rose to 18%.

Material

The material for our study of the ecology of polecats was collected between 1955 and 1967. The population density of polecats in various districts of the North-West was estimated from counting tracks along census routes covering about 500 km; 24 nocturnal hunting tracks were followed from beginning to end; and 91 carcasses were examined to determine feeding habits, breeding (histological preparation made from most of the material) and age and sex ratios (from the 91 carcasses plus 158 skins). Infection of the animals with filarioidea (35 specimens) and *Skrjabingylus* (37 specimens) was determined. Polecats in captivity were also observed. About 800 items of information from trappers, and computations of polecat density carried out by the State Hunting Inspectorate (over census routes of more than 30 km) were also used in the research.

Distribution

Comparatively recently (about 100 years ago) the polecat was very rare in the north of European Russia, and was found only in the southern districts of Karelia (Olonezk and Sheltozersk). K. F. Kessler (1868) considered that the northern limit of the distribution of the polecat was the township of Shoksha (61°20' latitude North).

Since then the polecat has spread northwards (Isakov 1939; Orlova 1948; Stroganov, 1949; Marvin, 1959; Heptner *et al.*, 1967). At present, according to our data, the northern boundary of polecat distribution in Karelia runs along the line Lendery - Rugozero - Nadvoitsy. Parovshshikov (1959) records a sighting of a polecat near the town of Kem in 1945 - 1946. The local researchers attribute the spread of polecats to changes in the habitat following the cutting of forests, building of settlements and development of agriculture (Lavrov, 1935; Isakov, 1939; Stroganov, 1949; Marvin, 1959; Parovshshikov, 1959). The Finnish zoologists associate the wider distribution with a general warming of the climate (Kalela, 1961; Siivonen, 1956). Heptner *et al.* (1967) consider that both factors are important.[2]

---

[1] Translated by Israel Program for Scientific Translations, Jerusalem 1962—Ed.

[2] See also Bakeev (1972), this volume—Ed.

At present, within the northern limits of its distribution (central and south Karelia), the polecat is found mainly in areas relatively modified and populated by man. Here it is found along railway tracks and open roads, near settlements, felling areas and farm lands. In the more southern districts (Leningrad, Pskov and Novgorod) the polecat inhabits mainly the banks of waterways (particularly medium sized rivers) and the edges of fields. Observations made in 84 sections of the North-Western districts along a census route of 1154 km during the winter of 1966/67, showed that most polecats (49.6%) were found on land adjoining the banks of waterways, where a large number of small rodents and frogs live. Polecats often live near villages and settlements (18% of sightings), in forests (11.6%) and near swamps (7.2%). They are also found along the edges of forests (5.8%), in meadows (5.2%) and in felling areas (2.6% of all sightings).

In Karelia the population density is low, and only in the southern districts (Sortavalsk, Olonezk, Prionezsk, Pudoszk) does the polecat reach commercial numbers (Table 1). Polecat density further south is markedly higher and is especially high in the Pskov district. Population estimates carried out over large observation areas according to the methods of Zarkov and Teplov (1958), covered routes of 1500-1600 km a year by the end of the commercial season (February) in 1956, 1959 and 1960, and gave results as follows: Leningrad district, 10 700 polecats; Novgorod district, 9600; and Pskov district, 14 100. Considering that during every commercial season as many polecats again were trapped, the number of animals during the pre-commercial season must have been twice as high. During recent years the population has noticeably declined, particularly in the Pskov district. For instance, computations during the 1966/67 season produced the results shown in Table 2.

TABLE 1: Population density of polecats in Karelia (number of tracks per 10 km census route)

Areas	1961	1962	1963	1964	1965	1966	Mean
Central Karelia	-*)	0.25	0.25	0.07	0.15	0.04	0.14
Segezesk	-	-	-	-	-	-	-
Medvezegorsk	-	0.25	-	0.07	0.14	-	0.12
Southern Karelia	0.50	0.44	0.50	0.40	0.39	0.44	0.45
Kondopozsk	0.50	0.25	0.75	0.44	0.21	0.12	0.38
Prionezsk	-	0.50	-	0.50	0.37	0.35	0.43
Olonezk	-	0.75	0.50	0.22	0.26	0.06	0.36
Sortavalsk	-	0.25	0.25	-	-	1.05	0.51
Pudozsk	-	-	-	0.45	0.64	0.64	0.58
Average	0.50	0.35	0.37	0.24	0.27	0.24	0.33

(* Length of census routes 11 189 km; a dash denotes that no census was made—Author)

TABLE 2: Numbers of polecats in the North-Western districts of the USSR during 1966-67 hunting season

District	Area covered by the census (sq. km)	Polecats recorded[1]	Polecats recorded per 1000 ha of hunting ground
Karelian ASSR	1250	55	0.44
Leningrad	3908	345	0.88
Novgorod	582	200	3.44
Pskov	4203	660	1.57
Total	9943	1260	1.26

---

[1] It is not clear whether this table is referring to carcasses or tracks—Ed.

Nesting behaviour

To build the nest, where the young spend the first few months of their life, the parents usually choose abandoned (but quite often also inhabited) dwellings (Table 3).

Nests are spherical and made of hay, pieces of skin of small rodents and the feathers of birds. The outside diameter is 30-35 cm, and the inner diameter 20-25 cm. The nests are relatively permanent. Beside these the polecats have temporary dens, which they visit at times when hunting. In winter, especially when food is scarce, polecats lie up during the day. We succeeded in following up completely the nocturnal trails of 24 polecats: 13 of them returned to the den which they had left and 11 settled down for the day in a new place.

TABLE 3: Distribution of locations where polecat nests were found, over several years, in the North Western districts of the USSR.

Location of nests	Number of nests	
	No.	%
In barns and other buildings	32	26.4
Under tree roots	18	14.9
In burrows on the banks of rivers, streams & lakes	17	14.9
Under haystacks	10	8.3
Under piles of brushwood and fallen trees	9	7.4
In the hollow of fallen trees	7	5.8
In piles of stones and boulders	7	5.8
Under tree stumps	6	5.0
In stacks of firewood and piles of logs	5	4.1
In ruined mud-huts and trenches	4	3.3
In large tussocks along banks of waterways	3	2.5
Under bridges over smaller rivers	3	2.5
	121	100

Territories and food habits

From tracking it is clear that polecats maintain more or less permanent hunting grounds. In the Karelian ASSR during the winter they occupy territories no larger than 4-9 sq. km, but in the Pskov district, from 1 to 25 sq. km. When the population density is high, territories adjoin each other, but when it is low, they remain separate. Apparently, the size of the territories is determined by the amount of food available.

The principle prey of the polecat are small rodents, frogs and birds (Table 4), of which the rodents are the most important. Similar data are recorded in other parts of the range of the polecat, e.g., the Moscow district (Lavrov, 1935) and the Tartar ASSR (Grigoriev and Teplov, 1939), where the proportion of rodents in the diet of the polecat is 95.8 and 74.8%. However, in contrast to these districts, amphibians (frogs) and large mammals were more often found in the stomachs of polecats in the North-West.

The percentage of fish in the diet is not high; in the Moscow district it was 0.8% (Lavrov, 1935), in the Tartar ASSR 6.9% (Grigoriev and Teplov 1939) and in our district 3.1%-7.1%. Traces of plants have not been recorded, although we did find them in small quantities (4.6-5%). In the North-Western district seasonal differences in food are pronounced. Frogs are much more often found in summer than in winter (Table 4). Birds are also eaten more often during the summer, but carrion, which is hardly ever found during the summer, becomes important in winter. In the guts of polecats we found traces of elks, raccoons, minks, ermines, owls, sheep and calves.

TABLE 4: Composition of the diet of the polecat in the North-Western districts of the USSR (91 samples)

Prey	Frequency occurrence (%)			
	Snow absent (26 samples)		Snow present (65 samples)	
	Karelia (9 samples)	Leningrad Novgorod & Pskov districts (17 samples)	Karelia (14 samples)	Leningrad, Novgorod Pskov (51 samples)
Mammals:	88.8	88.2	50.0	80.3
Rodents	88.8	82.3	50.0	78.5
White hares	-	-	7.1	-
Muskrats	-	-	7.1	4.6
Water voles	11.1	17.7	7.1	6.1
Grey voles	77.7	17.7	-	21.6
Common voles	-	11.8	-	6.1
Dark voles	-	11.8	-	15.5
Ginger voles	-	17.7	28.7	6.1
Norway rats	-	-	-	1.6
Forest mice	-	5.9	-	1.6
Insectivores	11.1	5.9	-	6.1
Moles	-	-	-	1.6
Shrews	11.1	5.9	-	4.6
Birds:	22.2	11.8	21.4	4.6
Galliformes	11.1	-	7.1	1.6
Passerines	11.1	11.8	-	3.1
Domestic birds	-	-	14.2	-
Frogs:	55.5	52.9	7.1	32.3
Fish:	-	5.9	7.1	3.1
Carrion:	-	5.9	21.4	27.1
Plants:	-	5.9	-	4.6

Tracking has shown that the polecat usually hunts only at night. In captivity (on a mink farm), polecats did not eat during the day the food given to them in the morning, but by the following morning the food had been eaten. In their natural habitat, especially if food is scarce, polecats sometimes hunt during the day. The distance covered during the night in search of food reaches up to 7.5 km, but averages 4.5 km. The greatest radius of activity (the distance from the start of the hunt to the farthest point visited, along a straight line) is 5.5 km, the shortest 0.1 km. The extent of polecat hunting activity is determined by weather conditions. During snowstorms and hard frosts they will not leave their nest for several days and nights. In captivity, at -25° and below polecats will not come out of their nests and will not even eat their food. At such times they sleep so deeply that they do not react to hand clapping, banging on their cages or any other noise.

During the autumn and winter the polecat often makes caches of food. In the middle of winter under a haystack in the Pskov district, we once came across a polecat in whose larder 47 frogs were found. In the same district over several winters we found another two larders: one containing 18 frogs, the other 9 mice and one vole. In the Karelian ASSR polecat larders were found twice; in one there were 3 grey rats, and in the other, 1 ginger vole and 4 frogs. Polecats often stay close to carrion and visit it over a long period (up to 1 month).

Reproduction

According to some authors (Tikhvinski, 1937; Novikov, 1956, 1963), the polecat reaches sexual maturity in its 2nd or 3rd year of life. Our data do not confirm this opinion. In November 1963 four male polecats of the current year, and probably of the same litter, were caught in the village of Svjatozero in the Karelian ASSR. The animals were kept in cages on an animal farm. At the end of April 1964, i.e., at the end of the natural mating season, two were killed. From histolotical analysis we established that the testes of these animals contained Sertoli cells, spermatogonia, primary spermatocytes, spermatids in various stages of development, and mature sperms. Interstitial tissue was present between the seminal tubules (Figure 1(a)). The average diameter of the seminal tubules was 225μ. The ducts of the epididymes were lined with tall cylindrical ciliated epithelium, and their cavities were filled with mature sperm (Figure 1(b)). The average diameter of the ducts in the epididymis was 243μ. The weight of the testes with epididymis (3830 and 4600 mg) was typical of polecats at the peak of breeding condition, being 10 times higher than the weight of the gonads when regressed (250-350 mg) (Figure 2). These gonads were certainly active, and show that male polecats become sexually mature in the first year of life, at the age of 10-11 months (Danilov 1965). However, in spring we found some polecats which were quite obviously not fertile. These animals probably become sexually mature in their second year of life at the age of 22-23 months.

There is no agreement in the literature about the duration and dates of mating in the polecat. Some authors (Lavrov, 1935; Tikhvinski, 1937; Novikov, 1956, 1963; Siivonen 1956; Marvin, 1959) maintain that the mating season is March to April. Others give longer periods, e.g., February to April (Hansl, 1958). Some researchers (Marshall, 1956) consider that the mating season lasts from April to August. This considerable difference in dates is apparently explained by climatic conditions. The sexual activity of polecats depends partly on photoperiodism (Bissonette, 1932; Hammond, 1951; Krohn and Zuckerman, 1953; Harvey and Macfarlane, 1958). Even in our relatively small region there were differences in the dates of the beginning of the mating season. In Karelia, for instance, mating begins in March and takes place mainly in April, but in the districts of Leningrad, Novgorod and especially in Pskov, mating sometimes begins as early as February. Out of 56 observations of mating animals, 2 (3.6%) occurred in February, 27 in March (48.2%), 26 in April (46.4%) and 1 in May (1.8%).

Courtship and mating are preceded by considerable changes in the condition of the gonads. In general, the sexual cycle of male polecats can be divided into three lengthy periods: (1) passive spermatogensis (November-February); (2) active spermatogensis (March-May); (3) regression (June-October).

The first period consists of two stages: (1) the beginning of mitotic activity in the spermatogonia, and (2) the development of the germinal epithelium to the spermatid stage. The epithelium develops from a single layer consisting of Sertoli cells and spermatogonia to a multi-layered structure consisting of Sertoli cells, spermatogonia, primary and secondary spermatocytes and spermatids. The testicles increase in weight from 350 mg at the beginning of November to 1800 mg in February. In November the seminal tubules contain Sertoli cells, spermatogonia and primary spermatocytes. The latter are not found in all tubules and most of them are degenerated. The interstitial tissue is prominent (Figure 3(a)). The average diameter of the seminal tubules is 125μ; the ducts of the epididymis measure 60μ. In December the germinal epithelium has two layers. The basal layer consists of Sertoli cells and spermatogonia, lining the fundamental membrane, and the second layer consists of primary spermatocytes, appearing in great numbers in all ducts (Figure 3(b)). The average diameter of the seminal tubules is 110μ, and of the ducts of the epididymis 67μ. At the end of January-February the germinal epithelium consists of three layers. The first layer consists of Sertoli cells

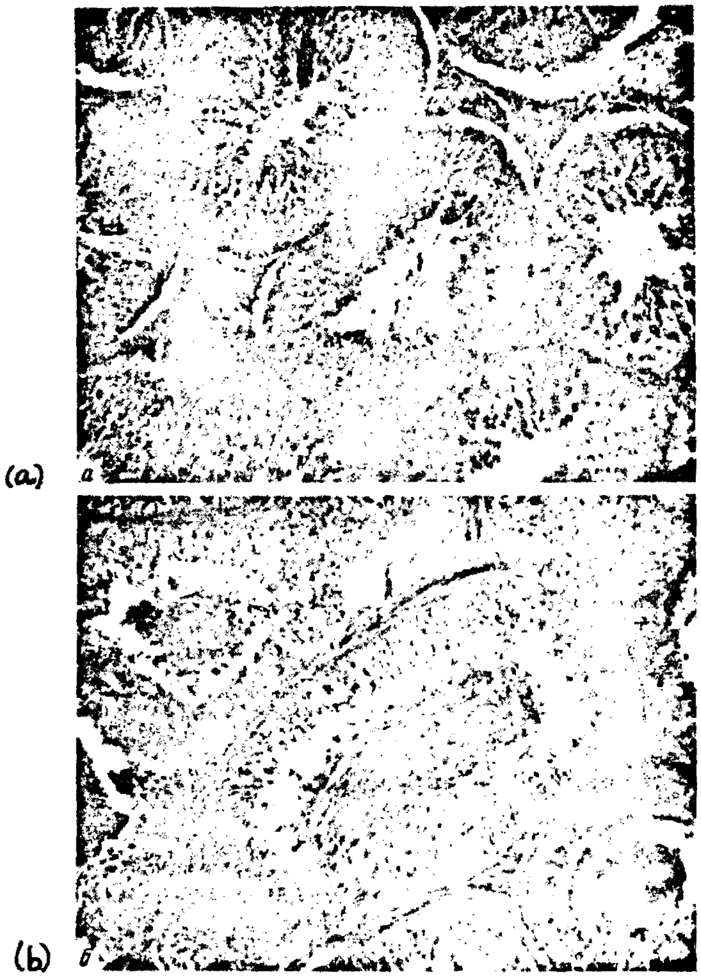


FIGURE 1: Cross-sections of (a) the seminal tubules and (b) the ducts of the epididymis of a yearling polecat in April.

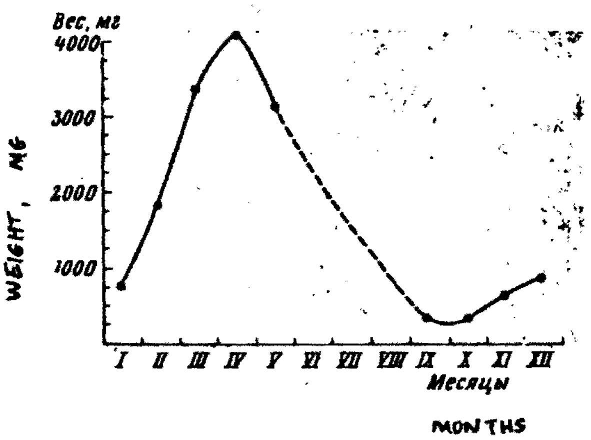


FIGURE 2: Seasonal variation in the combined weight of testes and epididymes.

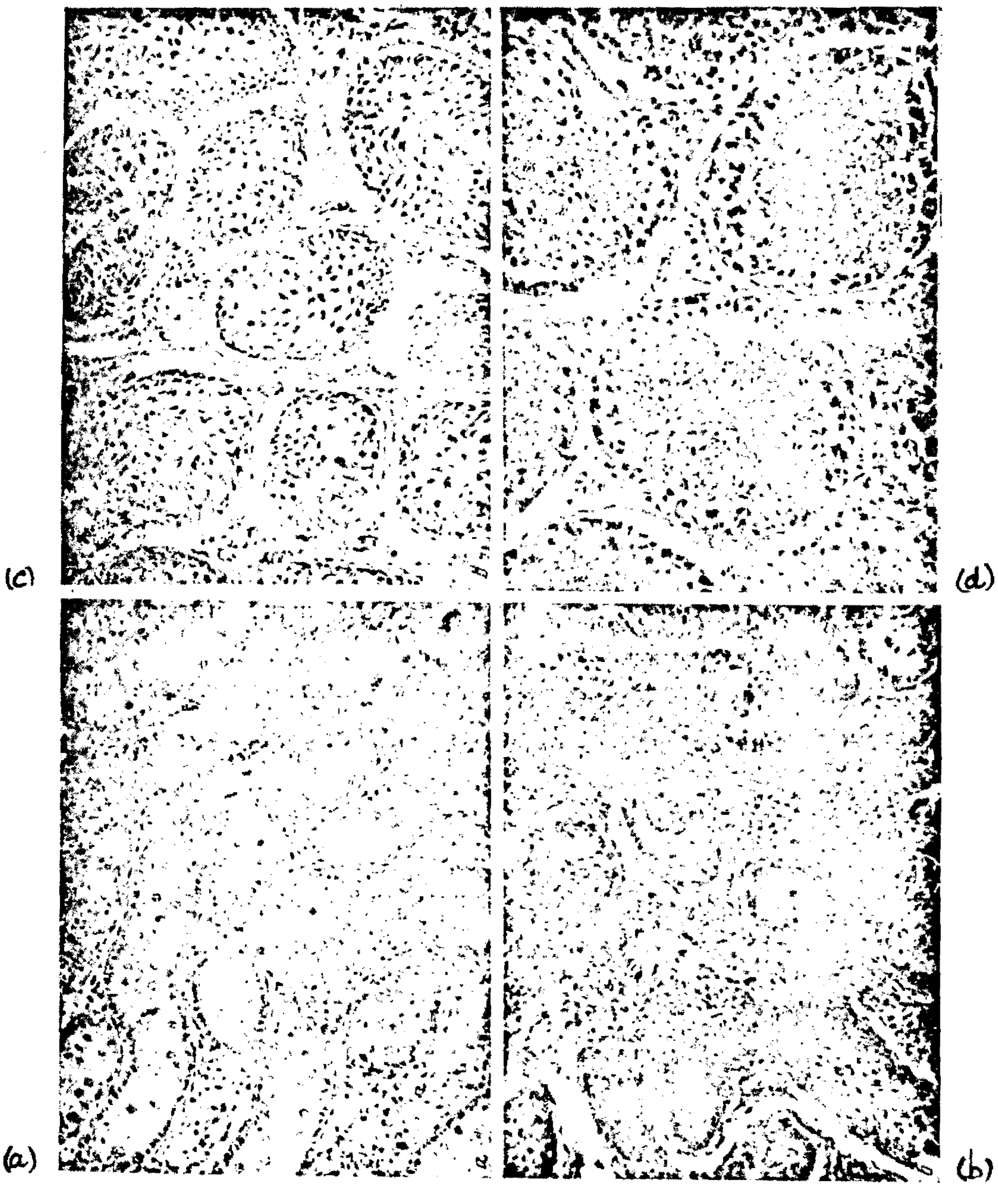


FIGURE 3: Cross sections of the testes of polecats showing the stages of spermatogenesis; (a) November; (b) December; (c) February; (d) March.

and spermatogonia, the second layer of primary spermatocytes, and the third layer of secondary spermatocytes and spermatids. At this time the next phase development begins (Figure 3(c)); the average diameter of the seminal tubules increases to 136μ, and those of the epididymis to 79μ. In a few cases, spermatozoa appear in February, but this occurs comparatively seldom, and therefore we refer this month to the period of passive spermatogenesis.

The second period (active spermatogenesis) also consists of two stages: (1) the formation of spermatids into mature gametes and (2) the intensive production of spermatozoa. This period is characterised by the active production and development of spermatids, and their transformation into mature spermatozoa. All cell types, from Sertoli cells and spermatogonia to mature spermatozoa (which are stored in the lumen of the tubules (Fig. 3(d)), are present in the seminal tubules. The testicles reach their maximum weight (Figure 2). The average diameter of the ducts in March is 210μ, and in April, 226μ: the diameter of the tubules of the epididymis is 203μ and 243μ respectively.

The third period includes the consecutive stages of regression of the germinal epithelium and a brief rest phase. It is characterised by the gradual fading of spermatogenesis and the degeneration of the embryonic epithelium down to a single layer of spermatogonia and Sertoli cells.

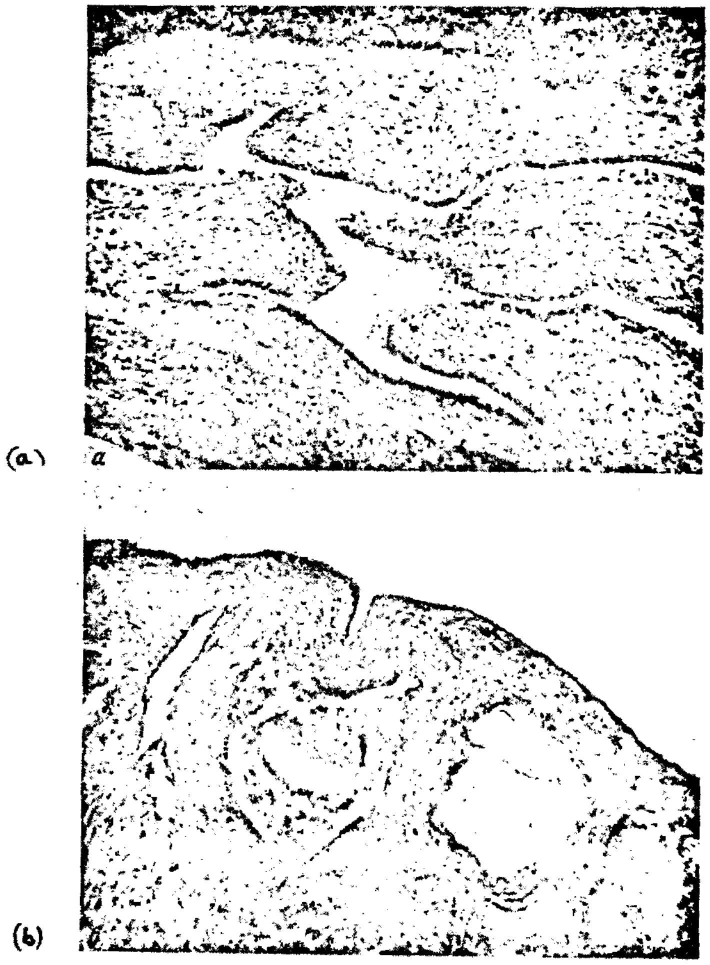


FIGURE 4: Cross sections of(a) the uterus of the polecat, and (b) the ovary, showing atretic follicles, in December.

From the above description it is evident that the peak of spermatogenesis in polecats is observed in March and April. At this time the females have mature follicles in their ovaries and are receptive to mating. The gonads of the females become active in February. Proliferation takes place quickly and in the North-Western districts most polecats are in oestrus in March-April, and in the Moscow district, at the beginning of May (Lavrov, 1935). Tikhvinski (1935), who studied polecats almost on the southern boundary of their distribution, is of the opinion that they are on heat in March and April. Other researchers agree (Ognev, 1931; Strogonov, 1949, Novikov, 1956, 1963).

According to our data the fertile season of the male polecat is longer than that of the female. While the latter are in oestrus mainly over the 2 months of March and April, the male polecats are fertile until June, and probably, in some individuals until July. The female genitalia obtained in December and January showed no signs of activity: they were in a state of metoestrum, characterised by an anaemic uterus (Figure 4(a)) and various stages of atresia of the follicles (Figure 4(b)).

Pregnancy lasts 40-43 days (Lavrov, 1935, and other authors). In the North-West the litters are born in May-June. The size of the litter (sample of 203 sightings) varies from 1 to 12 young (Table 5), usually between 3 and 8.

The eyes of the young open after 25-30 days. They grow fairly rapidly (Table 6) and at the age of 1½-2 months are able to leave the nest and follow their mother. Though they reach almost the size of an adult polecat by the time they are 7 months old, their development is not yet complete (Table 7).

This information was obtained from well-fed animals in captivity. Polecats in their natural habitat are much smaller. For instance, in the commercially exploited areas the yearlings (at the age of 7-9 months) often weigh only 250-400 g, but in captivity the weight at this age is 1250 g. Wild-caught young have never been recorded at this weight. However adult male polecats in the Leningrad district sometimes weigh up to 1400 g.

The young stay together for a comparatively long time. The last sightings of a group of several animals were recorded on 15, 17, 30 of October. However, often the litters begin to disperse at the beginning of September.

Usually the sex ratio is biased towards males. In Karelia, 56% of 34 polecats, and in Leningrad, Novgorod and Pskov provinces, 59.5% of 215 polecats sighted, were males.[1] The polecat population consists mainly of young of the year (52%); however, the presence of a considerable number of older animals (48%) is proof of an obvious under-harvesting of the polecat.

Parasites

The polecats in Karelia are infested with five types of helminth (Shahmatova, 1964). The following species are the most frequently found: *Skrjabingylus nasicola* (80%), *Capillaria putorii* (55%), *Molineus patens* (30%), *Filaroides martis* (30%). *Taenia taenicolis* appears to be a specific helminth of polecats. Up to 90% of the polecats of Karelia are infested by one or other species of helminth. In the southern districts, according to our data, the incidence of *Filaroides* (Table 8) was 91.5% (noticeably higher than in Karelia), but *Skrjabingylus* was detected in 70.3% of animals, that is, slightly less than in the Karelian ASSR.

The effects of these parasites on the polecat population have not been determined, and to date no mass mortality of polecats has been observed, nor any drastic reduction in numbers, due to helminth infestation.

---

[1] The original is not clear whether "sightings" refers to animals seen alive, or in fur warehouses or traps. The bias in the sex ratio could therefore be either in the population or in the catch—Ed.

TABLE 5: Frequency distribution of litter sizes of polecats in North-Western districts of the USSR (data from several different winters)

Number of young in the litter	1	2	3	4	5	6	7	8	9	10	11	12
Number of litters observed	1	8	16	25	32	37	30	22	16	8	4	4
	0.5	3.9	7.9	12.3	15.8	18.2	14.8	10.8	7.9	3.9	2.0	2.0

TABLE 6: Growth of the young of the black polecat

Age	Weight (g)	Body length (cm)	Author
New-born young	5	-	Siivonen, 1956
14-21 days	110	17.0	Lavrov, 1935
30 days	150	-	Siivonen, 1956
30-50 days	150	21.5	Lavrov, 1935
2 months	400	-	Siivonen, 1956
7 months	710	-	Our data
Adult	930	-	" "

TABLE 7: Changes with age of some characteristics of male polecats

Age	Head and body length (cm)	Condylobasal length (mm)	Zygomatic width (mm)	Baculum	
				Length (mm)	Weight (mg)
12 months	37.2	59.8	37.4	37.6	370
19 months	40.3	65.0	49.2	41.5	465
Over 3 years	41.5	67.5	41.8	43.1	520

TABLE 8: Infection of polecats with *Filaroides* and *Skrjabingylus* in the districts of Leningrad, Pskov and Novgorod (1960-1965)

Parasite	No. of polecats examined	No. of infected polecats		Intensity of infection[1]		
		No.	%	Min.	Max.	Mean
Filaroides	35	32	91.5	1	6	3.3
Skrjabingylus	37	26	70.3	1	58	14.1

[1] Intensity of infection with *Filaroides* = number of affected areas [of tissue?]: intensity of infection with *Skrjabingylus* = number of helminths per skull—Author

SUMMARY

The northern boundary of the distribution of polecats in Karelia at present runs along the Lendery - Rugozera - Nadvoitsy line. In 1966-1967 the density of polecats was 0.44 animals per 1000 hectares in the Karelian ASSR, 0.88 in the Leningrad district, 3.44 in the Novgorod district and 1.57 in the Pskov district. Rodents and frogs are the principals foods, comprising 78.5-82.3% and 7.1-55.5% of the diet respectively. In winter these animals were eaten less, and carrion more. Under favourable conditions sexual maturity is attained at the age of 10-11 months; otherwise, it is delayed to the age of 22-23 months. The sex ratio is biased towards males (56.0-59.5%), and young animals of both sexes exceed the adults in numbers (52% as against 48%). The infection of polecats by filaroidea and *Skrjabingylus* attains 91.5% and 70.3% respectively.

BIBLIOGRAPHY

Heptner, V. G., Naumov, N. P., Yurgenson, P. B., Sludski, A. A. Chirkova, A. F., Bannikov, A. G. (1967): The mammals of the Soviet Union. 2 (1): 1-1004, Izd-vo Vysshaya shkola, M.

Grigoryev, N. D. and Teplov, V. P. (1939): Results of research into the diet of fur animals in the Volga-Kama region. Tr. O-va estestvoispyt. pri Kazansk. un-te, 56 (1-2): 101-195, Kazan.

Danilov, P. I. (1965): When do polecat males become sexually mature? Tezisy dokl. nauchn. konf. In-ta biol. Petrozavodsk. un-ta: 35-37.

Zharkov, I. V. and Teplov, V. P. (1958): A guideline for the quantitative census of game animals on large areas: 3-25, M.

Ivanov, F. V. (1968): The numbers and hunting of the polecat in the Ryazan province. In a collection of articles: Nauchnotekhn. inform. Vses. n.-i. in-ta zhivotn. syrya i pushniny 22: 22-30, Kirov.

Isakov, Yu. A. (1939): Materials on the mammalian fauna of central and northern Karelia. Byull. Mosk. o-va Ispyt. Prir. Otd. Biol. 18 (2-3): 37-50.

Kessler, K. F. (1868): Materials for the knowledge of the Onega lake in the Onega region, in particular, with regard to zoology. Appendix to Tr. I syezda russkikh estestvoispytatelei [Transactions of the 1st conference of Russian natural scientists]; 1-145, St. Petersbourg.

Lavrov, N. P. (1935): Biology of the European polecat (*Putorius putorius*), Byull. Mosk. o-va Ispyt. Prirody, Otd. Biol. 44 (7-8): 362-372.

Lyalin, A. F. (1932): The polecat and its hunting. Zhizn i znanye: 3-70.

Marvin, M. Ya. (1959): The mammals of Karelia: 3-273, Izd-vo Karelsk. ASSR, Petrozavodsk.

Novikov, G. A. (1956): The carnivorous mammals of the USSR fauna: 3-293, Izd-vo AN SSSR, M.-L.

Ognev, S. I. (1931): The animals of eastern Europe and northern Asia 2: 666-683, M.-L.

Orlova, S. A. (1948): Migration of some game animals to the north of the Karelian-Finnish SSR. Izv. Karelo-Finsk. N.-i. bazy AN SSSR 1: 109-111. Izd-vo Karelo-Finskoi bazy, Petrozavodsk.

Parovshchikov, V. Ya. (1959): Changes in the areas of distribution, and new data on the distribution limits of some mammals of the northern European part of the USSR. In a collection of articles: Geografiya naseleniya nazemnykh zhivotnykh i metody ee izucheniya: 217-226. Izd-vo AN SSSR, M.

Rusakov, O. S. (1961): The polecat. Okhota i okhotn. kh-vo 3: 22-24.

Rusakov, O. S. (1963): Some data on the diet of the European polecat in the Leningrad, Pskov and Novgorod provinces. In a collection of articles: Promyslovaya fauna i okhotnichye khozyaistvo Severo-Zapad RSFSR 2: 195-199, L.

Stroganov, S. U. (1949): The identification of Karelian mammals: 5-198. Izd-vo Karelo-Finsk., Petrozavodsk.

Tikhvinski, V. I. (1937): The polecat, the ermine, and the marten.: 3-132, M.-L.

Shakhmatova, V. I. (1964): Helminths in Karelian Mustelidae and the development cycle of *Taenia intermedia* Rudolfi. Abstract of BSc dissertation. Moscow.

Yurgenson, P. B. (1932): Polecats: 3-32, Izd-vo Vneshtorgizdat, M.-L.

Bissonnette, T. H. (1932): Modification of mammalian sexual cycles. Reactions of ferrets (*Putorius vulgaris*) of both sexes to electric light added after dark in November and December. Proc. Roy. Soc., B: 110. London

Hammond, J. (1951): Control by light of reproduction in ferrets and mink. Nature 167 : 4239.

Hanzl, R. (1958): Raubwild und Raubzeug [Wild and predatory animals], Prague.

Harvey, N. E. and Macfarlane, W. V. (1958): The effect of daylight on the coat-shedding cycles, body weight and reproduction of the ferret. Austral. Biol. Sci.: 11.

Kalela, O. (1961): Nisäkäitten leviamisnopeutta Koskevia viimeaikaisia kokemuksia, Fenia 85 [Recent experiments on reproduction in mammals]

Krohn, P. Z. and Zuckerman, S. (1952): Reproduction. Ann. Rev. Physiol. 15.

Marshall, F.H.A. (1956): Physiology of reproduction 2. London.

Siiwonen, L. (1956): Suuri nisäkäskirja [The large mammal book], Helsinki.

RELATIONS BETWEEN THE MARTEN (*MARTES MARTES*), SABLE (*MARTES ZIBELLINA*), AND KIDAS (*M. MARTES x M. ZIBELLINA*) AS PREDATORS, AND THE SQUIRREL (*SCIURUS VULGARIS*) AS A PREY

by

Yu. P. Yazan (USSR)

[From: Trans. Int. Congr. Game Biol. 9: 530-38, Moscow 1970]

An interest in the "predator-prey" problem as exemplified by the marten, sable and squirrel began to develop a comparatively long time ago (Rayevsky, 1947; Nasimovich, 1948; Yurgenson, 1954, and others). It reached its peak, however, after the publication of two articles in the journal "Okhota i okhotnichye khozyaistvo" [Hunting and Game Economy], which blamed martens for a reduction in the numbers of squirrels everywhere (Kuznetsov, 1958; "The problem of the decrease in the numbers of squirrels", editorial article, 1959). Very soon these statements were supported by new facts, which in one way or another were taken to prove the detrimental influence of martens on the state of squirrel populations (Ivanter, 1961; Tsetsevinsky, 1962; Semionov, 1963, and others). Sentence was passed on the sable by Lavov (1967) on the basis of material collected on Sakhalin.

In the following years and at present, an overwhelming majority of experts working on this problem insists on the rehabilitation of martens and sables, which have been unjustly blamed for the extermination of squirrels (Gribova, 1958; Chashchin, 1958; Timofeyev, 1962; Monakhov and Baranovsky, 1967; Voilochnikov, 1967; Bakeyev and Bakeyev, 1967; Grakov, 1967, 1967a).

Our research (Yazan, 1962, 1962a, 1962b, 1966) which is based on extensive collections of material, does not leave any room for doubt that, in the Northern Ural, the marten and the sable are not the cause of the drastic reduction in numbers of squirrels, although, during some years, particularly when small rodents are scarce, these predators eat a considerable number of squirrels (Table 1).

The material in Table 1 indicates that squirrels occupy only the third place (19.7%) in the winter diet of martens, but in summer, when one might think it would be much easier to catch a young squirrel, they occupy one of the lowest places (3.8%).

The marten is a very agile animal. The squirrel's "experience" is not important to a marten. On occasions it catches an adult squirrel just as easily as a young one. Hunters have known this for a long time; they have also known that the bases of the marten's diet are the small rodents. In our study areas the marten eats them both in summer (40.3%) and in winter (39.1%).

In years with a good "harvest" of small rodents in the forest, the marten is at its plumpest, and its twenty-four-hours' [hunting] range is reduced to a minimum. On the contrary, in years when the rodent harvest is poor, the marten is less fat, hunts further each day, and often takes its day's rest on an empty stomach. During the 1954-1955 hunting season, for example, when in the winter diet of martens the number of small rodents (23.9%) and insectivores (5.9%) had noticeably decreased, the number of martens with empty stomachs reached its maximum at 13% (67 and 10 specimens)[1].

If the marten's diet is analysed year by year, with special reference to such prey as small rodents, squirrels, and birds of the *Tetraonidae* family, one quickly notices a very interesting regularity (Figure 1). If there is a lack of one or two of these food species, the martens turn to other types of food which are available close by.

---

[1] According to Table 1, the proportion of empty stomachs should be 15%, or 12% if the summer specimens are included—Ed.

TABLE 1: Summer and winter diets of the marten in the Pechora-Ilych reserve (as percentages of items found in all scats

TABLE 1: Summer and winter diets of the marten in the Pechora-Ilych reserve (as percentages of items found in all scats and guts with contents)

	1950-1951		1951-1952		1952-53		1953-1954		1954-1955		1955-1956		1958-1959		Average	
	winter	summer	winter	summer	winter	summer	winter	summer	winter	summer	winter	summer	winter	summer	winter	summer
Insectivores	21.2	22.3	30.7	15.0	1.4	0	0	0	5.9	0	2.6	0	15.0	-	11.0	6.2
Small rodents	17.5	24.0	45.3	22.0	26.3	48.0	28.0	69.0	23.9	27.0	59.0	42.0	40.0	-	39.0	40.3
Squirrels	20.0	2.3	20.0	18.0	18.8	0	20.0	0	41.7	3.0	5.1	0	12.5	-	19.7	3.8
Tetraonidae	41.2	7.4	34.6	8.0	13.0	5.0	28.0	8.0	21.0	0	20.5	0	15.0	-	24.8	4.1
Other birds	6.3	8.0	12.0	7.0	8.7	10.0	17.4	8.0	7.5	0	12.8	0	40.0	-	14.8	5.5
Other animal foods	22.0	29.9	6.7	11.0	7.2	17.0	6.7	7.0	1.5	10.0	7.7	42.0	10.0	-	8.7	19.5
Eggs	11.2	0	6.7	7.0	1.4	0	8.0	0	9.0	3.0	2.6	0	7.5	-	6.6	1.7
Carrion	4.0	0	10.7	0	1.4	0	2.7	0	9.0	0	5.1	0	10.0	-	6.1	0
Pine nuts	17.5	4.0	0	4.0	8.7	5.0	18.6	8.0	4.5	3.0	35.9	0	2.5	-	12.5	6.0
Berries	11.2	2.8	0	30.4	15.0	0	5.9	54.0	18.8	0	0	16.0	0	-	9.4	17.2
Number of guts and scats examined	80	109	75	17	69	16	75	9	67	15	39	6	40	-	455	171
Number of empty guts	10	-	7	-	6	-	4	-	10	-	3	-	2	-	42	-

The marten is not satisfied with only one species of prey, for example, squirrels, as is still unfortunately being assumed by some game economy workers. The marten feeds on any kind of food, and is not particularly fastidious. It mainly consumes whatever food is most abundant at the time and which is most available, i.e., the marten acts as a typical euryphage. This is clearly illustrated by the analysis of the marten's diet during the years when pine-nuts are either absent (Table 2) or abundant in forests (Table 3).

The fact that the marten feeds on squirrels is undeniable, but the extent of this pressure on the squirrel populations may be understood only on the basis of the following rough calculation. It takes 2-4 days for a marten to consume a squirrel. We repeatedly satisfied ourselves of this fact by following martens' tracks over many days. During the whole snowy period, which lasts for 6 months, a marten would therefore consume a maximum of 90 (i.e., 0.5 x 180) animals if it fed exclusively on squirrels. According to our calculations, however, squirrels make up an average of only 19.7% of the diet (Table 1). Thus, a marten consumes not 90 but only 18 squirrels during the snowy period, plus 3 more squirrels during the snowless period; the total is no more than 21 squirrels throughout the year. It should also be taken into account that these 21 squirrels include a considerable number which were already dead. Thus martens fulfill the functions of "sanitation workers" in the taiga. In February and March 1955 we found badly emaciated frozen rodents in 3 (13.3%) out of 37 squirrels' dreys which we examined. In December 1959 in the hollow of a dead tree (when it was sawn up for fire-wood) a dead squirrel was discovered, which was also emaciated and, apparently frozen to death. Martens had failed to find these squirrels and had not eaten them, and the question is: how many of such dead animals had been found and eaten by martens, and what is the percentage of dead squirrels among all the squirrels eaten by martens?

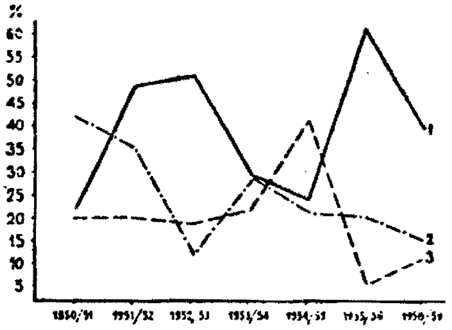


FIGURE 1: Annual variation in the diet of marten

1: Voles; 2: Tetraonidae; 3: Squirrels

And here is another case of a marten having consumed a dead squirrel. In December 1963 I obtained a marten whose stomach contained roughly half a squirrel. The marten had found the squirrel in a hollow of a tree round which there had been squirrel tracks over a radius of 300 metres for at least a week. We concluded from this that the marten had eaten either a dead or a sick squirrel, which had not been able to move about for a long period of time.

The fact should be also taken into account that the average weight of the stomach contents of a marten whose maximum weight is 105 g[1] does not

---

[1] This must be a misprint for 1050 g, the maximum weight for male martens in Russia recorded by Heptner *et al*. (1967)—Ed.

TABLE 2: Diet of martens in years of poor production of pine-nuts in forests

Food	% occurrence in the total guts examined		% occurrence in the number of guts with contents	
	Adults	Young of the year	Adults	Young of the year
Moles	0.0	4.8	0.0	6.6
Shrews	7.8	4.8	11.1	6.6
Small rodents	28.5	23.8	33.4	33.3
Squirrels	7.8	9.5	11.1	13.4
Wood lemmings	3.9	0.0	5.6	0.0
Hares	0.0	4.8	0.0	6.6
Capercailzies	9.8	4.8	13.9	6.6
Black grouse [?][1]	2.0	0.0	2.8	0.0
Partridges	2.0	9.5	2.8	13.4
Woodpeckers	3.9	0.0	5.6	0.0
Siberian jays	3.9	0.0	5.6	0.0
Dippers	2.0	4.8	2.8	6.6
Small birds	13.7	14.3	19.5	20.0
Frogs	2.0	4.8	2.8	6.6
Eggs	3.9	4.8	5.6	6.6
Pine nuts	2.0	0.0	2.8	0.0
Berries	0.0	0.0	0.0	0.0
Wasps	0.0	4.8	0.0	6.6
Carrion	7.8	4.8	11.1	6.6
Number of empty guts	-	-	2.0	0.0
No. with one type of food	-	-	69.4	60.0
No. with two types of food	-	-	19.4	40.0
No. with three types of food	-	-	11.2	0.0
Average weight of gut contents, g	-	-	20.9	23.0
Maximum weight of gut contents	-	-	105.0	71.0
Number of guts examined	51	21	36	15

---

[1] Author

TABLE 3: Diet of martens in years of good production of pine-nuts in forests

Food	% occurrence in the total guts examined		% occurrence in the number of guts with contents	
	Adults	Young of the year	Adults	Young of the year
Shrews	0.0	5.4	0.0	9.6
Small rodents	24.5	21.6	34.2	38.0
Squirrels	4.1	0.0	5.7	0.0
Wood lemmings	0.0	2.7	0.0	4.8
Water voles	0.0	2.7	0.0	4.8
Capercailzies	0.0	2.7	0.0	4.8
Willow grouse	0.0	2.7	0.0	4.8
Woodpeckers	2.0	0.0	2.9	0.0
Nutcrackers[1]	2.0	0.0	2.9	0.0
Small birds	8.2	2.7	11.5	4.8
Frogs	2.0	0.0	2.9	0.0
Pine-nuts	49.1	40.8	68.8	71.2
Berries	6.1	10.8	8.5	19.0
Carrion	2.0	8.1	2.9	14.0
Number of empty guts	-	-	3.0	2.0
No. with one type of food	-	-	46.8	9.5
No. with two types of food	-	-	49.9	57.2
No. with three types of food	-	-	3.3	33.3
Average weight of gut contents, g	-	-	23.7	15.4
Maximum weight of gut contents, g	-	-	68.5	33.5
Number of guts examined	49	37	35	23

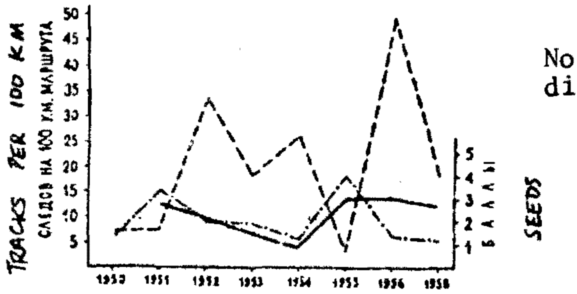
---

[1] *Nucifraga caryocatactes*—Ed.

exceed 30 g and that about 10% of all guts of martens when examined proved to be empty altogether. Consequently, the marten [often] goes partly or completely without food, and apparently consumes fewer squirrels throughout the year than we had calculated, perhaps 3-4 times less, i.e., not more than 5-7, and possibly even less than that.

Is this much or little? Of course, if these figures are multiplied by thousands of martens, the result will be impressive (Grakov, 1967). But, as applied to a whole region [the impact of martens on squirrels] is negligible, even if our figures were greatly increased. Thus, for example, the Troitsko-Pechorsk region of the Komi Autonomous Soviet Socialist Republic occupies an area of about 6 million hectares. According to the data of the game economy management (K. I. Keyukov) the numbers of martens in the region after the hunting season during the period from 1955 to 1966 were 2500, 580, 630, 1200, 1500, 2100, 1600, 1000, 800, and 660 respectively. The following numbers of martens were bagged in the same region during the same years: 965, 806, 874, 937, 790, 926, 825, 649, 774, 585, and 693. Even if one accounts for the fact that the martens bagged, just like those which had remained alive, [would have] consumed squirrels throughout the year, the damage to the squirrel populations caused by martens cannot exceed (7 x 3465) 24 255 specimens. And this figure is for a region the size of a considerable province.

The cause of the decrease in the numbers of squirrels in forests should be sought elsewhere. Let us direct our attention to the following diagram (Figure 2). It shows that the fluctuations in the numbers of squirrels do not depend, for all practical purposes (the connection has not been proved) on the numbers of martens; they depend however on the production of conifer seeds in the previous year.



Note: Author did not distinguish curves—Ed.

FIGURE 2: The effect of the conifer seed harvest and marten numbers on fluctations in the number of squirrels

1 - number of squirrel tracks per 100 km; 2 - number of marten tracks per 100 km; 3 - harvest of conifer seeds, on a five-point scale (1 point in 1950).

According to many reports received from hunter-correspondents, the conifer seed harvest in the Pechora taiga has on average been poor during the past few years (1, 2 and 3 points). There is also direct evidence of changes in the qualitative composition of tree stands. Huge areas of felling and forest fires, which have been accumulating during the past decades, have regenerated and changed the age composition of the stands, and in doing so have reduced the annual yield of seeds which are the basic food for squirrels.

Much of the dispute by zoologists as to "whose fault it is" has been solved by the paper by Reimers (1966). The qualitative changes in the taiga, which have been caused by the activities of man, lead, according to him, to a temporary replacement of coniferous trees by broad-leaved ones. The whole point however is that this process results not only in a reduction in the overall harvest of conifer seeds, but also in a considerable reduction in the numbers of rodents in the taiga. This last-mentioned circumstance certainly has a negative effect on the numbers of squirrels, because when there is a lack of small rodents, the martens and sables supplement [their diet] with other kinds of food including squirrels. According to our material, however, even when the numbers of small rodents are reduced, the martens do not cause any substantial losses in squirrel populations. But, in our opinion, a prolonged failure of crops and a reduction in the overall volume of the seed-producing conifers, due to man's transformation of the taiga, are the paramount causes of the problem in question.

In connection with the possible negative effect of the most recent manmade factors (pollution of the atmosphere, waters and soils by industrial waste, an increase in background radiation etc.) it is possible that changes have occurred for the worse and this also adversely affects the numbers of squirrels.

The squirrel is a very fecund animal. According to a picturesque popular saying, each female squirrel is "not alone but the fortieth in the lot" by the beginning of the hunting season. Consequently, in favourable conditions the squirrel is capable of restoring its numbers despite a certain pressure exercised by predators.

In the 1961-1962 season, for example, with very high numbers of martens present, the quota for half-finished squirrel furs was exceeded by 400%. This was completely unexpected by the officials in charge of procurements who knew that the squirrel numbers had previously been depressed. But two consecutive good years for spruce, pine and Siberian pine nuts, which preceded this rapid growth in the squirrel numbers, provided abundant nutrition for the female squirrels. They had become plump by the beginning of the breeding season and it did not take long for the result to appear despite the continuing effect of the pressure exercised by predators.

It follows from all that has been said that the marten, although it has a certain effect on the prey population, which increases when the prey are at low density, is not a limiting factor causing a reduction in the quantity of squirrels within any given area.

Let us now consider whether there is a difference in the diet of martens of different ages and sex (Table 4). First of all, it is evident that the marten eats a highly diversified range of foods of animal and vegetable origin, and the younger the marten is the greater variety of foods it utilizes. The list of foods eaten by the older marten sharply tapers off (this is particularly characteristic of females) and is mainly restricted to squirrels, pine nuts, and, to a lesser extent, Tetraonidae and other birds; and, in males, also to a group entitled "other food". There is almost no difference in the nutrition of males and females in the first two age classes of martens, and it is considerable only in the "other food" group. Apparently, the young female martens are more active than the males, but in older age groups, on the contrary, the males are more active than the females.

The ratio of empty stomachs found in the martens of all four age groups is generally constant overall and also in each sex and age group, i.e., 15-33% of the total number of guts studied. This is also true of the average and the maximum weights of the stomach contents only (without the gut).

The number of food types per stomach decreases in both the males and females of older age groups. In any case, we did not find [more than] three types of food in any one gut. This is because there is a very pronounced selective ability, or specialization, of individual martens for a particular type of food. Here is an example. In March 1959 we tracked a large marten for two days. It went mainly through the edges of overmature pine forests, i.e., the places where capercailzies usually spend the night in the snow. The marten scented capercailzies six times and, cautiously sneaking up, threw itself upon the birds which were under the snow. The presence of many old tracks of varying ages in the same places suggested the idea that the animal had used this method of hunting for a longish period of time, and not always unsuccessfully.

Unfortunately, we have fewer data available on the nutrition of the sable and the kidas than on that of the marten. We were therefore unable to examine the differences between all four age groups as had been done for martens, and had to limit ourselves to the analysis of the diet of only two age groups - the young of the year and the mature animals (Table 5).

By contrast with the marten, the young sable and kidases have a smaller range of food than the mature animals. The basic foods for sables at this age are: small rodents, Tetraonidae, pine-nuts and the "other food" group, in particular, frogs and toads; i.e., in their diet the most abundant and accessible foods are prevalent.

It is an interesting fact that neither the young sables nor kidases feed on squirrels, and in kidases even the adult animals do not eat squirrels. This is apparently a matter not only of the skill of the predators but also of an established habit of hunting.

TABLE 4

F

Insecti
Small r
Squirre
Tetraon
Other b
Bird eg
Carrion
Other a
Pine nu
Berries
Number
with
Number
Number
ing o
Number
types
Number
three
Average
stoma
Maximum
stoma

TABLE 4: Diet of martens (number of items as per cent of the number of guts examined) by sex and age

Food	Age of martens (years)							
	0		1		2		3	
	females	males	females	males	females	males	females	males
Insectivores	7.6	12.2	13.7	3.1	0	3.1	0	1.8
Small rodents	48.3	45.0	40.9	43.7	72.8	55.4	66.7	44.5
Squirrels	19.8	15.8	9.1	21.9	9.1	12.5	33.3	16.7
Tetraonidae	15.9	31.7	13.7	18.2	27.3	16.7	0	22.2
Other birds	7.6	14.6	27.4	15.6	27.3	12.5	0	0
Bird eggs	7.6	4.9	9.1	3.1	0	0	0	0
Carrion	5.5	8.9	4.5	9.3	0	0	0	0
Other animal food	46.9	4.9	18.2	9.3	0	21.8	0	11.1
Pine nuts	23.7	17.8	22.7	28.1	18.2	45.2	33.3	27.7
Berries	7.3	15.8	4.5	3.1	0	0	0	0
Number of guts with contents	110	84	22	32	11	36	3	18
Number of empty guts	23	33	6	5	2	5	0	6
Number of guts containing one type of food	56	50	11	20	6	23	2	11
Number containing two types of food	45	25	8	9	3	10	1	7
Number containing three types of food	9	9	3	3	2	3	0	0
Average weight of stomach contents	21.9	19.2	18.1	22.5	18.3	24.1	8.0	23.1
Maximum weight of stomach contents	91.0	87.0	65.0	81.0	59.0	69.3	24.0	103.5

TABLE 5: Diet of the sable and the kidas (number of items as per cent of the number of guts examined) by sex and age

Food	Sable				Kidas			
	Young of the year		Adults		Young of the year		Adults	
	F	M	F	M	F	M	F	M
Insectivores	0	0	0	10.0	0	0	0	0
Small rodents	66.7	50.0	33.3	10.0	100	100	33.3	20.0
Squirrels	0	0	16.7	30.0	0	0	0	0
Tetraonidae	33.5	50.0	33.3	40.0	0	0	0	20.0
Other birds	0	0	16.7	0	0	0	33.3	20.0
Bird eggs	0	0	0	10.0	0	0	0	0
Carrion	0	0	0	20.0	0	0	66.7	0
Other animal food	0	0	0	0	33.3	50.0	0	20.0
Pine nuts	0	50.0	50.0	30.0	0	50.0	33.0	40.0
Berries	33.3	0	0	0	0	0	0	20.0
Number of guts with contents	3	2	6	10	3	2	3	5
Number of empty guts	1	1	0	0	0	0	0	0
Number of guts containing one type of food	2	1	4	6	2	2	2	4
Number containing two types of food	1	1	1	3	1	2	0	0
Number containing three types of food	0	0	1	1	0	0	1	1
Average weight of stomach contents	5.5	22.5	24.9	17.5	20.0	30.0	10.6	60.1
Maximum weight of stomach contents	12.0	67.9	57.0	59.0	60.0	84.3	26.0	87.0

The adult sables eat a considerable quantity of squirrels (16.7% are consumed by females and 30.0% by males). As from the second year of life, there is almost no difference in diet between them and the adult martens. As they eat a smaller number of small rodents, the sables compensate by eating more Tetraonidae. But almost no Tetraonidae are found in the food of the kidas. According to our data the latter animal causes the least damage to game animals.

SUMMARY

The author has examined about 650 guts and more than 200 scats of marten, sable and kidas co-existing in the North Urals. As a result, he has revealed the main features of the winter and spring-summer feeding of the animals.

The marten feeds mainly on forest rodents, shrews, moles, tetraonids, small birds, and squirrels. When there are many rodents in the area, the marten feeds mainly on them; otherwise, it gets other types of food available at the time, including the squirrel. In years especially unfavourable for voles the frequency of observation of squirrels in the stomachs of martens increases to 50%; in other years it ranges from 0 to 20%. In the summer, this index does not usually exceed 10%. We must add that some squirrels eaten by predators were already dead (those which had already died of starvation or freezing).

The younger the marten, the greater the variety of food used by it. Quantities of squirrels, eaten by young and adult martens of both sexes, are approximately the same.

In contrast with the marten, the diversity of food of young sables and kidases is lower than that of the adult animals. The main components of the food of young sables are rodents, tetraonids, pine-nuts, and berries; those of kidases are rodents, pine-nuts, and amphibians. In the diet of both sables and kidases, the most easily available and abundant foods prevail.

Neither young sables nor kidases feed on squirrels. This prey is absent even in the diet of adult kidases. It can be accounted for by not only insufficient skill in the predators, but by their established habits of hunting.

Adult sables eat a considerable number of squirrels (females—26.7%, males—30%). After their second year their diet hardly differs from that of the adult martens. Sables eat fewer rodents, but more tetraonids. Kidases do not eat tetraonids at all. According to our data (though they are not numerous), this animal causes the least damage to game.

On the whole, the marten, sable, and kidas, despite the abovementioned differences, feed on the same species, having no competition among themselves. To a certain extent they affect the numbers of prey, e.g., squirrels especially when they are at low density. However, neither the marten, nor the sable, or especially the kidas, has a limiting influence over the numbers of squirrels in the habitats they share.

(Ed's Note: Bibliographies were not provided in the published volume from which this article was taken.)

INTRASPECIFIC RELATIONS [TERRITORIALITY] IN SABLE AND ERMINE

by

P. P. Tarasov

[From: Byull. Mosk. O-va Isp. Prir., Otd. Biol. 64(6): 37-43, 1959]

(Report delivered to a conference of the Zoology section,
14 February 1957)

The purpose of this report is to describe intraspecific relationships in carnivorous animals, their variation with ecological conditions, and their practical and evolutionary significance. For this purpose we examined two hunted species, the sable and ermine.

Territory in the Sable

This species is typical of the taiga, particularly the mountainous taiga; it prefers cedar forests and scattered stands of trees. Its basic diet consists of rodents, in particular the bank vole; it also hunts birds, and in summer a few insects. At all times of the year it readily eats berries and pine nuts.

The sable will catch any rodents which it meets by chance, and occasionally it hunts especially for mice, under piles of fallen trunks or in the bushes of the dwarf Siberian pine. It has excellent hearing, as is shown by its ears, which are prominent in comparison with those of other *Mustelidae*. It easily identifies hidden voles by their rustling in the snow. It has a fine sense of smell, which enables it to find nuts through a thick layer of snow when they have been hidden since autumn by a nutcracker or a squirrel, and also berries or cones which fell in autumn.

A difficult period in the annual life cycle is winter, which in the mountains brings a heavy snow cover and severe frosts. The sable's basic foods, voles and nuts, are hardly obtainable at this time; they are hidden by deep snow up to a metre and more, and so also are the berries. Birds are also scarce at this time.

Successful survival of individuals at this time of year depends on the dimensions of their hunting areas. It is quite obvious that the fewer individuals there are using the same piece of ground, the more productive will be the hunting on it. It is entirely natural that because of this there should arise, as in most other predatory animals, competition for territories and the necessity to defend them.

The sable does not tolerate invasions of its territory by competitors, irrespective of whether they are members of its own species or of another. The kolinsky, for example, is chased by the sable with such success that where the sable appears, the kolinsky as a rule disappears. The sable persistently chases even the ermine, although with less success, as the ermine is so small that the sable cannot pursue it into its burrow.

The sable does not tolerate invasions of its hunting territory by another sable. Anyone is convinced of this who has followed these animals for a long time by means of their winter tracks, and has observed not only the long and persistent pursuit of one sable by another, but has also seen the traces of fights, in the form of "stamped down areas" with drops of blood and scraps of fur left on the snow. Similar habits of the sable have been described repeatedly by many authors (Rayevski, 1947; Timofeyev, 1948; Abramov, 1952, and others).

The quarrelsome disposition of sables is well known also from keeping them in captivity, and this is incidentally one of the reasons why the actual rutting period was unknown for so long (it has been risky to put sables together for an extended period, as the animals quite often tear each other to pieces).

The quarrelsome disposition of sables and their exclusive individual territories also explain the failure of some management practices, such as the attempt to establish a high concentration of sables in hunting reserves.

For example, in the Barguzin reserve, over one and a half decades (1922 to 1936) there was no success in increasing significantly the number of sables in the protected area. On the other hand, during this time all the land adjacent to the reserve, where the sable was already completely exterminated in pre-Revolutionary times, proved to be inhabited by sables, and moreover at a population density scarcely less than that in the reserve. It has become clear that, as a result of the intense competition for territory, the entire population increase has moved out of the reserve. The same phenomenon has also been noted in other reserves, particularly the Kondo-Sosva (Rayevski, 1947).

A curious picture, explicable in terms of the practice of hunting, is revealed in the geographic centres of sparsely hunted sable grounds. It is mainly the old individuals of decreased fertility, as hunting experts believe, that stay in such places; the young animals invariably are forced out to the periphery, closer to the populated areas, where they are mostly caught by hunters. In this way, the most productive part of the population is shot while the "senescent" individuals remain untouched and die natural deaths (Abramov, 1946; Timofeyev, 1951).

Thus, both field observations and hunting experience bear witness to the severity of competition for territory among sables. This conflict requires the expenditure of a vast quantity of energy and undoubtedly entails additional mortality.

It is not by chance that, when the stomach contents of sables are analysed, claws of sables are found among the half-digested food.[1] On examining nearly a hundred stomachs, I came across this phenomenon twice. Similar records have been reported in the literature (Kalabukhov *et al.*, 1931).

By analogy with other species which compete for territory, for example the beaver, musk-rat, Russian desman, and other animals which mark out their own territories, sables may be expected to have special adaptations permitting moderation of intraspecific conflict. These indeed exist, and consist of the sable's habits of leaving markers or signs to show that a given territory is occupied.

