Studies on the wolf (Canis lupus L.) in Finland

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I. Introduction

The present range of the wolf (*Canis lupus* L.) in the northern hemisphere is very clearly bipartite. Within the sphere of western culture the species has been exterminated in vast areas. In North America, in the area south of the arctic tundra, the species occurs regularly only in the northern parts of Minnesota (ALLEN & MECH 1963, p. 203). In Western Europe the wolf breeds only on certain mountains, such as the Apennines and the Scandinavian mountains. In the other areas the species was exterminated in the eighteenth and nineteenth centuries as man extended his settlements (see e.g. PALMÉN 1913, JOHNSEN 1929, LÖNNBERG 1934). In Eastern Europe, in the area of the people's democracies, the wolf populations have shown the opposite trend during recent decades. At the end of the last century and in the beginning of the present one, wolves were hunted down indefatigably in these areas, but since the changes in landownership and in the structure of society which took place after the First World War the attitude of man to the wolf has also changed. A consequence of these structural changes in society (see KAURI 1957) has been that the range of the wolf has expanded very noticeably. Nowadays it covers, generally speaking, all the countries belonging to the East European bloc (see OGNEV 1931, pp. 185 – 193, ZIVANCEVIC 1951, FERIANCOVA & KOMAREK 1955, KNEZEVIC & KNEZEVIC 1956, KAURI 1957, ATANASSOV 1957, DULIC & TORTIC 1960, Anonymus 1960 a, RACA 1960, Anonymus 1960 b, CVIJETIC 1960, KORITNIK 1960, ATANASSOV & PESCHEV 1963). As a consequence of this expansion, wolves have also migrated farther westwards (see e.g. MOHR 1953, TENIUS 1956, KAURI 1957, PULLIAINEN 1962 a and b, 1963 c).

Studies on wolf populations have recently been carried out both in the east (e.g. KNEZEVIC & KNEZEVIC 1956, MAKRIDIN 1959) and in the west (e.g. BURKHOLDER 1959, ALLEN & MECH 1963), although for different reasons. The studies in the east have been linked with a vigorous campaign against wolves (KNEZEVIC & KNEZEVIC *op. cit.*, MAKRIDIN *op. cit.*, KALCKOV 1960, GEJDENREICH 1960). By contrast, the American investigators (BURKHOLDER *op. cit.*, ALLEN & MECH *op. cit.*; cf. also PIMLOTT 1964) have set out to study the biology of the species while this is still possible. The aeroplane has been used to aid the investigations both in the east and in the west (MAKRIDIN *op. cit.*, BURKHOLDER *op. cit.*, ALLEN & MECH *op. cit.*).

There has been no systematic investigation on the history, recent distribution and biology of the wolf in this country. However, attention has been paid to the disappearance of the wolf in the nineteenth and twentieth centuries (e.g. PALMÉN 1913, LEVANDER 1926, MUNSTERHJELM 1946, SIIVONEN 1949 and 1956, KORPIJÄRVI 1958). I have published some earlier accounts of the recent status of the Finnish wolf population (PULLIAINEN 1962 a and b, 1963 c).

The purpose of this paper is to provide records of the investigations which I have carried out during the years 1961 – 1964 on wolves in Finland at the Game Research Institute of the Finnish Game Foundation, and at the Department of Agricultural and Forest Zoology and the Department of Zoology of the University of Helsinki.

II. Occurrence of wolves in Finland

1. Material and methods

The following is a detailed survey of the occurrence of wolves in Finland during the years 1954 – 63. At the same time a short review will be given of the earlier occurrence of the species, based on previous investigations (see e.g. PALMÉN 1913, LEVANDER 1926, SALOVAARA 1930, MUNSTERHJELM 1946, SIIVONEN 1949 and 1956, KORPIJÄRVI 1958).

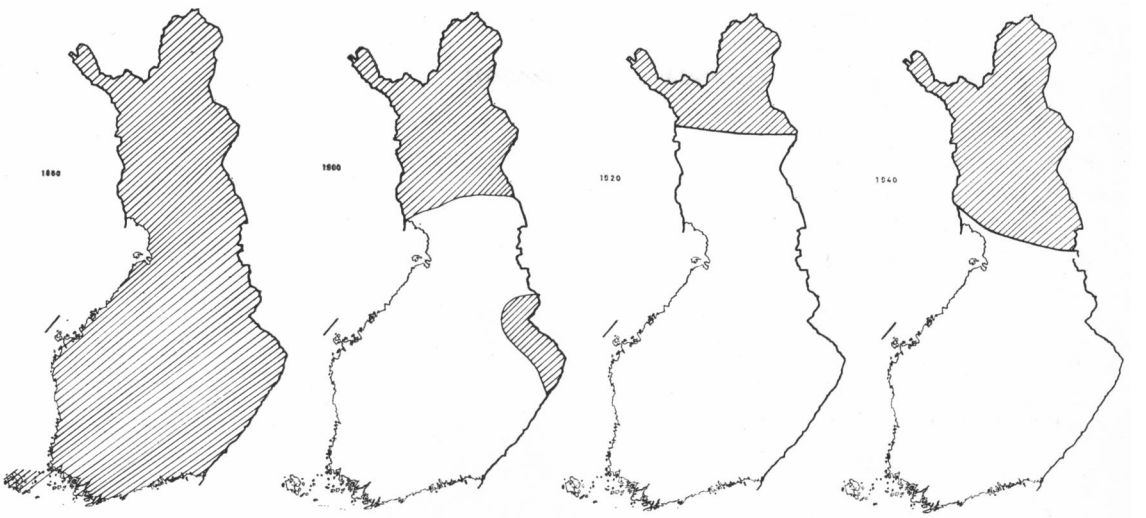
I have gathered data on wolf packs and on lone individuals by many different methods. Two inquiries (in spring 1962 and 1963) were sent to the observers of the Game Research Institute of the Finnish Game Foundation, who sent in reports on the wolves in their study areas (see also PULLIAINEN 1962 b, p. 101, 1963 c, pp. 136 – 137; about the reliability of these inquiries, see SIIVONEN 1951). I have also gathered data on wolves by reading all the numbers of the following newspapers: Helsingin Sanomat (1959 – 63; partly 1954 – 58), Kainuun Sanomat (1959 – 61), Karjalan Maa (1957 – 61), Koillis-Sanomat (1952 – 59), Lapin Kansa (1954 – 61). Some reports have been taken from the following newspapers: Ilta-Sanomat, Kaleva, Karjalainen, Länsi-Savo, Pohjolan Sanomat, Savonmaa, Savon Sanomat and Uusi Suomi. The data gathered from newspapers have been checked, if possible, by comparison with observations from different sources by sending a special inquiry to the observer in question and by following the movements of wolves according to reports published in newspapers, until, if the animal was eventually killed, it could be seen whether it was in fact a dog or a wolf. By this method it has been possible to establish that 50 – 60 % of the reports of wolves in West and Southwestern Finland actually refer to dogs (cf. VÄLIKANGAS 1926, RAND 1945 and 1948 a, ALLEN & MECH 1963). This is not the first time that newspapers have been used in investigations of this kind. LEVANDER (1926) used them in his studies on wolves in Finland. ARTIMO (1960) used them when studying the dispersal of the muskrat (*Ondatra zibethicus*) in Finland. RAND (1945), studying wolves in North America, gathered data from newspapers. OLSON (1938 a) and KNEZEVIC & KNEZEVIC (1956) used observations made by hunters in their studies on the biology of the wolf.

The data for the years 1948 – 53 have been obtained by means of inquiries made by the Game Research Institute of the Finnish Game Foundation.

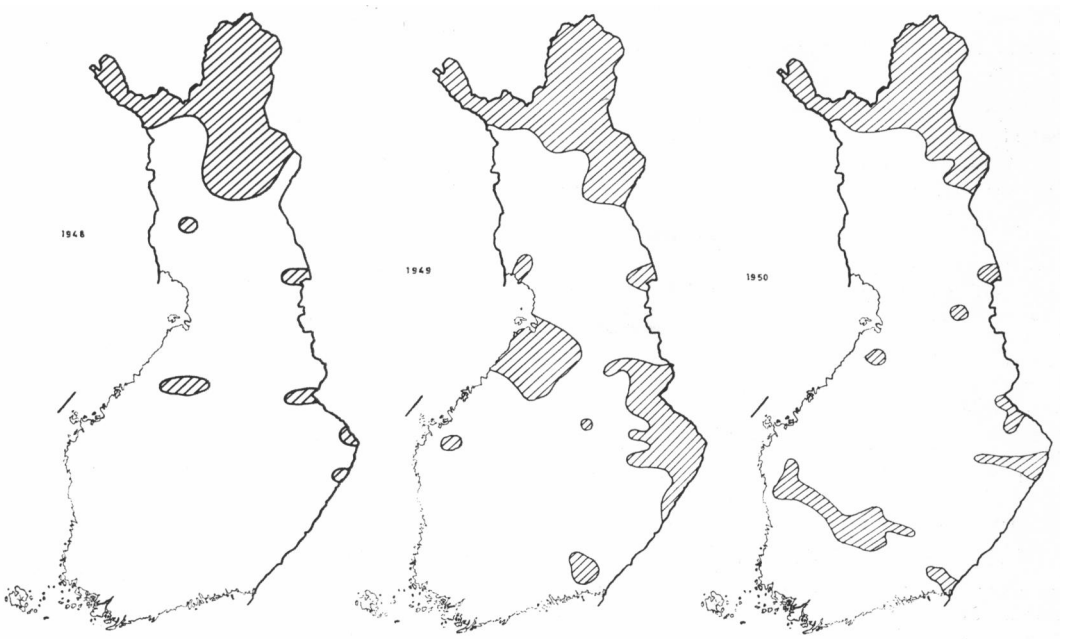
2. Changes in distribution and numbers

The decline in the Finnish wolf population began on the Aland Archipelago, where the last wolf was killed in the year 1844 (SALOVAARA 1930, p. 110). However, during the winter of 1875 – 76 wolves were again seen there (SALOVAARA *op. cit.*). Obviously they had come from the mainland. They were said to be crossed with dogs (SALOVAARA *op. cit.*; cf., however, RAND 1948 a, KNEZEVIC & KNEZEVIC 1956, ALLEN & MECH 1963, BARBERIS *et al.* 1964, HERRE 1965). I have found no later observations on wolves on the Aland Archipelago.

In the 1880's wolves still occurred in all parts of the Finnish mainland (SIIVONEN 1956; see Fig. 1), but the populations began to decline very rapidly. In the year 1900 (Fig. 2) the breeding area of the wolf included only the eastern and northern parts of the country, although occasional individuals were still seen in West Finland (SIIVONEN 1949). By the year 1920 (Fig. 3), the range of the wolf had contracted still further, comprising only northernmost Finland (the communes of Enontekiö, Utsjoki,



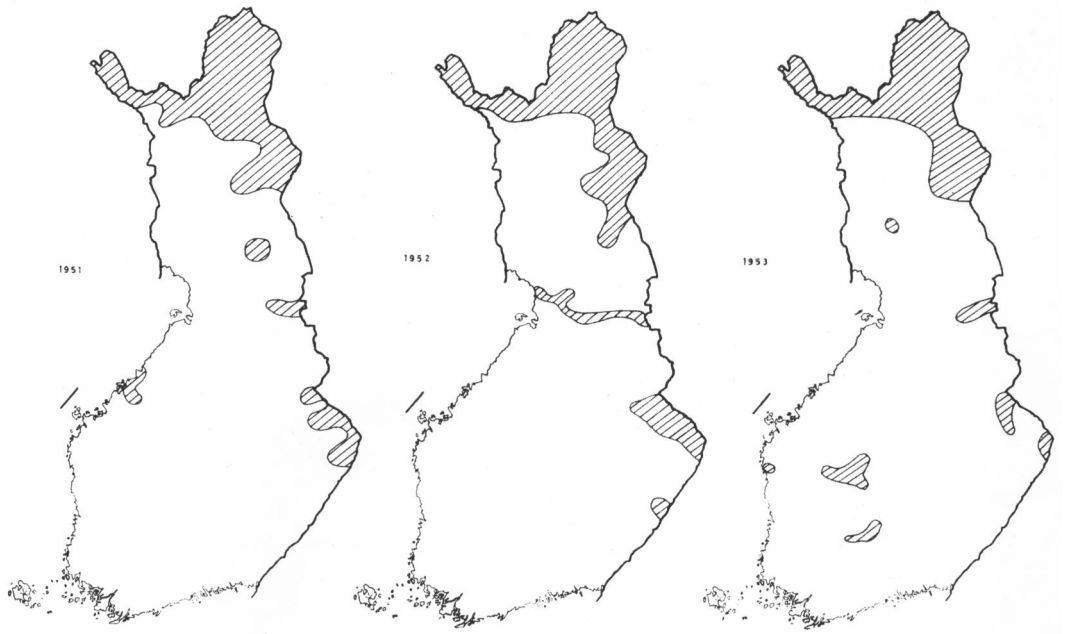
Figs. 1 – 4. The distribution of the wolf in Finland during the years 1880, 1900, 1920 and 1940, according to Siivonen (1949).



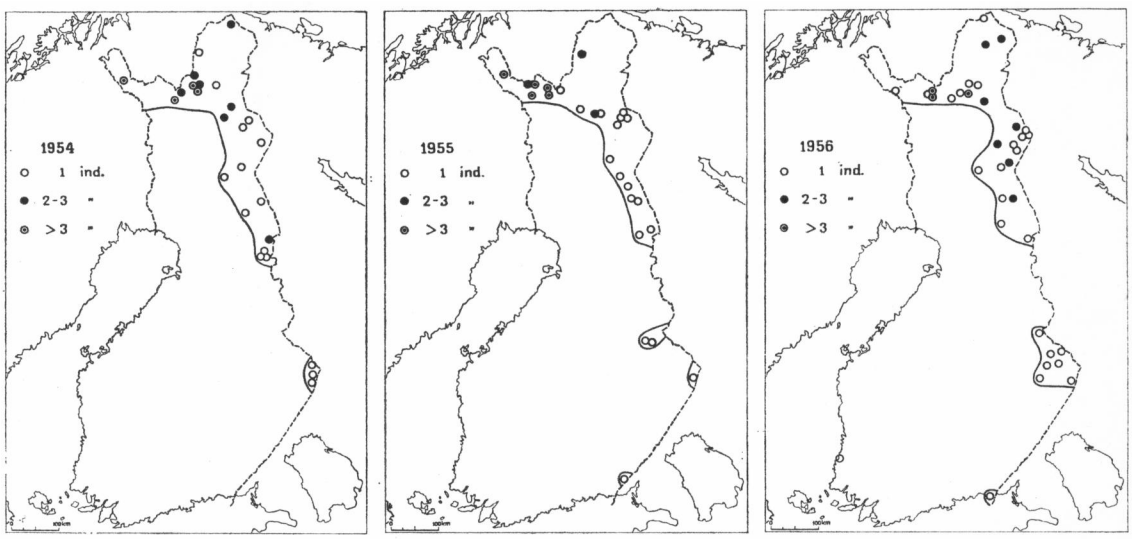
Figs. 5 – 7. The range of the wolf in Finland in 1948 – 1950. Observations on wolves were made in areas marked in the maps according to the game inquiries.

and Inari, and parts of the communes of Sodankylä and Savukoski, Siivonen *op. cit.*). At this time the range of the species was at its minimum. At the beginning of the Second World War (Fig. 4) there were wolves in the very sparsely settled area of North Finland and in some other parts of the country (Siivonen *op. cit.*), too.

Data on the annual changes in the distribu-



Figs. 8 – 10. The range of the wolf in Finland in 1951 – 1953. For explanations, see Figs. 5 – 7.

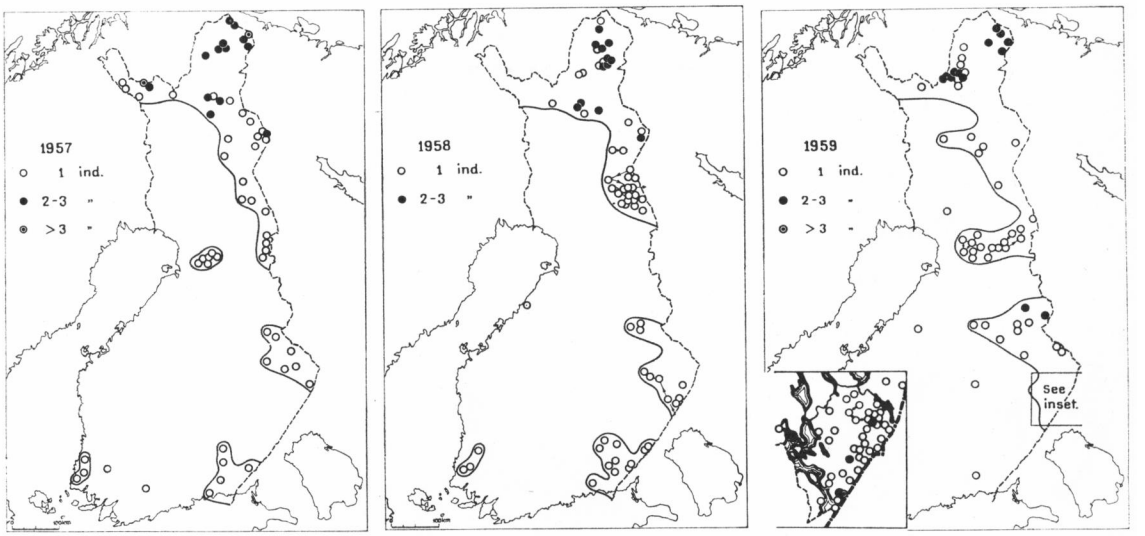


Figs. 11 – 13. Occurrences of the wolf in Finland in 1954 – 1956 (see also text).

tion of the wolf in Finland during the years 1948 – 1963 are presented below. Similar fluctuations took place during the period 1920 – 1947, too.

In 1948 (Fig. 5), wolves occurred in an area which included the communes of Utsjoki, Inari (InL), Sodankylä, Savukoski and Pelkosenniemi (KemL) in the east, and in the west only the commune of Enontekiö (EnL). Some of the wolves had come from beyond the eastern frontier. Several lone wolves were reported in Rovaniemi (PP) and in Ostrobothnia.

In 1949 – 1950 (Figs. 6 – 7), the range of the wolf extended over wide areas of Finland. In Lapland the situation was the



Figs. 14 – 16. Occurrences of the wolf in Finland in 1957 – 1959 (see also text).

same as during the previous year (see also INNOLA 1951), but in Ostrobothnia and East Finland the range was wider. The wolves observed were migrants which moved rapidly from place to place. In 1950, two migrating individuals were seen in South Finland. One of these animals was observed in the district of Parkano (St) and the other chiefly in South Häme.

In 1951 – 1953 (Figs. 8 – 10), the distribution of the wolf in Finland was much the same as in 1948. In 1953, a migrating individual was again seen in Häme.

In 1954 (Fig. 11), wolves were observed in the area which extended from the northern communes of Lapland along the eastern frontier to Kuusamo (Ks) and Suomussalmi (Kn). At Ilomantsi, in North Karelia, some wolves came over the frontier.

In 1955 (Fig. 12), the southern limit of the northern area coincided with the border of the communes of Kuusamo and Suomussalmi. Some individuals crossed the frontier into Pielisjärvi (PK) and Ilomantsi (PK).

In 1956, the northern part of the range was the same as the previous year. But in North Karelia the range had expanded, some individuals having migrated farther towards Central Finland (Fig. 13). Moreover, a wolf was seen at and near Rauma (St), and another wolf was observed on the southeastern frontier at Virolahti (EK).

In 1957, the northern area extended somewhat further southwards. At the same time the range had widened in North Karelia and Southeastern Finland (Fig. 14). Some migrating wolves were observed in Southwestern Finland, and an old wolf was seen at Pudasjärvi (PP).

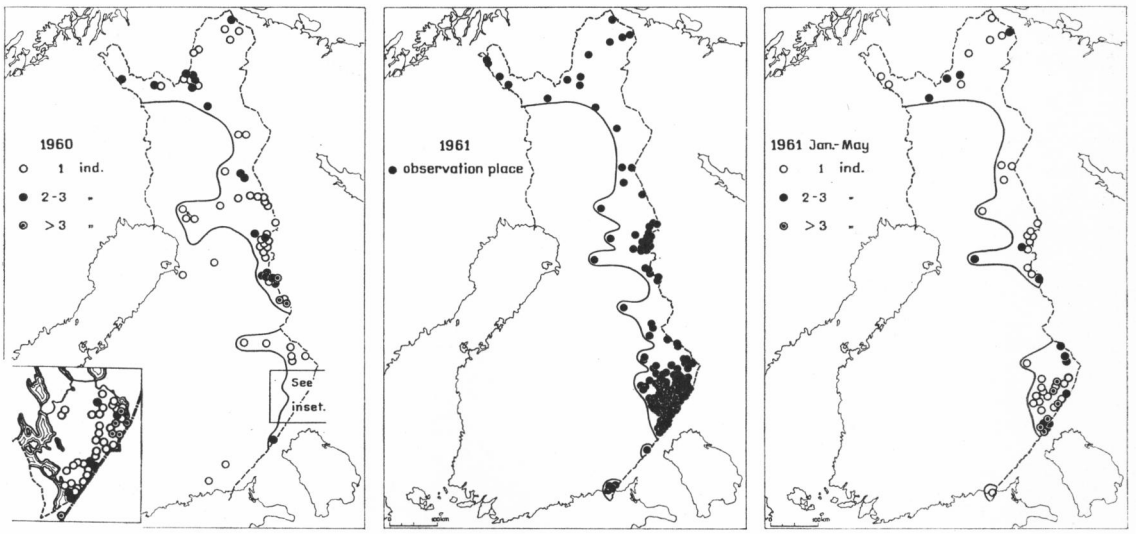
In 1958, the areas were much the same as the previous year (see Fig. 15).

In 1959, striking changes took place in the range of the species (Fig. 16). The northern area had widened westwards at the latitudes of Kittilä (KemL) and Pudasjärvi. The western limit of the range in North Karelia was at Vieremä (PS). Several migrating wolves were observed in the interior of the country.

