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The status, structure and behaviour of populations of the wolf (Canis l. lupus L.) along the Fenno-Soviet border[1]

Erkki Pulliainen

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Since 1950 Finland has received two expansions of the wolf (*Canis l. lupus*) from the east, mainly from Soviet Karelia into Finnish Northern Karelia and Kainuu, the first in 1959—63 and the second beginning in 1975. Before and during both expansions most of the wolves wandering in Finland were males, but as the breeding population approached the frontier the excess of males decreased. Groups reaching western and southern Finland (mainly along certain specific migration routes) usually consisted of one to four wolves, but in eastern Finland some packs were larger, and in 1969—79 pups aged 4—10 months were also seen. From studies carried out in Soviet Karelia and records of wolves crossing the Fenno-Soviet border it appears that under present-day conditions the saturation point of the Soviet Karelian wolf population is roughly five to seven individuals per 1000 km^2. Continuous hunting of a wolf population disturbs its self-regulation mechanism and enables it to attain its potential maximum productivity, which explains the rapid growth of populations in Soviet Karelia and the Leningrad Region of the USSR in the 1970s. In January 1979 there were about 100 wolves in Finland.

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1. Introduction

At the beginning of the 19th century the range of the wolf (*Canis l. lupus* L.) included the whole of Finland. The decline began on the Åland Islands, where the last wolf was killed in 1844 (Salovaara 1930), but in the 1880s wolves were still to be found in all parts of the Finnish mainland. Thereafter, the decline was rapid, and by 1900 the species bred only in the eastern and northern parts of the country (Palmén 1913).

In the Scandinavian Peninsula the wolf population had been decimated some decades earlier than in Finland, although the remnants were able to survive in northern Scandinavia for a considerable time with a surprisingly small population base (Haglund 1973). As far as Finland is concerned this base has been the wolf populations inhabiting the Kola Peninsula, Soviet Karelia and the surroundings of Lake Ladoga.

The purpose of the present paper is to provide records on the status, structure and behaviour of wolf populations along the Fenno-Soviet border.

2. Material and methods

When studying the wolf expansion of 1959—63, I was greatly assisted by the Finnish Border Patrol Establishment (Pulliainen 1965), and these experiences led me to suggest that the daily patrols along the frontiers between Finland and its neighbouring countries could record every crossing of the frontier by the large predators and estimate or calculate the numbers of these mammals in the areas under their surveillance three times a year. This proposal was accepted by the commander of the Border Patrol Establishment, and data from this observation line 2574 km long are now available for a period of over 11 years (1968—1979). The records made during this time show a total of 4195 crossings of the frontier by wolves.

Wolf tracks are easy to observe and identify in snow. In the northernmost parts of Finland the snow disappears in late May or early June and may appear by the end of September, or more normally in October, while in the south-east it may last only 3 or 4 months. This difference

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must be kept in mind when assessing the crossing data, although even in snowless conditions wolf tracks can be identified in sandy, wet or muddy ground, for instance. It should be noted that the members of the Border Patrol Establishment are taught during their preliminary training to recognize the tracks of wolves and other large predators.

The Russians follow the trends in the populations of the large predators by skiing along observation lines in different parts of the country and counting the numbers of tracks of these animals crossing the lines (Danilov et al. 1978). The results are then expressed as the numbers of tracks per 10 km of observation line.

It is interesting to compare the Finnish data with the corresponding Soviet Karelian data. Fig. 1 shows the total numbers of crossings of the frontier by wolves recorded in Finnish Northern Karelia and the numbers of tracks/10 km found in the corresponding Soviet Karelian area in 1968—76. Upward trends are clearly visible in both sets of data, and can be explained in terms of an increase in the numbers of wolves in Soviet Karelia from 1971 onwards, leading to an expansion into Finnish territory after 1974.