In sables, the primary territory markers are the droppings [scats], which the sable habitually leaves in any conspicuous place. Just as dogs and wolves leave their "signatures" at "information points" which are visible from afar (a pole, the trunk of a solitary tree), the sable deposits a scat on any raised object, such as the stump of a felled tree, a snow-covered mound, etc. It is interesting that the sable tests the need[2] for leaving signs of its sojourn in such places as a fresh ski-track, a kulyemka (sable trap) lightly covered with snow, a barn for produce, etc. Sable droppings can nearly always be found on a tree fallen across a stream, which sables often use as a bridge. It is most advantageous to leave a scat on these "bridges", as it is precisely there that it will be noticed by another individual. It is not by chance that dogs, for example, most frequently leave their "signatures" close to bridges.

The sable's habit of leaving scats in places where they may soon be found by another individual is also shown by its explicit preference for marking forest tracks, which is especially noticeable in summertime when the sable

---

[1] Commonly observed in mustelids caught in leg-hold traps, where they may chew at their own feet in an attempt to escape—Ed.

[2] Meaning unclear. Probably "... the sable is stimulated to leave signs..."—Ed.

uses them more often. My attention was drawn to this while working in the Barguzin reserve. According to the data of Rayevski (1947), along a two-kilometre stretch of forest track in July he found as many as 28 sable scats, which incidentally greatly simplified the problem of studying the diet of this species. A case observed jointly by me and the now deceased Timofeyev in the Barguzin reserve is not without interest. Checking the sable's reaction to "unusual objects", we placed piles of freshly chopped firewood within known sable territories, and also scattered ashes over several sections of the ski-tracks in the snow. In both cases the [resident] sable reacted to the new objects and, turning towards them, deposited a scat there. From the small size of the scat it could be judged that the beast did not have a natural urge to defecate [then] and emptied its bowels solely in order to deposit, in a prominent place, a material sign of its presence.

We point out that analogous habits - territory-marking by means of scats - are also characteristic of other animals, for example badgers, whose droppings are constantly found on their tracks. The same thing occurs in musk-deer, flying squirrels, and alpine species of voles (with the last, the droppings form large accumulations in certain places). Outside its own sanctuary the sable, as a rule, behaves differently (in movements, use of tracks and nests), and does not set its scats in conspicuous places.

While depositing a scat as proof of its residence, the sable often carries out a peculiar "ritual", apparently distinctive to and characteristic only of sables. In this ritual the sable, after the act of defecation, then leaves a so-called "drag-mark" - a track about a metre long where it has dragged its belly - which is quite visible in the snow. Sometimes the sable, coming across a ski-track, does not have the ability to leave a material sign, and limits itself to just a "drag-mark". These original habits of the sable are to be observed particularly often as spring approaches during the so-called "false rut", from which originates the well-known hunters' expression that the sable begins to be "tortured by the flesh" (Solovyev and Belousov, 1920).

The sable's habit of leaving a "drag-mark" has been reported in the literature, notably by such an authority on the sable as Rayevski (1947). Rayevski wrote of this habit: "In speaking of the sable's habit of rubbing itself in the snow, it must be kept in mind that it also rubs itself against objects such as branches and stumps which are sticking out from under the snow. The traces of this are most often found in the latter half of winter, although I have also seen such signs in autumn". Disputing the sexual basis of these habits and their connection with the phenomena of the pseudo-rut, Rayevski explained them as a means of getting rid of sticky snow adhering to the animal.

Originally, on noticing these habits of the sable [from tracking] in the Barguzin reserve, I did not attach any significance to the drag-mark and ascribed it to the urge to defecate. Later however, when I was able to observe the animals themselves (in the Chikhoi district of the Chita oblast), I noticed that on the sable's abdomen, i.e., that part with which the animal rubs itself in the snow and leaves its drag-mark, there is a distinctly marked special structure. It is in the shape of a tumour or fatty formation, lying in two parts in front of a thickening of skin, and slightly to the sides of the sexual orifice, and covered with short, thick, whitish hairs smeared with an oily secretion.

I have come to the conclusion that this formation is none other than a gland which is used, like the musk glands of the musk-rat or beaver, for marking occupied territory (Sludski, 1948; Tarasov, 1958). This gland, which is clearly evident when the skin is removed, and which hinders the scraping of it, is reminiscent of the shape of the wishbone of poultry, and itself consists of two shafts joined in front, each of which is about 4 cm long and 0.5 cm in thickness. In old males the gland is noticeably larger than in the young. It is also present in the females, in which, however, it appears under-developed. From October to January the dimensions of the glands do not change, from which it may be concluded that they function all the year round and have no direct connection with the reproductive cycle.

Judging from the dimensions of the glands described, it may be concluded that the function of defending occupied territory rests mainly on the males. It is therefore probable that the males always possess a larger hunting area than the females and always leave far longer trails in the snow.

Apparently it is not at all by chance that, on an autumn sable hunt with an Eskimo dog, one is far more likely to catch a male than a female. Of 27 sables caught by me in recent years in the Chikoi taiga (southern Trans-Baikal), 19, that is 70%, were males. A similar picture was revealed by other hunters working with dogs, whom I questioned.

Fairness demands a mention of the fact that these data refer only to the first half of the hunting season and to hunting with dogs (November-December). However, the same conclusions are reached if one takes into account the entire hunting season and different methods of capture. Thus, according to the data of Timofeyev (Timofeyev and Nadeyev, 1955), of 2494 sables caught at different times of the year by different methods, males composed 57.4% and females 42.6%.

Thus, disregarding the well-known equalisation of numbers of males and females in the capture process (which must inevitably occur in proportion to the number of males in the catch), all of these data illustrate the well-known predominance of males over females in the catch. Meanwhile the true ratio of the sexes among sables in the wild is approximately equal, and moreover females are even slightly more numerous (50.8%), as has been shown from an examination of this problem on sable farms (Zaleker, 1952).

Such a selective catching of the population, predominantly of males, is doubtless advantageous for a shorter period of reproduction, which once again underlines the practical significance of an intimate knowledge of intra-specific relationships.

The following observations illustrate the intense intra-specific competition for territory among sables, and the consequent existence of many transient animals searching for territories[1].

In December 1950 I set out with one of the local inhabitants on a sable hunt in a part of the taiga which had been well hunted since autumn. My guide assured me that, in the vicinity of the winter quarters where we planned to hunt, there were already no sables left, as they had all been killed off, and an artel of experienced sable hunters had recently returned from there after catching 6 sables in the vicinity of the winter quarters. Moreover, my guide was among those hunters. The immediately following days however, gave evidence of something different. During 15 days of hunting, to the great surprise of my guide, we caught another 4 sables there. Apparently, as a result of competition for territory, new sables had managed to settle this area in the 10-15 days before our arrival.

This story was precisely repeated in 1953, when we again found ourselves in the same spot, also after the local hunters had completely hunted it out. About two weeks after the hunters had left there, we caught there on the very first day two sables, and this was within a radius of no more than two kilometres of the winter quarters.

These observations confirm the existence among sables of animals searching for a territory, which rapidly fill up any "vacuum" which develops. They also explain the relatively rapid colonisation of territories adjacent to the reserves, and the extremely high productivity of these sable lands.

There is another conclusion of practical importance, arising out of observation of the biological peculiarities of the sable. For some time there have been great hopes of intensifying the stocking rate of the many hunting grounds in Siberia, using the so-called pre-hunting luring of sables by means of the construction of special sheds provided with meat and other lures. It

---

[1] The original refers vaguely to a "high 'population pressure'"—Ed.

was assumed that it is possible to lure a large number of sables (as many as ten) to each shed.

In autumn of 1953, in the Chikoi taiga, I filled 9 sheds with horse meat. I continued to observe them from October to December and, to my surprise, no more than one sable was lured to each individual shed.

I suppose that no other result could be expected in years of normal feeding conditions. [Hence, improving the catch] is hindered by intraspecific aggression among sables, due to their habit of defending individual territories.

Territory in the Ermine

This is a predator which usually catches its prey in their refuges. Such a method of hunting allows the ermine to obtain food in the most diverse conditions - from the tundra to the desert and from the plain to the greatest heights of the Tien Shan.

The basic foods of the ermine are the small rodents (Muridae), which are susceptible to large fluctuations in numbers. Often there are years when the number of Muridae falls to a low level, causing a tight spot in the life of the ermine. In years when the number of Muridae is depressed, the dimensions of the hunting area acquire a critical importance for the ermine, as for the sable. Therefore this animal, living for the most part in conditions where food is abundant, has similar [territorial] habits to the sable.

My observations illustrate well how ermines behave towards one another. I shall present them in the form of an almost full quotation from my diary.

"The ermine was caught alive and released in our living quarters. It quickly became accustomed to its new surroundings and soon ceased paying attention to people. After a day another ermine, larger in size, was released in the quarters; almost at once, without attempting to hide in a dark corner, it began to run around the room. Without noticing anything, the first animal also climbed behind boxes and under beds. Here they met, or more precisely caught sight of each other at a distance of 3 m, after which they stood still as though each of them was suddenly faced with great danger. They paid no attention to the people observing them. A minute passed, then quite unexpectedly one began chasing the other. It was impossible to make out which of the animals caused this. The ermines ran around the room, darting among the furniture and knocking over objects on the tables. When the larger animal had almost outrun the smaller, the latter managed to dart under a fold in the bedclothes, while the pursuing animal missed its mark and found itself above it. Puzzled by the sudden disappearance of its intended prey, the larger ermine began to fuss about, but feeling the other animal beneath it, it began to attempt to force its head through the bedclothes.

"The ermine in hiding, sensing that its attempts to save itself through flight were futile, squealed in despair, and we isolated the new animal."

After this "scene" it became completely understandable to us why, in the larder where game was stored and where hunting ermines were captured throughout the winter, there was not a single case of these animals appearing simultaneously, even as a pair. Over a full three years of observations, during which time more than 20 ermines were caught in the larder, it usually turned out that, after the capture of one animal, the larder was empty for some time, and then a new animal appeared and was also caught as soon as it was noticed.

However, occasionally during my absence no-one would catch any ermine. It might be expected that a certain concentration of ermines would arise during this time. However this did not occur. It was obvious that, where one ermine was already established, another could not settle. These observations demonstrate the presence among ermines of strict competition for territory and the possession by each individual of an individual territory.

The details of what methods are used by an individual to warn of its occupancy of a plot are not well known to me; however, according to available evidence on this subject, the same characteristic methods are used by the ermine as by the sable. Concerning this, Nasimovich (1948) writes: "With great regularity the ermine visits rocks and mounds where it has previously urinated or left droppings. By cautiously pushing aside the snow, it is possible to find here a whole series of ermine droppings at once. Most of them clearly belong to one and the same animal." The author does not explain these methods, but their meaning becomes clear in the light of what was said about the sable.

The strong-smelling anal glands in the ermine are also apparently [to be] regarded as organs which have the function of leaving "boundary marks" in appointed places.

The [previously] accepted opinion that the [function of the] anal glands of the Mustelidae is for protection from predators (Novikov, 1956) is, in our view, in need of revision. It is well known that these glands do not protect from dogs, for example, either the ermine or the kolinsky, even though in the latter the anal glands are exceptionally well developed. The anal glands do not protect the small carnivores from foxes or wolves either, as may be judged by the diet of the latter two, nor from sables, not to speak of birds of prey with their extremely weak sense of smell, for which a defensive smell can clearly have no significance whatsoever.

It is more difficult still to explain the origin of these glands, if the explanation is based on their protective function. The glands must have been fairly well developed before becoming organs of protection from enemies, as only in that case could they have any selective advantage.

Reproduction in Sable & Ermine

Comparing the sable and the ermine, we see that these two different species use methods which are generally similar. Both face the same problems of catching widely dispersed prey, which are of particularly great importance in wintertime. Judging by the numbers, the sable prefers mountainous areas; the ermine lives everywhere, but its home territory is ultimately in the north. Thus, both species live in conditions of prolonged snow cover, which makes the search for food difficult.

However, the similarities in the ecology of sable and ermine are not limited to the problems of obtaining food and the similar nature of their intraspecific relationships which arise from that. Both species possess, as is well known, a similar reproductive cycle, and have such remarkable adaptations as delayed implantation.

There is some reason to suppose that [another] common characteristic of both species, apart from delayed implanation, is the participation of the males in the rearing of the litter. For the ermine this may be regarded as proven. The presence of the male with the litter has been recorded simultaneously by observers (Bekshtrem, 1931; Grigoryev, 1938; Nasimovich, 1948). I happened to make a similar observation in Mongolia, where in July, while searching for colonies of Brandt's vole, a whole family of ermines, consisting of five half-grown animals, a full-grown male, and a female were caught in the course of a day and night.

With regard to the sable, there are far fewer similar observations in natural conditions, for reasons connected with the difficulty of access to the habitats of the sable in spring and summer and of observing them at this time. However, with all the antagonism characteristic of sables in general, males and females live more sociably. Their individual territories are usually adjacent, and overlap more often than those of individuals of the same sex. Rayevski (1947) refers to incidents of friendly mutual visits to dens by sables of the opposite sex.

Timofeyev (1955) cites reports of hunters who have observed that in the summer the male stays close to the female's litter and helps her with the feeding of the kits. An encounter with a male sable with a litter is described by Manteifel (1934).

Some interesting observations on the bahaviour of male and female sables kept together in captivity are cited by Dulkeit (1929). In March and at the beginning of April he kept sables in adjacent cages, which had communication between each other. Concerning this he observed the following: "... when the male attempted to enter the female's box, the latter prevented this, baring her teeth. Then, after several unsuccessful attempts, the male changed tactics and became accustomed to entering the female's den backwards. After this the male was repeatedly observed to spend prolonged periods in the female's den, although in general they preferred to live apart. It was curious that, when food was distributed, the male repeatedly carried into the female's box not only his own portion of meat, but also a portion intended for the female".

In these observations attention is paid to the male's method of entering the female's den as mentioned by the author (backing in). This method could scarcely be a result of the male's quick-wittedness. Rather these are innate habits, developed through natural selection as a result of the normal aggressiveness of sables.

Timofeyev (1955) reports that "the manifestation of the paternal instinct in several males in captivity was shown when, having picked up a piece of food, they began to run along the bars of the cage next door, in which was a female with a litter".

The facts cited compel us to propose that, as with other carnivores, for example polar foxes, sables and ermines in springtime look after their own females, so as to share with them the care of their offspring. Similar habits among polar foxes have been described in graphic detail by M. M. Prishvin. Perhaps the so-called false rut among sables, which had hitherto been interpreted in different ways (such as "excitement of the males caused by hormones in the urine of the females", as a "compensatory rut", as a re-distribution of hunting territories etc.), is also included with this.

Considering the problem of participation by the males in the feeding of the litter, it must be kept in mind that, as distinct from birds, this phenomenon among mammals is generally less widespread, and is apparently found only among carnivores, particularly the Canidae (wolf, fox, polar fox). With reference to Mustelidae, apart from the ermine and sable, the care of the offspring by the males is also recorded in the Siberian polecat (Sludski, 1955).

The care of the offspring is apparently connected with the fact that the individual territories of male sables and ermines are noticeable larger than those of the females, sometimes by 3 or 4 times, which obviously exceeds the requirements of one individual. Apart from that, the possibility cannot be ruled out that the males defend not only their own territories, but also those of the females. An indication of this is the numerical predominance in trapping of the males, which are more mobile; this is observed to a greater extent among sables, but is also well-known in the ermine. For example, according to the report of Nasimovich (1948), out of a group of 107 ermine carcases obtained by him from hunters in the Murmansk oblast in the winter of 1938/39, only seven were females and the remainder were males.

In this connection, the fact that the duty of guarding an individual territory rests on the male makes it possible to explain in a different way the larger size of the males in comparison with the females. Male sables weigh half again as much as their females, while male ermines are almost double the weight of their females.

Usually sexual dimorphism is regarded as a result of sexual selection (the advantage of the strong over the weak during rut), which is observed in polygamous animals (fur seals, deer), but polygamy could not arise among sables and ermines which live far apart[1]. Therefore the true reason for the larger size of the males of these species originates above all from competition, not for females, but for territory.

That this is evidently so is proved by the reversed sexual dimorphism in birds of prey, where the males, as is well known, are noticeably smaller than the females, for example the hawks and large falcons, among which competition for territory is very strongly pronounced. If superiority in sheer physical strength is necessary for males of ground-dwelling animals to defend their territories, for male birds of prey it is superior manoeuvrability in the air which is the most important consideration. It is not by chance that the female sparrow-hawk is almost twice the weight of the male.

Summing up what has been stated, we are entitled to draw the conclusion that there exists in nature not only the fact itself of intraspecific competition, with the ensuing struggle for individual territories, but also special habits and even organs which originate from this competition, in particular the various types of scent glands.

The development of these organs and the corresponding behaviour mitigates the severity of intraspecific competition and is an important means of escaping unfavourable effects of over-population. Consequently, over-population in nature is the same sort of continuously acting factor as many others, otherwise it would be difficult to imagine development of organs aimed at its elimination.

Charles Darwin once showed that, as a result of the struggle of males for females (for the right to beget offspring) in various groups of animals, such organs developed as horns in ungulates, tusks in elephants, canine teeth in wild boars and the walrus, spurs on the legs and wings of many birds, etc.

Severtsov (1951) shows that, in the process of evolution of such organs as horns in the ungulates, a process of diminution of their lethal nature and a consequent transformation of them into relatively harmless "tournament weapons" is observed.

It must be borne in mind that the presence of organs of attack also engenders a [means of] defence. Such are the powerful armour formed from special connective tissue on the flanks of the wild boar ("scales"), the mane of the lion, the breast shield formed from plumage in roosters, and the thickened skin on the necks of oxen, deer and antelope.

This shows beyond any doubt that intraspecific relationships have in many cases a formative evolutionary significance.

CONCLUSIONS

1. The shortage of food which is noticeable in winter-time, and especially in years of low abundance of prey, limits the number of carnivores in a given area of habitat. This causes competition within the species for feeding territories, and hence the development of adaptations for the marking of occupied territories.

2. In the ermine, marking of occupied territory is accomplished by means of a secretion of the anal glands, imparting a persistent odour to the scats. In the sable the function of the scent glands is carried out by a special glandular formation, situated alongside the sexual orifice.

3. The presence of adaptations which mitigate the severity of intraspecific competition for territory does not completely relieve the animals from territorial defence. This function in the ermine and sable is carried out by the males, which leads to an increase in their body size in comparison with the females.

---

[1] See comments by Kopein (1965), this volume—Ed.

4. Both sable and marten face similar ecological problems (e.g., in obtaining food), and hence they show similarities in competitive relationships, in sharply marked sexual dimorphism, and in the biology of reproduction. Delayed implantation, the males' search for the females in spring, and their participation in the feeding of the litter, are common to both species.

5. The presence of scent glands and sexual dimorphism in body size in the species examined proves the evolutionary role of intra-specific competition.

6. The existence of intra-specific competition and the great pressure for disposal of young animals associated with it also has benefits for the practical activities of man. Dispersal rapidly replaces animals removed from hunting areas, and allows swift re-colonisation of districts which are being hunted-out.

SUMMARY

On the basis of his own orignal investigations, and earlier published data, the author discusses the intraspecific relationships of the sable and ermine.

Both species are solitary and aggressive toward con-specifics, and both defend and mark their territories by means of special scent glands. The function of defending the territory is carried out by the male. The stronger individual survives and prevails over the rest in the struggle for territories hence, larger individuals are selected, i.e., those in which sexual dimorphism in body size is most pronounced.

BIBLIOGRAPHY

Abramov, K. G. (1952): The biology and ecology of the Far Eastern sables. Soobshch. Dalnevost fil. AN SSSR [Reports of the Far Eastern branch of the Academy of Sciences of the USSR] No. 4

Bekshtrem, E. A. (1931): Biology of the ermine. Prir. i sots. khoz-vo [Nature and Socialist Economy], No. 9-10.

Grigoriev, N. D. (1938): Reproductive biology of the ermine. Zool. Zhurn. 17 (5).

Darwin, C. The descent of man, and selection in relation to sex. Works, vol. 5. (1953 edition).

Dulkeit, G. D. (1929): On the biology of the sable, and sable farming on Bolshoi Shantar island. Izv. Tikhookeansk. naychno-promysl. st., [Transactions of the Pacific Scientific and fur-trading station] 3 (3).

Zaleker, V. L. (1952): Fertility of sables in nature. Karakulevodstvo i zverovodstvo [Sheep and animal breeding for furs], No. 3.

Kalabukhov, N. I., Folitarek, S. S., and Cheptsova, A. Ya. (1931): Materials on the nutrition of the sable. Izd-vo "Sov. Aziya".

Manteifel, P. A. (1934): The sable. KOIZ [All-Union Cooperative Joint Publishing House].

Nasimovich, A. A. (1948): Outline of the ecology of the ermine in the Lapland reserve. Tr. Laplandsk. gos. zapovedn. [Transactions of the Lapland State Reserve] No. 3.

Novikov, G. A. (1956): Carnivorous mammals of the USSR fauna. M.-L.

Raevskiy, V. V. (1947): Life of the Konda-Sosva sable. M.

Severtsov, S. A. (1951): The problems of animal ecology. M.

Sludskii, A. A. (1948): The muskrat and its acclimatization in Kazakhstan. Alma-Ata.

Sludskii, A. A. *et al.* (1953): The wild animals of Kazakhstan. Alma-Ata.

Soloviev, D. K. and Belousov, V. I. (1920): The sable and sable hunting. Sayanskii promyslovo-okhotnichii raion [Sayan hunting district], Pg. [Petrograd = Leningrad].

Tarasov, P. P. (1958): Characteristics of intraspecific relations in stenotopic rodents. Tr. Sredne-Aziatskogo n.-i. protivochumn. in-ta [Transactions of the Central-Asian Anti-Plague Scientific Research Institute], vol. 5.

Timofeev, V. V. (1951): The Irkutsk.
Timofeev, V. V. (1948): Ecology of the Barguzin sable. Tr. Barguzinskogo gos. zapovedn. [Transactions of the Barguzin State Reserve] No. 1
Timofeev, V. V. and Nadeev, V. N. (1955): The sable. Zagotizd. M.

CONTROL OF MOULT AND WINTER WHITENING
IN THE ERMINE (*Mustela erminea*)

by

V. E. Gaiduk

Faculty of Biology and Chemistry,
Brest State Teachers' Training College.

[From: Zool. Zhurn. 56(8): 1226-1231, 1977.]

Material and methods

The material for this article was collected from 1964 to 1977 in Belorussia. Twenty four ermines were examined in each season of the year. One hundred and seventy eight sightings of ermines in the wild were recorded (5-24 cases in each month). From 1965 to 1968, from 4 to 8 animals were kept in captivity, in conditions of light, temperature, and humidity approaching those of nature. I also examined 1267 ermine skins in the storage sheds and the fur centre of the republic in Zaslavl; and those in the collections of the Moscow University Zoological Museum (260 specimens), the Zoological Institute of the Academy of Sciences of the USSR (150 specimens), and the Institute of Plant and Animal Ecology in Sverdlovsk (64 specimens). For the investigation of moulting, Pavlova's scale of spring and autumn moulting scores (1959) was applied.

Fur colour was determined visually. Data on the climate of Belorussia (temperature, duration of daylight, snow cover) were taken from the papers of Shklyar (1973) and Alisov (1956), the Agro-climatic Handbook (1970), the Handbook on the Climate of the USSR (7th issue, 1965), and from meteorological stations: for other regions they were taken from the Agro-climatic Atlas of the World (1972), the Physico-geographical Atlas of the World (1964), and the Handbook on the Climate of the USSR (8th, 10th, 21st, 32nd issues, 1965-1969).

Control of the moult

The moult and the growth of fur in the ermine have not been studied thoroughly. The most extensive [previous] investigations of moulting in the ermine were carried out by Pavlova (1959), who found that the timing of the moult varies in different years and in different parts of the species' range (see Table 1). The duration of the moult in one individual is from 25 to 30 days, and for the population as a whole, about 60 days.

My investigations on moulting in *Lepus variabilis*, the winter hare, and other fur-bearing animals, and also data from the literature, suggest that the amounts of temperature and light, and combinations of these, determine the calendar period of moulting and the way in which it proceeds. According to the data of many investigations, light is a "starting mechanism" for moulting in wild animals (Belyaev, 1950, and others), while temperature has an influence on the speed and duration of its progress (Rothschild,1942, and others). Experimental data show (Novikov and Blagodatskaya, 1948, and others) that by lengthening or shortening the duration of the photoperiod it is possible to shorten or increase the duration of moulting in wild animals bred on farms or kept in captivity. In other cases this effect is not observed, or the result of supplementary lighting may even be, on the contrary, to inhibit moulting (Belyaev *et al.*, 1964). Obviously, a sharp change in daylength in an experiment can definitely affect the onset of the moult in wild animals kept at a given temperature. Since the temperature and humidity usually rise or fall in accordance with the lengthening or shortening of the daylength in middle and high latitudes, and other factors vary, it is possible to cause animals to moult by manipulating daylength [alone], although in nature moult is influenced by a complex of factors. On the other hand, the experiments of Ilyin (1926a) showed that by keeping *Alopex lagopus* (the Arctic fox) for an extended period at increased temperatures, it was possible to speed up the onset of the spring moult by more than 8 seeks. The data on moulting in fur-bearing mammals and in

TABLE 1: Average dates of the beginning and end of the spring and autumn moults of the ermine in different parts of its range (after Pavlova, 1959), in relation to the average temperature range over many years at the date of moulting, and the duration of the period of stable snow cover.

Regions	Spring moult			Autumn moult			Duration of snow cover, days
	Beginning	End	Temperature range, °C	Beginning	End	Temperature range, °C	
North European USSR	Mid May	Mid June	-2 to +6	From 20 September	From 20 October	+6 to -1	160-200
European USSR: central districts	End of March	Mid April	-2 to +7	Beginning of October	Beginning of November	+7 to 0	120-160
southern districts	End of February	End of March	0 to +7	-	-	-	40-80
south-eastern districts	March	April	-1 to +8	Mid October	Mid November	+8 to 0	100-140
Taiga districts of Siberia and the Urals	April	May	-2 to +6	End of August-beginning of Sept	1st 10 days of October	+6 to -1	160-220
South-eastern Siberia	April	Beginning of May	-1 to +7	End of September	End of October	+7 to -1	160-200
Central districts of Belorussia (author's data)	Mid March	2nd half of April	-2 to +7	1st half of October	Mid November	+7.5 to 0	100-120

birds show that the autumn moult in nature proceeds faster in years with lower temperatures and, on the other hand, moulting is delayed in years with temperatures a few degrees higher than normal. This is also characteristic of the spring moult.

The early spring of 1975 provided clear confirmation of the controlling role of temperature in the progress of seasonal processes in animals (moulting, reproduction, migration of birds). It begun in Belorussia, as in other regions of Europe, 30 to 50 days earlier than usual. In the republic the average temperatures each ten day period from January to March were 3-10° higher than the average values for many years, which brought about an earlier beginning (February) of moulting in several species of wild animals, including ermines.

From field and laboratory investigations, and from observing ermines in captivity, we have constructed a graph showing the correlation between the moult (expressed as a score) and the temperature and daylength, for ermines from the central parts of Belorussia (the Berezino and Borisov districts), in seasons with temperatures approaching the long term average (Figure 1.) Moulting among ermines in Belorussia in spring in a normal year begins in the first half of March and ends in the second half of April. The peak of moulting occurs from the 3rd ten day period in March to the 1st ten day period in April. At the peak the average moulting scores were 7-3 in spring and 3-7 in autumn. Moulting is correlated with an increase in daylength from 11 hr 30 min to 14 hr 30 min, and of temperature from -2° to + 7°. The upper side of the body (back, flanks, rump, thighs, shoulders) moult when the daylength is from 12 hr 10 min to 13 hr 40 min and the temperature from 0° to +4°. In seasons colder than average by 2°-6°, moulting begins and ends 12-25 days later; and in seasons warmer than average by 3°-7°, it begins and ends 15-30 days earlier.

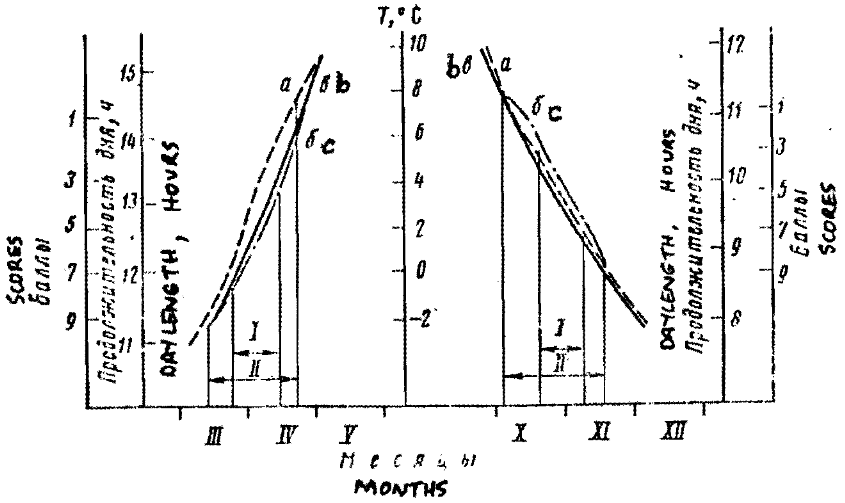


FIGURE 1: Correlation between spring and autumn moults of the ermine, and the temperature and daylength (in hours) in normal seasons in the central part of Belorussia.

a = daylength; b = moulting scores; c = temperature;
I = duration of peak of moult; II = total duration of moult.

The pattern and sequence of the moult in ermines in Belorussia are the same as in other parts of the species range. Moulting proceeds from one region of the body to the next in order . Each region moults at a certain critical range of temperatures. By plotting these temperatures on an outline of the animal's body, we obtained the temperature topography of moulting in the ermine (Figure 2, I, II). Moulting of each part of the body occurs within the limits of the temperatures shown.

In autumn in a normal year, moulting begins in the first ten day period of October and ends in the second ten day period of November. It takes place as daylength decreases from 11 hr 10 min to 8 hr 30 min, and temperature from +7.5° to 0°, with the peak between the limits 10 hr 20 min to 9 hr 0 min, and +4.7° to +1°, respectively. In years with autumns colder than average by 2°-6° or more, moulting begins and ends 10-20 or more days earlier.

It is noticeable that the temperature ranges of the spring and autumn moults, of the whole body and separate regions, are roughly the same (Fig. 2, I, II). The spring moult begins and the autumn moult ends at a temperature of -2° to 0°; the autumn moult begins and the spring moult ends at a temperature of about +7°. It is significant that, throughout the range of the species where seasonal dichromatism is usual, the spring and autumn moults proceed at ranges of temperature similar to those observed in Belorussia (Table 1). In regions with a more continental climate (Southern Siberia, Kazakhstan, etc.), the range of temperatures is greater by 2°-3°, and the duration of moulting is shorter by 5-10 days, because of an increase in the speed of progress of moulting.

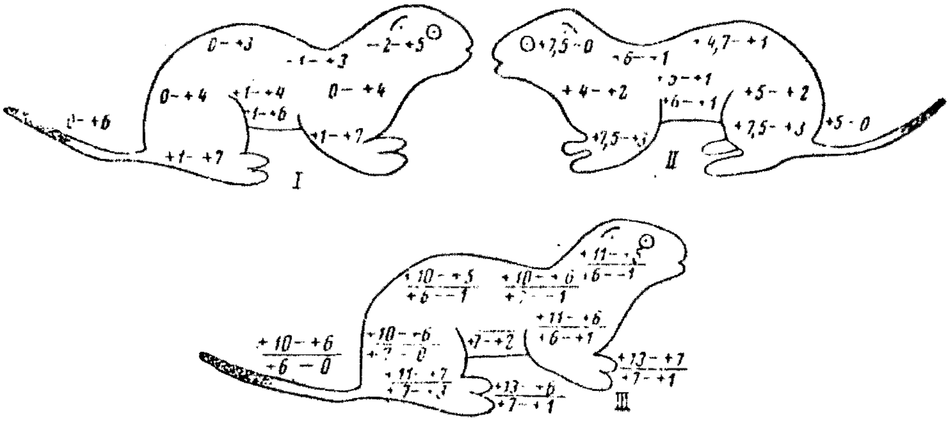


FIGURE 2: Distribution of critical temperatures for moulting on the body of the ermine from the central part of Belorussia (I = spring, II = autumn); and distribution of critical temperature ranges for growth of brown fur (numerators) or white (denominators) in autumn (III)

Moulting of the ermine in Belorussia, as in other districts in middle and high altitudes, coincides in spring with the probable disappearance of stable snow cover and in autumn with the probable falling of new snow. The time of the spring moult lags behind the time of disappearance of the stable snow cover by 15 to 25 days, while the autumn moult precedes its formation by 20 to 35 days. It should be noted that in Belorussia, a stable snow cover may fail to form once in 4 years in the south-western districts, and once in 20 years in the north.

Control of winter whitening

In middle and high latitudes, and in the mountains in lower latitudes, the ermine shows striking seasonal dimorphism in colour.

The change in colour of the fur occurs in the ermine as a result of the spring and autumn moults. Morphological and physiological processes occur in the skin during the moult, determining whether or not pigment will be formed. Hence, as the calendar period of moulting of the whole body and its separate parts is known, as are the temperature regimes at those times, the author proposes a model showing the possible range of temperatures at the time of the autumn moult; formation of pigment in the skin (and so in the fur) proceeds or does not proceed according to the temperature at the time (Fig. 2, III.). There is a definite temperature range, characteristic for each area of the animal's body, within the limits of which the formation of pigment in the skin either does (denominator) or does not (numerator) occur. Other investigations (Ilyin, 1926a, 1927; Kaufman, 1925; Schulz, 1935) have shown that the formation of pigments in the growing hairs of the Arctic hare is reduced at low temperature.

In districts with stable snow cover, ermine acquire white coats at the time when snow is likely to fall and lie; and in spring they return to brown at the time of the thawing and final disappearance of the snow cover. In districts where a stable snow cover does not form, the ermine remains brown in autumn. This flexible reaction has developed in the process of adaptation of the population to the environment, and has allowed maximum self-adaptation to the colour of the background. It comes about because of the control of temperature of pigment formation. The mechanism, genetically fixed in the process of evolution, [normally] operates in those regions where a stable snow cover is not formed, when the temperature regime in the moulting season is within normal limits. [In colder districts too,] in years when the temperature at the time of the autumn moult exceeds the upper limit for the production of a white coat, the winter fur remains brown. This also explains the phenomena observed in some years in the Fergana valley, in some regions of Europe, and in the southern and western states of the USA, where in autumn the ermine can either turn white or remain partially or fully brown. This is also characteristic of weasels. The flexible mechanism controlling colour change depends on the combination of photoperiod and temperature [prevailing at the time of the moult].

SUMMARY

From 1964 to 1975 the effect of photoperiod and temperature of the moult and hair colour of the ermine was studied. Moulting in the ermine in the central part of Belorussia in a normal spring proceeds when the daylength is between 11 hr 30 min and 14 hr 30 min, with the peak from 12 hr 10 min to 13 hr 40 min; in a normal autumn it proceeds when daylength decreases from 11 hr 10 min to 8 hr 30 min, with the peak between 10 hr 20 min and 9 hr. In the parts of its range where the ermine shows a striking seasonal dimorphism in colour, moulting occurs primarily within the following temperature limits: in spring between -2° and +7°, with a peak from 0 to +4°; in autumn between +7.5° and 0°, with the peak between +4° and +1°. Each part of the ermine's body moults at a critical range of temperatures. A model is suggested showing the temperature thresholds for the summer-brown areas in the skin of the ermine, which in autumn are associated with the growth of brown or of white hair. In regions where stable snow cover lies for less than 40 days or not at all, ermines do not turn white in winter.

BIBLIOGRAPHY

Agroclimatic World Atlas, 1972: 3-120, Gidrometeoizdat, Moscow - Leningrad.

Agroclimatic Handbook, 1970: 3-248. Izd-vo [Publishing House] "Urozhai", Minsk.

Alisov, B. P. (1956): Climate of the USSR. 5-127. Moscow University Publishing House, Moscow.

Belyaev, D. K. (1950): The function of light in the control of biological rhythms of mammals. Zh. obshch. biol. [Journal of General Biology] 11(1): 39-51

Belyaev, D. K., Utkin, L.G., Kulikov, B.A. (1964): The effect of lighting conditions on the development of the hair cover in minks (*Mustela vison* Schr.). Izv. Sibirsk. otd. AN SSSR [Proceedings of the Siberian Branch of the Academy of Sciences of the USSR] 4(1): 91-100.

Ilyin, N. A. (1926): Research into the effect of temperature on the pigmentation of varying hares. Tr. labor. eksper. biol. Mosk. zooparka [Transactions of the laboratory of experimental biology of the Moscow Zoo] 1: 128-180.

Ilyin, N. A. (1926a): Seasonal dimorphism in the colouring of the white fox. Ibid, 2: 239.

Ilyin, N. A. (1927): Analysis of the formation of pigment at low temperatures. Ibid, 3: 182-200.

Novikov, B. G., Blagodatskaya, G. I. (1948): The development mechanism of seasonal protective colouring. Dokl. AN SSSR 61(3): 577-580 [Transactions of the Academy of Sciences of the USSR].

Pavlova, E. A. (1959): Seasonal changes in the hair cover and moulting periods in the stoat. Tr. Vses. n.-i. inst. zhivotn. syrya i pushniny [Transactions of the All-Union Scientific Research Institute of animal raw materials and pelts] 18: 147-173, Moscow.

Handbook of the USSR climate, 1965-1969. 7, 8, 10, 21, 32. Gidrometeoizdat, Leningrad.

Physico-geographical World Atlas, 1964. Izd-vo AN SSSR i Gl. Upr. geodez. i kartograf. GGK SSSR [Publishing House of the Academy of Sciences of the USSR and the Main Office of Geodetic Survey and Cartography of the State Geodetic Committee of the USSR], Moscow.

Shklyar, A. Kh. (1973): The climatic resources of Belorussia and their utilization in agriculture, pp 8-430, Izd-vo [Publishing House] "Vysshaya shkola", Minsk.

Kaufman, L. (1925): An experimental study on partial albinism in the Himalayan rabbit. Biol. Gen. 1: 7-21.

Rothschild, M. (1942): Change of pelage in the stoat *Mustela erminea* L. Nature, 149: 78. London.

Schulz, W. (1935): Melanin development through chilling up to the visual evaluation of full albinos and up to the reproduction of hidden genetic traits without crossing. 2, 3: 259-291.

THE BIOLOGY OF REPRODUCTION OF ERMINE IN YAMAL

by

K. I. Kopein

[From: Trans. Inst. Biol. Ural 38: 33-40, 1965]

Ermine reproduction has been studied by a number of researchers (Yurgenson 1932, 1933;[1] Tikhvinsky, 1937; Grigoriev, 1938; Lavrov, 1939, 1941; Klimov, 1940;[1] Aspisov and Popov, 1940;[2] Asdell, 1929; Deanesly, 1935, 1943, and many others). Marshall's thorough summary (Marshall, 1958) should also be cited here. It summarizes all the works of overseas authors up to 1958 which deal with the physiology of the reproduction of mammals, and of ermine in particular. However a number of questions concerning the sexual cycle have still not been studied adequately. There are contradictions in reports of the periods of oestrus, in the times of birth of the young, and in the duration of delayed implantation; and, with the exception of two works (Popov, 1947; Petrov, 1956[1]), the question of the age structure of the population remains virtually untouched.

In all the works mentioned above information is provided on ermine reproduction in the southern and middle latitudes, but there is practically none for the polar region. We shall attempt to fill this gap.

In our research we used ermine carcasses taken during the 1959-1960 and 1960-1961 commercial [winter] seasons, plus some taken during the summer of 1961, and a few from 1959 and 1960; there were also some ermine supplied by Professor S. S. Schvartz. Altogether we had at our disposal the carcasses of 2373 ermine, of which 285 were from 1959-1960, 2046 from 1960-1961, and 42 from the summer of 1961. 8900 pelts were also examined. All the zoological material was collected within the Yamal-Nenets National Region. To study the reproduction and growth of the animals the generally accepted method was used, in addition to vivarium observations of live ermine (21 animals). A method worked out in our laboratory by Smirnov (1959) was used to determine age.

The climatic conditions of the polar region, and of the Yamal-Nenets Region in particular, are different from the climatic conditions of the central and southern areas of the country. Throughout this Region, above-zero average monthly temperatures are recorded only from June to September. So July must be regarded as being the first month of spring (average monthly temperature in the area of Salekhard is + 1.6°), while by October winter has already arrived (-2.9°). The snow cover settles between September and the beginning of October and remains up to June in the southern part, and to July in the northern part of the region. All of this plays an important part in understanding the phenology of ermine reproduction.

Our observations show that spermatogenesis begins in March. About this time, fresh tracks of males and females begin to appear [together] on the snow. All the males obtained in this month had enlarged testes (7.5 x 5.5 mm and 0.146 g), and live semen was discovered in three. In February all 26 males examined by us had testes measuring 5.0 x 4.0 mm and weighing 0.040 g. No live semen was found in them. Subsequently males with live semen were caught throughout the summer (size of testes up to 11.0 x 9.0 mm, weight up to 0.580 g). On 11 September a male was caught which had testes measuring 9.0 x 7.0 mm and weighing 0.200 g. Unfortunately a smear analysis under the microscope was not carried out. All the males which we obtained, in which spermatogenesis was present, turned out to be adult (i.e., older than a year). Of 23 young males caught from July up to August we found none which were sexually

---

[1] Translated in King (1975)—Ed.

[2] Translated in present volume—Ed.

mature. Our observations confirmed Deanesly's conclusions (Deanesly, 1943) that male ermine do not become sexually mature until they are a year old.

An analysis of the sexual organs of male ermine showed that sexual activity continues for almost 6 months, from March to August. Our data also support the observations of Schwartz (1959), who described the breeding of the ermine in Yamal. Thus the males obtained during the trapping season, between October and February, are not fertile. In the middle latitudes the males are capable of breeding from February to July (Marshall, 1958).

The dates of birth of the young are widely spread. On 30 May we were brought a young ermine which was still blind, weighing 35.0 g, and 123.0 mm in length. Assuming that the young begin to see in 9-10 days (Novikov, 1956)[1] then the date of its birth could be calculated as 20-22 May.

On 6 June a litter of young was found consisting of 4 females (weight 60.5; 68.0; 69.0; and 71.0 g) and 2 males (weight 90.0 and 97.0 g). They were about one month old, i.e., they had been born at the beginning of May. On 8 June a litter was taken which consisted of 5 young and 1 adult (male). They were caught in traps set on the runways of water-rats. It is known that the young leave the nest at about two months of age (Klimov, 1940; Aspisov and Popov, 1940). This means that the ermine caught had been born at the end of March or the beginning of April. On the same day we received two young males (teeth completely hollow and cranial sutures not closed) weighing 164.0 and 195.0 g and about two months old. On 6 June a young male weighing 220.0 g and 241.0 mm long was caught. On 9 June we found in the hollow of an old willow a litter of ermine consisting of an adult female and 6 young (3 males 65.0-70.0 g in weight and 3 females 55.0-60.0 g in weight) about three weeks old (eyes only just opened and unable to bite through skin on a human hand) which had been born at the end of May.

The examples cited indicate that the dates of birth extend through the spring from the beginning of April to the end of May. We might add in confirmation of this that at the beginning of June three nursing adult females were caught with developed (drawn out) nipples from which milk was secreted, but without scars in the uterus.

Thus the beginning of ermine reproduction in the polar region coincides with spring only in terms of the calendar, and phenologically this period is actually the end of winter (general covering of snow, below-zero temperature). This early reproduction, regardless of continuing snowy conditions, characteristic of many mammals of the north (lemmings, voles, and polar foxes), extends the general period of reproduction.

The development of the young is rapid. At about one month, i.e., shortly after they begin to see, the young stop taking milk and go on to an all-meat diet (after 5 weeks - Marshall, 1958). The nipples of the female caught with a litter on 9 June were already somewhat dried out. At least, we did not see the young of this litter, which were kept in a vivarium, taking milk from the mother (they were about four weeks old). They were perfectly capable of eating up small eggs, live, scarcely fledged nestlings, and water rats. They had already attained the weight of their mother (90.0 g) by the end of June, and the males even outstripped her (120.0 g). In the middle of July the young males weighed from 150.0-160.0 g and the females 110.0-120.0 g, i.e., over 3/4 of the weight of adult individuals, and by the beginning of September they had almost reached adult weight. They do not reach full adult ermine size until the second year of life (Marshall, 1958).

---

[1] Translated by Israel Program for Scientific Translations, Jerusalem, 1962. Novikov took this information from Klimov (1940) (translated in King 1975); but later work has shown that young ermine do not open their eyes until 34-42 days (Müller 1970). See also the paper by Tumanov and Levin, in this volume—Ed.

The teeth are replaced quickly, in the course of about two to three weeks. One to two month-old ermine[1] have two pairs of upper canines: one pair are small milk-teeth, the other pair are large, permanent teeth. The permanent tooth is still completely hollow with an open root. All the young of the litter obtained on 6 June (weight of females from 60.0-71.0 g, weight of males from 90.0 to 97.0 g) had exactly the same set of teeth. Of five young males weighing from 115.0 to 140.0 g, three still had small milk-teeth and two had already lost them. The open root hole of the upper canine had narrowed considerably. The replacement of the milk-teeth takes place quickly, then,being completed by 1.5-2 months[2] of age.

So far we have been citing examples of spring, or to be more exact, late winter ermine reproduction. But there is information suggesting that ermine reproduction finishes not in May, but continues on into summer too. On 6 and 7 August five young males were caught with body weights of between 115.0 and 130.0 g and 206.0-210.0 mm in length, and having milk-teeth along with their permanent teeth. They were no more than 1.5 months of age, i.e., they were born at the end of June.

In addition, on 28 July and 5 August two lactating adult females were obtained, one of which even had uterine scars. As we have already observed the young stop taking milk at about one month. Hence these lactating females must have had whelps no older than one month, i.e., born at the end of June or beginning of July. It has been established that uterine scars in the female ermine disappear soon after delivery of the young. One female dissected (killed on 26 June), the mother of a litter born at the end of May, had no scars.

Our material shows, then, that in the Polar region, apart from the spring (late winter) reproduction, summer reproduction of ermine is also possible. According to our observations the usual litter contained 5-6 young (three litters observed), although 12 dark scars were discovered in one parous female.

We have no direct observations on the duration of pregnancy. It would appear from the literature (Deanesly, 1935, 1943; Marshall, 1958) that the blastocysts have a period of delay (histologically proven) lasting from 8 to 10 months. Actual gestation is 42 days. First-hand observations of ermine in captivity have indicated that pregnancy can continue for 10 months (Asdell, 1929). Young females born in spring become sexually mature very early and mate 3-4 months after birth (Marshall, 1958).

To summarise what has been said so far we can list the following observations relating to the sexual cycle of the ermine:

a) variation in the duration of the delay in implantation;

b) the presence of oestrus both in spring and in summer;

c) absence of delayed implantation in a proportion of females;

d) presence of litters in spring as well as in summer;

e) presence of two litters in a proportion of females.

These features of the reproductive cycle should be reflected by the age structure of the population. So any conclusions drawn relating to reproduction should follow a discussion on the population dynamics of ermine.

To examine population structure it is first necessary to determine the ages of animals which have entered the population. As has already been noted the age of ermine is determined from the extent of occlusion of the canine root canal, expressed as a percentage (Smirnov, 1958). The healing process

---

[1] and [2] In contrast to statements about age on the previous page, these are correct—Ed.

of occlusion occurs as follows[1]. At one and a half months the milk teeth are replaced by the permanent teeth. Up to 2-2.5 months the canines are still hollow, but at 3-3.5 months the [internal] width of the root canal is about 60.0-62.0% of the exterior width of the root. Occlusion continues after this time, but at a slower rate. When the width of the canal reaches 12-16%, a visible ring or dark layer is formed in the cement of the tooth root, which indicates that the animal is more than one year old.

It should be mentioned that the occlusion of the root canal in males and females occurs unevenly. Because the female has smaller teeth than the male, and the canal width is also correspondingly smaller, occlusion occurs much more quickly in the females; whereas in males at 4-5 months occlusion is 40.0-42.0%, in females it will be 30.0-36.0%.

As has already been mentioned, our specimens were taken over two trapping seasons and two summer seasons. Initially we shall attempt to evaluate the summer catch i.e., 19 males and 21 females. The extent of occlusion varies in the males and females from 100.0 (hollow tooth) to 6.5% (canal almost fully occluded) in females and to 13.0% in males. Three groups stand out clearly on the chart: in the first the canal is hollow or has just begun to occlude (60.0-100.0%); in the second the canal width is 31.0-41.0%, and in the third the canal width is 6.5-21.5%.

There can be no doubt that the young of the current season come into the first group. Apart from the hollow teeth, their cranial sutures are still visible. The second group is also made up of animals born during the current year. Several of them have visible cranial sutures, and the tooth canal width is 31.0-41.0%. In addition, we know the exact ages of three of the ermine from this group which were held in captivity. Thus the first and second groups consist of animals born in the current year, but born in different months, from the beginning of April to the beginning of July. So, for example, a number of the ermine obtained in August have totally hollow canine roots, whereas others obtained at the same time already have a canal width of 60.0%, i.e., a difference of 1-1.5 months. Among the animals obtained at the beginning of September there are individuals with a canal width of 32.5-36.0%, and among those caught in the middle of August there are some with a hollow canal. It is quite clear that some of them were born at the end of winter (not later than the beginning of April), and others in mid-summer (June-July).

In the third group are the animals older than a year which were obtained from June to the beginning of August (only one was caught at the beginning of September). Of 11 adults there are two individuals which could be more than two years old (canal width 6.5 and 8.0%).

Thus the summer ermine population consists of two sharply differentiated groups: those less than a year old, making up 72.5% (n = 29) and adults making up 27.5% (n = 11) where m = ± 7.05%. It is evident from this correlation that adult animals make up a significant proportion of the ermine population in summer (the months before the trapping season).

We shall examine the age structure of the ermine population in the commercial seasons 1959-1960 and 1960-1961 from October to March inclusive. A total of 2331 carcasses were collected over the two seasons, including 1635 males with an upper canine canal width between 8.5 and 52.0%, and 696 females with a canal width between 9.5 and 45.5%. There were animals of different ages in this population; they can be divided into two groups: the young up to a year old, and the adults over a year old. But while these age groups were sharply differentiated in summer, in the winter population the differences are levelled out and [become] less distinct. The reason for this is that with age

---

[1] Note that there are some discrepancies between Kopein's account of this method of age determination given here, and the one he gives in his 1967 paper translated in King (1975)—Ed.

the rate of occlusion of the tooth canal is significantly reduced. Hence it is difficult to establish a clear limit between the two age groups, since there will be overlapping from both directions.

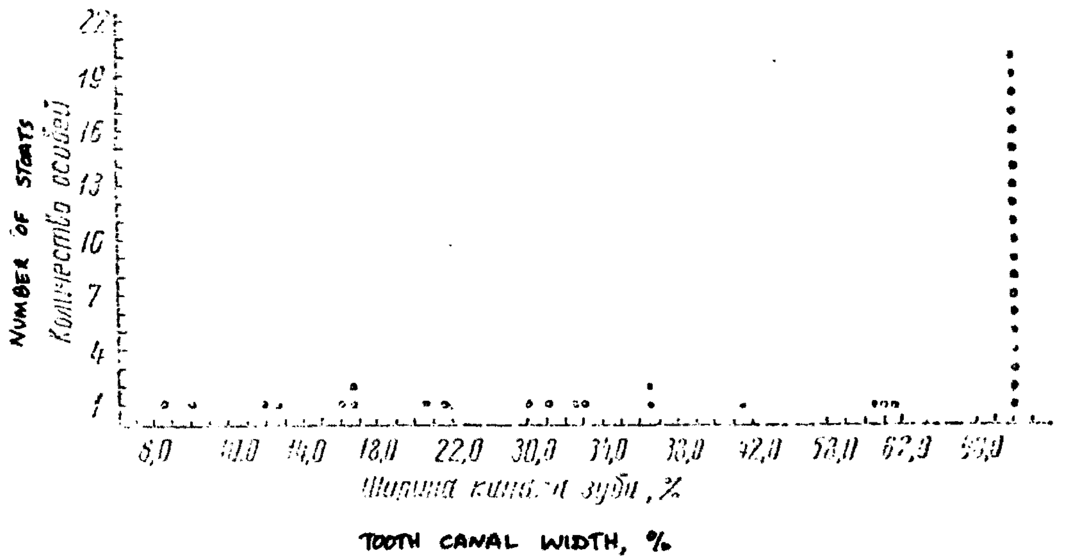


FIGURE 1: Age compositon of the ermine population sampled in summer 1961.

We shall take as a basis the distinction between the young and adult groups in the summer population. The adult group in summer has an average canal width of 15.4%, with m = ± 1.44%. This means that the average canal width can vary from 11.0 to 19.5% even with a threefold error.

Thus the boundary between the two groups in the winter ermine population will be within the same limits, though not less, since the occlusion of the canal will continue. So we can set a limit for males of 19.5%, classing all animals with a canal width of 19.5% and less as adults and those with a canal width of 20% and more as young (up to one year old). For females we take 16.5% as the limit in view of the fact that their canals occlude far more quickly.

Using this system of classification we find that in the females the young (i.e., those less than a year old) make up 95.1% (n = 662), and in the males they make up 94.1% (n = 1538); in adults these classes make up 4.9% (n = 34) and 5.9% (n = 97) respectively. The totals for both males and females are: young 94.4% (n = 2200) and adults 5.6% (n = 131), where M = ± 0.47%. The percentage of young, then varies, even with a threefold error, between 93.0 and 96.0%, and that of adults from 4.0 to 7.0% respectively. This means that the ratio of adult to young is 1:18, i.e., there are 35-36 young to each pair of adult animals.

Thus animals less than a year old make up the overwhelming majority of the winter ermine population. This becomes even more obvious when we use a conservative criterion to estimate the number of young. We shall illustrate this by an example.

As has already been pointed out above, even in the middle of summer the average canine canal width in the adult group is 15.4%. But since the occlusion of the canal continues with age, by winter the mean canal width in this group will be even smaller. In addition, the annual rings in the cement (which, along with canal width, are indicators of age, and form at the age of one year and over) were found only in animals with a canal width of 10% or less. From the mean error variation, [the average value for adults] could be down to 11.5%, and we would be just as correct to set the boundary between adult and young at around this figure rather than at 19.5%.

We did not record any substantial difference between the two commercial seasons 1959/1960 and 1960/1961 in the ratio of young to adult. The 1959/1960 winter population consisted of 3.8% (n = 11) adults and 96.2% (n = 276) young, and the 1960/1961 population 5.9% (n = 120) and 94.1% (n = 1924) respectively, although during this season there were 1.5 times more adults (t = 1.7).

We have already noted previous papers giving age ratios in ermine populations. The authors employed various methods to determine age. Popov (1947) investigated 695 ermine skulls collected over 12 seasons. Using the Stroganov method[1] to determine age (based on tooth wear), he divided the population into the following age groups: from 6 months to one year - 50.8%; 2 years -24.2%; 3 years - 15.4%; 4 years - 6.0%; 5 years - 2.6, and 6 years - 1.0%.

Petrov (1956) examined 1422 skulls collected from different places. Using his own method to determine age (33 measurements for each skull), he also made six divisions: from six months to one year - 47.0%; 2 years - 31.9%; 3 years - 16.5%; 4 years - 4.0%; 5 years - 0.5%, and 6 years - 0.1%.

As we have noted, our material showed that the winter ermine population contained 93.0-94.0% young animals under a year. Assessing the ratio of the age groups used in the works of Popov and Petrov, we observed that in both there is a sharp decrease in the number of four-year old animals in comparison with the number of three-year olds (a 250% decrease in the first sample and a 400% decrease in the second).

We are inclined to regard the groups of animals between six months and three "years" old given by Popov and Petrov as being young at the age of up to one year, and animals more than four "years" old as being adult. This is even more clearly suggested by the fact that in Popov's work the group of these animals makes up 90.4%, and in Petrov's study 95.3%. It is our opinion that if a more precise technique was available for determining the age of ermine, then the material dealt with by these authors would show that the winter (commercial) ermine population consists mainly of young animals less than a year old.

We shall now compare the samples taken in summer and winter. Our material shows that whereas in summer the adults over one year old comprise 27.5%, i.e., more than a quarter of the total, in winter this ratio drops sharply. In winter adults make up only 5.6% of the total, i.e., 1/18th of the population. The difference between the summer and winter populations is beyond question (t = 3.48).

So in winter, animals older than a year are five times less numerous than in summer. This means that for a short period (from the end of autumn to the beginning of winter) large numbers of older animals die off. Such a sharp difference in the ratio of young to old animals in the winter and summer populations cannot be put down to large-scale reproduction or output of younger animals, since reproduction in ermine is competed no later than at the end of July or the beginning of August. And even if there are occasional late litters they are not significant. (In the winter population the number of young animals with a canal width of less than 41.0-42.0%, i.e., aged about four months, is small, approximately 5-6%).

The large-scale disappearance of the older animals demonstrated here characterizes not only the ermine population, but also muskrats (Shvartz and Smirnov, 1959) and Muridae (Kopein, 1959). It would appear then, that the ermine's life span is very short, and that each year there is almost a complete renewal of the population. The average life span of individual ermines in the population investigated by us was 1.05 years, and the rate of population turnover (the time taken for 99.5% of a given generation to be replaced by its offspring) was 2.8 years (Martinson *et al*.1961). This means that only a few rare individuals can live for as long as 3 years, though it is possible to find adult animals over 2 years old (canine canal width less than 11%).

---

[1] Translation in this volume—Ed.

There is considerable dispute over the figures giving the ratio of males to females. In view of the fact that all authors use material collected principally during the commercial season, males predominate in [all] their collections of specimens. An analysis of the material available to us - 8900 ermine skins and 2350 carcasses - showed that males constituted an absolute majority (69.5%) of the winter (i.e., commercial) population. On the other hand, of 40 ermine caught in summer, 19 were males [47%] and 21 females. In two litters examined there were only 4 males and 7 females. As a result we are inclined to believe that the sex ratio at birth of ermines in the wild is 1:1, and the greater percentage of males [found] in winter is the result of a selective catch. To some extent this indicates a sex ratio in the summer population among adults of 7 females to 4 males. It is quite possible that because of intensive exploitation, which catches more males than females, polygamy is necessary to ensure the impregnation of the greatest number of females.

Our conclusions are as follows:

1. Under polar conditions ermine have two reproductive periods in a year: late winter and summer. In the June-August period an oestrus is observed in which the great majority of females less than a year old take part (reaching sexual maturity within 3-4 months after birth) along with adult males (born in the previous year). Males less than a year old reach sexual maturity and take part in breeding only in the following year.

After a delay in implantation lasting 9-10 months, these females bear the young in April and May of the following year. Then in spring oestrus occurs in the proportion of females which for some reason (insufficient supply of males, failure to reach maturity) did not participate in the summer oestrus of the previous year. They experience no delay in implantation and bear young after 6 weeks (in May and June).

The later litters recorded by us in July can be explained first of all by the possibility of a shortened period of delay in females which mated in spring (in which case the usual duration of their pregnancy is from 2-2.5 months, the same as for minks); secondly it can be explained by the presence of a second litter in females which have already produced one litter in the April-May period, the first litter having failed to survive for one reason or another.

2. The summer and winter ermine populations differ primarily in the ratio of young to adult animals. Whereas in summer the adults comprise around ¼ of the total population, in winter they make up only one sixteenth of it.

The average life span of an ermine in the wild is 1 year, and the period required for turnover of the whole population is about 3 years. The sharp decrease in the number of adults in the winter population (four to five-fold) in comparison with the summer population can be explained by the sudden disappearance of the older age groups in autumn.

3. Females less than a year old which take part in oestrus during the year in which they were born, as well as in the following year, are important in the production of ermine in the next year.

(No summary given—Ed.)

BIBLIOGRAPHY

Aspisov, D. I. and Popov, V. A. (1940): Factors influencing fluctuations in the numbers of the ermine. Tr. o-va estestvoispytatelei pri Kazanskom un-te 56 (3-4), Kazan.

Grigoriev, I. D. (1938): Biology of reproduction of the ermine. Zool. zh. 17 (5).

Klimov, Yu. I. (1940): Materials on the biology of the ermine. Tr. biol. nauch.-issled. in-ta Tomskogo gos. un-ta 7, Tomsk.

Kopein, K. I. (1959): Population ecology of the large narrow-skulled vole and of the Siberian lemming on Yamal. Avtoref. diss. Sverdlovsk (Fondy UFAN SSSR).

Lavrov, N. P. (1939): The ermine. "Sov. okhotnik", No. 12

Lavrov, N. P. (1941): Reproduction of the ermine, and forecasting its numbers. Tezisy dokl. ekolog. konf. po probl. "Massovoe razmnozhenie zhivotnykh i ikh prognozov" 2, Kiev.

Novikov, G. A. (1956): Carnivorous mammals of the USSR fauna. M.-L. Izd-vo AN SSSR.

Petrov, O. V. (1956): The sexual dimorphism of the skull of the ermine. Vestn. LGU 15.

Popov, V. A. (1947): Age structure, forage reserve and helminths of the ermine as indicators of fluctuations in the numbers of this species. Tr. O-va estestv. pri Kazanskom un-te 57 (3-4), Kazan.

Smirnov. V. S. (1959): Age determination and age structure of the Arctic fox on Yamal. "Mat-ly po faune Priobskogo severa i ee ispolzovaniyu". Tr. Salekhardskogo statsionara UFAN SSSR", ed. 1, Tyumen.

Shvarts, S. S. (1959): The question of the biology of ermine reproduction beyond the polar circle. "Mat-ly po faune Priobskogo Severa i ee ispolzovaniyu". Tr. Salekhardskogo statsionara UFAN SSSR, ed. 1, Tyumen.

Shvarts, S. S. and Smirnov, V. S. (1959): The comparative ecological and physiological characteristics of the muskrat in the forest steppe and the near-polar areas. Tr. In-ta biol. UFAN SSSR 18, Sverdlovsk.

Tikhvinski, V. I. (1937): The polecat, ermine and weasel. M.-L., KOIZ.

Yurgenson, P. B. (1932): The ermine. M.-L. KOIZ.

Yurgenson, P. B. (1933): Variability in the skull of the ermine. Zool. zh. 12.

Asdell, S. A. (1929): Patterns of mammalian reproduction. J. agric. Sci. N.-Y, 1929.