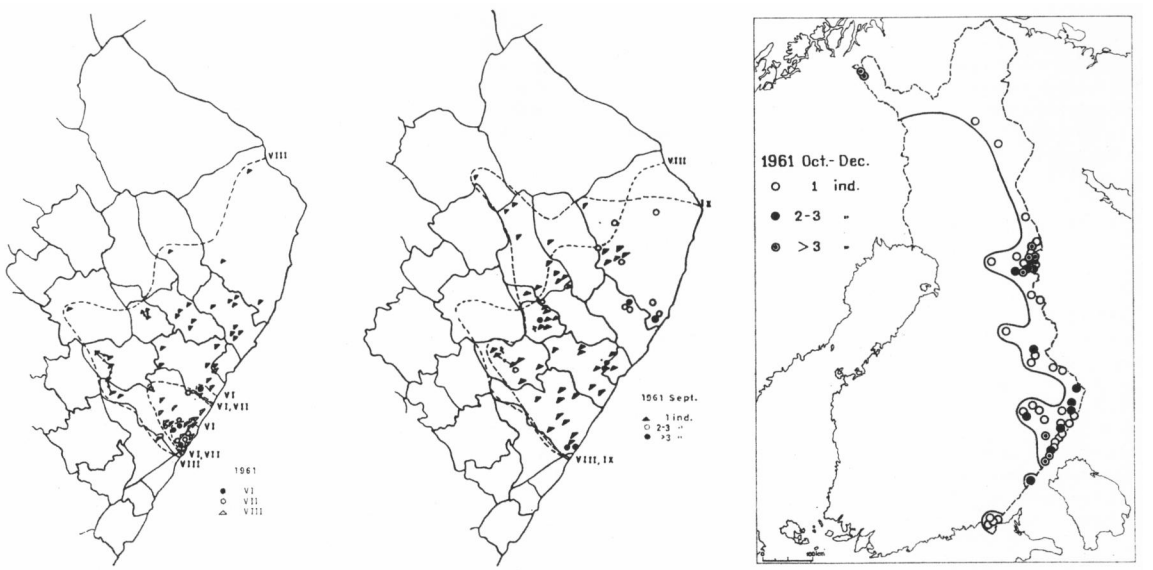
The most remarkable change was in the season at which the wolves appeared in North Karelia. All the previous, rather infrequent observations had been made in wintertime, but now a few wolves were seen near the frontier in summer. Some appeared in the vicinity of dwellings and the identification of the species was confirmed. However, it is possible that there had been wolves in North Karelia during previous summers, which escaped observation during the snowless conditions, for the number of inhabitants in this district is small.

In 1960, the situation in the area north of Suomussalmi (Kn) was almost the same as during the previous year (Fig. 17). In the southern parts of the commune of Suomussalmi wolves were observed for the first time after a long interval. The observations in question were made in the district of Vuokki. Moreover, wolves were observed at Kuhmo (Kn), south of Suomussalmi. At the border of the communes of Pudasjärvi (PP) and Utajärvi (PP) a migrating wolf was killed. At Kempele (PP), tracks of a wolf were seen. Wolves occurred throughout the area between the communes of Parikkala (LK) and Pielisjärvi (PK) in East Finland, and in the west as far as Rautavaara (PK). At the frontier between the communes of Kitee (PK) and Ilomantsi (PK) a number of wolves were seen during the summer. In the winter, packs of wolves were observed. The largest pack consisted of 11 individuals. At the same time some wolves crossed the frontier into Southeastern Finland. One of them went as far west as Savitaipale (ES).

In 1961, the northern area of the species, north of Suomussalmi, was much the same as during the previous year



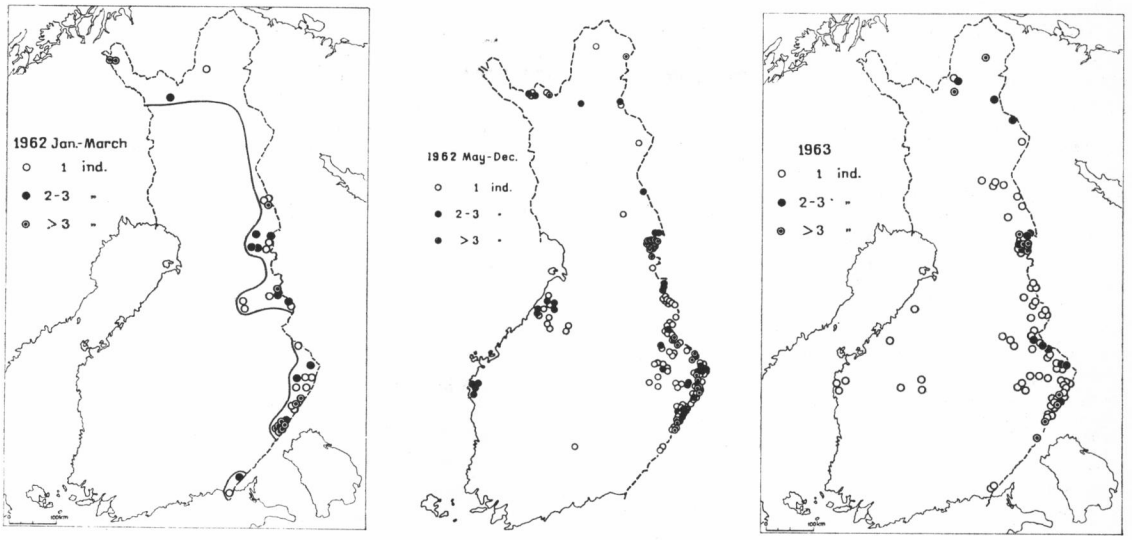
Figs. 17 – 19. Occurrences of the wolf in Finland in 1960 – 1961 (see also text).



Figs. 20 – 22. Occurrences of the wolf in Finland in June–December 1961 (see also text).

(Fig. 18). In North Karelia and at the border of the communes of Kuusamo and Suomussalmi wolves were observed in larger numbers than during any year after the Second World War. Wolves were observed throughout the area from Rautjärvi (ES) to Nurmes (PK). Further, a wolf was seen at Sotkamo (Kn). Thus it can be said that there was a continuous range extending from northernmost Finland down to North Karelia, although there is no confirmed observation from Kuhmo (Kn). The western limit of the range was at Liperi (PK) and Juuka (PK). At Virolahti a wolf crossed the frontier in summer. For a long time it moved in a rather restricted area. During the year the dispersal and occurrence of wolves could be followed from season to season (Figs. 19 – 22).

In January – April (Fig. 19), wolves were seen in the main in packs, throughout North Karelia from Uukuniemi (LK) to Pielisjärvi (PK). In the west the limit was at Juuka (PK). Most of the packs were observed at the frontier, which they crossed and recrossed. Lone wolves migrated farther inland. I have no certain observation made in May, but after



Figs. 23 – 25. Occurrences of the wolf in Finland in 1962 – 1963 (see also text).

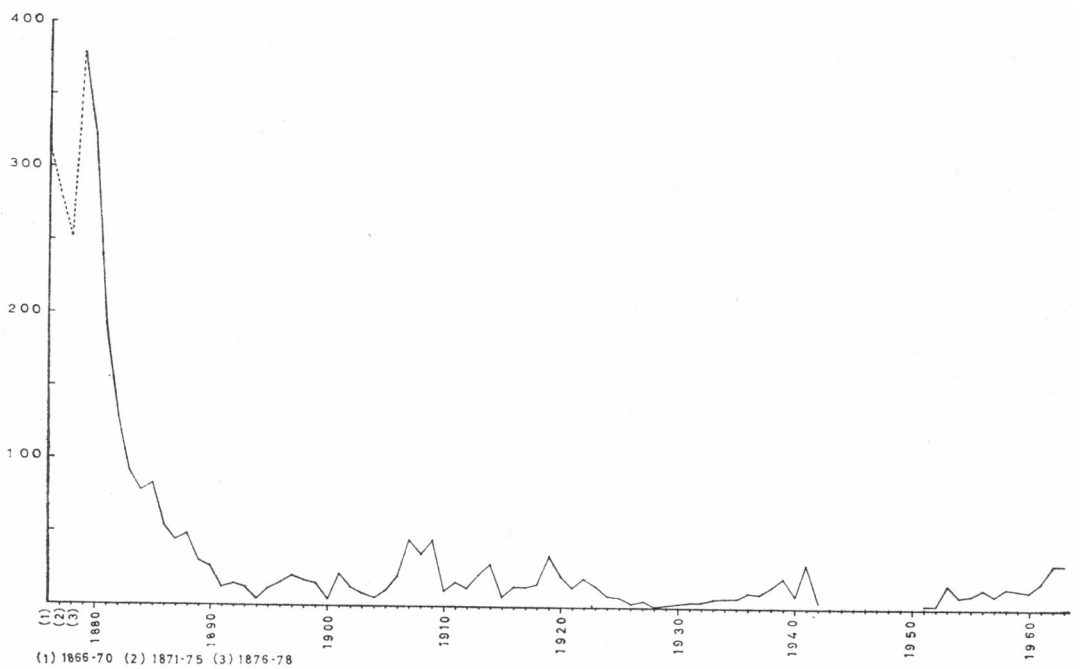


Fig. 26. The numbers of wolves killed during the years 1866 – 1963, according to the official statistics. For the years 1943 – 50 no data are available.

15. VI wolves were seen at Kitee (PK) and Tohmajärvi (PK). In July the range included Kitee and the eastern part of Rääkkylä (Fig. 20). In the beginning of August, a strong and rapid expansion took place to Liperi (PK), Eno (PK) and Ilomantsi (PK). At the end of August and in September, wolves were seen in packs (families; see Fig. 21), too. In September the range extended to Juuka (PK) in the northwest. During this month the number of wolves in North Karelia increased greatly. In the period October – December (Fig. 22) the number of wolves decreased, the packs returning

to the U.S.S.R. Most of the wolves recorded were observed on the frontier.

In 1962 (Figs. 23 – 24), wolves were observed in the same areas as during the previous year, but the numbers had decreased to some extent.

In 1963, wolves were observed during the winter months in the same areas as in the two previous winters (Fig. 25). In North Karelia the numbers had decreased still further. In the Kuusamo-Suomussalmi district, in contrast, wolves were observed in great numbers. The decrease in the number of wolves in North Karelia took place chiefly during the summer months. Only a few lone wolves were observed, and these were moving near the frontier. At Kitee (PK), where wolves had previously been very numerous, not a single one was observed. In autumn, packs of wolves were reported both in North Karelia and in the Kuusamo-Suomussalmi district. Some individuals were seen in West Finland, too.

Fig. 26 shows the official statistics of wolves killed in Finland during the years 1866 – 1963. The values for the years 1866 – 1870, 1871 – 1875 and 1876 – 1878 are presented as the means of these years (see also PALMÉN 1913). During the 1880's, especially at the beginning of that decade, a very great decrease took place in the numbers of wolves killed. In the first half of the present century the numbers of wolves killed yearly are seen to have fluctuated to some extent. Not one of the peaks reaches the level of the 1870's. In the beginning of the 1960's a typical increase in the numbers of wolves killed is visible.

3. Structure of the populations

A. General

This investigation was intended to include data on the age-class composition and sex ratio of the Finnish wolf populations. With the help of Mr. Einari Kuosmanen, 24 newly-shot wolves were studied in order to determine the age classes of the animals. Because MAKRIDIN (1959) has recently emphasized that age determination in wolves on the basis of the teeth is impossible, we tried to use the pelage, bones (skeleton) and general physiological condition of the animals as criteria, but we could not find any scientifically tenable method. For this reason no exact data on the age classes of the Finnish wolf populations can be presented.

But it is easy to determine the sex of newly-shot wolves. All the sex determinations used were made on newly killed individuals.

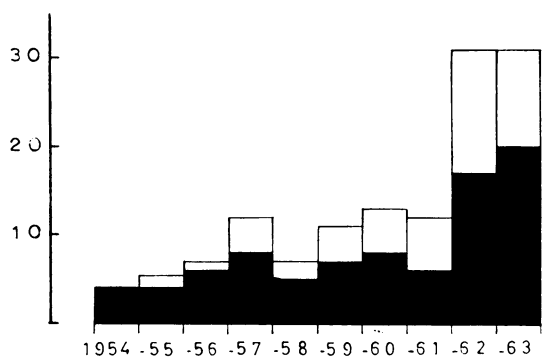


Fig. 27. Changes in the sex ratios of the Finn sh wolf populations during the years 1954 – 63. Black columns = males white columns = females.

B. Sex ratio

During the years 1948 – 63 the sex of 139 wolves was determined. The data for Lapland, where the wolf breeds regularly (see below), include records from the years 1948 – 1953. The data for other areas are for the years 1954 – 1963. The material studied is presented in the following tabulation. Lapland comprises the communes of Enontekiö (EnL), Utsjoki (InL) and Inari (InL), i.e. the breeding area of the wolf in Finland. The Savukoski-Kuhmo district includes all the communes along the eastern frontier of Finland between the two mentioned. The administrative district of North Karelia and the commune of Uukuniemi are referred to as North Karelia.

	♀♀	♂♂	n
I Lapland	36.0	64.0	9 + 16 = 25
II The Savukoski-Kuhmo district	27.7	72.3	13 + 34 = 47
III North Karelia	53.1	46.9	26 + 23 = 49
IV The other parts of Finland	11.1	88.9	2 + 16 = 18

There is no significant difference in the sex ratio of the wolf populations of areas *I* and *III* (*I*[1] $\chi^2 = 1.440$, *III* $\chi^2 = 0.081$). On the other hand, the difference in the sex ratio of the wolf populations of areas *II* and *IV* is statistically highly significant (*II* $\chi^2 = 8.510$, *IV* $\chi^2 = 9.388$).

There is no significant difference in the sex ra ios of the populations between areas *I* and *II* ($\chi^2 = 1.000$), or *I* and *III* ($\chi^2 = 1.309$). Between areas *II* and *IV* the difference is statistically almost significant ($\chi^2 = 3.048$, P = .05 – .10). The corresponding differences between areas *I* and *IV*, and *II* and *III* are statistically significant ($\chi^2 = 4.838$, $\chi^2 = 5.407$). The difference between areas III and IV is statistically highly significant ($\chi^2 = 11.326$).

[1] Yates's correction used.

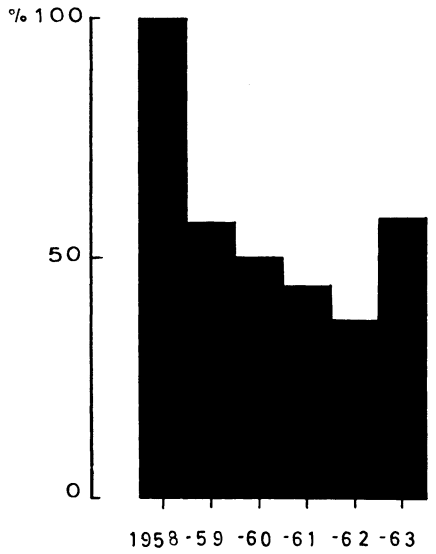


Fig. 28. Changes in the sex ratio of the wolf population of North Karelia presented as the percentage of males during the years 1958 – 1963.

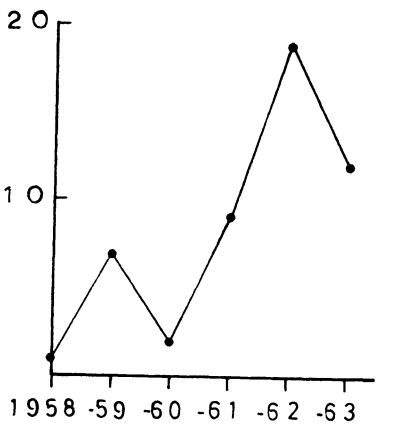


Fig. 29. The numbers of wolves killed in North Karelia during the years 1958 – 1963.

In Fig. 27 I present the figures for the sex ratios of the whole country according to the statistics of wolves killed. There are differences between these figures and the official statistics, owing to the following facts. I have not been able to check the sex of every wolf killed, or the reports have been contradictory. There is a methodical difference, too. The official statistics are arranged according to the dates when a bounty has been paid. On the contrary, I have used the actual dates of killing. For this reason some wolves are omitted, because the dates of killing are unknown.

The data available show that the proportion of females increased during the decade 1954 – 1963, especially at the end of the period. In Fig. 28 the figures for the proportion of males in North Karelia during the years 1958 – 1963 are presented. The same trend is also visible in these statistics, i.e. the proportion of males has decreased. At the same time the total number of wolves killed has clearly increased (see Figs. 26 and 29).

III. The colour variations in the wolf

1. General

Ognev (1931, pp. 163 – 193) discussed the races and colour forms of wolves in Eastern Europe and Asia. According to him (p. 165), the summer coat of the forest wolf (*Canis lupus lupus* Linnaeus 1758) is of a characteristic ochraceous tawny shade with a tinge of grey. Black-tipped hairs, especially on the back, darken the general colour of the wolf. The winter coat is greyer and more bushy. Ognev (*op. cit.*, p. 171) regarded the black stripe down the front of the fore-leg as a typical feature of the race. He (*op. cit.*, p. 183) described the colour of the tundra wolf (*Canis lupus albus* Kerr. 1792) as follows:

»The general colour of the fur is light, whitish. There is a little red colour, especially on the shoulders and on the middle of the back. The flanks, paws and stomach are white. The mean length of the hairs on the middle of the back is 110 – 130 mm, while the corresponding value for the winter fur of the forest wolf is at most 85 mm».

Ognev (*op. cit.*, pp. 177 – 178) especially emphasized that in certain cases the characteristic black stripe on the fore-leg of the forest wolf may be absent (see also Noack 1910). When I studied wolves killed in Finland, I also took note of this stripe (see also Suomalainen *et al.* 1922, p. 283).

2. Material and methods

The inquiries concerning the colour forms of the wolf were sent to the following museums (in parentheses the number of wolf skins studied):

Table 1. Data concerning the distribution of wolves of different colour phases in Finland. B = black stripe on the fore-leg, G = no black stripe on the fore-leg.

Biological province	Commune	Date	Sex	Age class	Type
EnL	Enontekiö	1963	?	ad.	B
PK	Ilomantsi	15. IV. 1959	♂	ad.	B
»	»	VI. 1959	♂	ad.	B
»	»	23. III. 1962	♂	ad.	G
»	»	19. VIII. 1962	♀	juv.	G
»	»	10. XII. 1962	♂	ad.	B
»	»	11. XII. 1962	♂	ad.	B
»	»	31. XII. 1962	♀	ad.	B
»	»	12. I. 1963	♀	ad.	G
»	»	21. II. 1963	♂	ad.	G
»	»	27. III. 1963	♀	ad.	B
InL	Inari	1905 – 08	?	ad.	B
»	»	1905 – 08	?	ad.	B
»	»	1905 – 08	?	ad.	B
»	»	III.–IV. 1963	♂	ad.	B
»	»	15. VI. 1963	♀	ad.	G
»	»	15. VI. 1963	♀	juv.	B
»	»	15. VI. 1963	♂	juv.	B
»	»	15. VI. 1963	♂	juv.	B
PK	Kitee	22. I. 1960	♀	ad.	B
»	»	20. IV. 1961	♀	ad.	B
»	»	6. X. 1961	♀	ad.	B
»	»	15. I. 1962	♀	ad.	B
»	»	21. VIII. 1962	♀	ad.	B
»	»	9. IX. 1962	♀	juv.	B
»	»	27. IX. 1962	♂	juv.	B
»	»	24. X. 1962	♀	ad.	B
»	»	20. XII. 1962	♀	ad.	B
»	»	13. II. 1963	♀	ad.	B
PK	Kontiolahti	1946	♂	juv.	G
EP	Korsnäs	10. II. 1963	♀	ad.	B
Kn	Kuhmo	20. X. 1963	♂	ad.	B
PS	Kuopio commune	28. I. 1902	♂	ad.	G
Ks	Kuusamo	?	♂	ad.	B
»	»	4. XI. 1963	♂	juv.	B
EH	Lammi	1879 – 82	?	ad.	B
»	»	1879 – 82	?	ad.	G
KP	Lestijärvi	12. I. 1963	♂	ad.	B
PK	Lieksa	23. XII. 1962	♂	juv.	B
V	Lieto	XI. 1921	♂	ad.	G
PK	Liperi	19. I. 1962	♀	ad.	B
PS	Maaninka	14. XII. 1937	?	ad.	B
KP	Nivala	III. 1934	♀	ad.	B
»	»	16. III. 1949	♂	ad.	G
EP	Närpiö	?	♀	ad.	G
»	»	2. VII. 1962	♂	ad.	G
EH	Padasjoki	27. II. 1950	♂	ad.	B
PK	Pielisjärvi	1954	♂	ad.	B
PK	Pielisjärvi	20. XII. 1961	♂	ad.	B
»	»	26. XI. 1962	♀	juv.	B
»	»	20. XII. 1962	♂	ad.	B
»	»	27. XII. 1962	♀	juv.	B
»	»	6. I. 1963	♂	ad.	B
»	»	3. IX. 1963	♂	ad.	B
St	Pori commune	1907	♂	ad.	B
U	Pornainen	26. IX. 1845	♀	ad.	B
KP	Pyhäjoki	29. XII. 1962	♂	ad.	G
PK	Pyhäselkä	25. IX. 1961	♀	ad.	B
EP	Pörtom	24. XI. 1955	♂	ad.	B
St	Surroundings of Rauma commune	1950's	♂	ad.	G
»	»	18. VII. 1956	♂	ad.	G
ES	Rautjärvi	17. I. 1958	♀	ad.	B
»	»	10. VII. 1962	♀	ad.	B
»	Ristiina	13. IV. 1957	♀	ad.	B
PK	Rääkkylä	5. IX. 1961	♂	ad.	B
PH	Saarijärvi	14. IV. 1957	♂	ad.	B
Ks	Salla	4. IV. 1963	♂	ad.	B
KemL	Savukoski	9. III. 1957	♂	ad.	B
»	»	18. II. 1957	♂	ad.	B
EK	Sippola	1950	?	ad.	G
»	»	25. XII. 1958	♀	ad.	B
Kn	Suomussalmi	25. X. 1962	♂	ad.	B
»	»	25. X. 1962	♂	ad.	B
»	»	27. X. 1962	♂	juv.	B
»	»	5. I. 1963	♂	ad.	B
»	»	20. I. 1963	♂	ad.	B
»	»	8. II. 1963	♂	ad.	G
»	»	12. II. 1963	♀	ad.	B
»	»	16. II. 1963	♀	ad.	G
PK	Tohmajärvi	9. IX. 1962	♂	ad.	B
»	»	24. XII. 1962	♂	juv.	B
V	Surroundings of Turku	1882	♂	ad.	B
PK	Tuupovaara	25. I. 1962	♀	ad.	B
»	»	30. I. 1963	♂	ad.	B
»	»	24. II. 1963	♀	ad.	B
»	»	3. III. 1963	♀	ad.	B
LK	Uukuniemi	1. III. 1962	♂	ad.	G
PK	Valtimo	7. II. 1959	♂	ad.	G
»	»	9. VI. 1963	♂	ad.	G
St	Vampula	17. IV. 1957	♂	ad.	B
EK	Virolahti	6. IV. 1956	♂	ad.	B
PK	Värtsilä	19. XII. 1958	♂	ad.	B
»	»	22. XI. 1961	♀	ad.	B

U.S.S.R.: Leningrad, the Zoological Institute of the Academy of Science (15).

Norway: Zoological Museum of the University of Oslo (4), State Game Research Institute, Vollebekk (2).

Sweden: Zoological Institute of the University of Uppsala (1), Naturhistoriska Riksmuseum, Stockholm (10), Zoological Institute of the University of Lund (0).

Finland: Zoological Museum of the University of Helsinki (8), Zoological Museum of the University of Turku (1), Zoological Museum of the University of Oulu (7), Museum of Natural History, Kuopio (2) and the Ostrobothnia australis collections, Vaasa (1).