The crossing data give a reliable picture of the relative changes in the mobility of wolves (see also Pulliainen 1979b), but do not reveal the actual number of animals involved, for one individual may cross the frontier several times during a year. Nor is it reasonable to calculate rates of immigration or emigration from these figures, as few observations can be made during the snowless season, and possibly the wolves return to the USSR to breed at that time of year.

Information on all wolves killed and found dead in Finland was sought through every available channel of enquiry.

3. Results

3.1. Finnish wolf populations

Of the 4023 crossings of the frontier by wolves recorded in 1968—78 by the Border Patrol Establishment 4007 (99.6 %) took place across the border between Finland and the USSR, 14 (0.3 %) on the Norwegian frontier and two (0.1 %) on the Swedish frontier. During 1968—72 the number of crossings varied between 70 and 115, in 1973 the records showed 192 crossings, and there was then a very sharp rise, from 129 in 1974 to 1259 in 1977 (Fig. 2). This rise took place especially in Northern Karelia (Lieksa and Ilomantsi) and southern Kainuu (Kuhmo), although in 1976 and 1977 wolves were recorded all along the border between Finland and the USSR (Fig. 3). At that time no rise was shown by the figures for the Norwegian or Swedish frontiers, although a few wolves did enter Swedish Lapland from Finnish Lapland. The crossing data and other observations made indicate that 1977 may represent the peak year for the present expansion of wolves from the east, for the total number of crossings was smaller in 1978, and this downward trend has continued during the first 5 months of 1979.

The patrols have estimated the numbers of wolves three times a year (1 January, 1 June and 1 October) over the 11-year period within a zone

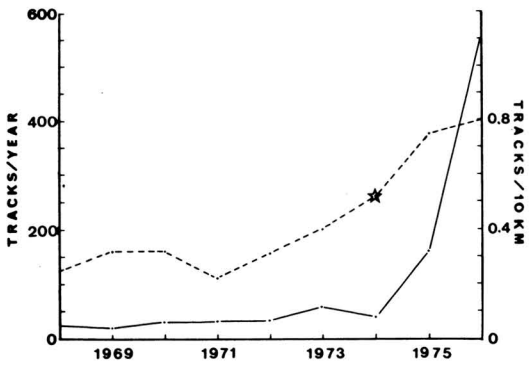

Fig. 1. The total numbers of crossings of the frontier in Finnish Northern Karelia (left scale; solid line) and the mean numbers of crossings of observation lines by wolves in the adjacent Soviet Karelia (right scale; dotted line; Danilov et al. 1978). A star indicates the saturation point of the wolf population of this part of the Karelian ASSR (see also text).

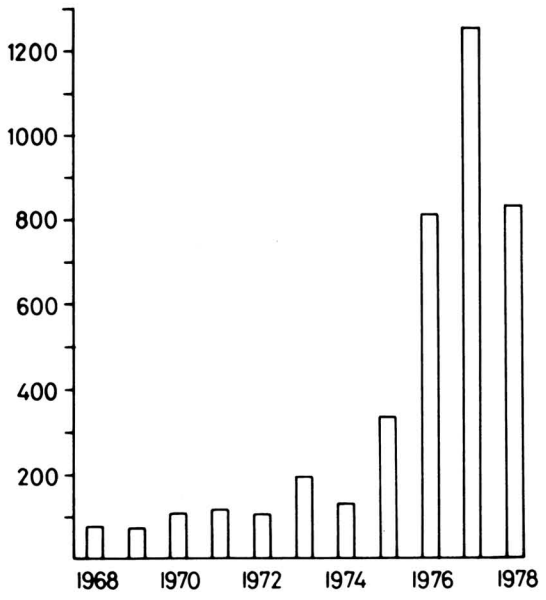

Fig. 2. The total numbers of crossings of the Finnish frontier by wolves recorded by the Border Patrol Establishment in 1968—78 (see also text).

