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Ecology of the otter (*Lutra lutra*) in central Finland and methods for estimating the densities of populations. - University of Joensuu, 2006, 128 pp.
University of Joensuu, PhD Dissertations in Biology, No. 43, ISSN 1457-2486.
ISBN 952-458-882-X

Keywords: activity, breeding, carrying capacity, competition, density, density-dependence, diet, distribution, food, habitat quality, home range, juveniles, litter, monitoring, population, S-shaped growth curve, snow-tracking, source-sink.

The otter (*Lutra lutra*) is a semiaquatic Mustelid with wide distribution. However, its populations decreased in many areas in the 20th century. Otters are well adapted to life in the water. Their body is elongated, the tail flattened and the fur is thick and waterproof. The main food is fish all over the otter's range. However, amphibians have also been important food for otters in Finland. Finding suitable feeding areas is problematic in the North, due to the thick ice layer in winter, and otters have to move over large home ranges searching for food and possible new feeding areas.

In this long-term study, the ecology of otters was studied extensively in central Finland. The diet of otters was studied by analysing spraints (faeces). The activity of otters was investigated by following sprainting activity in summer and by snow-tracking in winter. Snow-tracking was also used to study the home ranges, breeding and density of otters. To estimate population densities two new snow-tracking methods were developed. The home range mapping method (HMM) is very intensive, but gives an exact estimate of the number of otters. The one-visit census (OVC) is a sampling method that provides a faster way to estimate the population densities.

The one-visit census method was used in a large project for monitoring the Finnish otter population in 1995-1998. In this study the possibility of monitoring Finnish otter populations by snow-tracking was evaluated. The results were found to be promising and the method applicable for nation-wide studies. The number of otters in Finland was approximately 2000-2550 individuals in the above-mentioned years.

In the study area (1650 km^2) in central Finland, the otter population increased from about 20 individuals in 1985 to 50 individuals in 2002. It was possible to estimate the density of otter populations in different river systems by exact annual counting of all otter individuals by HMM. Finding an S-shaped growth curve made it possible to determine the local carrying capacity for the otter population in the study area. The density of otters depends on used method. It was 0.7 individuals per 10 km of riverbed in summertime (2002), but increased up to 5.2 individuals per 10 km if only available winter feeding areas was used. The length of the home range for female otters or litters was typically 20-40 km of watercourse. Otters used all the available feeding areas in winter, but in summer there was abundant free space and food available.

The density-dependent offspring production for the population of otters was documented for the first time in this study. Density-dependent reproduction indicates the existence of intraspecific competition in otter populations in central Finland. Food was scarce and competition took place only in the winter, when most of the feeding sites were covered by ice. The ice cover limits the availability of food resources enormously, and creates a "bottleneck" for the otter populations in central Finland.

In the study area most of the otter cubs produced in a few river systems, resulting in a source-sink structure between the network of habitats or local populations. The increase of local populations was equal in all river systems. Highly productive source populations rendered population growth possible in other river systems. In central Finland the mean number of cubs per female was 1.51 in autumn. All known litters were born between May and September.

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CONTENTS

LIST OF ORIGINAL PUBLICATIONS

This thesis is based on the following articles, which are referred to in the text by their Roman numerals:

I Sulkava, R.T. 2006: Snow tracking - A reliable method for estimating otter (*Lutra lutra*) populations (accepted to Wildlife Biology).

II Sulkava, R.T. & Liukko, U-M. 2006: Use of snow-tracking methods to estimate the abundance of otter (*Lutra lutra*) in Finland with evaluation of one-visit census in monitoring purposes (manuscript).

III Sulkava, R.T., Sulkava, P.O. & Sulkava, P.E. 2006: Source and sink dynamics of density dependent otter (*Lutra lutra*) populations in rivers of Central Finland (manuscript).

IV Sulkava, R. 1996: Diet of otters (*Lutra lutra*) in Central Finland. Acta Theriologica 41: 395-408.

I designed all the studies (I-IV). Although I had many field and other assistants involved in different parts of the study, I was also responsible for the data collection and analyses. I wrote all the articles, I and IV myself, and articles II and III in collaboration with the co-authors.