The total Finnish material amounts to 93 skins. The museum collections contained 19 of these, and I found 74 in other places. The method used was as follows. On discovering that a wolf or wolves had been killed during the last ten years in a certain commune, I sent to the rural police chief of the commune, who had probably paid the bounty for shooting the wolf or wolves, an inquiry concerning the present whereabouts of the skin or skins, and asked him, if possible, to look for the black stripe on the fore-leg of the wolf or wolves. All the rural police chiefs to whom the inquiries were sent replied. After this I sent a similar inquiry to the holders of the skins. Over 80 per cent of the holders answered the inquiries. Mr. E. Kuosmanen studied 23 skins killed in North Karelia and supplied me with the data. The other 51 wolf skins studied were situated in the house of the killer of the wolf, at some school of the commune, in the communal meeting-house or in the house of the buyer of the skin. Most of these 51 skins were studied at least twice by different persons. The Finnish data are presented in Table 1 and those from Scandinavia in Table 2. Table 3 shows the data relating to the U.S.S.R. 75 of

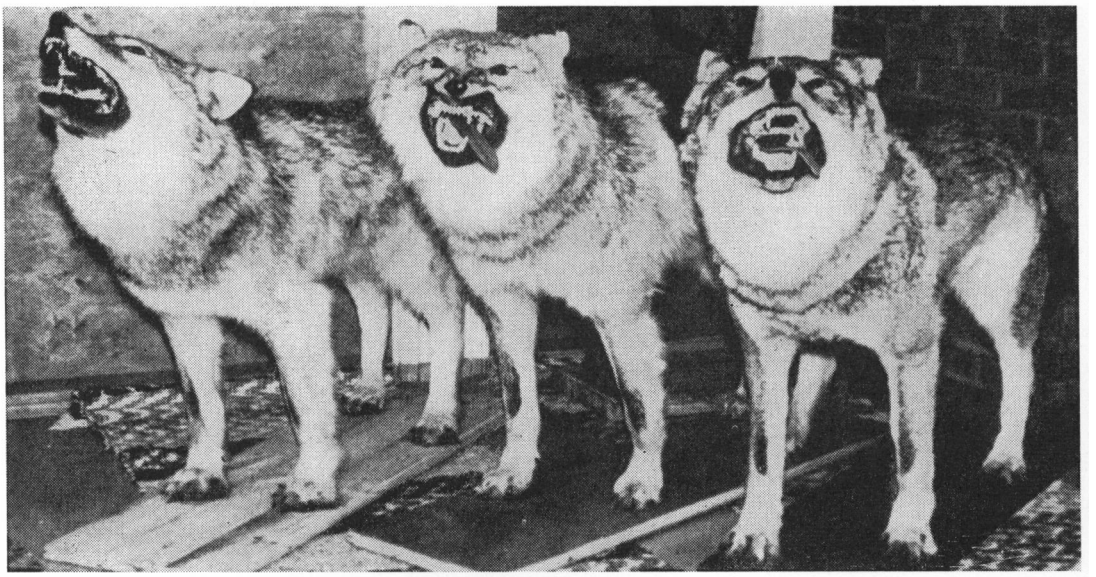


Fig. 30. Wolves with a black stripe running down the front of the fore-leg. – Photo E. Kuosmanen.

Table 2. Data concerning the distribution of wolves of different colour phases in Norway and Sweden. B = black stripe on the fore-leg, G = no black stripe.

Country	Locality	Date	Sex	Age class	Type
Norway	Akershus	II. 1842	?	ad.	B
»	Jevsjøen	25. III. 1939	♂	ad.	B
»	Kautokeino	10. VIII. 1906	?	juv.	B
»	»	1957/58	♂	ad.	B
»	»	1963	?	ad.	B
»	Nedenes	I. 1862	?	ad.	B
Sweden	Alsike	4. I. 1857	♂	ad.	B
»	Arjeplog	24. II. 1932	?	ad.	B
»	Jokkmokk	9. IX. 1912	?	ad.	B
»	Kiruna	8. II. 1909	♀	ad.	B
»	»	15. IV. 1959	♀	ad.	B
»	Ramsjö	12. II. 1926	♂	ad.	B
»	Torneträsk	XII. 1909	♂	ad.	B
»	The district of Stockholm	3. I. 1831	♂	ad.	B
»	Vilhelmina	1. XII. 1935	?	ad.	B
»	»	15. I. 1937	♂	ad.	B
»	Västerbotten	19. III. 1935	?	ad.	B

Table 3. Data concerning the distribution of wolves of different colour phases in the U.S.S.R. B = black stripe on the fore-leg, G = no black stripe.

Locality	Date	Sex	Age class	Type
Leningrad oblast:				
Gatchina	?	?	ad.	B
Region of Novaya Ladoga	13. X. 1919	♀	ad.	B
» » » »	13. X. 1919	♀	ad.	B
» » » »	13. X. 1919	♀	ad.	B
» » » »	13. X. 1919	♂	ad.	B
Vologda oblast:				
Cherepovets	18. II. 1919	♂	ad.	B
»	18. II. 1919	?	ad.	B
Novgorod oblast:				
Region of Staraya Russa	?	♀	ad.	B
Taimyr Peninsula:				
Region of Hatan	IX. 1934	♂	juv.	B
» » »	28. II. 1935	♂	ad.	B
» » »	IX. 1934	♂	juv.	B
» » »	5. I. 1933	♂	ad.	G
» » »	1. II. 1935	♂	ad.	B
» » »	25. XII. 1933	?	ad.	G
» » »	24. XII. 1933	♂	ad.	G

the Finnish skins (80.6 %) were those of wolves killed during the years 1954 – 1963. So the material available provides a very good picture of the recent situation. By contrast, the Scandinavian data and the data of the U.S.S.R. are from the first three decades of this century. This must be remembered when discussing the data. It must be taken into account that the data from the U.S.S.R. are very meagre compared with the wolf population of the country, whereas in Fennoscandia the situation is just the reverse.

3. Colour of fore-legs

A. Colour phases and their distribution in Fennoscandia

The ground colour of the fore-legs of the wolf is mostly grey, sometimes with a brownish or reddish-brown tinge. It is likely that there are seasonal changes in this respect (see also Ognev 1931, Knezevic & Knezevic 1956, p. 192; cf. Lönnberg 1934). A black stripe down the front of the fore-leg is characteristic. The mean size of this stripe is 2 × 10 cm (see Fig. 30). The dimensions of the stripe vary somewhat, but the shrinking of the skins, and the state and direction of the hairs influence the records so much that I have not been able to classify the stripes according to size. The stripe may be absent (see Fig. 31). The wolves which have a black stripe on their fore-leg are indicated with

Fig. 31. A wolf without a black stripe down the front of the fore-leg.

B. The wolves without a black stripe are indicated with G. In the following tabulation I present wolves of groups B and G, which were killed during different months.

	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	Total
B:	10	6	5	7	0	4	1	1	7	6	4	12	63
G:	2	4	3	0	0	2	2	1	0	0	1	1	16

The data presented show that the characteristic in question is present in the wolves throughout the year. So the stripe is not confined to either the summer or the winter coat.

When the wolf cubs have their cub fur, these characteristics are naturally not visible. When the cub fur changes to the first winter coat (at the age of 3 – 5 months), these distinctive features become clearly visible. I have followed the growth of the black stripes in penned cubs and observed that they reached full size at the age of about four months. 13 of the wolves killed were less than eight months old. Eleven of them had a stripe and two had not.

The sex distribution of the two colour phases is visible in the following tabulation.

	B	G	n
Males	57.6	78.9	38 + 15 = 53
Females	42.4	21.1	28 + 4 = 32
Total	77.6	22.4	66 + 19 = 85

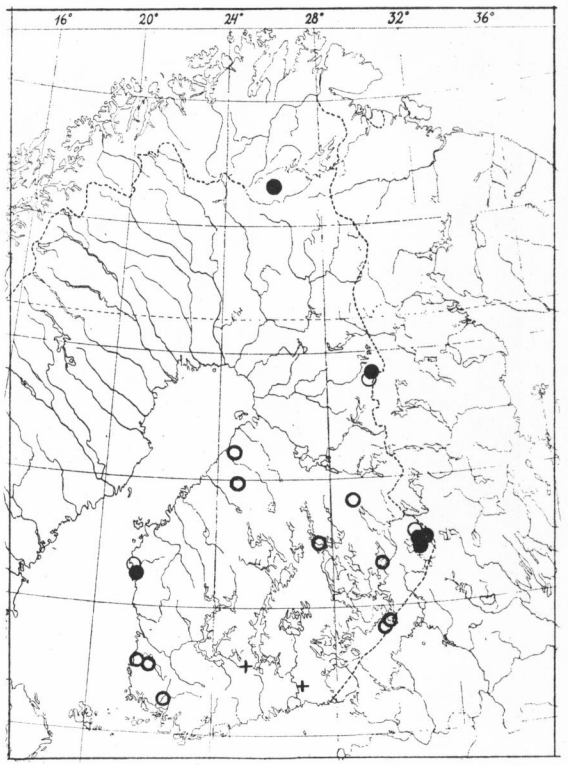


Fig. 32. The distribution of the wolves without a black stripe on the front of the fore-leg in Northern Europe. Explanations as in Fig. 33.

In the following tabulation the distribution of the Fennoscandian data on the two colour phases are presented.

	Finland	Scandinavia	n
B	77.4	100.0	72 + 17 = 89
G	22.6	0.0	21 + 0 = 21

In Figs. 32 – 33 the distribution of the different colour phases in Fennoscandia are presented.

B. Differences between the populations of Fennoscandia

I have divided Fennoscandia into four areas. The first area (*I*) covers Norway, Sweden and the communes of Enontekiö and Inari in Finnish Lapland. The second area (*II*; cf. also Voipio 1956 and 1962 b) consists of Savukoski, Salla, Kuusamo and Suomussalmi, on the eastern frontier of Finland. The third area (*III*) covers the administrative district of North Karelia and the communes of Kuhmo, Uukuniemi and Rautjärvi. The other parts of Finland form the fourth area (*IV*). The distribution of the two

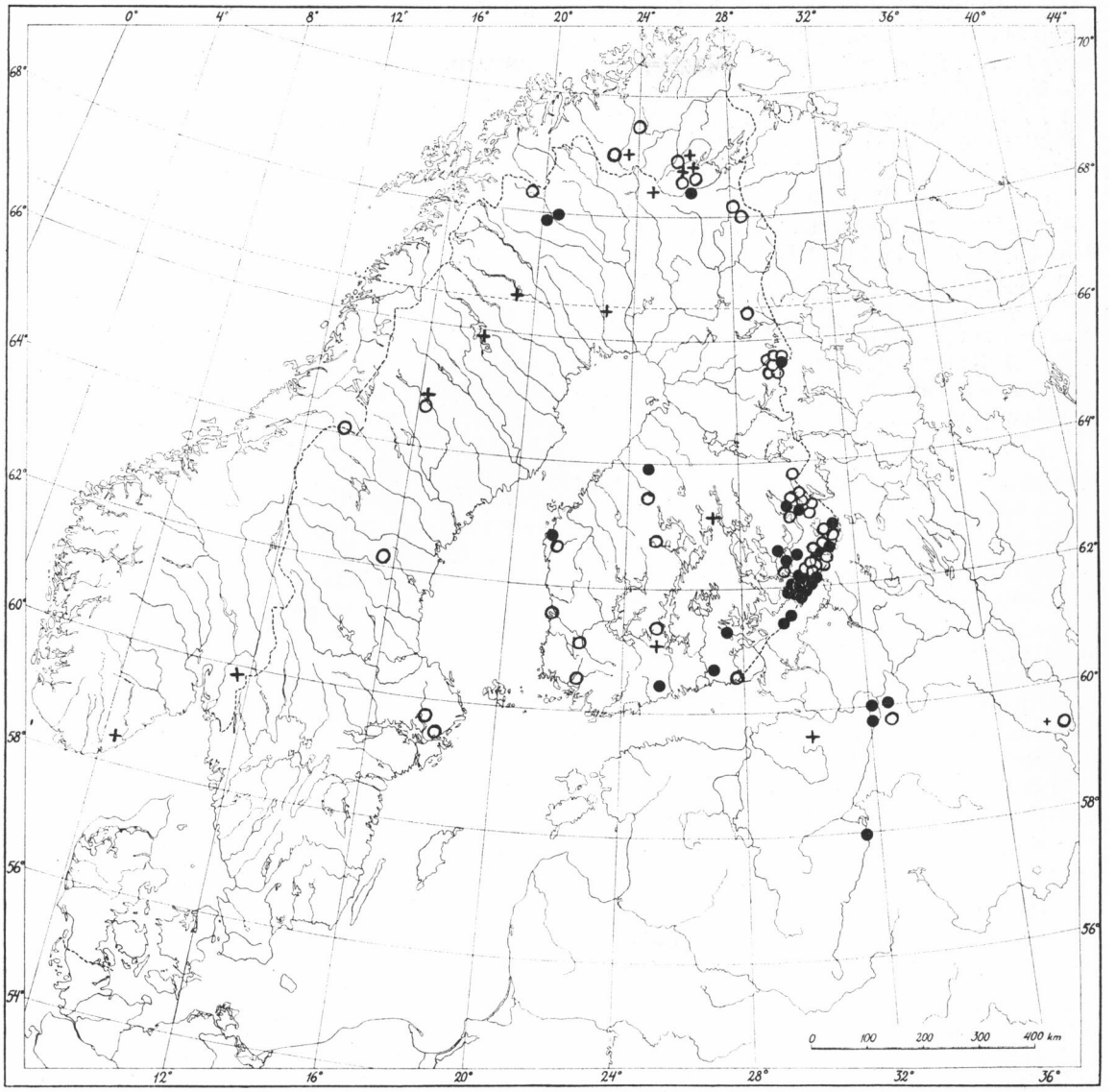


Fig. 33. The distribution of the wolves with the black stripe on the front of the fore-leg in Northern Europe (see also Tables 1 – 3). Explanations: open circle = a male, black circle = a female, + sex unknown.

colour forms in these areas can be seen from the following tabulation.

	B	G	n
I	96.2 %	3.8 %	25 + 1 = 26
II	84.6 »	15.4 »	11 + 2 = 13
III	82.6 »	17.4 »	38 + 8 = 46
IV	60.0 »	40.0 »	15 + 10 = 25
Total	80.9 »	19.1 »	89 + 21 = 110

In areas *I* and *III* the difference between the numbers of the two colour phases is statistically highly significant (I $\chi^2 = 20.346$ [1], III $\chi^2 = 18.282$), and in area *II* the corresponding difference is statistically significant ($\chi^2 = 4.922$), but in area *IV* the difference is not statistically significant ($\chi^2 = 0.640$).

There are no statistically significant differences in the distributions of the two colour phases

[1] Yates's correction used.

between the populations of the following areas: *I* and *II* ($\chi^2 = 0.406$), *I* and *III* ($\chi^2 = 1.685$), *II* and *III* ($\chi^2 = 0.062$), *II* and *IV* ($\chi^2 = 1.394$). The corresponding difference between areas *I* and *IV* is statistically highly significant ($\chi^2 = 7.827$). The difference between areas *III* and *IV* is statistically almost significant ($\chi^2 = 3.262$, P = .05 – .10). The difference between the western and northern area *I* and area *IV* should be noted, and likewise the almost significant difference between North Karelia (*III*) and area *IV*. If areas *II*, *III* and *IV* are united, a large area is formed which covers Finland except for its northernmost parts. The difference between area *I* and this large area is statistically significant ($\chi^2 = 3.912$).

C. Distribution of the colour phases in Northern U.S.S.R.

The scanty data available originate from the northern parts of Europe and Asia. The European data were obtained from the districts of Leningrad, Novgorod and Vologda. Since these lie to the southeast of Eastern Fennoscandia, the data available have been dealt with separately from the Fennoscandian data. The Asian data originate from the tundra zone of the peninsula of Taimyr.

Area *I* covers the European area and area *II* correspondingly the Asian area (see Table 3). The occurrence of the two colour phases in these areas is shown in the following tabulation.

	B	G	n
I	100.0	0.0	8 + 0 = 8
II	57.1	42.9	4 + 3 = 7

It can be seen that in area I all the wolves studied had the black stripe on the fore-leg. In area II both phases were found.

4. Discussion

Even when the wolf occurs in some area in great abundance, its population density is rather low compared with other mammals (see Olson 1938 a, Stebler 1944, Cowan 1947, deVos 1950, Thompson 1952, Allen & Mech 1963; cf. e.g. the red fox, *Vulpes vulpes*, Lampio 1951 a). In order to understand the distribution of the two colour phases in Fennoscandia we must look at the occurrence of the wolf in that area.

During recent decades the wolf has bred in Fennoscandia only in the northern and to some extent in the middle parts of the Scandinavian mountains (see also Haglund 1965, Curry-Lindahl 1965). In Finland this breeding area comprises the communes of Enontekiö and Inari. Earlier, the species bred in all parts of Fennoscandia, but in the eighteenth and nineteenth centuries the populations decreased very rapidly and strongly (see also Johnsen 1929, Lönnberg 1934).

In Finland the wolf population underwent a clear decrease in the 1880's (see Fig. 26). Subsequently only migrating wolves have occurred in West and South Finland in winter. On the eastern frontier, however, more observations have been made. During the years 1959 – 63, a clear expansion was observed in this area. Against this general background Fennoscandia was divided into four areas. The breeding population thus occurs in the Scandinavian mountains and the other individuals have come from the U.S.S.R., where the wolf occurs in great abundance (see also Marwin 1959).

The statistical analysis of the distribution of the two colour phases in the western (*I*) and eastern Finnish (*II* + *III* + *IV*) areas shows that wolves without a black stripe are significantly more common in the east than in the west. According to the data available, only one female wolf without a black stripe originates from the western area. It is worth mentioning that this wolf was killed in the easternmost commune (Inari) of the area.

There was no difference in the abundance of the two phases in area *IV*. These wolves were either killed when the wolf bred in all parts of Finland or else they migrated during the last decades, mainly via the communes of Kuusamo and Suomussalmi, along the Suomenselkä into West and Southwest Finland. A few individuals from over the frontier migrated via Southeast Finland. In the area which extends along the eastern frontier from Savukoski to Rautjärvi an expansion was observed. These wolves must have come from the U.S.S.R. Most of these wolves had a black stripe on the fore-leg. The difference between the ratios of the two colour phases is significant.

In Figs. 32 – 33 the occurrence of the two colour phases is visible. It can be seen that the wolves without stripes are more abundant in the east than in the west.

As already mentioned (p. 223), *Canis lupus lupus* L. has a typical black stripe down the front of the fore-leg and *Canis lupus albus* Kerr.

has no such stripe. The distribution of these two races (forest wolf and tundra wolf) can be seen from their names. The former inhabits the taiga and the latter the tundra. According to OGNEV (1931, pp. 177 – 178), wolves which have no stripe on the fore-leg occur in the Altai mountains and on the Irkutsk plateau in Asia (see also NOACK 1910, pp. 461 – 467).

According to the available Fennoscandian data, it seems that in the eastern parts of this area there occurs, although rather rarely, a wolf type which resembles that of Altai and Irkutsk.

The wolves found in the other parts of Finland were lone, migrating individuals. The female killed at Inari was the mother of the cubs which were reared in pens (see below). All the cubs had black stripes down the fronts of their fore-legs. All the other wolves observed in that area had the black stripe in question. Thus it is probable that the cubs were the progeny of a male with the black stripe (?) and a female without the black stripe (certain). In this case it is possible that the presence of a black stripe is governed by a dominant gene. A male was killed in North Karelia on 23. III. 1962 (see also pp. 245 – 246). This male had been observed to copulate with a female. During the summer the female ranged the same forest district with her cubs. On 19. VIII. 1962, one of these cubs, a female, was killed. On 12. I. 1963 and 21. III. 1963, in the same forest district a male and a female were killed which may have belonged to the same family mentioned above. None of the wolves in question had a stripe. Thus the gene in question must have occurred in homozygous form. On 8. and 16. II. 1963 at Suomussalmi a male and a female which had no stripes were killed. The killers said that the wolves were members of the same pack.

According to the data available, in Fennoscandia the two colour phases occur side by side within the populations, i.e. we are dealing with a case of polymorphism (cf. e.g. VOIPIO 1957, 1962 a and b). Because wolves without the fore-leg stripe are more abundant in the east, it seems that this character originates from the tundra wolf. It is a fact that this race is characterized by grey limbs (entirely without stripes). This is supported by the scanty data from the U.S.S.R., too, according to which wolves without the stripe occur in the northernmost parts of Eurasia.

OGNEV (1931, pp. 165, 183) mentioned that in the winter coat the length of the hairs of the middle of the back is at most 85 mm in the forest wolf and generally 110 – 130 mm in the tundra wolf. The mean length of these hairs in forest wolves with fore-leg stripes killed in Finland was 91.3 ± 5.6 mm, whilst in the wolves without stripes the corresponding value was 106.1 ± 7.7 mm. The difference between the values mentioned is not statistically significant ($t = 1.56$). However, it is possible that the latter have longer hairs than the former. If this is true, it supports the hypothesis that the tundra and forest wolves have crossed. There are still too few skulls available for exact studies on this problem.

IV. The growth of the wolf

1. Material and methods

Exact data on the growth rate of the wolf were obtained by rearing three wild wolves (2 ♂♂, 1 ♀) on a farm. Mr. Yrjö Korhonen took the cubs from their den near the river Lemmenjoki at Inari (InL) on 15. VI. 1963. Their eyes opened on 22. VI. We can thus conclude that they were born on 10. VI (cf. e.g. OGNEV 1931, 1959).

When the cubs were found, their weight was about 0.5 kg. At first they were fed with milk. In July, they were brought to Viiala (EH) by Director Antti Mustakallio, who took care of them until they were brought to the Viikki Experimental Farm on 11. X. At Viiala the cubs were weighed every Tuesday during the period 6. VIII – 15. X. At Viikki weighings were performed regularly after the date mentioned above. The cubs were weighed in the morning before being fed. They were fed regularly every day. From milk they were promoted to fresh fish. After 13. VIII the cubs were also given fresh meat in addition to the food items mentioned above. After September the wolves were fed mainly with offal (lungs, bones with meat, fat, etc.), but during the experiments they were fed with rabbits and guinea-pigs and with mutton, too. At Viikki, the food given to the wolves was weighed (see Table 4). In fact, at Viikki the growth conditions as regards amount of food and regularity of feeding were ideal. By contrast, opportunities for exercise were restricted and may have influenced the growth rate of the wolves. For this reason the records obtained cannot be regarded as absolutely natural. I think that the records describe almost the maximum growth rate of the species.

During the wolf expansion in North Karelia some wolves were killed which were clearly cubs

Table 4. Data concerning the food (kg) of the penned wolves (2 ♂♂ and 1 ♀) during the period 11. X. 1963 – 25. II. 1964. The quantity of food not consumed has not been deducted from the values given. The remains amounted to 15 – 20 % of the values given, but consisted of the parts with little nutritive value.