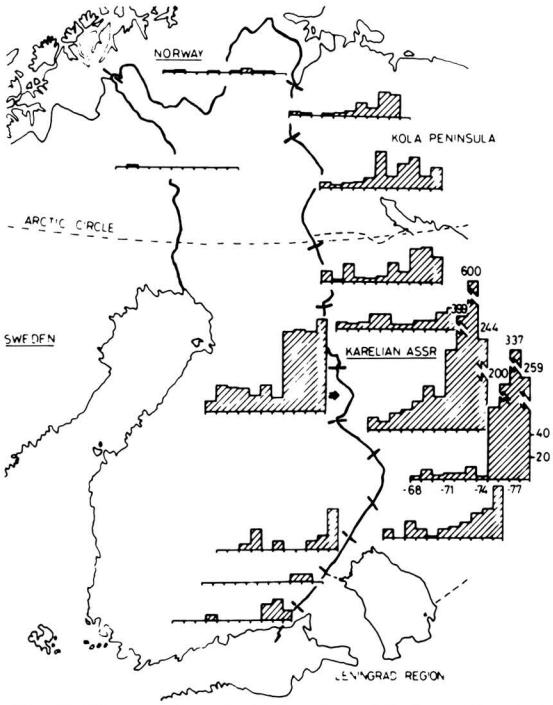

Fig. 3. The numbers (calculated per 100 km of frontier) of crossings of the different parts of the Finnish frontier by wolves recorded by the Border Patrol Establishment in 1968—78.

at least 20 km wide adjacent to the frontier. The most reliable estimates are naturally those based on observations in the snowy season, i.e. 1 January. These show that the majority of wolves occurred in the vicinity of the frontier between Finland and the USSR (Fig. 4), the numbers varying between 6 and 24 in 1969—75, but increasing from 1976 to 1978. The total figure reported for 1 January 1978 was somewhere between 77 and 89, but on 1 January 1979 it was again smaller (between 63 and 70).

The majority of the "Finnish" wolves taken into account in these estimations have been moving in the vicinity of the border between Finland and the USSR in units of 1 to about 10 individuals, and may have crossed the border almost daily. When pursued on the Finnish side, they retreated to the Russian side. In the inner parts of Finland wolves have also been seen moving in units of 1—4. They use the old migration routes (Fig. 5), and since 1970 individuals have been seen in western and southern Finland. The total information available indicates some 30 wandering wolves in January 1979. Thus at the beginning of 1979 Finland had about 100 wolves.

The sexing of 123 dead wolves in Finland in 1969—1979 showed that 65.8 % were males, a disparity which is statistically highly significant. The 48 wolves examined in 1968—75 included 38 males (almost 80 %), and correspondingly the 75 wolves examined in 1976—79 included 43 males (57.3 %), there being still a slight, although statistically non-significant, excess of males.

Table 1 shows the sex ratios of wolves killed in different parts of Finland in 1948—63 and 1969—79. The wolf is known to have bred in the north of Finland (Lapland) in 1948—53, and at that time the 25 dead individuals included nine females. In 1969—79 almost all the wolves moving in this area were killed by reindeer-owners, and among nine individuals sexed there were seven males.

Both the district between Savukoski and Kuhmo and that of Northern Karelia lie along the border between Finland and the USSR (Fig. 5). The expansion of the wolf from the east, which reached Northern Karelia and the southern part of the Kuhmo-Savukoski district in 1958—63, led to an even sex ratio in the former area but an excess of males in the latter. In 1969—79 the Savukoski-Kuhmo district also had a statistically significant excess of males. In Northern Karelia there were five males and one female among the dead wolves encountered in 1972—75, but an even ratio of 16:15 in 1976—79. Excesses of males among the dead wolves were found in 1948—63 and 1969—79 in the other parts of Finland where wandering wolves occurred.