Deanesly, R. (1935): The reproductive processes of certain mammals. Part IX. Growth and reproduction in the stoat (*Mustela erminea*) Philos. Trans. [Roy. Soc. Ser. B.], 1935.

Deanesly, R. (1943): Delayed implantation in the stoat (*Mustela mustela*) Proc. Zool. Soc., Lond.[1]

Marshall, F. H. A. (1958): Physiology of reproduction. Vol. 1, London.

Martinson, R. K., Holten, J. W., and Brakhage, G. K. (1961): Age criteria and population dynamics of the swamp rabbit in Missuri. J. Wild. Mgmt. 25 (3).

---

[1] Ref. incorrect - should be Nature 151: 365-66, and *mustela* should be *erminea*—Ed.

MALE REPRODUCTIVE CYCLES IN THE MUSTELIDAE

by

P. I. Danilov and I. L. Tumanov

[From: Zool Zhurn. 51: 871-80, 1972.]

Despite the great importance of mustelids to the hunting industry, some aspects of their biology, and particularly of their reproduction, have not been examined until now. The present work sets forth the results of research into the processes of spermatogenesis among several species of the Mustelidae.

The species investigated were those inhabiting the Northwest of the European part of the Russian Soviet Federative Socialist Republic (Pskov, Novgorod, and Leningrad oblasts, and the Karelian Autonomous Soviet Socialist Republic). From 1962 to 1970, 332 animals were processed (Table 1).

TABLE 1: Material examined

	No. of animals obtained per month												Total
	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	
Weasel	1	-	2	-	1	-	3	2	1	2	1	3	16
Stoat	5	3	3	5	2	2	3	2	3	-	4	4	36
Polecat	7	3	3	6	1	3	2	1	1	6	21	15	69
European mink	-	2	-	5	-	1	-	-	-	4	12	3	27
American mink	3	6	7	4	1	2	4	-	1	6	27	19	80
Pine marten	18	16	4	-	1	-	-	1	-	4	10	22	76
Badger	-	1	-	1	1	3	1	1	1	2	-	4	15
Otter	-	1	1	-	2	-	1	-	-	1	5	-	11
Wolverine	-	-	2	-	-	-	-	-	-	-	-	-	2

The age of each animal was determined from the wear of the teeth, the closure of the cranial sutures, and the development of the sagittal and occipital crests (Danilov and Ivanter, 1968). In certain specimens age was established from the lamellar structure of the teeth (Klevezal and Kleinenberg, 1967)[1].

The general condition and degree of fatness were assessed from dissection of the carcasses. Diseased or severely emaciated males were not used for histological analyses. The gonads were fixed in 10% formalin or Bouin's solution. Normal histological procedures were followed. Paraffin wax sections 7-10 microns thick were stained with haematoxylin-eosin. The slides were photographed at low magnification (objective X^{10}, ocular X^{10}).

As is conventional, we classify the seasonal changes in the male sexual organs into 3 periods: I - passive spermatogenesis; II - active spermatogenesis; and III - period of regression and rest. Preliminary research showed (Danilov, 1965, 1967) that the cyclical changes in the sexual organs of various species of Mustelidae are similar but differ in time. Thus, after giving a brief description of the three phases, we shall discuss below only the details of the individual species' cycles, indicating the times when the various changes occur.

---

[1] Translated by the Fisheries Research Board of Canada, Transl. series no. 1024, ed. D. E. Sergeant.—Ed.

The first period (passive spermatogenesis) includes 2 stages: a) the beginning of mitotic activity in the spermatogonia, and b) the development of the germinal epithelium of the seminiferous tubules up to the spermatid stage. This period is characterised by the development of the embryonic epithelium of the seminiferous tubules, consisting of Sertoli cells and spermatogonia, into a multi-layered epithelium which contains Sertoli cells and spermatogonia, primary and secondary spermatocytes and spermatids. External changes (2-3 fold enlargement) in the testes become noticeable towards the end of the period.

The second period (active spermatogenesis) also includes two stages: a) the formation of mature gametes, and b) intensive production of spermatozoa. Throughout this period the development of the spermatids, and their transformation into mature sperm cells, continues. In the seminiferous tubules all stages occur, from Sertoli cells and spermatogonia to spermatozoa accumulating in the lumina of the tubules. The testes achieve their maximum size at this time. They exceed by 8-10 or more times the dimensions and weight of testes during the period of rest.

The third period (regression and rest) is a gradual decline of spermatogenesis and reduction of the embryonic epithelium to spermatogonia and Sertoli cells. The weight of the genitals gradually drops.

Weasel (*Mustela nivalis L.*)

Information about the reproduction of the weasel is very contradictory. According to the data of some authors, rut (and hence active spermatogenesis) takes place at the beginning of spring; others consider that this species generally lacks a definite mating period (Yurgenson, 1931, 1932; Nasimovich, 1949;[1] Novikov, 1956,[2] 1963; Marvin, 1959; Rubina, 1960;[3] Siivonen, 1956; Hartman, 1964; Heidt *et al.*, 1968; Heimpel, 1968).

According to our observations in the wild, and also of animals held in captivity, weasels become more active in March-May. This is confirmed by studies of their cycle of spermatogenesis. In adult weasels the testes achieve their greatest dimensions and weight at the beginning of spring, remaining in this condition until the middle of summer. A certain increase in the weight of the testes is noticeable in January (Figure 1). However, proliferation of the germinal epithelium of the seminiferous tubules (passive spermatogenesis), begins from the end of October to November. At this time primary spermatocytes appear in the seminiferous tubules. The first spermatids are often noticeable in the ducts in January; however, they do not develop into spermatozoa, but undergo atresia. This condition can be observed in the animals' testes until March. The period of passive spermatogenesis lasts about 4 months (November to early March).

Spermatozoa are found in the testes only at the end of March, and in the gonads until the middle of July. Thus the second period, or active spermatogenesis, also takes 4 months: late March to early July. Evidently the males retain their fertility throughout this whole period. The most likely time of mating is the middle of this period, i.e., April - May, when the production of mature gametes is at its maximum rate.

The involution of the embryonic epithelium of the seminiferous tubules begins at the end of July. A state of functional rest in the testes is observed from August to the beginning of October, i.e., the regression of the spermatogenous epithelium and the state of rest last from July to October.

---

[1] Translation available in the Elton Library, Department of Zoology, Oxford University.—Ed.

[2] Translated by Israel Program for Scientific Translations, Jerusalem 1962.—Ed.

[3] Translation available from the British Library, Lending Division, Boston Spa, Yorks.; No. RTS 2292—Ed.

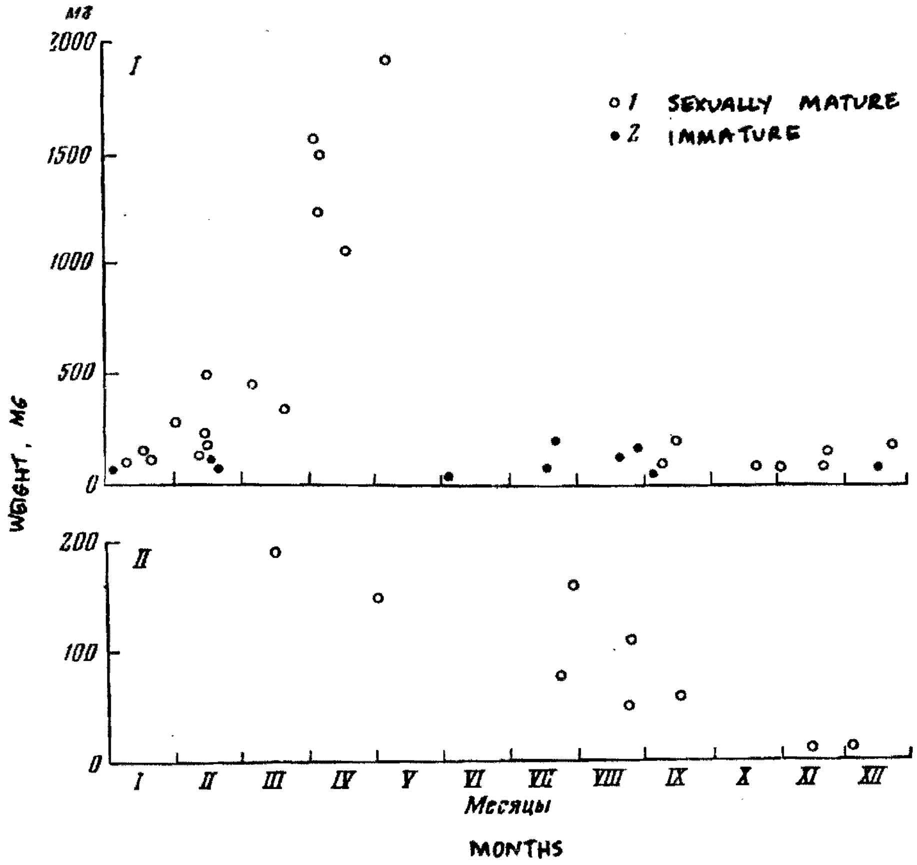


FIGURE 1: Seasonal changes in weight of paired testes plus epididymes in the weasel (I) and ermine (II)

Male weasels do not breed in their first year. Their testes, during the period when the gonads of adult males are active, weigh only 15-20 mg., and the germinal epithelium of the seminiferous tubules consists merely of Sertoli cells and primary spermatogonia.

Ermine (*Mustela erminea* L)

Male ermine in the Northwest reach sexual maturity in their second year. In a young male, the weight of the paired testes with accessory glands is stable through three seasons (summer, autumn, winter) of the first year of life (Figure 1). Sexual maturity comes only at the beginning of spring, when the weight and dimensions of the testes increase, and the first phase of passive spermatogenesis (the first meiotic division) is observed in the seminiferous tubules. Mature gametes are noted in the testes of young males from the end of May to the beginning of June, i.e., at the beginning of their second year of life.

The change in the structural and functional state of the sexual organs in adult males occurs in two stages: (1) the first meiotic division and formation of primary spermatocytes, marking the beginning of passive spermatogenesis, takes place at the end of December (Figure 2 (1)); (2) the second phase of passive spermatogenesis ends in March with the appearance of spermatids (Figure 2 (2)). The period of passive spermatogenesis in the ermine lasts almost 4 months, from the end of December to March.

In the wild a marked change in the animals' activity (an increase in the number of tracks made per day, while hunting activity decreases), is observed from the beginning to the middle of March. This is a sign of the beginning of spermatogenesis in the males, which [at this time begin to] seek females intensively, and also to extend and mark out their territories before reproduction.

FIGURE 2: Sections of the testis of the ermine illustrating the annual cycle.

(1) initial phase of passive spermatogenesis (end of December)
(2) final phase of passive spermatogenesis (March)
(3) intensive production of spermatozoa (June)
(4) regressed (September)

Spermatozoa are first noted in the seminiferous tubules in April, when the beginning of active spermatogenesis is recorded. Apparently males are often already fertile at this time, since many spermatozoa accumulate in the ducts of the epididymis. The most intensive production of sperm cells is observed from the second half of May to June (Figure 2 (3)). A decline in spermatogenesis becomes noticeable at the beginning of August. By the end of this month spermatozoa are absent from the testes. Hence, active spermatogenesis in the ermine lasts from April to the middle of July. Most matings probably occur from the end of April to the beginning of June. In September and October the embryonic epithelium regresses after which a short rest follows (Figure 2 (4)), and then the cycle is repeated. Therefore, the period of regression and rest also lasts about 4 months, from August to November.

Polecat (*Mustela putorius* L.)

The age at which the male polecat becomes sexually mature has been considered previously (Danilov, 1965; Danilov and Rusakov, 1969).[1] The new data [presented here] corroborate the suggestion made earlier that sexual maturity is achieved by male polecats at the end of their first year of life. The testes of the young of the year, obtained in February - April, are greatly enlarged. The fertility of these animals' gonads, judging by their weight[2], corresponds to that of adult males in the periods before and during rut (Figure 3).

---

[1] Translated in this volume—Ed.

[2] The original says "judging by the histological picture", though the reference is to a graph showing weight—Ed.

Changes in the genitalia of adult males in the course of a year occur in the typical sequence. Passive spermatogenesis begins in November and continues up to February. During this time a slow increase in the weight of the testes occurs, from 350 mg in November to 1 200 mg in January.

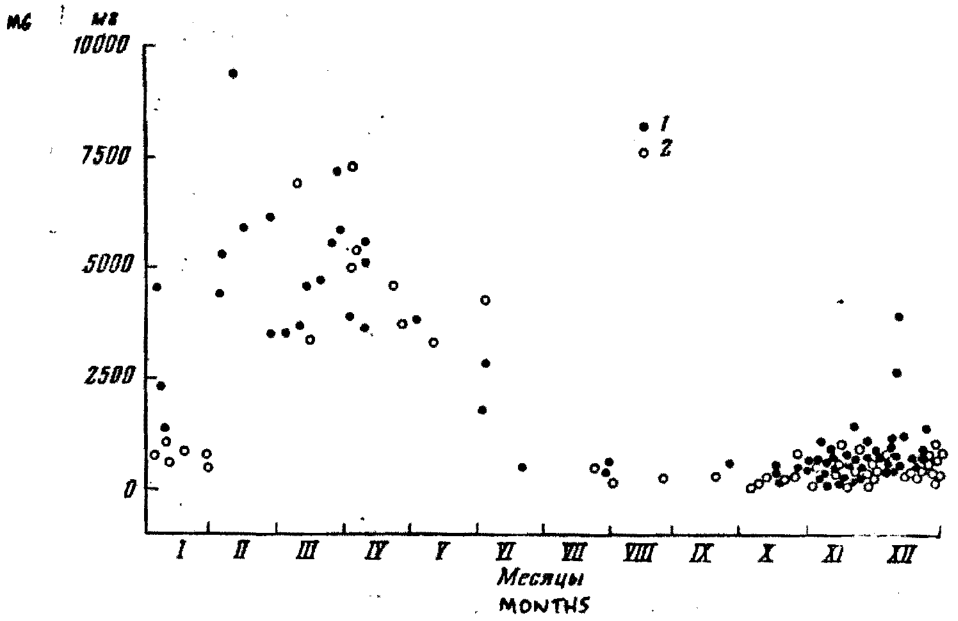


FIGURE 3: Seasonal changes in weight of paired testes plus epididymes in the American mink (1) and polecat (2).

The beginning of active spermatogenesis (appearance of spermatozoa in the seminiferous tubules) occurs from March to the first half of June. The most intensive production of mature spermatozoa is observed in early April. At that time the testes are at their maximum dimensions and weight, and their ducts have the largest diameter. Evidently the peak of the breeding season for the polecat in the Northwest of the U.S.S.R. occurs from the end of March to the beginning of April. In the wild, increased activity is observed in the Pskov district in the last third of February, and in the Karelian A.S.S.R., in the middle of March. In this period the tracks of polecats are often met with even in places not typical for them, e.g., pine forests, mossy swamps, or on the ice of large lakes.

The third period is the decline of spermatogenesis, regression of the embryonic epithelium of the seminiferous tubules and relative sexual quiescence, and is the longest (from the end of June to the beginning of November).

European mink (*Mustela lutreola* L.)

We have insufficient data to describe the whole cycle of spermatogenesis in this species. In December the testes are markedly enlarged (the weight of a pair of testes with epididymes is 800-1 400 mg). There are many spermatids in the embryonic epithelium of the seminiferous tubules; however, spermatozoa are not yet being formed. In the February and April specimens examined, the active process of the differentiation of spermatids is proceeding, and large numbers of mature sperms are observed in the ducts of the epididymis. In October-November the weight of the testes is minimal (300-600 mg), and Sertoli cells, spermatogonia and isolated primary spermatocytes are present in the seminiferous tubules, indicating a state of rest.

American mink (*Mustela vison* Briss.)

The reproduction of this species in captivity has been studied in captivity has been studied sufficiently completely. We shall touch only a few details of spermatogenesis in animals taken from natural populations. Activation of the mitotic processes in the germinal epithelium of the seminiferous tubules is noticeable at the end of November. From this time onwards, primary spermatocytes appear in the tubules, i.e., passive spermatogenesis begins. An increase in the dimensions and weight of the testes becomes noticeable in December (Figure 3). The length of the first period is 3 months, November to January. At the beginning of February the animals' testes are greatly enlarged, and in the seminiferous tubules a mass of spermatids appear. Several of them are developing into spermatozoa. The peak of spermatid differentiation is observed from the middle to the end of February. The presence of sperm cells in the gonads is detectable until the beginning of June, from which one can conclude that the second period (active spermatogenesis) in the American mink is extended and takes place in February - May. After this the seminiferous tubules gradually clear, concluding with a short rest in October, i.e., the third period covers June - October.

Rut in the American mink occurs in the wild at the same time as in captivity - from the second half of February to March. One of the proofs that the European and American minks do not interbreed is alleged to be the lack of coincidence of fertile seasons in these 2 species. But the duration of active spermatogenesis in the American mink overlaps the period of sexual receptivity of the female of the European mink. Therefore this hypothesis does not explain the non-interbreeding of these species.

Pine marten (*Martes martes* L.)

The spermatogenesis of the pine marten has been described by us previously (Danilov, 1967; Danilov and Ivanter, 1968). We will discuss here some further data.

According to the preliminary data, the majority of male martens reach sexual maturity from the end of the second to the beginning of the third year of life: this is confirmed by the condition of the gonads of young animals of the previous year's litter, obtained at the end of March and in August. The weight of a pair of testes with epididymis does not exceed 400 mg, which corresponds to the weight of adult gonads in the period of quiescence. There is no activity in the seminiferous tubules, and their embryonic epithelium consists of cells........[1]

In adult animals the weight of the testes in spring is almost at its maximum - 1800 - 2000 mg. In March spermatids are observed in the seminiferous tubules, and by May, mature spermatozoa.

Wolverine (glutton) (*Gulo gulo* L.)

Data on the breeding seasons of this species are very contradictory. Adlerberg *et al.* (1935) show that rut in the wolverine, in the European part of the U.S.S.R. and southern Siberia, occurs in December - January. Novikov (1956, 1963) writes that the mating of these predators takes place in September, but according to some data, in July. Dulkeit (1953) notes that, in the Altai, rut in the wolverine occurs at the end of summer. Parovshchikov (1960) makes the same statement for the Arkhangelsk district. Makridin (1964) considers the end of March to April a possible time for the mating of wolverines in Taymyr, and, finally, Mohr (1938, 1939) (quoted by Wright and Rausch, 1955) describes an instance of mating by wolverines in the Copenhagen Zoo in summer.

---

[1] There is a printer's error on this page; one line has been repeated twice in a slightly different typesetting, and another has obviously been lost here. The meaning is probably "consists of Sertoli cells and spermatogonia" (and possibly other elements as well).—Translator.

Reproduction of wolverines and, in particular, their spermatogenesis, has been studied most fully in Alaska, Finland and Sweden. Wright and Rausch, (1955), having analysed quite a large number of animals, came to the conclusion that sexual activity in adult males in Alaska occurs in late spring or early summer. All the males they obtained in November - January were infertile. Krott (1959, 1960) reports that in Sweden and Finland wolverines mate in April - July.

Microscopic analysis of our specimens (2 adult males obtained in the middle of March) showed that the seminiferous tubules contain all stages from spermatogonia to spermatozoa. In the ducts of the epididymis can be seen a large number of mature sperm cells. The average diameter of the seminiferous tubule is 187 microns. The average weight of the testes with epididymis is 12 500 mg. Evidently the males are already fertile by the middle of March. To summarise, the breeding season for wolverines appears to be in spring and early summer.

Badger (*Meles meles* L.)

We observed the histology of the testes of adult badgers throughout almost the whole year. When the animals emerge from their burrows (April), the genitals of the males are already greatly enlarged (weighing up to 16 700 mg). In the seminiferous tubules the first phase of active spermatogenesis is going on. All stages are found in them except mature sperms. From May to July, the most active phase of the cycle, the peak of spermatozoa production, is observed. The weight of the testes reaches its maximum of 20 000 mg.

In the south of France the greatest weight of gonads in badgers is noted in January - February, with a second small rise in July. In Sweden the increase in mass of the reproductive organs occurs 1.5 months later than in France (Canivenc *et al.*, 1968). In the Northwest of the R.S.F.S.R. active spermatogenesis in the badger lasts until the end of summer. In the first third of August the gonads are still active; the embryonic epithelium of the seminiferous tubules has 4-5 layers and consists of Sertoli cells, spermatogonia, primary spermatocytes, spermatids, and mature spermatozoa. The latter arrange themselves in small numbers in the lumina of the tubules (Figure 4 (1)). Thus, the most likely period of rut in the badger is May-July.

At the end of September the embryonic epithelium of the seminiferous tubules is single-layered and consists of Sertoli cells, spermatogonia, and isolated primary spermatocytes, not forming secondary ones, which indicates extreme atresia and regression of the germinal epithelium. A similar condition in the reproductive organs is seen in males in the middle of October. But by December the testes of adult animals show not only external changes (increase in weight), but also significant changes in the microstructure of the seminiferous tubules, indicated by the development of the embryonic epithelium as far as the phase of spermatid formation (Figure 4 (2)).

The rapid regression of the spermatogenous epithelium in the badger has, apparently, an adaptive significance, since after a comparatively short autumn the animals must accumulate a sufficient quantity of fatty deposits for hibernation, and the physiological processes taking place in the gonads require an additional output of energy.

The males reach sexual maturity in their third year. The testes of animals aged 1-1.5 years, obtained in the period when adult animals are most active (June), are undeveloped (weight 800-1000 mg). The epithelium of their seminiferous tubules is one-layered and consists of Sertoli cells and primary spermatogonia.

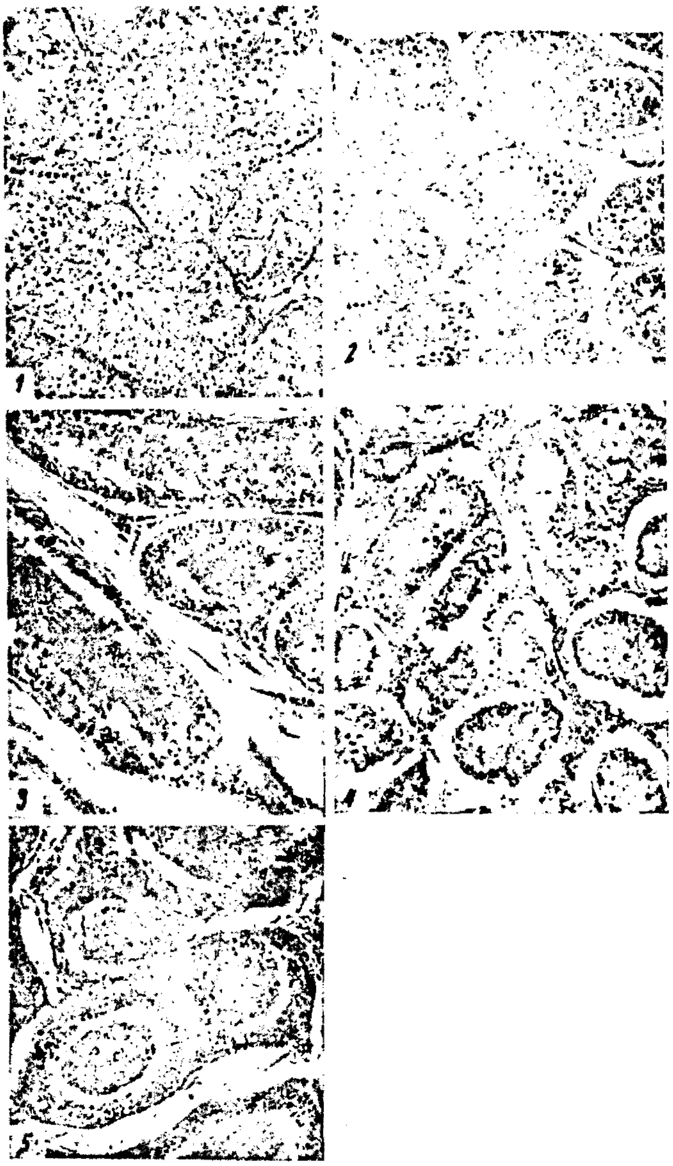


FIGURE 4: Cross-sections of the testes of badgers (1, 2), of sexually mature otters (3, 4), and of a young otter (5).

1. decline of spermatogenesis (August)
2. activation of the spermatogenous epithelium of the seminiferous tubules (December)
3. active spermatogenesis (November))
4. extreme regression of the embryonic epithelium (July)
5. ducts of the epididymis of the testis of a young male, filled with spermatozoa (May)

Otter (*Lutra lutra* L.)

The reproduction of the otter has not been studied until now. Our observations show that with the onset of the spring thaws (March) the otters' mobility increases. At this time the animals cover significant distances on the ice of reservoirs; the tracks left by adult animals are often found in pairs.

The gonads of the sexually mature male are fully fertile by the middle of November; the weight of a pair of testes with epididymes is 7800 mg; in the seminiferous tubules the active process of spermatogenesis is going on

(Figure 4 (3)), and the ducts of the epididymes are filled with sperm. A similar state is observed in specimens collected in February. By July, regression of the embryonic epithelium of the seminiferous tubules is complete, and the general condition is close to that of quiescence (Figure 4 (4)).

Evidently the cycle of changes in the gonads of adult males in the course of the year occurs as follows: passive spermatogenesis - end of summer to autumn (August - October); active spermatogenesis - winter to beginning of spring (November - March); regression of the spermatogenous epithelium and rest - spring to summer (April - July). In young males which have reached sexual maturity and are breeding for the first time, spermatogenesis occurs at other times. In March the initial phase of active spermatogenesis is observed in them: spermatozoa are forming in the seminiferous tubules, although there are still none in the ducts of the epididymes. In May the active phase of the cycle, the mass production of spermatozoa is observed, and the ducts of the epididymes are filled with sperm (Figure 4 (5)). Apparently the breeding season for young otters differs somewhat from that of older animals and occurs from spring to the beginning of summer.

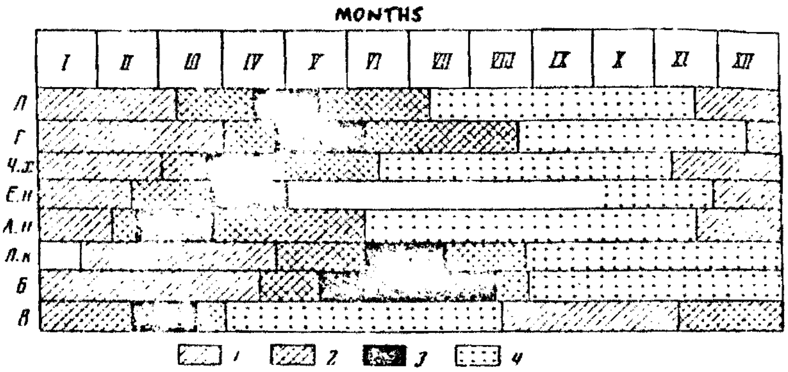


FIGURE 5: Spermatogenesis in the Mustelidae

1. Passive spermatogenesis
2. Active spermatogenesis
3. Most likely period of mating
4. Regression and quiescence.

Species, from top to bottom: weasel, ermine, polecat, European mink, American mink, pine marten, badger, otter.

Conclusion

Comparative analysis of spermatogenesis in the species examined allows the distinction of 3 groups (Figure 5) according to breeding season:

(1) Early spring mating (polecat, European and American minks and some otters).

(2) Early summer mating (weasel, ermine and young adult otters).

(3) Summer mating (marten and badger).

The wolverine, evidently, belongs to the first or to the second group, since the gonads of two adult animals, obtained in the middle and end of March, were fertile. In the seminiferous tubules of specimens obtained in March, intensive production of spermatozoa was going on.

Spermatogenesis in all the species examined is characterised by 3 stages of almost equal length, lasting on average, about 4 months each. A similar cycle has been observed by us in the lynx, and occurs in the arctic fox

(Sokolov, 1957) European bear (Erickson *et al.*, 1968) and European beaver (Ivanova, 1961). It appears that changes in the male reproductive organs of monocyclical species follow a single pattern and differ only in time.

Numerous investigations have shown that the reproductive cycle in predators is stimulated by the reaction of the hypothalamic-hypophysical system to changes in daylength and, seemingly, in the light spectrum. The time of parturition is usually determined by ecological conditions: warm weather during the period of whelping and nursing the kittens, an adequate food supply for the time when the young begin to live independently, and so on. The date of whelping is regulated on the whole by the length of the pregnancy. Exceptions are the late summer and early autumn whelpings of otters which are apparently explained by the fact that the mating season and the length of the delay in implantation are different in otters of different ages.

SUMMARY

All species studied typically have a sexual cycle of 3 stages of equal length, each stage lasting on average, about 4 months. Changes in the reproductive organs of male Mustelidae follow a single pattern, and differ only in time. Animals such as the polecat and the European and American minks have early spring periods of rut. Rut in the summer is characteristic of the marten and badger. The weasel and the ermine are among the species which mate in early summer. In older male otters, active spermatogenesis is observed in the winter and beginning of spring.

BIBLIOGRAPHY

Adlerberg, G. P., Vinogradov, B. S., Flerov, K. K. and Smirnov, N. A. (1935): The animals of the Arctic; 1-135. Izd-vo Glavsevmorputi, L.

Danilov, A. I. (1965): When do polecat males become sexually mature? Tezisy dokl. nauchn. konf. In-ta biol. Petrozavodsk. un-ta: 35-37.

Danilov, A. I. (1967): Reproduction of the pine marten in Karelia. Ibid.: 86-87.

Danilov, P. I. and Ivanter, E. V. (1968): The pine marten in Karelia. Uch. zapiski Petrozavodsk. un-ta 15(4): 179-197.

Danilov, P. I. and Rusakov, O. S. (1969): The ecology of the polecat (*Mustela putorius*) in north-western European Russia. Zool. zh. 48(9): 1383-1394.

Dulkeit, G. D. (1953): The significance of the lynx and wolverine as predators in the ecosystem of the Altai taiga. Source: Book entitled "Preobrazovanie fauny pozvonchnykh nashei strany" [Transformation of our country's vertebrate fauna]: 147-152. Izd-vo Mosk. o-va ispyt. prirody.

Ivanova, T. M. (1961): The annual recurrence of spermatogenesis in the European beaver. Tr. Voronezhsk. zapovedn. 12: 117-138.

Klevezal, G. A. and Kleineberg, S. E. (1967): Determining the age of mammals by means of the layered structure in the teeth and bones; 1-142. Izd-vo "Nauka", M.

Makridin, V. P. (1964): Distribution and biology of the wolverine in the Far North. Zool. zh, 43(11): 1688-1692.

Marvin, M. Ya. (1959): The mammals of Karelia: 1-236. Izd-vo Karelsk. ASSR, Petrozavodsk.

Nasimovich, A. A. (1949): Biology of the weasel on the Kola peninsula and its competitive relationship with the ermine. Zool. zh. 28(2): 177-182.

Novikov, G. A. (1956): The carnivorous mammals of the USSR; 1-293. Izd-vo AN SSSR, M.-L.

Novikov, G. A. (1963): Order Carnivora. From the book by Gromov, I. M., Gureev, A. A., Novikov, G. A. Strelkov, P. P. and Chapski, K. K.: Mlekopitayushchie fauny SSSR - [The mammals of the USSR fauna] 2: 740-895. Izd-vo AN SSSR, M.-L.

Parovshchikov, V. Ya. (1960): On the biology of the wolverine and otter. Zool. zh. 39(7): 1111.

Rubina, M. A. (1960): Some ecological traits of the weasel *Mustela nivalis* L. according to the observations in the Moscow province. Byull. Mosk. o-va Ispyt. Prirody 65(4): 27-33.

Sokolov, N. N. (1957); Histological analysis of the sexual cycle of the tundra fox. Zool. zh. 36(7): 1076-1083.

Yurgenson, P. B., (1931): The ermine and the weasel in the North. Sov. Sever 2: 1-35.

Yurgenson, P. B. (1932): The weasel : 1-25. Vneshtorgizdat, M.

Canivenc, R., Bonnin-Laffargue M., and Relexans, M. (1968): [The seasonal genital cycles in some European Mustelidae]. Ser. physiol. 85-104, Paris

Erickson, A. W., Mossman, H. W., Hensel, R. J. and Troyer, W. A. (1968): The breeding biology of the male brown bear (*Ursus arctos*). Zoologica (Scientific contributions of the New York zoological society) 53(3): 85-105

Hartman, L. (1964): The behaviour and breeding of captive weasels (*Mustela nivalis* L.). New Zealand Journal of Science, 7(2): 147-156.

Heidt, G. A., Peterson, M. K., and Kirkland, G. L. (1968): Matin behaviour and development of the least weasel (*Mustela nivalis* L.) in captivity. J. Mammal. 49(3-4): 413-419.

Heimpel, H. (1968): The weasel, Europe's smallest carnivore. Natur und Land, 54(1): 34-35.

Krott, P. (1959): The wolverine. Monographie der Wildsaugetiere 13, Jena.

Krott, P. (1960): The wolverine. Die neue Brehm-Bucherei, Wittenberg-Lutherstadt.

Siivonen, L. (1956): [The large mammal book] Helsinki, Ottawa.

Wright, P., and Raush, R. (1955): Reproduction in the wolverine *Gulo gulo* L. J. Mammal. 36(3): 346-355.

FEMALE REPRODUCTIVE CYCLES IN THE MUSTELIDAE

by

P. I. Danilov and I. L. Tumanov

[From: Byull. Mosk. o-va Isyt. Prir. Otd. Biol. 80 (1): 137-45, 1975]

This paper presents the results of studies on the sexual cycle of female mustelids. An earlier paper (Danilov and Tumanov, 1972)[1] described the sexual cycles of the males of these species.

The material was gathered from 1963-1973 in the Pskov, Novgorod, Leningrad, and Murmansk regions and in the Karelian ASSR. In all, 244 females were studied (Table 1).

TABLE 1: Material examined

	Months												
	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	Total
weasel	-	-	-	-	2	-	5	1	2	-	2	2	14
ermine	8	7	2	1	3	1	1	3	-	3	1	2	32
polecat	11	3	-	2	-	-	1	-	1	4	10	7	39
European mink	-	-	-	1	3	-	1	-	-	2	20	4	32
American mink	3	3	2	-	3	4	8	3	1	5	8	10	50
pine marten	11	21	7	-	-	-	-	-	-	1	10	24	77

The gonads were weighed, measured, fixed in 10% neutral formalin or Bouin's alcohol and chloroform and embedded in paraffin wax. Sections cut at 7-8 microns were stained with haematoxylin-eosin or Mallory's compound. They were photographed at low magnification (objective 8X, eyepiece 15X).

The stages of the oestrous cycle were established from observation of changes in the sexual organs; the state of the vaginal epithelium, the intensity of blood supply to the uterus, the appearance of the muscular walls, epithelium and glands of the uterus, and the development and atresia of the follicles and copora lutea in the ovaries and their dimensions. At the same time use was made of a table drawn up from data in the literature (Lavrov, 1944; Borodulina, 1951; Zaleker, 1955; Abramov, 1961; Shell, 1956) and our our studies [see Appendix].

External signs of rut were recorded during the process of tracking and observing these animals in their natural environments and in captivity. Fertility was defined as the number of embryos and whelps in a litter.

Weasel (*Mustela nivalis* L.)

As has been established (Danilov and Tumanov, 1972), male weasels become sexually mature at the age of one year. Probably the females in our region also come on heat for the first time at the same age. In young (3-4 months) females, caught in July-August, only primordial and small cavity follicles at various stages of development and atresia were observed in the ovaries. Their maximum diameter did not exceed 200 microns. The attainment of sexual maturity at an earlier age (3-4 months), as noted by Fog (1969) in Denmark, does not take place in our conditions. In an adult weasel (3+) caught in May the gonads were active, showing the characteristics of the last stage of pre-heat.

---

[1] Translated in this volume—Ed.

Adult females collected from the wild at the end of July had embryos that were in the last stages of development. Their reproductive organs were hyperaemic and greatly enlarged. The ovaries contained large, well-developed corpora lutea with diameters of up to 1050 microns, and also primordial and cavity follicles no more than 220 microns in diameter. Clearly these animals would give birth in no more than a week's time, i.e., at the beginning of August.

In November-December the sexual system of the adult females is in anoestrus: the vaginal epithelium is 2-3 layered, the uterus thin and anaemic, the glandular layer weakly developed, the epithelium cylindrical; in the ovaries there are primordial and cavity follicles, mostly atretic, of up to 250 microns in diameter.

Some data in the literature (Yurgenson, 1931, 1932; Tikhvinsky, 1937; Novikov, 1956,[1] 1963; Marvin, 1959; Rubina, 1960;[2] Walker, 1972 and others), and our own material, suggest that the principle season of births in weasels is in spring - from the end of April through to May; but according to the opinion of other researchers (Hartman, 1964; Heimpel, 1968; Heidt *et al.*, 1968) mating and whelping are observed in this species in all seasons of the year.

It seems to us most likely that young females of the early spring generation, i.e., those born in April-May, attain sexual maturity and are mated at the end of the winter following the season of their birth i.e., in early spring (March-April) of the next calendar year. As has been shown by the researchers of D. B. Ternovsky (1974), Hartman, (1964) and Heidt *et al.* (1968), pregnancy in weasels proceeds without delay in implantation and lasts 35-37 days. Consequently, after the spring rut, the young are born in April-May.

In females of the late summer generation (those born in July-August) sexual maturity and rut are delayed until the beginning of summer, and the young are born at the end of summer and even in autumn (instances are known when nests have been found occupied by blind whelps even in September). Judging by the composition of 6 litters, and the number of embryos in 5 pregnant females, there are from 4 to 10 in a litter, and the average is 7.1.

Our observations of wild animals in captivity have shown that lactation is continued for about 1½ months, but that from the age of a month the young begin to eat meat too.

The litters of the spring generation break up in July-August, and of the summer generation, in autumn.

Ermine (*Mustela erminea* L.)

Up to the present time zoologists have disagreed over the age of sexual maturation and time of rut in the ermine. Some authors consider that young females and some of the males breed in their first year, at the age of 3-4 months; others believe that sexual maturity is deferred to the second year. Evidently the age of sexual maturity in the ermine varies considerably, depending on the latitude of the area and its climate. According to the observations of Grigoriev (1938) in the Kazan zoological park, of Lavrov (1944) in Kazakhstan, of Ternovsky (1974) in western Siberia, of Deanesly (1935) in England and Müller (1954, 1970) in Central Europe, females attain sexual maturity and mate in the first year of life. Our region is considerably further north than the

---

[1] Translated by Israel Program for Scientific Translations, Jerusalem, 1962—Ed.

[2] Translation available from British Library Lending Division, Boston Spa, Yorks, No. RTS 2292—Ed.

territories mentioned above, and according to our data, female ermine reach sexual maturity at the end of the first or beginning of the second year of life. Thus only overwintered animals breed.

Let us compare the state of the reproductive organs in the young of the current year and in adults, in the summer-autumn period. In a young female, aged approximately 3 months at the end of July, the epithelium of the mucous membrane of the vagina had 4-6 layers, and cornification was not observed in its upper, flattened layers. The muscular walls of the uterus were thin, and its blood vessels were few in number and of small diameter. The epithelium of the mucous membrane had an almost cubical form. The ovaries contained primordial and small (maximum diameter 360 microns) growing follicles. There were also fairly large (up to 600 microns) atretic follicles with advanced degeneration. There were no copora lutea. Evidently the most active period of follicle development was already past, but the female had not reached sexual maturity.

Approximately the same picture is observed in August too, when the vaginal epithelium is 4-6 layered and cornification is absent. The walls of the uterus are thin, anaemic, and the glands weakly developed. The ovaries contain primordial and average-sized (maximum diameter 330 microns) cavity follicles at various stages of development and atresia, and no corpora lutea.

The weight of the gonads of young females changes as they mature and breed for the first time. In animals aged 3-4 months (August) the uterus and ovaries together weighed 100 mg; in 6-7 month-old animals (October) they weighed 125 mg; and subsequently in January they weighed 115 mg, in February - 160 mg, in April - 250 mg, in May (in 12 month-old animals) - 280 mg, in October (in 18-19 month-old animals) - 230 mg.

The reproductive organs of animals born in the preceding year or before appear quite different. A one-year-old female which died in captivity at the end of April had in her ovaries primordial and numerous fairly large (up to 410 microns in diameter) cavity follicles, which indicate the initial period of prooestrum.

Adult females, collected at the beginning of May, were lactating. At the same time, judging by the state of their gonads, they were in an early stage of pre-heat: the epithelium of the mucous membrane of the vagina was multi-layered (from 10-12 rows of cells); its surface layers were cornified,

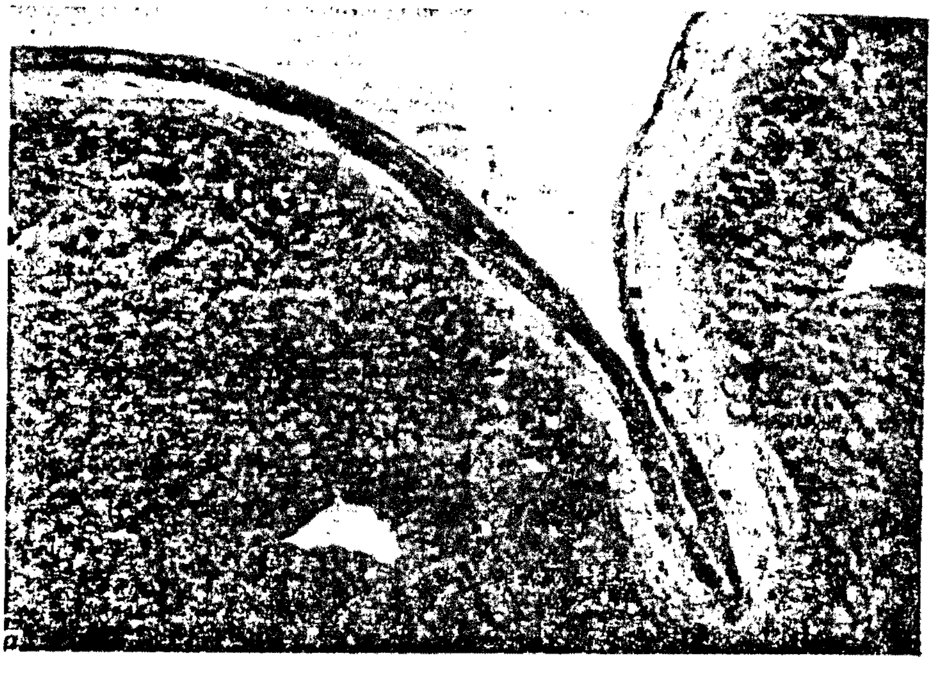


FIGURE 1a: Reproductive organs of the ermine in May: the vagina

FIGURE 1b: Reproductive organs of the ermine in May: the uterus

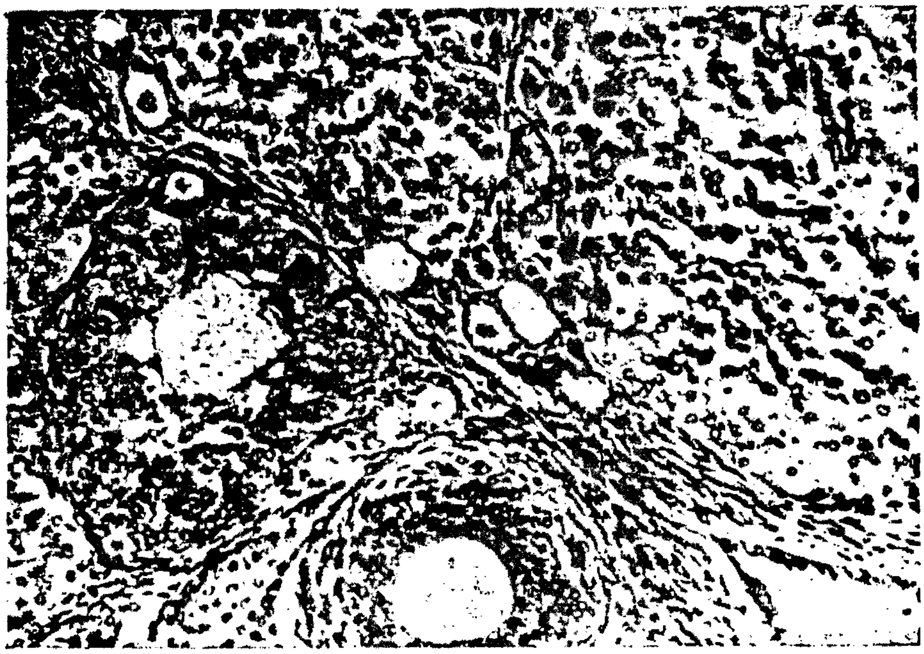


FIGURE 1c: Reproductive organs of the ermine in May: the ovary

and their cells had lost their nuclei, and in places desquamation of the horny cells could be observed (Figure 1a). The lumen of the uterus was star-shaped and it contained a secretion of the uterine glands; the muscular walls were noticeably thickened and hyperaemic, and the epithelium of the mucous membrane was dense and cylindrical (Figure 1b). The ovaries contained numerous primordial follicles; the cavity follicles were at various stages of development and atresia, and the atrẽtic follicles were fairly large (up to 490 microns in diameter). The maximum diameter of the developing follicles was 250 microns. The corpora lutea of lactation represented loose formations of lutein cells (up to 500 microns in diameter) with marked involution (Figure 1c).

In June, the ovaries of the adult animals showed corpora lutea of pregnancy (up to 440 microns) and infrequent primordial follicles; most of the cavity follicles were atretic, and measured up to 275 microns in diameter. These females were pregnant, and their follicular activity suppressed. The same condition could be observed in specimens collected in August. Hence, the period of heat in the ermine occurs at the end of May-June: and evidently, later periods of mating are also possible in females who are breeding for the first time or have whelped late. The peak of spermatogenesis in males is also at the beginning of summer. The rut period of the ermine in our region is therefore from the end of spring to the beginning of summer (May-June); somewhat earlier in the south and approximately 2 weeks later in the north.

Comparison of our data with those of various other researchers demonstates again that breeding seasons of given areas depend very strongly on latitude. In the southern parts of the range of the ermine, rut occurs in early spring (Grigoriev, 1938; Klimov, 1940;[1] Lavrov, 1944), and in the northern parts, in mid-summer (Nasimovich, 1948; Laptiev, 1958; Shwartz, 1959). The reports of Novikov (1956), Kolosov *et al.* (1961), Gromov *et al.* (1963) and Heptner *et al.* (1967)[2] refering to the whole range of the species, state that rut in the ermine is generally observed at the end of spring through to the beginning of summer.

At the same time the majority of foreign researchers (Deanesly, 1935; Müller, 1954, 1970; Siivonen, 1956; Hanzl, 1958; Zimmermann, 1959) consider that there are two periods of rut in the ermine: in spring leading to a pregnancy lasting 8-10 weeks, and in summer, leading to a pregnancy of 9-10 months. We have never observed anything of this kind. All adult animals collected from July through to April were pregnant, and the young born in the current season were infertile and their sexual organs were undeveloped.

The pre-implantation stage of pregnancy in the ermine (the period of delayed implantation), lasts from July to February, and during this stage the vaginal epithelium is 2-4 layered and consists of polygonal cells. The muscular walls of the uterus are thin and the lumen has the appearance of a narrow slit, and the blood vessels are scarce and of small diameter. The ovaries contain corpora lutea of pregnancy (450 microns in diameter at the beginning and up to 550 microns at the end of the period), and primordial and small growing and atretic follicles (from 200 microns at the beginning and up to 330 microns at the end of the period).

Some signs of preparation for implantation become noticeable in isolated animals at the end of January, such as an enlargement and hyperaemia of the uterus, proliferation of the mucous membrane (stimulated by the secretion of progesterone by the corpora lutea) and growth of the corpora lutea (up to 570 microns). At the same time the dimensions of the growing follicles also increase (up to 330 microns). These signs become more obvious at the end of February-March, when, evidently, implantation takes place.

After implantation the pregnancy continues for little over a month. In unmated females, at the end of winter an intensification of follicular activity is observed; the developing follicles increase in number and in size, reaching in January-February up to 390 microns.

In the southern districts of the region the young are born from the middle to the end of April, and in the northern districts in the middle of May. Thus the usual duration of pregnancy in the ermine is close to 10 months: 8.5-9 months delayed implantation, and 1-1.5 months normal pregnancy. The average number of young in the litter is 7 (27 litters counted).

---

[1] Translated in King (1975)—Ed.

[2] Chapters on *nivalis* and *erminea* translated by British Library, Lending Division, Boston Spa, Yorks, No. RTS 6458—Ed.

The break-up of the litters and dispersal of the young takes place from the end of July to August. Litters which had not yet dispersed were encountered on the 3rd, 5th, 11th, 15th and 20th of July, but by the end of the month, on July 26th, we observed a pair of young on their own. At later periods - on August 20th and 26th, and then on September 7th, 13th, 19th and 24th - we encountered only single animals or young ones in a pair.

Polecat (*Mustela putorius* L.)

Both male and female polecats attain sexual maturity in their first year. The signs of sexual maturity in young females may be observed as follows. In October-December the vaginal epithelium of females in their first year is 2-3 layered, the uterus is infantile, and there are primary and small cavity follicles not exceeding 120-130 microns in the ovaries. In January the vaginal epithelium is still 2-3 layered and the uterus is infantile, but in the ovaries cavity follicles are already up to 330 microns in diameter. At the beginning of February the epithelium of the membrane of the vagina thickens noticeably, and becomes 7-layered; the cells of the outer rows flatten and their nuclei become pycnotic. The muscular walls of the uterus are slightly thickened, the glandular layer is well-developed and the glands secrete; hyperaemia takes place. In the ovaries the primordial and growing follicles enlarge; some of these reach 380-400 microns in diameter. This state of the reproductive organs, close to prooestrum, is also observed at this time in the adults. Young and adult females obtained at the end of April had embryos in the final stages of development, covered with a light embryonic down, i.e., 3-5 days before birth.

Thus rut in the polecat in the north-west European part of the USSR occurs at the end of February through to the beginning of April.

As field observations and the reports of hunter-correspondents have shown, young polecats are born in the southern areas of the region from the end of April to the beginning of June, in northern regions later by 10-15 days. Fertility, judging by 203 litters (Danilov and Rusakov, 1969),[1] ranges from 1-12, with an average of 6.1 whelps. The young remain with their mother till September, when they reach almost the size of adults and become independent.

The ovaries of adult females in October-November contain average cavity follicles up to 275 microns in diameter, the majority of them degenerating. The sexual organs are completely quiescent.

European mink (*Mustela lutreola* L.)

Reproduction in the European mink has been littled studied until now. Even in the monograph of Novikov (1939), devoted to this species, there are no clearly defined statements on the breeding season.

The material at our disposal allows us to begin a description of the oestrous cycle only from the metoestrum, or the first days of pregnancy. In an adult female, collected at the end of April, the muscular walls of the uterus were shrunken, and the epithelium showed signs of degeneration (flattening of the cells and pycnotisation of their nuclei). The folds of the mucous membrane had a strongly twisted dendroid appearance ([produced as a] reaction to the progesterone). The uterine glands were secreting intensely, and the lumen of the uterus contained the secretion of these glands. The ovaries contained corpora lutea at the stage of vascularisation. Their centres were filled with blood, and growth of the lutein cells was taking place. The maximum diameter of a corpus luteum was 990 microns. Ovulation had recently taken place. The ovaries also contained some primordial and developing follicles,

---

[1] Translated in this volume—Ed.

up to 440 microns in diameter.

Two females procured on May 5th and 6th were pregnant, each of them with 6 embryos at early stages of development (the average dimensions of the embryos were 2.5-3.3 mm). The lumen of the uterus in these females had a greatly twisted dendroid appearance, and the glandular layer was well developed. The ovaries contained functioning corpora lutea of pregnancy, up to 1700 microns in size, and also isolated large atretic follicles of up to 770 microns.

The periods of heat and rut in the European mink evidently occur at the end of March and in April. At the end of April minks were observed mating in the Moscow Zoological Park (Rubetskaya *et al.*, 1933).

Pregnancy in the European mink proceeds without delay of implantation, as proved by a number of investigations including studies of wild animals in zoos. It lasts for 35-37 days. Birth of the young occurs at the end of May through to the beginning of June. A case is known of a female, caught when pregnant, whelping in captivity on June 12th. In the litter (11 litters counted) there are from 3 to 6 young, on average 4.5. Lactation lasts for about 1.5 months. The young begin to disperse in September-October.

At this time and somewhat later, in November, the reproductive organs of animals born in the current year are in anoestrus, and only at the end of November does some increase in follicular activity in the ovaries become noticeable. In autumn the vaginal epithelium in young of the current year is 2-3 layered. The uterus is infantile, the glands weakly developed. In the ovaries there are a few primordial and small cavity follicles up to 190 microns in diameter. From the end of autumn to the beginning of winter the number of primordial and small cavity follicles in the ovaries increases, and some of them reach up to 275 microns in diameter.

In adult animals the vaginal epithelium and uterus appear similar to those of young, but in the ovaries, along with the growing follicles, atretic follicles are often encountered. In October the diameter of the developing follicle does not exceed 130 microns. In November their number increases markedly, and their dimensions reach 275 microns. In December isolated follicles reach 440 microns. Thus the period of an oestrous is between September and November.

American mink (*Mustela vision* Briss.)

The first signs of sexual activity in the adult, and of the maturation of the young American mink females, are observed at the beginning of February. The total weight of the uterus and ovaries increases significantly from 260-380 mg at the end of summer and in autumn, and 450-500 mg towards the end of winter, to 650 mg (adults only) in March. Histological changes appear: an increase in the thickness of the mucous membrane of the vagina of up to 5-6 layers of cells, thickening of the walls, a slight hyperaemia of the uterus and the growth of the grandular layer; and the beginning of secretion of the glands. The greatest changes take place in the ovaries, where follicles develop markedly, and some of them reach 880 microns. The sexual organs at this time may be classified as being at the end of the anaoestrum and the beginning of the pro-oestrum.

In adult females these changes become noticeable from the beginning of January, when the follicles reach somewhat larger dimensions [than in young], up to 940 microns. However, by the end of February these differences are levelled, and in all the animals studied a pre-heat or heat state is observed, in which observable differences are related to the individual rather than to age.

The vaginal epithelium of females at this time is 10-13 layered, the upper layers are cornified, and significantly desquamated. The walls of the uterus are thickened and hyperaemic, the lumen has a star-shaped form, and the uterine glands are well developed and actively secreting. In the ovaries are large cavity follicles, close to graafian follicles, reaching 1050 microns in diameter.

The females collected from the middle to end of March were pregnant. At this time the epithelium of the vaginal mucous membrane was 4-6 layered, with the upper layers flat, but cornification was already absent. The thickness of the muscular walls of the uterus was not great, and hyperaemia had gone down. The ovaries contained the corpora lutea of pregnancy with a diameter of up to 770 microns. Small cavity follicles measuring up to 110-120 microns were present.

In the middle of May the ovaries of the females that had given birth still had the corpora lutea of lactation, measuring up to 880-1000 microns, and average-sized, growing and atretic follicles up to 440 microns in diameter were beginning to appear. The vagina and uterus were quiescent; the epithelium of the vaginal mucous membrane was 2-3 layered, the uterus was thin and anaemic; uterine scars were barely noticeable, and towards the end of the month they disappeared. A limited growth of the follicles in the ovaries of adult females continues till August, when sections show cavity follicles of varying sizes. The largest of these reach 550 microns in diameter.

In the following months, in September-October, rapid involution of the ovaries is observed, and in sections, only primordial and small cavity follicles, generally atretic and not exceeding 250 microns in diameter, are seen.

In November some signs of stimulation of sexual organs are observed in adult females, such as a thickening of the mucous membrane of the vagina to 4-6 layers, and an enlargement of the growing follicles in the ovaries (on average up to 350 microns in diameter) increases; individual large follicles also appear, but as a rule they quickly become atretic. In young females similar signs are not observed.

All the processes connected with rut, pregnancy and the birth of young in wild American mink take place at the same times as in animals kept in farms, where these phenomena have been studied fairly fully (Petrayev *el al.*, 1934; Clair, 1941; Abramov, 1960, 1961; Bayevsky, 1961; Hansson, 1947; Enders, 1952; Venge, 1959; and others).

Judging by 18 litters and pregnant females, the litter of the wild female contains 4-7 whelps, on average 4.7, i.e., approximately the same number as in captivity. The litters break up in September-October, but the separation and dispersal of the young sometimes continues until the end of November.

Pine marten (*Martes martes* L.)

The majority of young reach sexual maturity in their third year (Starkov, 1940, 1947, 1948; Leblet, 1951; Gribova, 1956; Novikov, 1956, 1963; Kotov and Riabov, 1963; Heptner *et al.*, 1967), but between 15% and 50% do so in their second year, (Starkov, 1947; Kotov and Riabov, 1963; Gribova, 1956). According to our observations, such females comprise no more than 10%. Of 38 young pine martens we studied in February-March, the typical signs of pregnancy (hyperaemia and increase in the weight of the sexual organs up to 110 mg, and corpora lutea in the ovaries) were observed in only three.

Probably in this case too the age at sexual maturity depends largely on the geographical position of the area.

Macro- and micro-changes in the sexual organs in animals reaching maturity (age 1+) and pregnant (2+ and older), become noticeable by the end of February or the beginning of March. The total weight of the vagina, uterus, and ovaries increases markedly, reaching on average 940 mg (680-1280 mg). The length of the vagina in females aged 2+ and older on average is 28.6 (26.3-32.4) mm; of the uterus 21.4 (17.3-27.0) mm; of its left horn 48.8

(37.1-59.0) mm; and of the right horn 53.8 (43.2-76.5) mm.

The reproductive organs of young females aged up to a year have at this time an average weight of 330 (280-430) mg; the length of the vagina is 25.3 (19.6-29.2) mm; the uterus 20.4 (14.2-27.2) mm; its left horn 35.9 (29.3-44.8); and its right horn 41.2 (28.7-53.6) mm.

The microstructure of the reproductive organs is characteristic of sexually immature animals. The vaginal epithelium is 1-2 layered. The uterus is infantile, the glands little developed. In the ovaries there are primordial and small cavity follicles, both developing and atretic; their maximum diameter in January-February is 240-330 microns and even in March they do not exceed 450 microns.

At the same time in young (1+) females approaching their first breeding season, some stimulation of the sexual organs is observed . The mucous membrane of the vagina thickens to 4-6 layers of epithelial cells. The body and horns of the uterus are thin and anaemic, but the growth and secretion of the uterine glands are intensifying. As well as primordial and small cavity follicles, the ovaries contain fairly large growing follicles, whose dimensions increase from 330-450 microns (in January-February) to 550-580 microns (in March). Adult (3+) females which have not bred appear similar.

In pregnant females the sexual organs show substantial changes in February, when preparation for implantation of the embryos begins. Back in January the epithelium of the uterus becomes cubical and the glandular layer is sufficiently developed, but the muscular walls remain thin, and hyperaemia is not marked. The ovaries contain the corpora lutea of pregnancy, reaching 1200 microns in diameter. In the middle of February the general hyperaemia of the uterus becomes noticeable, especially of its glandular layer. The functioning corpora lutea of pregnancy reach 1300-1500 microns in diameter. Follicular activity is suppressed; follicles attaining 400-450 microns become atretic.

Preparation for implantation and implantation proper continue to the middle or end of March. At this time the corpora lutea in the ovaries reach their greatest dimensions (1700-1800 microns); their lutein cells are large and clear. True pregnancy lasts about 1.5 months. The young are born at the end of April or beginning of May. In 34 litters there were 2-6 whelps, an average of 3.3. Lactation continues for 1.5-2 months. Martens probably mate in July.

In autumn and at the beginning of winter the reproductive organs in animals of the current year and yearlings (1+) are almost identical. The vaginal epithelium is 2-3 layered, the uterus infantile, its walls thin, the blood vessels few in number. Only the ovaries show substantial differences. From October to December, the ovaries of young of the same year contain primordial and very small cavity follicles (110-220 microns), whereas in yearlings the maximum diameter of growing follicles is 2-3 times greater, up to 330-450 microns. In pregnant females at this time, the vaginal epithelium remains 2-3 layered, and the walls of the uterus thin; hyperaemia is not observed, but the glandular layer is developed and the glands active. In the ovaries there are corpora lutea with dimensions of 650-770 microns. Growing and atretic follicles are up to 330 microns in diameter.

SUMMARY

A study was made of the sexual cycles of weasel, ermine, polecat, European and American mink and pine marten females. The gonads of 244 females were histologically examined. Data are given on age at sexual maturity, mating season, duration of pregnancy, fertility etc.

BIBLIOGRAPHY

Abramov, M. D. (1960): Peculiarities of the biology of reproduction of the mink (*Mustela vison* Schreb.). Tr. NII pushn. zverovodstva i krolikovodstva 5, M.

Abramov, M. D. (1961): Mink farming. M., Selkhozgiz.

Baevski, Yu. B. (1961): Some peculiarities of the embryonic diapause in the mink (*Mustela vison*). DAN SSSR, 139 (2).

Borodulina, T. L. (1951): The latent period in the embryonic development of the Altai mole. DAN SSSR, 80 (4).

Heptner, V. G., Naumov, N. P., Yurgenson, P. B., Sludski, A. A. Chirkova, A. F. and Bannikov, A. G. (1967): The mammals of the Soviet Union 2 (1). M. Vysshaya shkola.

Gribova, Z. A. (1956): Materials on the reproduction of the pine marten in the Vologda province. Tr, Vses. n.-i. in-ta okhotn. promysla 16. M.

Grigoriev, N. D. (1938): Biology of reproduction in the ermine *Mustela erminea* L. Zool. Zhurn. 17 (5).

Gromov, I. M., Gureev, A. A., Novikov, G. A., Strelkov, P. I. and Chaiski, K. K. (1963): The mammals of the USSR fauna, part 2, M.-L. Izd-vo AN SSSR.

Danilov, P. I. and Rusakov, O. S. (1969): The ecology of the polecat (*Mustela putorius*) in the north-western regions of the European USSR. Zool. zhurn. 48 (9).

Danilov, P. I. and Tumanov, I. L. (1972): Male reproductive cycles in the Mustelidae. Zool. Zhurn. 51 (6).

Zaleker, V. L. (1955): Histological analysis of the reproductive organs of rejected female sables. Karakulevodstvo i zverovodstvo 4.