Period	Heads of cattle	Lungs of cattle	Offal	Rabbits	Guinea-pigs	Bones of cattle	Other food items
1963:							
11. – 15. X	5.5	12.7	–	–	–	–	
16. – 22. X	4.9	22.9	5.8	–	–	–	bread 1.1 kg
23. – 29. X	1.4	26.3	0.7	3.9	–	–	
30. X – 5. XI	–	–	–	24.8	–	–	meat, etc. 3.0 kg, blood 1 ltr.
6. – 12. XI	–	3.4	–	23.8	–	–	
13. – 19. XI	4.4	13.6	–	9.4	–	–	
20. – 26. XI	10.3	24.3	–	–	–	–	
27. XI – 3. XII	14.6	21.1	–	–	–	–	
4. – 10. XII	10.0	24.4	–	6.0	1.8	–	
11. – 17. XII	3.2	22.1	–	16.8	–	–	
18. – 23. XII	3.5	19.8	–	5.0	1.6	–	
24. – 31. XII	5.0	21.9	–	10.5	1.3	–	
1964:							
1. – 7. I	5.2	23.3	–	–	–	–	
8. – 14. I	7.3	15.0	–	4.0	–	–	meat 0.5 kg
15. – 21. I	4.2	8.0	–	–	14.0	–	
22. – 28. I	5.5	16.8	–	1.5	5.0	–	
29. I – 4. II	8.0	15.7	–	4.0	–	–	
5. – 12. II	6.0	12.7	–	–	5.0	28.5	
13. – 19. II	–	–	20.0	–	–	–	
20. – 25. II	0.6	–	17.0	–	1.5	–	

of the previous spring (the age criteria, see e.g. OGNEV 1931). It is impossible to determine the exact age of these wolves, but 1. V can be regarded as the mean birth-date (see p. 235). For the sake of comparison, these values are shown alongside the experimental records (see Figs. 34 – 35).

In order to determine the weight of full-grown wolves (over eight months old) weight records of the wolves killed during the last 15 years were gathered. Most of the records were obtained from the killers themselves. Almost all the wolves killed are weighed very exactly, because for the large predators, including the wolf, sportsmen use the weight as the measure of the value of the animal killed. Because of the variation in measuring instruments and observers, the data are recorded here to the nearest kilogram.

Table 5. Comparison of the weights of wolves as reported by the weighers themselves and by the newspapers.

Females		Males	
Actual weight kg	Report in newspaper kg	Actual weight kg	Report in newspaper kg
9	9	44	44
30	30	44	44
39	39	31	30
30	27	30	30
30	30	40	40
31	27	40	36
34	34	42	42
20	20	25	25
20	30	40	40
24	24	50	50
31	31	48	48
30	30	28	28
41	42	39	39
31	31	38	38
31	31	31	31
35	35	45	45
28	30	40	40
30	30		
32	32		

Whilst collecting the data I had an opportunity to test the reliability of reports in the newspapers concerning the weights of wolves. The weights of 19 females and 17 males were gathered from the newspapers and from the killers themselves. The comparison of these two series is shown in Table 5. The test was performed by t-analysis. It showed that at least in this case we can trust the newspapers ($t = 0.130$).

33 full-grown female and 52 full-grown male wolves were weighed. The distribution of these wolves in the different communes is shown in Table 6.

Table 6. Data concerning weights of wolves killed in the different communes.

Province	Commune	Weights, kg Males	Females
EnL	Enontekiö	40, 50	
PK	Ilomantsi	38, 38, 40, 40, 44, 45, 45	30, 39
InL	Inari		30, 45
PP	Kemijärvi	40	
PK	Kitee		28, 30, 30, 31, 34
»	Kontiolahti	28	
Kn	Kuhmo	44, 50	30, 36
Ks	Kuusamo	35, 35, 40	29, 29
KP	Lestijärvi	43	
PK	Liperi		24
EP	Närpiö	42	31
EH	Padasjoki	39	
PK	Pielisjärvi	26, 40, 42, 42	30, 30, 32
Ks	Posio	35	33
KP	Pyhäjoki	42	
PK	Pyhäselkä		41
PH	Rautalampi	55	
ES	Rautjärvi		25, 35
»	Ristiina		40
PK	Rääkkylä	50	
PH	Saarijärvi	43	
Ks	Salla	30, 40, 45, 45, 50	
KemL	Savukoski	40	
Kn	Suomussalmi	35, 35, 40, 40, 40, 40, 41, 45	31, 35
PK	Tohmajärvi	48	
»	Tuupovaara	39	28, 29, 31, 32, 35
InL	Utsjoki	45	
LK	Uukuniemi	32, 38	
PK	Valtimo	31, 45	
St	Vampula	35	
EK	Virolahti	39	
PK	Värtsilä	40	30, 32
EK	Ylämaa		30

2. Results and discussion

In Figs. 34 – 36, the weight increase of penned wolves and weights of wild wolves are presented to the age of 51 weeks. Three periods can be seen in the weight increase of penned cubs: a period of maximal growth (0 – 14 weeks), a period of rapid growth (14 – 27 weeks) and a period of

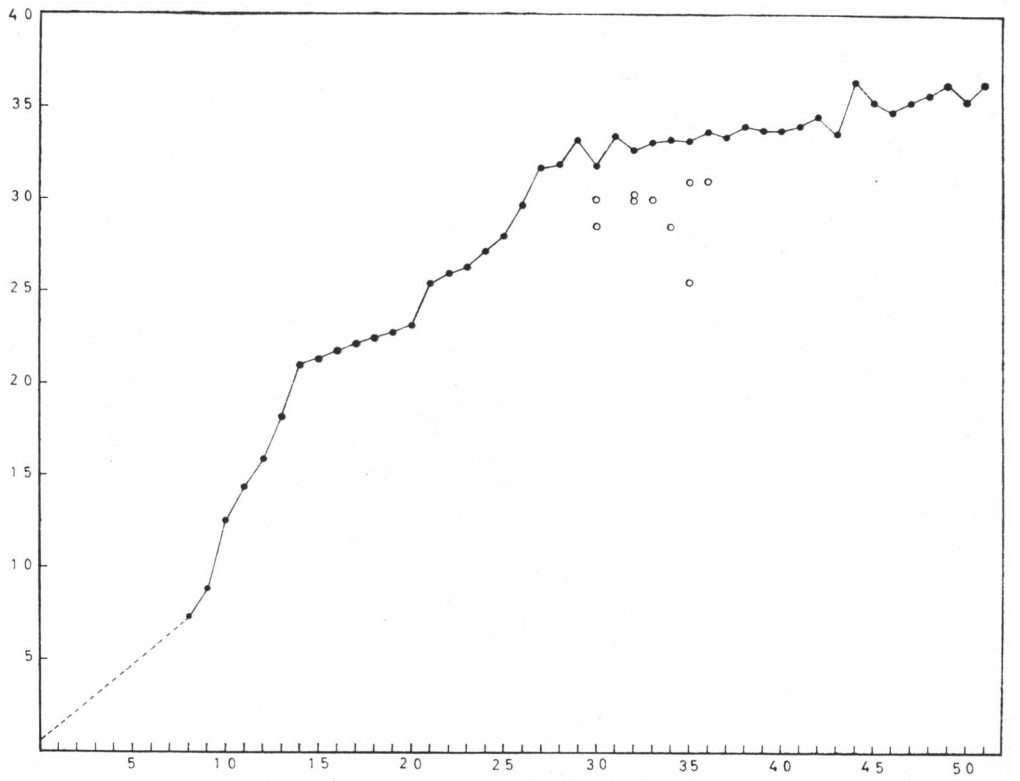


Fig. 34. The mean weight increase of the two male wolf cubs. Records of wolves killed in natural conditions are marked with open circles. Ordinate: weight in kilograms. Abscissa: age in weeks.

slow growth (27 – 51 weeks). The weight of the female increased during the first period by an average of 1.2 kg per week, during the second period by 0.8 kg and during the slow period by 0.03 kg. The corresponding values for the males were as follows: 1.5 kg, 0.8 kg and 0.2 kg. The growth rate of the males was clearly greater during the first and third periods, whereas during the second period the two sexes grew at the same rate.

Similarly in the growth of human children, for instance, three periods can be distinguished. The first period ends at the age of ten years. During this period the differences between boys and girls are very small (see e.g. TAKKUNEN 1962). The weight increase during the following three years is distinctly higher in girls than in boys. After this the situation is quite the reverse (TAKKUNEN *op. cit.*).

During the 27 (– 29) first weeks of the cubs' life, a weak rhythm of 6 – 7 weeks is discernible. In the beginning of each of these periods the weight increase is slower than at the end of the period, which is characterized by a rapid weight increase. The rapid weight increase which took place in the period 13. – 20. VIII (the tenth week) was perhaps partly due to the fact that the wolves were fed with meat for the first time. The reduction in the weight increase during the second growth period was attributable to the fact that then the cubs were teething (14th – 23rd week). The third growth period was characterized by great changes in the weights from week to week. KRAMER (1961) has previously drawn attention to the same phenomenon.

The weights of the male wolves killed in natural conditions are lower than those of the penned individuals, but this is not always the case with the females.

The nature of the food consumed seemed to have very little influence on the weight increase of the cubs (cf. e.g. the small mammals, KALELA 1957, PEARSON 1962). During the 20th week the cubs were fed only with offal. During this week

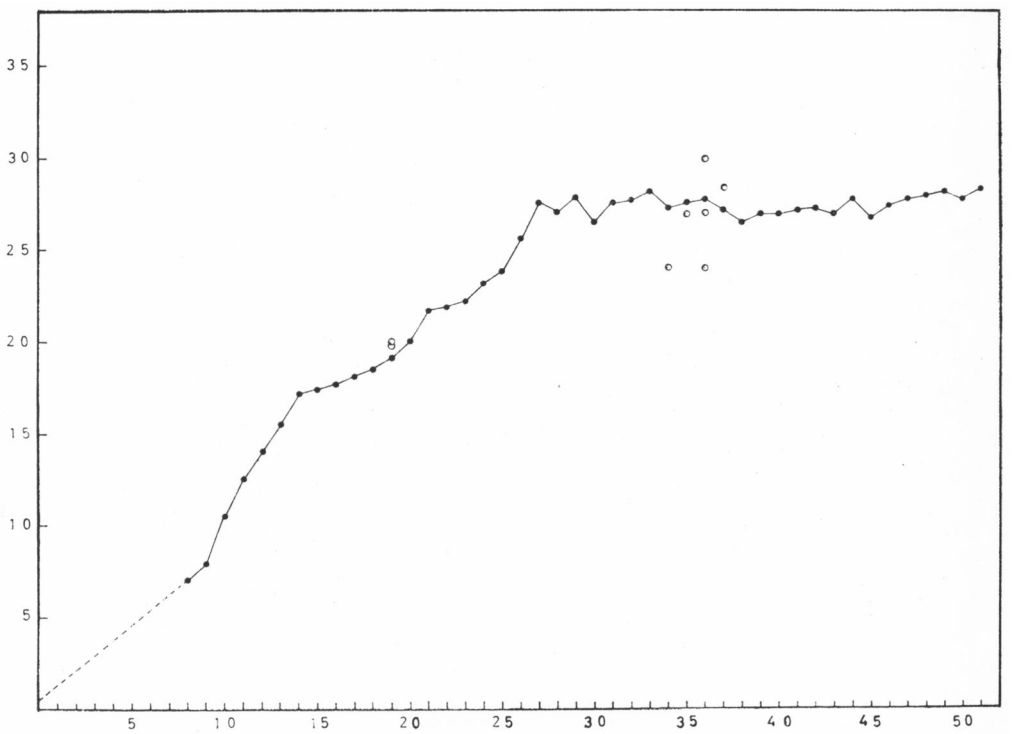


Fig. 35. The weight increase of the female wolf cub. Records of wolves killed in natural conditions are marked with open circles. Ordinate: weight in kilograms. Abscissa: age in weeks.

their weights increased as follows: the males 0.3 – 0.4 kg and the female 0.9 kg. During the following week the cubs were fed on the following diet: six rabbits (total weight 25.7 kg), mutton, liver, etc. (total weight 3 kg) and one litre of blood. The wolves consumed the food offered almost entirely. During this week their weights increased as follows: the males 2.1 – 2.4 kg and the female 1.7 kg. During the following week the amount and quality of the food offered remained unchanged. However, the weights of the cubs increased only as follows: the males 0.2 – 0.4 kg and the female 0.2 kg. Other experiments carried out gave similar results. Hence it can be concluded that the effects of the quality of the food consumed by the cubs are only temporary and their weight increase is controlled by an internal rhythm (cf. e.g. the small mammals, MORRISON *et al.* 1954, PEARSON 1962, PENGELLEY & FISHER 1963, and the hedgehog, *Erinaceus europaeus*, KRISTOFFERSSON & SUOMALAINEN 1964).

The weights of wolves after the age of eight months are shown in Table 6. The height of the penned wolves reached its maximum at this age. For this reason it has been taken as the limiting value. However, according to the experimental records of the present study, the weights increase even after this age. According to the data available, the mean weight of the males is 41 ± 4.4 kg and the corresponding value for the females is 32 ± 4.4 kg. The difference between the weights of the two sexes is statistically significant ($t = 7.82$). In the preliminary studies I had recorded exactly the same values (PULLIAINEN 1962 b, p. 111).

According to ZVORIKIN (1939), weights of male forest wolves vary between 42 and 55 kg. According to him, the male may reach a weight of 80 kg. According to MERTS (1953), the weight of the male wolf (without the stomach contents) is between 34 and 48.5 kg and that of the female between 31 and 42.1 kg. MAKRIDIN (1959) killed 23 males and 23 females. Their mean weights were 40 and 33.6 kg (the maximum values correspondingly 49 and 41 kg). HESSE *et al.* (1951, p. 464) mention that wolves increase in size toward the northeast and decrease in size toward the southwest according to Bergmann's Rule.

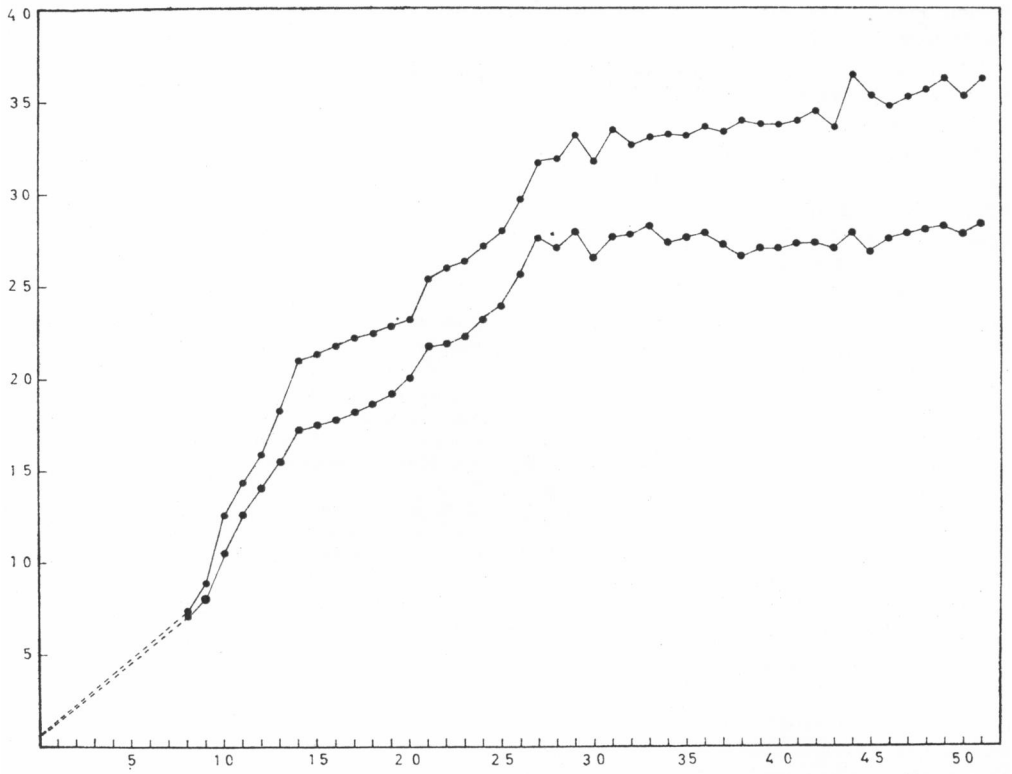


Fig. 36. The comparison of the weight increases of female (lower curve) and male (upper curve) wolf cubs. Ordinate: weight in kilograms. Abscissa: age in weeks.

If a comparison is made between my data on *Canis lupus lupus* and that of MAKRIDIN (*op. cit.*) on *Canis lupus albus*, no significant differences can be found between the two wolf races. The males of MAKRIDIN's data are 1 kg lighter than those of the present study and in the females the situation is the reverse (the difference being 1.6 kg). KNEZEVIC & KNEZEVIC (1956, p. 192) mentioned that in Yugoslavia wolves generally weigh 30 – 35 kg, although they may reach as much as 63 kg. According to these data, it seems that the weight of the wolf decreases toward the south.

V. The biology of the wolf

1. General

MAKRIDIN (1959) has recently reviewed the literature published in the U.S.S.R. on the biology of the wolf. In North America the biology of the species has recently been studied by a number of investigators (see e.g. STENLUND 1955, CRISLER 1956, BURKHOLDER 1959, MECH 1962, 1963, ALLEN & MECH 1963). The general features of the biology of the wolf are as follows, according to the literature available.

The wolf is monogamous (YOUNG & GOLDMAN 1944, OGNEV 1959, p. 239). Pairing begins in January (OGNEV 1931, KNEZEVIC & KNEZEVIC 1956), but rut fights are most common in February – March, according to the locality in question (e.g. SETON 1929, ROMANOV 1941, MUNSTERHJELM 1946, SDOBNIKOV 1948, OGNEV 1959, MAKRIDIN 1959). The female gives birth in her den to an average of five to six young after a gestation period of 60 – 63 days (OGNEV 1931, 1959). Depending on the locality, the wolf digs

a new den every year or breeds from year to year in the same den (OGNEV *op. cit.*, HORNBY 1934, ROMANOV 1941, MUNSTERHJELM 1946, CRIDDLE 1947, MAKRIDIN 1959). Both parents take care of the young (OGNEV *op. cit.*). According to MURIE (1944), other wolves may also help the parents take care of the young. These wolves are generally young of the previous spring. The female is capable of taking care of her young alone (PULLIAINEN 1963 c). According to OGNEV (1959), the female suckles for 35 – 45 days. After this the young are fed with food vomited by the female (SIIVONEN 1956). As the young grow up their range continuously increases (KNEZEVIC & KNEZEVIC 1956, OGNEV 1959).

In the autumn and winter wolves occur in packs (see e.g. BANFIELD 1951, MAKRIDIN 1959, BURKHOLDER 1959, KALELA 1961, MECH 1962, 1963, ALLEN & MECH 1963). A pack is a closed social unit (SCHENKEL 1948). Its behaviour is characterized by howling (SCHENKEL 1948, WYNNE-EDWARDS 1962), migrating and hunting together and by fights between the members of the pack to determine the hierarchical order (e.g. SCHENKEL 1948).

Ungulates are the chief food of the wolf (see e.g. MURIE 1944, COWAN 1947, THOMPSON 1952, STENLUND 1955, CRISLER 1956, KNEZEVIC & KNEZEVIC 1956, MAKRIDIN 1959, BURKHOLDER 1959, ALLEN & MECH 1963). Many investigators (see e.g. WRIGHT & SIMPSON 1920, CRITCHELL-BULLOCK 1930, HORNBY 1934, OLSON 1938 a, PORSILD 1945, MAKRIDIN 1959, KUYT 1962; cf. MURIE 1944, THOMPSON 1952) have reported that in winter the movements of wolves are dependent on the movements of ungulates. On the other hand, it is known that snow conditions affect the movements of these animals (see e.g. ZHITKOV 1904, OGNEV 1931, FORMOZOV 1946, MUNSTERHJELM 1946). OGNEV (1931, p. 196) emphasized that in winter their movements are affected by a number of factors simultaneously.

Packs break up in late winter when pairing takes place and the young become independent (SCHENKEL 1948, OGNEV 1959).

2. Material and methods

The data here described were collected during the expansion of the wolf from the east and are also based on observations made on penned individuals. I will present only such data as are necessary for an understanding of the biological background of the history and expansion of the species.

Observations on the breeding biology of the wolf were made in the northernmost communes of the country, Enontekiö and Inari (Seppo Aho, Yrjö Korhonen, Aslak Magga and Arvi Ranta). Some observations on breeding were also made by Erkki Hyttinen and Heimo Rautava in North Karelia.

The data on wolf packs are almost the same as those used for the study of the recent history of the species in this country (see also pp. 219 – 222). They were 705 checked observations made during the years 1954 – 63. If a lone wolf, or a pack, roamed a certain area for several days or was followed from place to place, the data are counted as a single observation.

The basic information on the food biology of the wolf was obtained by means of the so-called second predator inquiry (see also PULLIAINEN 1963 c, pp. 136 – 137, 1965 a). Mr. Mikko Rantanen gathered almost complete records of the domestic animals killed by wolves during the years 1959 – 63 (911 ind.) in North Karelia. The corresponding statistics of the local authorities were also used. The statistics concerning the reindeer killed by wolves during the years 1958 – 62 were gathered by the Paliskuntain Yhdistys (942 ind.). Some observations on animals killed by wolves were obtained from the newspapers. However, they were checked by sending a special inquiry to the observer in question. Altogether 1066 animals are known to have been killed by wolves in 1962. During that year the observers followed wolves 1047 km (during 48 days) in the forest zone and many hundred kilometres in the tundra zone. In January-February 1958, a wolf was followed by sportsmen 330 – 350 km (during 17 days) at Kuusamo (Ks). These data have also been used.

The recent studies on wolves in North America and the U.S.S.R. were performed with the aid of aeroplanes (see MAKRIDIN 1959, BURKHOLDER 1959, MECH 1962, 1963, ALLEN & MECH 1963) and a great number of research workers. These methods gave very good results in the conditions where they were used. Aeroplanes are of great value in the tundra zone, but in our forest zone their use is very limited or even impossible. For this reason the methods used here are almost the only ones possible in Finnish conditions. It must also be emphasized that I have been able to obtain data from all parts of Finland simultaneously. 150 observers of the Game Research Institute sent in their observations continuously and I could follow the distribution of the wolf from day to day. The same was true of the newspapers. All the news could be checked when it was only a few days old. With the method used I could also continuously compare all the sources with each other (see also p. 230). Some observations were checked by carrying out corresponding experiments with penned wolves (see also PULLIAINEN 1964 a).

3. Annual rhythm of the wolf

A. Breeding biology

According to OGNEV (1931, p. 197; 1959, p. 233), pairing begins in the middle of January when the young females are expelled from the pack (see also KNEZEVIC & KNEZEVIC 1956). According to ROMANOV (1941), MUNSTERHJELM (1946, p. 71) and OGNEV (1959, p. 233), fighting takes place or at least begins in February. According to SETON (1929, p. 274), SDOBNIKOV (1948) and MAKRIDIN (1959), the rut and pairing take place mainly in March. The Finnish data on the mating time of the species are very scanty. At Ilomantsi (PK), Ahvensalo, copulation took place on 9. III. 1962 (H. Rautava, personal communication; see also PULLIAINEN 1962 b, p. 110). At Inari (InL) copulation took place about 8. IV. 1963; this date was calculated from the date when the cubs in question opened their eyes (according to OGNEV 1959). PALMGREN (1920, p. 25) mentions that the copulation of penned wolves took place as follows: 15. II. 1903, 25. II. 1907 and 20. III. 1910. It seems likely that copulation mainly takes place at the end of February and in March, but in northern conditions it may even be postponed to the beginning of April (see also SIIVONEN 1956). This is supported by the observations made in the fells of Tsuukisautsi in Enontekiö (EnL). During the last ten years littering has mainly occurred in June (Seppo Aho and Aslak Magga).