Among the 29 wolf pups aged 4—10 months killed in Finland in 1969—79 (Table 2), there

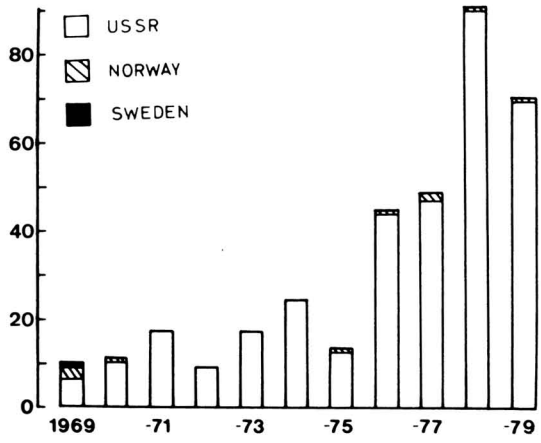

Fig. 4. The numbers of wolves in the vicinity of the Finnish frontier on 1 January 1969—79 according to the estimate of the Border Patrol Establishment (see also text).

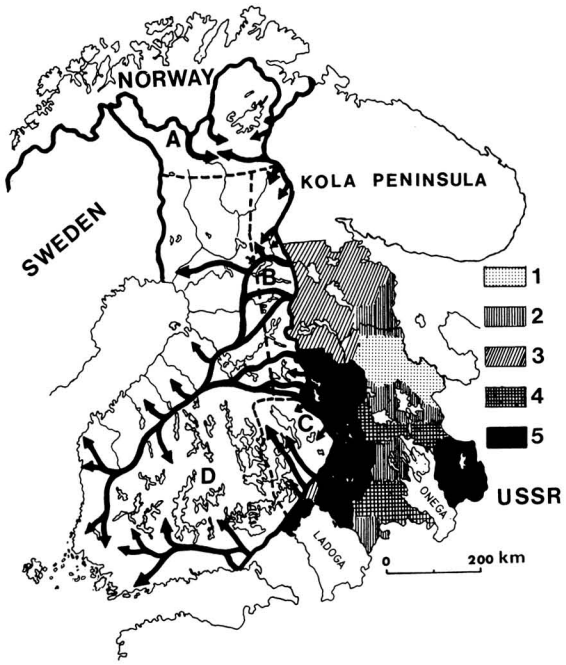

Fig. 5. The main migration routes of wolves in Finland, numbers of crossings of observation lines by wolves in the Karelian ASSR in winter (according to Danilov et al. 1978; abbreviations: 1 = 0.19 or less, 2 = 0.20—0.29, 3 = 0.30—0.39, 4 = 0.40—0.49 and 5 = 0.50 or more tracks/ 10 km of observation line) and the Finnish study areas mentioned in Table 1 (A = Lapland, B = the Savukoski-Kuhmo district, C = Northern Karelia and D = the other parts of Finland).

was a slight, but statistically non-significant, excess of males (58.6 %). There are probably only two cases (Nos. XI and XVI) in which the figures represent a complete litter.

3.2. Soviet Union wolf populations

According to Danilov et al. (1978), the mean number of wolf tracks per 10 km in the whole of Soviet Karelia in 1961—76 was 0.4. The population was largest (0.5—0.6 tracks/10 km) in the southern and central parts of this area (Fig. 5), which are characterized by abundant populations of moose (*Alces alces* L.) and reindeer (*Rangifer tarandus* L.); in the northeastern part there are fewer moose and reindeer, and also fewer wolves (0.2—0.3 tracks/10 km).

Danilov et al. (1978) report that before 1940 wolves were rare in northern Soviet Karelia (see also Marvin 1959), the few individuals inhabiting cultivated areas and the coasts of the White Sea. Practically no wolves occurred in the taiga. In the late 1940s intensive clear-cutting was commenced in these forests, and the conifers were replaced by deciduous trees, which offered food for the moose populations and enabled these to increase greatly. At the same time reindeer husbandry was discontinued in the area, and the semi-domestic reindeer (*R. t. tarandus* L.) returned to the wild state, while the wild forest reindeer (*R. t. fennicus* Lönnberg) were no longer hunted. Thus there was abundant food for the wolves, which could move freely along the forest roads, trails of ungulates, and other paths. Consequently, the wolf population expanded northwards at the same time both in Karelia and in the adjacent Arkangelsk area (see also Semenov 1976).