1 INTRODUCTION

The distribution range of the European otter (*Lutra lutra*) has been extensive; from Portugal to Japan and from North Africa to arctic areas, including Finnish Lapland. The populations declined in many areas between the 1950s and the 1980s (e.g. Macdonald & Mason 1994). Distribution became patchy, mostly in isolated areas on the periphery of Europe (Foster-Turley et al. 1990). However, in the 1990s and the 2000s, the populations have been increasing, at least in some parts of Europe (e.g. Sjöåsen et al. 1997, Kranz 2000, Roos et al. 2001, Conroy & Chanin 2002, Reuther 2002). The otter was a threatened (V; vulnerable) species in Europe until 2004, when it was re-evaluated as "near threatened" (NT) (IUCN 2004).

At the beginning of this work in 1980, the otter was rare and listed as a threatened species in Finland (Rassi et al. 1985). Erlinge (e.g. 1967a, 1967b, 1968a and 1968b) studied otters in southern Sweden, but only a few local studies were carried out in Finland in the 1980s (Skaren & Kumpulainen 1986, Skaren & Jäderholm 1987, Skaren 1988, Cronström 1989, Storrank 1989, Sulkava & Sulkava 1989). In the 1980s very little was known about the distribution, population dynamics or biology of otters in Finland or other climatically similar areas. The need to improve our knowledge of the biology and distribution of otters was urgent. With very limited knowledge of the otter, it was difficult or even impossible to plan the conservation and management of the species.

Only little is known world-wide about the numbers or densities of otters. Techniques for estimating the size of populations of otters are difficult to use and time consuming. A basic field survey method for estimating the presence of otters is based on counts and observations of spraints (faeces) and footprints on riverbanks. Studies based on this so-called "standard method" have been carried out in many areas (e.g. Jenkins & Burrows 1980, Conroy & French 1987, Mason & Macdonald 1991, Sulkava & Storrank 1993, Brzezinski et al. 1996, Trindade & Farinha 2002, Chanin 2003). This field survey is recommended as the best method for investigating otter distribution in large areas (Macdonald & Mason 1994). It gives knowledge about the distribution and relative status of otters (Mason & Macdonald 1987, IUCN 2000), but only little information about population size, density and the vitality of populations, or the spatial organization of otters.

Although all the currently used methods are difficult to use and time consuming, the monitoring of otter populations is very important for the purposes of conservation and management (e.g. Foster-Turley et al. 1990, Rassi et al. 1992, Anon. 1994, Stjernberg & Väisänen 1998,

IUCN 2000, Chanin 2003). For the countries belonging to the European Union, it is a legal duty to collect data on the distribution and population trends of threatened species such as the otter (Habitat directive; 92/43/EEC,1992). The otter is listed in appendices II and IV in the list of Interested Species of Community. However, even today, the monitoring of otters functions well only in England (Crawford 2003).

Our knowledge and understanding of the otter's distribution, population dynamics and biology in Finland is now much better than it was at the beginning of this study period. In the 1990s, many otter studies were carried out in Finland (Skaren 1990, 1992a and 1992b, Skaren & Jäderholm 1990, Stjernberg & Hagner-Wahlsten 1991 and 1994, Storrank 1993, Sulkava 1993, Sulkava & Storrank 1993, Mäkelä & Rajala 1995), and the Finnish wildlife triangle scheme, which included the otter, began to produce a snow-track index each year (e.g. Helle et al. 1992, Lindén et al. 1996). At the end of the 1990s otter studies was perhaps at most active in Finland (e.g. Sulkava 1995, Sulkava & Storrank 1995, Höglund 1996, Kauhala 1996, Lindgren & Tornberg 1996, Luhta 1996, Wikman 1996, Liukko 1997, Cronström & Liukko 1999, Helle & Wikman 1999, Liukko 1999, Rydbäck & Stjernberg 1999, Skaren 1999, Sulkava & Liukko 1999), (IV). At the beginning of the 2000s, most Finnish otter study projects had come to an end. However, much material from the studies carried out in the 1990s was still unpublished, and some new articles were published (Ludwig et al. 2002, Storrank et al. 2002, Hyvärinen et al. 2003, Hellsten 2004, Sulkava 2006a and 2006b, Sulkava & Liukko 2006, I II, III).

One of the most pleasing results of my studies was the finding that the otter population was rapidly increasing from the 1980s to the 1990s (I, III). Results of my study were among those that contributed to the otter being located in the new category, "of least concern", i.e. the species is no longer threatened in Finland (Rassi et al. 2001).

The aim of this study was to develop methods for investigation and monitoring of otter populations, and to investigate the distribution and population density of otters in central Finland (Fig. 1), and to study the biological factors influencing otters' reproduction and survival in the Finnish environment, where there is long-lasting ice cover on lakes and rivers in winter. The main aims of the study were:

1. To create a reliable method for studying the density of otter populations in northern Europe climate conditions,

2. To find out whether there is trend in population density, and

3. To find the essential factors like food and feeding

habitats that affects the survival of otters.