Kler, R. V. (1941): The heat and pregnancy of some Mustelidae (mink, sable, marten). Tr. Mosk. zooteckhnich. in-ta 1.

Klimov, Yu. N. (1940): Materials on the biology of the ermine. Tr. Biol. n.-l. in-ta Tomsk. un-ta 7.

Kolosov, A. M., Lavrov, N. P. and Naumov, S. P. (1961): Biology of the game animals in the USSR. M., Vysshaya shkola.

Kotov, V. A. and Ryabov, L. S. (1963): The game and valuable mammals of the foothill and mountain districts of the Krasnodar Territory. T. Kavkazsk zapovednika 7, Maikop.

Lavrov, N. P. (1944): Biology of reproduction of the ermine. Tr. Tsentr. n.-i. laboratorii biologii i okhotn. promsyla Narkomzaga SSSR 6, M.

Laptev, I. P. (1958): The mammals of the taiga zone of West Sibera. Izd-vo Tomsk. un-ta.

Leble, B. B. (1951): The marten. M., Zagotizdat.

Marvin, M. Ya. (1959): The mammals of Karelia. Petrozavodsk.

Nasimovich, A. A. (1948): An essay on the ecology of the ermine in the Lapland Reserve. Tr. Laplandsk. zapovednika 3, M.

Novikov, G. A. (1939): The European mink. Izd-vo LGU.

Novikov, G. A. (1956): The carnivorous mammals of the USSR fauna. M.-L., Izd-vo AN SSSR.

Novikov, G. A. (1963): Carnivores. From the book Mlekopitayushchie fauny SSSR. [The mammals of the USSR fauna] 2. M.-L. Izd-vo AN SSSR.

Petryaev, P. A., Orlov, B. M., Khomyakov, E. N. and Rebrova, E. M. (1934): Biology of reproduction and variability in the American mink. M.

Rubina, M. A. (1960): Some ecological traits in the weasel *Mustela nivalis* L., from observations in the Moscow province. Byull. Mosk. o-va Isyt. Prir. Otd. Biol. 65 (4).

Rubetskaya, Shcherbakova, Zeidel (1933): Biology of the European mink in the Moscow zoo. Byull. zooparkov i zoosadov 13. [No initials given].

Starkov, I. D. (1940): The breeding of martens. M., KOIZ.

Starkov, I. D. (1947): Biology of sable and marten breeding. M., Mezhdunarodnaya kniga.

Starkov, I. D. (1948): Physiology of reproduction of fur animals of the Canidae and Mustelidae families. Autoref. kand. diss. [thesis] M.

Ternovski, D. V., (1974): Reproductive peculiarities in the weasel and the ermine. Okhota i okhotn. khoz-vo 6.

Tikhvinski, V. I. (1937): The polecat, the ermine and the weasel. M.-L., KOIZ.

Shvarts, S. S. (1959): Biology of the reproduction of the ermine beyond the Polar circle. Tr. Salekhardsk. statsionara Uralsk. fil. AN SSSR 1, Tiumen.

Yurgenson, P. B. (1931): The ermine and the weasel in the north. Sovetsk. Sever 2.

Yurgenson, P. B. (1932): The ermine. From the book "Pushnye zveri SSSR" [The fur animals of the USSR], M.

Deanesly, R. (1935): Reproductive processes in certain mammals IX, Growth and reproduction in stoat (*Mustela erminea*) Phil Trans. Roy. soc. 225.

Enders, R. K. (1952): Reproduction in the mink (*Mustela vison*). Proc. Amer. Philos. Soc. 96 (6).

Fog, M. (1969): Studies of the weasel (*Mustela nivalis*) and the stoat (*Mustela erminea*) in Denmark. Dan. Rev. Game Biol. 6 (2).

Hansson, A. (1947): The physiology of reproduction in the mink (*M. vison* Schr.), with special reference to delayed implantation. Acta zool. Stockholm 28: 1-136

Hanzl, R. (1958): Raubwild und Raubzeug [Wild and predatory animals], Prague .

Hartman, L. (1964): The behaviour and breeding of captive weasels (*Mustela nivalis* L.). N.Z. Jl Sci. & Techn. 7(2).

Heidt, G., Petersen, M. and Kirkland, G. (1968): Mating behavior and development of least weasels (*Mustela nivalis*) in captivity. J. Mammal. 49 (3).

Heimpel, H. (1968): Vom Mauswiesel, European kleinstem Raubtier. [The weasel, Europe's smallest carnivore]. Natur und Land 54 (1).

Müller, H. (1954): Zur Fortpflanzungs Biologie des Hermelins (*Mustela erminea* L.) [The biology of reproduction of the ermine]. Revue suisse zool. 61 (5).

Müller, H. (1970): Beitrage zur Biologie des Hermelins [Contributions to the biology of the ermine], (*Mustela erminea* L.). Saug. Mitt. 18 (4).

Siivonen, L. (1956): Suuri Nisäkäskirja [The large mammal book]. Helsinki.

Shell, G. (1956): Biology of the laboratory mouse. N.Y.

Venge, O. (1959): Breeding experiments with mink. Amer. Fur Breeder 32 (4).

Walker, D. (1972): Observations on the collection of weasels (*Mustela nivalis*) from estates in south-west Hertfordshire. J. Zool. 166 (4).

Zimmermann, R. (1959): Taschenbuch unserer wildlebenden Saeugetiere [Handbook of our wild mammals]. Leipzig-Jena.

APPENDIX

States in the oestrous cycle in mammals

1. Vaginal epithelium

a. Dormancy (anoestrum): mucuous membrane gathered into longitudinal folds; epithelium consists of 2-4 layers of low polygonal cells; growth of the epithelium begins at the end of the stage.

b. Pre-heat (pro-oestrum): epithelium multi-layered (5-9 rows of cells); surface layers of the functional epithelium flattened, with pycnotised or lost nuclei; desquamation of the epithelium beginning in places.

c. Heat (oestrum): epithelium of 10-17 layers of cells; surface layers flat, without nuclei, cornified, intensified desquamation takes place; in the lumen of the vagina there is a large number of cornified cells (scales) of the epithelium.

d. Post-heat (meteostrum): at the beginning of this stage the horny layer disappears, the epithelium contracts to 4-7 layers, and finally to 2-4 layers.

2. Uterus

a. Dormancy (anoestrum): uterus anaemic, the muscular walls thin, the blood vessels scarce and of small diameter; epithelium cubical in form; uterine glands developed, secreting especially intensely before implantation.

b. Pre-heat (pro-oestrum): uterus enlarged, slightly oedematic and hyperaemic; blood vessels of the walls widened; epithelium transitional between cubical and cylindrical form; uterine glands well developed.

c. Heat (oestrum): uterus markedly enlarged, hyperaemic; mucous membrane forming large folds with even edges, as a result of which the lumen has a star-shaped form (indicating the activity of folliculin); epithelium tall-cylindrical.

d. Post-heat (metoestrum): enlargement and hyperaemia decline; folds of the mucous membrane take on a strongly twisted dendroid shape (reaction to progesterone); involution of the epithelium begins; uterine glands secrete abundantly; embryos at the stage of free-floating blastocysts.

Ovaries

a. Dormancy (anoestrum): Ovaries contain primordial (100-150 microns), small and average growing and atretic follicles (up to 400 microns); atresia especially marked in the middle of the stage; in pregnant females there are distinct corpora lutea of pregnancy of average dimensions (400-900 microns); at the end of the stage growth in the number and dimensions of the follicles (up to 600 microns) is observed; corpora lutea enlarge up to 1300-1800 microns.

b. Pre-heat (pro-oestrum): active growth of the follicles takes place; some reach dimensions 800-1000 microns; their cavity is stretched by follicular fluid, in which the ovum lies freely; the capillary network is well developed; corpora lutea of lactation are involuting.

c. Heat (oestrum): individual follicles are ovulating; their maximum diameter reaches 1500-1800 microns; formation of mature follicles continues; at the same time atresia of follicles at various stages of their development is observed.

d. Post-heat (metoestrum): corpora lutea of pregnancy set apart distinctly from the surrounding tissue; their diameter at the beginning of pregnancy is 800-1000 microns; many atretic follicles.

A METHOD OF AGE DETERMINATION AND AN ANALYSIS OF THE AGE STRUCTURES OF ERMINE POPULATIONS (*MUSTELA ERMINEA* L.).[1]

by

S. U. Stroganov

[From: Zool. Zhurn. 16: 113-129, 1937]

The estimation of the stock and the prediction of the yield of commercially valuable animals are among the most urgent problems in the planning and organisation of hunting, which plays a great part in our country's Socialist economy.

The growth of research into the prediction [of annual variations in] productivity of commercially valuable species makes the development of methods of age determination for these animals urgently necessary. Several researchers have recently tackled this problem. After the publication of Naumov's paper (1934) on the age of squirrels, techniques were evolved for determining the age of the squirrel (*Sciurus vulgaris exalbidus* Pall.) by Holzmaier (1935), the chipmunk (*Eutamias asiaticus* Gmel.) by Teplov (*in litt.*) and the little marmot (*Citellus pygmaeus* Pall.) by Naumov (1935). In all these papers the writers used changes in the structure of the teeth as the criterion of age differences. The experience of cattle breeding shows that teeth provide the main age criterion in mammals (cf. Korneven and Lesbr 1932). Research into the process and rate of tooth abrasion enabled us to devise a method for determining the age of the ermine (*Mustela erminea* L.).

An examination of other cranial characteristics which change with age did not give satisfactory results. Changes in the proportions of the skull provide criteria for age-determination only in young animals: after the age at which the permanent teeth are completed, the skull measurements of the ermine give a transgressive series, not useful for age determination. Such conclusions were reached by Yurgenson (1933)[2] in his paper on the development of the ermine skull, and Naumov (1935) in his research on changes with age in the skull of the little marmot (*Citellus pygmaeus* Pall.).

We did not find any useful criteria in the fur, claws or body dimensions of ermine.

To work out an age scale, we investigated about 400 skulls from the collections of the Zoological Museum of the Moscow State University and of Professor S. I. Ognev of Moscow State University. All the examined skulls are well labelled, indicating the exact dates when they were obtained. Using the age scale we devised, we made an analysis of the age structures of [several] ermine populations, using an additional 592 skulls. Thus, an examination of more than 1000 ermine skulls forms the basis of the present paper.

To determine the age of the ermine of this year's litter it is necessary to know the date of birth of the young.

We now have the following data on the periods of heat and littering in the ermine.

According to L. P. Sabaneev the heat[3] period of the ermine in the central region of the Soviet Union occurs in March, but in the more southern regions it

---

[1] The work was carried out at the Soyuzzagotpushnina biostation on Pogonno-Losinyi Island—Author

[2] Translated in King (1975)—Ed.

[3] Stroganov here apparently assumes direct implantation in the ermine, though later acknowledging the possibility of delay—Ed.

is in February. On the 30th April[1] A. A. Silantev, in the former Balashov District of former Saratov Province, was presented with a pair of adult ermine, obtained from a destroyed burrow, in which there were several blind young. E. P. Spangenberg told me that on the 4th May 1922 he procured 3 young ermine, about 5 inches long, from a burrow near the Kudinovo Nizhegorod railway station. On the 2nd of April A. Raiko obtained a female ermine in the former Borispol District of Poltava Region. On autopsy this female was found to be pregnant with 10 embryos. According to data of Brauner (1923) the period of ermine reproduction in the Ukraine is the end of March, but sometimes earlier. On the 9th[2] February 1898, near Kherson, 3 blind young ermine were found in their burrow. Yurgenson (1932) states that in the southern part of the Ukraine the heat period of ermine is observed at the end of December. In Germany the heat period of ermine, according to the data of local observers (for example L. Heck, Brehm, "Tierleben", Vol. III, 1915), occurs early in spring. On the 6th of June 1931 E. P. Spangenberg obtained 4 young ermine with their eyes just opened in the region of Ak-Bulak on the Turgai steppes.

From observations of Zverev (1931) the ermine's heat period in the northern part of Western Siberia occurs in about March. A litter of young was found there in April. According to the data of Dulkeit (1929) ermine are born in April on Bolshoi Shantar Island.

Troitsky (1930) states that in the former Kansk Region the heat period of ermine "begins at the end of February and continues to the middle of March. At the very end of April, but more often at the beginning of May, young can be found." There are usually between 6 and 8 of them. At the end of April this writer cut open a female ermine, obtained near the Duplensk Omsk railway station. The female proved to be pregnant, with embryos already forming.

Zharkov (1934) was given a female ermine in Tartary at the beginning of March 1931. The animal was pregnant with nine embryos, about 20 mm long. Between the 11th and 24th May, Zharkov examined in different areas of Tartary 11 ermine burrows with young of different ages, the oldest being about $\frac{3}{4}$ of the length of the adult ermine. Pershakov (1928) observed a female ermine with blind young on the 25th April 1925.

According to Heinrath (Brehm, l.c.) and Mantejfel (1927) pregnancy continues for 74 days, i.e., almost 12 weeks. However, there is a theory that, as in the sable, the pregnancy of the ermine can be much longer, including a period of delayed implantation. Zharkov reports on an ermine pregnant with 11 embryos, captured in May 1934, and dying in the Kazan Zoo on the 20th April 1935. She was kept in an isolated cage.

In general, as the above information indicates, the breeding season of the ermine varies, depending on the geographical locality and other, as yet unknown, factors.

Nevertheless, comparing the dates when the young of different ages were found, the period of birth should be late March, April and May, except in the Ukraine, where the ermine apparently gives birth earlier.

If we assume that the young are born in April or May, the change from milk to permanent teeth takes place when they are about 3 months old. In the second half of July, young ermine already have their permanent teeth.

The skull of a young ermine with its milk teeth preserved is oval to round and without the characteristic nuchal and sagittal crests. In comparison with the adult, the brain case is large and the basal area small. The foramina infraorbitalia are narrow and stretched sideways. The sutures are very pronounced. After the change from milk teeth to permanent teeth (end of July-

---

[1] These dates are given according to the old Julian calendar, which is 13 days earlier than our present calendar—Ed.

[2] Text gives 9th (22nd) February; the date as reckoned by the old and new calendars respectively—Ed.

August) the sutures coalesce, except for the suture marking off the ossa nasalia. The nuchal and sagittal crests are developing. The teeth are the same size as those of adult ermine.

In October and November the nuchal and sagittal crests are more sharply pronounced and the sutures are coalesced. The surface of the bones consolidates and becomes, as it were, glazed. Concentric ridges are noted on the surface of the brain capsule. The skull loses its juvenile features, becoming less distinguishable in configuration from that of the adult ermine. From this time on the age of the ermine can only be judged from the changes occurring in the teeth i.e., from the abrasion of the carnassial and molar teeth of the upper jaw and the carnassial teeth of the lower jaw.

Description of the teeth of the ermine

Development

$$\mathrm{i}\,\frac{3-3}{3-3}\,;\quad \mathrm{c}\,\frac{1-1}{1-1}\,;\quad \mathrm{pm}\,\frac{3-3}{3-3}\,;\quad \mathrm{M}\,\frac{1-1}{2-2} = 34$$

The milk teeth of the ermine differ from the permanent teeth in the following characteristics. The incisors and canine teeth are less developed, but sharper. The second upper premolar and the second and third lower premolars are tricuspid, whereas the permanent teeth corresponding to them are unicuspidate.

The permanent upper incisors are stronger than the lower and are arranged in one row. They curve inwards slightly and, on meeting the teeth opposite, somewhat overlap them. The front edges of their cusps are oval. The biting surface of the upper incisors is truncated and turned inward. The teeth are chisel-shaped. The outer two upper incisors are considerably larger than the central incisors and resemble the canine teeth in shape.

Apart from size, the incisors of the lower jaw differ from those of the upper jaw in shape and distribution. The tips are truncated, the biting surfaces are horizontal and they are arranged in two rows; the 2nd pair are placed slightly behind the row formed by the 1st and 3rd pairs and are turned inward towards the oral cavity.

The canine teeth are strongly developed in both sexes. There is a gap for the canine teeth of the lower jaw between the canine teeth of the upper jaw and the 3rd upper incisors. The canine teeth of the lower jaw are positioned adjacent to the incisors themselves. The crowns are conical and bent back. The canine teeth of the upper jaw are stronger than those of the lower jaw. The roots are shaped like a bent cone.

The first[1] premolar teeth of the upper jaw are poorly developed. Their blade-like crowns are shaped like a right-angled triangle, lying on its base, with the hypotenuse facing the adjacent second premolar teeth. The latter are better developed and have a single-cusped blade in the form of an isosceles triangle. The carnassial, the most powerful tooth in the dental arch, has three roots (two in front and one behind); the latter is larger. The crown of the tooth is in the form of a blade, roughly divided into two parts, back and front. The back blade is poorly developed and terminates in a right angle at the rear. The front blade is much larger and has a sharp cusp, and inside there is a tubercle on the inner column.

The first[1] premolar teeth of the lower jaw are very poorly developed and have a flattened chewing surface. The second and third premolar teeth are similar in structure to the first and second premolar teeth of the upper jaw, but rather larger.

---

[1] Technically, the first premolar is absent in both jaws: this is the second. See the description of Hall (1951)—Ed.

The molar tooth of the upper jaw lies at right-angles to the row of teeth and the masticatory surface of the crown has two tuberculate areas, one outside, the other inside (facing the tongue). It has only one root, flattened from the front rearwards, sometimes bifurcating at the end.

The molar teeth of the lower jaw [are very different]. The crown of the first molar, the lower carnassial, has three prismatic blades with sharp tips, the most powerful of which is the middle blade, which has a very sharp point. On the inside the crown has two depressions or grooves between the blades. It rests on two roots. The second and last molar is greatly reduced in size and shaped like a truncated cone. It has one root.

The nature of tooth abrasion

All the teeth of the ermine are subject to abrasion. The abrasion of incisors, canines, and premolars, with the exception of the upper carnassial tooth, does not seem to follow any set pattern, since individual variations are very great. However, examination of the abrasion process of the carnassial teeth and the upper molars gives a completely different picture. When food is being chewed, the upper carnassial overlaps the lower, not unlike the blades of a pair of scissors, and where they touch, friction must occur. The outer tuberculate area of the upper molar tooth also overlaps the outside of the last blade of the lower carnassial, and the recess between the middle and back blades of the lower carnassial covers the space between the outer and inner tuberculate areas of the upper molar, dividing it into two parts. There is no pressure on the inner tuberculate area of the upper molar when this happens.

Obviously, these teeth are most consistently in use and subject to constant stresses, and that is why abrasion proceeds more regularly than on other teeth and why the degree of their abrasion may be accepted as the most accurate criterion of their age.

The signs of tooth abrasion in the ermine appear late, when it is about a year old.

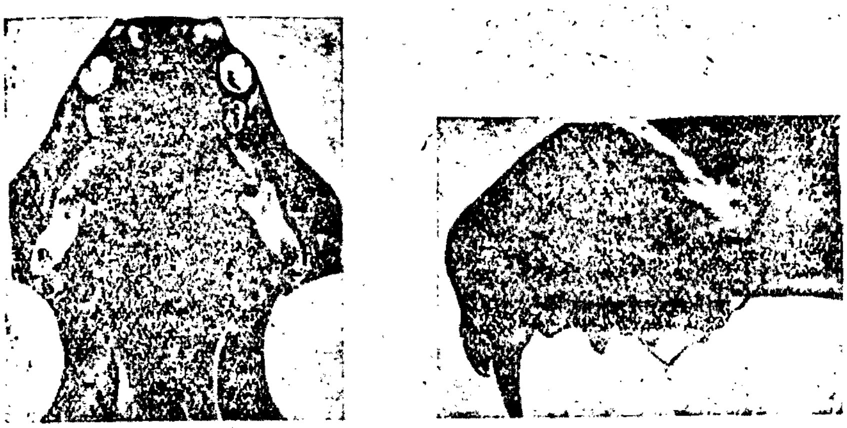
Having verified this description on a series of 700 ermine skulls, we selected the wear of the carnassial teeth as an age criterion, and so in future we shall focus our attention on them.

Age changes in the teeth

As was shown above, at the end of July and in August, after the change from milk teeth to permanent teeth, the latter quickly develop and by October-November are fully formed. In this period all teeth are very white, their surface glistening, the tips of the blades of the upper carnassials are unblunted, and the enamel is perfect. This is characteristic of an ermine of about 6 to 7 months.

During the following winter months right up to March, the sharp cutting edge of the blade of the upper carnassial is somewhat blunted as the result of abrasion of the enamel. A skull with teeth in this state will be found in material collected in the autumn-winter hunting season and corresponds to the age of a litter of the current year, i.e., from 6-7 months to 1 year old (Figures 1 and 2).

Specimens obtained during the summer months, showing increasing bluntness, i.e., abrasion of the sharp cutting edge of the blade of the upper carnassial, represent a further stage of development. Analysis of this material shows that the next stage is the appearance of a narrow strip of dentine along the edge of the blades of the upper carnassial, though the profile of the tooth is still basically unchanged. Similar signs are noted in specimens obtained between November and March, i.e., presumably between the ages of 1 year 7 months and 2 years (Figures 3 and 4).

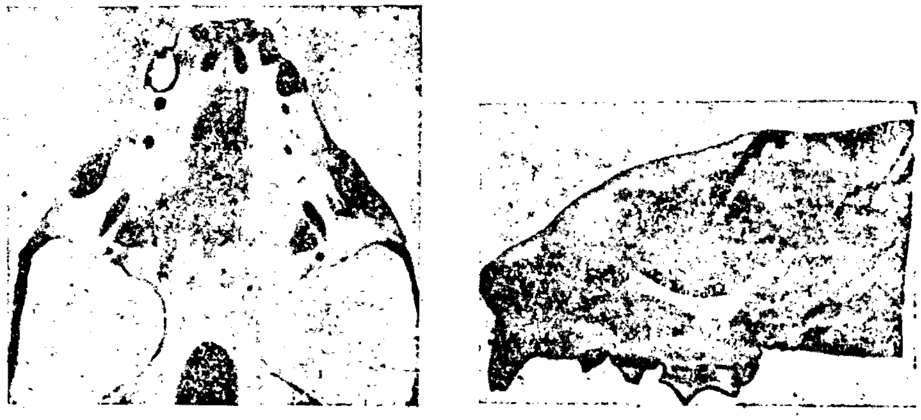


FIGURES 1 and 2: One year old

The establishment of later age classes from tooth abrasion becomes more difficult. However, by comparing the dates of capture with the degree of abrasion of the teeth, we consider it possible to distinguish the later age classes from the rate of abrasion in the first year of life, determined above.

FIGURES 3 and 4: Two years old

The following characteristics are peculiar to the 2½ to 3 year age group. Approximately twice the amount of dentine is exposed on the edge of the blade of the upper carnassial. The profile of the tooth looks like an arch with a semi-circular crown. Moreover a dentine patch appears on the outer tuberculate area of the upper molar (Figures 5 and 6). The inner recess between the first and middle blades of the lower carnassial is affected by abrasion which did not occur in the first two years (Figure 7).



FIGURES 5 and 6: Three years old

By the time the ermine is about 4 years old, the abrasion of the teeth is considerable. The rear blade of the upper carnassial is smoothed down almost to the base of the crown. Thus this tooth becomes, as it were, single-bladed. The lower tip of the remaining blade only just reaches the alveolus of the lower carnassial tooth. The profile of the tooth loses its arched appearance and resembles a triangle with blunted apex (Figure 9). The surface of the outer tuberculate area of the upper molar is ground down for about half its area (Figure 8). All three blades of the lower carnassial, and the inner depression between the first and second blades, are affected by abrasion (Figure 10).

FIGURE 7: Three years old

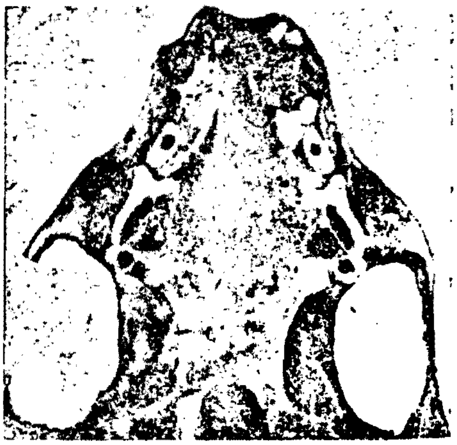
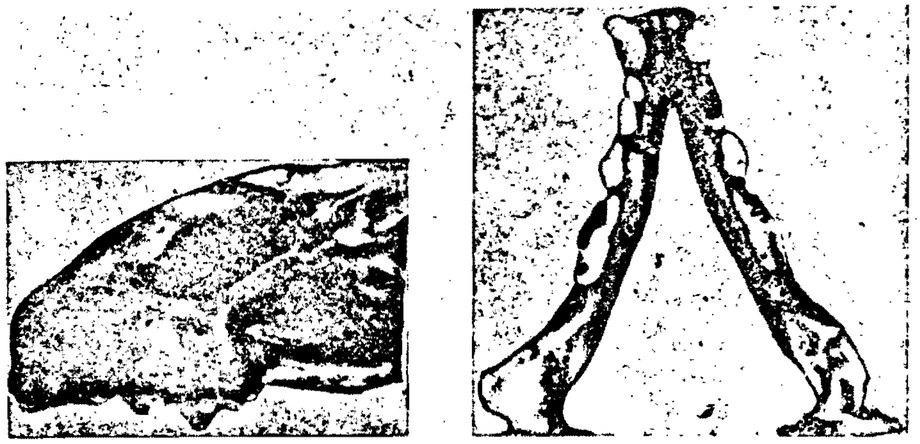


FIGURE 8: Four years old



FIGURES 9 and 10: Four years old

When the ermine is about 5 years old, heavy abrasion of the edge of the blade of the upper carnassial unites the strip of exposed dentine on this tooth with the dentine patch on the outer tuberculate area of the upper molar which occupies almost all its area (Figure 11). The profile of the upper carnassial is triangular with an obtuse angle at the apex (Figure 12). The tip of this tooth does not reach the aveolus of the lower carnassial tooth.

Finally, in the group which can be referred to as the oldest age group - about 7 years old - the dentine strip of the upper carnassial occupies almost the entire area of the base of the crown. The blades are smoothed. The profile of the examined tooth resembles a trapezium, the long base of which is formed by the neck of the tooth (Figure 14).

Concerning possible differences in the rate of abrasion of the teeth due to variations in the composition of the diet in different years and in different geographical areas and habitats, later studies show that they are insignificant.

FIGURES 11 and 12: Five years old

FIGURE 13: Five years old

FIGURE 14: Six to seven years old

The diet of the ermine is similar in all the habitats in which it lives. All known variations in the diet of ermine can be assumed to cause similar abrasive effects on the teeth, apparently not exceeding the extent of the variation within any one age group. The food of the ermine consists basically of mouse-like and some other, sometimes fairly large, rodents. This food varies, of course, depending on the habitat and its fauna. Thus, according to Yurgensen (1932), in river valleys and low-lying land around lakes the water-vole is the chief source of food for the ermine, and the next most important item is fish; on the tundra, lemmings, and on plains, susliks etc., form the diet. Small rodents may be considered the basic source of food for ermines.

It is quite possible that these variations in the diet of different populations of ermine have some effect on the rate of tooth abrasion, but the effect is not great and will not affect analysis of the age composition of the populations. This fact enables us to assume that the age scale described is fully valid for determining the ages of ermine in all districts.

A synoptic table for age determination in the ermine (*Mustela erminea* L.) from the teeth[1]

1. (a) The skull has milk teeth. It is bulging and has a rounded oval shape. The sutures are clearly visible, and the outlines of individual bones are distinct. The characteristic nuchal and sagittal crests are absent or barely noticeable. ....juvenile, about 3 to 4 months old.

(b) The skull does not have milk teeth .... 2.

2. (a) The permanent teeth are adult in form. They are snowy white, their surfaces glisten, their enamel is perfect. There are no traces of tooth abrasion whatsoever, either as wear of the enamel or as exposure of dentine. The sagittal and nuchal crests are well developed. The skull has lost its juvenile features and its shape is hardly distinguishable form that of the adult ermine. .... subadult, about 6 to 7 months old.

(b) The teeth show signs of abrasion; either the edges are blunted or the dentine exposed ....3.

3. (a) Traces of abrasion are visible on only one upper carnassial tooth. There is no dentine exposed but the sharp cutting edges of the blades are blunted (Figures 1 and 2). ....adult, about 1 year old.

(b) Dentine is exposed .... 4.

4. (a) Patches of exposed dentine do not merge to form a single strip of dentine on the two most posterior teeth of the upper jaw .... 5.

(b) The condition described in (a) above is observed .... 6.

5. (a) A dentine strip is found only on the tip of the upper carnassial. The strip passes across the rear cutting edge of the tip of the upper blade and the tip of the back blade. The profile of this tooth is basically unchanged (Figures 3 and 4). .... adult, about 2 years old.

(b) The dentine strip passes along the cutting edge of the upper carnassial and is twice as large as in (a) above. The profile of this tooth is arched with a semi-circular crown (Figure 6). The outer tuberculate area of the upper molar has a dentine patch in the shape of a crude isosceles triangle or square (Figure 5). .... adult, about 3 years old.

(c) The profile of the upper carnassial is pectinate with a very blunt tip (Figure 9). The rear blade of this tooth is levelled almost to the base of the crown. The rear blade of the upper carnassial is very worn and does not cover the alveolus of the lower carnassial when the jaws are closed. The dentine patch on the outer tuberculate area of the upper molar occupies about half its area (Figure 8). .... adult, about 4 years old.

6. The patches of exposed dentine on the carnassial and molar of the upper jaw have merged and form a single strip.

(a) The strip of exposed dentine passes across the tip of the blade of the upper carnassial and merges with the dentine patch on the outer tuberculate area of the upper molar. This dentine patch occupies almost the whole surface of the outer tuberculate area (Figure 11). The profile of the upper carnassial is triangular, with an obtuse angle at the apex (Figure 12)...................

adult, about 5 years old.

---

[1] When determining the age by means of teeth it is necessary to use a binocular microscope, as even a strong lens does not reveal all the details of the characteristic teeth abrasion patterns. With some experience the age of one skull can be correctly determined in 2-3 minutes.—Author.

A few extra lines have been inserted so as to make this table a workable key. —Ed.

(b) The dentine strip on the upper carnassial covers almost the entire area of the crown base; its blade is levelled. The profile of this tooth resembles a trapezium with the neck of the tooth forming the large base (Figure 14)...... senile adult about 6-7 years old.

Analysis of the age structure of ermine populations

We had available the following material for analysis of the age structure of ermine populations: a set of 83 ermine skulls, collected in the 1925-26 hunting season by G. D. Dulkeit on the Bolshoi Shantar Islands; 192 skulls collected in the 1933/34 hunting season by workers of the Volzhsk Kanskoye Biological Station; 119 skulls collected in the 1930/31 season by the same station in the Menzelinsk and Krasnoborsk regions of the Tartar Autonomous SSR, and 198 skulls collected by M. D. Zverev between February and April 1929 in Western Siberia. 592 skulls were examined in all. All the material was collected from ermine trappers, as indicated above, in the trapping season. Thus, the skulls examined show the state of the population during the hunting season and are a fairly accurate reflection of the age composition of ermine in the wild. They represent samples of ermine populations obtained during the hunting season in regions in which hunting differs in intensity.

Using the scale which we had evolved for determining the age of ermine, we analysed the age structure of the samples. The results are given in Table 1 and Figure 15.

TABLE 1. The Age structure of ermine populations

	1 year		2 years		3 years		4 years		5 years		6 years or more	
	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%
Bolshoi Shantar Is.	56	69.0	19	23.5	6	7.4	2	2.3	-		-	
Tartar SSR (1933/34)	74	38.5	65	33.8	32.	16.7	13	6.8	6	3.1	2	1.1
Menzelinsk & Krasnoborsk regions of the Tartar SSR (1930/31)	72	60.5	24	20.2	12	10.01	6	5.04	4	3.3	1	0.8
Menzelinsk region (1929/30)	14	62.5	4	20.8	5	25.0	1	0.5	-		-	
Western Siberia (1929)	98	49.5	45	22.8	32	17.2	14	7.0	7	2.5	2	1.0

The results enable us to reach some conclusions on the rates of mortality in populations of ermine in different years, in different regions and under different hunting conditions.

Three characteristics of the age structure of the samples examined must be noted:

1. The variation in the proportion of the young of the first year to the older age group.

2. The distinct difference in the proportions of the adult age groups between samples from the Tartar SSR and Western Siberia on the one hand, and those from Bolshoi Shantar Island on the other.

3. The low maximum age in the Shantar sample in comparison with the samples from Western Siberia and the Tartar SSR. Whereas in the latter two regions a number

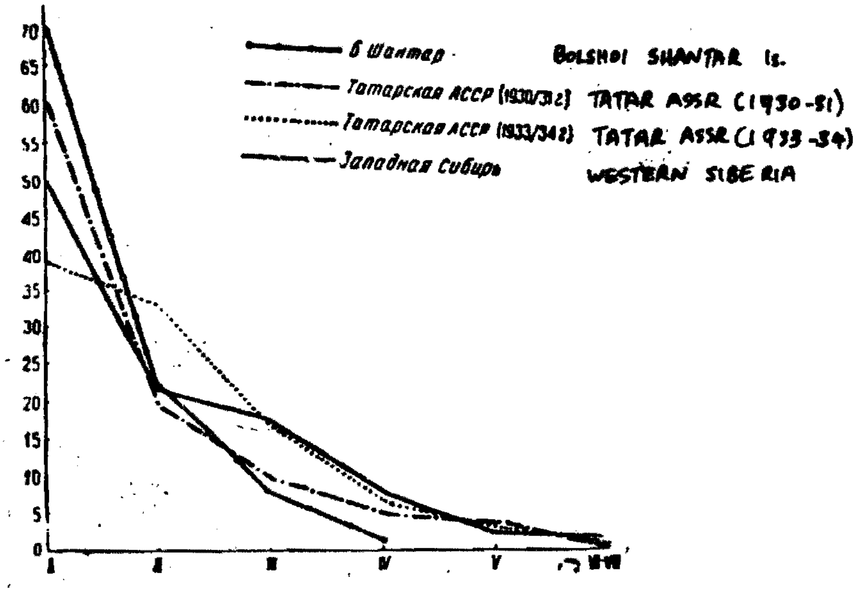


FIGURE 15: Maximum longevity and mortality rate of ermine in 4 populations

of ermine live till the age of 6-7 or more, the maximum age of the Shantar ermine, according to our data, is 4 years.

These characteristics can be explained as follows.

The variation in the proportion of the young animals to the adults in different regions and in different years undoubtedly indicates differences in ecological conditions. As shown in Table 1, the young ermine comprise 69.1% of the ermine population on Bolshoi Shantar Island and 60.5% in the Menzelinsk and Krasnoborsk regions of the Tartar Autonomous SSR. This ratio of young to old appears to be typical of the results of hunting ermine throughout the season. Approximately the same results (5 young to 2 adults) were obtained by Kozlov (1931) in the steppe polecat (*Putorius eversmanni* Les.) in the Lower Volga region. It must be noted that Yurgenson (1933), using a combination of cranial characters, classified 54 of 74 skulls of Shantar ermine as young animals, a similar result to my own. This consistency confirms the accuracy of my age criteria, since we had both been examining the same material.

Comparing our data with similar information obtained by Naumov (1934, 1935) for the squirrel and the little suslik (*Citellus pygmaeus* Pall.), we observe first of all a clear difference in the ratio of young to adults (Figure 16). From 66.6% to 82.5% of the specimens taken from the squirrel population are young. Kalabukhov shows that 67% of the total suslik population consists of young. This percentage is closer to that of the ermine population, especially as Naumov (1935) found, in the same suslik, the 1 year old age group comprised 54.7%. The reasons for this lie in the biology of the species. Each year the squirrel gives birth to 8 to 10 young, reproducing twice, while the suslik produces one litter per year, with an average of 5 to 6 young per litter. The ermine also reproduces once a year, but the number in the litter varies from 4 to 13.

The proportion of young ermine in the Western Siberian population (49.5%) must also be considered "normal". As indicated earlier, this sample was obtained between 26th January and 1st April, i.e., at the end of the trapping season. Without doubt a large proportion of the young are caught in the first half of the season, when they enter traps much more often than the more experienced adults. Hence, towards the end of the season the ratio of young to adult should level out slightly.

There is an extremely low percentage (38.5%) of young among the ermine from the Tartar SSR during 1933/1934. The possibility of error in determining the age of the 1 year old ermine can in our opinion be completely ruled out, since apart from tooth abrasion, the skull of the young ermine is easily distinguished from that of the adult by the cranial characteristics. The sample is also valid because, as reported by V. P. Teplov and V. Tikhvinsky, the skulls were collected indiscriminately from hunters at all times during the season. Consequently, a mass mortality of the young ermine must have taken place in the spring or summer preceding the hunting season. Confirmation is also provided by data on state purchases of ermine [pelts].

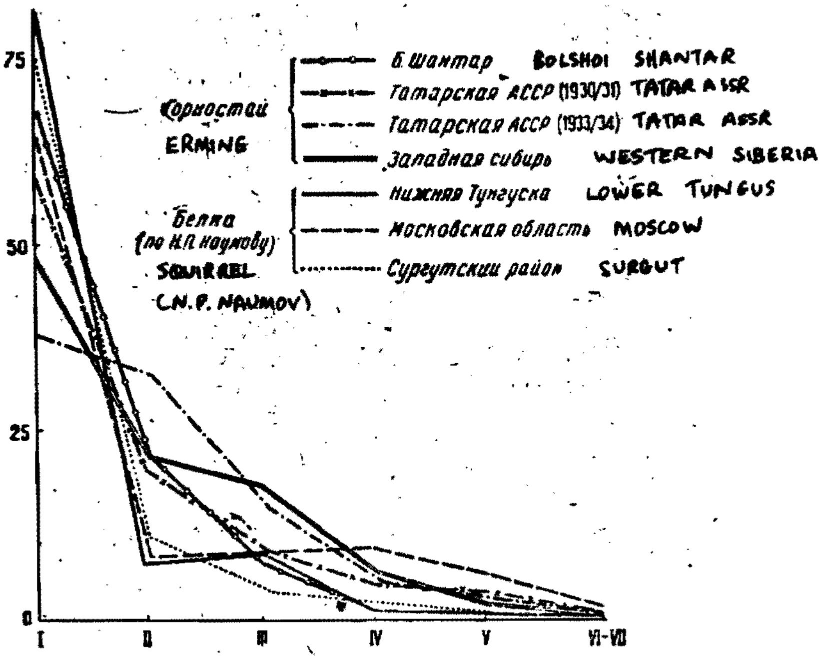


FIGURE 16: Mortality rates in samples of ermine compared with those in samples of squirrels (data from N. P. Naumov).

The graph (Figure 17) shows [the annual variations in the number of] ermine caught in the Tartar SSR from 1927/28 to 1933/34, inclusive. As can be seen from the curve, the lowest yield occurred in 1929/30, 1930/31, 1931/32 and 1932/33. According to V. Tikhvinsky the reason for the drop in the yield of ermine in 1929/30 was the switching of hunters to agriculture. Most hunters were diverted to farm work in the newly formed kolkhozes. Only with the more stable organisation of the kolkhozes, beginning in 1931/32, did state purchases of ermine begin to increase, but it was still far from the level reached in 1927/28 and 1928/29. This level was not reached in 1932/33 or 1933/34 either, but the reasons here are different. In addition to general factors causing fluctuations in the number of these animals in different areas, the flood level of the Kama in spring, and perhaps in autumn, has a bearing on the number of ermine in the Tartar SSR. As is generally known, the ermine in the Tartar SSR, like everywhere else, chiefly inhabits flood-plains. According to data of Zharkov (1934) "the index of density of ermine in the flood-plain regions in Tartary and Bashkiria ranges from 1 to 5 per 1000 hectares; other regions, even where heavily wooded, give indices from 0.01 - 0.1 and seldom higher than 1.0. The difference between the indices of 1926 and 1934 is so great that it often exceeds the difference in annual fluctuations." Bashkirov and Grigorev (1931) indicate that "the population drops sharply in flood areas after high water, especially in areas which have been almost entirely deforested, where ermine, particularly young ermine, often have had no refuge at all." The destruction of young ermine when the Kama overflows its banks is also confirmed by Pershakov (1928) who observed on the 25th April 1925 the attempts of a female ermine to rescue her young from their flooded home. At flood-time the inundation areas of the lower Kama and Volga are submerged in water and the beginning of the flood coincides with the birth of the young. Undoubtedly, the high overflow of the Kama and Volga in the coastal regions of the Tartar SSR has tremendous significance as an ecological factor, and greatly influences the population fluctuations of ermine by its effect on the survival of the newborn and nestling young.

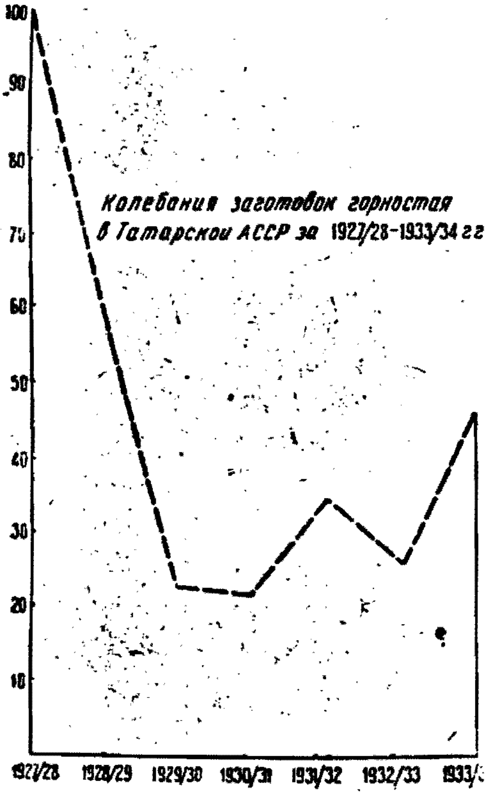


FIGURE 17: Annual variations in state purchases of ermine in the Tartar SSR from 1927/28 to 1933/34 (1927/28 = 100%)

From a comparison of the data of State purchases of ermine in the Tartar SSR with the annual flood levels of the Kama, it is clear that the flood of spring 1932 (the highest in recent years) coincided with the minimum number of state purchases of ermine in 1932/33 (Figure 18).

The level of the spring flood of the Kama in 1933 was apparently favourable for the production of ermine. However, the state purchases of 1933/34 did not reach even 50% of the 1927/28 level; so there are apparently other factors also causing a sharp decline in the number of ermine.[1]

The above information confirms the conclusion reached by us concerning the mass mortality of young ermine in the spring and summer of 1933. Unfortunately the causes of these deaths could not be determined. There is the possibility that the ermine suffered from an epizootic disease. Formosov (1935), reporting on the capture of a tularemic steppe polecat in Kazakhstan, considers this "a fact which has tremendous significance in explaining the connection between the fluctuations in the number of tularemic rodents, and in the animals which hunt them."

In examining the questions of the longevity and the mortality rate of ermine in different regions and in different years, we used mathematical methods for more exact analysis. For determining the percentage of deaths and survivals we used the formula employed by Baranov (1918):

---

[1] See Lavrov (1956) in King (1975)—Ed.

$$K = \frac{\lg n_1 - \lg n_2}{(t_1 - t_2)\ 0.434}$$

$$\lg f = K.0.434$$

$$M \quad = 100 - f$$

where K is the mortality factor; f the percentage of specimens still alive by the end of the chosen period of time; M - the percentage of deaths per annum; t_1, t_2 - the extreme age groups examined; n_1 and n_2 - the numbers of the extreme age groups examined. The results are shown in Table 2.

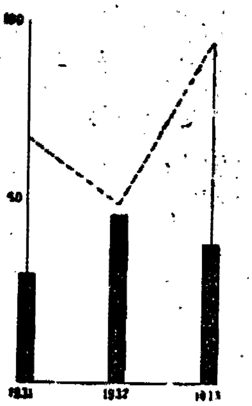


FIGURE 18: Comparison of the number of ermine purchased by the state (dotted line) with the level of the spring flooding of the Kama at Yelabuga.

The data below show that the mortality and survival rates of the ermine in Western Siberia and the Tartar SSR are very similar. This shows that the ecological conditions and the intensity of ermine hunting are the same in both regions.

TABLE 2: Percentage mortality and survival in ermine populations[1].

Region and year	f	M(%)	K
Tartar SSR 1931/1934	46.14	53.86	0.774
Menzelinsk and Krasnoborsk regions of the Tartar SSR 1930/1931	49.34	50.66	0.707
Western Siberia II-IV, 1929	50.08	49.92	0.692
Bolshoi Shantar Island 1925/1926	32.46	67.54	1.126

Judging by the available data, the ecology of the ermine has been studied more fully in Western Siberia and the Tartar SSR than in other regions; the habitats, diet, and reproductive characteristics etc., are similar in both regions. In taxonomy the West Siberian ermine (*Mustela erminea tobolica* Ogn.) is very close to the Volga-Kama ermine.

---

[1] In the calculation we used only ermine aged between 2 and 6½ years, since the mortality rate of the ermine during the first year of life, and the rate of reproduction in the years when the samples were taken, were so different for all examined regions, that a special examination is needed, the results of which I shall discuss below.—Author

Yurgenson (1931) who recently studied the question of ermine hunting, writes that "a characteristic of ermine hunting statistics is that the highest yields come from semi-hunting regions, for example, the former Vyatsk and Cherepovets provinces and the regions on either side of the Urals. This is because, on the one hand, non-professional hunters frequently hunt the ermine as secondary employment and, on the other, the population density of ermine is particularly high in these regions."

The researches of Bashkirov and Grigorev in the Tartar SSR and of Troitsky (1930) in Western Siberia show that in these regions the available hunting opportunities are not used to the full. The ermine is hunted with gun, dog and traps only as a spare time job.

These factors are apparently responsible for the similar rates of mortality and survival in Tartar SSR and Western Siberia. It is natural that the ermine's life span should also be the same in both regions.

The data on the age structure of the ermine population of Bolshoi Shantar Island give an age curve of quite a different sort, unlike the curves described for the Tartar SSR and Western Siberia. A comparison of these curves, and the data of Table 2, reveals a higher mortality and a lower maximum age of ermine on Bolshoi Shantar Island. While there were quite a number of 6 to 7 year old specimens, and even older ones, in the material from the Tartar SSR and Western Siberia, no specimens more than 4 years old were found on Bolshoi Shantar Island.

It seems to us that the reasons for this, as established by Naumov (*loc. cit*) for squirrels, lie partly in differences in the intensity of hunting. Hunting appears to be fairly intensive on Bolshoi Shantar Island. G. D. Dulkeit (1929) says that in 1920/21, 20 Yakut and Tungus hunters caught 350 to 400 sables; moreover they hunted them only in the first half of winter, the rest of the time they searched for dens and shot squirrels, foxes and otters. They ceased hunting by mutual consent, leaving about 40 or 50 sables on the island. With such experienced hunters as the Yakuts and Tungus, using dogs and traps on the restricted area of an island, hunting is non-selective and the age-classes are harvested, in proportion to their numbers in the population. Here qualitative selection and natural mortality are not of any great significance. This, according to Naumov (*loc. sit*) lessens the chances of wild animals living to an old age "and the biological life span is reduced to 2 to 3 years. It should be mentioned also that Mejsner (1933) in "Commercial Ichthyology" states that the maximum age of fish decreases when fishing increases.

With the evidently reduced scale of hunting in Western Siberia and the Tartar SSR the life span of the ermine increases and individual specimens live to a very old age, when they are bound to die of starvation after losing all their teeth. There are no data in the literature on the life span of ermine in their natural state. But judging from the fact that Severtsov (1930) established a life span for the pine marten of 8 to 9 years, depending on the rate of growth and the age at puberty, we can assume that the life span of the ermine is up to 7-8 years. If this is so, then in areas where there is very little hunting, the life span of the ermine nearly reaches its biological maximum.

Conclusion

Data on the age structure of samples of hunted ermine enable us to determine the yield and the effect of hunting on the stocks of ermine. Analysis of the age structure of ermine populations may indicate the state of the populations.

1. Constant proportions over a number of years of the age groups in samples from a given area, taken at the same time in similar environments, indicate the the intensity and extent of regular hunting. The fluctuations in the number of state purchases will be governed only by fluctuations in the numbers of ermine, which depend on other factors.

2. An increase over a number of years in the percentage ratio of older animals, and a high percentage of young in the population at the end of a hunting season, may be a sign that the species is being under-harvested.

3. When the number of state purchases remains relatively stable or drops over a period of years, and there is a predominance of young in the population and a heavy reduction or absence of the older age groups in the yield (Bolshoi Shantar Island), we can say that hunting is over-intensive.

4. An abrupt change in the percentage ratio of the age groups due to a sharp decline in the number of first year animals collected even when hunting is stable or less intensive than in previous years, indicates a drop in the number of births or a mass mortality of young from some external cause.

5. As yet we are unable to define precisely just what proportion of young to adults reveals the most satisfactory yield and success in hunting. To solve this problem we require systematic observations of the ermine over a number of years in one region, or, better still, simultaneously in several regions.

6. The weakest point in papers on age-determination methods for game is the absence of any direct data for the evaluation of the authenticity of the age scale. If further research is conducted in this direction, the young ermine in a particular region will have to be tagged and thorough observations of the tagged population made. This will enable us in future both to define the age scale more exactly, and also to study the dispersal of ermine and to determine the reasons for it. The most suitable region to carry out these projects appears to me to be the region of the Lower Kama in the Tartar SSR. At flood-time there it is easier and cheaper than anywhere else to organise ermine tagging and to conduct further observations on the tagging of the ermine population by the Volga-Kama Zonal Biostation.

SUMMARY

From the practice of cattle-breeding it is clear that the teeth are the principal index of the age of a mammal. An investigation into the process and rate of the wear of the teeth of the ermine (*Mustela erminea*) allowed the author to work out a method for age determination for this species, described in the text and presented in the form of a synoptic table or key.

The age structure of ermine populations sampled over a number of years from the Tartar ASSR,, from Western Siberia and from Bolshoi Shantar Island, are compared.

Data obtained from an analysis of the age structure of samples of ermine may indicate the state of the population as follows:

1. Constant proportions of the age groups in samples from one region, taken over a number of years when environmental conditions are relatively stable, indicate a satisfactory level of hunting. Fluctuations in supplies of ermine will be due only to natural variations in the ermine population.

2. If more older ermine are found, and a higher proportion of young at the end of the hunting season, hunting is too light.

3. If the yield is stable or decreasing over several years, and there is a great predominance of young combined with a scarcity or absence of older ermine (as on Bolshoi Shantar Island), hunting is too heavy, probably exceeding the limits of rational exploitation of the stock.

4. If there is a sharp reduction of young even though the level of hunting has not changed, a failure of reproduction or a mass mortality of young ermine may be be suspected, due to some external cause.

5. As yet it is not possible to define precisely the proportion of young to adult ermine which gives warning of reproductive failure or an unsatisfactory level of hunting. To solve this problem it is necessary to carry out systematic observations on the ermine in one, or even better, several regions simultaneously, for a number of years.

6. The weakest point in works on methods of age determination in furbearers is the lack of data for validation of the criteria of the age scale. When developing further investigations on this it will be necessary to tag young ermine and observe them carefully. This will in future permit criteria of age to be made more precise, and will also provide information on the causes and extent of dispersal of young ermine.

[No references given—Ed.]

FACTORS DETERMINING FLUCTUATIONS IN THE NUMBERS OF ERMINES

by

D. I. Aspisov and V. A. Popov

*The Volga-Kama Game Hunting Scientific Research Bio-station
of the Main Fur Trade*

[From: Arb. d. Naturforsch. Ges. an der Univ. Kasan, 6: 41-64, 1940].

The ermine is a significant member of our fur-bearing fauna. According to Guber and Gavrilova [6] ermine supplies 5.7%-6.2% of the USSR fur harvest, which exceeds the contribution of so widespread a species as the blue hare (*Lepus timidus*) (data collected 1927-32). In the fur export trade, ermine is even more important. The yield of ermines, as can be seen from the available supplies of pelts, fluctuates considerably from year to year. For instance, in the Tatar SSR the output of ermine pelts, taken as a percentage of the previous year, varies from 7 to 324%. Similar variations occur in other regions.

Fluctuations in the output of ermine pelts reflect fluctuations in their numbers. Therefore it is extremely important to determine the factors that explain these fluctuations, because only thence may we try to predict the yield of ermines, and also to conserve them.

Research on the theme "Ermine Forage Reserves" was done at the Volga-Kama area bio-station in 1938/39, as undoubtedly changes in prey populations are a significant factor affecting the fluctuations of ermine numbers.

Although work on this subject has not been finished, we can already point out the main factors which influence the fluctuations in ermine numbers, and in some cases even use these factors to forecast the yield of ermines. This is possible because even before 1938 members of the staff carried out a series of studies on ermines. Beginning in 1929, the feeding habits of this species were systematically studied by Grigoriev, Teplov, and Tikhvinski [7]. In 1934-35 I. V. Zharkov [11], from examining the methods used in the ermine trade, gave a summary of biological information on this species and worked out an original method of estimating ermine numbers.

In 1938 A. A. Sukharnikov [20] studied the distribution of small mammals, the principal food of ermines on flood plains. Between 1935 and 1937, data collected incidentally allowed us to establish the presence of a period of delayed implantation, which extends the total gestation period in the ermine to 7-8 months (N. D. Grigoriev, [8]). In 1936/37 V. I. Tikhvinski [22] showed a correlation between fluctuations in the ermine population and some meteorological factors. Finally, material collected in 1938 allowed us, as can be seen later, to determine a close relationship between the yield of ermine pelts and fluctuations in prey of ermine, and even to point out some methods of forecasting the yield of ermines from this relationship. A summary of this material is urgently needed, because, as will be shown later, in order to obtain data from which to make accurate forecasts of the yield of ermine in future, the work programme of the Fur Trade System must be supplemented.

In the following account we will summarise available data on the basic ecology of ermine, and will discuss the various factors which influence the population dynamics of this species.

Beside the authors, the following members of the staff at the station took part in research and data collection: N. F. Mironov, F. N. Azantsevski, and A. A. Vlasov. V. I. Tikhvinski greatly helped with work on the section dealing with the forecasting of ermine pelt stocks.

Brief summary of ermine biology

Habitat

The hunting grounds most densely populated by ermines in the Volga-Kama area are the flood plains of the big rivers: the Kama, Volga, Belaya and Vyatka. This is shown clearly in Figure 1, which was drawn up using data from the Tatar Republic.

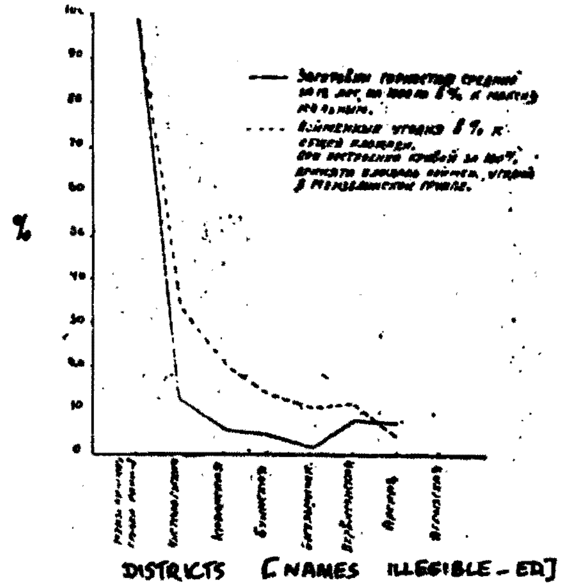


FIGURE 1: Relationship between the yield of ermine and the proportional area of flood-plains in different districts

———— average yield of ermine per 1000 ha. over 12 years, expressed as a % of the maximum.

---------- Flood-plain areas as a % of the total area of each district, taking the area of the flood-plain of the Mengelinsk group as 100%.

As the graph shows, the yield of ermine in different districts varies with the percentage of flood plain areas. Indeed, in Tatary, the number of ermines caught in the flood-plain districts is often six times higher per unit area than in the dry valley districts. Outside the flood plains the ermine is found in marshes, along lakes, in damp gullies, and along forest and steppe streams, that is, almost always near water. Ermines avoid huge forest blocks, open plains and fields. Small numbers of ermine are also found in felled and burnt areas and forest outliers. The majority of writers describing distribution of ermine in the various physico-geographical zones, also show that the most populated ermine habitats are those near by water, as follows: Shantar Islands: G. D. Dulkeit [10]. West Siberia: M. D. Zverev [12], I. D. Kiris [13], and V. N. Troitski [21]. Altai: B. A. Kuznetsov [14]. The Urals: Kuklin [15]. The forest steppe zone: G. A. Velizhanin [4] and Dobrokhotov [26]. Central European USSR: L. I. Girshfeld [5], E. A. Bekshtrem [1], A. A. Pershakov [18], and I. V. Zharkov [11] The Ukraine: A. A. Brayner [2]. In the tundra of the Gydan peninsula, as S. P. Naumov [17] points out, the distribution of ermine is patchy, as it is correlated with the habitats of lemmings, the ermine's principal prey in the tundra.

The restriction of ermines to localities close to water is probably related to the abundance of food in such places, particularly to the concentration there of the water vole. Some confirmation of the comparatively high food resources of the flood plains can be seen in the results obtained from transect censuses of small rodents, which were carried out in the flood plains of Kama and in the Cheremshan forest. The data are shown in Table 1. The table shows that the number of murine species in the flood-plain, compared with the forest, is extremely high. This indicates a stable reserve of prey, and the possibility of substituting one type of food for another, should the numbers of one kind drop for a time. This is of great significance in assessing the prey populations of different habitats. The density index of small rodents on flood plains is higher than that in the forest. And finally, in flood-plain areas, even during the years of low numbers of water voles, on average 14 water voles per kilometre of the shore line can still be found. Considering that there are also opportunities for catching fish, birds and other prey on the flood-plains, and that the most common rodents of the flood-plains are those that are most preferred by ermine (see below), it is clear that the potential prey resources of flood plains are higher than those of other habitats.

The distribution of ermines in the flood plain is uneven. The censuses of ermine tracks carried out here in 1934 by Zharkov [11], and in 1937/38 and 38/39 by us, show that ermines are concentrated along the shores of reservoirs and brushwood lowlands. Table 2 shows the distribution of ermine tracks in various localities on the Kama flood plains in 1937, estimated over a route covered on foot (a distance of 25 550 paces, or 23-24 km, along four parallel lines, crossing the open country and 800 paces apart from each other).

The table shows that the maximum density of tracks occurs in the brushwood, usually in damp lowlands, lake shores, and marshes. The somewhat lower density of tracks in the last-named habitat type is due to the inclusion of routes crossing frozen lakes and marshes, not usually frequented by ermine and having only transit tracks. Excluding these areas, there were 3.5 ermine tracks to 100 paces along the shores of reservoirs.

In 1938 a second census of ermine tracks was carried out, which gave similar results to that of 1937. From the distribution of prey resources in the flood plain, we can see that the concentration of ermine tracks along the shores or reservoirs and brushwood lowlands is not incidental, but occurs because it is here that the ermine finds most of its food.

This hypothesis is confirmed by Table 3, which shows the distribution of small rodents by habitat. Table 3 shows that along the shores of lakes and marshes the density index of small rodent populations is comparatively high (0.14) and, an especially important point, there are many common and root voles, both readily eaten by the ermine. Considering that the shores of reservoirs are also favoured habitats of water voles, it is clear that lake-shores and marshes in a flood plain have undoubtedly the best feeding and hunting conditions, which accounts for the concentration of ermine tracks.[1]

The considerable concentration of ermine tracks along the brushwood lowlands is also understandable. It is related to the parching of the open meadows, which is known to be the cause of autumnal migrations of common voles to the brushwood lowlands and fields. On the other hand, by the time snow falls, the population density of voles on open meadows undoubtedly drops, because of the effects of predation by birds [of prey].

---

[1] Our data on the distribution of prey species by habitat in the flood plain basically agree with the data obtained by A. A. Sukharnikov [20] in August/September 1935, in a different flood plain area. The differences that do appear are probably seasonal. We carried out our census through the whole vegetation season, while Sukharnikov did his at the end of summer. On the other hand, there are also differences in character between the flood plain where we worked and that where Sukharnikov worked—Author.

TABLE 1: Density estimates of small rodents in floodplains compared with forest.

Locality of census	DATE	Trapnights ("Gero" type traps)	Numbers caught	Density index	Species						
					Bank vole %	Grey vole %	Root vole %	Striped field mouse %	Northern birch mouse %	Common red-backed vole %	Harvest mouse (*Micromys minutus*) %
Cheremshan forest massif of the Tatar Republic. Mixed leafy forest (linden oak, elm, aspen)	June 1938	175	9	0.05	66.7	-	-	-	22.2	11.1	-
Kama flood plain, Alekseyev area, Tatar Republic. Areas of the flood plain totalling a hectare	June 1938	175	15	0.09	26.7	39.6	6.7	17.5	8.1	0.7	0.7

TABLE 2: Distribution of ermine tracks in the Kama flood plain, according to the census taken on a walking-route on 8 December 1937

Habitat	Length of the census route		Number of tracks found	Number of tracks per 100 paces
	Paces	%		
Open meadows	13 750	58.4	61	0.44
Brushwood meadows	1 400	6.0	14	1.00
Brushwood lowlands	650	2.8	16	2.46
Shores of lakes and marshes	2 000	8.5	47	2.35
Oak crests[1]	4 050	15.1	16	0.39
Coastal high forest	1 600	6.7	12	0.75
Forest clearings	600	2.5	-	-
	23 550	100%	156	0.62

[1] Stopbanks, levees or low hills?—Ed.

TABLE 3: Distribution of small rodents in various habitats on the flood plain

Habitat	DATE	Trap-nights ("Gero" trap type)	Numbers caught	Density Index	Species					
					Bank Vole %	Grey vole %	Root vole %	Field mouse %	Long tailed field mouse %	Common redbacked vole %
High forest along shoreline		150	21	0.14	42·8	23·8	-	9·6	23·8	-
Shoreline of lakes and marshes	from April to November	1555	218	0.14	18·1	16·7	17·6	38·8	8·8	-
Open fields		1630	126	0.08	0·8	83·4	-	11·9	3·1	0·8
Brushwood		2875	369	0·12	46·6	13·5	1·6	27·2	11·1	-
Oak crests[1]		1875	275	0.14	54.9	6.2	0.7	21.8	13·8	2.6
Areas totalling one hectare of the flood-plain		8085	1009	0.09	25.9	44.5	2.7	18.2	8.2	0.5

[1] See footnote, Table 2.