Table 1. Sex ratios of wolves killed in Finland in 1948—63 and 1969—79.

Area	1948—63 ♂%	*n*	1969—79 ♂%	*n*
Lapland	64.0	25	77.8	9
The Savukoski-Kuhmo district	72.3	47	67.2	58
Northern Karelia	46.9	49	56.8	37
The other parts of Finland	88.9	18	73.6	19

Danilov et al. (1978) drew attention to the threefold increase in the Karelian wolf population from 1966—69 (0.2 tracks/10 km) to 1973—76 (0.7 tracks/10 km), attributing this to two factors, the improved food situation mentioned above and the reduced control during the years when small numbers of wolves were recorded.

Bibikov (1973) reported that there were 300 wolves in Karelia in the early 1970s. These two sets of data, taken together, can be used to estimate that at the time of the maximum in 1976 there may have been 800—900 wolves in Soviet Karelia. During the 1978 hunting season 151 wolves were killed in the area (official statistics).

Bibikov (1973) further stated that at that time there were 140 wolves in the Leningrad area, where the population probably also increased, for, according to the local authorities, there were some 500 in that area in 1978. The official goal is to reduce the number to 150 in a forest area of about 60 000 km^2.

In 1973 Bibikov reported that there were 30 wolves in the Kola Peninsula, inhabiting its western and southern parts. No later reports are available, but observations made in eastern Finnish Lapland can tell us something about the later history of this population.

Thus there are breeding wolf populations beyond Finland's eastern frontier throughout its length, although the western edges of these

Table 2. Sex ratios of wild wolf pups in Finland according to kill statistics.

Date of death	Litter no.	Locality where a wolf died	Pups ♂	Pups ♀	Other members of the pack killed
IX.1969	I*	Suomussalmi, Raate	1	0	—
XI.1969—					
II.1970	II*	Kuhmo, Lentua-Kalliojoki	1	1	—
III.1972	III	Lieksa, Lehmivaara	1	0	—
XI.1972	IV	Savukoski, Lipakkaselkä	0	1	—
XI.1972	V	Salla, Onkamojärvi	2	0	—
I.1973	VI	Kitee, Papinniemi	1	0	—
II.1973	VII	Ilomantsi	0	1	—
X.1973	VIII	Salla, Kulvakkovaara	2	0	adult ♂
XI.1974	IX	Kuusamo, Liikanen	1	0	—
II.1976	X	Nurmes	1	0	—
X—XII.1976	XI	Salla, Niemelä-Selkälä	1	2	adult ♀
I.1977	XII	Tyrnävä	1	0	adult ♂
I.1977	XIII	Ilomantsi, Hoskansalo	0	1	adult ♀
III.1977	XIV	Valkeala, Kääpälä	1	0	—
X.1977	XV	Kuhmo, Rastinkylä	1	0	—
XII.1977	XVI	Ilomantsi, Ilaja	2	3	adult ♂
IX.1978	XVII	Lieksa, Ruunaa	0	2	—
X.1978	XVIII	Salla, Tuntsa	1	0	adult ♀
I.1979	XIX	Ilomantsi, Ijala	0	1	ad. ♀ + ad. ♂
			17	12	

*may belong to the same litter.

populations may or may not reach Finnish territory (Fig. 3).

4. Discussion

In northern Europe the wolf has for decades occupied a greatly restricted range. Within the area of western culture the species has been exterminated almost entirely, while in eastern Europe its populations have made rapid growth. The eastern frontier of Finland forms a border between these two cultures. This dichotomy is reflected very strikingly in the occurrence of the species on the frontiers of Finland during the last decade; very few crossing have been recorded on the Swedish and Norwegian frontiers, while more than 4000 observations have been made on the eastern frontier. The crossing data also appeared to agree fairly well with our knowledge of the sizes of the wolf populations beyond the borders of Finland.