Wolves are mature at the age of 22 months at the earliest (MAKRIDIN 1959; see also BAILEY 1926, MURIE 1944). The young females have their first rut a little earlier than the young males (OGNEV 1931, p. 197). The older wolves generally have an earlier rut than the younger ones (OGNEV 1959, p. 233). Wolves have very violent fights, which are generally won by the old males (MUNSTERHJELM 1946, p. 71). Males which are left without a female may even follow female foxes (CRITCHELL-BULLOCK 1930). According to MURIE (1944) and HERRE (1965), wolves can copulate with dogs, too. According to HERRE (*op. cit.*), it is the wolf that selects its mate, not the dog.

The numbers of cubs found in wolf dens in Lapland during recent years are visible in Table 7. It can be seen that the average number of young is 2.8. According to OGNEV (1931, p. 198, 1959, p. 242) and KNEZEVIC & KNEZEVIC (1956, p. 192), the average number of cubs is 5 – 6. The position and structure of the den depend on the nature of the ground in the locality (OGNEV 1931, 1959, HORNBY 1934, ROMANOV 1941, MUNSTERHJELM 1946, CRIDDLE 1947, MAKRIDIN 1959). If possible, the wolf digs a new den every year in sandy ground. The wolf can also use old dens of red foxes, or rock caverns, and dens may even be under bushes. Recent observations made in Lapland (Seppo Aho, Aslak Magga, Yrjö Korhonen, Esko Suomalainen and Arvi Ranta) show that in the fell region wolf dens are generally in the valleys, not on the tops of the fells. In Finnish Lapland wolves mostly dig new dens every year, but some wolves have taken over the old dens of red foxes.

Table 7. Wolf dens found in Finland during the years 1955 – 63.

Province	Locality	Date	No. of cubs	Observations
EnL	Enontekiö, Tsuukisautsi	VI. 1955	2	
»	» »	VI. 1959	4	
»	» »	VI. 1961	5	
»	» »	VI. 1962	1	
»	» »	VI. 1962	2	
InL	Inari, the fells of Vibus and Marasto	V. 1958	?	A nursing female was shot
»	» »	VI. 1963	3	

According to OGNEV (1931, 1959), both parents take care of the young. MURIE (1944, p. 24) observed other wolves helping to take care of the young, too. These wolves were males and females of the previous summer. For the first few days after the birth of the cubs the female and the cubs are fed by the male (OGNEV 1931; cf. also MURIE 1944, p. 31). The observers of the present study did not see males in the neighbourhood of dens. However, the reason may be that the males are very wary. It is also a fact that wolves do not hunt in the neighbourhood of the den (KOPONEN 1914, MURIE 1944, MAKRIDIN 1959, KORHONEN, personal communication). On the other hand, it was observed that the female can take care of the young alone (see PULLIAINEN 1963 c, p. 144).

Whilst suckling, the female remains within a radius of about two kilometres from the den (Yrjö Korhonen, Aslak Magga and Arvi Ranta; cf. also MURIE 1944, p. 31).

When suckling ceases, the cubs are fed with vomited matter (see SIIVONEN 1956). The observations made on penned wolves showed that at the age of one and a half months the cubs ate fresh fish and milk very eagerly. At this age MURIE (1944, p. 46) already gave fresh

meat to his cub. At the age of two months my cubs ate fresh meat very eagerly. In nature the cubs are fed by the adult wolves at the den at this age (MURIE 1944, p. 31). As the cubs grow up, their range continuously expands (MURIE *op. cit.*, p. 34, KNEZEVIC & KNEZEVIC 1956, p. 192, OGNEV 1959, p. 263). In North Karelia Mr. Erkki Hyttinen observed that at the age of 3 – 4 months the cubs accompany their mother when she is in the surroundings of the den. However, at this age the den still serves as a hiding-place. MURIE (1944, p. 34) made similar observations. I observed that the penned cubs behaved very similarly in captivity. When the door of their pen was left open they gradually ventured outside. If they took fright they hid in their pen. Two weeks after the first sortie they moved daringly outside the pen. In North Karelia cubs were seen with their mother in July – August (H. Rautava). It is likely that these cubs were then about 3 – 4 months old. The female was observed to carry her prey to a great distance from the place where she had caught it. Usually a lot of sheep disappeared in North Karelia in July – August.

Mr. Erkki Hyttinen observed that at the age of 5 – 6 months cubs feed at the place where the prey is caught (see also PULLIAINEN 1962 a and b). They begin to catch for themselves at the age of 7 – 8 months (PULLIAINEN *op. cit.*; cf. MURIE 1944, pp. 36 – 37). A number of observations made in North Karelia during the wolf expansion support these observations very well.

B. Winter activities

As mentioned above, the cubs begin to take an active part in hunting at the age of 7 – 8 months. It is by then late autumn or early winter. Their development naturally leads on to pack formation (see also MURIE 1944, YOUNG & GOLDMAN 1944, SCHENKEL 1948). In September the female and her cubs keep together and form the natural basis for packs, the female being the natural leader of the pack (see also SETON 1929, MURIE 1944, p. 40, MUNSTERHJELM 1946; cf. SCHENKEL 1948). The autumn howling of wolves serves to link up the members of the pack (MURIE 1944, YOUNG & GOLDMAN 1944, MUNSTERHJELM 1946, p. 74, WYNNE-EDWARDS 1962, p. 60; see also SETON 1909). This concerns both the female and cubs and the lone wolves of the previous summer. A remarkable increase in the sociability of the latter is to be noted. Later on they may join a pack formed earlier by a family (see also MURIE 1944). In North Karelia observations were made on packs comprising nine or more wolves. These are called here large packs. Large packs are first observed in North Karelia in November – December. By then the cubs hunt, too. In Lapland, however, observations on these large packs have been made as early as September. In these large packs, too, the leaders are females (see SETON 1929, p. 342, MURIE 1944, p. 40).

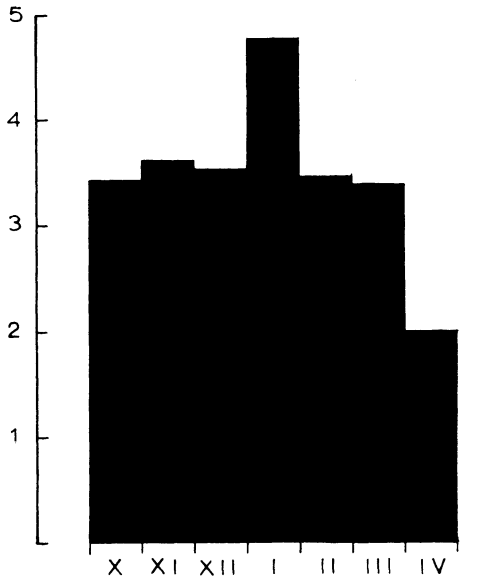


Fig. 37. The average sizes of wolf packs during the winter months (X – IV).

During the autumn and winter, wolves may separate from the pack and join it again (e.g. MURIE 1944, ALLEN & MECH 1963). However, there is a tendency for the family to keep together until the rut fights. In Fig. 37 the mean size of the packs (consisting of two or more wolves) during the months October – April is presented. The 142 observations recorded were made during the years 1954 – 63 in the following communes: Kuusamo, Suomussalmi, Kuhmo, Pielisjärvi, Ilomantsi, Tohmajärvi, Tuupovaara, Kiihtelysvaara, Värtsilä, Kitee and Uukuniemi. It can be seen that the mean size of the packs was almost the same during all months except January and April. The maximum mean size was observed in January (4.8 ind.) and the minimum size correspondingly in April (2.0 ind.), while

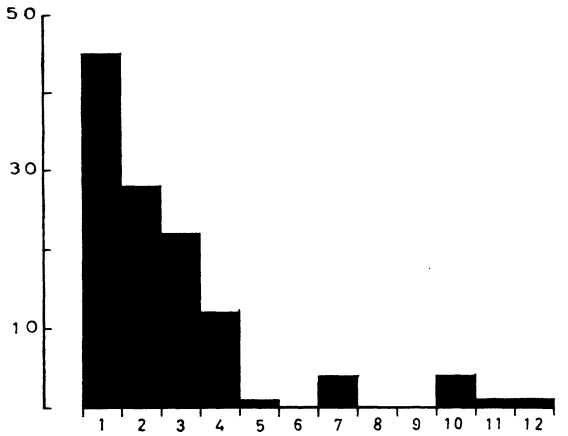
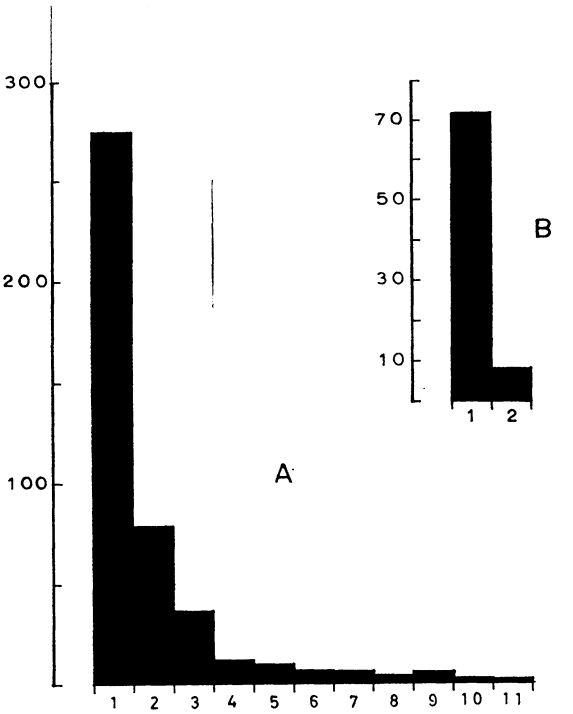


Fig. 38. Frequency distribution of the sizes of the wolf packs studied in Lapland (see text). Ordinate: number of observations. Abscissa: sizes of packs.



Figs. 39 (A) – 40 (B). Frequency distribution of the sizes of the wolf packs in East Finland (Fig. 39) and in the other parts of Finland (Fig. 40) (see text). Ordinates: number of observations. Abscissas: size of pack.

during the other months it was 3.5 ind. That the maximum should occur in January seems natural, in view of the great mobility of the wolf as the mating season approaches (see OGNEV 1931, 1959, MUNSTERHJELM 1946). It is biologically significant that the wolves are in packs at the start of the mating season. On the other hand, it is surprising that the packs are not at their minimum in February and March when the fights are at their peak. I think that the sociability of the species is so great that although the fights break up the packs temporarily the wolves have a great tendency to join together again (see also MURIE 1944, p. 39). I think that most of the fights in North Karelia take place in the U.S.S.R., where the changes in the sizes of the packs mainly take place (cf., however, PULLIAINEN 1962 b, p. 115). The results mentioned above also support the view that the wolves join up into packs for a short time after the fights (see PULLIAINEN *op. cit.*, p. 115). It can also be seen from the diagram (Fig. 37) that in April, when the birth of the cubs approaches, the packs finally break up into pairs and lone wolves (cf. also OGNEV 1931, MURIE 1944).

In order to examine the distribution of the packs according to their size, I have divided the country into three areas. The area of Lapland covers the communes of Enontekiö, Inari and Utsjoki, and the northern part of Sodankylä, i.e. the breeding area of the species. The communes of Savukoski, Salla, Kuusamo, Suomussalmi, Kuhmo, Uukuniemi and Saari, and the administrative district of North Karelia represent the expansion area of the species in the east. The other parts of Finland form the third area. The lone wolves are also included. In Fig. 38 the data of Lapland, consisting of 118 observations, are shown. 38.1 per cent of the observations concern lone wolves. According to STENLUND (1955), the corresponding value in the breeding area in North America was 41 per cent. I think that the packs consisting of 2 – 7 individuals are formed by a family and possibly some lone wolves of the previous summer (cf. HORNBY 1934, OLSON 1938 a and b, MURIE 1944, STENLUND 1955, MAKRIDIN 1959). There are only six observations (5.1 per cent) on packs consisting of 10 – 12 wolves. It is likely that in these cases two or more families had joined up (cf. SETON 1929, OLSON 1938 a and b, MURIE 1944, OGNEV 1959). I think that the relative scarcity of large packs is dependent on the low population density in the area (cf. also OGNEV 1959). Moreover, according to these data, it seems that the pairs in the area have fewer

Table 8. The trend of the mean sizes of wolf packs (two individuals or more) in two areas in East Finland during the years 1958 – 63.

	1958	1959	1960	1961	1962	1963
I. The administrative district of North Karelia, the communes of Saari and Uukuniemi	–	2.7	5.1	3.5	3.4	4.2
No. of observations	–	10	14	26	42	10
II. The communes of Kuusamo, Suomussalmi and Kuhmo	2.0	2.0	4.1	2.5	4.6	3.6
No. of observations	2	1	14	13	14	9

cubs than usual (see also p. 235). The average size of the packs (2 – 12 ind.) was 3.7 individuals.

In Fig. 39 the corresponding data of the expansion area are presented. The average size of the packs (2 – 11 ind.) was 3.5 individuals, which is only a little smaller than the value for Lapland.

In Fig. 40 the data relating to the other parts of Finland are presented. During the study period the packs observed, amounting to 10 per cent of the observations, never consisted of more than two wolves. All the other observations were made on lone wolves.

In the following tabulation I present the data of the whole country relating to summertime (May – August).

	No. of wolves seen together			Total
	1	2	3	
No. of observations	69	4	3	76
Percentage	90.8	5.4	3.9	100.0

The wolves seen in twos and threes were observed either in May or in August. They were probably immature individuals that had joined company (cf. CRITCHELL-BULLOCK 1930, MURIE 1944). The observations made in August may also concern a female and her cubs. The fact that the immature wolves join up indicates the remarkable sociability of the species (cf. MURIE *op. cit.*, SCHENKEL 1948). On the other hand, it is known that males which have had no mate migrate over vast areas in late winter and spring. In Finland these migrations may even extend to the southwesternmost parts of the country (see also PULLIAINEN 1962 b).

In Table 8 I present the trend of the mean size of the packs in two areas of the country during the years 1958 – 63. In the first area only lone wolves were observed in 1958. After 1959, wolf packs were observed regularly every winter. The maximum mean size was already reached in 1960. In the second area three packs were observed in 1958 and 1959. The observations were made at Kuhmo, the southernmost commune of the area. After 1960, the size of the packs clearly increased. The number of packs also increased. The average size of the packs reached a maximum in 1962.

4. The food biology of the wolf

A. Prey animals

General. – There are great differences between different parts of Finland with respect to the proportion of farmed land. For this reason I divided Finland into different areas when studying the food biology of the wolf (see also PULLIAINEN 1963 c). There is an important difference between the tundra zone and the forest zone and similarly between the reindeer area and the rest of Finland. In the latter area a small number of wild reindeer have recently been observed, too. In consequence, for the present purpose I have distinguished the following areas: North Karelia, Ostrobothnia (see Fig. 41), Kainuu (the communes of Kuusamo, Suomussalmi and Kuhmo) and Lapland (the area north of the commune of Kuusamo where wolves were observed, see pp. 219 – 222).

Table 9. Data concerning prey of wolves in North Karelia and Ostrobothnia in 1962. The data were gathered with the help of the observers of the Game Research Institute.

	Bear	Elk	Elk calf	Horse	Cow	Calf	Sheep	Dog	Cat	Hare	Squirrel	Black grouse	Gallinaceous bird (not identified)	Total
North Karelia	1	14	4	3	9	15	149	28	1	3	1	–	7	235
Ostrobothnia	–	2	–	–	–	5	30	7	–	2	–	2	–	48
Total	1	16	4	3	9	20	179	35	1	5	1	2	7	283
%	0.3	5.7	1.4	1.0	3.2	7.1	63.3	12.4	0.3	1.8	0.3	0.7	2.5	100

In Table 9 data of the animals killed by wolves in 1962 in North Karelia and Ostrobothnia are presented. The corresponding localities are shown in the map (Fig. 41). The statistics available concern the numbers of animals, not their weights or volumes. The last method, especially, is very exact, but in Finnish conditions it was impossible to use. In the statistics presented domestic animals are strongly represented. The data of North Karelia are almost complete. However, the data of wild animals are naturally incomplete, although a number of wolves were tracked. The wild animals killed by wolves were eaten almost entirely. Domestic animals, on the contrary, were generally only partly eaten. In North Karelia, for instance, in 1962, wolves ate the following domestic animals entirely: 31 sheep, 3 cows, 5 calves and one horse. The corresponding figures for domestic animals killed by wolves (see Table 13) were 149 sheep, 9 cows, 15 calves and three horses. It can be seen that 20 – 30 per cent of the domestic animals killed by wolves were eaten entirely. It is also to be noted that human activities often disturb wolves feeding on domestic animals. The small domestic animals like cats and dogs are generally eaten entirely.

The cattle mentioned in Table 9 were caught mainly in summer and the wild animals mainly in winter.

In summer and autumn 1962, two male wolves were roving in Ostrobothnia. The animals killed by these wolves are presented in Table 9. One of these males was killed on 29. XII. 1962 at Pyhäjoki (KP) (weight 42 kg, cf. p. 232) and the other on 12. I. 1963 at Lestijärvi (KP) (weight 42.5 kg, cf. p. 232). These wolves, whilst moving within a rather restricted area, killed at least 48 animals in seven months (see Fig. 41).

In June 1962, two wolves (♂ and ♀) were seen at Närpiö (EP). The former was killed on 2. VII. 1962 at Närpiö and the latter on 10. II. 1963 at Korsnäs (EP). During the summer months these wolves ate at least 12 sheep, two calves, two cats and a dog (these animals are not included in Table 9).

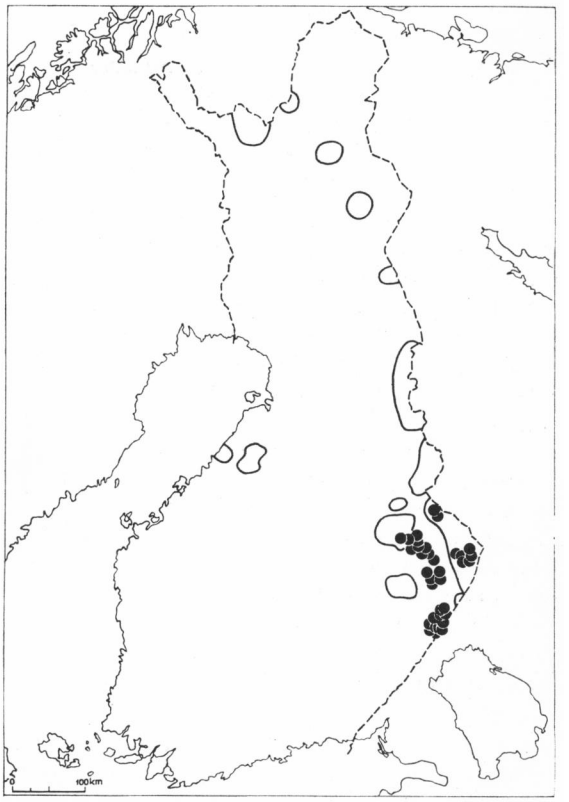


Fig. 41. The studies summarized in Tables 9 and 10 were performed in the areas delimited. In the places marked with black circles wolves killed domestic animals in North Karelia in 1962.

It is worth mentioning that the bear (*Ursus arctos*) is one of the animals that may be devoured by wolves. In autumn 1962, a bear den was found by Mr. E. Tapola at Ilomantsi (PK), Jorkansalo. There were plentiful remains of a bear in the vicinity of the den. It could be seen that a wolf pack had been eating at the place. The mean weight of a female bear over three years old is 135 kg (23 individuals) and that of a corresponding male 165 kg (84 individuals) (own data; see also KOMONEN 1953). It may be concluded that a large pack had been eating

Table 10. Data concerning prey of wolves in North Finland (see text) in 1962. The data were gathered with the help of the observers of the Game Research Institute.

	Elk	Elk calf	Wild reindeer	Reindeer	Sheep	Dog	Red fox	Har	Capercaillie	Total
Kainuu	2	1	1	600	2	10	2	1	1	620
Lapland	–	1	–	155	–	7	–	–	–	163
Total	2	2	1	755	2	17	2	1	1	783
%	0.2	0.2	0.2	96.4	0.2	2.2	0.2	0.2	0.2	100

Table 11. Data concerning the contents of the stomachs of wolves.

Date	Province and commune	Sex	Age class	Stomach contents	Investigator
1960	Kn: Suomussalmi	♀	juv.	Flesh and hair of a red fox and dog	Y. Karttimo
III. 1962	PK: Ilomantsi	♂	ad.	Hair of an elk	H. Rautava
X. 1962	Kn: Suomussalmi	♂	juv.	Flesh and hair of a reindeer, feathers of birds (volume about 2 l)	H. Kangasperko and S. Sulkava
XII. 1962	KP: Saloinen	♂	ad.	Hair of a dog, and a black grouse (0.5 l)	– » –
XII. 1962	PK: Lieksa	♂	juv.	Two small rodents, hair and flesh of a dog, leaves and grass, remains of a bird (2 l)	– » –
XII. 1962	PK: Ilomantsi	♀	ad.	Flesh and hair of a dog	H. Rautava
I. 1963	PK: Tuupovaara	♂	ad.	» » »	V. Piironen
III. 1963	» »	♀	ad.	Remains of a carcass	– » –
IV. 1963	Ks: Salla	♂	ad.	Flesh and hair of a reindeer (0.5 l)	H. Kangasperko and S. Sulkava
X. 1963	Kn: Kuhmo	♂	ad.	» » of an elk	V. Piirainen
XI. 1963	Ks: Kuusamo	♂	juv.	Two heads of a vole, hair, and feathers of a bird	P. Åkerlund
XI. 1963	Ks: Posio	♂	juv.	Flesh and hair of a sheep, hair of a vole, twigs of blueberries, hairmoss, some dipterous larvae (2 l)	H. Kangasperko and S. Sulkava
XI. 1963	PK: Tuupovaara	♂	ad.	Flesh, skin and hair of a dog	T. Huovinen
I. 1964	Kn: Kuhmo	♂	juv.	Meat bait, horse manure, feathers of a tetraonid (1.5 l)	H. Kangasperko and S. Sulkava
I. 1964	PS: Maaninka	♀	juv.	Bones and hair	O. Liimatainen
I. 1964	ES: Haukivuori	♂	ad.	Remains of a dog	T. Hänninen
X. 1964	Kn: Suomussalmi	♂	juv.	Hair of an elk, offal, cow manure, a shrew, head of a fish, cowberries, blueberries, leaves (1.5 l)	H. Kangasperko and S. Sulkava

the bear. However, it is uncertain whether the bear was killed by the wolves or not (see also PULLIAINEN 1963 c).

In Table 10 I represent the statistics of the study areas of Kainuu and Lapland. I think that all the prey animals that are usually killed by wolves in this northern area are mentioned in this table. Because reindeer are of great economic importance to man, their relative numbers are perhaps too high. The animals mentioned in Table 10 were mainly killed in winter.