Biology of reproduction

It is not the immediate task of this article to discuss ermine reproduction, and we will touch on these questions only generally and only as much as is relevant. The latest investigations by Zharkov [11] and Grigoriev [9] have demonstrated delayed implantation in ermines, leading to a pregnancy of the order of 7-8 months. Hence, ermines must mate at the end of summer or in autumn. In the spring there is probably a false rut, stimulating the development of the foetus or the mating of some animals which for some reason did not breed in the summer.[1] Information on numbers and the dates of birth of the young is shown in Table 4.

As with other Mustelidae, the date of birth of the young ermine is correlated with latitude, and usually coincides with the setting in of stable and favourable temperatures. In Tatary the young are born at the end of April or in the first ten days of May.

Ermines usually nest in the burrows of water voles and hamsters, less often in tree hollows: out of 12 nests found by the members of the staff of the Volga-Kama Biostation, 6 (50%) were made in the burrows of water voles and hamsters, 4 (33%) in tree hollows, and two, probably temporary ones, under rotten tree stumps. The inside of the nest, as a rule, is lined with scraps of water vole's fur, and near the nest a "toilet" can always be found.

TABLE 4: Bibliography on the breeding season and numbers of young of the ermine.

Author, region	Date of birth	Numbers of young in the litter
Browner, A. A. [2] Ukraine	End of March or earlier	3 (1 litter)
Beckstrem, E. A. [1] former Ryazan province	1st half of May	3 - 5
Zharkov, I. V. [11] Tatary	Beginning of May	5 - 6, up to 11
Zverev, M. D. [12] West Siberia	April	3 - 10, up to 12
Troitski, V. N. [12] West Siberia	End of April	6 - 8, up to 12

In the rearing of the young the male probably takes part as well as the female. Usually the male can be seen near the nest burrows (Dulkeit [10], Zharkov [11], and Grigoriev [9]). It is interesting to note that the majority of the ermine nests found in the Kama flood plain were situated on patches of higher ground, which are seldom flooded.

The young are born completely helpless and blind, and for up to one month do not crawl out of their burrow. For about 2 months they need the complete care of their parents. They become independent in July. By September the young reach the size of a fully grown female, but the males sometimes

See footnote, Table 2.

---

[1] Because accurate information on these questions is important in working out the reasons for fluctuations in the ermine populations, we are including them in our future research—Author.

overtake her in size. The sex ratio of the young is close on one to one. Carcasses of ermines obtained in the Volga-Kama area during the 1928-1937 hunting seasons (940 specimens) show a predominance of males - 60% [8]. Zverev [12] examined 1734 ermines, and found 53% males, 47% females. Similar data have been obtained by Zharkov [11] in the flood plain of the lower reaches of the river Kama, whilst taking censuses of ermine tracks showing 57% males: 43% females. Considering the greater activity of the males, we can assume that in reality the sex ratio is closer to equal.

Diet

We obtained 1585 ermine stomachs in the Volga-Kama area, most of which were used in the papers of Grigoriev, Teplov and Tikhvinski [7]; Grigoriev and Teplov [8]; and Zharkov [11]. The ermine's diet was particularly fully studied during the winter hunting season (1055 samples). The processing of these stomachs by N. D. Grigoriev and V. P. Teplov gave the information in Tables 6 and 7.[1]

From the list of prey, we see that small rodents predominate; they were found, on the average over 8 years, in 68.9% of dissected stomachs. The first place among small rodents invariably belongs to the common vole. The percentage of small rodents found in the stomachs of ermines fluctuates between the years, reaching a maximum in the years of their population peaks, as for example in the years 1932/33. According to Falkenstein [23], 1932 was a year of high numbers of small rodents (this is also confirmed by observations carried out by members of our research station) and we see that in Tatary the percentage of small rodents found in the food of ermines increased to 82.3%, its absolute maximum. By contrast, in years of low populations of small rodents, their presence in the ermine's diet in the flood plain environment fell to 42.8%.

Second place in the ermine's diet, in terms of the number found, is taken by the water vole. In the peak years for water voles, this species was found in 49.1% of dissected stomachs, but in the years when the numbers of water voles dropped, as happened in 1932/33, the numbers of stomachs containing water voles fell to 2.7%. Through a period of years, the water vole was found on the average in 13.8% of dissected stomachs.

Since on average the weight of a water vole is higher than that of the common vole (the common vole was taken as the prey unit by Greigoriev and Teplov, [18]) by 5 times, the water vole is clearly the principal item in the diet of ermine. Other types of food, as the table shows, are seldom found. Their unit weight in the ermine's diet is mostly measured in tenths of one percent.

Unfortunately, the diet of ermine during the summer, which is of great interest to us, is represented by only 200 stomachs. Because of the small sample, we have to present data from all years combined (Table 8). The tables show that there is no substantial difference in the diet of winter compared with summer (snowless) seasons. In summer, as should be expected, the intake of small rodents and birds increases somewhat.

Investigations carried out by Zverev [12], who processed 1600 data on the diet of ermines collected in Western Siberia during the years 1928/29, show that there too the water and common voles are the principal prey.

We conclude that the common and water voles are the most important prey of ermine. Tests carried out by feeding various prey to ermines in captivity also show the ermine's preference for common voles and water voles. By giving the ermines some of each species found on the flood plain, we usually noted that they preferred common and root voles to other types of small rodents. But when the water vole was also given to the ermine, we

---

[1] There is no Table 5—Ed.

TABLE 6: Annual variation in the diet of ermine in the Volga-Kama area (1055 items)

Years	No. of items	Water vole	Other rodents	Insectivora	Birds	Amphibians	Fish
1928/29	56	35.7	59.0	18.0	5.4	-	10.7
1929/30	85	17.6	65.9	6.0	3.5	1.1	8.9
1930/31	157	18.4	67.5	16.5	0.6	-	2.5
1931/32	16	-	75.0	-	12.5	-	12.5
1932/33	74	2.7	87.8	5.4	1.3	-	-
1933/34	522	9.0	68.5	11.6	4.2	0.9	5.1
1934/35	57	49.1	49.1	5.3	-	1.7	7.0
1936/37	88	5.6	78.1	3.4	10.2	5.4	3.0
1928/37	1055	13.8	68.9	10.6	3.6	0.6	5.0

TABLE 7: Composition of the winter diet of ermine, from 1055 items identified during the years 1928/29-36/37.

Ser. No.	Prey	Nos of items found	%
1	Mammalia	948	89.8
2	Rodents	863	81.8
3	Water voles (*Arvicola amphibius* L)	146	13.8
4	Bank vole (*Evotomys glareolus* Schr)	16	1.5
5	Common vole (*Microtus arvalis* Pall)	302	28.6
6	Root vole (*M. oeconomus ratticeps* Keys *et* Blas)	8	0.75
7	Striped fieldmouse (*Apodemus agrarius* Pall)	10	0.94
8	Other small murids	356	33.7
9	Hamsters (*Cricetus cricetus* L)	9	0.85
10	Hares (*Lepus europaeus* Pall, *L. timidus* L)	12	1.13
11	Insectivora	112	10.6
12	Shrews (*Sorex*)	104	9.8
13	Birds (*Aves*)	38	3.6
14	Fish (*Pisces*)	53	5.02
15	Insects (*Insecta*)	6	0.56
16	Plant remains	16	1.5

TABLE 8: Diet of the ermine during the summer (snowless) season

Ser. No.	Prey	Nos of items found	%
1	Mammals	179	86.1
2	Rodents	178	85.6
3	Water vole (*A. amphibius* L)	34	16.3
4	Common redbacked vole (*E. glareolus* Schr)	4	2.0
5	Common vole (*M. arvalis* Pall)	75	33.9
6	Root vole (*M. oeconomus ratticeps* Keys et Blas)	20	9.6
7	Striped field mouse (*A. agrarius* Pall)	13	6.2
8	Long-tailed field mouse (*A. sylvaticus* L)	2	1.0
9	Small murids	30	14.4
10	Insectivora	1	0.5
11	Water shrews (*Neomys fodiens* Schub)	1	0.5
12	Birds (Aves)	11	5.3
13	Fish (Pisces)	1	0.5
14	Insects (Insecta)	1	0.5
15	Plant remains	16	7.7
	Total	208	

became convinced that the latter is preferred even to the common and root voles. As a rule, bank voles are eaten as second choice, with mice following. With great reluctance, after forced hunger periods, the ermine eats shrews (*Sorex araneus, S. minutus*).

Some information about the ermine's diet preferences in its natural habitat was collected in areas where the populations of prey were known. In the summer of 1938, on the Kama flood plain in the vicinity of the permanent [field] station, we collected 60 scats of ermines. The results of processing this information are shown in Table 9, as well as the [relative abundance] (%) of the small mammal prey in the areas where the scats were collected. The latter information was obtained as a result of laying pit traps [19] and noose traps in census transects. Comparing the biomass of various species of small vertebrates in the diet of ermines and in the areas where the ermine scats were collected, we find that despite the considerable biomass of bank voles, wood and field mice, and shrews, these species are of little significance in the ermine's diet. The ermine is clearly able to choose, and its preference is for the common and water voles. Summarising the above data, we consider that the common vole and the water vole are the principal prey of ermine in the Volga-Kama area through all seasons of the year.

Influence of Meteorological factors on changes in ermine populations

The influence of some meteorological factors on fluctuations in the numbers of ermine in Tatary was studied by Tikhvinski [22]. He established that the following factors influence the yield of fur, and therefore presumably also the populations, of ermine, in the conditions prevailing in Tatary:

1. the level of flooding (we obtain the highest pelt yield at times of average flooding);
2. the average temperature during the period 1 April - 20 June; and
3. the average temperature in July.

Using a combination of these factors, Tikhvinski was able to predict the yield of ermines in Tatary with an average deviation of 36.2% from the actual yield, when the average yearly fluctuation in yield was 90.5%. However, Tikhvinski obtained these results purely from statistics. In his work he only assumes the causes of the correlations he found. Our data, from a series of cases, provide factual evidence, on the causes of Tikhvinski's results, which basically confirm his assumptions.

As was to be expected, the positive influence of average flooding on the ermine population is because floods create favourable conditions for the hunting of the nursing female, whose nests are built on crests.[1]

TABLE 9: Comparison between prey taken by ermine during the summer of 1938, and the prey available.

	Composition of ermine diet during summer 1938		Relative biomass of small rodents in the areas where scats were collected
	No.	%	%
Common vole	12	20.0	28.5
Root vole	14	23.3	8.6
Water vole	14	23.3	4.2
Bank vole	4	6.3	10.2
Striped field mouse	12	20.0	12.8
Long-tailed field mouse	2	6.8	3.0
Harvest mouse	-	-	4.2
Shrew	-	-	28.7

The census carried out on small rodents during the flooding of 1938 showed (see Table 10) that the density of small rodents on half-flooded crests increases more than tenfold (from 0.07 to 0.72-0.80). As further evidence, we can quote the results of a census on water voles carried out by an expedition made by members of the research station. "In May 1931, along the flooded shoreline of the Kama Flood plain, 59 water voles were counted over a distance of 150 metres, and at the same time a dog caught 26 water voles in 20 minutes and discovered two steppe-polecats, who feed exclusively on water voles. (Plenty of fur, guts, tails, paws and other remains were found around the burrows"—I. V. Zharkov [11]).

On the other hand, heavy floods reduce the prey populations of ermine (not to mention that in such years many ermines are also drowned). After a heavy flooding, the areas which have been covered by water are repopulated by small rodents at a slower rate than after a light or average flooding, because of their distance from the "survival localities" (crests) and also because of the loss of a considerable number of rodents during the floods. In such cases, the ermine will probably have to concentrate near the remaining pockets of small rodents, and will experience food shortages. The conditions

---

[1] See footnote, Table 2.

TABLE 10: Census of small rodents during the flooding of 1938.

Date	Locality of census	Trapnights	Nos. caught	Density index	Species											
					Field mouse		Common vole		Root vole		Bank vole		Long-tailed field mouse		Shrew	
					No.	%	No.	%	No.	%	No.	%	No.	%	No.	%
9 May 1938	Brushwood crest with a black poplar clump 50% flooded (Volozhka)	25	20	0.80	5	25.0	6	30.0	-	-	6	30.0	2	10.0	1	5.0
10 May 1938	Oak crest 75% flooded (Plotzkaya)	25	18	0.72	6	33.3	-	-	12	66.7	-	-	-	-	-	-
4 May 1938	Oak crest not in flood near lake Krivoye	125	9	0.07	5	55.5	-	-	-	-	2	22.2	2	22.2	-	-

prevailing during average floods will be more favourable for the ermine. Varshavski [3], who studied seasonal movements of small rodents, found that in the Don flood plain the density of rodents on flooded areas was restored by about the end of May (1936), that is a month after the floods. According to our observations, repopulation of the flooded areas begins the moment the water starts to recede. Such species as the water vole and root vole, then the fieldmouse and the common vole follow the receding waters. However, the population density is restored extremely unevenly, depending on the size and distance away of "survival localities" of the small rodents and the population density in these localities. In areas that are remote from the crests, the population density of the rodents is not restored even by autumn, whilst in areas close by the numbers of animals restored considerably faster.

Our observations show that the reduction of the yield of ermine pelts in years with a cold spring is explained by the death of the young, due not to low temperatures, but to the lesser availability of small rodents to the ermines in such years. The activity of small rodents in spring is closely related to the minimum temperatures as illustrated by Fig. 2, drawn up from the results of B. A. Popov's studies in the south of Tatary. Ermines hunt small rodents mainly in the open; therefore, when rodents are not very active, and stay in their burrows, it is much more difficult for the ermine to catch them, and this must have a considerable effect during the period of rearing the young. The small rodents probably also increase less rapidly in years with a cold spring, because in such years the conditions for reproduction are not optimal.

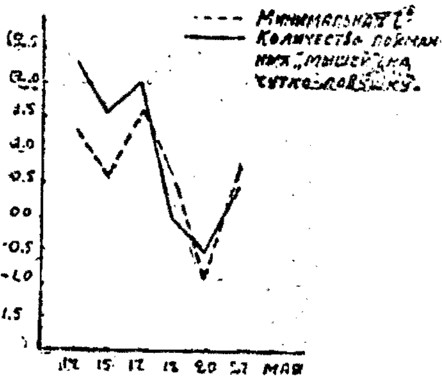


FIGURE 2: Activity of small rodents in relation to minimum temperatures.

-------- Minimum temperature

________ No. small rodents caught per trapnight

So far, we have no data to explain the relationship between the yield of ermine pelts and the July temperatures. Nevertheless, it is probably due to the influence of meteorological conditions on small rodents, which in colder, damper years are more exposed to sickness, and probably breed less. This illustrates that when studying the reasons for changes in the ermine population, simple correlations with meteorological conditions are insufficient; it is necessary to try to relate changes in the ermine populations directly with changes in prey populations, so that a closer relationship may be obtained.

Fluctuations in ermine populations in relation to changes in food supplies

We have already established that the water vole is one of the main food resources of the ermine. Hence, it follows that a correlation may be expected between the numbers of these two species in places where they co-exist.

Data on the yield of the pelts of both species exist and can be used to some extent as an index of their numbers. We will now proceed to examine this information.

We have at our disposal information from several provinces and republics of the Volga-Kama region on the stocks of ermine and water vole pelts [held in the fur warehouses] over the last few years, which are on the whole typical of the ermine and water vole pelt stocks from areas of similar size [in other regions].

The range of information from separate administrative units is not the same. The most complete data we received had been obtained from the pelt stores of the Tatar Republic. One can judge the [annual] changes in pelt stocks from Table 11. The figures were calculated as follows. The number of water voles (as indicated by stocks of vole pelts), may affect the yield of ermine only after the breeding season, so we compared the vole pelt stocks recorded for a whole calendar year with those of the ermine from the last quarter of the same calendar year and for the first three-quarters of the following year. The results are shown in Figure 3.

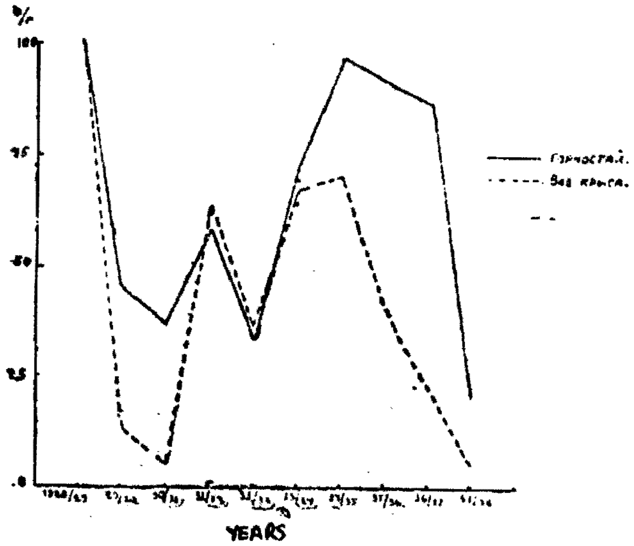


FIGURE 3: Annual variations in pelt stocks of ermines and water voles in the flood plain of the Kama River (Tatary), expressed as a % of the maximum yield.

——————— ermine -------------- water vole

These curves clearly confirm the correlation between the ermine and the water vole fur stocks. They are drawn from data on the pelt stocks in the districts of Tatary adjoining the Kama River flood plain, and therefore demonstrate the correlation very clearly. As the flood plain is the ermine's main habitat, the correlation is probably valid for the whole of the republic.

From the graph we see that a drop in the water vole pelt stocks is always followed by a drop in the ermine pelt stocks and vice versa; when water vole pelt stocks increase, the pelt stocks of ermines increase as well (Lavrov [16] also points out the correlation between fluctuations in the numbers of the Siberian weasel [Kolinsky] and the water vole). However, in some seasons, as for example in 1935/36 and 1936/37, after water vole pelt stocks had dropped sharply, the drop in the ermine pelt stocks was comparatively slight. Undoubtedly, the drop in water vole pelt stocks reflected a sharp decline in the population of voles (this is confirmed by the information received from

TABLE 11: Annual variations in the yield of water voles and their use in forecasting the yield of ermine in the following season in different regions or republics of Russia.

Region or Republic	Years	Water vole pelt stocks as a % of the stocks of previous year	Ermine pelt stocks as a % of the maximum	Deviation of the actual ermine pelt stocks from stocks of previous year, as a % of the former	Anticipated ermine pelt stocks as a % of the actual stock of previous year	Deviation of the anticipated stocks from the actual, as a % of the latter	Index of forecasting success
Tatar ASSR	1928-29	-	100.0	-	-	-	
	1929-30	15	43.4	- 130.4	49.5	+ 12.3	
	1930-31	32	34.0	- 27.6	60.1	- 23.4	
	1931-32	1206	53.7	+ 36.7	158.0	0.0	
	1932-33	59	40.5	- 32.6	75.0	- 0.5	
	1933-34	179	74.5	+ 45.6	120.0	- 30.0	
	1934-35	102	99.1	+ 24.8	100.0	- 24.8	
	1935-36	58	87.4	- 13.4	75.0	- 14.7	
	1936-37	64	93.7	+ 6.7	78.0	- 27.2	
	1937-38	23	22.1	- 323.5	55.0	+ 133.0	
	Average			71.3	-	29.6	41.5
Mari ASSR	1933-34	-	60.3	-	-	-	
	1934-35	340	96.1	+ 37.2	159.9	+ 0.3	
	1935-36	75	62.9	- 53.0	83.0	- 26.9	
	1936-37	157	100.0	+ 37.1	121.3	+ 23.7	
	1937-38	34	30.0	- 233.3	61.9	- 106.8	
	Average			90.1		39.4	43.7
Kirov Region	1932-33	-	53.0	-	-	-	
	1933-34	204	66.0	+ 19.7	141.0	- 12.1	
	1934-35	68	62.2	- 6.0	80.0	+ 15.7	
	1935-36	427	100.0	+ 37.8	157.8	+ 1.7	
	1936-37	40	64.5	- 55.1	44.0	+ 31.8	
	1937-38	47	19.3	- 234.2	66.9	- 122.6	
	Average			71.0	-	36.8	52.0

TABLE 11: continued

Region or Republic	Years	Water vole pelt stocks as a % of the stocks of previous year	Ermine pelt stocks as a % of the maximum	Deviation of actual ermine pelt stocks from the stocks of the previous year, as a % of the former	Anticipated ermine pelt stocks as a % of the actual stock of previous year	Deviation of the anticipated stocks from actual, as a % of the latter	Index of forecasting success
Gorki Region	1932-33	-	51.0	-	-	-	
	1933-34	114	60.2	+ 15.3	104.9	+ 11.0	
	1934-35	275	100.0	+ 39.8	153.0	- 7.7	
	1935-36	67	70.5	- 41.3	83.5	+ 18.4	
	1936-37	42	53.1	- 32.8	65.0	- 13.7	
	1937-38	84	22.9	- 131.8	88.0	+ 104.0	
	Average			52.2		30.9	59.2
Bashkir ASS Republic	1931-32	-	86.0	-	-	-	
	1932-33	154	100.0	+ 14.0	120.9	+ 4.1	
	1933-34	123	83.0	- 20.5	108.0	+ 30.0	
	1934-35	85	78.0	- 6.4	89.0	- 5.1	
	1935-36	58	97.4	+ 20.0	74.0	- 40.8	
	1936-37	71	85.0	- 14.6	82.0	- 6.3	
	1937-38	41	21.2	- 301.0	64.0	+ 156.0	
	Average			62.8		40.4	64.3
Chuvash ASS Republic	1934-35	-	100.0	-	-	-	
	1935-36	31	61.8	- 61.8	98.5	+ 59.2	
	1936-37	75	59.2	- 4.4	83.0	- 13.2	
	Average			33.1		36.2	109.4
Udmurt ASS Republic	1933-34	-	72.2	-	-	-	
	1934-35	46	97.0	+ 25.6	67.0	- 50.0	
	1935-36	155	100.0	+ 3.0	120.8	+ 17.3	
	1936-37	44	65.9	- 51.8	65.0	- 1.3	
	1937-38	159	22.8	- 189.0	122.2	+ 252.0	
	Average			67.3		80.1	119.0

our own observations), and hence their availability as food for ermine was considerably reduced. Hence, a great drop in the ermine pelt stocks should have been expected, but it did not happen. This could occur only if, in the habitats populated by ermines, sufficient alternative prey species were available to replace the water vole in the ermine's diet. The principal alternative prey are in fact small rodents. And indeed, if we refer to the data on ermine diet, it is clear that this substitution always occurred, particularly in the seasons 1935/36 and 1936/37. This is clearly confirmed by Figure 4, which shows as a percentage the [annual variations in the relative] number of water voles and of small rodents found in the guts and scats of ermine.

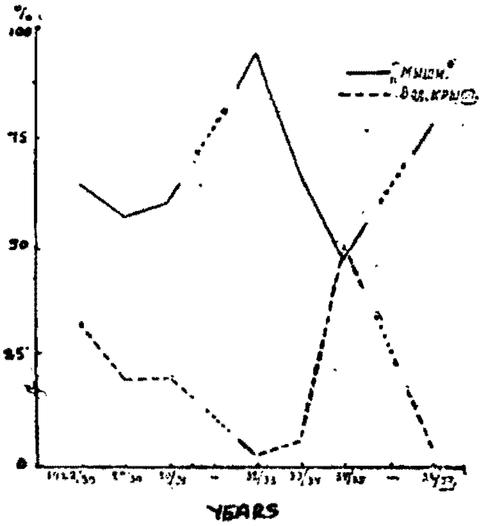


FIGURE 4: Annual variations in percentage occurrence of small rodents and water voles in the diet of ermine from the flood plain of the Kama River, Tatary.

———————— small rodents -------------- water voles

However, we must remember that such replacement of the water voles by the small rodents is possible only in years of peak populations of the latter, which, of course, will not always coincide with the years when there is a drop in the numbers of water voles. Therefore, in order to forecast the yield of ermine, it is necessary to consider the changes in the numbers of small rodents as well as water voles. If, at the same time as the water vole numbers fall, the numbers of small rodents increase, a drop in the ermine pelt stocks can be expected, though not a significant one. But a drop in numbers of small rodents *and* water voles will inevitably bring a sharp decline in the ermine population and hence in the yield.

The close relationship between the pelt stocks of the water vole and ermine makes it possible to attempt a forecoast of ermine pelt stocks from the water vole pelt stocks. However, the economic situation should also be taken into account, as it has a significant influence on pelt stocks. In order to reduce this influence to a minimum, V. I. Tikhvinski has suggested that we do not use the absolute pelt stock figures, but we express them as a percentage of the figures of the previous year. This considerably lessens the influence of the economic situation, as the conditions of two consecutive years are more similar than those compared over a more lengthy period. Besides, the number of a species in the present season depends largely upon the number born in the previous season and now reproducing. In considering the pelt stocks as a percentage of the previous year, we take this into account. We followed the method described above, of comparing the water vole pelt stocks for one calendar year (for example 1931), with the ermine pelt stocks for the last quarter of that year and for the 1st, 2nd and 3rd quarters of the following year (in this case 1932).

Here we met with a serious difficulty: the vole, as a pelt producing species, has shown up only comparatively recently in the pelt stocks, and in some years the yield, depending on the hunting trade situation, increases too fast.[1] Hence, for certain areas we used only the data from the years following the years of maximum yield. However, even with this restriction the vole pelt stocks in some years increased too rapidly. Considering that it is unlikely that the vole population could increase fourfold, we set a ceiling of 400% as the maximum possible increase, and, in years in which the pelt stocks had increased more than fourfold, reduced the increase recorded to 400% (we had to do this for only 2 figures). These procedures gave 34 pairs of figures for correlation, namely; in Tatary for 9 years, in Bashkiria for 6, in the Kirov and Gorki regions for 5 years, in the Urdmurt republic for 4 years, in the Mari republic for 3 years and in the Chuvash republic for 2 years (see Table 11).

The correlation coefficient between the water vole and the ermine pelt stocks turned out to be very high and quite reliable (0.71 ± 0.09). After further analysis we found that a curve expressed relationship between the water vole and ermine pelt stocks better than a straight line. This curve is shown in Figure 5.

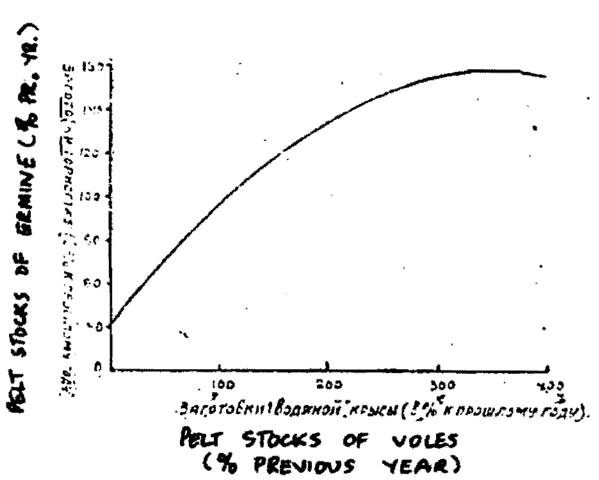


FIGURE 5: Correlation between stocks of pelts of water voles and ermine.

As can be seen from the curve, the ermine pelt stocks increase in the beginning as quickly as the water vole pelt stocks do, but later on the increase slows down, and eventually, after the increase in water vole pelt stocks exceed 320% compared to the previous year, further increase ceases to influence the ermine pelt stocks, which is quite understandable from the biological point of view.

As might be expected, when the pelt stocks of water voles are stable (100% of the production of the previous year) the ermine pelt stocks also remain stable (about 97% of those of the previous year).

Figure 5 illustrates the possibility of forecasting the ermine pelt stocks from figures available on the water vole pelt stocks. The results of this forecast, for single years and provinces, are shown in Table 11. The table shows that in most cases the trend of changes in ermine pelt stocks is forecast well from calculations based on Figure 5.

---

[1] i.e., the increase in production was due more to economic than biological factors—Ed.

To express the extent of agreement between expected and actual stocks, Tikhvinski [22] suggested a special index of success in forecasting. In order to calculate this index, the average deviation of the anticipated pelt stocks from the actual, expressed as a percentage of the latter, is shown as a percentage of the figure derived from the same calculation for the previous year. This index is used with the minus sign[1] and the smaller its absolute value, the more accurate is the forecast. If the absolute value of this index is more than 100, the forecast is unsuccessful. According to the figures in Table 11, the forecasts of ermine pelt stocks based on the water vole pelt stocks are successful in all regions except for Udmurtia (index of success -119.0%) and for Chuvashia (-109.4%). These provinces do not have many large rivers, therefore the water vole is probably less important in the diet of ermine in these areas compared with areas with well-developed flood plains (Chuvashia adjoins the Volga only with a mountainous shore line.) If these provinces are excluded, then the forecasts deviate from the actual pelt stocks by an average of 39.7% while fluctuations of pelt stocks shown as a percentage of the previous year average 67%.

We calculated the anticipated pelt stocks above from the figures of the water vole pelt stocks over a calendar year. However, when using this method in practice it is quite possible to obtain a forecast from the figures of the water vole pelt stocks for the 2nd quarter of the calendar year only, expressed as a percentage of the corresponding period of the previous year. This makes it possible to forecast the ermine pelt stocks in the forthcoming season by as early as the 15th of July. The method of forecasting ermine pelt stocks from water vole pelt stocks is more accurate than other methods of planning, as can be seen from Table 12.

Diseases and parasites of ermines

So far, we do not know of any cases of mass destruction of ermines due to an epizootic. No such event is reported in the literature. However, Formosov [23] refers to a case of tularemia in a polecat found in the district of Dzhambeity (Kazakhstan). As the polecat and the ermine are closely related, it is reasonable to expect to find tularemia among ermines too[2] - particularly as the water vole in the Volga-Kama district is subject to this disease.

We did not carry out any special research into diseases affecting ermines, but used the information collected earlier on helminthiasis in ermines. A total of 39 ermines were obtained during the winter season of 1937/38 in Tatary and were examined for helminths by complete dissection according to Skriabin's method. Eleven of these ermines turned out to be infested (28.2%). The extent of infestation was insignificant. As can be seen from Table 13, trematodes predominate.

Regrettably, we do not have a list of helminths affecting ermines, and at present we are unable to assess their importance in the biology of the animal.

A considerable infestation of ermines with parasites affecting the major organs such as lungs and liver, together with the discovery by A. M. Formosov of tularemia in a steppe-polecat, certainly means that future work on the causes of the fluctuations in the ermine population must include parasitological studies.

---

[1] Omitted from Table 11, probably by a printer's error—Ed.

[2] Lavrov (1944) found tularemia in ermines: see King (1975)—Ed.

TABLE 12: Percentage deviation of the expected ermine pelt stocks in Tatary from the actual, over the last 9 years (1929/30 - 1937/38) (expressed as a % of the actual pelt stocks).

Forecasting method	From	To	Average
Based on the average [ermine] pelt stocks over the last 3 years	8	128	72.0
Based on the actual [ermine] pelt stocks of the previous year	7	324	71.3
Based on the flood level, average temperatures during the period 10 April - 20 June and average temperatures of July (data obtained by V. I. Tikhvinski)	1	76	33.2
Based on the water vole pelt stocks	0	133	29.6

TABLE 13: Helminths of ermine in Tatary in 1937/38

No. of ermines examined	39
No. infected	11
Trematodes	
Lungs	2
Liver	4
Intestines	4
Stomach	3
Total	8
Nematodes	
Intestines	1
Stomach	3
Total	3
Cestodes	
Liver	1
Intestines	2
Total	3

CONCLUSIONS

We can state the following list of factors determining the fluctuations in ermine numbers:

1. The size of the water vole population. The significance of this factor for the Gorki and Kirov regions and the Tatar, Bashkir and Mari republics has been proved. For the Udmurt and Chuvash republics it has not yet been confirmed. Its effect is shown in Figure 5. It can already be used in forecasting by calculating the expected yield of ermine next season from figures for the water vole pelt stocks in the 2nd quarter of the current year.

2. Numbers of small mammals. This factor can modify the accuracy of forecasts made from water vole yields. Particularly large errors are possible if the minimum numbers of water voles coincide with the maximum numbers of small rodents; therefore the latter factor has to be always kept in mind when making the forecast. Regrettably we cannot yet describe more accurately the correlation between the populations of ermine and of small rodents because we do not have even a rough index of the fluctuations in the numbers of small rodents over a long enough period of years.

3. The level of floods.

4. Spring temperature (10 April - 2 June).

5. Summer temperature (July).

The influence of these factors has been confirmed only in Tatary, but they are probably important in other regions as well.

It is obvious that when forecasting the ermine yield, all the factors listed have to be considered to some extent. The accuracy of the forecast will be sufficient only if, on the one hand, the relationship between the ermine pelt stocks and all 5 determining factors is established sufficiently accurately, and, on the other hand, the inter-relationships between the factors themselves are established.

Unfortunately, this is not yet possible, but a programme can be outlined which will provide the necessary information within a few years. For this purpose it is necessary to collect enough numerical data over a sufficiently long series of years.

1. First of all, it is necessary, of course, to regulate the process of the stocktaking of pelts. This must be done by the fur-trading organisations from a cross-section of separate pelt collecting points (otherwise it is impossible to assess fluctuations in pelt stocks in different areas, or to obtain information from a region which has changed its boundaries). Furthermore, in the same cross-section it is absolutely necessary to take the census of the stock of pelts for the four quarters of the year, as the population of the species in the current season is computed from the pelt stocks of the 4th quarter plus the pelt stocks of the three quarters of the following year.

2. The census data for water voles and for small rodents can be supplemented by analysing the ermine's stomachs. The percentage of stomachs in which one or the other species was found shows with the utmost accuracy the numbers of these species in the environment, which in future can be used to make a forecast of the yield of ermine.

Therefore a collection of ermine carcasses (50 from each region, or from a [representative] part typical of the natural conditions of the region; or even better 50 carcasses each at the beginning and end of the hunting season) must be included in the programme of studies of the yield by fur-trade organisations. The Biostations must process the material in good time.

However, until this work is begun, the numbers of water voles and small rodents may be estimated, from less accurate data, obtained from correspondents, on the numbers of these species in the 2nd quarter. Also the pelt stocks of water voles can be used as an indirect indicator of their population levels.

3. In order to confirm the influence of climate on the ermine pelt stocks outside Tatary it is necessary to collect sufficient information on the pelt stocks taken from a cross-section of the separate pelt collecting points [in other regions]. Within the next few years this material will be gathered.

Already we have the possibility of forecasting ermine pelt stocks from a single factor (the water vole pelt stocks), with an average deviation of 39%, and an average fluctuation of the pelt stocks of 67% (in Tatary alone the corresponding figures are 29.6 and 71.0). We can expect that future forecasts, using additional data on all the factors noted above, will be quite satisfactory. However, we cannot yet consider to have found all the factors determining the ermine population. The extent of the influence of such factors as diseases and parasites is still unclear.

SUMMARY

This article presents data collected by the authors mainly in 1939, during their research work on the lower part of the Kama River valley, near its mouth. They also made use of other information and data obtained by the Biological Station over a number of years. A summary of the research is given as the following hypotheses:

1. The ermine is most common on the flood plains of river valleys. Here it finds a great variety of prey; the main items are small rodents, particularly water voles (*Arvicola*) and common voles. Analyses of stomach contents showed that ermines prefer water voles and common voles; and this was also demonstrated by experiments with ermines kept in captivity.

2. The summer and winter diets of ermine are similar.

3. The distribution of ermines on flood plains is uneven. Marshes, damp scrub and riverbanks are preferred. Such places are rich in prey, and often the dens of water voles and hollows of logs are used by ermines for nests.

4. The development of ermine embryos includes a long delay in implantation. After mating in late summer the female does not give birth until next spring. The newborn ermine are helpless, but they are weaned by two months, and by four months they are about the same size as the adults. Sex ratio is close to one to one.

5. The population density of ermines is directly correlated with that of rodents, and particularly of water voles (Figure 5).

6. Reports of the number of pelts of watervoles collected in June are a sufficient basis for an approximate forecast of the yield of ermine pelts in the following winter. The forecast will be more reliable if additional data on the populations of small rodents are available.

7. Yields of fur are influenced by economic conditions, and therefore it is preferable to express a forecast in terms of a ratio to the crop of the previous year, not as an absolute number.

8. Climatic factors influencing the population of ermines in the wild include (a) the level of the spring flood of the Kama River (average levels are favourable); (b) the air temperature between 10 April and 20 June and through July (low temperatures are unfavourable). These factors act indirectly through their effects on the populations of prey of ermine. If only [climatic] data are available a forecast can still be made, but it will be less reliable.

BIBLIOGRAPHY

[1] Bekshtrem, E.A.K. (1931): Biology of the ermine. Zh. "Priroda i sotsialisticheskoe khozyaistvo" 9-10.

[2] Brauner, A. A. (1923): Selsko-khozyaistevennaya zoologiya [Agricultural zoology].

[3] Varshavski, S. N. (1937): Regularities in the seasonal movements of rodents. Zool. zhurn.

[4] Velizhanin, G. A. (1931): Zoological description of the polecat reserve of the Siberian branch of the Siberian Plant Protection Institute [Zoologicheskoe opisanie khorkovogo zakaznika Sibirskogo otd.] Institute zashchity rastenii Sibiri 1(8).

[5] Girschfeld, L. I. (1927): The game fauna of animals and birds of the Krasno-Bakov district of the Nizhegorod province. Materialy k izucheniyu flory i fauny centr. prom. obl., 1927.

[6] Guber, V. V. and Gavrilova, L. A. (unpubl.): The game economy of the USSR in figures. Manuscript, 1934.

[7] Grigoriev, N. D., Teplov, V. P. and Tikhvinski, V. I. (1931): Materials on the feeding of some game animals in the Tatar Republic. Records of the Volga-Kama Biological Station, 1.

[8] Grigoriev, N. D. and Teplov, V. P. (1939): Results of research into the diet of fur animals in the Volga-Kama region. Trudy ob-va estestvoispytatelei pri K.G.U. 56 (1-2).

[9] Grigoriev, N. D. (1938): Biology of the reproduction of ermine. Zool. zhurn. 17 (5).

[10] Dulkeit, G. D. (1929): Research on the sable, and sable farming on Bolshoi Shantar Island. Izvest. Tikhook. N. Prom. st. 3 (3).

[11] Zharkov, I. V. (unpubl.): Materials on the organisation of ermine hunting in the Tatar ASSR. Manuscript, 1935.

[12] Zverev, M. D. (1931): Materials on the biology and agricultural significance of polecats and other small carnivores of the family Mustelidae in Siberia. Trudy po zashchite rast. Sibiri 1/8.

[13] Kiris, I. D. (1934): Ecology of the Central-Obdorsk [Salekhard] squirrel. Sbornik [collected articles] "Ekologiya belki", KOIZ.

[14] Kuznetsov, B. A. [no date given]: Rodents of the Semipalatinsk district in Kazakhstan. Byull. Mosk. O-va isp. prirody 41 (1-2).

[15] Kuklin, S. A. (1938): The animals and birds of the Urals and their hunting. OGIZ, 1938.

[16] Lavrov, N. P. (1937): Materials on the biology of the Siberian weasel. Zool. zhurn. 16 (4).

[17] Naumov, S. P. (1931): The mammals and birds of the Gyda peninsula. Trudy Polyarnoi Komissii Akad. Nauk 4.

[18] Pershakov, A. (1938): A little about the ermine. Zh. "Okhotnik" 12.

[19] Popov, V. A. (unpubl.): An experiment in the acclimatization of the mink (*Mustela vison* Schr.) in the Tatar Republic. Manuscript.

[20] Sukharnikov, A. A. (1939): An experiment in determing the food value of the various habitats of the flood-lands for small Mustelidae and the fox. Trudy O-va Estestvoispytatelei pri KGU 15 (3-4).

[21] Troitski, V. N. (1930): Hunting in the Chuna-Angara district near the Kan River region. Izv. Sibirskoi Kraevoi prom. Biostantsii 1.

[22] Tikhvinski, V. I. (1938): Correlation between meteorological factors and fluctuations in the numbers of some hunted species. Trudy O-va Estestvoispytatelei pri KGU 15 (3-4).

[23] Fankelshtein, B. Yu. (1934): A survey of harmful rodents and measures for their control in 1932. Zashchita rastenii, 1934.

[24] Formozov, A. N. (1935): Fluctuations in the numbers of hunted animals. KOIZ, 1935.

[25] Yurgenson, P. B. (1933): Variability in the skull of the ermine. Zool. Zhurn. 12 (1).

[26] The world of animals in the Central Volga region. Sbornik OGIZ, Kuibyshev, 1937.

THE RELATIONSHIP BETWEEN AGE AND INDIVIDUAL VARIATION IN THE ERMINE

by

K. I. Kopein

[From: Akademija Nauk SSSR, Uraljskij Filial. (Works of the Institute of Plant and Animal Ecology) 71: 106-112, 1969.]

Introduction

The study of natural selection in the wild is one of the central problems of modern ecology. In recent years the opinion has often been expressed that a selective advantage spreads much more rapidly through a population than was formerly supposed (Sheppard 1959, and others). It therefore seems probable that, if not the results, then the trend of the selection can be observed in a relatively short space of time.

A great deal of material collected in a few years is required to study this problem. Moreover, this material must be collected from a relatively long-lived species in which the effects of natural selection can be followed in a single generation. The ermine, which lives 3-4 years, fits these conditions.

One possible way of solving the problem of the trend and effectiveness of natural selection is to study the differences in size between animals of different ages in natural populations. The study must concern itself only with those traits which are not affected by age changes in morphological features e.g., length of body, feet, tail, skull, row of teeth, etc., which remain virtually constant after adult size is attained). Differences which occur in these features between groups of different age provide a means of judging the direction of natural selection, and the size of the differences a way of judging its effectiveness. But selection cannot be judged from traits reflecting age variation (height of skull, size of [its bony] crests, wear of teeth, etc.) since the form of the skull will change with age to the same extent in all individuals of the same age.

For the main characteristics we took the condylobasal length (CBL) of the skull as the most stable indicator capable of accurate measurement, and also body length. The adult measurements of ermines, as observations have shown (Kopein, 1965)[1], are reached very quickly. By the beginning of the commercial hunting season, animals under a year old have almost the same measurements as adults. Other observers have also noted this (Klimov, 1940)[2].

Further growth takes place much more slowly and ends in the second year. This means that, other things being equal, every adult must be larger than a young animal (we are of course referring to individuals of the same subspecies). In previous papers on the ermine (Stroganov, 1937[1]; Klimov, 1940; Morozova-Turova, 1961) it is stated that the largest animals are old adults while the small ones are young, under a year old. Naturally, this is true for the species as a whole, not for single individuals. Thus, e.g., Klimov (1940) says that larger, and consequently older, animals are caught first, take part in migrations, etc. The whole population is divided into adults which are the biggest and the young which are small.

That is what we thought: but a preliminary processing of our material for two hunting seasons (1959/60, 1960/61) revealed that among adult animals there are small individuals (CBL of 44.2 mm), and among the young, large individuals (CBL of 52.0 mm). A more careful study of the material showed that large animals are found quite often among those under a year old, and small ones among adults. This occurs equally among males and females. Thus, e.g.,

---

[1] Translated in this volume—Ed.

[2] Translated in King (1975)—Ed.

in the 1963/64 season the 10 biggest young under a year old had an average body length of 286.7 mm and CBL of 51,5 mm for males, and 231.6 and 44.2 respectively for females. The figures for the 10 smallest adults were: 244.0 and 46.2 for males, and 218.0 and 42.0 for females. The same thing was found in other years (Kopein, 1961).

Material and Methods

Material for this article consisted of ermine carcasses collected in the northern Tjumen region over five hunting seasons (1959-1964), and also summer collections made in 1959/61. As additional material we had skulls, kept in museums and institutions, and collected over a number of years (1937-1940) from various parts of the country (Northern Kazakhstan, Krasnojarsk district, Irkutsk, Kirov and Omsk regions).

We had all together more than 4000 carcasses and skulls. All skull measurements were taken by the same person with calipers, 2-3 months after the skulls had been boiled. Age was determined from the teeth (Smirnov, 1959; 1960; Klevezal and Kleinenberg, 1964; Kopein, 1965). The method was checked against captive animals (27 ermine) and found to be reliable.

We distinguished three age groups: (a) under a year (age 6-8 months); (b) adults (1.5 years); (c) old (2.5 years and over). The reliability of the classification varies from 98-99% for males to 96-98% for females.

Results

Skull and body measurements of ermine of various ages.

A comparison between the measurements of animals of different ages caught in different years showed that animals under a year old have bigger skull and body measurements than adults, both over all the years as a whole and in separate years (Table 1). This we found both in males and females. In some years this difference is significant, (e.g., in males for 1960/61, males and females 1963/64); in other years the significance of the differences between the two age classes was only about 92% (t = 1.4). There are years when the difference is insignificant (1961/62, 1962/63). If all the material is combined (all years taken together), the difference in skull and body measurements between these two groups is significant (t >3). If we compare adults with old animals, the same phenomenon is found, although the differences are smaller and less significant (probably because of insufficient material). It may therefore be concluded that animals over two and a half years old have smaller measurements than one-and-a-half-year-olds and that the latter have smaller measurements than under-one-year-olds (6-8 months).

We have found no evidence (either in the literature or our own material) to indicate that ermine or other mustelids become smaller with age[1]. Published information on variation in skull measurements relates only to the smallest mammals (shrews). There is therefore only one possible explanation. Small individuals have some advantage over larger ones and live to a mature age in relatively larger numbers. As might be expected, this difference can be found only in large series, but the fact that it persisted over five years indicates that we are dealing with a regular, not a fortuitous, phenomenon connected with natural selection.

This conclusion is supported by comparing the measurements of individuals of a single generation at different ages. The average skull measurements of each of the generations we studied diminish with time (Table 1).

---

[1] In our vivarium 3 male ermine reached the age of 2.5 years, and one [female] reached 3.5 [years]. The CBL of the three males averaged 48.50 mm (47.1; 48.7; 49.7) and of the old, nearly 4-year-old, female, 42.4 mm)—Author.

TABLE 1: Changes in body measurements with age in the ermine

Sex	Age	body length (mm)		CBL (mm)	
		n	M ± m	n	M ± m
			1959/60		
Male	Young	150	258.5 ± 0.8	160	47.91 ± 0.10
	Adults	5	254.0 ± 5.0	5	47.83 ± 1.00
Female	Young	33	222.4 ± 1.5	47	42.25 ± 0.14
	Adults	1	-	2	42.55 ± 0.47
			1960/61		
Male	Young	1135	255.5 ± 0.3	1235	48.28 ± 0.04
	Adults	83	248.7 ± 1.1	84	47.81 ± 0.14
	Old	3	257.7 ± 0.5	3	47.67 ± 0.39
Female	Young	426	223.0 ± 0.4	557	42.39 ± 0.04
	Adults	25	220.0 ± 1.6	32	42.17 ± 0.16
	Old	-	-	1	-
			1961/62		
Male	Young	493	258.2 ± 0.5	525	47.75 ± 0.06
	Adults	130	258.2 ± 1.0	144	47.73 ± 0.13
	Old	15	258.2 ± 3.4	17	47.50 ± 0.32
Female	Young	170	223.2 ± 0.7	198	42.33 ± 0.09
	Adults	58	222.0 ± 1.1	63	41.97 ± 0.13
	Old	5	218.0 ± 3.0	6	41.48 ± 0.21
			1962/63		
Male	Young	-	-	13	47.63 ± 0.34
	Adults	-	-	3	47.63 ± 0.43
Female	Young	-	-	19	42.25 ± 0.20
	Adults	-	-	3	42.10 ± 0.13
			1963/64		
Male	Young	438	261.5 ± 0.9	476	48.62 ± 0.06
	Adults	20	248.9 ± 2.5	22	47.31 ± 0.31
	Old	-	-	2	47.30 ± 0.14
Female	Young	123	221.5 ± 0.9	146	42.54 ± 0.08
	Adults	6	218.0 ± 2.3	8	41.95 ± 0.23
	Old	-	-	1	-
			All years combined		
Male	Young	2216	259.4 ± 0.2	2409	48.20 ± 0.03
	Adults	221	255.9 ± 0.8	258	47.75 ± 0.09
	Old	20	256.8 ± 2.7	22	47.51 ± 0.25
Female	Young	752	229.9 ± 0.3	967	42.47 ± 0.04
	Adults	90	221.3 ± 0.8	108	41.98 ± 0.09
	Old	5	218.0 ± 3.0	8	41.69 ± 0.17

The diagram (Figure 1) shows the progression of these changes. Thus, e.g., if for under-one-year-olds born in 1959/60 the average skull measurement is 47.91 mm, then after a year (in 1960/61), when they have become adult (1.5 years old), the average skull measurement is less (47.81 mm). In the next year (1961/62) it has dropped further to 47.50 mm (2.5 years old)[1]. These observations are of special interest, since in different years the measurements of under-one-year-olds differ and are related to the population density. We discovered a law governing the changing measurements in different years (Table 1). The average figures for under-one-year-olds were highest in 1960/61 and 1963/64. These were the years of the highest population density of the ermine. The figures for under-one-year-olds were lowest in the years of lowest population density (1961/62, 1962/63). This may explain why the differences between the measurements of under-one-year-old and adult males were not significant in these years.

Our material shows that during the period of our observations there was a perceptible reduction in the average measurements of adult and old animals of the northern ermine population. Thus, if we compare the skull measurements of the adult group over five years, it turns out that these measurements dropped every year. This can be seen in Table 1 and Figure 2. This decrease goes on in spite of the fact that at this age the skull of each individual is still growing. This means that there is selection for animals of smaller size. We could identify a definite trend of selection. For how long it will go on is as yet impossible to say.

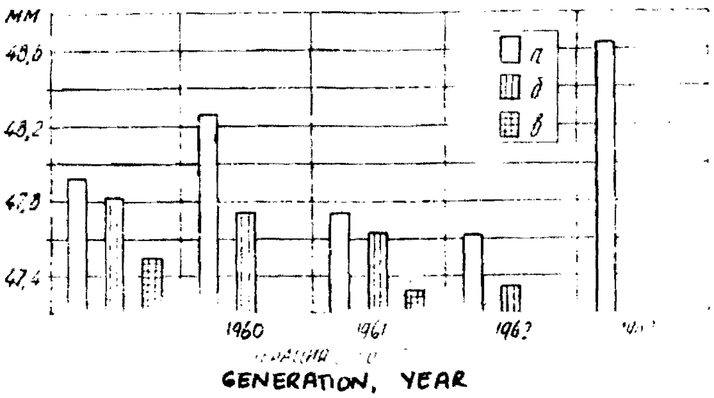


FIGURE 1: Average change in CBL with age in ermine of different generations ▭ Under one year old (6-8 months); ▥ Adults (1.5 years old); ▦ Old (over 2.5 years old).

This decrease in the average figures for adults is not confined to the northern ermine populations. It goes on in other areas (Table 2), although the significance of the difference in measurements is much less than in the northern ermine (the samples are small). It is interesting to note that the process of selection for small animals can be determined even in one season. Let us give an obvious example of the reduction in [average] measurements of ermines during one winter in one of the areas where our work was done (Labytpangi, Yamalo-Nenetskij district). The CBL of the skull of males by months was:-

Oct - 48.93 ± 0.12 (n = 120)
Nov - 48.57 ± 0.22 (n = 36)
Dec - 48.37 ± 0.27 (n = 35)
Jan - 48.23 ± 0.27 (n = 17)
Feb - 48.12 ± 0.23 (n = 44)
Mar - 48.20 ± 0.38 (n = 11)

---

[1] Turnover of the ermine population takes 3-4 years, i.e., animals may live for up to 3-4 years in the wild (Kopein, 1965)—Author.

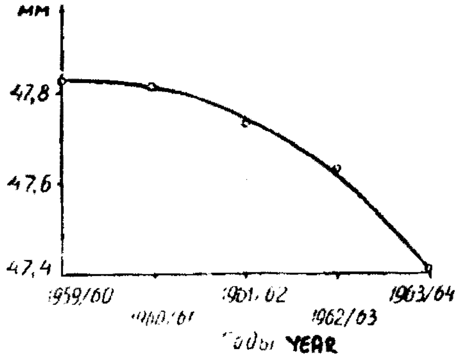


FIGURE 2: Decline of the average CBL in adult ermine

TABLE 2: Decrease with age in skull measurements of male ermine from various regions, mm.

Region	Year	Young		Adult	
		n	M ± m	n	M ± n
Northern Kazakhstan	1937/38	27	47.10 ± 0.26	24	46.37 ± 0.38
	1938/39	45	47.04 ± 0.23	26	46.29 ± 0.28
	1939/40	24	47.80 ± 0.24	5	46.86 ± 0.52
Krasnojarsk	1937/38	25	47.01 ± 0.28	8	46.25 ± 0.38
	1938/39	26	47.35 ± 0.27	6	46.65 ± 0.61
	1939/40	20	47.55 ± 0.25	6	46.47 ± 0.45
Kirov region	1938/39	34	47.41 ± 0.18	21	46.75 ± 0.28
Omsk region	1938/39	24	47.41 ± 0.26	8	46.91 ± 0.41
Irkutsk region	1937/38	11	47.22 ± 0.32	17	46.38 ± 0.22
TOTAL		236	47.32 ± 0.08	121	46.54 0.14

Some physiological features of animals of different ages.

It is possible that the physical demonstration of the law we found (the drop in average size of adults) is due to the nature of hunting (large animals are removed [first]). But the regular drop in average figures for adults over the whole period of our observations (in spite of the great variations in the measurements for the young) makes us think that the general trend of the changes we found is related to certain natural differences between animals of different sizes. We attempted to estimate the physiological state of large and small ermine from two very important indicators: fatness, and the vitamin A content in the liver.

In the 1963/64 season most of the samples we collected were tested for fatness and Vitamin A. In one instance we found a relationship between fatness and the age of the animals (Figure 3). It appeared that under-one-year-olds are less fat than adults. This applies both to males and females. It further emerged that females under one year old are fatter than their male contemporaries. To exclude the possibility of the influence of age (young, growing organisms usually have less fat than adults), we studied the relationship between measurements, fatness and vitamin A content in animals of all ages.

Table 3 shows that the smaller animals, both male and female, were fatter than the large ones. The vitamin A content is also higher in smaller animals than in larger ones. Admittedly, the reliability of this is only 82% for males and 90% for females. Here apparently, there are additional factors which we as yet have not identified. Incidentally, the group of males having the most vitamin A (more than 700 mg %) has an average CBL of 47.96 mm (n=16).

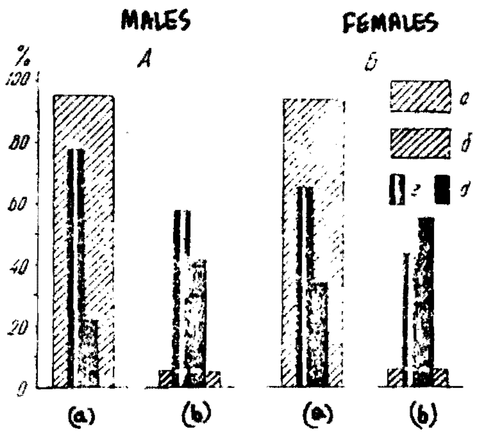


FIGURE 3: Relationship between fatness (left, males; right, females) and age.
(a) Under one year old; (b) Adults.
▯ lean; ■fat.

TABLE 3: Relationship between measurements (CBL), fatness and Vitamin A

	Males		Females	
	n	M ± m	n	M ± m
Fatness				
low	386	48.76 ± 0.07	99	43.05 ± 0.10
high	114	47.88 ± 0.13	55	42.28 ± 0.14
Vitamin A content				
low (44 mg%)	180	48.60 ± 0.10	56	42.69 ± 0.14
high (45 mg%)	160	48.50 ± 0.12	46	42.44 ± 0.15

Our figures therefore show that small animals have an advantage over large ones (the possibility of differences in diet of animals of different sizes cannot be excluded). In any case, these facts support our conclusions on natural selection in the northern ermine population in the years in which we studied it.

Conclusion

Our evidence indicates a real possibility of ascertaining the trend of selection in natural ermine populations. We cannot say with certainty what are the actual causes of the selection of smaller animals. Nor is it possible to determine the rate and limit of the phenomenon on a historical time scale. Indeed, that was not our aim in this work. All this requires further study. It would be interesting to check the problems raised here in other mammal species and, perhaps, other classes. This may be clarified by further research.

SUMMARY

The author studied 4000 skins and skulls of ermine (*Mustela erminea* L.) from the lower part of the Ob river, and also animals kept in captivity.

The data show that the mean sizes of the skull and body of young animals were bigger than those of older ones. The sizes of adults and old animals decreased during the period of observation, especially in northern populations. It is possible to determine the direction of selection in natural populations of ermine.

BIBLIOGRAPHY

Klevezal, G. A. and Kleinenberg S. E. (1964): Methods for an accurate determination of age in connection with the study of the mammal population structure. Sovremennye problemy izucheniya chislennosti populyatsii zhivotnykh (Mat-ly soveshch.), M.

Klimov, Yu. N. (1940): Materials on the biology of the ermine. Tr. biol. nauch.-issl. in-ta Tomsk. gos. un-ta 7.

Kopein, K. I. (1961): Materials on the biology of the ermine in Yamal. Pervoe Vsesoyuznoe soveshchanie po mlekopitayushchim. Tez. dokl. 2.M., Izd-vo MGU.

Kopein, K. I. (1965): Biology of reproduction of the ermine in Yamal. Ecology of the vertebrates of the Far North. Tr. In-ta biol. UFAN SSSR 38.

Morozova-Turova, L. G. (1961): Geographical variability in the ermine (*Mustela erminea* L.) in the territory of the USSR. Sbornik trudov zoologicheskogo muzeya MGU 8.

Smirnov, V. S. (1959): Age determination and age structure of the Arctic fox in Yamal. Materials on the fauna of the northern Ob and its utilization. Tr. Salekhard. stats. 1.

Smirnov, V. S. (1960): Age determination and age ratios in mammals, taking the squirrel, the muskrat and five species of carnivores as examples. Flora and fauna problems in the Urals. Tr. In-ta biol. UFAN SSSR 14.

Stroganov, S. U. (1937): Methods of age determination and an analysis of the age structure of ermine populations. Zool. zh. 16 (1).

Sheppard, P. M. (1959): Natural selection and heredity. Hutchinson University Library, London.

STABILITY AND VARIABILITY OF THE AGE STRUCTURE IN SABLE POPULATIONS

by

G. I. Monakhov

*All-Union Scientific Research Institute of
Hunting and Fur Farming (Kirov)*

[From: Zool. Zhurn., 53: 1376-1384, 1974.]

Age structure is one of the elements of population dynamics. The structure and density of a population[1] is determined by the age at sexual maturation, the proportion of sexually mature animals in total and in each sex, the survival rate in each age class, and the age-specific breeding rate of females. Variations in age structure can also influence the sex ratio.

The basic aim of this work is to study the influence of the stability or variability of the age structure in [the dynamics of] sable populations in the Soviet Union. In the research we used data collected from the All-Union Scientific Research Institute of Hunting and Fur Farming and its branches. The age of the animals was determined by the relative width of the canine canal[2] or by the number of annual layers in the tooth cement.

Length of Lifespan and Reproductive Period

The sable is a comparatively long-lived mammal. According to the data of Manteyfel (1934), sables have lived in a zoo for about 15 years, and in the Povenets Nursery up to 18 years. In the Pushkino State Fur Farm individual animals have lived to the age of 19 years.

Both males and females become sexually mature in the second year of life; females in state fur farms may be still fertile at the age of 17 (Starkov, 1947), but are usually replaced at about the age of 13-14 (Afanasyev and Pereldik, 1966). The age composition of sable populations on state farms is maintained as follows: young under one year of age (1-) (which are retained for herd restocking) usually make up 20-22%; animals older than a year (1+) 15-21%; and all other age groups 58-62% (Table 1). The bulk of the population consists of animals older than 3 years, of which females in the 3-10 year age group comprise 85-95%. With the sex ratio of 1:3 and an average litter size of 2 kittens, the actual annual increase over the whole farm is 120-130% and, for the breeding stock alone, 150-160%. These rates are significantly higher than the average increase observed in natural sable populations, and are more stable.

Wild sables have a markedly shorter life span. An analysis of the age structure of the populations of Cisbaikalia and Transbaikalia done in 1969 found that the maximum individual lifespan was less than 8 years, while the average calculated over several years proved to be a little over 2 years; in the majority of samples very old animals were only rarely found. In all natural populations studied by us (Table 2) the largest group is composed of animals under 1 year of age (1-); animals older than a year (1+) make up about one-third; and all other animals over 2 years (2+) comprise 18-36% of the total population.

It is known that in the wild, female sables of the middle age groups have the greatest reproductive capacity (Zaleker, 1953; Bayevsky, 1956; Vershinin, 1963; Monakhov, 1968; Belov, 1972). In captivity, the data of Portnova (1962) and our own findings (Mamatkina, Monakhov and Pavlov, 1970), show that females aged 5-10 years produce the greatest number of offspring.

---

[1] We use the term "population" according to the interpretation of Mayr (1968). —Author.

[2] See Kopein 1965, this volume—Ed.

TABLE 1: Sex ratio and age structure of the sable population on state fur farms

Age groups	Pushkino state fur farm			Krasnoyarsk state fur farm			Average over state fur farms, %		
	Total	Males %	Females % ± m	Total	Males %	Females % ± m	Males	Females	Total % ± m
2+	2588	15.5	46.6 ±0.77	652	13.4	44.4 ±1.48	15.1	46.1	61.2 ±0.67
1+	641	1.9	13.4 ±0.53	243	3.2	18.4 ±1.15	2.2	14.5	16.7 ±0.51
1-	940	3.4	19.2 ±0.61	232	1.7	18.9 ±1.17	3.0	19.1	22.1 ±0.57
Total	4169	20.8	79.2 ±0.63	1127	18.3	81.7 ±1.14	20.3	79.7	100.00

However, in natural populations the number of females of this age is very small (Table 2), so their contribution to the total productivity is insignificant. It is the females aged 3-5 years that produce the majority of young; females over a year (1+) produce somewhat fewer, though sometimes also equal numbers of young. Thus in natural populations the sex and age structures of the reproductive stock differ substantially from those which give such a high reproduction rate for sables in captivity. As a result of this the potential increase of wild sable populations varies in different regions from 51.0 to 79.0%, and never exceeds 165.2% (Vershinin, 1963; Kiselev, 1964; Numerov, 1965; Poluzadov, 1965; Monakhov, 1968; Belov, 1972; Kryuchkov, 1972). The actual increase is on average 48% of the autumn population numbers (Table 2).