In Soviet Karelia and the Leningrad region the increase in the wolf populations has been rapid, even threefold during less than a decade. In areas where there is no human impact on the wolf population, e.g. on Isle Royale, such increases do not seem to occur (see Mech 1970, Peterson 1977, Allen 1979). The reason for this is probably the self-regulation mechanism of the wolf population, for the suppression exerted by the α-pair is so great that the other mature females of the pack do not produce offspring. This has been verified in nature (Haber 1977) and in captivity (Zimen 1976, Ginsburg, pers. communication), but if the α-male is removed, all the mature females give birth to pups (Ginsburg, pers. communication). The α-pair is chiefly responsible for the care of the young, and it is therefore most vulnerable (of the adults) to the hunter (see also Table 2). Wolf hunting thus allows the potential maximum productivity of the pack to be realized (see also Mech 1970). The wolf populations of Soviet Karelia and the Leningrad region have been hunted continuously, although at varying intensities (Danilov et al. 1978).

A wolf population at saturation point naturally disperses in directions where there are no barriers and into suitable empty territories. In the case of Soviet Karelia and the Leningrad region the latter were available in Finland, which is part of the former range of the species. The wolf was protected in the southern half of Finland from September 1973 until the end of 1977, and events showed that the species would probably very soon regain its former territories, despite the drastic changes made by man in the structure of the landscape. Indeed, wolves might successfully inhabit even the most settled areas in southern Finland, if they were not faced with the hazards of our "civilized world" in the form of busy roads and unintentional disturbance by man (see Pulliainen 1979a).

Bibikov (1973) estimates that the 300 wolves in Soviet Karelia represent a density of 2.5 wolves per 1000 km^2. Since expansion can be regarded as an expression of population pressure in a population at saturation point, recent observations on the increase in the Soviet Karelian wolf

population and the commencement of a powerful expansion into Finnish Northern Karelia allow us to estimate (see Figs. 1 and 3) that the saturation point of the wolf population under the conditions prevailing at present in Soviet Karelia is roughly 5—7 wolves per 1000 km^2. In the European part of the USSR the wolf populations have reached even higher densities (10 or more ind./1000 km^2) in the more southerly regions (Bibikov 1973).

Concerning the behaviour of a wolf population at saturation point under present-day conditions in Soviet Karelia, one might speculate that the use of forest roads and the trails of ungulates as pathways in deep, soft snow (see also Danilov et al. 1978) would lead to increased numbers of encounters between wolf units (lone wolves and packs) and thus to increased mobility, which may be manifested both in an increased number of crossings of the observation line (e.g. the border between Finland and the USSR), and also in a strong tendency for the population to disperse. I have taken these aspects into account in estimating the size at which the Soviet Karelian wolf population reached saturation point.

The majority of the wolves which crossed into Finland from Soviet Karelia in 1959—63 were killed, and expansion was thus blocked (Pulliainen 1965). Before and during that expansion most of the wandering wolves were males, but as the breeding population approached the frontier the excess of males decreased. The same trend in sex ratios has been recorded during the present expansion from Soviet Karelia into Finnish Northern Karelia (Table 1), and a similar blocking of the expansion is now in progress, for at least 72 wolves have been killed in Finland in 1977—79.

In 1959—79 wolf packs comprising more than five individuals have been observed only in the easternmost part of Finland (Pulliainen 1965, present data). Units which have wandered to the western and southern parts of the country have consisted of one to four individuals. Most of these wandering groups were probably formed by low-ranking adults and juveniles from the packs in the breeding area, which show a greater tendency to emigrate than do the other members of the packs (see also Zimen 1976). It is worth noting that no return of such wandering individuals has been recorded so far, which suggest that (a) this is real dispersal of a population(s) from a saturated area and (b) the wandering individuals have found suitable habitats and enough available food in their new areas.

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