The reindeer mentioned in Table 10 were killed in Kainuu in rather a limited area. Most of them were killed at Hossa, situated on the boundary of the communes of Kuusamo (Ks) and Suomussalmi (Kn). The area where wolves roamed there covers about 70 km². In winter the western limit of the range is 15 km from the frontier and in summer the corresponding distance is 20 – 30 km. Besides about 600 reindeer, wolves killed at least three dogs and an elk (*Alces alces*) in this area. The greatest number of wolves observed at a time in this area was over 10.

It is worth mentioning that wolves very often eat only parts of a reindeer they have killed.

MAKRIDIN (1959) mentions that the wolf digests all its food during a few hours, so that only keratin (e.g. hair, hoofs, feathers and claws) and tendons remain unchanged. BURKHOLDER (1959) has reported that the wolf digests its small prey animals entirely. My observations on penned wolves fully support these statements. Of the rabbits eaten by the cubs only the hairs remained unchanged during digestion. This fact makes the study of the food of the wolf from the stomach contents rather difficult. In Table 11 the contents of the stomachs of the wolves studied are listed. It can be seen that these data support the picture of the food of the wolf obtained from the data presented earlier. However, it is also to be noted that there were remains of small-sized birds and small rodents in a number of the samples studied.

Mr. J. Kivistö (see also Table 11) observed faeces of wolves containing berries, e.g. cowberries (*Vaccinium vitis-idaea*). It is likely that these originated from the stomachs and crops of prey animals (e.g. tetraonids) eaten by wolves. The same thing was observed by THOMPSON (1952), too. It is also worth mentioning that the penned wolf cubs ate bread, cabbage, and other plant material, too.

Domestic animals killed by wolves in North Karelia. – In the previous chapter I already dealt with the domestic animals killed by wolves in North Karelia in 1962. Before July 1961, the state compensated farmers for the loss of domestic animals only if these were killed by bears, not by wolves. For this reason no official statistics concerning the domestic animals killed by wolves prior to this date are available. After July 1961, farmers were indemnified for the damage caused by wolves. All the domestic animals for which compensation is paid by the state are checked by impartial persons who make official reports. For this reason these statistics are regarded as reliable. I gathered corresponding data from the years 1958 – 1960. These

Table 12. Domestic animals killed by the large predators in North Karelia during the years 1959 – 1963.

	1959		1960		1961		1962		1963		Total	
Domestic animals	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%
Horses	–	–	–	–	2	0.4	3	1.5	–	–	5	0.4
Cows	–	–	–	–	29	5.6	9	4.4	1	4.6	39	3.6
Heifers and young bulls	–	–	3	1.4	8	1.5	11	5.4	–	–	22	2.0
Calves	3	2.2	19	8.9	39	7.5	17	8.3	3	13.6	81	7.4
Sheep	132	97.8	191	89.7	437	84.4	164	80.4	18	81.8	942	86.3
Pigs	–	–	–	–	3	0.6	–	–	–	–	3	0.3
Total	135	100.0	213	100.0	518	100.0	204	100.0	22	100.0	1 092	100.0

data are naturally not so reliable as those mentioned above. The most important uncertain factor is the predator which inflicted the damage in question. In certain cases the owners lied, stating that the damage was done by a bear, because then the state paid indemnity. In Table 12 all the domestic animals killed by the large predators (the lynx, *Lynx lynx*, the bear and the wolf) are presented. It can be seen that during the summers of 1959 – 1963 predators killed at least 1092 domestic animals in North Karelia. 86.3 % of these animals were sheep. Cows, heifers and calves constituted only 13.0 %. Horses and pigs were clearly secondary in this respect. The domestic animals included in this table were killed by the predators in general. I think that the bear and the wolf show the same preferences. In Table 13 I present the data of domestic animals killed by wolves, on the one hand, and by the other predators, on the other hand. The data of the years 1959 – 60 were collected by the author and the corresponding data of the years 1962 – 63 were collected by Mr. Mikko Rantanen. It can be seen that wolves killed at least 70 % of the domestic animals lost yearly. No data are available for the year 1961 but according to Mr. Rantanen the relation was almost the same as during the year 1962.

Table 13. Data concerning domestic animals killed by wolves and other large predators (the bear and lynx) in North Karelia during the years 1959 – 1963.

Year	Predator	Horses	Cows	Heifers and young bulls	Calves	Sheep	Total	%
1959	Wolf	–	–	–	1	111	112	83.0
	Others	–	–	–	2	21	23	17.0
1960	Wolf	–	–	3	12	135	150	70.4
	Others	–	–	–	7	56	63	29.6
1962	Wolf	3	9	–	15	149	176	86.3
	Others	–	–	11	2	15	28	13.7
1963	Wolf	–	1	–	3	15	19	86.4
	Others	–	–	–	–	3	3	13.6

It is interesting to know to what extent domestic animals were kept in North Karelia during the experimental period. In Table 14 I present the corresponding data according to the agricultural statistics. It can be seen from Table 14 that the total number of domestic animals in North Karelia did not change remarkably during the experimental period. Cattle made up 63.8 – 73.7 % of the total number of domestic animals. The proportion of these animals increased by about two per cent yearly. The number of sheep correspondingly decreased fairly steadily during this period, from 19.8 % to 10.2 %. The numbers of horses and pigs remained almost unchanged. If these values are compared with the numbers of domestic animals killed by wolves, it can be seen that the ratio between cattle and sheep is reversed. According to these data, it seems that wolves clearly prefer sheep. This is especially supported by the comparison of calves and sheep, which belong to the same size class. The percentage of calves kept by cattle owners is somewhat higher than that of sheep. By contrast, the ratio of calves

Table 14. Numbers of domestic animals in the district of the North Karelian Agricultural Society during the years 1959 – 1963 (according to the agricultural statistics).

	1959		1960		1961		1962		1963	
	No.	%	No.	%	No.	%	No.	%	No.	%
Horses	16 505	7.6	16 700	8.0	15 600	7.3	15 600	7.1	15 000	7.2
Bulls	292	0.1	200	0.1	300	0.1	200	0.1	300	0.1
Cows	77 757	35.6	80 500	38.7	80 400	37.3	82 300	37.4	84 500	40.3
Heifers and young bulls	14 941	6.8	13 300	6.4	14 000	6.5	17 500	8.0	15 200	7.3
Calves	46 448	21.3	42 600	20.5	51 500	23.9	52 700	24.0	54 400	26.0
Pigs	19 228	8.8	19 300	9.3	22 100	10.3	22 800	10.3	18 600	8.9
Sheep	43 372	19.8	35 400	17.0	31 400	14.6	28 700	13.1	21 400	10.2
Total	218 543	100.0	208 000	100.0	215 300	100.0	219 800	100.0	209 400	100.0

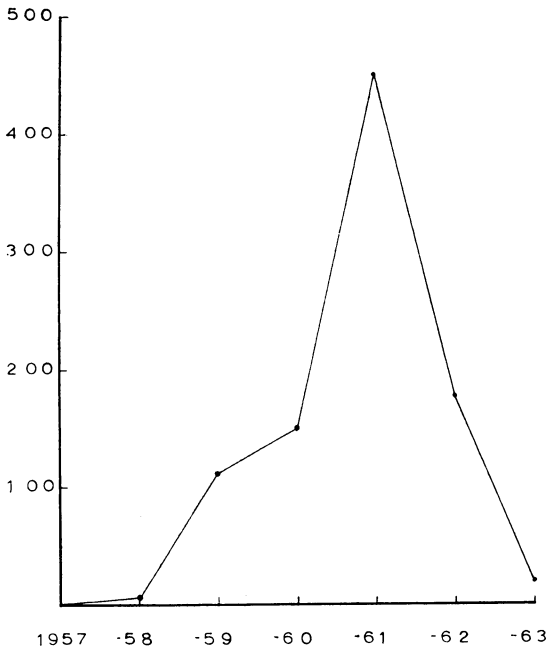


Fig. 42. The numbers of domestic animals killed by wolves in North Karelia during the years 1957 – 63.

to sheep killed by wolves is 1 : 10. However, I think that the problem is not so simple. The data presented above do not give a true picture of the availability of domestic animals. Most of the sheep are kept on pastures situated far from residences. Cattle, by contrast, are kept in pastures near residences, and are even tended by herdsmen. Some of the domestic animals (e.g. bulls and pigs) are even kept in sheds, as are all the domestic animals in winter. It is clear that these animals are much less available than animals kept in distant pastures. It can be concluded that both availability and active selection influence the composition of the food consumed by wolves.

As already mentioned, the number of sheep in North Karelia decreased during the experimental period (1959 – 1963). It is likely that wolves and other predators were partly responsible for this. Because large predators killed large flocks of sheep, cattle owners in many areas of North Karelia gave up sheep-farming. However, at the same time the percentage of sheep in the whole country decreased from 11.4 % to 9.0 %, too.

In Fig. 42 I present the trend of the numbers of domestic animals killed by wolves in North Karelia during the years 1957 – 1963. A total of 914 domestic animals were destroyed by wolves. The numbers reached their peak in 1961. During the two following years a great decrease took place in these numbers.

Reindeer killed by wolves. – The state compensates the reindeer owners for reindeer killed by predators. An ear of the reindeer bearing the mark of the owner must be shown and the killer of the animal must be determined before the owner can obtain indemnity from the state. For this reason statistics of reindeer killed by predators are available. However, some mistakes may be included in these statistics. The most important factors are as follows. On vast forest and fell areas tens or hundreds of reindeer killed by predators are never found. Many fawns which are killed by predators are unmarked. For this reason no indemnity can be claimed. Sometimes predators and/or other animals eat the ears so that no marks can be found. The following comparison shows how many of the killings in question are not included in the statistics. In 1962, in the area of the reindeer-owners' associations of Hossa and Kallioluoma in the communes of Kuusamo (Ks) and Suomussalmi (Kn) about 600 reindeer were killed by wolves (see Table 10). Only 284 of these animals were officially checked and paid for. Thus half the reindeer killed were not included in the statistics.

Table 15. Data concerning reindeer killed by the different predators during the years 1958 – 1962.

	1958		1959		1960		1961		1962		Total	
Predator	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%
Wolf	139	46.3	125	47.9	65	22.8	220	44.3	395	56.3	944	46.1
Wolverine	152	50.0	127	48.6	210	73.7	235	47.3	265	37.8	989	48.3
Bear	9	3.0	8	3.1	4	1.4	28	5.6	26	3.7	75	3.7
Lynx	–	–	–	–	4	1.4	10	2.2	8	1.1	22	1.1
Golden eagle	–	–	–	–	2	0.7	1	0.2	8	1.1	11	0.5
Red fox	–	–	–	–	–	–	2	0.4	–	–	2	0.1
Others [1]	2	0.7	1	0.4	–	–	–	–	–	–	3	0.2
Total	302	100.0	261	100.0	285	100.0	496	100.0	702	100.0	2 046	100.0

[1] During the years 1958 – 1959 the reindeer killed by the lynx, golden eagle and red fox were recorded together.

Table 16. The distribution of the reindeer killed by wolves in different age classes.

	1958		1959		1960		1961		1962		Total	
Age classes of reindeer	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%
Older than a year	112	80.6	100	80.0	56	86.2	163	74.1	326	82.5	757	80.2
Fawns	27	19.4	25	20.0	9	13.8	57	25.9	69	17.5	187	19.8
Total	139	100.0	125	100.0	65	100.0	220	100.0	395	100.0	944	100.0

In Table 15 I present the reindeer killed by the different predator species during the years 1958 – 62 according to the statistics of the Paliskunta Association. During this period wolves and wolverines killed almost the same numbers of reindeer. The other predators mentioned in Table 15 killed reindeer only occasionally. During the years 1958 – 61 wolverines had slightly greater importance as killers of reindeer than wolves, but in 1962 the situation was reversed. The reason for this was that the wolf expansion occurred in the communes of Kuusamo and Suomussalmi. For this reason the number of reindeer killed by wolves increased from the year 1961 to the year 1962 by 79.5 %.

Reindeer are generally classified as adults over one year old and fawns. Thus the age of the reindeer killed by wolves can be studied. Here again the possible mistakes mentioned above should be noted. In Table 16 reindeer killed by wolves during the years 1958 – 62 are classified by age. The percentage of fawns among the reindeer killed by wolves varied only a little during the experimental period (from 13.8 % to 25.9 %). The corresponding mean values among reindeer killed by bears and wolverines are 33.3 and 20.9, respectively.

In the following tabulation the data mentioned above and the percentages of fawns in the reindeer populations during the years 1958 – 59 and 1961 – 62 are presented. The data of 1960 are not available.

Year	Percentage of fawns among the reindeer killed by wolves	Percentage of fawns in the corresponding reindeer populations
1958	19.4	22.9
1959	20.0	24.9
1960	13.8	
1961	25.9	23.4
1962	17.5	22.3

It can be seen that the percentages correspond very well with each other.

In Fig. 43 I present the distribution of reindeer killed by wolves in 1958 in the areas of the reindeer-owners' associations. The southern limit of the area where reindeer are kept is shown in the map, too. The most numerous wolves were killed near our eastern frontier and at Enontekiö (EnL) in the north.

B. Home range

Hunting routes of wolves. – During recent years observations concerning runways or hunting routes regularly used by wolves have been made in Finland (see also PULLIAINEN 1962 b, p. 117, 1963 c, p. 144). In the following tenable records obtained are described.

In January – February 1962, the movements of a wolf pair were followed at Ilomantsi (PK). The home range of this pair extended about 30 km in the north-south direction and about 30 – 40 km in the east-west direction. The eastern limit of their range was behind our eastern frontier. The distance travelled by the wolves in the U.S.S.R. was estimated from the time spent behind the frontier and the average

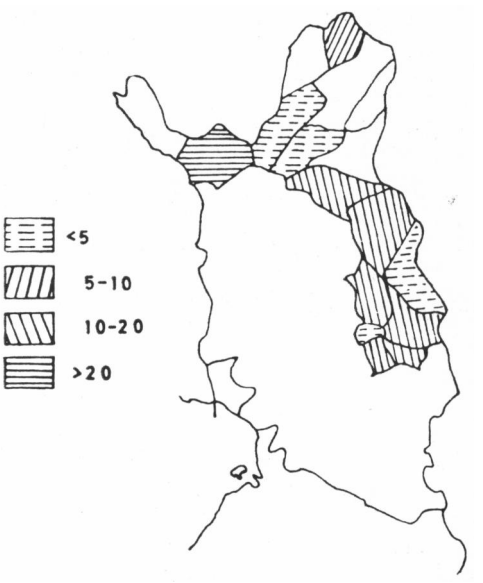


Fig. 43. Map showing the numbers of reindeer killed by wolves in the areas of the reindeer owners' associations in 1958. The southern limit of the area where reindeer are kept is shown in the map, too.

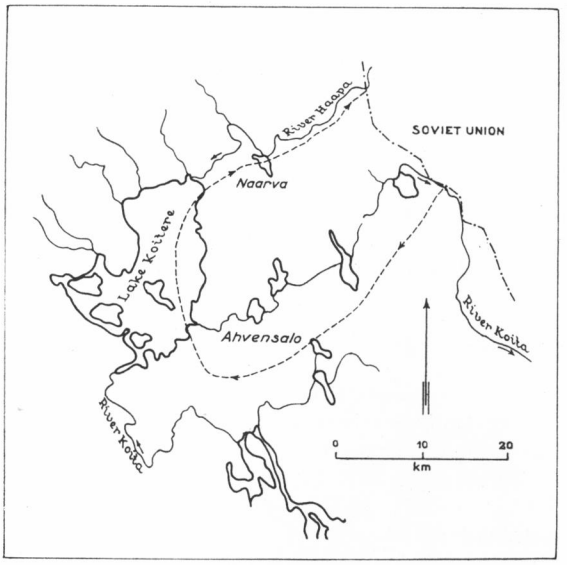


Fig. 44. The movements of a wolf pair at Ilomantsi (PK), East Finland (see text).

rapidity of movement of the pair. When travelling (Fig. 44), these wolves kept to a certain time-table. On 11. III they were observed at Ahvensalo. From there they travelled over Lake Koitere and past the village of Naarva to the U.S.S.R. On 20. III they returned to Finland and on 22. III they were observed at Ahvensalo. Thus a circuit took 11 days. Throughout the study period (January – February) this time-table was followed (H. Rautava). This pair moved with the male as leader (cf. p. 236). On 23. III the male was shot (weight 44.5 kg). After this the female used the same runways as before. It littered in the area, too.

In January – February 1958, a young male was tracked in the northern parts of Kuusamo (Ks) and in the northeastern parts of Posio (Ks). Tracking was begun on 19.I and discontinued on 4. II, when the wolf was killed at Kuusamo (Juuma). Its weight was 34.5 kg. The movements of this animal are shown in Fig. 45. The fact that the wolf was being tracked by sportsmen may have affected the records obtained. When travelling, the wolf made circuits such as are characteristic of hunting routes. The distance covered by the wolf was 330 – 350 km. Thus the male travelled an average of 20 km a day. It used lake ice, beds of streams and roads, too. During these 17 days it killed 21 reindeer, but ate only parts of them. It tried to kill almost all the reindeer it came across.

A clear rhythm was also observed in the movements of wolves at Hossa, Suomussalmi (Kn). The wolves visited this area at intervals of one week, except in late winter, at the time of the rut fights, when the intervals were longer (M. Kuhlman).

In summer and autumn 1962, two wolves roamed Ostrobothnia. Their summer movements could be traced from the domestic animals they killed and their winter movements by tracking. No exact data are available, however. They returned to the same place at intervals of one or two weeks.

In summer and autumn 1962, a female was observed in and around Närpiö (EP). A similar rhythmicity to that of the wolves of Ostrobothnia was observed in this case, too. The home range of this wolf covered a rather restricted area, too.

Winter and summer habitats of wolves. – The winter habitats of the wolf vary very much, depending on the locality in question. The species breeds at Tsuukisautsi, Enontekiö (EnL), but it also spends the winters there. The area occupied is rather restricted. Its diameter in the north-south direction is about 20 km and from east to west only about 2 km, the width of the ravine. A great many reindeer are kept there. Wolves kill them throughout the year. To some extent wolves follow the seasonal movements of reindeer (A. Ranta). In their breeding areas at Inari (the Vibus and Marasto fells; InL) and Utsjoki (InL) wolves have selected as their winter habitats fells with sharp outlines. These fells are also characterized by a thin and hard snow cover. These wolves keep clear of the forest zone, where the snow is soft and deep.

In the first wolf inquiry questions were asked of the observers concerning the winter habitats of wolves. Answers were obtained from 31 study areas. In the tundra zone wolves showed a marked preference for fells with sharp outlines (100 %). In the forest zone the order of preference was as follows: ice and shores of lakes (53.8 %), spruce stands (23.0 %), swamps (15.2 %), beds of streams and rivers (4.0 %) and edges of fields and meadows (4.0 %). All these habitats are characterized by a relatively thin and hard snow cover. The observations mentioned above were made when the wolves had selected their habitats freely. If wolves are pursued, they use

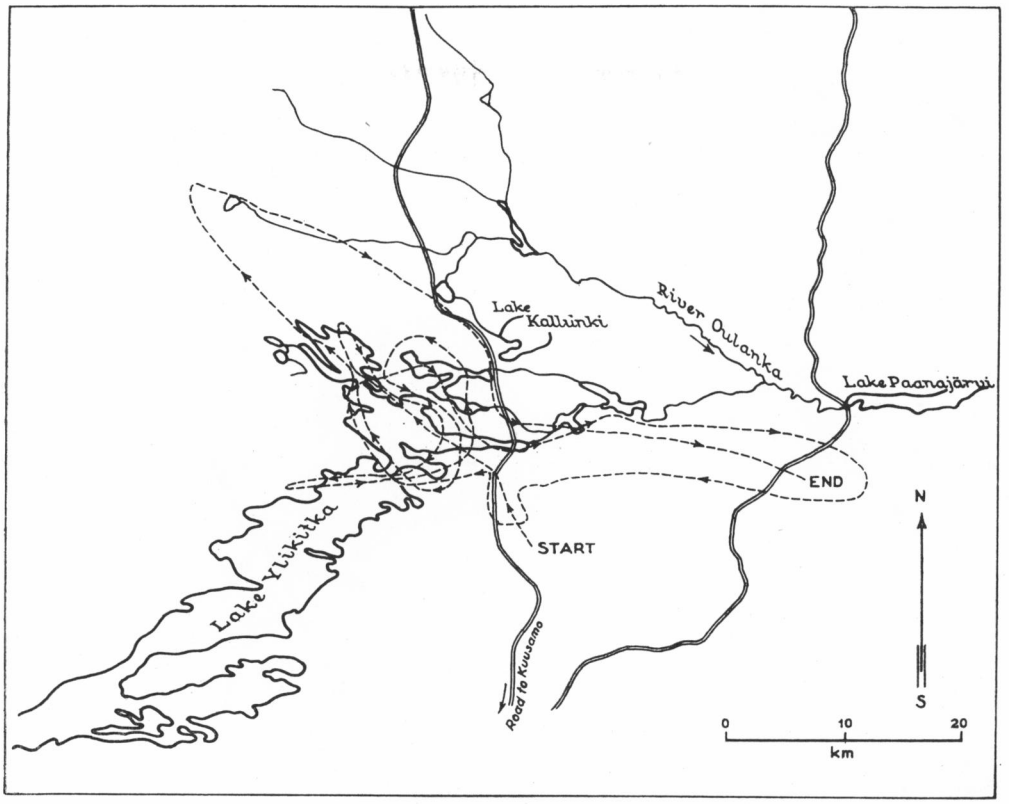


Fig. 45. The movements of a wolf at Kuusamo (Ks) (see text).

routes where they can move with ease. They may then follow highways, roads, paths of forest workers, logging routes, ski tracks, etc. From the top of a hill they look down at their pursuers (see also PULLIAINEN 1962 b, 1963 c). Wolves prefer to rest and sleep on the tops of hills, too.

Exact data on the summer habitats of wolves are not available, because they are very difficult to study. However, the observers made most of their observations in the following habitats: game trails and their immediate vicinity, lake shores, edges of fields and meadows, etc. The observers emphasized that wolves do not go right out into the open in such places as fields. They swim to the islands in lakes, too, probably on account of the sheep that are very often kept there.