Comparison of samples of farm and wild sables show that the age structure of state farm populations is determined so as to make the fullest use of the species' reproductive potential. Differing radically from the structure of natural populations, it creates the highest [possible] economic productivity. However, the age structure of natural populations is under the constant influence of natural selection. The number of individuals in each new generation progressively decreases in the course of time, and an accumulation of the most valuable animals for reproduction (the principle on which state farm stocks are managed) seems practically unrealizable under normal conditions (though apparently possible under the most difficult living conditions).

The principles of development of highly productive state farm sable populations can and should be taken into consideration in the planning of programmes for conservation of wild sables.

Mortality of Sables in Various Age Groups of the Population

Natural mortality, despite the well-known ecological adaptability of the sable, sometimes reaches very considerable proportions. Measuring its extent is difficult, in fact not always possible, as this work requires long-term research and sufficiently accurate age-determination. At present there are still very few such studies reported. Bayevsky (1956) found that the total mortality among sables of the Barguzin mountain range did not exceed 35% of the total population numbers, of which 30% fell on the young animals. Vershinin (1963) showed that the mortality of embryos and nestlings of sables in Kamchatka averaged 38.6% with fluctuations from 18.6 to 64.5%. According to our data (Monakhov, 1968) the mortality of embryos and nestlings of sables in North-west Baikalia averaged 36.5%, ranging from 7.2 to 77.8%. The sexes of the young which died could not be determined.

TABLE 2: Geographical variation in sex ratios and age structures of sable populations in the USSR

Geographical regions	n	Sex ratio(% male)		Percent. aged (1-)			Percent. aged (1+)			Percent. aged (2+)		
		n	% ± m	Males	Females	Total % ± m	Males	Females	Total % ± m	Males	Females	Total % ± m
Patom & Northern Baikal uplands	1756	1027	58.5 ± 1.18	27.9	19.8	47.7 ± 1.19	15.1	10.9	26.0 ± 1.05	15.4	10.9	26.3±1.05
Northwestern & Northeastern Baikalia	2277	1245	54.7 ± 1.04	21.6	20.6	42.2 ± 1.03	18.8	13.4	32.2 ± 0.98	14.3	11.3	25.6±0.92
Angara	1891	1040	55.0 ± 1.15	30.7	24.2	54.9 ± 1.15	14.7	12.3	27.0 ± 1.02	9.5	8.6	18.1±0.88
Khamar-Daban & Eastern Sayan	1395	781	56.0 ± 1.33	24.5	20.7	45.2 ± 1.33	17.8	12.7	30.6 ± 1.23	13.6	10.6	24.2±1.15
Southern Transbaikalia	138	82	59.4 ± 4.18	23.9	21.8	45.7 ± 4.24	21.0	12.3	33.3 ± 4.01	14.5	6.5	21.0±3.47
Sikhote-Alin	700	379	54.1 ± 1.88	23.9	22.1	46.0 ± 1.88	10.0	8.1	18.1 ± 1.46	20.3	15.6	35.9±1.81
Chulym River basin	314	170	54.1 ± 2.81	25.2	22.0	47.2 ± 2.82	16.6	11.4	28.0 ± 2.53	12.4	12.4	24.8±2.43
Southwestern Altai	187	93	49.7 ± 3.66	34.7	38.0	72.7 ± 3.26	9.1	6.4	15.5 ± 2.65	5.9	5.8	11.8±2.36
TOTAL	8658	4817	55.6 ± 0.53	26.0	21.8	47.8 ± 0.54	16.1	11.8	27.9 ± 0.48	13.6	10.7	24.3±0.46

The figures cited above were calculated from the difference between 'potential' gain (the number of corpora lutea of pregnancy) and actual gain (the number of young under 1 year of age in a sample taken in the following hunting season). Their close agreement may be taken as indirect confirmation of their objectivity.

An approximate estimate of the mortality among older sables was made merely by comparing the number of animals in consecutive age groups. We conducted lengthy observations of the variability of the age structure in the sable population of Northwest Baikalia (Table 3). The age structure in this population varied between years very considerably. Therefore, to estimate the mortality rate among animals in group 1+ in relation to the group 1-, and in group 2+ in relation to group 1+, we compared their longterm average ratios. In the first case the total decrease in animals of both sexes was 28%, in the second 13%. Since all animals older than 2 years are included in the third age group (2+), mortality in every subsequent group (3+, 4+ and so on) must be somewhat less than in group 1+. In this population the mortality of males in group 1+ was 21%, and in group 2+, 11%; of females, respectively 35% and 15%.

For the Cisbaikalia and Transbaikalia populations (Table 4) analogous calculations gave the following results: mortality of both sexes in group 1+, 42%; in group 2+, 21%; among males in group 1+, 36%; in group 2+, 19%.

From these data and from those in Tables 2, 3, and 4, we conclude that the sex ratio in each age group is near the average for the species, and also that the annual mortality of both sexes in each generation increases fairly uniformly. In most cases the survival of males is higher than that of females. Under normal conditions the most numerous age group is always the young under 1 year of age.

A different picture is observed during unfavourable years. In the population of Northwest Baikalia in the year following the season of 1961-62, which was difficult (very bad weather and food conditions), there were only 12.8% of young under one year of age, and of them only 3.8% were female (Table 3). In the Cisbaikalia and Transbaikalia populations the number of young animals in that same season was the smallest for the whole period previously recorded (Table 4). Conditions in 1968-69 and 1969-70 were even more difficult for the sables of this region; then, the high mortality of young under one year of age decreased their numbers to 22.0 and 12.5% respectively. During these years, just as in 1961-62, young females died much more often than males.

The fact that during the hard years the number of adult females (1+ and especially 2+) exceeded considerably the average long-term proportion (Tables 3 and 4) is both characteristic and important. As a result of this the reproductive nucleus is better preserved in the years of hardship and is ready to compensate in the shortest time for the large losses in population caused primarily by mortality of the young under one year of age, whose deaths in such years amount to about 80% of the annual production.

These data allow us to make the following conclusions. The age structure of a sable population is sensitive to the effects of external environmental factors on rates of increase and mortality. Under normal living conditions the mortality of animals in each age group is apparently proportional to their numbers. Young animals born in the current year always predominate in the population. Under extreme conditions, on the other hand, it is primarily the young animals which die, while older animals predominate in the population, and the survival of older females is usually higher in such conditions than it is over the long-term average.

Thus, one can say that in harsh conditions the population "sacrifices" the sexually immature young animals to preserve the reproductive nucleus, which is capable of rapidly restoring the population to the ecological optimum[1]. This appears to be a mechanism for population homeostasis.

---

[1] A situation in which the population density corresponds to the carrying capacity of the land for sables.—Author

TABLE 3: Annual variations in the sex ratio and age structure of the sable population of Northwestern Baikalia

Seasons	n	Sex ratio (% males ± m)	Percent. aged (1-)			Percent. aged (1+)			Percent. aged (2+)		
			Males %	Females %	Total % ± m	Males %	Females %	Total % ± m	Males %	Females %	Total % ± m
1956/57	75	49.3 ± 5.8	17.3	22.7	40.0 ± 5.56	29.4	17.3	46.7 ± 5.76	2.6	10.7	13.3 ± 3.92
1957/58	81	51.8 ± 5.6	25.9	28.4	54.3 ± 5.54	16.0	6,2	22.2 ± 4.62	9.9	13.6	23.5 ± 4.71
1958/59	58	56.8 ± 6.5	17.2	20.8	38,0 ± 6.37	17.2	19.0	36.2 ± 6.31	22.4	3.4	25.8 ± 5.75
1959/60	131	54.2 ± 4.4	18.3	16.0	34.3 ± 4.15	19.1	20.6	39.7 ± 4.12	16.8	9.2	26.0 ± 3.83
1960/61	75	65.3 ± 5.5	17.3	9.3	26.6 ± 5.10	20.0	16.0	36.0 ± 5.54	28.0	9.4	37.4 ± 5.89
1961/62	131	53.5 ± 4.4	25.2	22.9	48.1 ± 4.36	13.0	7.6	20.6 ± 3.53	15.3	16.0	31.3 ± 4.08
1962/63	78	69.2 ± 5.2	9.0	3.8	12.8 ± 3.78	25.6	9.0	34.6 ± 5.39	34.6	18.0	52.6 ± 5.65
1963/64	71	59.1 ± 5.8	22.5	15.5	38.0 ± 5.76	16.9	11.3	28.2 ± 5.34	19.7	14.1	33.8 ± 5.61
1964/65	116	49.2 ± 4.6	33.6	36.2	69.8 ± 4.26	12.1	7.7	19.8 ± 3.70	3.5	6.9	10.4 ± 2.83
1965/66	65	55.4 ± 6.2	26.2	7.6	33.8 ± 5.86	12.3	21.6	33.9 ± 5.87	16.9	15.4	32.3 ± 5.80
1966/67	51	49.0 ± 7.0	21.6	29.4	51.0 ± 7.00	15.6	9.8	25.5 ± 6.10	11.8	11.8	23.6 ± 5.95
1967/68	47	51.1 ± 6.7	27.7	29.8	57.5 ± 7.23	14.9	14.9	29.8 ± 6.67	8.5	4.2	12.7 ± 4.75
TOTAL	979	55.2 ± 1.6	22.2	20.4	42.6 ± 1.6	17.5	13.2	30.7 ± 1.5	15.5	11.2	26.7 ± 1.4

TABLE 4: Annual variation in the sex ratio and age structure in the sable populations of Cis- and Transbaikalia

Seasons	n	Sex ratio (% males + m)	Percent. aged (1-)			Percent. aged (1+)			Percent. aged (2+)		
			Males %	Females %	Total % + m	Males %	Females %	Total % + m	Males %	Females %	Total % + m
1951/52	113	53.0 ± 4.69	36.3	27.4	63.7 ± 4.52	13.3	11.5	24.8 ± 4.01	3.5	8.0	11.5 ± 3.0
1953/54	75	58.7 ± 5.69	18.6	17.4	36.0 ± 5.54	22.6	12.0	34.6 ± 5.49	17.4	12.0	29.4 ± 5.26
1955/56	81	55.6 ± 5.52	22.2	26.0	48.2 ± 5.55	22.2	9.8	32.0 ± 5.18	11.1	8.7	19.8 ± 4.43
1956/57	142	51.4 ± 4.19	28.9	29.6	58.5 ± 4.14	20.4	12.0	32.4 ± 3.93	2.1	7.0	9.1 ± 2.42
1957/58	81	51.9 ± 5.55	26.0	28.4	54.4 ± 5.54	16.1	6.1	22.2 ± 4.41	9.8	13.6	23.4 ± 4.73
1958/59	223	57.8 ± 3.31	35.4	29.6	65.0 ± 3.19	15.2	10.0	25.6 ± 2.92	7.2	2.2	9.4 ± 1.95
1959/60	131	54.2 ± 4.35	18.3	16.1	34.4 ± 4.15	19.1	20.6	39.7 ± 4.27	16.8	9.1	25.9 ± 3.83
1960/61	176	62.0 ± 3.66	31.2	22.8	54.0 ± 3.76	13.6	10.2	23.8 ± 3.21	17.0	5.2	22.2 ± 3.13
1961/62	205	56.5 ± 3.46	26.8	22.5	49.3 ± 3.49	16.1	9.3	25.4 ± 3.04	13.7	11.7	25.4 ± 3.04
1962/63	190	59.5 ± 3.56	13.1	12.1	25.2 ± 3.15	25.8	16.4	42.2 ± 3.58	20.5	12.1	32.6 ± 3.40
1963/64	887	56.2 ± 1.67	26.3	22.4	48.7 ± 1.68	15.5	11.4	26.9 ± 1.49	14.5	9.9	24.4 ± 1.44
1964/65	861	55.7 ± 1.69	40.3	33.9	74.2 ± 1.49	9.0	6.9	15.9 ± 1.25	6.4	3.5	9.9 ± 1.02
1965/66	1322	56.4 ± 1.36	33.6	23.6	57.2 ± 1.36	14.1	13.1	27.2 ± 1.23	8.8	6.8	15.6 ± 1.00
1966/67	568	53.5 ± 2.09	22.0	17.6	39.6 ± 2.05	18.0	13.4	31.4 ± 1.95	13.5	15.5	29.0 ± 1.91
1967/68	1081	56.0 ± 1.51	28.1	23.5	51.6 ± 1.52	17.7	13.2	30.9 ± 1.41	10.2	7.3	17.5 ± 1.16
1968/69	851	57.0 ± 1.70	13.9	8.1	22.0 ± 1.42	23.1	17.4	40.5 ± 1.68	20.0	17.5	37.5 ± 1.66
1969/70	344	56.7 ± 2.67	6.7	5.8	12.5 ± 1.78	16.8	9.9	26.8 ± 2.39	33.2	27.6	60.7 ± 2.63
1970/71	518	56.6 ± 2.18	20.6	16.7	37.3 ± 2.12	21.6	15.1	36.7 ± 2.12	14.3	11.7	26.0 ± 1.93
TOTAL	7849	56.2 ± 0.56	26.4	21.2	47.6 ± 0.57	16.8	12.5	29.3 ± 0.50	12.9	10.2	23.1 ± 0.48

Stability and Variability of the Age Structure

One of the characteristic featues of age structure is its fairly high lability in comparison with, for example, the sex ratio. This was confirmed by our data as well. In the population of Northwest Baikalia very considerable fluctuations in the proportions of the age groups were observed over a 12-year period (Table 3). In the young under one year of age (1-) the range of fluctuations was 57.0% (from 69.8% to 12.8%); in the group 1+ it was 26.9% (from 46.7 to 19.8%); and in the group 2+ it was 42.2% (from 52.6 to 10.4%). In the Cisbaikalia and Transbaikalia populations over 17 years this range was 61.5% in the group 1-, 26.3% in the group 1+, and 51.6% in the group 2+. In populations of other regions, where the observation period was comparatively short, the range of fluctuations was markedly less. Thus, for example, in southern Transbaikalia, over 6 years, the amplitude of fluctuations in the age groups was equal: in group 1-, 35.2%, in group 1+, 25.7%, and in group 2+, 39.7%, while in the population of the Chulym basin over 3 years of observation it was 9.6, 6.4, and 8.2% respectively.

Clearly, the age structure can vary very widely between years, and this is caused principally by the influence of environmental factors. The data show that the greatest variability is characteristic of the young under 1 year (1-), while the greatest constancy in numbers of animals in a generation is observed among sables older than a year (1+).

The year to year variation in age structure [in a given population] can be very considerable, but geographical variation in age structure, in a given year and in the long-term, is much less. In different populations in Cisbaikalia and Transbaikalia in 1964-65, the amplitude of variation within age groups was 19.2% in group 1-, 14.2% in group 1+ and 5.6% in group 2+. In 1965-66 in the same populations it had these values: 1-, 22.3%; 1+, 8.7%; 2+, 15.8%; (Table 5). If we trace the longterm mean variation of that same index of variability in a number of sable populations studied in the USSR (Table 2), we obtain the following results: in group 1- the amplitude of variation was 12.7%, in group 1+ 15.2%, and in group 2+ 17.8%. Evidently geographical variation in age structure, in any one year and also over the longterm, is relatively small. The similarity between the age structures of populations from very remote regions suggests that there is a tendency, caused by heredity and typical of the species, to maintain a quite definite ratio between age groups under normal conditions, and an equally definite tendency to restore rapidly to normal an age structure temporarily unbalanced by exceptional environmental circumstances.

Table 2 suggests that differences in age structure between populations are more frequently discernable from the nature and range of variation in numbers of animals in each generation, than from differences between populations in average indices.

Here it is appropriate to call attention to the age structure of sables in southwest Altai. This population is situated on the edge of the range of distribution of the sable. Over 2 years of observation the number of young under 1 year (1-) was invariably much higher than average for the species (Table 2). We suggest that this was not due to selective hunting, but may be because the dynamics of peripheral populations are different in some way. It may be related to the fact that in the outlying districts of the species' range the animals have a relatively shorter lifespan, so an unusual age structure is observed: "a negligible percentage or total absence ... of old animals" (Lavrovsky, 1964). Another reason may be because shortage of food leads to greater activity of the animals, particularly young ones (Naumov, 1945).

TABLE 5: Geographical variation in age structure of sable populations in Cis- and Transbaikalia in the 1964-65 and 1965-66 seasons, sexes combined.

Geographical regions	1964/65				1965/66			
	n	Age groups, %			n	Age groups, %		
		I	II	III		I	II	III
Patom & Northern Baikal uplands	148	69.6	18.9	12.1	260	55.7	25.8	18.5
North-western & North-eastern Baikalia	255	66.6	21.9	11.5	222	40.0	33.4	26.6
Angara	183	85.8	7.7	6.5	384	62.3	24.7	13.0
North-eastern Transbaikalia	77	73.0	15.6	11.4	-	-	-	-
Khamar-Daban & Eastern Sayan	121	80.9	12.4	6.7	352	60.8	28.4	10.8
Total	784	74.5 ± 1.56	15.9 ± 1.31	9.6± 1.05	1218	56.4 ± 1.42	27.6 ± 1.28	16.0 ± 1.05

Conclusion

The data presented in this paper show that age structure is one of the most important elements in the mechanism of population regulation in sables. On state sable farms the age structure is managed so as to fully realize the species' reproductive potential, which leads to sustained population increases of a magnitude practically impossible for wild populations with their natural age structure.

Generations of sables of various ages react differently to changes in the environment by appropriate changes in their rates of reproduction and survival. In both good and bad conditions the effect is to adjust the population density to the current level of carrying capacity of the land for sables.

The age composition is one of the most variable elements of the ecological structure of sable populations. Its lability has nevertheless its own characteristics and boundaries. Fluctuations in age ratios from year to year are greater than from region to region, and the greatest deviations from the average are levelled fairly rapidly (in the course of 2-3 years) as a result of the selective mortality appropriate to the ecological conditions. The greater survival of adult females in years of ecological hardship is a characteristic feature of the age structure in sable populations.

SUMMARY

The age structure has been studied in natural and state farm populations of the sable. The reproductive abilities of wild and captive populations differ markedly under their different conditions, suggesting the primary role of age structure in the control of population density in the sable. The state farm populations are managed to permit the fullest realization of the species' reproductive abilities. They obtain high and stable annual increases which are practically impossible in wild populations with natural age structures. The age composition is one of the most labile elements of the population dynamics of the sable. Fluctuations of the ratio of generations between years are greater than between regions. The greatest fluctuations in ratios from the average are levelled rapidly (in 2–3 years) as a result of the selective mortality of specimens of different age and sex in different ecological conditions. The greater survival of adult females in the years of ecological hardship is a characteristic feature of the age structure of the sable populations.

BIBLIOGRAPHY

Afanasyev, V. A. and Pereldik, N. Sh. (1966): Fur animal breeding in captivity: 1-398. Izd-vo "Kolos", M.

Baevski, Yu. B. (1956): Variability in the fecundity of Barguzin sables. Byull. Mosk. o-va ispyt. prirody, otd. biol. 61 (6): 15-26.

Belov, G. A. (1972): Population peculiarities of the potential fecundity of the Kamchatka sable. Materialy nauchnoi konf. posvyashch. 50-letiyu Vses. n.-i. in-ta okhot. kh-va i zver-va, part 2. Voprosy ekologii: 40-45, Kirov.

Vershinin, A. A. (1963): The dynamics of reproduction and the control of utilizing the stocks of Kamchatka sables. Tr. Vses. n.i. in-tazhivotn. syra i pushniny, 20: 8-33. Izd-vo Tsentrsoyuza.

Zaleker, V. L. (1953): Materials on the fecundity of wild sables. Tr. Vses. n.-i. in-ta okhotn. promysla 12: 80-91. Zagotizdat.

Kiselev, V. A. (1964): The sable of the North Yenisei and the rational utilization of its stocks. Autoref. kand. diss. 1-20, M.

Kryuchkov, V. S. (1972): Materials on the ecology of the sable in the silkworm breeding areas of the Chulym basin. Materialy k nauchn. konf. posvyashch. 50-letiyu Vses. n.-i. in-ta okhot. kh-va i zver-va: 36-39, Kirov.

Lavrovski, A. A. (1964): Some peculiarities in the structure of populations and in the dynamics of the numbers of animals on the boundaries of their distribution areas. Sb. [Collection] "Sovremennye problemy dinamiki chislennosti populyatsi' zhivotnykh, M.

Mayr, E. (1968): Zoological species and evolution: 1-597, Izd-vo "Mir", M.

Mamatkina, E. G. Monakhov, G. I. and Pavlov, M. K. (1970): Reproductive rate of sables on farms and in nature. Byull. Mosk. o-va ispyt. prirody, otd. biol. 75 (2): 146-151.

Manteifel, P. A. (1934): The sable: 1-108, KOIZ, M.-L.

Monakhov, G. I. (1968): The population structure, reproductive dynamics and the problems of rational utilization of sable stocks in Cis- and Transbaikalia. Zool. zh., 57 (4): 602-609.

Naumov, N. P. (1945): Geographical variability in the dynamics of numbers and evolution. Zh. obshch. biol. 6 (1): 37-52.

Numerov, K. D. (1965): The sable of the Yenisei Siberia. Autoref. kand. diss.: 1-24, Krasnoyarsk - Irkutsk.

Poluzadov, N. B. (1965): Reproduction and rational utilization of sable stocks in the Urals. Sb. "Voprosy okhotnichyego khozyaistva i zverovodstva": 93-102, Izd-vo "Ekonomika", M.

Portnova, N. T. (1962): Our experiment in sable breeding. Krolikovodstvo in zverovodstvo 12: 24-27.

Starkov, I. D. (1947): Biology and breeding of sables and martens: 1-130, M.

THE DISTRIBUTION AND POPULATION DYNAMICS OF THE SIBERIAN KOLINSKY IN THE WESTERN PART OF ITS RANGE IN THE USSR

by

Yu. N. Bakeev

[From: Byull. Mosk. o-va Iskt. Prir. Otd Biol. 76 28-38, 1971]

The kolinsky[1] (*Mustela sibirica* Pall.) is a species typical of the South Taiga and parts of the Central Taiga areas of Siberia. West of the Urals it reaches the Volga, and the furthest westerly point where it is found is in the Vetluga Basin.

Its range was first described in some detail by N. P. Lavrov (1937); then further information was added by I.P. Laptev (1958) and S. U. Stroganov (1962)[2]. By collating all data published earlier and adding some new ones we can give a more detailed description of the western part of this animal's range.

The present western boundary of the distribution of the kolinsky lies between 50° and 45°E., and it is found over a relatively wide area stretching from the Orenburg Region to the Komi ASSR, or between 50° and 61°N.

In the SW districts of the Komi ASSR the kolinsky was found on the left bank of the upper reaches of the Sysola in the 1930s (Lavrov, 1937). It was noted in roughly these same places, i.e., the Letsky and Priluzsky districts of the Komi ASSR, by N. A. Ostroumov (1949), N. A. Ostroumov and V. V. Tureva (1953), and V. Ya. Parovshchikov (1958). The latter states that it was rare in these areas but had become common by 1949.

The kolinsky is found in the southern districts of the Kirov Region. In what was formerly the Vyatsky district and on the borders of the Tartar ASSR it has been known since the 1920s (Plessky, 1928; Ognev, 1931).

The most westerly points of its distribution in the European part of the USSR were investigated by A. N. Formozov (1935). According to his information the kolinsky was being trapped in the 1920s and early 1930s in the Sharinsky district of the Kostrom Region (the former Gor'kovsky district), near the village of Drjablovo in the Mundyrsky Rural District Council area, in the basin of the Kaksha (Prudovka village) and in the Krasnye Baki district of the Gor'kovsky Region. In the former Gor'kovsky district (now the Gor'kovsky, Kostromsky and Kirovsky regions) the species was not rare: in 1925-1930 the average catch for the hunting season was 25, and the maximum 456 (reported by V. A. Guber and L. A. Gavrilova).

In the Tatar ASSR the kolinsky is found in commercial numbers in the area bounded by the Kama and its tributary the Vjatka, and also the adjacent left bank of the Kama (Baskirov, Grigoriev, 1931). In the general kolinsky-trapping area, which we estimate to be 856 000 hectares, the average catch per hunting season was 422 in the 1920s with a maximum of 711, or 0.49-0.83 animals per 1000 hectares. The kolinsky was only rarely found in the Mamadyshky, Chistopolsky and Bugulminsky districts (Bashkirov and Grigoriev, 1931), from where it spread into the Melekessly district of the Kujbyshev Region.

In the Orenburg Region trapping of the kolinsky began in 1902 (Darkshevich, 1950). Its population density up to the present continues to be low. It is usually found in the Sharlyksky, Octjabrsky, Zijanchurinsky, Kuvandysksky, Saraktashky and Troitsky districts. According to S. V. Kirikov (1952), it is only very rarely found in the Guberlinsky area of low, rounded hills. In the former Middle-Volga district, now the modern Kujbyshev and Orenburg Regions, the number of pelts per season was quite large, averaging 437, with a maximum of 824, in 1925-1930 (Guber and Gavrilova).

From the Orenburg Region the southern boundary of distribution stretches into the Kazakh SSR.

The northern boundary of kolinsky distribution in the European part of the USSR runs from the above-mentioned places in the upper reaches of the Sysola to the upper reaches of the Pechora, where the species is found along

---

[1] Also called the Siberian weasel. Its magnificent fur is marketed as kolinsky or Siberian mink—Ed.

[2] Translated by Israel Program for Scientific Translations, Jerusaleum, 1969—Ed.

the river Ljapin and on the Ilych approaching 63° N. (Lavrov, 1937; Teplova and Teplov, 1947). The kolinsky is very rare in all the northern forests of the Komi ASSR and the Perm Region. In the Nyrobsky, Cherdynsky and Krasnovishersky districts only a few dozen animals were caught per season in 1925-1936 in a forest area of about 5 million hectares. In the Komi-Permjatsky National District the kolinsky is found only in the southern part, in the Kosinsky, Kudymkarsky, Yusvinsky and Yurlinsky districts, and even then only a few isolated animals are caught (Tomilin, 1953).

In the mountain forests of the Urals the kolinsky reaches 63° N. (Lavrov, 1937), but it is rare everywhere. Even at 59°-60° N., in the territory that was formerly part of the Denezhkin Kamen reserve, it is in fact found in the forests adjoining the flood-plains of the Sosva and Shegultan and along other rivers, but in very small numbers (Chernjavskaja, 1959).

In western Siberia (Tjumensky Region) the northern boundary of distribution runs through the Yamalo-Nenetsky National District, where from 1931-1933 between 92 and 127 pelts were treated. Here the kolinsky is found from the Sub-Ural district in the west, where no more than 5 pelts per year are obtained, to the Tazovsky district in the east. The animal was observed in the Nadymsky district in the 19th century by I. S. Poljakov (1877); there are no subsequent reports from this locality. In the southern part of the Pur river basin isolated animals are caught now and again (report by N. I. Chesnokov), and along the river Taz in the past the species reached almost as far north as the mouth of the Taz (Stroganov, 1962). As in other parts of the Yamala-Nenetsky District the animal's population in the Taz basin has greatly decreased in the last decades.

There is only a small population of kolinsky in the enormous expanses of the northern forests in western Siberia, which lie to the west of the distribution boundary, and in European USSR and the Urals. For example, in the Berezovsky area of the Khanty-Mansijsky National District a forest area of about 7 million hectares gave a yearly yield of only a few dozen pelts in the 1930s. The greatest number (206) was caught in 1947, but in recent years there have been only 3-9 per season. It is found along the river Kazym, where L. N. Shuchov (1915) classed it as an animal of commercial importance. There is no later information from this locality. V. N. Pavlinin (1959), on a visit to the basin of the northern Sos'va. reports that the kolinsky is extremely rare and that in 1956 he could manage to find only one record of its being trapped in this area, near the mouth of the Ljapin, in the last 20 years.

In the former Kondo-Sosvinsky reserve the kolinsky was very rare (Vasilev, 1928), and according to a later report from V. V. Raevsky and V. N. Skalon in the mid 1940s there was not a single sighting. Cases of kolinskys being caught along the rivers Khanlazin, Bolshaja Evva, Nagra-Agan, Tugr and Tapsuj are known. It is more regularly trapped along the Konde and Ejtje, i.e., west and south of the reserve. It has evidently become even rarer here in recent years. In 1961 a count of commercial animals was carried out in the middle reaches of the Ejte from tracks in the snow, but there was no sign of the kolinsky. According to the trappers, they did not come across it in the area of Lake Aran-Tur on the river Konde either (report by N. N. Bakeev and G. A. Babakov).

It is also rare in the Octjabrsky district of the Khanty-Mansijsky National Park District where, in a vast territory containing many flood-plain areas which the kolinsky favours, particularly along the Ob, not more than 86 skins per year have come in over the last 25 years.

The kolinsky population achieves commercial density in the more southern districts of the Khanty-Mansijsky National Park District: there is regular trapping in the Samarovsky, Surgutsky, Larjansky and Kondinsky districts, south of 62° N.

In the Sverdlov Region the kolinsky is regularly trapped south of 60° N. In the Serov District there was a yield of up to 525 skins per season in the 1930s (report by S. A. Kuklin), and of more than 300 in Garinsky in the 1950s (report by B. F. Korjakov).

In the Perm Region the northern limit of regular trapping moves even further south, south of 58°N. (Chusovsky, Lysvensky, Dobrjansky and districts further south.) In the eastern districts of the region the species has always been rare.

In the western part of its range the kolinsky was most numerous from 1925-1936, although it was then being intensively trapped. In those years there were two large areas of high population density, - the Prikamsky (left bank) and the Tobolo-Irtyshky (Figure 1).

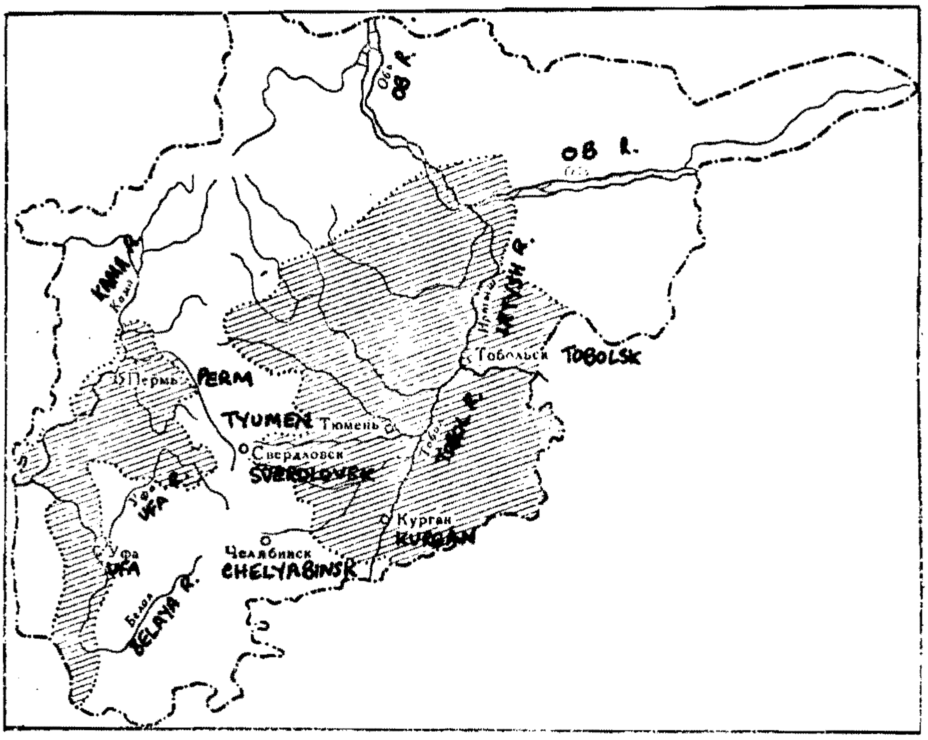


FIGURE 1: The Prikamsky and Tobolo-Irtyshki areas (shaded) of high population density of kolinsky from 1925-36.

In the period 1950-1964 the general density of kolinsy greatly decreased over almost the whole area of its range. The previous pattern of distribution has generally remained, though the figures are down and the population density in the centres of distribution and beyond them is lower.

Only the Prikamsky area of former high density remains in the Bashkiri ASSR, in an area of forest-steppe districts abounding in flood-plains (river Belaja) like the Birskij, Kushnarenkovsky, Narimanovsky, Blagoveshchensky, Karamaskalenkovsky, Ufimsky, etc. In the vast remaining territory of the Perm, Cheljabinsk and, in part, the Sverdlov Regions as well as in the Bashkiri ASSR, the density has dropped sharply.

A similar drop is also found in the Khanty-Mansijsky National Park District. The present low population density is shown not only by the five-fold decrease in skins, but also by a census of mustelids from tracks in the snow, carried out in 1953 in the Samarovsky, Surgutsky and Uvatsky districts of the Tjumen Region, which returned only five sets of kolinsky tracks over census lines totalling 480 km.

To a slightly lesser extent there has been a decrease in density in the Tobolo-Irtysksky area, i.e., in the forest-steppe and southern forest districts of the Kurgan, Tjumen and Sverdlovsk Regions. However, here too the area of highly productive kolinsky range is noticeably less, dropping from 15 to 4.8 million hectares, while the average yield in skins over the area as a whole has dropped 1.27 to 0.80 pelts per 1000 hectares.

The yield is still the same (0.8-1.9 pelts per 1000 hectares) in the northern forest-steppe districts of the Kurgan Region, (Katjsky, Chashchinsky, Dalmatovsky, etc., districts). This strip of high density also includes the southern forest and northern forest-steppe areas of the Omsk Region - Bolsheukovsky, Kolosovsky, Tarsky, Tjukalinsky, etc., districts.

There has been a sharp drop in density and yield in the southern part of the forest-steppe zone of the Omsk, Kurgan and Cheljabinsk Regions. In parts of the most markedly steppe areas the species has completely disappeared. There are isolated records of kolinskys being trapped in the Isilkulsky, Kalachinsky, Okoneshnikovsky and more southerly districts of the Omsk Region, in the Polovinkinsky, Zverinogolovsky and Sarafulinsky districts of the Kurgan Region, and in the Troitsky, Plastovsky and more southerly districts of the Cheljabinsk Region.

Although there are in these steppe areas, just as in the more northerly forest-steppe, lakes fringed with swampy thickets of reeds which are typical kolinsky habitat, the population density is low. In the last decades the area under forests in these districts has noticeably declined and this may have an unfavourable effect on the species, which tends towards forest habitats. It often uses holes in trees and tree-stumps for storing food and making nests (Sasov, 1965; Ternovsky, Danilov, 1965). But there is no direct correlation between the area under forest and the population density. It is probable that, we have here a whole complex of factors adversely affecting the animal's living conditions. The species composition of rodents, their population density and fluctuations may be of particular importance, since rodents are the principal food of the kolinsky.

Our observations in the Cheljabinsk Region on lakes Bolshoj and Malyj Kuyash and the adjacent forest outliers in the steppe showed that the kolinsky avoids the forest outliers in winter, and hunts small rodents in the marshes round the lakes, often visiting muskrat nests on the lakes themselves. Over a distance of 105 km through aspen and birch outliers with small swamps we found only 4 kolinsky tracks, while on the other hand we found 382 ermine tracks and 92 weasel tracks; but on a 7 km section cutting across the lakes and their surrounding marshes we counted 11 kolinsky tracks, 2 steppe polecat tracks, 20 ermine tracks and 21 weasel tracks. All this shows that in the forest-steppe zone the relationship between the kolinsky and forest vegetation is largely disappearing.

It is known that the kolinsky population density, particularly in the forest-steppe zone of western Siberia, is directly proportional to the population density of the water vole (Lavrov, 1937; Ternovsky and Danilov, 1965). In the southern, markedly steppe and forest-steppe areas of western Siberia, conditions for the water vole are less favourable, since the farther one goes south, the fewer low-lying, permanent bogs there are and the less is the marshland character of the habitat. Moreover, stretches of water often dry up over the whole district (Maksimov *et al.*, 1965).

The drop in the kolinsky population in the 1950s and early 1960s over a vast area in the western part of its range must apparently be attributed to a number of periodic phenomena.

The long-term records for kolinsky pelts show that the population density is subject to wide variations both from year to year and in cycles of years. In the western part of the range several records of population expansion are found from 1883 to 1964 inclusive, i.e., in the last 80 years. The first, according to Lavrov (1937), took place in 1884-1886 when, from Silantev's figures (1898), 80 000-100 000 skins appeared yearly on the Irbitsk market. From 1887 to 1895 inclusive the number of skins varied between 40 000-65 000 on the same market, [except for the years] 1889 and 1894, when the total was 75 000-80 000. The increase in the number of kolinskys in 1894 coincided with a population peak among rodents, including the water vole, which began in 1893 (Vinogradov, 1934). For the period 1895-1909 there is no information on the kolinsky population density. In 1910 there were few in western Siberia. In 1916-1917 the population there increased sharply, Lavrov, 1937), and this was preceded by a great increase in the number of rodents in 1913-1914, an increase which continued in some areas until 1915 (Vinogradov, 1934).

We can assess the changes in population density in the next period from 1924 from the figures for skins. The population stayed at a particularly high level from 1925-1929, 5 hunting seasons in a row. This increase occurred over the whole range; it was also noted by Lavrov (1937) and coincided with an equally large increase in the numbers of small rodents over almost all the European part of the USSR and western Siberia (Vinogradov, 1934).

The next increase was observed in 1935-1939 and, finally, the last population peak affecting the whole area occurred in 1950-1953.

The next increase, 1960-1964, only affected the southern forest and forest-steppe areas of the Sverdlovsk, Tjumen and Kurgan Regions.

All the above increases in population were preceded by large increases in the numbers of rodents, including water voles. In the Khanty-Mansijsky National Park District population increases in the water vole were noted in 1937-1938, and 1949-1950 (Ageenko, 1959). In the western Siberian forest-steppe there were a lot of water voles in 1927-1929, 1936-1939, 1947-1951 and from 1956 to 1962 (Maksimov *et al.*, 1965).

Therefore, large increases in the kolinsky population have occurred roughly once every ten years, and even less frequently in some areas.

In the area under review some regional differences in population dynamics due to local natural features were observed. Thus, on the periphery of the range in the Perm Region and the Bashkir ASSR there rarely occurred any particularly large increases - only twice in 36-38 years. Here the population is evidently limited by a scanty food supply. There are few water voles in the Ural foot-hills, and small rodents do not completely satisfy the kolinsky's needs. Research by Lavrov (1937) and Grigoriev *et al.* (1931) showed that the water vole is the chief item of the kolinsky's diet in the Tartar and Bashkir ASSR, but by comparison with the forest-steppe areas of western Siberia, small rodents, the mole and other items are more important there.

A periodic drop in the kolinsky population evidently occurs as a result of decreased fertility in years when food is scarce. The number of young in a litter varied from 2 to 14 (Stroganov, 1962; Vojlochnikov, 1965). Presumably the animal makes full use of its potential fertility in years when food is plentiful, and this leads to a rapid growth in the population in 2-3 years.

In the Sverdlovsk Region the kolinsky finds more favourable living conditions, especially in the southern forest and forest-steppe areas which abound in lakes and small forest- and flood-plain marshes. As can be seen from Table 1, in the 33 years for which information is available, a high population density occurred in 22 years (67%), a low density in only 3 years (9%). Large increases occurred 4 times. As far as population dynamics are concerned, the forest-steppe of the Kurgan and Tjumen Regions is similar to the Sverdlovsk Region (Table 1).

Transformation of the countryside through the cutting down of forests, the extending of the area of agriculture, land-reclamation, etc., has a lot to do with the subsequent changes in the population density of the kolinsky.

We were able to observe the effect of tree-felling on the kolinsky and other mustelids on the western slopes of the Urals, at Bisertsky station in the Nizhne-Serginsky district of the Sverdlovsk Region. Observations on the mustelid population density were begun here in 1959 in a diminishing spruce and fir forest, heavily obstructed by felling debris and with an admixture of lime, elm and birch, and were completed in 1964, when 80% of the overmature tree-stands had been cut down (felling started in 1956).

The results of our observations on the populations of kolinsky and other mustelids are given in Table 2.

TABLE 1: Distribution of years with high, average, and low kolinsky population density in the Urals and neighbouring regions from 1924 to 1964

Regions	Number years info. available	Population (according to pelts)					
		High					
		Years	%	Years	%	Years	%
Sverdlovsk	33	22	67	8	24	3	9
Kurgan	18	8	44	8	44	3	12
Forest-steppe Tjumen	17	9	53	3	18	5	19
Khanty-Mansijsky National Okrug:							
Kondinsky, Samarovsky	31	9	29	13	42	10	32
Surgutsky	34	10	29	11	32	13	38
Cheljabinsk	37	9	24	18	49	10	27
Bashkiri	38	14	37	9	24	15	39
Perm	36	6	17	9	25	21	58

TABLE 2: Changes in mustelid populations at Bisertsky station, from track counts

Month and Year	Length of census line (km)	Tracks per 100 km				
		Kolinsky	Marten	Weasel	Ermine	Small Rodents
Feb-March 1959	61.4	3	237	10	-	37
" " 1960	113	9	178	68	3	15
Oct-Nov 1960	132	13	67	36	5	120
Dec 1962	30	7	20	10	13	7
Nov 1963	98	80	7	104	10	16
Nov 1964	40	72	0	17	36	130
Mar-Apr 1965	73	60	11	No	census	taken

At the beginning of the observations in 1959 and 1960, when felled areas were small, the most numerous species was the pine marten. Over 100 km of census line, which went mainly through the diminishing forest, there was an average of 178-237 criss-crossing marten tracks and only 3-9 kolinsky tracks. The kolinsky was numerous in the flood-plain of the Biserta and its tributary the Baska,where there were 30 tracks over 28 km, or 107 per 100 km. In the forests there were only tracks of isolated animals which occasionally went in. There were none at all on the 3-year felling sites.

According to a local trapper, Kadochnikov, a similar distribution of mustelids had been observed by him in the 1930s, when there had been few martens and many kolinskys. Even then the kolinsky had kept to the flood-plain and adjacent areas where food was more abundant. In the forests, with their admixture of broad-leaved species, which should seemingly have attracted the kolinsky because of the debris and abundance of holes, the animal was practically absent.

They appeared in great numbers on the felling sites in 1963 and 1964; over 100 km of census line 123-150 tracks were found. By this time, in a vast area of felling sites of different ages and covering scores of kilometres, there had developed a typical fauna of commercially useful animals and birds. There were big flocks of grouse, and a lot of ermine, weasels, blue hares and elk. Among small rodents the grey voles - the field vole, *Microtus oeconomicus* and the dark vole - became very numerous. The species composition of the voles must have been very important for the kolinsky. At the same time, such typical forest species as the hazel-grouse, capercailzie and pine marten disappeared, the latter holding out for a long time in undercut areas.

Thus intensive and large-scale felling in the Urals creates favourable conditions for a population increase of the kolinsky and other small mustelids.

Our observations show that even in a forest zone in the west of the kolinsky range its typical habitats are scrubland, felled areas, burnt areas and marshy flood-plain or lake-shore land (Table 3).

TABLE 3: Distribution of kolinsky tracks by habitat at Bisertsky station, 1959-64

Habitat	length of census line (km)	Tracks per 100 km
Diminishing spruce-fir forest with lime and birch	215	13
Mixed average-age spruce-birch-aspen forest	80	14
Biserta flood-plain, including swamps, spruce, willow, bird-cherry copses	70	47
Felling sites of various ages (up to 10 yrs)	100	60
Aspen-birch outliers and hay-fields	8	63

In taiga forests the main enemy adversely affecting the kolinsky population density is usually thought to be the sable (Doppelmair, 1926; Kazarinov, 1954; Timofeev and Nadeev, 1955; Shaposhnikov, 1956[1]; Laptev, 1958; Stroganov, 1962; Vojlochnikov, 1965, *et al.*). For the most part the data given by these writers refer to the mountainous areas of the Altai, the Far East and eastern Siberia, where the sable and kolinsky co-exist. In the area that concerns us here, the subzone of the taiga forests (Khanty-Mansijsky National Park District), the kolinsky mainly inhabits flood-plain lands with willow, bird-cherry and alder coppices, or marshy sites and over-grown burnt areas (Barabash-Nikiforov, 1937; Laptev, 1958), i.e., the very areas where the sable appears either rarely or not at all. Therefore the effect of the sable on the kolinsky population in the western part of the range cannot be great. Hence, in several cases the drop in the kolinsky population cannot be due to the sable. For example, in the Larjaksky district in the basin of the Vakh there was a large decrease in the kolinsky population from 1953-58, which had nothing to do with the sable. The sable was liberated here only in 1958 and it is not numerous even now. Further, in the Khanty-Mansijsky National District in 1950-1951 there was a considerable increase in the kolinsky population in spite of a high density sable production.

---

[1] Translated in the book "Studies on Mammals in Government Preserves" (P. B. Yurgenson, ed.) pp. 18-30. Israel Program for Scientific Translations, Jerusalem 1961.—Ed.

V. F. Korjakov (unpubl. report) also came to the conclusion that the sable has little effect on the kolinsky population density in western Siberia.

The kolinsky and the pine marten live in different habitats and they cannot often meet. At the Bisertsky station the marten showed no interest in fresh kolinsky tracks. There have been reports of instances where a fox has caught kolinskys, killed them and then abandoned them. In years of food shortages the fox has eaten kolinskys (Abashkin, 1965; Ternovsky and Danilov, 1965). But none of this allows us to attribute the main role in the regulation of the kolinsky population density to the fox.

The literature gives a case of a mass mortality of kolinskys due to some epizootic disease (Naumov and Lavrov, 1941) but it was not studied in detail.

Inadequate exploitation by trappers might also have an adverse effect on population density, since this would lead to an increase in the average age of the population and a reduction in the reproductive rate. But a population increase and an extension of the kolinsky's range were observed in a period of intensive trapping between 1924 and 1940. A ban on trapping in the years of population decline of 1947-1960 produced no positive results. On the contrary, it caused even greater disorganization in kolinsky trapping and evidently had negative consequences.

The large periodic changes in population density on the western fringes of the range make us take a critical attitude to a prevailing opinion that the species extended beyond the Urals only recently.

In describing the spread of the kolinsky Bobrinsky (1951) wrote: "It was evidently at the end of the 19th century that the animal crossed the Urals. In 1911 it appeared in Bashkiri, in 1925 it was found in the Kirov Region and in large numbers in Tartary, in 1927 it was caught in the northwestern part of the Gorkovsky area, and in 1932 in the Kujbyshev Region".

Bobrinsky's picture of the gradual spread of the kolinsky is inaccurate. It is known, for example, that around Orenburg, in the former Okhansky and Solikamsky districts of the Perm Region, the animal was trapped as early as 1900, 1902 and 1905 (Ushakov, 1930; Lavrov, 1937; Darkshevich, 1950). In Tartary it was regularly trapped in 1913/14, and, according to information collected by Bashkirov and Grigoriev (1931), it appeared in the republic "20 years ago". At the beginning of the 20th century the kolinsky was also known in the north of the Perm Region in the Verkhnekamsky area (Sjuzev, 1911).

If the hypothesis that the kolinsky spread from east to west is to be defended, and if the available evidence of its presence West of the Urals is taken into account, we shall have to accept that it suddenly appeared over a vast territory, almost the whole of its present range in the European USSR, and that this range subsequently underwent no important changes.

Of course, such a rapid spread and subsequent rapid colonisation of its range, its settlement of all suitable areas, and its increase by 1924-25 to trapping density in the former Middle-Volga and Gorkovsky areas, in the Perm region and the Bashkiri ASSR, at least for the last 40 years, is quite improbable. The logical assumption is that there has occurred a population growth, not a spread of the species,

The discovery of a large number of kolinsky habitats West of the Urals between 1924 and 1930, taken as evidence of the extension of the animal's range, coincided with a period of intensive research into the trapping industry, and this in turn was instigated by the great attention which economic organizations were paying to hunting and trapping, The sharp rise in the kolinsky population led to more intensive trapping than usual and this is what led to the discovery of numerous small habitat areas which had previously passed unnoticed.

The present fall in population density, when the animal has become a rare species difficult to find West of the Urals, can be taken as a confirmation of our views. In recent years there has been no information that the kolinsky survives in the Kujbyshev, Orenburg and Kostrom Regions. In the last 10 years it has not been trapped in the Tartar ASSR, but it survives as a species (Aspisov unpubl.). It is now very rarely caught in the Kirov region.

The main criterion for supposing that the animal did not exist West of the Urals in the last century has usually been that it had not been found there by contemporary writers. But this is not a reliable criterion, especially as the kolinsky attracted little attention for a long time, and even now has been little studied. Information about it that has entered into zoological works has usually been well behind what is known locally. For example, Ognev, in a major review called "Animals of Eastern Europe and Northern Asia" (1931) reports the spread of the kolinsky in Bashkiri on the catching of a single specimen in a park in the town of Ufa, while remaining ignorant of the fact that the republic at that time (1924-30) had a yearly catch of between 5000 and 11 000 pelts per season.

Ognev only assumed the existence of the animal in the Perm Region, where in fact between 1925 and 1930 there was a catch of 5000 skins per season. He wrote: "The kolinsky can probably be found in Perm Province as a rarity (nobody has as yet seen it), since it is difficult to allow that the range of the Vjatsky, Orenburg and Ufa kolinsky can be so detatched from western Siberia".

S. A. Kuklin (1937) considers that the kolinsky crossed the Urals much earlier, "about 100 years ago". Formozov and Isakov (1963) suppose that the westward spread of the kolinsky and the retreat eastward of the sable in the European USSR have been going on during the last 2-3 centuries, i.e., a lengthy period. However, these assumptions, like that of Bobrinsky (1951) that the animal crossed the Urals at the end of the 19th century, are unsupported by facts. The discovery of sub-fossil remains in the future may bring us nearer a solution to this interesting problem.

No less complex is the question of the ecological barriers that have checked the westward spread of the kolinsky. It may be assumed that the following factors have some importance;- (1) deterioration in food supplies further westward, especially the low density of water vole populations; (2) the presence of the stronger and better adapted polecat which occupies roughly the same habitats and is also polyphagous, feeding not only on small rodents but also on birds and amphibians (Lavrov, 1935).

This last assumption is supported by a comparison of the numbers of polecat, European mink and kolinsky pelts, as the yield per unit area. The kolinsky inhabits those parts of the region where the polecat is rare, and the output of skins of all three species is about 1 per 1000 hectares. As the polecat population density increases that of the kolinsky at first decreases, and then it disappears completely from the fur trade.

SUMMARY

The western boundary of the range of *Mustela sibirica* Pall. is placed between 50° and 45°W. Here the species is widely distributed from Orenburg oblast to the Komi ASSR (50°—61°N). A characteristic feature of its distribution in the Middle and Southern Urals and in the adjacent plains is the concentration of the main mass of the population in river valleys. Very high fluctuations in abundance are observed in the western part of the range. During the last 80 years peaks of abundance recurred every 10-20 years. During periods of low abundance the kolinsky became very rare over vast areas, producing the mistaken impression of a contracting range and a subsequent dispersal of the species to the west. The discovery of a great number of its habitats to the west of the Urals between 1924 and 1930, which was regarded as evidence of an expansion of its range, coincided with just another peak of abundance.

BIBLIOGRAPHY

Abashkin, S. A. (1965): Materials on the trophic interrelations of the fox, ermine, kolinsky, and water vole in Baraba. Collection of articles "Zhivotnyi mir Baraby", Novosibirsk.

Ageenko, P. D. (1959): Hunting areas and hunting the water vole in the Khanty-Mansi district. Collection of articles "Vodyanaya krysa in borba s nei v Zapadnoi Sibiri", Novosibirsk.

Barabash-Nikiforov, I. I. (1937): The animal and bird fauna of the Tobolsk district. "Uch. zap. Saratovsk. un-ta", vol. I (14), ser. biol. ed.1.

Bashkirov, I. S. and Grigoryev, N. D. (1931): Essay on the hunting in Tatary. "Raboty Volzhsko-Kamsk. kraevoi promysl. biol. stantsii", ed. 1, Kazan.

Bobrinski, N. A. (1951): Geography of animals (zoo-geography course). M., Uchpedgiz.

Vasilyev, V. (1928): Hunting in the Tobolsk north, its organisation and prospects. Uralsk. okhotnik 23-24.

Vinogradov, B. S. (1934): Materials on the dynamics of the fauna of murid rodents of the USSR. Istoricheskii obzor massovykh razmnozhenii, L.

Voilochnikov, A. T. (1965): The kolinsky and its hunting in the Far East. Collection of articles "Vopr. okhotn. khoz-va SSSR" (Mat-ly k VII kongressu Mezhdunar. okhotn. soyuza nauchn. rabotnikov po okhotovedeniyu). M., "Kolos".

Grigoriev, N. D., Teplov, V. P. and Tikhvinski, B. I. (1931): Materials on the diet of some game [fur] animals in the Tatar Republic. "Raboty Volzhsko-Kamsk. kraeboi promysl. biol. stantisii", ed. 1. Kazan.

Darkshevich, Ya. (1950): The birds and animals of the Chkalov province and their hunting. (Sputnik okhotnika i naturalista). Chkalov.

Doppelmair, G. G. (1926): Geographical distribution of the sable and the sable hunting districts. Uralsk. okhotnik No. 4 and 5.

Kazarinov, A. P. (1954): "The sable of the Far East", Khabarovsk.

Kirikov, S. V. (1952): The birds and mammals of the Southern Urals., M., Izd-vo AN SSSR.

Kuklin, S. A. (1937): The animals and birds of the Urals and their hunting. Sverdlovsk.

Lavrov, N. P. (1937): Materials on the biology of the kolinsky *Kolonocus sibiricus* Pall.). Zool. zhurn. 16 (4).

Laptev, I. P. (1958): The mammals of the taiga zone of Western Siberia. Tomsk.

Maksimov, A. A., Folitarek, S. S. and Barbash, A. A. (1965): A survey of the massive reproduction of water voles in the forest-steppe zone of Western Siberia in 1956-64. Collection of articles "Zhivotnyi mir Baraby", Novosibirsk.

Naumov, S. P. and Lavrov, N. P. (1941): Foundations of biology of game [fur] animals of the USSR. M.

Ognev, S. I. (1931): The animals of Eastern Europe and North Asia, vol. II.M.-L., Gosizdat.

Ostroumov, N. A. (1949): The world of the animals of the Komi ASSR. Syktyvkar.

Ostroumov, N. A. and Turyeva, V. A. (1953): The world of the animals of broad-leaved forests. Collection of articles "Proizvod. sily Komi ASSR", vol. III, part 2, M., Izd-vo AN SSSR.

Pavlinin, V. N., (1959): Distribution of the kolinsky and European mink in the basin of the Northern Sosva river. Mat-ly po faune Priobsk. Severa i ee ispolzovaniyu, vol. I. Tr. Salekhard. statsionara Uralsk. fil. AN SSSR, ed. 1, Tyumen.

Parovshchikov, V. Ya. (1958): The banding of the pine marten. Priroda 1.

Plesski, P. V. (1928): The kolinsky in the Vyatka province. Okhotnik i rybolov 2.

Polyakov, I. S. (1877): Letters and reports on the journey into the valley of river Ob commissioned by the Academy of Sciences. Zap. Akademii Nauk 30, annex No. 2.

Sasov, N. P. (1965): The winter supplies of the kolinsky. Collection of articles "Zhivotn. mir Baraby", Novosibirsk.

Silantyev, A. A. (1898): A survey of fur-hunting in Russia. SPb.

Stroganov, S. U. (1962): The animals of Siberia. Carnivores. M., Izd-vo AN SSSR.

Syuzev, P. V. (1911): A list of the animals of the Kama region.M.

Teplova, E. N. and Teplov, V. P. (1947): The significance of snow cover in the ecology of mammals and birds in the Pechoro-Ilych reserve. Tr. Pechoro-Ilychsk. zapovednika 5. M.

Ternovski, D. V. and Danilov, O. N. (1965): Materials on the biology of Mustelidae in the centres of a massive reproduction of water voles in Baraba. Collection of articles "Zhivotn. mir Baraby", Novosibirsk.

Timofeev, V. V. and Nadeev V. N. (1955): The sable. M.

Tomilin, A. G. (1953): The mammals of the Komi-Perm district. Tr. Moskovsk. pushno-mekhovogo in-ta 4. M.

Ushakov, V. (1950): Distribution of the kolinsky in the Urals. Uralsk. okhotnik 2-3.

Formozov, A. N. (1935): Essays on the fauna of terrestrial vertebrates of the Gorky region. Collection of articles "Priroda Gorkovsk. i Kirovsk. kraev. Nauchno-populyarnye ocherki". Gorky.

Formozov, A. N. and Isakov, Yu. A. (1963): The world of animals. From the book "Zapadnaya Sibir". M., Izd-vo AN SSSSR.

Chernyavskaya, S. I. (1959): The mammals of the "Denezhkin Kamen" reserve. Tr. zapovednika "Denezhkin Kamen" 1. Sverdlovsk.

Shaposhnikov, F. D. (1956): Ecology of the sable of the north east of Altai. "Sbornik" Materialov po rezultatam izuch. mlekopitayushchikh v gos. zapovednikakh". M.

Shukhov, I. N. (1915): The Kazym and its inhabitants. Exhegodnik Tobolsk. gubernsk. muzeya, 24th year (1915), 26.

THE EFFECT OF HUNTING ON THE SEX RATIO AND POPULATION DENSITY OF ERMINE

by

K. I. Kopein

Berdichev Teachers' College

[From: The Productivity of the Ecosystems of the Subarctic, Academy of Sciences of the USSR, Ural Branch, pp. 140-142, Sverdlovsk 1970. Proceedings of a symposium on the study, rational use and protection of renewable natural resources of the Far North of the USSR]

The sex ratio of an animal population depends largely on environmental conditions, and greatly influences the population dynamics of the species. Disturbances in the proportion of the sexes often lead to a reduction in the reproductive rate, and eventually to a reduction in the density of the population.

This applies particularly to animals with a short life span. The ermine - a species important to the fur trade and whose numbers have been sharply declining in recent years - is such an animal.

We analysed the sex ratio of populations of ermine from the tundra and forest-tundra regions, and also attempted to assess the influence of hunting on the sex ratio.

Field observations and collections of ermine carcases (4500 specimens) caught in 1959-1964 in the north of the Tyumen Region were the material for this article.

Examination of six ermine litters which had not yet dispersed showed that there were 17 males and 22 females among them. In addition, there were 19 males and 21 females among the animals caught during continuous hunting of the ermine in summer over a limited area. From these data we believe that the sex ratio at birth in the ermine is approximately 1:1 (36 males and 43 females).

The young of the year comprise the majority of the ermine population (the ermine's average life span is about 1-1.5 years, although some individuals reach the age of 3-4 years).[1]

The sexes mature at different ages; the females at 3-4 months and the males a year later. Hence it may be concluded that the ermine is a polygamous species. If they were monogamous, 50% of the females would not reproduce.

The body measurements of male ermine are considerably greater than those of the female. They therefore need more food, and their individual territories are larger in comparison with those of the females (this is corroborated from tracking).

All these features of the males' biology cause them to be more active than the females, which eventually leads to their higher natural mortality.

Ermine are hunted by various methods, usually with traps. Males usually predominate the catch (from 53 to 93% according to the data of different authors). Males comprised 71.8% of the ermine we caught.

Bearing in mind that at birth the sex ratio in the ermine is about 1:1, the higher percentage of males found in traps suggests that males have a higher probability of being caught than females. Especially many males(70-80% of all the males caught in the year) are caught in the fourth quarter. In this period there are three males in every four ermine caught.

---

[1] See other papers by Kopein in this volume and in King (1975)—Ed.

Thus hunting, acting selectively on the males, disturbs the sex ratio of the ermine population, and may lead to a reduction in the reproductive rate and in density. This may be particularly significant in thickly populated[1] regions, where hunting is carried on very intensively and the whole region is regularly hunted.

The intensity of hunting is shown by the sex ratio of a sample. A high percentage of males (65-75%) in a sample taken over the whole season indicates a low rate of hunting, while a low percentage (40-50%) indicates a high rate, at which the reproductive rate is greatly reduced (because of an almost complete lack of sexually mature males at the period of mating).

Just such a low sex ratio is observed in regions where there is a small number of ermine (the Omsk Region, Kazakhstan, etc.). In northern regions the percentage of males in trapped samples is considerably higher, which indicates a considerably lower intensity of hunting in these regions. In recent years in the tundra and especially the forest-tundra regions, the percentage of males has begun to decrease, which suggests [the beginning of] a disturbance of the sex ratio in the ermine populations in these areas also.

(No summary or references provided—Ed.)

---

[1] By man—Ed.

THE DYNAMICS OF SABLE POPULATIONS AND THE REGULATION OF THE HARVESTING OF SABLE IN THE USSR

by

N. N. Bakeyev and G. I. Monakhov
(USSR)

[From: Transactions of the International Congress of Game Biologists 9: 353-56, 1970.]

Over-exploitation of the sable, a valuable fur-bearing animal, has led to a lengthy depression of sable resources. At the present time, owing to a number of economic and protective measures, sable resources have returned to the level of the 16th-17th centuries, when intensified exploitation of fur resources in Siberia began.

Sables have become a common game species in the forests of Siberia and of the Far East, including Kamchatka and Sakhalin.

The total area of distribution of the species amounts to 497 million hectares. At present, hunting is carried out in most of it. The proportions of the total area graded as low, medium and high in productivity are shown in Table 1.

TABLE 1: Proportions of the sable hunting area of low, medium and high productivity (1956-1965).

Population density	Area (% of the total distribution area)	Yield of pelts per 1000 hectares	Stocks of pelts (% of the total stocks for the USSR)
Low	31.7	0.005-0.18	7.7
Medium	41.2	0.20-0.50	36.3
High	27.1	0.55-2.00	56.0

During the last decade, the total number of sables in the USSR has been estimated at not less than 600 000 individuals.

Estimates of the population density and rate of harvesting of sables per unit area permit classification of populations in different regions according to their reproductive capacity and productivity (Table 2).