The habitats mentioned above include over 90 per cent of the habitats recorded. It can be seen very clearly that the wolf selects its habitats. Thus wolves, when travelling, follow certain routes. This was observed very clearly when the movements of wolves over the eastern frontier were studied. The same thing was visible when wolves were migrating through South and West Finland. Since 1956, the recording of game animals crossing the frontier has been officially included in the programme of the Border Patrol Establishment. Thus, reliable data are available concerning the movements of wolves over the frontier. In Fig. 46 I have marked the places that were regularly used by wolves when crossing the frontier. The relative thickness of the arrows describes the frequency of the use of the place in question. In South and West Finland wolves have used the same migration routes for decades (see Fig. 47). The interval between two observations at a certain place might be several decades. However, the wolves observed used exactly the same route when travelling, even to within a

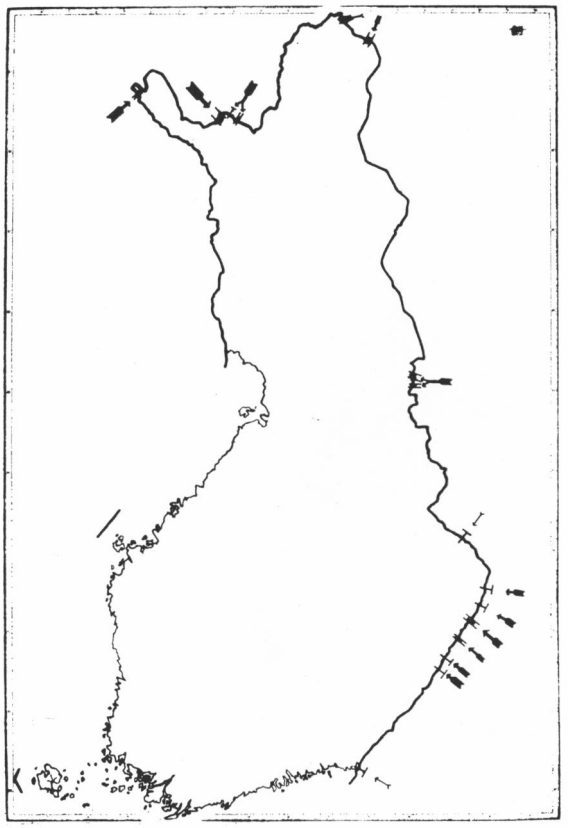


Fig. 46. The places where wolves regularly crossed the frontier. The thickness of the arrows indicates the frequency.

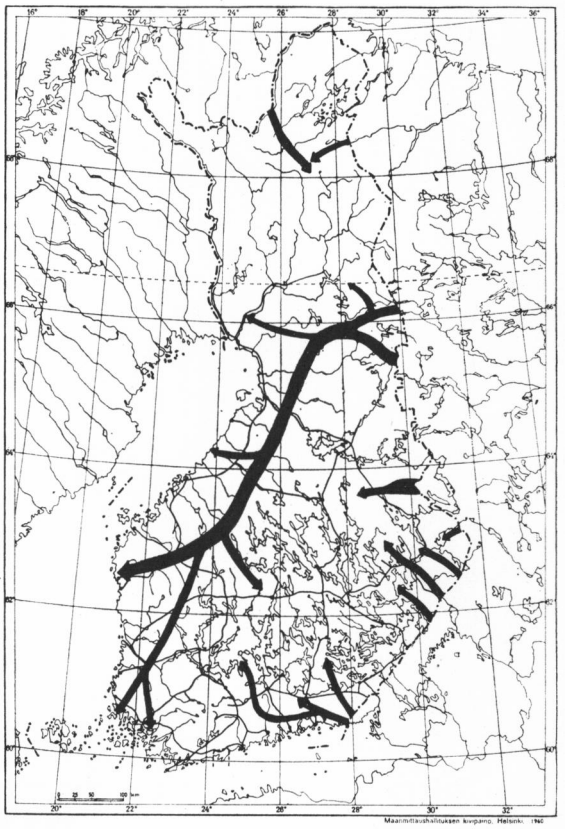


Fig. 47. The main migration routes of wolves in Finland. Made according to all the records on migrating wolves available. The most commonly used migration route (the Suomenselkä) marked with the thickest arrow.

few metres. In fact, there are hills, eskers and islands on wolf routes that bear names proving them to have been used by wolves from ancient times. The Suomenselkä is one of the most commonly used migration routes. This explains many of the observations of wolves in Southwest Finland, which otherwise seemed surprising. In the southeast wolves have migrated to Finland via Virolahti. One of the common routes goes via the following communes to South Savo: Ylämaa (EK), Luumäki (ES), Savitaipale (ES), Suomenniemi (ES) and Ristiina (ES). This habitat selection system of the wolf has already been known to Finnish hunters and sportsmen for a long time (see e.g. MUNSTERHJELM 1946).

Distances travelled daily by wolves. – As already mentioned (p. 244), the so-called »wolf of Kuusamo» travelled 20 km a day on an average.

The observers, when tracking wolves, made exact notes on the distances travelled by them daily. In the following tabulation I present the records obtained in the forest zone. All cases in which tracking had to be discontinued at the frontier are omitted.

Area	No. of tracking days	Total distance travelled, km	Speed km/day
North Karelia	21	464	22
Kainuu	11	310	28
Ostrobothnia	8	172	22
Lapland	3	55	18
Total	43	1001	23

It can be seen that the variation in the values is comparatively small. The mean distance travelled by wolves per day is 23 km.

No corresponding data from the tundra zone are available. One of the observers in this zone, J. Magga, kept some records. These showed that on hard snow wolves might travel as much as 200 km a day.

C. Discussion

MURIE (1944) carried out thoroughgoing investigations on the food biology of the wolf in Alaska. He examined a great number of scats. The scat analysis method was also used by COWAN (1947), THOMPSON (1952) and STENLUND (1955), for instance. COWAN (*op. cit.*) calculated the number of prey animals killed by wolves in his study area, too. According to MURIE (1944), caribou (*Rangifer arcticus*) are the main food of the wolf in Alaska (43 %). Mountain sheep (*Ovis d. dalli*) take second place (about 26 %). The percentage of ungulates is thus 69. The other food items of wolves are the ground squirrel (*Citellus citellus*; 13 %), the marmot (*Marmota marmota*; 8 %), voles and mice (5 %) and the elk, beaver, snowshoe hare, fox, ptarmigan, etc. (total about 5 %). MURIE (*op. cit.*) emphasized that if the population of some major prey animal of the wolf is low, some other major prey animal can take its place. According to MURIE (*op. cit.*), the proportions of the different prey animals vary considerably from year to year, but some animals, like the ground squirrel and marmot, are consumed only during the five months of summer.

COWAN (1947) found that ungulates made up about 80 per cent of the food consumed by wolves in the Rocky Mountain National Parks of Canada (according to scat analyses). When the number of killings observed in nature was taken as the basis of calculations, the percentage of ungulates increased. THOMPSON (1952) carried out investigations in Wisconsin, USA. The only ungulate in the area, *Odocoileus virginianus*, made up about 97 per cent of the food consumed by wolves. Rodents took second place. In Minnesota, USA, the corresponding percentage of *Odocoileus virginianus* was 95.5 % (STENLUND 1955), the other 4.5 % consisting of hares, porcupines and gallinaceous birds. Among others, the following investigators have emphasized the importance of ungulates as the food of wolves: PLESKE 1887, JOHNSEN 1929, CRITCHELL-BULLOCK 1930, HORNBY 1934, OLSON 1938 a and b, SDOBNIKOV 1939, ROMANOV 1941, PORSILD 1945, MUNSTERHJELM 1946, RAND 1948 a and b, SEMENOW-TJAN-ŠANSKIJ 1948, KNEZEVIC & KNEZEVIC 1956, BURKHOLDER 1959, MAKRIDIN 1959, ALLEN & MECH 1963.

Some investigators have pointed out special features of the food biology of the wolf. PREBLE (1908, p. 212) observed that wolves took hares from primitive traps of Canadian Indians (cf. the Arctic fox, *Alopex lagopus*, MUNSTERHJELM 1946, PULLIAINEN 1965 a). STANWELL-FLETCHER (1942, pp. 138 – 139) mentioned that at the end of February, when the snow cover was hard, wolves mainly caught hares. OGNEV (1931, 1959), FOWLER (1937) and RAND (1945) emphasized the importance of cattle in the diet of wolves. HARPER (1955) observed that wolves would eat carcasses (see also MURIE 1944). ELLIS (1957) mentioned that wolves were seen feeding from garbage heaps.

In both North America and Eurasia ungulates seem to be the most important food items of wolves. The results of the present investigation confirm this impression. The percentage of small-sized animals, such as rodents and birds, varies according to the method used, the locality and the season. Generally it is below 10 %. They are only make-weights in the diet. This was already emphasized by MURIE (1944). The ease of catching seems to be an important factor, especially in areas under cultural influence (see also OGNEV 1931, 1959, FOWLER 1937, RAND 1945).

ROWAN (1950) reported that wolves use certain hunting routes (see also OLSON 1938 a and b). However, MURIE (1944), DEVOS (1950), THOMPSON (1952) and BANFIELD (1953), among others, were unable to observe their existence. The investigations of ROWAN (*op. cit.*) and BANFIELD (*op. cit.*), for instance, were performed in the Rocky Mountains (Alberta, Canada) in areas with very similar natural conditions. Thus this contrast between the different investigations does not, at least entirely, depend on differences between the natural conditions of different areas. The Finnish data are still scanty, but they seem to indicate that wolves have a tendency to use hunting routes, especially in areas where prey animals are plentiful and in summertime.

DEVOS (1950) studied wolves on Sibley Peninsula, in Ontario, Canada. The travel routes of timber wolves in his study area were apparently mainly influenced by three factors: the topography of the area, the distribution of the most important prey animals, and the seasonal changes in the climate. CRITCHELL-BULLOCK (1930), MUNSTERHJELM (1946) and THOMPSON (1952) reported that wolves regularly use the same travel routes when moving in a certain area. MACLULICH (1936), OLSON (1938 a and b),

THOMPSON (1952) and HARPER (1955, p. 20) observed that wolves use the same routes as their prey. The next step in this argument is that wolves follow the herds of their prey animals (see e.g. WRIGHT & SIMPSON 1920, CRITCHELL-BULLOCK 1930, OGNEV 1931, p. 195, HORNBY 1934, OLSON 1938 a, p. 327, PORSILD 1945, THOMPSON 1952, FERIANCOVA & KOMAREK 1955, MAKRIDIN 1959, KUYT 1962). MURIE (1944) verified that during the winter wolves were only locally dependent on the movements of the caribou herds, because they could use mountain sheep as their food.

In areas where only migrating individuals occur it is very often clear that wolves use certain travel routes. If there are ungulates which move in herds in the area, wolves often use game trails, i.e. the same routes as the prey animals. It is biologically very fitting that wolves should select the same routes as their prey animals, because in this way they avoid unnecessary travel.

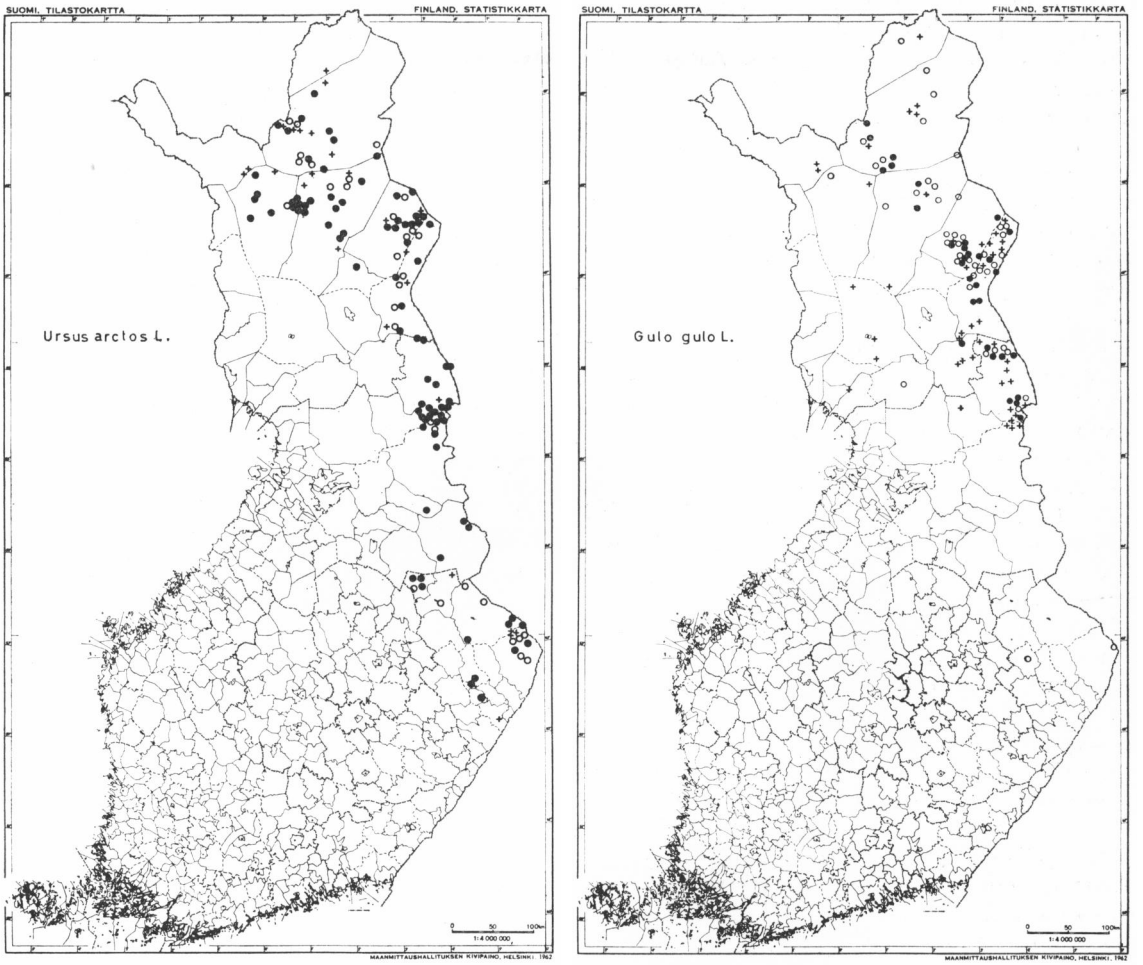
As long ago as 1904, ZHITKOV stated that the winter movements of wolves are dependent on the snow conditions (OGNEV 1931, p. 196). Thus snow forms a special problem in the winter ecology of wolves. OGNEV (*op. cit.*, p. 194) stated that deep, soft snow with no crust on it prevents the wolf from catching its prey and interferes with its movements. MUNSTERHJELM (1946, p. 78) reported the same thing. In the classical work of FORMOZOV (1946) concerning the adaptation of mammals to snow conditions, these animals are divided into the following categories: chionophobes (avoid snow), chioneuphores (adapted to snow conditions) and chionophiles (highly adapted to snow conditions or bound to them). According to him, the wolf is one of the chioneuphores.

A number of investigators (e.g. Anonymus 1914 b, OLSON 1938 a and b, DUNNE 1939, DEVOS 1950, BANFIELD 1954, BURKHOLDER 1959, FRANCIS 1960, PULLIAINEN 1962 b, 1963 c, ALLEN & MECH 1963) have reported that wolves like to travel on ice. ELLIS (1957) reported that wolves moved along the shores of lakes. DEVOS (1949) and BROWN & LANNING (1954) observed wolves on highways. It can be seen that the results of the present investigation support the investigations mentioned above.

It is also worth mentioning that snow conditions play an important role in the winter ecology of the caribou, too (PRUITT 1959).

BURKHOLDER (1959) reported that wolves travelled on an average 24.8 km a day (the longest distance travelled was 72.0 km). Thus the Finnish data are in excellent agreement with the results obtained in North America. PRUITT (1960) calculated that the mean running speed of the wolf was 6.4 km/h. The corresponding speed of the caribou, its prey animal, was 9 km/h. MUNSTERHJELM (1946), however, reported that when running on firm ground the wolf can overtake all the other animals of the North.

Many investigators (e.g. MURIE 1944, STENLUND 1955, CRISLER 1956, BURKHOLDER 1959, MECH 1962, 1963, ALLEN & MECH 1963) have recently concerned themselves with the following problem. Does the wolf select its prey animals according to their age, sex or condition? According to MURIE (1944, p. 231), the caribou killed by wolves are generally the slowest and weakest animals (see also MCCANN 1956). According to STENLUND (1955), wolves attack deer that are in good condition; only 7 per cent of the deer killed were old animals. Wolves did not select prey animals according to their sex. CRISLER (1956) carried out painstaking investigations on the relations between the wolf and the caribou. The main results of his studies are as follows. Healthy caribou may escape when wolves attack them. Calves may keep alive better when alone or in a small herd than when in a large herd. Injured and sick individuals readily fall prey to wolves. Half the killings observed by him fell into this category. CRISLER (*op. cit.*) concluded that wolves select their prey according to the condition of the animals. According to BURKHOLDER (1959), a wolf pack does not distinguish between the elk and the caribou; the kill is a function of the place. Nor do wolves select caribou according to their sex, age or state. All the caribou were in good condition. Wolves have no difficulty in catching their prey. They kill by biting and tearing. ALLEN & MECH (1963) carried out admirable studies in the Isle Royale National Park (Lake Superior, USA) (see also MECH 1962, 1963), where special efforts were made to observe hunts by the large wolf pack living there. In watches totalling 68 hours, 66 hunts involving 132 moose were witnessed. The pack actually tested 77 moose but killed only 6 of these, a »predation efficiency» of 7.8 %. In all, fifty-seven kills were found and 51 examined: 18 were calves, but most of the others were 8- to 15-year-olds. None was 1 – 6 years old.



Figs. 48 – 49. The occurrences of the bear and the wolverine in Finland. Symbols indicate places where bears and wolverines were killed during the years 1954 – 1963. Explanations: open circle = female, black circle = male, + sex unknown.

Thus a clear selection of prey animals was visible. In Finland it was observed that wolves preferred to kill certain species of domestic animals, especially sheep, which are easy prey. A great many reindeer are also killed by wolves in Finland every year. The wolves did not seem to select according to the age of the reindeer. Thus a kill is a function of the place. However, it is possible that seasonal variation exists in this respect.

5. Interspecific relations with the other large predators

In earlier papers (Pulliainen 1963 a, b, 1964 b, 1965 b) I have discussed the biology and distribution of the bear, wolverine (*Gulo gulo*) and lynx in Finland. In the following chapters I shall briefly discuss the interspecific relations of these four large predators in Finland.

A. The bear (Ursus arctos)

Ognev (1931, p. 194) already reported that where there are a large number of wolves, there are few bears and vice versa. In the northern parts of Eurasia this means that bears inhabit the inner parts of the taiga zone and wolves correspondingly live near the limit of the tundra and taiga zones and in the tundra zone. It is also a fact that wolves migrate far southwards to the taiga zone along the river valleys and

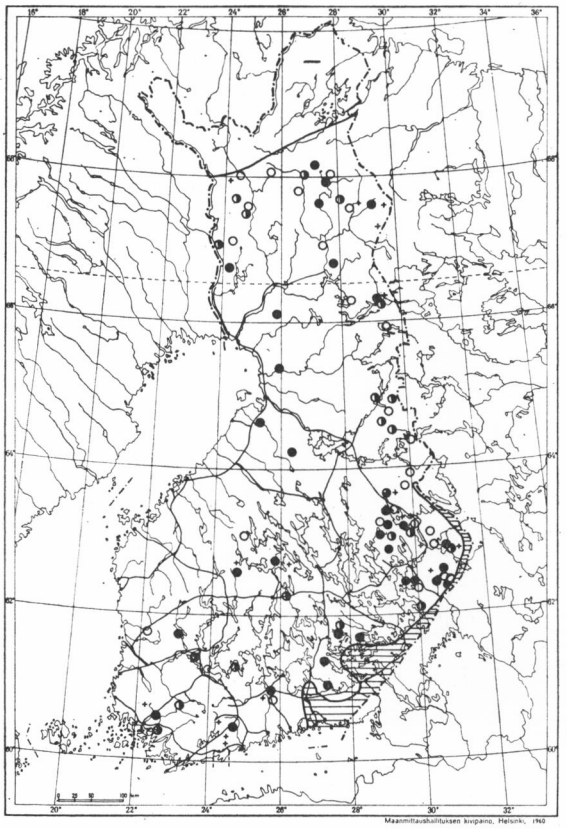


Fig. 50. The occurrence of the lynx in Finland during the years 1959 – 1962 according to the inquiries of the Game Research Institute. Explanations: open circle = 1959, black circle = 1960, half black circle = 1961 and + = 1962 (single observations), hatched area = area with a number of observations.

inhabited districts. The Arctic fox (*Alopex lagopus*) behaves in the same way, too (see the review by PULLIAINEN 1965 a).

In Finland, the bear is found in an area extending from the western to the eastern frontier in the north. Along the eastern frontier the area extends southwards to North Karelia (see Fig. 48; see also PULLIAINEN 1963 a). If a comparison is made between the northern breeding area of the wolf and the Finnish distribution of the bear, it can be seen that the two species do not inhabit the same ranges in Finland. It is obvious that they may migrate across the same areas, but nowadays they breed in different areas. The situation is clearer if it is dealt with topographically. The wolf tends to keep to the fells and the bear correspondingly to the forest zone. The same thing is also observed in Sweden (see HAGLUND 1965).

Bears kill few reindeer in comparison to wolves and wolverines. The bear is said to be one of the prey animals of the wolf (MUNSTERHJELM 1946, the present investigation).

I think that the predator-prey relation between the wolf and the bear influences the intolerance between the two species (see also KNEZEVIC & KNEZEVIC 1956). When the wolf expansion in North Karelia began, bears disappeared over vast areas. The same thing was observed on the boundary of the communes of Kuusamo and Suomussalmi, too.

Some exceptions to this rule were observed, however. In the breeding area of the wolf at Enontekiö, Tsuukisautsi, a bear appeared in summer 1963 only about 25 kilometres from a wolf den.

B. The wolverine (Gulo gulo)

No wolverines have been observed for many decades in the breeding area of the wolf at Enontekiö, Tsuukisautsi. In an area some ten kilometres southwest of this area occasional tracks of wolverine have been observed during this period (S. Aho). On the Marasto and Vibus fells at Inari wolves and wolverines occur on the same fells, but it was emphasized by the observers that the two species do not occupy the same areas. The district in question is part of the regular breeding area of the wolf, whereas the main breeding area of the wolverine is in the communes of Sodankylä and Savukoski, where the population density is highest (see Fig. 49).

The wolf and wolverine kill almost equal numbers of reindeer yearly (Table 15, pp. 242 – 243). Over 90 % of all the reindeer killed by predators are killed by these two species. In fact, the species in question may be considered food competitors. I think that this is one of the reasons why they do not inhabit the same areas. When the population densities of these species are as low as they are today, the species can very easily occupy different areas.

It is known, however, that the wolverine will eat reindeer killed by wolves, if these are available. If the wolf enters a new area within the home range of the wolverine, the latter abandons the area. This was very clearly observed on the boundary of the communes of Kuusamo and Suomussalmi. When the wolf expansion took place, the wolverines of the area moved away. In the communes of Savukoski

and Salla it was observed that the bear and the wolverine prefer to inhabit different areas (see PULLIAINEN 1963 a).

C. The lynx (Lynx lynx)

The lynx is one of those members of the Finnish fauna whose distribution does not extend to the northernmost parts of Lapland (see also STOLLMAN 1963). For this reason it does not occur in the northern breeding area of the wolf. Most of the Finnish lynxes are migrants that have come over the southeastern frontier (between the communes of Ilomantsi and Virolahti; see Fig. 50). Sometimes lynxes cross over the frontier as far north as Salla. It is interesting to note that most of the lynxes in the southeast crossed the frontier in the area where the population density of the wolf during the expansion was lowest (cf. Figs. 16 – 25).