Sable populations of low densities are typical of the whole northern and north-eastern part of the distribution area, particularly Yakutia, the Magadan region, and the northern areas of the Khabarovsk Territory. This is due to the scarcity of food in the sparse pre-tundra and larch forests, and also to adverse climatic conditions i.e., strong frosts with a shallow snow cover (Abramov, 1967). These factors reduce the reproductive rate and increase the natural mortality rate compared with other populations.

The best conditions for the sable are in the mountain taiga of South Siberia, where there are many Siberian pine forests with an admixture of spruce, fir, larch and other tree species. Particularly high population densities, reaching 16-18 animals and a yield of 5-7 skins per 1000 hectares, have been recorded in the Altai and West Sayan forests.

The sable populations of the central part of Central and East Siberia are less dense than those in the southern mountainous parts. The sables of these regions live in highly diverse conditions. An intact virgin taiga with many Siberian pine forests (typical sable habitats) alternate with forests of secondary origin, mainly birch forests which are unsuitable habitats for

TABLE 2: Geographical variation in density and reproductive capacity of sable populations, from the data of A. A. Vershinin (1963), V. L. Zaleker (1962) and our own research.

Region	Forest type	Average density per 1000 ha	Average yield of pelts per 1000 ha per year	Average no. of embryos per pregnant female	Population structure				Longterm average potential % increment
					males		females		
					adult	young	adult	young	
South-eastern	Larch forests with dwarf Siberian pine and forest tundra	0.08-0.6	0.08	2.96	-	-	-	-	27.1
Northern	Northern taiga larch and spruce-larch forests	0.6 -1.0	0.26		21.3	38.6	14.0	21.1	
Central	Siberian-pine birch-pine forests	1-6	0.60	3.47	32.6	22.2	23.2	22.0	60.5
West-Siberian	Pine/Siberian-pine	2	0.44	3.80	46.7	16.3	24.4	12.6	78.9
The Far East (southern)	Spruce/Siberian-pine/larch and Siberian-pine/broadleaved	2	0.40	3.27	-	-	-	-	-
South-Siberian (mountain)	Siberian pine with larch and spruce-fir	5-10	1.24	3.14	26.7	26.6	18.9	25.8	47.3
Kamchatka	Larch-*Betula ermanii* with dwarf Siberian pine	3	1.0	4.03	38.7	10.7	33.9	16.7	59.9
Sakhalin	Spruce-larch and fir-birch	2-3	0.75	3.51	-	-	-	-	-

sables. Birch forests occupy 30-45% of the afforested area in some districts of Central Siberia. These populations are hunted to varying extents, and this in the end leads to uneven densities of sable populations, which on an average fluctuate from 1 to 6 with a maximum of 10 and even 18 animals per 1000 hectares (Bakeyev, 1968).

The West-Siberian population inhabits the Siberian pine and pine taiga, which is relatively homogeneous, low-lying and very waterlogged. Large areas are occupied here by [one word unknown][1] low-growing pine forests distributed through the marsh, which are completely unsuitable for sables, and this noticeably reduces the productivity of the district for sables.

Siberian pine forests on the western borders of their distribution area seed infrequently, and are poor in food supplies for sables. In the years of poor seeding they have no pine-nuts, which are an attractive and easily accessible food for sables. Therefore sables in West Siberia eat more animal food (Zaleker and Poluzadov, 1955), and this stimulates their reproduction to a certain extent. On an average there are 3.8 embryos per pregnant female, judging from the corpora lutea of pregnancy (Zaleker, 1962). The general shortage of food observed in some adverse years increases the embryonic and post-embryonic mortality rate. Therefore, though the potential increment of the population is high (about 79%) the actual recruitment is lower (41-43%).

The Kamchatka sable population inhabits larch (with dwarf Siberian pine) and *Betula ermanii* forests which are rich in foods, both plants (mainly berries) and also animal prey.

The abundance of food on Kamchatka changes greatly from year to year: some years there is no food at all. Therefore indices of reproduction and recruitment fluctuate in the Kamchatka sable population. In favourable years 7-8 young were found in a litter, and up to 9 corpora lutea were recorded in histological analyses of the ovaries of female sables. The average number of embryos per pregnant female increased to 4-4.7 in such years. The potential increment of the population reached 80 and even 134%.

In adverse years, when there were no plant foods, and few small rodents, most female sables, worn out during the lactation period, did not breed next season. In such cases the proportion of the sexually mature females which were pregnant dropped to 15-30%. The average number of embryos per pregnant female decreased to 2.9, while the potential recruitment in the population was 16-28% (Vershinin, 1963).

As has been shown (Table 2), there is marked geographical variation in the reproductive capacity of different sable populations. The reproductive rate varies to a considerable extent from year to year, due to the effects of both external and intra-populational factors (Table 3). Therefore the rate of exploitation of a sable population cannot remain constant.

It is essential to introduce a hunting system which is adjustable to the annual variations in rate of reproduction of the population. To do this, it is necessary to know the potential recruitment to the population each year.

Delayed implantation in sables makes it possible to determine the average number of embryos per sexually mature female by means of histological analyses of the ovaries, 8-10 months before the start of the hunting season. If the age structure and the sex ratio in the population are known, it is easy to calculate the potential recruitment to the stock. In the northwestern Baikal region we determined it for each season (Table 3).

We observed almost twofold fluctuations in the potential recruitment in different seasons. In order to plan the harvest it is also necessary to know the possible waste (mortality) of individuals in the population before the

---

[1] Translator.

beginning of hunting. This depends on environmental conditions, mainly the food supplies in the forest. The embryonic and post-embryonic mortality rate may be assessed to a certain extent from the difference between the potential and the actual recruitment (number of the young-of-the-year in a population sample). In favourable years, which, in the north-western Baikal region, were 1957-1958 and 1958-1959, the mortality rate of the young ranged from 7.2 to 12.0%. In adverse years the mortality rate of the embryos and young reached 77.8%. (Monakhov, 1968).

TABLE 3: Potential annual recruitment to the sable population of north-western Baikal region

Seasons	Number of sables sampled	% adult females	Average number of corpora lutea per adult female	Potential % recruitment to population
1956-57	75	28.0	2.20	61.7
1957-58	81	19.8	2.8	40.8
1958-59	58	22.4	1.77	39.6
1959-60	131	29.8	2.74	81.7
1960-61	75	25.4	2.57	65.2
1961-62	131	23.6	2.48	58.5
1962-63	78	27.0	2.42	65.3
1963-64	191	22.5	2.64	59.4
Total	820	24.8	2.44	60.5

When determining the rate of harvesting it is necessary to take into account the present population structure, and the present and potential resources for future increase of the population. It would be advisable to discontinue hunting if the density of sables is 0.5 per 1000 hectares in forests which are typical for sables and whose carrying capacity is considerably higher than this figure. At a density of 0.5 to 2.0 individuals per 1000 hectares, a harvest of 10-50% of the increment stimulates reproduction and assists in re-establishment of the optimum density. If the forests are rich in sables (10 or more individuals per 1000 hectares) then it is possible to harvest the total increment.

The existing methods for analysing the dynamics of the populations of game animals allow the regional branches of the All-Union Scientific Research Institute of Game Economy and the Breeding of Animals for Furs to determine annually the permissible sable harvest, in order to ensure the rational utilization of this resource.

SUMMARY

The sable (*Martes zibellina*) has become a common species in the forests of Siberia and the Far East. It occupies an area about 500 million hectares.

Northern and northeastern populations are not numerous, with low density (0.08-1.0 animals per 1000 hectares), low fertility (the average number of embryos per pregnant female is 2.96), and low increase of population (27% a year); they inhabit mainly larch forests—the least favoured habitat of the species. These populations occupy 57% of the whole area and produce 8% of the total harvest of sable skins. The populations of the central part of

Siberia and of the southern part of the Far East, which have a density of 1-6 animals per 1000 hectares, average fertility (3.27-3.47 embryos per female), and potential increase of population 60-80%, occupy 36% of the area.

The populations of southern Siberian mountain forests (mainly cedar forest) in the optimum habitat for the species, have high density (5-10, at most 18 animals per 1000 hectares) which probably results in lower fertility (3.14 embryos per female) and decreases the population increase to 47%. These populations occupy 7% of the area.

The increment of population varies greatly with the years (in the northwestern Baikal region from 40% to 82%). For determining the increment one should know the population structure and fertility, the food resources, and the meteorological conditions, especially in the breeding season. The difference between the potential (the number of embryos) and the actual (the number of animals in the year's litter) recruitment to the population may be rather great—from 7% to 80%. Therefore, when the rate of harvesting is fixed, the probable mortality of the young stock should be taken into consideration.

It is not advisable to hunt sable when the density of population is less than 0.5 animals per 1000 hectares. If the density is 10 and more animals per 1000 hectares, the number of animals harvested may equal the total population increase.

(No references provided—Ed.)

SELECTIVITY OF SABLE HUNTING

by

V. K. Melnikov

[From: Byulleten M. O-va Isp. Prirody, Otd. Biol.,
80 (6): 36-41, 1975].

Our material is based on data from 769 sables caught over 4 seasons in the Krasnoyarsk region. We divided them into age groups on the relative width of the canal of the canine tooth (Smirnov, 1960)[1], which is a very reliable method, particularly for distinguishing the young-of-the-year (Monakhov, 1967). The animals obtained were divided into 3 groups according to the date killed and the method used, and also by sex and age. Only those animals were used for which the dates and the hunting methods were known. In order to determine the selectivity of the various hunting methods, the sex ratios and age structure of the sables caught were analysed. We assessed the selectivity of hunting from changes in the ratio of the young-of-the-year caught per adult sable through the hunting season and with the use of different hunting methods, and also from the changes in the sex ratio of the catch. The significance of the differences in these ratios was determined from t-tests (Lakin, 1973).

Selectivity with respect to age and sex

In the course of a hunting season (Table 1) the ratio of the young-of-the-year per adult markedly decreases. The difference between the age ratios at the beginning and at the end of hunting ($P > 0.99$) is significant in four cases out of five (Table 1). The only statistically insignificant difference was the one in the Turukhan district, which may be due to a relatively small sample: only 15 sables were caught here in January and February.

A regular decrease in the numbers of the young-of-the-year caught per adult can be caused only be selective removal of the young during the first stage of the hunting season, independently of the methods used. At the beginning of the hunting season the young-of-the-year usually comprise a high proportion of the sables caught (Belov, 1972), far higher than their proportion in the sable population at this time of the year, and considerably more than the calculated potential production of the previous breeding season. A similar pattern has been recorded by N. B. Poluzadov (1965) in the Urals.

Hunting selects for young-of-the-year even in years when their proportion within the population at the beginning of the season is not great. In the 1969/70 season, unusually few young were observed in the samples from most of the areas of the Krasnoyarsk Region. Among 322 sable carcasses received during that season from the Tashtyp district (which amounted to about 10% of the total yield of the Shorsk hunting enterprise) there were only 20.2% young-of-the-year. The proportion of young-of-the-year among the sables trapped decreased drastically (by 6 times) during the later stages of the hunting season. The proportion of adults caught usually increases considerably from the second half of December.

At the beginning of the hunting season it is usual to obtain a relatively greater number of males, both among the adults and the young-of-the-year. Among the adults, the relative number of males obtained per female gradually decreases as hunting proceeds, reaching its minimum at the end of the season. In January/February sexually mature females are quite often in the majority (Table 2). The sex ratio in the young-of-the-year changes little up to the

---

[1] Method described by Kopein, 1965 (this volume)—Ed.

TABLE 1: Change in age ratio (number of young of the year per adult[1] in samples of sable taken through the hunting season.

Seasons	Districts	Total Number of sables caught	Young per adult			Reliability of difference between the data from the beginning and the end of the hunting season [t]	P
			October-November	December	January-February		
1969-70	Tashtyp	200	0.7	0.4	0.12	3.64	0.99
1970-71	Baikit	114	1.2	-	0.3	2.91	0.99
1971-72	Baikit	190	4.0	1.8	1.5	2.60	0.99
1972-73	Baikit	161	5.9	2.2	0.6	5.05	0.99
1971-72	Turukhan	104	4.6	3.3	2.7	0.73	0.53

TABLE 2: Sex ratio among adult sables (males per female) through the hunting season

Seasons	Districts	October-November	December	January-February	Average per hunting season
1969-70	Tashtyp	1.6	1.1	0.7	0.95
1970-71	Baikit	1.2	1.1	1.0	1.15
1971-72	Baikit	2.0	1.5	1.4	1.57
1972-73	Baikit	1.7	0.6	0.9	0.90
1971-72	Turukhan	1.5	1.4	0.3	1.10

TABLE 3: Sex ratio among young sables (males per female) through the hunting season

Seasons	Districts	October-November	December	January-February	Average per hunting season
1969-70	Tashtyp	1.7	2.0	1.25	1.9
1971-72	Baikit	1.4	1.4	0.95	1.3
1972-73	Baikit	0.7	0.7	0.27	0.6
1971-72	Turukhan	1.0	1.2	0.75	1.1

middle of the season (December) compared with the beginning of hunting (Table 3). After that the proportion of males in the bag drastically decreases (in three instances) or else increases (in one instance). However the (average) difference in the sex ratio of young between the beginning and the end of hunting is not statistically significant.

---

[1] It is possible to assess the number of young-of-the-year per adult female by multiplying the given ratios by 2, assuming that the sex ratio is 1:1—Author.

Calculations showed that the probability of an increase in the proportion of females trapped at the end of the hunting season attains 80-90%. Deviations in the difference in sex ratio may be explained by the different degrees of selectivity of the various hunting methods used at different stages in the season. In order to eliminate such an effect, which distorts the effect due to the stage of the season alone, theoretical regression coefficient were calculated from the data of Tables 2 and 3 (Plokhinskii, 1961). They confirm (Figure 1) that a decrease in the proportion of males and a corresponding increase in the proportion of females caught in the course of a hunting season is not accidental.[1]

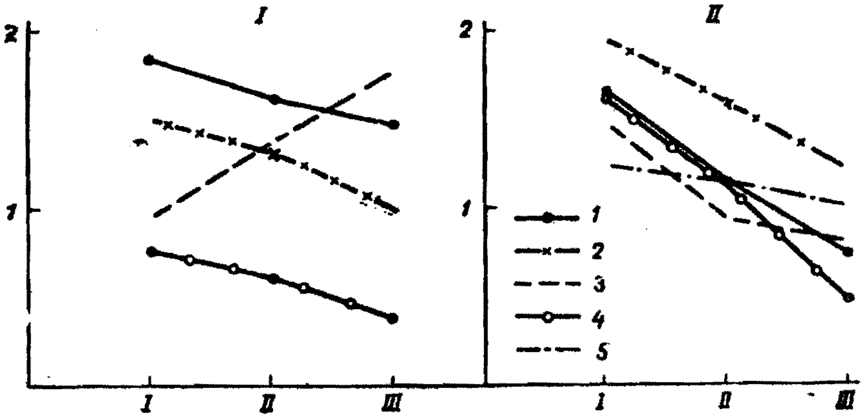


FIGURE 1: Calculated regressions of the decline in the numbers of males caught per female through the three stages of the hunting season.

Key: I - the young-of-the-year; II - adults. 1 - Tashtyp district, 1969-1970; 2 - Baikit district, 1971-1972; 3 - Turukhan district, 1971-1972; 4 - Baikit district, 1972-1973; 5 - Baikit district, 1970-1971.

A higher mortality rate of males compared with that of females occurs in many species. It is highly probable that the selectivity in the hunting of male sables, obvious at the beginning of the hunting season, may be explained by their higher activity as compared with that of the females, their longer travelling distance during a 24-hour period, their larger home ranges, their lesser attention to safety, etc. All this increases the likelihood of a dog encountering their fresh tracks. It is possible to find more males than females at any stage of the hunting season among the sables obtained from a relatively small area.

It is known to hunters that some areas always produce more males or females; therefore an analysis of the selectivity of hunting for one sex should use data from a sufficiently large district. It should be emphasized that the real sex ratio of the sable population cannot be estimated from data collected at the beginning of the season, as the proportion of males will always be artificially high. Some samples contain very few females, due to highly selective hunting of males and of the young-of-the-year [all through the season]. Thus, during the 1971/72 season in the Turukhan district, the proportion of females amount to only 7.8 ± 2.4%, while in 1972/73 in the Kezhma district it was 4.4 ± 1.99%. Many more examples could be given.

---

[1] As the young and male animals are removed from the population, females begin to get caught in large numbers. The Turukhan district is the only exception; and this may possibly be explained, as said before, by the small size of the sample at the end of the hunting season—Author.

Selectivity of different hunting methods

A comparison of the number of the young-of-the-year per adult obtained, from the same area during the same period, with the use of dogs or baited traps, shows that the probability of trapping young ones is considerably higher if food baits are used (Table 4). Of the young-of-the-year (per adult sable), 25-27% more are caught in baited traps than by hunting with dogs.

TABLE 4: Proportion of young-of-the-year per adult sable caught by different hunting methods.

		October-November		After 15 December		
Seasons	Districts	With dogs	In baited traps	On runways	With bait	In the whole sample
1969-70	Tashtyp	1.6	-	0.25	1.25	0.32
1971-72	Baikit	3.75	4.7	-	-	2.30
1971-72	Turukhan	4.34	5.5	-	-	3.95

The analysis of trapping (Table 4) shows that in a given period of time considerably more adult animals are trapped in traps set on their runways (105 sables); but the young-of-the-year, even when their proportion in the total sample is small (20.2%), still comprise the majority of the catch of baited traps even at the end of the hunting season (difference significant at 99.7%) Therefore there cannot be the slightest doubt that traps provided with food bait selectively catch the young-of-the-year. The young are caught more often with bait because they are inexperienced and less cautious than adults.

Our material (145 sables from 2 districts) proved to be inadequate for examining the selectivity of different hunting methods by both sex and age, and therefore Table 5 shows only the sex ratio of sables caught by two methods.

There are somewhat fewer males caught by the use of baited traps than by hunting with dogs. An interesting sex ratio was found among the sables caught in the Tashtyp district in traps set on runways. During the 1969/70 season an average of 6.1 males were caught for every 10 females, while the general sex ratio of sables caught during the season was 1:1. It may be assumed that the larger number of females caught in traps set on runways is because this method was used during the later stages of hunting, when large numbers of males had already been caught.

In summary, the following generalization can be made. Selectivity of all hunting methods is highest for the young-of-the-year. It is particularly well marked at the beginning of the hunting season and when using traps with food bait, and is the least marked when hunting with dogs. Young animals are caught first even in the years when their proportion in the population at the beginning of the hunting season is small. In the later stages of hunting, particularly after 15 December, the proportion of adults (mainly females) drastically increases. Males of all ages are preferentially caught at the beginning of the hunting season. The selective hunting of the young-of-the-year and males at the beginning of the season increases the relative reproductive potential of the sables population, as it results in the conservation of sexually mature animals, particularly females.

Continued selective hunting of the young-of-the-year and males at the beginning of the season could be detrimental, because the systematic preferential removal of one age or sex group changes the structure of the sable population; and these changes could become irreversible. However, the extent

TABLE 5: Ratio of male and female sables obtained by two hunting methods

Seasons	Districts	October-November With dogs	 In baited traps	In the whole sample
1971-72	Baikit	1.72	1.48	1.5
1971-72	Turukhan	1.29	0.95	1.1

of the selectivity of hunting is not fixed, and is most distinct in the areas where the rate of exploitation is low. As different hunting areas are exploited to varying extents, including some which act as a kind of reserve, where there is no hunting at all, the effects of selectivity are largely levelled out. Also, selective hunting is detrimental only if it is so heavy that the production of the population is insufficient to reestablish its normal structure. Each species has its own normal population structure for optimal homeostasis.

By comparing the age and sex ratios in samples of animals caught with the calculated ratios in the population, we found that in cases showing the most extreme deviation, the number of young-of-the-year caught exceeds by 30-46% the number which should have been found in the sample if the hunting were proportional. The annual increment in sables, according to the data of Monakhov (1968) varies from 22 to 142%, i.e., the range of fluctuations in the increment greatly exceeds the extent of selectivity. Consequently, the selectivity of hunting the young-of-the-year remains within the limits of the potential of the population to compensate, and therefore selective hunting cannot cause irreversible changes in the structure of the sable population.

Hunters always aim to harvest their usual number of furs, whatever the population density of sables. In the years of reduced fertility and low survival of the young, as for example in 1969, this can be done only by harvasting the basic reproductive stock i.e., sexually mature animals. Thereby the total number of sables decreases to a considerable extent, not only during the hunting season, but also during the subsequent years. It seems possible to us to use indices showing the selectivity of hunting (the age ratio) in the control and effective regulation of sable hunting, in order to conserve their numbers, and, consequently, also the structure of the population. A prevalence of older age groups at the beginning of the hunting season (in test samples taken in October-November) indicates poor reproduction and a need to stop hunting before the appointed time. In order to increase the reproductive potential of sables during poor years, it is advisable to permit hunting only up to the middle or the end of December, the time when the first indications of reduction in population appear in the intensively hunted areas.

The sex and age structure of samples taken at the beginning of the hunting season do not reflect the actual structure of the population. Owing to the selectivity of hunting the ratio of the young-of-the-year and of males is usually over-estimated in samples. Therefore these data cannot be used to calculate the expected increment without the necessary corrections. In order to determine the actual structure of the sable population, carcases which are to be used for analysis must be obtained throughout the whole hunting season in the district sampled. Only the intensity of sable hunting in a given area can be assessed from the structure of the test samples.

SUMMARY

At the beginning of the hunting season mainly young sables are taken, irrespective of the mode of capture and of the percentage of young-of-the-year in the population at the time; young are also preferentially caught in baited traps at all stages of the hunting season. At the start males prevail, but the percentage of sexually-mature females increases sharply during the second half of the season. The selective capture of males and young-of-the-year distort the natural structure of the population, a fact that has to be taken into account in calculating estimates of the expected recruitment.

BIBLIOGRAPHY

Belov, G.A. (1972): Methods for determining an increase in the numbers of sables. "Sb. NTI VNIIOZ", ed. 37-39, Kirov.

Lakin, G. F. (1973): Biometry. M.

Monakhov, G. I. (1967): Comparative evaluation of some methods for the age determination of sables. "Sb. NTI VNIIOZ" ed. 19. M.

Monokhov, G. I. (1968): The rational utilisation of sable stocks. "Okhota i okhotn. khoz-vo", No. 10.

Plokhinski, N. A. (1961): Biometry. Novosibirsk.

Poluzadov, N. B. (1965): Reproduction and rational utilisation of sables in the Urals. In the collection: "Vopr. okhotn. khoz-va i zverovodstva". M.

Smirnov, V. S. (1960): Age determination and age ratios in mammals, taking the squirrel, the muskrat and five species of carnivores as examples. Tr. In-ta biologii UFAN SSSR 14. Sverdlovsk.

TAKING A CENSUS OF OTTER, SABLE, MARTEN AND SMALL MUSTELIDS

by

V. P. Teplov

[From: 'Methods of determining the numbers and geographical distribution of terrestrial vertebrates.' Institute of Geography, Academy of Sciences of the USSR, pp. 165-72. Publishing House of the Academy of Sciences of the USSR, Moscow, 342 pp, 1952.]

Methods of censusing populations of most species of mustelids are still not particularly well developed. Most easily counted are otters and mink, because of their close ecological relationship with lakes and rivers.

The best time to carry out observations is at the beginning of winter, when the snow is not deep and the lakes are not yet frozen over or are just covered with thin ice. A count is made as follows: (1) the banks of rivers and lakes are searched; (2) all tracks are carefully noted and the prints measured; (3) the extents of the home ranges of individual animals or families (young otters stay with their mothers for their first winter) are determined. The present method is therefore one of quantitative calculation of individual ranges.

With experience, male and female tracks of mink and otters, and even those of young otters, can be distinguished. Otters and minks are scarce in most regions, and the hunting ranges of adult animals of one sex hardly ever infringe upon one another. The banks of lakes are not suitable for otter and mink along their entire length, which contributes even more to the isolation of the territories of separate individuals and families.

A census carried out around lakes can be done by one person, but in the vicinity of small rivers and streams it is better done by two, who maintain constant communication with each other as they go along each bank. If snow should cover the banks before a lake freezes over, and if the banks and nature of the lake permit, a boat can be used to move around it, which greatly facilitates the job.

The home range of an otter often occupies several kilometres of shore line, and in winter these animals are often very unevenly distributed. Hence a survey must be carried out along most of a lake shore and even over its entire length.

With the increasing weight of the cover of snow and ice and the settling of the ice, hollows form under the ice along the banks of the lake, often up to a kilometre in length, which are readily used by otter and mink. During this time the animals often do not appear on the surface of the snow for several days. In periods of frost and deep snow otters often manage to cross from one lake to another. This is not a particularly good time for observing them.

On small reserves and game-farms it is advisable to carry out a survey for otters and mink on all the lakes. On large areas a survey can be limited to the most typical lakes and the results extrapolated to all lakes populated by otters and mink. The calculations are carried out as follows: (1) inventory of the lakes in the area under observation is made; (2) the topographical distribution of otters and mink are plotted on a schematic distribution map; (3) lakes classified as typical are identified, examined, measured and described; (4) a census of otter and mink on these lakes is made; (5) the results obtained are evaluated from a survey of all lakes of the type.

In making a census of the otter in the Volga delta in February, A. T. Romashova used a specially trained dog to hunt out the winter dens of the otter in the Astrakhan reserve. The environmental conditions of the otters in the reserve were rather unique and we cannot recommend this method without having tried it out in other regions, so we shall not go into the work of A.T. Romashova in further detail.

Counting sable in their winter "nests", a method developed by V.V. Rayevsky,[1] is a striking example of a successful and simple solution to a complex problem, based on a detailed study of the ecology of a species. Having established that the winter hunting ranges of the sables are exclusive, and having proved the practicality of conducting a survey of sable in their winter "nests", even in areas of very high population density, Rayevsky evolved a census method which could be applied to most mustelid species. The information we have on the ecology and habits of the pine marten, kolinsky, polecat and ermine leads us to believe that the winter behaviour of these species is similar to that of the sable, which suggests that a census of them could be conducted by Rayevsky's method. This requires much time and effort, but gives accurate figures which enable the figures from comparative surveys to be converted into absolute [densities]. The numbers of marten in experimental census areas were established from counting the number of winter "nests". Observers automatically kept a record of their itinerary while travelling through the area along a network of observation routes. The number of fresh tracks of marten per unit of area covered were compared with the results of a count of their winter "nests", and from this experiment we can obtain accurate co-efficients for converting relative indexes into absolute.

There can be no doubt that the number of tracks of a particular species encountered on a determined route under specific ecological conditions in a particular year depends directly on the population density of that species in that habitat. Hence, we can establish the population density of the species in the most divergent habitats of the locality by counting, in the control area, both winter "nests" and tracks, and in all other areas, tracks only. From the correlation between the incidence of tracks and the density of the marten population over a number of years, taking into account the record of the ecological characteristics of the winter season each year (depth of snow cover and structure, air temperature, availability of food, etc.), on which the activity of the predators depends,[2] figures will in future be available whereby the population density of mustelids can be accurately ascertained from track counts alone.

The conversion of relative to absolute figures would not of course apply in a winter season which stands out as being particularly unusual.

This being said, the following scheme for conducting a census of the sable, marten, polecat, kolinsky and ermine[3] in our large reserves and hunting areas can be put forward (the schedule of work to be carried out in this sequence.)

1. The distribution of the species of interest in each type or group of types of the main habitats in the study area should be plotted.

---

[1] See "A census of the population density of the sable" by V. V. Rayevsky, in this symposium—Author

[2] During a shortage of food the marten often covers a wider area, leaving more tracks, so that during a count of the tracks criss-crossing the observation route, a false impression of marten numbers may be obtained. This possibility should be taken into consideration—Author

[3] It is probable that a census of [two words whose meaning could not be established - Trans.] can also be carried out in this way—Author

A series of routes of a pre-determined length should be marked out, along which all tracks will be counted. The work can be carried out in any month during the snowy period of the year, but should not take too long or the gathering of data can be distorted by differences in the seasonal activities of the animals. The length of the routes is determined by the size of the area to be studied and by how easily the work can be organised and carried out. It is desirable that in each group of types of the main habitats there should be routes of from 50-100 kilometres in length.

2. Permanent experimental areas in the main habitats of the species should be established.

The type of habitat is decided by the results of the route survey. The size and configuration of the experimental areas are determined by the nature of the land and by how easy it is to organise and carry out the work. As a result of a survey of sable in their "nests" on the Taiga plain, Rayevsky,[1] recommends square areas 10 km by 10 km in size. Experiments on areas of this size would be acceptable in a census of pine marten in their "nests" on level terrain. When carrying out a survey in mountainous areas it is preferable, instead of one square area, to have several experimental areas in the form of long rectangles, 0.5-1 kilometre in width, situated across the slopes in various ways. For ermine, kolinskys and polecats, the size of the experimental areas can be reduced to 3-5 kilometres^2. The boundaries of the experimental areas and the network of census routes should be marked in unobtrusive ways - with paint on trees and with special markers at the entrance of dens. The spacing of the census routes depends on the species being studied. For sable and marten the census route should be up to 1 kilometre long, whereas for a count of the smaller mustelid species, the distance can be reduced to 0.5 km.

3. An overall estimate of the numbers of marten in the experimental areas should be made by counting their winter "nests".

This should be done with the shortest possible delay in the frosty winter period by systematically tracking all animals detected, and determining their home ranges and the location of their winter nests. The animals are detected by walking along the network of census routes. While doing this, all tracks found are noted on a map. This means that a special count of tracks in the experimental areas need not be made. The winter nests and home ranges of the individual animals found are plotted on a map of the area.

4. An itinerant check should be made for tracks in the main types of habitat in the region, including the area in which the experiment is being carried out.

5. Maps and tables relating to the population density of the species in the whole region should be drawn up. For this, the data from the itinerant surveys are evaluated from the correlation between the number of tracks found and the population density in the areas where both tracks and nests were counted.

On small reserves and game farms surveys are carried out over the whole of their area.

To carry out a successful census, detailed descriptions of the census routes and areas, and diagrammatic maps of their distribution in the locality should be made. In the reserves these are called "animal record books". This should be borne in mind for most other methods of carrying out a census of an animal population also.

---

[1] Cf. V. V. Rayevsky's article, "A Census of the Population Density of the Sable" in this symposium—Author

We successfully undertook a comparative survey of marten tracks along observation routes, without an attendant survey of their winter "nests" in the control areas, to monitor the general population changes of marten in the Pechora-Ilych game reserve. The survey was carried out twice every winter for some years; from the beginning of November to the beginning of December and then in March. In the first case this was done simultaneously with a survey of squirrels, and the second time with a survey of elk. The total length of census routes covered by observers in the reserve during a survey of marten fluctuated in different years from 1000 to 3000 km. The tracks found during each survey (early winter and late winter) were counted [separately] over the first 100 km of route, after which the index figure for the tracks found through the whole of the winter was taken as the average of the early and late winter survey figures. Figures were worked out separately for the dark conifer (spruce, fir) forests and the predominantly pine forests. This was because in the pine forest region the marten is more easily flushed out by hunters than in the dark conifer forests, and so for some years after the reserve was established the marten was rare in the pine forests.

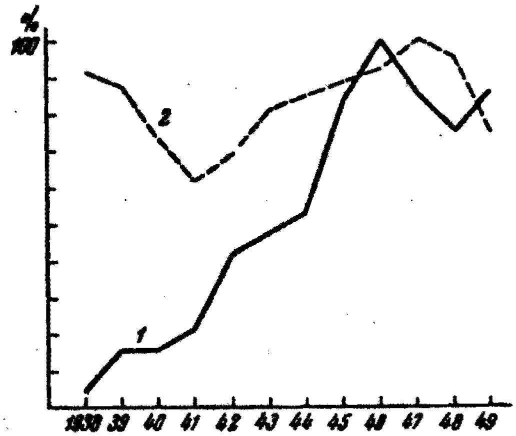


FIGURE 1: The results of annual counts of the tracks of the pine marten in the Pechora-Ilych reserve, expressed as the average number (in percentages) per 100 kilometre observation route (the greatest number encountered was taken as 100%).

1. Region of pine forests. 2. Region of dark conifer forests.

From Figure 1 it can be seen that in the pine forest region the number of marten has almost continuously increased. This increase is due both to a significant influx of marten from the neighbouring dark conifer forests, and to the reproduction of marten living in pine forests.

The index for the last year exceeds that for the first year by 16 times, which indicates a significant increase in the marten population in the reserve.

The situation differs in the dark conifer forest regions. Index figures for severe winters are very close (1938-39; 12 tracks, and 1945-46; 11.5 tracks). From these we can assume that the marten population was the same at the beginning and end of this series of counts.

A reduction in the numbers of marten recorded in the winters of 1939/40 and 1941/42, and their increase over the next four winter seasons, can perhaps be explained by numbers of marten moving into the pine forest region and the hunting grounds bordering on the reserve, and then the repopulation of different areas of young animals.

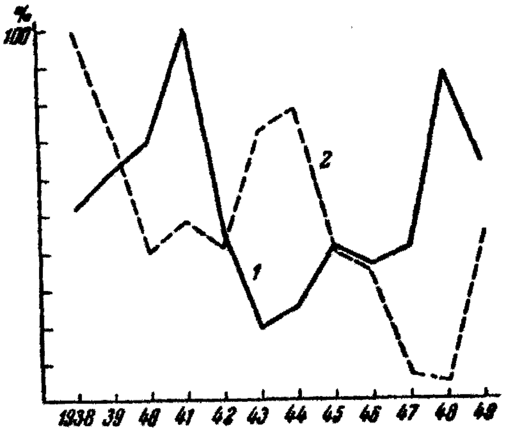


FIGURE 2: The average number of ermine tracks over 100 kilometres of observation route in the Pechora-Ilych reserve in November (the greatest number encountered being taken as 100%) and the supply of pelts from areas adjoining the reserve (in percentages) for the years 1938-1949. 1 = tracks; 2 = pelts.

Figure 2 gives the results obtained over a number of years of surveying the ermine from its tracks along the observation routes in the Pechora-Ilych reserve, and the harvest of pelts of this species in the regions adjoining the reserve. It can be seen that in most years the two lines form "scissors": in years when peak numbers of ermine are found in the reserve, the supply of pelts drops, and vice versa. In the Pechora taiga country, the ermine is trapped almost exclusively with edible bait, but the number of ermine trapped in this way depends less on their numbers than on their hunger. In years when ermine are not short of food, fewer are caught, and in years of famine the catch increases. The woodland vole is the ermine's main food in the Pechora taiga country. As twelve years of observation have shown, the number of woodland voles greatly influences the ermine's rate of reproduction and the number of ermine captured. In years when peak numbers of voles occur in the Pechora, peak numbers of ermine are found, and there is a drop in the harvest of pelts. In years when voles are scarce the population of ermine falls, but the pelt harvest increases. This regular relationship is well illustrated by the following. One year when peak numbers of ermine were found in the Pechora-Ilych reserve, the average number of voles caught per 100 trap-nights was 25, and the average index for the harvest of ermine that year was 30%. In a year when the population of ermine dropped, the index for the number of voles fell to 10 per 100 trap-nights, and the harvest of ermine rose to 70%.

Both examples graphically demonstrate that a comparative survey of marten by their tracks, even if not accompanied by a controlled check of animals in their "nests", can be quite valuable. Though the actual number of animals is unknown, this method allows a general monitoring of the number of marten present provided that a survey of tracks is carried out from year to year along observation routes over significant areas.

Among other methods of taking a census of marten, we should mention that developed by Zharkov (1941) for counting ermine in the flood-plains of large rivers. The hunting grounds of ermine here are mostly along the banks of marshes and lakes, which generally run parallel with the river, forming flood-plains. The home ranges of individual ermine during heavy winter snowfalls are generally isolated from each other, but if they do happen to be close together, then in most cases they belong to animals of different sexes.

The male's home range, according to Zharkov, is almost 3 times greater in area than that of the female (the average area of the male's range in the Kama river basin is 20.5 hectares, and that of the female, 7.8 hectares). The average length of the male ermine's range (the distance between the furthermost points of the area) would be somewhere in the region of 800 metres, and a corresponding figure for that of the female would be about 320 metres. A census of ermine using Zharkov's method would be conducted in the following way:

1. In flood-plain areas where ermine are numerous, an observation route is marked out across the entire breadth of the flood-plain right up to the river banks. This will cut across marshes and lakes as well as the ermine's hunting grounds which, as already mentioned, are most frequently found on the banks of lakes;
2. Ermine home ranges crossed by the route are surveyed and measured. At the same time the sex of each animal is determined by the size of the tracks;
3. The size of the census area is determined. For length, the overall length of the observation route is taken, and for width, the average diameter of the home ranges of male and female ermine, calculated in step 2 above;
4. From the figures obtained in steps 2 and 3, the number of ermine is calculated per unit area of flood-plain.

Zharkov's method is perfectly acceptable for a census of ermine in the particular environment of the flood-plains of large rivers which, we should point out, are one of the species' main habitats. Unfortunately, it is no less laborious than Rayevsky's method of censusing sables in their "winter nests".

If Zharkov's method is to be successfully applied, data must be available on the size of the ermine's home ranges. To obtain this information, special preliminary work on tracking down sufficient numbers of animals (not less than 10 specimens of each sex) must be carried out. This would not present much difficulty if the indices obtained could be used for a given region over a number of years; but since the length of the ermine's hunting excursions, and therefore the dimensions of its territory, change abruptly from year to year depending on the food supply and other conditions, the size of the home ranges must be determined each year. This makes this method as difficult as the "winter nest" method, and as the latter undoubtedly gives more accurate results, it should, in our opinion, be given preference.

In order to compare the relative numbers of sable and marten in summertime in different regions and habitats, the method of recording animal droppings (scats), which are usually deposited on paths or fallen tree trunks, can be used. In the Caucasian reserve, where the number of marten at various altitudes was determined by both collecting scats on the paths in summer and by counting tracks in winter, [we found that] counting the scats on the paths can yield some useful information about the number of marten in the region.

The smallest representative of the marten family, the weasel, although of no particular commercial value, is useful because it exterminates vast numbers of noxious rodents. Specially adapted for travelling under the snow, the weasel in many regions spends a great deal of time beneath it, and therefore it is virtually impossible to survey the weasel population at the same time as the other mustelids. The only time when weasel tracks appear on the surface of the snow in fairly large numbers in the middle and north-eastern parts of the European USSR is during the short period [in autumn] when the newly-fallen snow is no more than 5 cm thick. However, even at this time a survey of weasel tracks can be made only in open areas devoid of tall grassy vegetation, for example in fields sown in winter corn, in pastures, in meadows or fields, in the mossy tundra, in Alpine meadows etc. In places like these a survey can be made by marking the area out into experimental strips.

The best method is to carry out the survey with two people. This does away with the need to mark the area out in advance. Conducting the survey itself consists of the observers walking parallel with one another and keeping 10-15 metres apart, and noting and recording on a plan of the route all weasel tracks found and their direction. The latter is extremely important as ultimately it is from the number of in-coming and out-going tracks that the number of animals in the experimental strip is determined. The general length of each inhabited observation strip should be no less than 10 km, so that with a 10-15 m gap between observers, this gives an area of 10-15 ha. Two people can examine an area of this size in a day.

In forest habitats and in scrub and tall, grassy vegetation a survey of the weasel in this manner is impossible, as the first light snowfalls do not give a continuous cover (some of the snow falls on plants) and also in most regions the weasel soon spends almost all its time beneath the snow.

Among comparative methods of counting weasels, we might point out (a) counting the number of weasels observed while turning and gathering in haystacks and grain ricks in the fields and on the threshing floor, and (b) the number of weasels caught in traps set for moles. (The latter method was suggested by Formozov, 1948.)

It goes without saying that in both cases the number of weasels noted should be expressed in relative figures - the average number of weasels detected in 100 m^3 of hay or straw in stacks, the number of weasels in a defined area of a field, or the number of weasels caught in a given number of moletraps.

(No summary provided—Ed.)

BIBLIOGRAPHY

Zharkov, I. V. (1941): New methods for the ermine census. Nauchno-metod. zapiski Gl. upr. po zapovednikam, ed. 8. M.

Formozov, A. N. (1948): The small rodents and insectivores in the Sharya district of the Kostroma province during the period from 1930 to 1940. - Materialy po gryzunam, ed. 3. Fauna in ekologiya gryzunov. M. [Materialy po poznaniyu fauny i flory SSSR. Novaya seriya, otd. zool., ed. 17 (32)]

SEXUAL DIMORPHISM IN THE DEVELOPMENT, SIZE, AND PROPORTIONS OF THE SKULL IN THE PINE MARTEN (*MARTES MARTES* L.: MAMMALIA, MUSTELIDAE)

by

O. L. Rossolimo and I. J. Pavlinov

[From: Byull. Mosk. O-va Isp. Prir. Ot. Biol. 79: 23-35, 1974]

Pronounced sexual dimorphism in the size and morphology of the pine marten (*Martes martes* L.) has often been noted (Aspisov, 1959; Pavlinin, 1959; Yurgenson, 1956a;[1] Ryabov, 1962[2]; Yazan, 1970; Rode and Didier, 1944; Schmidt, 1943; Lampio, 1951). However most of these observations were made on extremely restricted material and concerned a small set of characters. Moreover, the lack of any exact method of age-determination did not allow sufficiently detailed study of the development of the sexual dimorphism. All this restricted both the full examination of sexual dimorphism in the structure of the skull and also attempts to give a functional interpretation of the differences detected.

A series of 642 pine marten skulls from the Pechora-Illych Reserve, kept in the collection of the Moscow University Zoology Museum, served as the material for the present study. The sex of the specimens was known. The age of each specimen was determined from the cemental layering of the upper canine tooth observed in sections stained with haemotoxylin. The whole collection was arranged in the following age groups:

Age groups	Absolute age		Quantity of material	
	males	females	males	females
0	5-12 months		89	112
1	2 years		82	64
2	3 years		76	43
3	4 years		55	18
4	5 years		27	15
5	6-7 years	6-8 years	23	10
6	8-9 years	9 years or more	19	4
7	10 or more	-	9	-

The following characters were measured:

1. the condylo-basal length of the skull;
2. the length of the facial section of the skull;
3. the length of the cerebral section;
4. the length of the rostrum (from the anterior edge of the orbits to the anterior edge of the first incisor alveolus);
5. the length of the orbits;
6. the post-orbital length from the apex of the post-orbital process to the point of flexure of the calvaria of the skull in the region of its greatest post-orbital constriction;
7. the height at the frontal bone;
8. the height at the region of post-orbital constriction;
9. the height of the brain case (without tympani);

---

[1] Translated by Israel Programme for Scientific Translations, Jerusalem, 1961—Ed.

[2] Translated in King (1975)—Ed.

10. the width of the rostrum;
11. the interorbital width;
12. the supraorbital width;
13. the post-orbital width;
14. the zygomatic width I (at the level of the post-orbital constriction);
15. the zygomatic width II (maximal);
16. the width of the brain case I (at the level of the anterior edge of the articular fossae);
17. the width of the brain case II (behind the roots of the zygomatic arch);
18. the width of the dentition at the level of Pm^4;
19. the width between the articular fossae;
20. the length of the lower jaw;
21. the height of the coronoid process;
22. the weight of the lower jaw;
23. the volume of the cerebral chamber.

Differences between the sexes in the values of each measurement were calculated as percentages from the formula

$$D = \frac{\bar{X}M - \bar{X}F.\ 100}{\bar{X}F}$$[1]

where D = the index of sexual dimorphism, and $\bar{X}M$ and $\bar{X}F$ = the average values of the measurements of a given character in males and females. The maximal and minimal percentage differences were tested with t-tests.

The characters used for analysis of sex-related differences in rates of growth were the ones showing maximum variation with age: 1, 2, 4, 6, 9, 10, 13, 14, 16, 20, 22, 23. Differences between the sexes in growth rates were assessed by comparing the absolute values of the specific rates of growth for each sex. $(\alpha F) - (\alpha M)$ where αF, αM = specific rates of growth for a given character during the interval between two adjacent age groups.

For the comparison of sex-related differences in skull proportions, indices were calculated expressing the relationships of characters 2-18, 20, and 23 to the condylobasal length, and characters 19, 21, and 22 to the length of the lower jaw.

Differences between the sexes in growth rate

Pavlinin (1959) and Rottcher (1965) showed that in the very early period of post-natal development in the pine marten (2-4 months) the growth rate in females is considerably less than in males. Up to now, possible sex-related differences in the later stages of development of the skulls of pine martens have not been examined. This question is investigated below.

During the age interval 0-1, the great majority of characters (eleven out of twelve) develop more rapidly in females than in males (Figure 1). The specific rates of increase of the measurements of females average 0.0490 (range 0.0122 to 0.1218; and in males, .0220 (0.0034 to 0.0600). The specific rate of growth varies between characters. The growth rates of the volume of the brain case and the weight of the lower jaw in females are less than twice those of the males (0.0525 and 0.0325; 0.1045 and 0.0600 respectively); the growth rates of the condylo-basal length, the postorbital length, and the width of the rostrum are 3-4 and even 5 times greater in females than in males (0.0122 and 0.0034; 0.1218 and 0.0374; 0.0386 and 0.0072 respectively). It is necessary to point out that the growth rates of characters included in various functional complexes is on the average fairly similar for both sexes:

---

[1] In the original, an additional malformed character appears in this formula, but on checking the translators say that it is a printing error—Ed.

in the groups of characters characterising the general growth of the skull (1, 2, 4) and the characters of the "temporal" (6, 9, 13, 14, 23), and the maxillary (10, 20, 22) complexes, the specific growth rate in females is on the average 2-2.5 times higher in males.

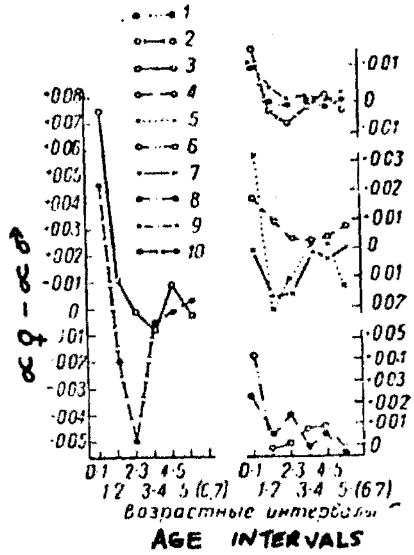


FIGURE 1: Sex-related differences in the growth rates of various skull characters during post-natal development from 5 months onwards:

1. condylo basal length of skull;
2. length of face;
3. post-orbital length;
4. height of brain case;
5. width of rostrum;
6. post-orbital width;
7. zygomatic width I;
8. width of brain case I;
9. length of lower jaw;
10. weight of lower jaw.

In succeeding age intervals (1 - 2 - 3 - 4) the difference in growth rates of females and males assumes a different character. The rate of growth in the females decreases markedly, whereas in males this decrease is minor. In some characters (condylo-basal length, length of the rostrum, post-orbital width, width of the brain case I, volume of the brain case), the difference between the growth rates of males and females remains the same in sign as in interval 0-1, but is considerably reduced. The value of the specific growth rate in females fluctuates between 0.0046 and 0.0370, and on the average constitutes 0.0102; for the males between 0.0050 and 0.0270, and on the average 0.0082. In other characters (length of face, width of rostrum, width between the articular fossae, weight of the lower jaw) the difference between the values of the specific rates of growth reverses sign, that is to say, the rates of growth of these characters in females (from 0.0008 to 0.0277, and on the average 0.0075) become less than those in males (from 0.0009 to 0.0545, and on the average 0.0208).

The zygomatic width is different: in this character, the specific growth rate in males exceeds that of females throughout the whole of the first four age groups. However in this character there is also a change with age in the extent of the difference in its growth rate in males and females. In the interval 0-1 the specific growth rate of the zygomatic width is practically identical in both sexes: 0.0418 for males and 0.0403 for females: but in the interval 1-4 sex-related differences appear as the rate of growth for males on the average equals 0.0206, and for females 0.0071.

In later age groups (5, 6, 7) differences in the growth rates of most characters of males and females are absent or are very insignificant. It should be emphasised that this applies both to characters which change only very slightly during this span of ages (condylo-basal length, length of the face, zygomatic width, width between the articular fossae, length of the lower jaw, weight of the lower jaw), and also to characters which show a "secondary" stage of development at this age, which is associated with intensification of the activity of the temporal muscle (almost all characters of the "temporal" complex, i.e., post-orbital length, post-orbital width, width of the brain case I, volume of the brain case). For the first group of characters the values of the specific growth rate comprise, for males, from 0.0016 to 0.0065 (on the average 0.0023) and for females, from 0.0001 to 0.0075 (on the average 0.0020); for the second group, for males - from 0.0032 to 0.0308 (on the average 0.0129), for females - from 0.0055 to 0.0212 (on the average 0.0121). In the characters of the "temporal" complex, this acceleration typically occurs earlier (Table 1) in females (in group 5) than in males (in group 6). However, these differences are apparently due to the purely technical fact of the discrepancy in the ages of males and females in the older age groups, because the division of females among the age groups is not comparable to that of males [see unnumbered table at beginning of paper].

TABLE 1: Specific growth rates of characters of the "temporal" complex in the age intervals 4 - 5 - 6 - 7

Characters	Age interval			
	4-5	5-6	6-7	sex
Length of post-orbital constriction	0.0033	0.0308	0.0166	M
	0.0122	0.0212	-	F
Post-orbital width	-0.0019	-0.0210	-0.0214	M
	-0.0104	-0.0186	-	F
Width of brain case I	-0.0010	-0.0164	-0.0063	M
	-0.0070	-0.0055	-	F
Height of brain case	-0.0010	-0.0050	-0.0012	M
	-0.0020	-0.0132	-	F

In two further characters examined in this age group (5 - 6 - 7), sex-related differences are observed also in the very nature of growth. In males an increase in rostrum width at age 6 - 7, similar to the "temporal" complex feature, is somewhat intensified in comparison with the age interval 3 - 5; the specific rate of growth increases to 0.0110. Such a change in the growth rate is not found in females; throughout the whole period the specific rate of growth of the rostrum width is 0.0007. In the height of the brain case, sexual dimorphism in the change of rates of growth is in an inverse ratio. In males in the period 5 - 7 growth rates of this character compared with the period 3 - 5 virtually do not change, and the specific growth rate on the average equals 0.0042. In females changes in the height of the brain case in the interval 5 - 6, on the contrary are considerably more marked than at the age 3 - 5, and the specific rate of growth at the older age attains 0.0132.

Changes in the extent of sexual dimorphism in the growth rates of various characters in the course of development demonstrate differences between males and females in the character of the skull growth in general and also in the peculiarities of the development of its functional sections. Thus the more rapid growth rates of almost all skull characters in females compared with males in the period 0 - 1, with the subsequent levelling off of these differences with age, indicates that the inhibition of active juvenile growth, which takes place at independence,either begins somewhat earlier in males than in females, or else is more marked. The females, dropping behind the males in growth at the age of 3 - 5 months, "catch up" with them at the age of 6 - 17 months. The final slowing down in growth of the female skull comes about, evidently, in age group 1 (the beginning of age interval 1-2). Differences in the growth rates of different characters in older age groups (5, 6, 7) indicate differences in the functional activity of the parts of the skull characterised by the given measurements.

Sex-related Differences in Absolute Size of the Skull

Sexual dimorphism in skull size has been evaluated quantitatively by few authors. Aspisov (1959) and Yurgenson (1956a) reported that [frequency] distribution curves for the measurements of a series of characters (condylo-basal length, zygomatic width, and several others) in males and females virtually do not overlap. According to Yazan (1970) the average value of "t" for six characters fluctuates on average from 2 to 15. There are no data on the variation with age of sex-related differences in skull characters through the range of ages investigated by us. The work of Yazan (1970) produced data obtained from a study of age groups identified by a most inexact method, and are therefore not very reliable.

Our material gave the following results. In the age group 0 sexual dimorphism ranged from 2% (post-orbital width) to 40.5% (weight of lower jaw), giving a value for "t" of 3.4 and 27.4. In the age group 6 sexual dimorphism ranged from 5.1% (length of the cerebrum) to 44.0% (weight of the lower jaw) giving a value for "t" of 3.3 and 11.2. The statistical significance of all differences found was of the order of 0.01.

The greatest average sexual dimorphism is in the weight of the lower jaw and the post-orbital length (41.8% and 31.4%), and also the volume of the brain case (20.0%). The least sexual dimorphism is in the length of the orbits and the length of the brain case (on the average 5.2% and 5.6%). The sexual dimorphism for the remaining characters averages from 6.5% to 13.6%.

If the characters are grouped according to their functional relationships, it appears that the greatest [average] sexual dimorphism is in the characters of the dental maxillary (from 7.4% to 45.1%, averaging 15.4%) and zygomatic (from 8.0 to 13.9%, averaging 11.3%) complexes, and in the group of characters associated with the activity of the temporal muscle (2.2%-37.9%, averaging 11.1%). For the rest of the characters, which reflect the general growth of the skull and do not enter into the above groups, the sexual dimorphism constitutes from 4.2% to 13.4%, averaging 10.1%. These differences, although insignificant, confirm the data of Yurgenson (1947)[1] on sexual dimorphism in the structure of the masticatory apparatus. The characters with the least sexual dimorphism in group 0, the post-orbital width and width of the brain case anterior to the zygomatic processes of the squamosal bones (2.2% and 3.1%), are characters closely associated with the development of the temporal muscle; this fact does not contradict this confirmation but on the contrary, reaffirms it, because the insignificant sexual dimorphism in those two characters is determined by the fact that the anterior section of the brain case is laterally more compressed in the age group 0 in males than in females (see below).

All the characters considered fall into two groups according to the nature of the age variation in sexual dimorphism (Figure 2).

The first group (condylo basal length, length of the face, length of the rostrum, post-orbital length, weight of the lower jaw, height of the coronoid process), includes characters which decrease in sexual dimorphism from age group 0 to age group 1, and for several also to group 2, after which sex-related differences increase right up to age groups 5 and 6. In this group of characters the sexual dimorphism in the age group 0 is either somewhat less than in the older age groups, or else generally is the greatest for the given character.

In the second group of characters (post-orbital width, width of the brain case I, height of the brain case, volume of the brain case, zygomatic width I) are included those which show a continuous increase in sexual dimorphism from age group 0 to the older age groups. However, in the zygomatic width on the one hand and in the other characters of this group on the other,

---

[1] Translated in King 1975—Ed.

the increase in sexual dimorphism is brought about for different reasons. The increase in sex related differences with age in the zygomatic width, which is increasing absolutely, is because of higher rates of growth for this character in males than in females. The increase in sex-related differences in the width and volume of the brain case, which both decrease with age, is because of higher rates of change in these characters in females compared with males.

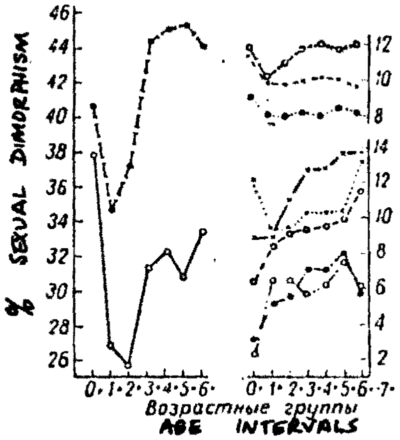


FIGURE 2: Changes with age in the sexual dimorphism of the skull of the pine marten during post-natal development from 5 months onwards. Key as in Fig.1.

Sexual dimorphism in Skull Proportions

Data on sexual dimorphism in skull proportions are quite limited. The authors (Ryabov, 1959; Yurgenson 1956b[1]; Pavlinin, 1959) who have studied this question have considered few characters and have usually restricted themselves to the most general observations about the more infantile structure of the female skull in comparison with the male.

When we examined this question we divided the skull into four sections, based on the topographical relationships of the characters (Table 2).

1. The relative values of characters of the facial section of the skull, excepting the length of the face and the post-orbital length, are typically similar in both sexes. Sexual dimorphism in the relative post-orbital length are great, and this, most probably, determines the significance of sexual dimorphism in the relative length of the face. All the indices of the facial section of females, except the length of the orbits, are less than those of males. It should be noted that the relative indices for the facial section change with age synchronously in both sexes; only the relative supra-orbital width reveals weak indications of differences in its rate of change in males and in females.

2. Relative values of characters in the cerebral section have more marked sexual dimorphism and are more diverse in their relationships with age. The index of the length of the brain case, which is greater in females, changes with growth in both sexes synchronously. Hence, sexual dimorphism in this character does not vary with age. The relative indices for volume of the brain case and its height in the region of the post-orbital narrowing are less in females than in males. These differences are traced throughout all age groups, their range increasing with age. For the remaining indices of the cerebral section there is a characteristically gradual smoothing out of sexual dimorphism with age. In the age groups 0 and 1 the value of the relative indices of brain case width I, brain case width II, post-orbital width, and

---

[1] Translation available from British Library Lending Division Boston Spa, Yorks. No RTS 1946—Ed.

the height of the brain case are more for females than males, but in the age groups 5 - 7 these indices either become equal in both sexes (the first three) or else become somewhat less in females than in males (height of the brain case).

3. From most indices of the dental-maxillar section, clear sexual dimorphism is characteristic and they are virtually constant with age. Sexual dimorphism is particularly marked in the relative weight of the lower jaw, which is considerably less in females. In contrast, the sex-related differences in the relative width of the rostrum are not great, and in the relative width of the dentition at the level of Pm^4 they are completely absent.

4. The indices of the zygomatic section are identical for both sexes in age group 0, but in these indices there is a characteristic appearance and intensification of sexual dimorphism with age. In males both zygomatic widths increase more quickly in relation to the condylo-basal length, and the sexual dimorphism in the zygomatic width at the level of the post-orbital narrowing becomes larger with age.

As may been seen from these data, sexual dimorphism in the relative values of most characters is distinct. As in the absolute values, the greatest sexual dimorphism in proportions is found in the sections of the skull associated with mastication. The age variation of many of the indices considered is great; in the whole series of relative indices there have been recorded sex-related differences in the extent of age changes, as a result of which the comparative indices for females and males also changes with age. In group 0 the female skull, in almost all indices reflecting its general configuration, displays a significant infantilism in comparison with the male skull: the relatively shorter length of facial section and post-orbital section, and a wider, higher, and longer brain case, determine the "juvenile" aspect of the female skull. In subsequent age groups the relationship between the skull proportions of males and females changes. According to several indices (length of the facila section, the post-orbital length, the length of the orbits, and the length of the brain case) females remain more "infantile" than males. In other indices (all brain case widths and the height of the brain case) a levelling of sex-related differences takes place and the indices for females approach those for males. The extent of sexual dimorphism in both zygomatic widths and the volume of the brain case characteristically increases with age. This means that the male skull, in which the zygomatic arches are wider in the older groups, acquires a more "adult" configuration than the female.

A comparative study of the relative proportions of male and female skulls, perhaps more than any other method of craniometric analysis, gives the opportunity to determine sexual dimorphism in the structure and functioning of the chewing apparatus. The existence of sex-related differences in the relative weight of the temporal and masticatory muscles of pine martens was shown by Yurgenson (1947). In planning future studies on this question it is interesting to note the following sex-related differences in proportions of the skull. (In considering this question we were guided by the data on the functional morphology of the chewing apparatus in the works of Schumacher (Schumacher, 1961) and Turnbull (Turnbull, 1970)). In females of age group 0, all relative widths of the brain case were greater than in males; with age the proportions become practically the same in both sexes. This indicates that sex-related differences in the work of *m. temporalis pars profunda* are slight, and are apparently explained only by the general retardation in development of the female skull in the first year of life. But the change with age of the relative proportions of the height of the brain case shows that the parietal portion of this muscle influences the vault of the brain case more actively in females than in males. Significant differences in relative post-orbital length, which do not diminish with age, show the same significant differences also in the work of the *m. temporalis pars superficialis*, which in males is apparently more strongly developed. This is confirmed by the lesser development of the sagittal crest in the female, a feature whose shape is much influenced by the superficial portion of the temporal muscle.

TABLE 2: Sex related differences in the proportions of the pine marten skull

Character	Age group								Sex
	0	1	2	3	4	5	6	7	
				Facial section of the skull					
Length of the facial section	0.542	0.544	0.547	0.551	0.551	0.552	0.554	0.551	M
	0.526	0.531	0.530	0.532	0.530	0.534	0.530		F
Length of the rostrum	0.309	0.310	0.309	0.309	0.310	0.311	0.310	0.310	M
	0.305	0.306	0.305	0.307	0.309	0.309	0.309		F
Length of the orbits	0.169	0.169	0.170	0.170	0.169	0.170	0.170	0.169	M
	0.175	0.175	0.176	0.176	0.176	0.177	0.177		F
Postorbital length	0.105	0.109	0.111	0.115	0.118	0.119	0.123	0.126	M
	0.083	0.092	0.096	0.096	0.097	0.098	0.102		F
Height of the frontal bone	0.323	0.323	0.321	0.322	0.320	0.321	0.319	0.316	M
	0.321	0.319	0.318	0.318	0.318	0.318	0.315		F
Interorbital width	0.242	0.246	0.247	0.246	0.249	0.253	0.251	0.253	M
	0.242	0.243	0.244	0.247	0.248	0.247	0.247		F
Supraorbital width	0.274	0.284	0.286	0.287	0.297	0.295	0.294	0.292	M
	0.280	0.280	0.282	0.284	0.288	0.288	0.288		F
				Cerebral section of the skull					
[Length] of the cerebral sectn	0.585	0.585	0.584	0.585	0.585	0.584	0.585	0.585	M
	0.606	0.605	0.606	0.606	0.605	0.605	0.606		F
Volume of the brain case	0.435	0.423	0.418	0.415	0.415	0.411	0.400	0.388	M
	0.395	0.376	0.369	0.366	0.364	0.357	0.343		F
Postorbital width	0.226	0.218	0.212	0.208	0.205	0.204	0.197	0.190	M
	0.242	0.222	0.216	0.212	0.210	0.207	0.198		F
Width of brain case I	0.345	0.337	0.334	0.330	0.328	0.327	0.320	0.315	M
	0.365	0.346	0.341	0.334	0.332	0.330	0.325		F
Width of brain-case II	0.436	0.431	0.430	0.428	0.430	0.430	0.429	0.431	M
	0.444	0.438	0.435	0.434	0.431	0.430	0.432		F
Height at post-orbital constriction	0.305	0.303	0.299	0.297	0.297	0.300	0.298	0.295	M
	0.303	0.298	0.292	0.287	0.290	0.287	0.288		F
Height of brain case	0.348	0.344	0.340	0.338	0.335	0.336	0.334	0.332	M
	0.358	0.343	0.336	0.337	0.332	0.333	0.329		F

continued —

Table 2 continued.

Characters	Age groups								
	0	1	2	3	4	5	6	7	Sex
	Dental-maxillary section of the skull								
Width of rostrum	0.200	0.201	0.202	0.204	0.206	0.206	0.207	0.209	M
	0.193	0.197	0.197	0.200	0.202	0.202	0.201		F
Width of dentition at Pm^4	0.320	0.322	0.321	0.321	0.322	0.322	0.321	0.321	M
	0.322	0.321	0.321	0.320	0.320	0.322	0.321		F
Length of lower jaw	0.654	0.657	0.659	0.658	0.658	0.657	0.657	0.657	M
	0.643	0.645	0.651	0.648	0.646	0.647	0.647		F
Weight of lower jaw	0.964	1.012	1.063	1.114	1.126	1.148	1.144	1.147	M
	0.760	0.832	0.850	0.847	0.848	0.859	0.860		F
Width between articular fossae	0.742	0.741	0.742	0.742	0.743	0.744	0.745	0.745	M
	0.760	0.767	0.766	0.764	0.768	0.769	0.768		F
Height of coronoid process	0.451	0.446	0.447	0.447	0.447	0.449	0.446	0.447	M
	0.442	0.437	0.438	0.436	0.436	0.438	0.435		F
	Molar section of the skull								
Zygomatic width I	0.497	0.518	0.528	0.536	0.542	0.546	0.546	0.547	M
	0.498	0.513	0.514	0.514	0.519	0.520	0.519		F
Zygomatic width II	0.551	0.572	0.578	0.584	0.584	0.586	0.585	0.585	M
	0.556	0.563	0.563	0.562	0.569	0.577	0.576		F

Sexual dimorphism in the structure and function of the maxillary apparatus is reflected by differences in the structure of the lower jaw of males and females: In females the mandibular rami are shorter relative to the condylobasal length and are placed wider apart; the coronoid process is also relatively shorter. This probably means that there are sex-related differences in the proportion of force applied to the lower jaw.

Conclusion

Sexual dimorphism in the size of pine marten skulls is quite marked. It is reliable for all characters (significant at 0.01) in all age-groups examined.

Sexual dimorphism in average skull proportions is less pronounced (without being quantitatively tested): the entire series of relative indices for males and females are the same or similar in value. Significant age variations are characteristic of several indices of sexual dimorphism.

Pronounced sex-related differences in the growth rates of particular characters are found only in the age interval 0 - 1.

In general, the greatest sexual dimorphism is found in the characters and proportions of the masticatory apparatus.

Sexual dimorphism was most marked in age group 0: the female skull is smaller and considerably more infantile than the skull of the male (Figure 3E). These differences are due to the lag of females behind males, both in the growth of the skull and the formation of its characteristic shape, reflecting the type of work of the chewing apparatus. In the age interval 0-1 the rates of

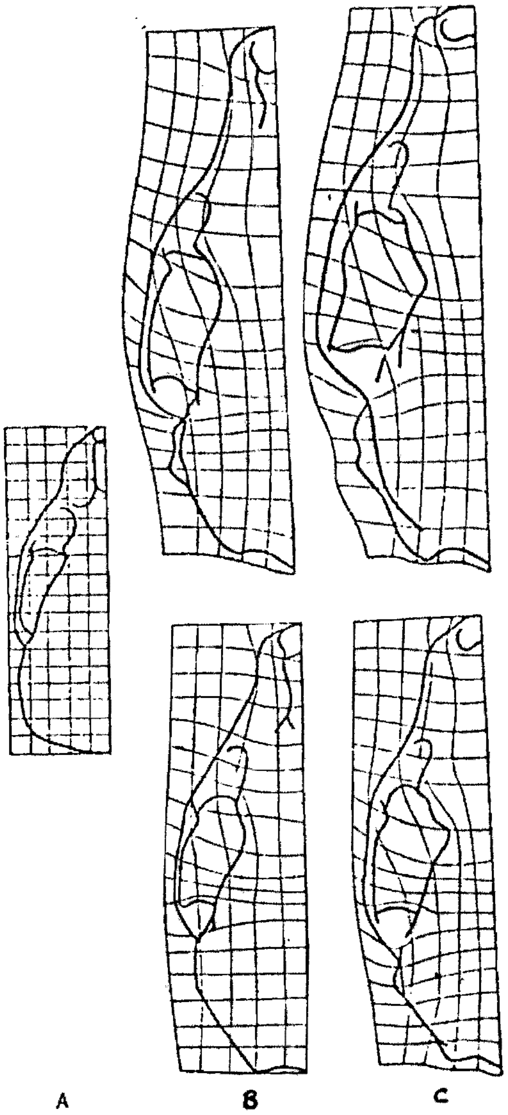


FIGURE 3: Changes with age in the proportions of the skull of male [above] and female pine martens (using the method of d'Arcy Thompson, 1917).

A: 2-3 months; B: 8-10 months; C: 8-10 years

change in the values of almost all observed characters are greater in females than males. The change in ratio of growth rates is explained by the fact that in males an inhibition of active juvenile growth and development apparently takes place earlier than in females. In this interval the females catch up with the males both in general growth and the formation of an "adult" configuration of the skull. As a result of this, sexual dimorphism, both in the absolute and in proportion, is reduced quite considerably.

In the age groups 1 - 2 - 3, sex-related differences in the growth rates of characters are significantly reduced. The growth rate in females becomes less than in males. Evidently at the beginning of this interval (age group 1) the female skull completes its growth. At the same time most of the characters of the "temporal" complex in this age interval develop, as before, more intensively in females, that is to say, the formation of the "adult" configuration of the female skull proceeds more actively than that of the male. Sexual dimorphism of the characters showing a diminution in growth rate in age group 1 increases towards age groups 2 and 3. It should be noted, however, that in these characters the sexual dimorphism in age group 0 either is the greatest or else slightly less than that in age groups 2 and 3.

Most characters showed a material change in sexual dimorphism during the later age groups (4, 5, 6, 7). The values of the sex-related differences in most characters remain in the range attained before age group 3. In both males and females the values of most characters in the interval 3[1] - 6 - 7 change at an almost identical specific rate. Marked sex-related differences in growth rates were noted in the interval 5 - 6 - 7 for two or three characters. There is a further and marked change in the difference between the sexes in most of the proportions of the "temporal" complex, as a result of which the configuration of the female skull approaches that of the male (Figure 3B).

The data examined suggest that the nature and development of sex-related differences in the size configuration of the skull are mainly the result of the females lagging behind the males in growth and development at 2 - 4 months of age. Specifically, the characters studied reflect the development and function of the temporal muscle and the sections of the skull connected with it. It is significant that in males, during the secondary period of development, it is the surface layer of the temporal muscle which is apparently most active, whereas in the females it is the inner one that is most active. Hence, this process is essentially similar in both sexes, and is expressed in each of them within the range of resources provided by the structure of the temporal muscle which was reached towards 6 - 12 months of age.

SUMMARY

Noticeable sex-related differences in growth rate were discovered within the age interval 0 - 1; nearly all characters develop more rapidly in females than in males. The sex-related differences in absolute measurements are reliable for all characters at a level of significance of 0.01, during the whole period under consideration. A decrease of sex-related differences was observed for a number of characters from the 0 to the 1 age group with a subsequent increase towards the 2, 3 groups. The sex-related changes in skull indices are most pronounced in the 0 group: the skull of the female is more infantile than the skull of the male in all the indices. In older age groups the configuration of the female skull is near to that of the male skull.

BIBLIOGRAPHY

Aspisov, D. I. (1959): Dynamics of the pine marten population in the Volga-Kama region and some indices for the forecasting of changes in its numbers. Tr. Vsesoyuzn. n.-i. in-ta zhivotn. syriya i pushnini 18. Kirov.

Pavlinin, V. N. (1959): Notes on the morphology of the Ural pine martens. Tr. Uralsk. otd. MOIP 2. Sverdlovsk.

Ryabov, L. S. (1959): The Caucasian pine and stone martens in the Krasnodar region. Tr. Kavkazsk. zapovednika 5. Maikop.

Ryabov, L. S. (1962): Some age related peculiarities in the morphology of the Causcasian pine and stone martens. Zool. zhurn. 41 (11).

Yurgenson, P. B. (1947): Sexual dimorphism in the diet as an ecological adaptation of a species. Byull. Mosk o-va. Ispyt. Pirir. Otd. Biol. 52 (6).

Yurgenson, P. B. (1956a): Essays on the comparative study of sable and martens. Mat-ly po resultatam izuch. mlekopitayushchikh v zapovednikakh [Materials on the results of the study of mammals in forest reserves]. Moscow.

---

[1] Misprint for 5?—Ed.

Yurgenson, P. B. (1956b): Determining the age of the pine marten. Zool. zhurn. 35 (5).

Yazan, Yu. P. (1970): The question of morphological similarity of martens, sables and kidases. Tr. Kirovsk. s.-kh. in-ta 22 ed. 52.

Lampio, T. (1951): On the sex ratio, sex differentiation and regional variation of the marten in Finland. Papers on Game Research 7 (7).

Rode, P. and Didier R. (1944): Differences entre la tete osseuse de la marte et celle de la fouine. Mammalia 8.

Rottcher, D., (1965): Beitrage zur Altersbestimmung bei Nerz, Steinmarder und Iltis. Inaugural-Dissertation, Giessen.

Schmidt, F. (1943): Naturgeschichte des Baum- und des Steinmarders. Monogr. Wildsäugetiere 10.

Schumacher, C. H. (1961): Funktionelle Morphologie der Kaumuskulatur. Jena.

Thompson d'Arcy. (1917): Growth and Form. Cambridge.

Turnbull W. D. (1970): Mammalian masticatory apparatus. Fieldiana Geol. 18(2).

AGE AND SEASONAL CHANGES IN SOME PHYSIOLOGICAL CHARACTERS IN THE WEASEL (*MUSTELA NIVALIS* L.) AND ERMINE (*MUSTELA ERMINEA* L.)

by

I. L. Tumanov and V. G. Levin

The Western Branch of the All-Union Research Institute of Hunting and Fur Breeding, Leningrad Zoo.

[From: Vestnik Zoologii 2: 25-30, 1974.]

The mode of life of a species is related to its metabolic rate. The study of metabolic processes is an important part of ecologo-physiological research, as it helps in understanding the adaptation of the species to environmental conditions. This paper describes observations made by the authors on age and seasonal changes in the respiration rate and the cardiac activity in the weasel (*Mustela nivalis* L.) and ermine (*M. erminea* L.). In this subject, no Mustelidae have yet been sufficiently studied (Titova, 1950; Slonim, 1952; Makridina & Melkina, 1964).

Post-embryonic development was studied in 11 ermine whelps and three weasels which had been born in captivity from captured pregnant females. We determined changes with age in the body weight and temperature, basal metabolism, and the rates of external respiration and cardiac activity. Seasonal changes in these characters were observed in 7 adult ermine and four weasels. Altogether we carried out about 500 different physiological measurements. Oxygen consumption was determined in a respiration chamber (Kalabukhov, 1951) at an ambient temperature of 20-22°. Rectal temperature was taken by means of the "Temp-60" electro-thermometer. The cardio-vascular measurements were made under urethane anaesthetic, by means of electro-cardiograms producing ink and hot-wire cardiographs from "cuff" type electrodes. Simultaneously, respiration was recorded by means of microresistances and a measuring bridge from a medical electrothermometer which perceives temperature gradients in respiration[1].

Age and seasonal changes in the weight of weasels and ermine

Analysis of the data on the daily growth of the young of both species showed that they develop very slowly up to the age of one month; their weight increases by an average of 0.4-0.8 g per 24-hours (Table 1). After their

TABLE 1: Body weight (g) and its daily increment (g) in weasels and ermine in the early stages of ontogenesis.

Species	Index	Age (days)									
		1	4	9	16	25	36	42	44	57	59
Weasels	Body weight	1.5	3.2	6.3	10.4	15.8	26.8	36.2	38.5	60.8	64.5
	Daily increment	-	0.5	0.6	0.6	0.7	1.0	1.6	1.1	1.7	1.8
Ermine	Body weight	3.5	4.7	7.6	12.0	17.4	27.8	46.4	52.1	77.5	80.5
	Daily increment	-	0.4	0.6	0.6	0.6	0.9	3.1	2.8	1.9	1.5

---

[1] The authors are grateful to V. P. Galantsev for his assistance in the work with the electro-physiological equipment—Author.

eyes have opened (30th - 33rd day) the average daily growth of the young increases markedly, reaching its peak on the 41st-42nd day of the post-embryonic development. The considerable increase in daily growth during this period is apparently related to the emergence of the young from their nesting chamber, and substantial changes in their respiratory reactions.

The suckling period of the young (according to observations made in captivity) lasts in weasels up to the age of 1½ months, and in ermine up to 2 months, after which they begin to feed independently, and their daily growth drastically increases. Sexual dimorphism in weight and body size does not show in the 4-5 week old young of the two species, but as from the age of 6 weeks males are noticeably larger and heavier than females.

Seasonal changes in live weight are extremely significant as indicators of periodical shifts in the level of energy metabolism. As in most mammals, the live weight of weasels and ermine gradually increases from the beginning of September to the end of autumn. This happens mainly because of the depositing of fat reserves, which are localised under the skin (first of all in the groin area) and the abdominal cavity. Peak weight is reached in October-December, but decreases towards the end of winter. The weight of weasels and ermine is lowest in summer (Table 2). Fat reserves and the thicker winter fur of these species lower the emission of heat and protect the animals from the effects of low temperatures.

TABLE 2: Changes in live weight of adult weasels and ermine in the course of a year (g).

Species	Sex	Month					
		January	March	May	July	September	November
Weasels	Males	92.2	93.8	88.6	81.2	90.5	94.5
	Females	57.8	60.3	57.6	54.6	56.3	59.4
Ermine	Males	224.6	217.5	194.2	161.6	195.3	227.1
	Females	141.4	136.6	129.5	128.9	135.5	149.2

Changes in some physiological characters during the development of weasels and ermine

The rectal temperature in three-day old young which have been taken away from their mother is rather low - from 25° to 31°C. As the weight and size of the young increase, and they become covered with thick fur and their thermoregulation becomes established, their body temperature increases, reaching (by the age of one month) 38°-40°C. Later it changes negligibly. In weasels the temperature averages 0.5-0.7° higher than in ermine, which reflects a higher level of energy metabolism (Table 3). At the age of one to six months the musculo-cutaneous temperature of the postfemoral group of muscles increases on average from 37.2 to 37.9° in weasels and from 36.8 to 37.3° in ermine. Increases in the temperature of femoral muscles in ontogenesis may be related to the development and maturation of the animals in the process of growth, and with an increase in blood circulation to their working organs.

In most mammals the basal metabolic rate increases negligibly during the first month of post-embryonic development, until the period of the opening of the eyes of the young and the increase in their motor activity which follows (Tashevskaya, 1968). Then more energy is used for oxidative metabolism, and oxygen consumption increases. [In contrast], during the process of growth and development of young weasels and ermine, oxygen consumption per gram markedly decreases (Table 5). In animals over the age of one month some increase in

TABLE 3: Changes with age in oxygen consumption of weasels and ermine (ml/g./hour).

Age (days)	Weasels			Ermine		
	Number of repetitions of the experiment	Average body weight (g)	Oxygen consumption (M ± m)	Number of repetitions of the experiment	Average body weight (g)	Oxygen consumption (M ± m)
30	7	20	7.1±0.09	9	25	4.1±0.05
45	8	38	7.4±0.06	8	52	4.4±0.09
60	10	64	6.2±0.06	12	80	3.9±0.08
75	9	68	5.9±0.08	15	93	3.7±0.07
90	11	72	5.5±0.10	11	107	3.5±0.05
120	9	79	4.7±0.07	14	131	3.3±0.06
150	8	82	4.6±0.05	12	135	3.4±0.08
180	10	84	4.3±0.08	9	141	3.3±0.06

energy matabolism and respiration rate are observed only on the 40th to 43rd day after birth, which may be related to the exit of the animals from the nest and a sharp change in their motor reactions.

The basic metabolic rate in weasels (both in males and females) proved to be higher than that in ermine. This is apparently due to the smaller live weight and body size of weasels.

The respiration rates of weasels and ermine decrease insignificantly with age. For example, the respiration rate of weasels at the age of one month is 110-124 breaths per minute, but at 6 months old 96-104 breaths per minute. In the ermine, for the same period, the respiration rate decreases from 96-120 to 86-100 breaths per minute.

During development, parallel with the changes in the body weight and the metabolic rate, a slowing down of the pulse rate is observed. Thus, in young ermine aged from one to ten months, the average pulse rate decreases from 503 to 421 beats per minute in males and from 435 to 402 in females. Similar changes in the rate of cardiac activity occur during development of young weasels (Table 4).

Our research showed that oxygen consumption (per unit of weight) in the females of both species is higher than that in the males, which is largely due to the smaller size and mass of their body.

TABLE 4: Changes with age in the pulse rate in weasels and ermine (beats per minute).

Species	Sex	Age (months)					
		1		2		3	
		Mean	Range	Mean	Range	Mean	Range
Weasels	Males	483	450-540	475	420-540	451	420-480
	Females	516	480-570	482	450-540	468	420-510
Ermine	Males	435	420-480	421	390-450	402	360-480
	Females	503	450-540	462	420-510	421	360-510

Seasonal changes of some physiological characters of weasels and ermine

Seasonal changes in the body temperature of these species may be traced quite accurately. The highest rectal temperature in weasels and ermine kept in laboratory conditions is recorded in spring, and the lowest in winter. Thus, whereas in April the body temperature of *M. erminea* females fluctuated between 38.6 and 40°C, in July it was 38.4 and 39.2°C, and towards December it decreased to 37.6 - 38.4°C. In autumn, as compared with the summer months, the body temperature increases by an average of 0.3 - 0.4°. Seasonal changes in metabolism occurs also in the Arctic fox (*Alopex lagopus* L.), raccoon-dog (*Nyctereutes procyonoides* Gray) and *Vulpes vulpes* L. (Sokolov, 1949; Firstov, 1952; Pozdnyakov, 1953). The highest level of oxygen consumption in weasels and ermine is in summer and spring (Figure 1), which may be due to preparations for the rut and the related increase in activity. It is interesting to note that in the common fox - *Vulpes vulpes* L. (Isaakyan and Akchurin, 1953) the spring peaks in the curve of seasonal changes in oxygen consumption coincide with their mating season (February - beginning of March).

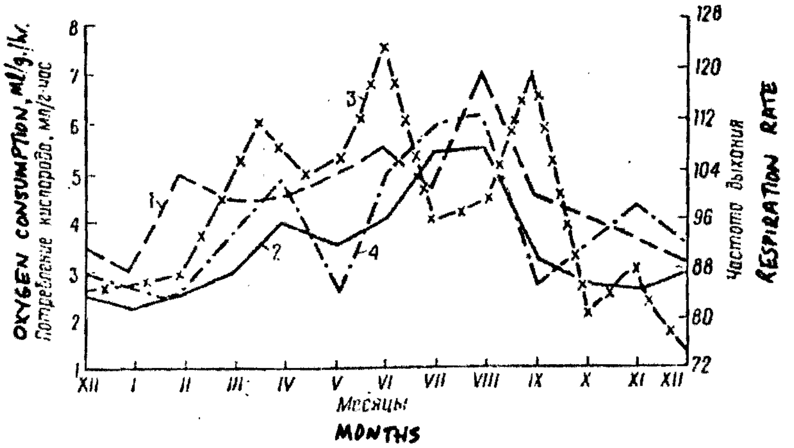


FIGURE 1: Seasonal changes in oxygen consumption and respiration rate in weasels and ermine.

1 - respiration rate in weasels; 2 - oxygen consumption in weasels;

3 - respiration rate in ermine; 4 - oxygen consumption in ermine.

At the end of summer the oxygen consumption of small Mustelidae decreases, but in autumn it increases again, though not reaching the spring level (Figure 1). In winter the basal metabolic rate in both species drastically decreases. These changes cannot be related to a deterioration in nutrition during a period of poor food supplies, because the experimental animals received the same rations throughout the year. But in both weasels and in ermine a change from the summer fur to a thick and dense white winter fur takes place in October. It is quite possible that the reduction in oxygen consumption in these species in winter months is largely due to changes in the body weight and the thermal conductivity of the fur. It is however necessary to point out that even in those individuals which were kept in warm quarters and which had moulted only partly, the basal metabolic rate also decreased considerably in winter. Therefore, these reactions are not simply due to the physical properties of the skin cover but are composite specific characteristics of the nervous and the humoral mechanisms of heat regulation (Slonim, 1952).

Seasonal changes in the cardiac activity rate in the weasel and the ermine are not well-defined, and remain within the limits of individual variability.

An analysis of the seasonal changes in the basic metabolic rate and rate of respiration indicates the interrelationship between the basic physiological functions in the body (Figure 1). The plumpness of the weasel and the ermine in winter, and their thick fur, reduce the need for intensive energy metabolism at that season. A reduction in the general heat insulation during the spring-summer period increases the emission of heat by the body. The main factors which determine periodic changes in the metabolic processes in animals are the seasonal shifts in the activity of the endocrine system, which is regulated by the central nervous system (Sokolov, 1949, Firstov, 1952). The above-mentioned changes in the intensity of the energy metabolism and the respiration and pulse rates are a striking example of the interrelationship between seasonal fluctuations in the environment and the physiology of the living organism.

SUMMARY

During the development of the young of both weasels and ermine, basal metabolic rate (oxygen consumption per gram of body weight) and cardiac activity (respiration and pulse rates) decrease with age. In adult weasels and ermine, the basal metabolic rate shows seasonal changes, reaching its maximum in spring and summer.

BIBLIOGRAPHY

Issakyan, L. A. and Akachurin, R. I. (1953): Seasonal changes in the gas exchange in carnivorous mammals. From the collection "Opyt izucheniya regulyatsii fiziologicheskikh funktsii", ed. 2, M.-L.

Kalabukhov, I. I. (1951): Methods for experimental studies of the ecology of terrestrial vertebrates. M.

Makridina, K. V. and Melkina, A. N. (1964): Comparisons of the level of metabolism during the growth process of mink whelps of the Hedlund and standard varieties. Uch. zap. Petrozavodskogo un-ta 12, ed. 2.

Pozdnyakov, E. V. (1953): Seasonal metabolic changes in the blue fox. Tr. Mosk. pushno-mekhovogo in-ta 4, M.

Rashevskaya, D. A. (1968): Age-related changes in the blood circulation in some rodent species. From the book: "Sravnitelnaya i vozrastnaya fiziologiya", M.

Slonim, A. D. (1952): Animal heat and its regulating in the organism of mammals. M.-L.

Sokolov, E. A. (1949): Seasonal changes in the basic metabolism of the raccoon-dog. Tr. Mosk. pushno-mekhovogo in-ta, 2. M.

Titova, M. I. (1950): Standards for the supplementary feeding of adult sables. Tr. TSNIL pushnogo zverovodstva 5.M.

Firstov, A. A. (1952): Biological peculiarities of the basic metabolism of fur animals. Tr. Mosk. pushno-mekhovogo in-ta 3. M.

SEXUAL DIMORPHISM IN MUSTELIDS (*Mustelidae, Carnivora*)

by

I. G. Shubin and H. G. Shubin

Institute of Zoology of the Academy of Sciences of the
Kazakh SSR, Alma-Ata, Tomsk State University

[From: Zhurnal obshchei biologii 36(2): 283-90, 1975.]

Sexual dimorphism is a widespread phenomenon in the animal world. It is observed, in the colouring, sizes, and structure of some internal and external organs (Davitashvili, 1961; Darwin, 1871, quoted according to 1908 issue; Dementyev, 1940; Kistyakovski, 1958, and others). In mammals, differences in the body sizes of males and females are observed in the Insectivora, Pinnipedia, Ungulata, primates, and land carnivores. In some animals dimorphism is always well defined, but in others it is variable. But so far we have no clear idea of its biological meaning.

In order to investigate the variation and regulation of sexual dimorphism in mustelids we used mainly the body weight. For this purpose a summary table was compiled for each species of this group living within the boundaries of the Soviet Union, recording weight, sex, and region. According to our data, seasonal fluctuations in the fatness of most mustelids are relatively small, and usually the heaviest animals are the largest. For this paper we used data both from our own studies and from the literature. It should be mentioned that the latter are still extremely scarce and often do not show the time of the year and the region in which animals had been caught. Furthermore, the seasonal, annual, habitat, etc., variations in mustelids have been little studied, although they are known to occur. All this hampers the use of published data.

There is considerable geographical variation in body size in the mustelines, such as weasels (*Mustela nivalis* L.) and ermines (*Mustela erminea* L.) (Figure 1). The largest ermines live in the Ala-Kul basin, where males, according to the data of Lobachev (1970) weigh 291 g on an average, some of them reaching 350 g; fairly large ermines live in the Ukraine (Abelentsev, 1968) the Aktyubinsk region, and in northern Siberia (our data; Kopein, 1967)[1], but in other districts they are about half this size. Particularly small ermines (average [males] 145-150 g) are observed in the montane regions of Tien Shan and the Dzungarian Ala-Tau (Stroganov, 1962[2]; Lobachev, 1970). In spite of such geographical variation, sexual dimorphism in the ermine is pronounced almost everywhere. Males are always 1.5-2 times larger than females (Figure 2). In the weasel, a large difference in the sizes of males and females is observed only in Kazakhstan and Central Asia, although the geographical variation in body weight is larger [than the variation in sexual dimorphism] (Figures 1 and 3). In the greater part of Western Siberia (our data; Stroganov, 1962) , Transbaikalia (Stroganov, 1962), and Yakutia (Tavrovski, *et al.*, 1971), the average weight of weasel males does not exceed 50-55 g, but in North Kazakhstan it increases to 65-70 g, and in South Kazakhstan it is up to 90 g (our data). In South Balkhash (Sludski, 1953) and Tadzhikistan (Chernyshev, 1958) where there are no ermines, weasels reach a weight of 187-250 g. Large weasels also live in the Ukraine (Abelentsev, 1968).

We have little material on the [kolinsky or] Siberian weasel (*Mustela sibirica* Pall.). In Yakutia (Tavrovski *et al.*, 1971) males are 1.7 times larger than females. In the north of Kemerovo region 9 males, which we caught in winter, averaged 410.7 (220-650) g, but the three females weighed 310 (245-410) g; i.e., the males were only 1.3 times heavier than the females. Similar measurements were given by Stroganov (1962). In some regions of Western

---

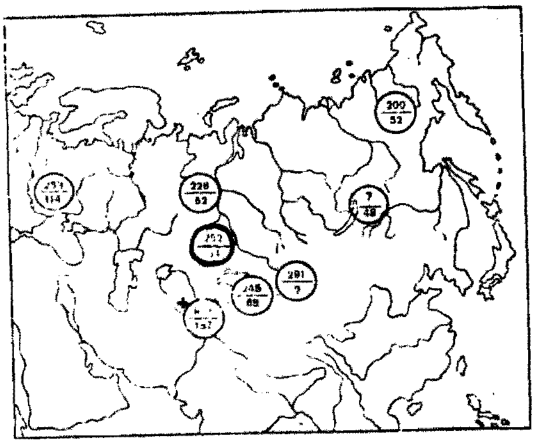
[1] Translated in King (1975)—Ed.

[2] Translated by Israel Program for Scientific Translations, Jerusalem, 1969—Ed.

Siberia, the Baraba Steppe, for example, "giant Siberian weasels" are found. These reach 820 g (Zalesski, 1930; Zverev, 1931; Stroganov, 1962). Marked sexual dimorphism is observed here, but it is apparently best developed in the itatsi weasel on Sakhalin, where, according to Benkovski (1971) females weigh only 162-267 g and males 425-943 g, i.e., 3-4 times as much.

Mustela altaica Pall. inhabits some regions of the Far East, Transbaikalia, Altai, Kazakhstan and Central Asia. In Altai, according to Stroganov (1962), males are 1.6 times heavier than females; in the Balkhash, according to Sludski (1953) 1.7-1.8 times; but according to Zlobin and Shiriyaev (1970), 1.8-1.9 times.

Mustela putorius L. is a European species. In the Ukraine the average weight of males is 812.27 g and that of females, 464.21 g (Abelentsev, 1968). In Central Europe the weight of the polecat reached 1580 and 624 g respectively (Herter, 1959). Thus the males of this animal are 1.7-1.8 times heavier than the females.



+ absent

FIGURE 1: Geographical variation in the mean body weight of ermine males (numerator) and weasel males (denominator).

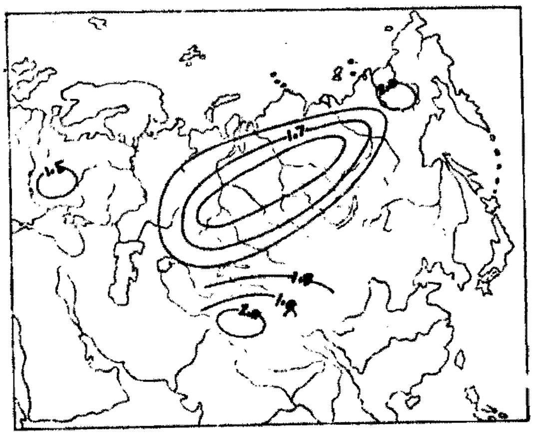


FIGURE 2: Geographical variation in sexual dimorphism in the body weight of ermines.
(For explanation see the text.)

The Siberian polecat (*Mustela eversmanni* Less.) inhabits a considerable part of Europe and Asia. It shows great geographical variation and in some regions attains "gigantic" dimensions (Zverev, 1931; Stroganov, 1962). Sexual dimorphism is quite considerable in most regions, particularly the Ukraine and the Tselinograd region (Table 1), where males are about twice as large as females. The largest polecats inhabit Western Siberia and Central Kazakhstan.

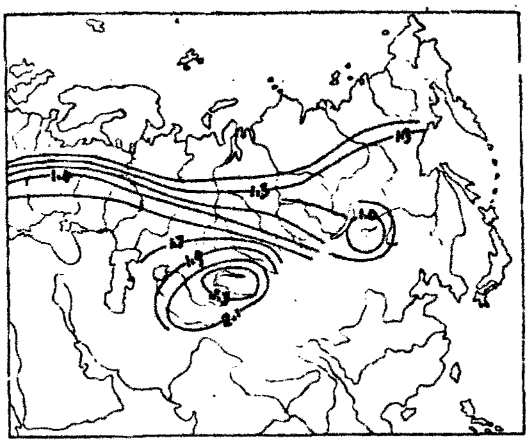


FIGURE 3: Geographical variation in sexual dimorphism in the body weight of weasels.
(For explanation see the text.)

In European mink(*Mustela lutreola* L.) sexual dimorphism in body size is apparently only slight. According to the data of Abelentsev (1968), in the Ukraine the weight of males is 707.5 (502-949) g and that of females is 650.3 (370-700) g.

TABLE 1: Geographical variation in the body weight of the Siberian polecat, g.

Regions	Males			Females			Times by which males are larger than females
	n	Mean	Range	n	Mean	Range	
The Ukraine (Abelentsev, 1968)	108	990	480-1530	38	529	330-763	1.9
Kemerovo region, July 1968 (our data)	6	932	740-1100	4	596	590-605	1.6
Western Siberia (Stroganov, 1962)	-	-	to 2050	-	-	to 1350	1.5
Transbaikalia, (Yurgenson, 1947)	10	811	550-1150	10	584	405-745	1.4
Aktyubinsk region April-June 1970	4	1042	952-1260	3	596	520-638	1.7
April-July 1971 (our data)	19	768	607-1145	6	550	457-692	1.4
Tselinograd region: in the vicinity of Ladyzhenka settlement, April-May 1957	10	1168	740-1570	2	618	345-375	1.9
in the vicinity of lake Shoindykol, April-July 1958 (our data)	29	1286	820-2200	10	757	550-900	1.7
in the vicinity of Alma-Ata, 1968-1972 (our data)	3	776	470-1000	7	747	270-964	1.0

The American mink (*Mustela vison* Briss.) is larger than the European mink, and shows quite marked sexual dimorphism. Males are usually 1.7-1.8 times heavier than females (Popov, 1941, Ternovski, 1955; our data). But geographical variation in the body weight of this species is insignificant. In Altai, Tartaria, and the plain of Western Siberia, the [mean] weight of these animals is almost identical.

The mottled polecat (*Vormela peregusna* Guld.) is distributed in Eurasian steppes and deserts. In Tadzhikistan males weigh 419.7 (370-500) g and females about 380 g (Chernyshev, 1958). Seven males and 1 female were caught in the northern Kyzyl-Kum; their weights were 442.8 (340-580) and 380 g respectively (according to verbal report by A. Bekenov).

The sable (*Martes zibellina* L.) is found mainly in the taiga in the Asian part of the Soviet Union. According to our data, individual and seasonal variations in weight of sables in Western Siberia are much higher than geographical variations. Thus, in the basins of Vasyugan and Chulym rivers the weights of sables differ not only between different seasons but also between years (Table 2). The largest sables inhabit Kamchatka and the East Sayan mountains (Bakeev, 1973). The greatest difference between the sexes is found in the Amur region, where males are 1.7 times larger than females (Abramov, 1967), but in other regions it is relatively small.

The pine marten (*Martes martes* L.) is found mainly in Europe. In the Ukraine males weigh 1259.2 (830-1515) g and females 933.4 (750-1190) g (Abelentsev, 1968); in Timan (Komi Autonomous SSR) 1024 (950-1100) and 763.3 (700-800) g respectively (Romanov, 1969); in the Central and Southern Urals 795-850 (670-1050) and 542-620 (484-850) g respectively (Pavlinin, 1959, from weight of carcases)[1]. Thus the male pine martens are only 1.3-1.4 times heavier than the females.

The stone marten (*Martes foina* Erxl.) is distributed more widely. However, differences between sexes in body weights of stone martens are also rather small. In the Caucasus males are 1.2 times heavier than females (Ryabov, 1958). In the Trans-Ili Ala-Tau 25 males weighed from 110[2] to 1600 g, averaging 1300.25 g: and 25 females from 900 to 1200 g, averaging 1050 g (according to a verbal report by Yu. S. Lobachev). Somewhat heavier (1.4-1.5 times) than females are the males in Central Europe (German Democratic and German Federal Republics), and in the Ukraine (Schmidt, 1949; Abelentsev, 1968).

Martes flavigula Bodd. mainly inhabits south-west Asia. In our country it is found only in the Far East, where, according to Bromley (1956)[3] males are only 1.2 times heavier than females.

The badger (*Meles meles* L.) is widely distributed in Europe and Asia. Animals inhabiting plains and foothills are larger than those inhabiting mountains (data by Yu. S. Lobachev), and show different degrees of sexual dimorphism. In Tadzhikistan (Chernyshev, 1958) and England (Neal, 1948) females are the same size as males: in Western Siberia (according to our data) and the Ukraine (Abelentsev, 1968) they are 1.5 times lighter.

In the otter (*Lutra lutra* L.), which has an extensive distribution area, the geographical variation in weight is apparently small. Both in the Ukraine and the Far East the mean weights are almost identical (Abelentsev, 1968; Heptner, *et al.*, 1967), and males are 1.4-1.5 times heavier than females.

In comparing the mustelids examined we see that the differences in body weight between sexes are small in badgers, otters, *Martes flavigula* Bodd., stone martens, and European mink, whereas in weasels, ermines, kolinskys, *Mustela altaica* Pall., and polecats, the males can be up to twice as heavy as the females. According to the data by Yurgenson (1947)[4], Zeleker and Poluzadov

---

[1] ... "from weight of carcasses" would mean that weights were taken after pelting—Ed.

[2] This must be a misprint for 1100—Ed.

[3] Translation in "Studies of Mammals in Government Preserves" (ed. P.B. Yurgensen): Israel Program for Scientific Translations, Jerusalem 1961—Ed.

[4] Translated in King (1975)—Ed.

TABLE 2: Geographical variation in body weight of sables(g)

Regions	Males			Females			Times by which males are larger than females
	n	Mean	Range	n	Mean	Range	
Sverdlovsk region (Pavlinin, 1963)	56	1330	1000-1780	24	910	790-1050	1.5
Western Siberia (Raevski, 1947)	-	1290	1034-1659	-	864	760-1115	1.5
Vasyugan basin							
November 1968	12	1158	1000-1300	13	884	800-1100	1.3
February 1968	8	1462	1300-1600	7	888	750-1000	1.6
November 1969	9	1205	1000-1300	5	780	700-800	1.5
Chulym basin							
November 1970	9	1400	1200-1600	8	937	700-1100	1.5
November 1971	9	1144	900-1300	5	860	800-900	1.3
(our data)							
East Kazakhstan region November-February 1964 (Data of Yu. S. Lobachev)	25	1376	1100-1800	25	954	750-1100	1.4
Altai, winter 1953-54 (Ternovski, 1955)	4	1065	990-1140	5	746	600-920	1.4
Eastern Siberia							
January	22	1472	1110-1810	21	1132	820-1560	1.3
July	-	1433	1200-1800	-	980	870-1300	1.4
(Kuznetsov, 1941)							
Yakutia (carcases without pelts)							
west	172	810	539-1078	100	601	418-773	1.3
south	59	759	555-950	52	525	410-633	1.4
(Tavrovski *et al*. 1971)							
Kamchatka (Kuznetsov, 1941)	4	1500	880-1869	5	1100	600-1140	1.4
Sakhalin (Kuznetsov, 1941)							
January	22	1193	880-1500	25	916	740-1120	1.3
July	22	1289	940-1600	25	905	800-1130	1.3
Amur region (Abramov, 1967)	40	1360	1100-1750	23	768	500-1000	1.7

(1967), and others, even in pine martens and sables, although their sexual dimorphism in body weight is small, there are considerable differences in the diets of males and females. No morphological differences have been found in the structure of the digestive organs, musculature, or skulls of the sexes (Yurgenson, 1947) and therefore it may be assumed that these species show only the initial stages of the intraspecific ecological divergence which separates the niches and thereby weakens the competition for food between males and females. In contrast to martens and sables, in most species of *Mustela* there is not only a distinct ecological divergence but also substantial morphological differences between sexes in the organs and muscles related to the catching and killing prey, as shown by Yurgenson (1947), in the Siberian polecat and weasel. The ecological differences between the females and males in these species are so great that, particularly in their methods of hunting, their behaviour, and their activity, they are as different from each other as absolutely different species. When tracking Siberian polecats in January/February 1972 in the vicinity of Alma-Ata, it was observed that the largest male covered 5-7 km, in an area of 40 km^2, almost every night, and always caught Muridae above the ground. He seldom entered the nests of rodents and did not dig them out; and he also frequently changed burrows for his day-time rest. In contrast, the small-sized female, during the same period, appeared on the surface every 6-8 days and covered not more than 1 km in searching for a burrow containing a hibernating souslik. Having found one, she dug it out for two-three days and afterwards remained in it for a long time. She spent five weeks in an area of less than 1 km^2. Similar data have also been given for the ermine (Vershinin, 1972)[1]. Considerable ecological separation between males and females is probably peculiar to small, relatively slow-moving, Mustelidae which feed mainly on animals. It is quite obvious that, in less favourable habitats, sexual dimorphism should be more pronounced, and this is confirmed by the present data. Thus, in weasels a large increase in the size of males compared with females is found in the flat areas of Central Asia and South Kazakhstan; in kolinskys in Yakutia and Baraba forest-steppe; and in Siberian polecats in the Ukraine and the steppe zone of Kazakhstan, i.e., more frequently on the periphery of the distribution area, where conditions are apparently unfavourable.

It is quite possible that these differences also depend on interspecific competition. The ermine and weasel have similar distribution areas and are potential competitors. In Siberia there is not much difference in the weight of male and female [weasels], but here they are 3-4 times smaller than the males of the ermine, which allows the two species to avoid one another by having different-sized nests. These species live in the same habitats, and if there were no separation in their sizes, it is doubtful whether they would be able to co-exist. In Kazakhstan they have different habitats. The ermine confines itself to damper places, such as fluvial plains, and lake and intermontane basins; but the weasel lives in the scrub and weed thickets of watersheds where the ermine is absent. It is quite possible that this difference in habitat was the prerequisite for the development of considerable sexual dimorphism in the weasel in the plains of Kazakhstan and Central Asia. The same competitive relationship probably explains the fact that the heaviest weasel males and females are found in the regions where the ermine is absent (the plains of South Kazakhstan and Central Asia) or very large (the Ukraine).

Sexual dimorphism in weasels increases with their general size and is best developed in the largest races (Heptner, *et al.*, 1967)[2]. This trend may also be clearly observed in Kazakhstan. For example, in the vicinity of Semiyarskoe and Basaga villages, male weasels are 1.7-1.9 times larger than females, but 2.3 times larger in the vicinity of Alma-Ata, where weasels are larger. In the Ukraine, however, the differences between sexes in the body weight of weasels are less pronounced, although they are larger here than in Kazakhstan.

Furthermore, in populations showing a less pronounced sexual dimorphism, the females are often larger than the males in populations where sexual dimorphism is great. Apparently the rule of sexual dimorphism, formulated by Geodakyan and Smirnov (1968), cannot always be applied to Mustelidae. According to this rule, if males are larger than females then the species concerned becomes larger through evolution. The development of sexual dimorphism probably depends on a number of factors such as intraspecific selection, interspecific competition, diet and food supplies, etc.

The greatest sexual dimorphism is usually observed in the small, relatively slow-moving, species of Mustelidae (weasel, ermine, kolinsky, *Mustela altaica* Pall.); in those whose habitats are in open country (polecats, mottled

---

[1] Translated in this volume—Ed.

[2] Translated by British Library, RTS No. 6458 (chapters on weasel and ermine only)—Ed.

polecats) and in those which experience the greatest competition for food from large predators (sable, corsac fox, fox, wolf, lynx, etc.) especially in the places where there are no permanent populations of prey. In the large Mustelidae (badger, otter, *Martes flavigula* Bodd. and others) sexual dimorphism is less pronounced, apparently because these animals are more specialized, less fertile, or better supplied with food, and so suffer less from competition. Probably, this also applies to some small Mustelidae which inhabit favourable places only. Thus, in stone martens in the Trans-Ili Ala-Tau mountains, where food supplies are relatively constant and abundant, sexual dimorphism is negligible. In the Ukraine, females and males of the European mink are similar in body weight, and it may be assumed that this region is ecologically favourable for them. Sexual dimorphism in the badger is more pronounced in the least suitable habitats, such as in Western Siberia and the Dzungarian Ala-Tau. But in other parts of the distribution area of this animal, sexual dimorphism is almost absent.

We conclude that the ecological and morphological differences between females and males become more apparent in unfavourable environments because they serve to weaken the results of inter- and intraspecific competition. By means of sexual dimorphism the animals become better adapted to the environment. The smaller sizes of the females enable them to find more refuges from their enemies and also to find food more easily, because they are able to enter a wider range of burrow sizes of potential prey. This is particularly important, because in most Mustelidae only the female rears the young, and these begin to eat flesh very early (Sviridenko, 1935; our data).

From the data given in this paper it appears that in many cases the degree of sexual dimorphism in the body weight of Mustelidae has a strongly pronounced tapering variation. Environmental conditions have a definite effect on these animals. The less favourable they are, the greater is the sexual dimorphism in the body size, but in better habitats the weight differences of males and females decrease. Furthermore, the degree of sexual dimorphism in closely related species changes in parallel. Thus weasels and ermines increase in sexual dimorphism together from the north to the south. On the whole, in large Mustelidae (badger, otter, *Martes flavigula* Bodd.) sexual dimorphism is less pronounced than in the small ones (weasel, ermine, kolinsky, *Mustela altaica* Pall., Siberian polecat) which need a greater ecological adaptability in order to survive.

SUMMARY

The sexual dimorphism in body size and weight in mustelids (Mustelidae) reduces intraspecific competition. There is only a slight difference in more specialized larger species better provided with food (*Meles meles, Lutra lutra, Martes flavigula*). The greatest weight differences between males and females are found in the smaller sized mustelids (*Mustela nivalis, M. erminea, M. sibirica, M. altaica, M. eversmani*) which move slowly and experience greater competition. Sexual dimorphism increases the ecological adaptability of the species to different habitats. The sexual dimorphism of mustelids depends on environmental conditions: as a rule the less favourable the latter are, the more sharply it is defined. In optimum habitats the weight differences between males and females are usually lower. Most commonly males become relatively largest in the most unfavourable habitats.

BIBLIOGRAPHY

Abelentsev, V. I. (1968): The fauna of the Ukraine, vol. 1. Mlekopitayushchie, ed.3. Kunyi, Kiev, 1-280.

Abramov, K. G. (1967): The sable in the game economy of the Far East. M., "Nauka", 1-160.

Bakeev, N. N. (1973): In "The sable, the marten and the yellow-throated marten". M., "Nauka", M., 49-52.

Benkovski, L. M. (1971): Byull. Mosk. o-va. Ispt. Prir., Otd. biol., 76 (2): 44-51.

Bromley, G. F. (1956): Collection: Materialy po rezultatam izucheniya mlekopitayushchikh of gosudarstvennykh zapovednikakh[Materials on the results of the study of mammals in State Reserves], M.

Vershinin, A. A. (1972): Byull. Mosk. o-va. Ispyt. Prir. Otd. Biol., 77 (2): 16-26.

Geodakyan, V. A. and Smirnov, N. N. (1968): Sexual dimorphism and evolution of the lower Crustacea. Problemy evolutsii, vol. 1, Novosibirsk. "Nauka".

Heptner, V. G., Naumov, N. P. Yurgenson, P. B., Sludski, A. A., Chirkova, A. F. and Bannikov, A. G. (1967): The mammals of the Soviet Union, vol. 2, part 1. Morskie korovy i khishchnye[sea cows and carnivores]. M., "Nauka", 1-1003.

Davitashvili, L. Sh. (1961): Theory of sexual selection. M., Izd-vo AN SSSR, 538.

Darwin, C. (1908): The descent of man, and selection in relation to sex. Collection of works, vol. 5-6, M.

Dementyev, G. P. (1940): Manual of zoology, vol. 6, Birds. M. Izd. AN SSSR.

Zaleker, V. L. and Poluzadov, N. B. (1967): Animal husbandry and furs, Kirov. Tr. Vses. nauchno-issled. in-ta, ed. 21, 25-33.

Zalesski, I. M. (1930): Reports of the Siberian regional plant protection station, 4 (7), Novosibirsk.

Zverev, M. D. (1931): Papers on plant protection in Siberia [Tr. po zashch. rast. Sibiri], 1 (8), Novosibirsk.

Zimina, R. P. (1964): Regularities in the vertical distribution of mammals after the example of the northern Tien Shan. M., "Nauka", 1-158.

Zlobin, B. D. and Shiryaev, V. V. (1970): Tr. Kirovskogo s.-kh. in-ta [Transactions of the Kirov Agricultural Institute], 22, (52), Kirov, 188-194.

Kopein, K. I. (1967): Tr. MOIP[Moscow Society of Naturalists], 25 M.:33-39.

Kistyakovski, A. B. (1958): Sexual selection and specific identifying characters in birds. Izd-vo Kievskogo un-ta, 199.

Klimov, Yu. N. (1940): Tr. Biol. n.-i. In-ta Tomskogo gos. un-ta [Transactions of the Biological Research Institute of the Tomsk State University], vol. 7.

Kuznetsov, B. A. (1941): Tr. Mosk. zootekh. in-ta [Transactions of the Moscow Zoo-Technical Institute] 1: 23, M.

Lobachev, Yu. S. (1970): Izv. AN KazSSR, [Reports of the Academy of Sciences of the Kazakh SSR], Biology series, No. 1.

Nekipelov, N. V. (1962): Dokl. Irkutskogo protivochumnogo in-ta [Papers of the Irkutsk Anti-Plague Institute], No. 4, Irkutsk, 106-116.

Pavlinin, B. N. (1959): Tr. Uralsk. otd. MOIP [Transactions of the Ural Branch of the Moscow Society of Naturalists] 2, Sverdlovsk, 15.

Pavlinin, B. N. (1963): Tr. In-ta biologii, UF AN SSSR [Transactions of the Institute of Biology, Ural Branch of the Academy of Sciences, USSR], Sverdlovsk, 1-112.

Popov, V. A. (1941): Tr. Vses. n.-i. in-ta okhotnichyego promysla [Transactions of the All-Union Hunting Research Institute], M.5, 13-19.

Raevski, V. V. (1947): The life of the Kondn-Sosva sable. M.

Romanov, A. N. (1969): Tr. Vses. n.-i. in-ta zhivotnovodstva i pushniny [Transactions of the All-Union Scientific Research Institute of animal husbandry and fur], No. 22, Kirov, 19-25.

Ryabov, L. S. (1958): Tr. Kavkazskogo gos. zapovednika [Transactions of the Caucasian State Reserve], 4, Maikop, 31.

Sviridenko, P. A. (1935): The Siberian polecat and its agricultural significance in combating rodents, M.-L., Selkhozgiz.

Sludski, A. A. (1953): The order Carnivores. From the book: Zveri Kazakhstana, Alma-Ata, 1-536.

Stroganov, S. U. (1962): The animals of Siberia. Carnivores. M., Izd. AN SSSR, 1-458.

Ternovski, D. V. (1955): The economic significance, ecology and acclimatisation of the American mink in Altai. Kand. dis. [Thesis], Novosibirsk.

Tavrovski, V. A., Egorov, O. V., Krivosheev, V. G., Popov, M. V. and Labutin Yu. V. (1971): The mammals of Yakutia. M., "Nauka", 1-660.

Chernyshev, V. I. (1958): Tr. In-ta zoologii i parazitologii AN Tadzhikskoi SSR [Transactions of the Zoology and Parasitology Institute of the Academy of Sciences of the Tadzhik SSR] 85, Stalinabad.

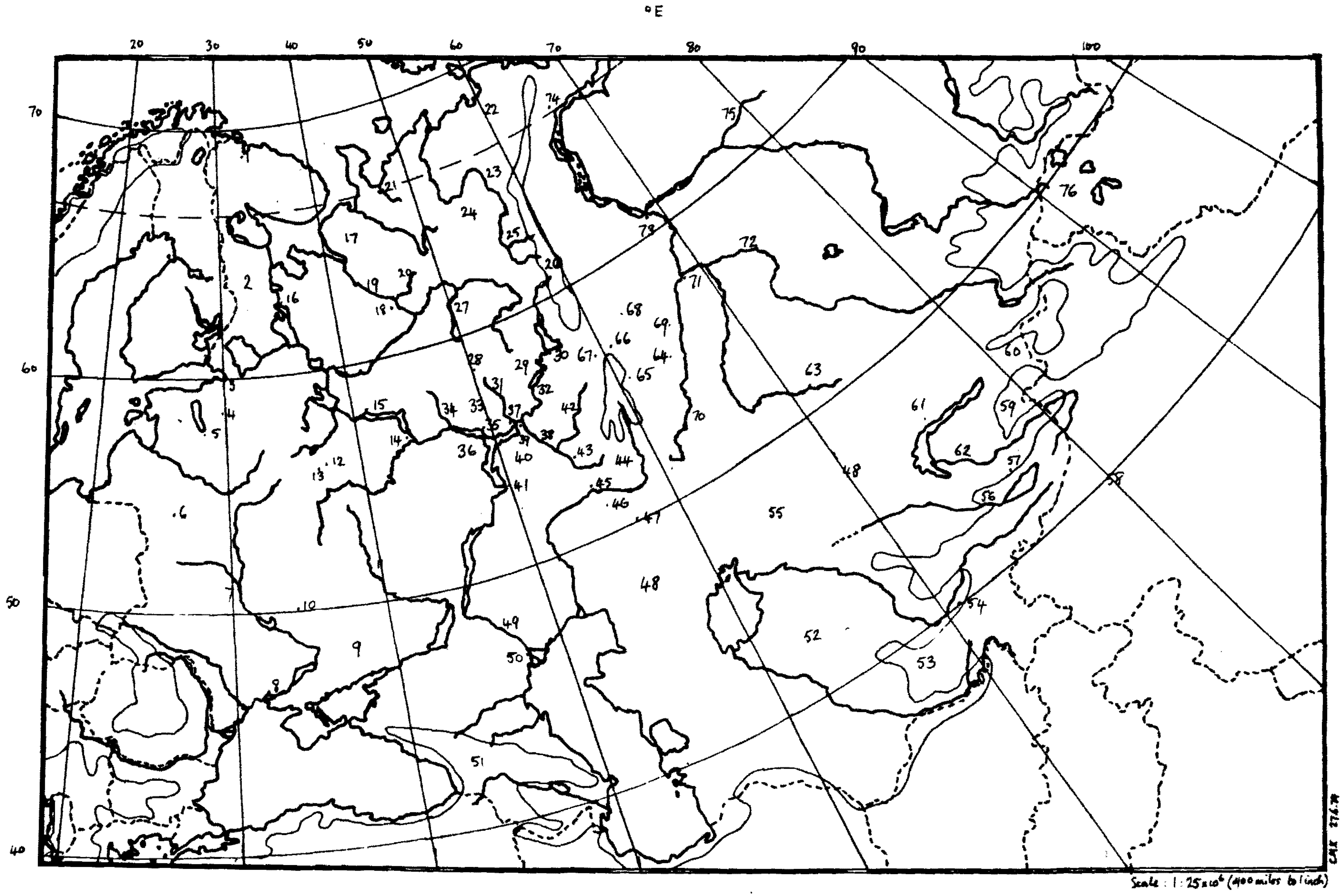
Shubin, I. G. (1970): Materials of the scientific and industrial conference on hunting and fur-breeding in Kazakhstan. Alma Ata, 197-199.

Yurgenson, P. B. (1947): Byull. Mosk. o-va. Ispyt. Prir., Otd, biol. [Bulletin of the Moscow Society of Naturalists, biology section] 52 (6): 33-35.

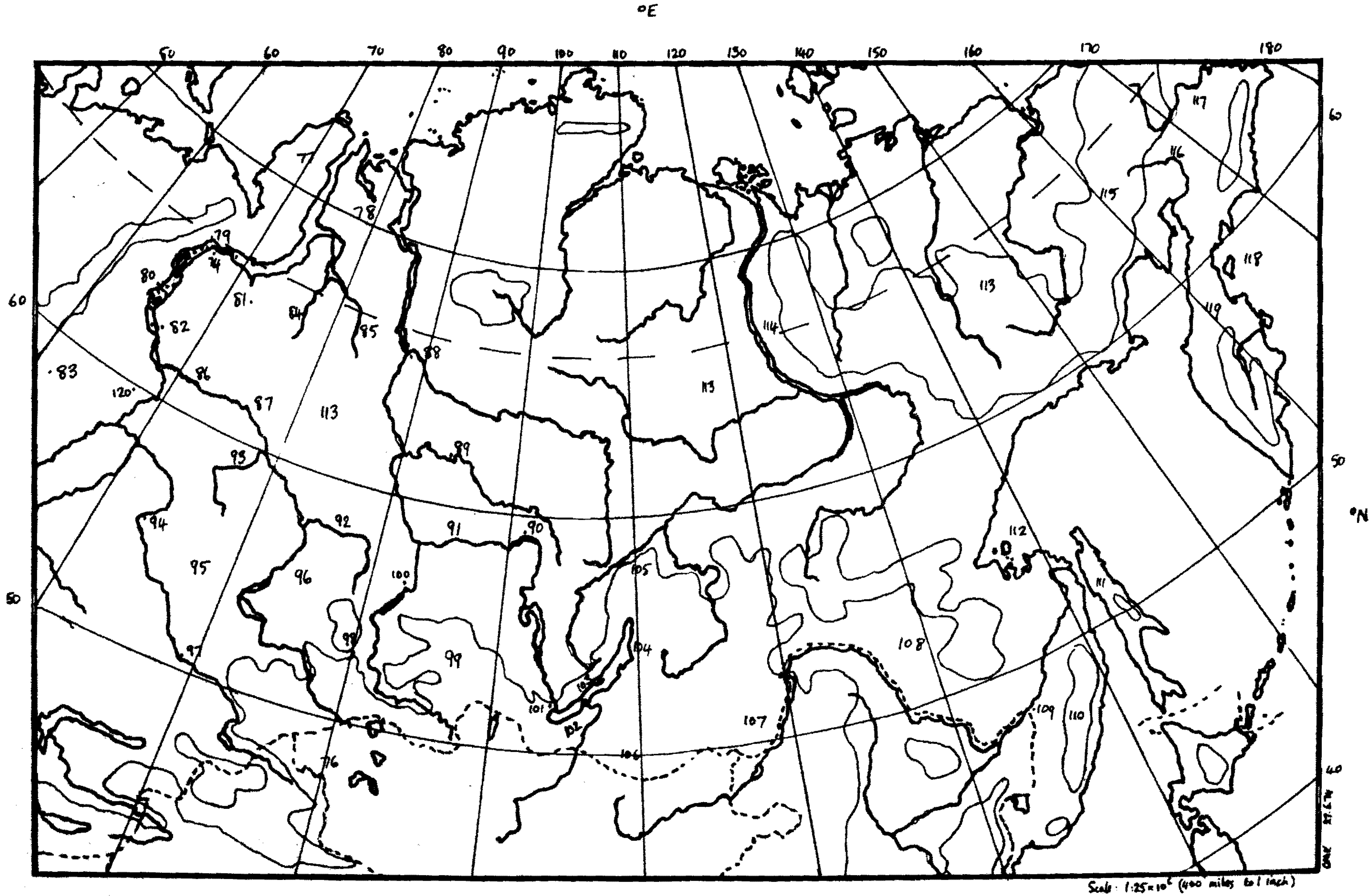
Herter, K. (1959): Polecats and ferrets. Die neue Brehm-Buecherei, Wittenberg.

Neal E. (1948): The badger. London.

Schmidt, F. (1949): Natural history of the pine and stone martens. Monographien der Wildsaeugetiere [Monographs of wild mammals] 10, Leipzig.



Locality map - European Russia



Locality map - Asian Russia

Key to maps

Minor places are not mapped or indexed if the context gives a clear indication of their position relative to places that are, or if they are not mentioned in the "Times Atlas of the World" (1959).

Number		
1	Murmansk	81
2	Karelia, prov.	24-34, 70, 81
3	Leningrad	24-34, 70, 81, 192
4	Novgorod	24-34, 70, 81
5	Pskov	24-34, 70, 81
6	Zaslavl	56
7	Belorussia, prov.	56-60
8	Kherson	94
9	Ukraine	94, 110, 197-9
10	Poltava	94
11	Don, R.	121
12	Moscow	26, 32, 56, 93, 180
13	Pushkin	139-40
14	Gorki	124-6, 149, 156
15	Kostrom	149-57
16	Povenets	139
17	Archangel'sk, prov.	1-10
18	Cherevkovo	2, 8
19	Northern Dvina, R.	1-10
20	Uftyuga, R.	1-10
21	Oma, R.	1-10
22.	Nenets, district	1, 62, 135, 150
23	Pechora, R.	1-10, 37, 41, 149, 176-7, 180
24	Komi, ASSR	40, 149-50, 200
25	Ilych, R.	37, 150, 176-7, 180
26	Ural, Mts	36, 106, 110, 149-57, 200
27	Sysola, R.	149
28	Kirov, prov.	1-10, 123-6, 129, 133-6, 149, 156
29	Udmurtia	124-7
30	Perm	150-7
31	Vyatka, R.	106, 110, 149, 157
32	Kama, R.	103, 110-30, 149, 151
33	Mari ASSR	123-6
34	Vetluga, R.	149
35	Kazan	94
36	Chuvash, prov.	124-7
37	Yelabuga	105
38	Belaya, R.	110, 151
39	Menzelinsk	101, 110
40	Tartar SSR	26, 94, 101-6, 109-30, 149, 153, 200
41	Kuybyshev	149, 156-7
42	Biserta, R.	154
43	Ufa	151, 157
44	Bashkiria	103, 124-6, 129, 151-7
45	Orenburg	149, 156-7
46	Ak-Bulak	94
47	Aktynbinsk	197-9
48	Kazakhstan, prov.	59, 127, 133-6 149, 161, 197-8, 201-02
49	Volga, R.	104, 110-30, 149
50	Astrakhan	173
51	Caucasus Mts	200
52	Kyzl-Kum, desert	200
53	Tadzikistan, prov.	197, 200
54	Fergana	60
55	Turgai, steppe	94
56	Trans-Ili Alatau, Mts	200-203
57	Alma-Ata	199, 202
58	Tien Shan, Mts	197
59	Dzungarin Alatau, Mts	200, 203
60	Ala-Kul, lake	197
61	Balkhash	197-8
62	Ili, R.	200, 203
63	Tselinograd	198-9
64	Kurgan	151-4
65	Chelyabinsk	151-4
66	Sverdlovsk	56, 150-5, 201
67	Nizhne-Sergi	153
68	Irbit	152
69	Tyumen	133-7, 150-4, 160-1
70	Tobol, R.	151
71	Tobolsk	151
72	Irtysh, R.	151
73	Khanty-Mansijsky	150-5
74	Salekhard	62
75	Vakh, R.	155
76	Altai Mts	110, 141, 145, 155, 162, 198, 200-1
77	Yamal	62, 135, 150
78	Gydan, Peninsula	110
79	Labytpangi	135
80	Berezovo	150
81	Nadym	150
82	Octjabr'sk ye	150
83	Serov	150
84	Pur, R.	150
85	Taz, R.	150, 156-7, 200
86	Ob, R.	150-151
87	Surgut	151-4
88	Turukhan	167-71
89	Baikit	168-71
90	Kezhma	169
91	Angara, R.	141, 146
92	Chulym, R.	141, 145, 200-1
93	Vasyugan, R.	200-1
94	Omsk	133-6, 152, 161
95	Baraba, steppe	198, 202
96	Kemerovo, prov.	197-9
97	Semiyarskoye	202
98	Tashtyp	167-71
99	Sayan, Mts	141, 146, 162, 200
100	Krasnoyarsk	133-6, 139-40, 167-71
101	Irkutsk	133-6

Geographical Index

Minor places are not mapped or indexed if the context gives a clear indication of their position relative to places that are, or if they are not marked in the "Times Atlas of the World" (1959).

*Marked only on map on page 20

Number on map and page reference

Number on map and page reference

Number on map and page reference

Subject Index

7

4,

Species Index

Mustelids

Other animals

P. D. HASSELBERG, GOVERNMENT PRINTER, WELLINGTON, NEW ZEALAND—1980

42208E—400/2/80