The wolf is the most important natural enemy of the lynx (MUNSTERHJELM 1946). In the diagram (Fig. 51) I present the official statistics of wolves and lynxes killed in Finland during the years 1866 – 1906. The statistics of the years 1866 – 1878 are presented as three means. The numbers of wolves killed yearly decreased greatly after 1879. The decrease was rapid and no return to the former level occurred. When the numbers of wolves decreased, the population density of the species also decreased. At this time the population density of the lynx began to rise. At the same time the numbers of lynxes killed yearly also began to increase. The peak was reached in 1885. After this year the numbers of lynxes killed began to decrease again. Perhaps two factors affected this situation. At first, when the population density of the wolf was great, wolves kept the population density of the lynx low. After the decrease of the wolf

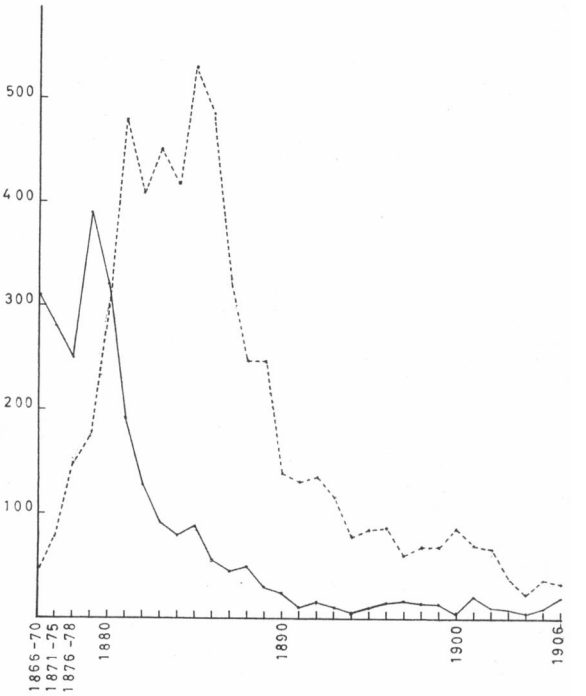


Fig. 51. The numbers of wolves (even line) and lynxes (broken line) killed in Finland during the years 1866 – 1906, according to the official statistics.

population the population density of the lynx may have increased. It can also be assumed that when wolves became scarcer, the hunters began to shoot lynxes in greater numbers.

I do not think that there is any food competition between these species (see also HAGLUND 1965). The main food of the wolf is ungulates (the present investigation), whereas the food of the lynx is hares, foxes, etc. (see e.g. MUNSTERHJELM 1946, SIIVONEN 1956, HAAPANEN 1960, PULLIAINEN 1964 b).

VI. General discussion

In the 1800's, great changes took place in the Fennoscandian wolf populations. Official statistics of the wolves killed are a fairly reliable index of these changes. However, JOHNSEN (1929) already emphasized that there are some uncertainties in these statistics.

The Swedish statistics in question (Fig. 52) show that the first remarkable decrease in the numbers of wolves killed took place in the 1830's and 1840's (LÖNNBERG 1934). Twenty years later a second decrease took place. After this, the numbers of wolves killed fluctuated within relatively narrow limits. In Norway (Fig. 53) a remarkable decrease parallel to the second Swedish decrease took place in the 1860's (JOHNSEN 1929). After this the situations in the two countries were similar. In Finland the first remarkable decrease only took place in the 1880's (Fig. 26). After this, the corresponding numbers of wolves fluctuated fairly evenly

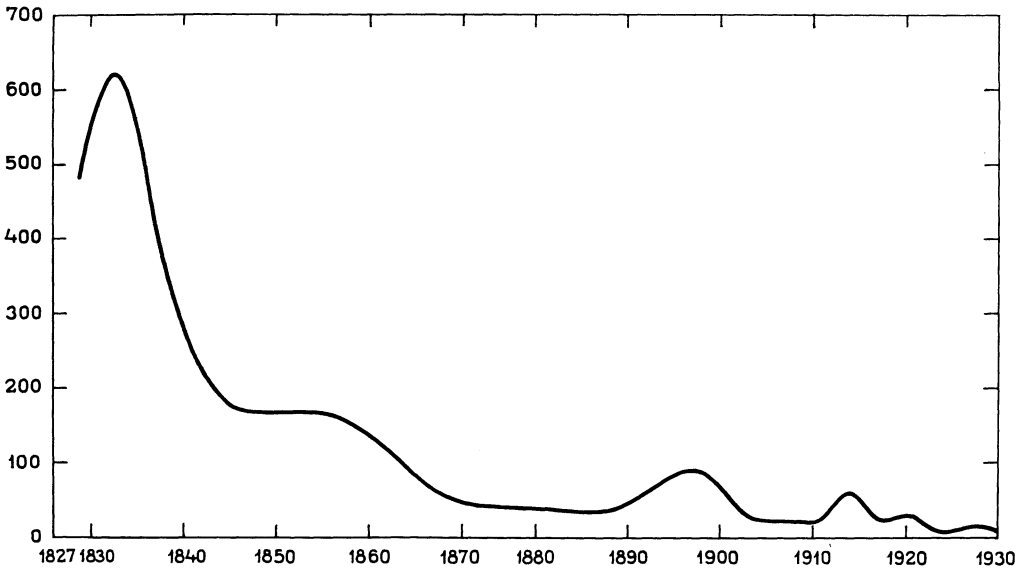


Fig. 52. The numbers of wolves killed in Sweden during the years 1827 – 1930, according to LÖNNBERG (1934).

from year to year. At times there have been small increases, as in the beginning of the 1960's.

In Norway and Sweden the last remarkable decrease in the numbers of wolves killed thus took place simultaneously and in Finland 20 years later. The causes which led to these changes in the wolf populations were common to all these countries. The most important factor was man and his activities. When the populations of the great predators were dense, these animals killed great numbers of domestic animals yearly (see e.g. SUOMALAINEN 1922, JOHNSEN 1929, LÖNNBERG 1934; see also pp. 238 – 242). It is natural that in these conditions the state paid a bounty for wolves shot (see LÖNNBERG 1934, pp. 1 – 2). Many decades of keen hunting of these predators produced a result, i.e. their numbers decreased strongly and did not increase again remarkably. Over vast areas the large predators, including the wolf, were exterminated. However, small populations still survived in the vast forests and on the fells. The expansion of settlement and agriculture was also a factor aiding in the extermination of the large predators, especially the wolf.

As mentioned above, the numbers of the bear, wolverine and lynx likewise decreased. The decline in the population began simultaneously in the bear and the wolf, but it took place more slowly in the former (see KUJALA 1932, SIIVONEN 1956, PULLIAINEN 1963 a). At the same time a decrease in the wolverine population took place, but likewise continued somewhat more slowly than with the wolf (see SIIVONEN 1956, PULLIAINEN 1963 b). The lynx population decreased somewhat later than the wolf population (see p. 251), but eventually the lynx was almost totally exterminated (PULLIAINEN 1964 b, 1965 b). As the numbers of the large predators decreased, some regularities could be observed. At first these predators disappeared from the southwestern archipelago, the southern coastal zone and the surroundings of Lake Saimaa. In the settled parts of Finland the last wolf populations were to be found on the Suomenselkä ridge. Later, the boundary between the unsettled and settled parts of the country has been the southern limit of distribution of the bear and wolverine (for further details, see PULLIAINEN 1963 a and b).

When the wolf populations of South and Central Finland were destroyed, the last wolves retreated to the most suitable habitats in Lapland where food resources and snow conditions were favourable. The best areas in this respect were the Scandinavian Mountains and the sharply outlined fells of Finnish Lapland. In the tundra zone the distribution of the wolf is limited by the distribution of the reindeer and wild reindeer (MIDDENDORF 1875). Because reindeer are abundant, the wolf population might have been expected to increase. However,

man can very effectively regulate the density of wolf populations, if he wants. The reindeer-keepers of Finnish Lapland know the wolves of the district individually by their tracks. By destroying wolf dens and cubs they keep the wolf population below a certain limit. They can distinguish the sexes from the size of their tracks, and do not kill the females, because they then lose the easy bounty for the cubs. For this reason the mean age of wolves has increased. It was shown by PALMGREN (1920) that in bears the number of progeny decreases with age. Perhaps the same is also true in the case of wolves. It is very difficult to say to what extent a low population density and inbreeding have led to degeneration of the Fennoscandian wolf stock (cf. the other mammals, VOIPIO 1948, 1950, 1952, BUTLER 1953; cf. also INGLES 1963). Many factors are known to play a role in the population dynamics of the species (cf. also ANDREWARTHA & BIRCH 1954). The following factors, for instance, are known to be significant in this respect: itch, distemper and rabies (e.g. PIKE 1892, SETON 1911, 1929, ANDERSON 1938, MURIE 1944), endoparasites (e.g. CRITCHELL-BULLOCK 1930, MAKRIDIN 1959, OGNEV 1959, RAUSCH & WILLIAMSON 1959), scarcity of food (e.g. HORNBY 1934, CLARKE 1944, ERRINGTON 1946, BANFIELD & TENNER 1958; cf. MURIE 1944), cannibalism (e.g. OGNEV 1931, p. 197, MUNSTERHJELM 1946, MAKRIDIN 1959, FRANCIS 1960) and intraspecific intolerance (e.g. MURIE 1944, 1945, SCHENKEL 1948). In Finnish conditions, at least, diseases (cf. LAMPIO 1946 a, MUROMA 1951 a and b) and food resources are not known to have had any noticeable influence on population dynamics. MUNSTERHJELM (1946) emphasized the importance of rut fights and cannibalism in this respect.

A population has a tendency to grow when one or more of the limiting factors are removed. According to the experiences obtained in Fennoscandia, it is known that man can very effectively regulate wolf populations. Before the First World War people in both Eastern and Western Europe took action against wolves. From the west to the east wolves were gradually exterminated (see KNEZEVIC & KNEZEVIC 1956). Since the First World War great changes have taken place in the political structure of Europe. The centralized economic system dominates in the east. In the west traditional free enterprise dominates. When the new political system came into being in the Eastern European countries,

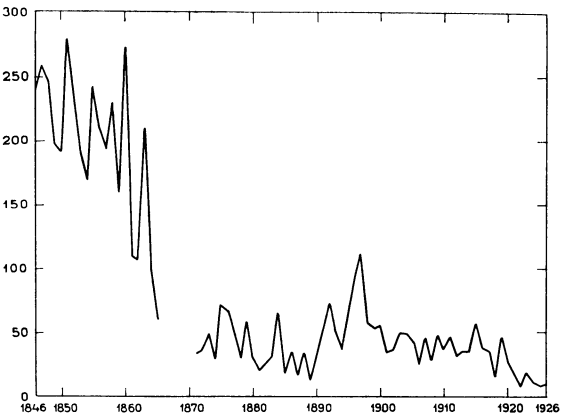


Fig. 53. The numbers of wolves killed in Norway during the years 1846 – 1926, according to JOHNSEN (1929).

great structural changes (see KAURI 1957) took place in society. Factors of biological importance were the changes in landownership, agriculture and hunting, for instance. Hunting as a sport and trade ceased to exist. Hunting under state control took its place. Official hunters were mainly interested in fur-bearers, and little attention was paid to wolves and other predators. Landownership and game management were the province of the state. The status of the individual as a sportsman and hunter had changed. It is not surprising that in these conditions game tended to increase. In many strategically important areas fields returned to forest. Many different animal species have adopted niches in the pioneer stages of natural forest succession (see SEISKARI 1962). Increases in populations of small game tend to be followed by increases in the populations of their predators. Since the destructive effect of man on predator populations was absent, the chances of such an increase were perhaps optimal. Besides wild animals the predators could use as their food domestic animals, such as cattle (see e.g. KNEZEVIC & KNEZEVIC 1956). As the numbers of predators increased, the population pressure naturally increased and the species widened their ranges. It is to be noted that this took place simultaneously throughout the eastern bloc (see e.g. ZIVANZEVIC 1951, FERIANCOVA & KOMAREK 1955, KNEZEVIC & KNEZEVIC *op. cit.*, KAURI 1957, ATANASSOV 1957, DULIC & TORTIC 1960, Anonymus 1960 a, RACA 1960, Anonymus 1960 b, CVIJETIC 1960, KORITNIK 1960, IVKOVIC 1960, ATANASSOV & PESCHEV 1963). The ex-

pansion of the species took place into the former ranges of the species. It is clear that during recent years a great deal of attention has been paid to the great abundance of wolves in Eastern Europe (see also MAKRIDIN 1959).

The most interesting area from the standpoint of the present study is that just beyond Finland's eastern frontier. Before the Second World War the wolf bred at Pieninkä, a vast primaeval forest in the area of Aunus (Olonetz) and Viena (Onega), behind the eastern frontier (see also MARWIN 1959). After the Second World War Finland ceded large areas in Karelia to the U.S.S.R. Most of the ceded land remained neglected. Fields and meadows returned to forest. These areas became very suitable for game (cf. the rented area of Porkkala, BERGMAN 1957, 1958). I think that in these conditions the wolf population of Pieninkä as well as the more eastern wolf populations increased and spread westwards. Before the Second World War the wolves of Pieninkä extended their winter migrations to the north coast of Lake Ladoga (A. J. Valkama, pers. communication). As the range of the wolf population widened, these animals reached the area ceded after the Second World War. There they found a very plentiful game population, and very soon occupied the area. Then (in the beginning of the 1950's) the wolves migrated to Finnish North Karelia in winter. During the years 1956 – 58 (Figs. 13 – 15), the winter migrations of the species to this area increased very markedly. In 1959, wolves were seen in the neighbourhood of the eastern frontier before the summer was over. Perhaps they had even been there earlier, but had not been observed. In 1960, the migrations clearly increased. This could be seen from the increase in the numbers of domestic animals killed by wolves, the increase in the number of reports, etc. In 1961, the expansion was so strong that it could be followed throughout the year and compared with the annual rhythm of the wolf. If one looks at the recent (1956 – 63) history of the wolf in North Karelia, one can understand the expansion mechanism of the species.

During the years 1956 – 58, the population was still a considerable distance from the frontier and only in winter, the season when the wolf's range is at its widest, were wolves seen on the frontier. In summer 1959, wolves were seen on this side of the frontier, which was connected with the widening of the range in late summer. In 1960, the numbers of wolves were greater and they appeared earlier than they had the previous year. In 1961, the population was so near the frontier that some wolves were observed in June, and in August the females took their cubs with them on this side of the frontier. During the summer the range of the wolves continuously expanded in North Karelia. At the same time, there was a great increase in wolf-hunting. Using many different methods, people succeeded in killing a great number of wolves (see also RANTANEN 1962, 1964). Simultaneously, the wolves learnt to avoid traps set by the hunters (cf. also OGNEV 1931, p. 210). When wolves were hunted they very often returned to the U.S.S.R. (where they were undisturbed). Partly owing to man's activities and partly owing to population pressure, wolves migrated first to Kuhmo (Kn) and later on to the boundary of the communes of Kuusamo (Ks) and Suomussalmi (Kn). In the latter area the expansion reached its peak during the winter of 1962/63. In summer 1963, only a few domestic animals were killed by wolves in North Karelia. Likewise the observations on wolves decreased. Here again man demonstrated that he can regulate the numbers of wolves [cf. the effect of man on red fox (*Vulpes vulpes*) populations, SIIVONEN 1959]. If these activities had been absent, it is likely that wolves would have repopulated large areas of Finland. It was observed that wolves showed a tendency to become resident even when they migrated to Southwest Finland via the Suomenselkä (cf. the birds, KALELA 1954 a and b, 1958 and the Arctic fox, PULLIAINEN 1965 a). If these wolves had not been killed, they would have caused an expansion of the range of the species. When migrating, wolves use definite migration routes (see Fig. 46; see also SIIVONEN 1952 a and b).

MAYR (1939) divided the sex ratios of birds into the following categories: the primary sex ratio occurs during the embryonic period, the secondary sex ratio is that at hatching and the tertiary sex ratio relates to the time at which the offspring reach maturity, i.e. to birds that have passed the nestling or juvenile stage in general. In the present work only tertiary sex ratios have been considered. According to STENLUND (1955), there is an excess of males in wolf populations. However, MAKRIDIN (1959) killed 133 tundra wolves, and of these 78 (58.6 per cent) were females and 55 (41.4 per cent) males, the difference between the numbers being statis-

tically significant ($\chi^2 = 3.978$). MARKLEY (1945) studied coyote (*Canis latrans*) populations in the western United States. In one population there was an excess of females and in two cases the situation was the reverse. LUND (1959) studied the sex ratio of the Norwegian red fox populations. He reported an excess of males. The same situation is known to occur among dogs (*Canis familiaris*) (according to LUND *op. cit.*) and muskrats (*Ondatra zibethicus*) (in Finland, LAHTINEN 1953; see also the review by LAMPIO 1965). According to LAMPIO (*op. cit.*), a sex ratio of 50.8 ± 0.2 per cent of males occurs in the Finnish squirrel (*Sciurus vulgaris*) populations. I have observed an excess of males in the mallard (*Anas platyrhynchos*) populations overwintering in Finland (PULLIAINEN 1963 d; see also the review by HILDÉN 1964). There is an excess of males at the edges of the populations of some animal species (e.g. the roe-deer, *Capreolus capreolus*, KALELA 1948, the marten, *Martes martes*, LAMPIO 1951 b, p. 19, the bear, *Ursus arctos*, PULLIAINEN 1963 a, some small bird species, v. HAARTMAN 1952). It is also a fact that male wolves migrate over large distances at the edges of populations (see e.g. MOHR 1953, TENIUS 1956, the present investigation). The lynx (*Lynx lynx*) differs from the species mentioned above, because most of the migrants are females (PULLIAINEN 1964 b, 1965 b). From the present study it seems that in the wolf it is mainly the males that migrate, whilst in the breeding area and its vicinity the sex ratio is very near 1 : 1. In North Karelia it could be seen that as the breeding area of the species approached the frontier, the sex ratio came nearer the ratio 1 : 1.

The fact that the Finnish (and North Karelian) wolf population has been in close connection with the wolf population of Northeastern Europe can be seen from the distribution of the two colour phases, too. The wolf population of the Scandinavian mountains has been much more isolated.

Summary

1. The data of the present study were collected by many different methods. The basic material consists of information gathered from different newspapers (over 10 000 numbers checked) and inquiries made by the Game Research Institute of the Finnish Game Foundation. 125 wolf skins were studied in the Zoological Museums of the Nordic countries and Leningrad (the U.S.S.R.), private and official collections, etc. Three cubs (2 males and a female) taken blind from a den at Inari, Lapland, were studied in captivity. The data relating to various aspects of the biology of the wolf were subjected to numerous comparisons and analyses.

2. In the 1880's, a great decrease took place in the Finnish wolf population. In 1900, wolves were still to be found in the eastern and northern parts of Finland. Since that date the numbers of wolves in Finland have fluctuated to some extent from year to year. This can be seen from the statistics of wolves killed and from the numbers of reports of wolves. The last typical expansion of the species began in North Karelia in 1959. It reached its peak in 1961, after which there was a rapid decrease. The expansion in question began when the wolf population beyond the eastern frontier increased and expanded westwards. The occurrence of wolves in North Karelia was studied in the light of the annual rhythm of the life of the species.

3. Most of the migrating wolves were males, but as the breeding wolf population neared the eastern frontier, the excess of males decreased.

4. Two colour phases can be distinguished among forest wolves (*Canis lupus lupus* Linnaeus 1758). The individuals of the first phase have a black stripe running down the front of the fore-leg. In the other phase this stripe is absent. Among Fennoscandian wolves the former phase is more abundant than the latter. Wolves without the black stripe become significantly more abundant towards the east.

The relationships of the two races, *Canis lupus lupus* L. and *C. lupus albus* Kerr., the tundra wolf of the arctic coasts of U.S.S.R., are discussed.

5. Three periods can be distinguished in the weight increase of wolf cubs: a period of maximal growth (at the age of 0 – 14 weeks), a period of rapid growth (at the age of 14 – 27 weeks) and a period of slow growth (27 – 51 weeks). The weight continues to increase slowly after the age of 51 weeks, but no exact data are available. During the first and third periods the weight increase of males is greater than that of females. During the second period the weight

of the two sexes increases at the same rate. An inner rhythm is suggested to regulate the weight increase of the cubs.

6. The mean weight of wolves over eight months old is 41 ± 5.7 kg and the corresponding value for females is 32 ± 4.4 kg.

7. Most of the copulations of Finnish wolves take place in March.

8. In Finnish Lapland the wolf still breeds in the fells of the communes of Enontekiö (EnL) and Inari (InL). Generally both parents take care of the young, but in North Karelia it was observed that the female can rear her young alone.

9. During the development of the cubs there are different stages characterized by a widening of the home range and increasing versatility of their activities.

10. Females are generally leaders of the packs in winter. The size of the packs depends on the population density and season. In winter two packs may combine to form a large pack (even more than 10 individuals in Finland nowadays).

11. The packs break up in late winter, but the individuals may join together again for a short time. Generally, wolves show great sociability throughout the year except for pairs during the breeding season.

12. The winter habitats and migration routes of wolves are characterized by a thin snow cover and terrain where movement is easy. Wolves very often use the same routes as their prey animals.

13. Domestic animals and elk are the most important food of wolves in the forest zone. In Lapland and in other areas where reindeer are reared, this species constitutes their most important food. Small animals like rodents and birds are only makeweights in the diet.

14. Wolves do not select reindeer according to their age or size. The kill is a function of the place and time.

15. Wolves travel 23 km a day, on an average, in the forest zone.

16. The food biology of the species is discussed and compared with the results obtained in North America.

17. The bear, wolverine and lynx avoid the range of the wolf.

18. The history and recent distribution of the species in Northern Europe and the population dynamics of the species are discussed.

Acknowledgements. I wish to tender my thanks to all those persons who have kindly helped me in the completion of this work. My deepest gratitude is due to Dr. JUKKA KOSKIMIES, who suggested the subject of this study and who has afforded me his encouragement and generous advice on many problems throughout the course of the work. Further, I express my sincere thanks to Professor ERNST PALMÉN, Professor OLAVI KALELA, Professor PONTUS PALMGREN and Professor ESKO KANGAS, for their valuable criticisms concerning the manuscript. I wish to thank Professor ESKO KANGAS, Head of the Agricultural and Forest Zoological Institute, Professor ERKKI KIVINEN, Rector of the University and Professor PAAVO ROINE, Head of the Department of Nutritional Chemistry, for working facilities.

My sincere thanks are also due to Mr. KALERVO SALONEN, M. For., for helping me during this work. I am also indebted to Mr. HELMER OKSANEN, M.Sc., Miss LEENA JOUSINEN, Mrs. AUNE JANTUNEN and Mr. MATTI RINNE for their practical assistance. I also wish to thank those 300 observers and collaborators who helped me during the course of the field work.

I am indebted to Mr. ANTTI MUSTAKALLIO, Director, and Mr. YRJÖ KORHONEN for the gift of the wolf cubs.

I express my gratitude to Mr. HANNU ESKELINEN, M.A., for translating the Russian publications, and to Mrs. JEAN MARGARET PERTTUNEN, B.Sc., who has checked the English of my manuscript.

This study has been aided by grants from the University of Helsinki, the Finnish Game Foundation, the Finnish Cultural Foundation and the Foundation for Research on National Resources in Finland, for which I would like to record my sincere gratitude.

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Received 20 IX. 1965
Printed 1. XI. 1965