The diet was predicted to be one of the essential factors in survival. Because only limited information was available on this factor in the 1980s, I studied the diet first. At the same time, I started to develop new snow-tracking methods. Studying the movement of otters in different seasons and conditions, their home ranges and their scent marking activity had to be figured out when the goal was to develop a reliable method of estimating the density of otter populations.

Once the new reliable snow-tracking method had been established, more detailed new questions on the population dynamics of otters were raised. These were:

4. What kind of demographic process is going on in the local otter population?

5. How high is the carrying capacity for otters in my study area?

6. Is there intraspecific competition and is population size limited in a density-dependent processes?

In addition, based on the method developed in this study, these factors were applied to estimate the size of the total population of otters in Finland.

2 MATERIALS AND METHODS

2.1 Home ranges and activity

The spraint marking activity of otters was studied over a period of three years (1989-91), from some 30 permanent study sites. All the study sites located near bridges or other places easily reached by car. The sites were in all kind of waters, from small streamlets to large rivers and from oligotrophic to mesotrophic waters. Each study site was carefully examined at the end of every snow-free month (from May to October). Otter spraints were collected from all sites, and therefore it was possible to know exactly whether any faeces had been deposited at a particular site within one month. The most important sprainting sites were under spruce trees or bridges. Since a large tree or bridge covered the place, the spraints were not dissolved by rain. The differences between monthly spraint marking activity were measured by the monthly number of positive sprainting sites. Spraints were also used in summertime as an indicator of moving of the otters in different waters.

The home ranges (Fig. 1) were studied using snow-tracking (I, II). I studied the density of otters in every winter between 1985 and 2003, and followed all individuals or litters during each winter (I, III, Sulkava 2006b). I also studied the length of the daily cruising distance of otters inside

their home range in winter (Fig. 2) (I). These extensive data on the movements of otters gave a clear picture of their typical home range. In 1990-1991 I also followed one otter family (a female with one cub) every day over a two-month period. There was only one litter in this particular river system, one male and two other lone individuals in that year. In central Finland lake and river systems of this kind are common, and also the number of otters in a single system is usually low. In such conditions, it is possible to identify individuals by measuring size, direction of trail and age of tracks. This was easily accomplished, at least when the otters were followed every day, and nearly all movements of individuals could be seen in the snow.

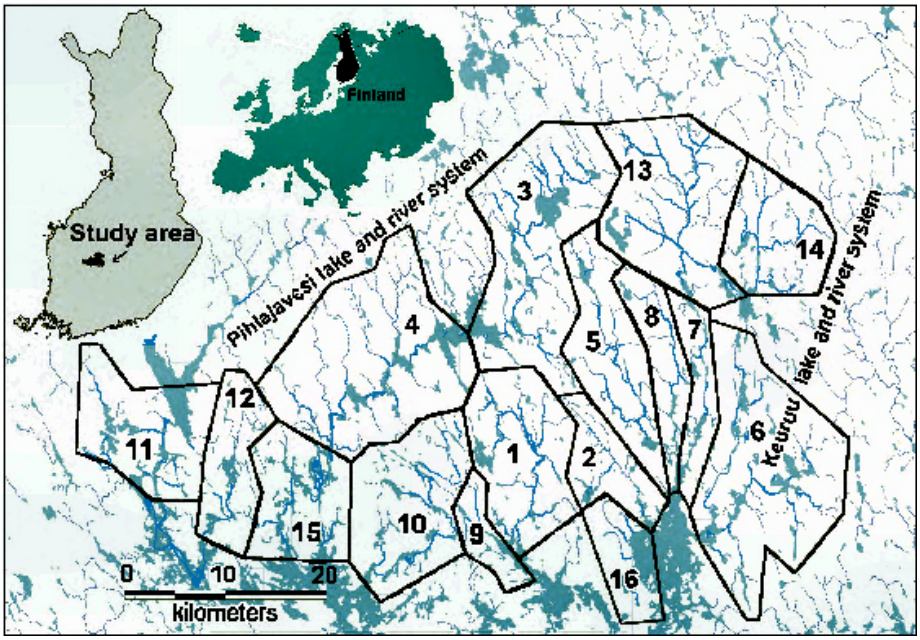

Figure 1. The otter home range river systems of the study area. The number of area (1-16) is used later in the text and figures.

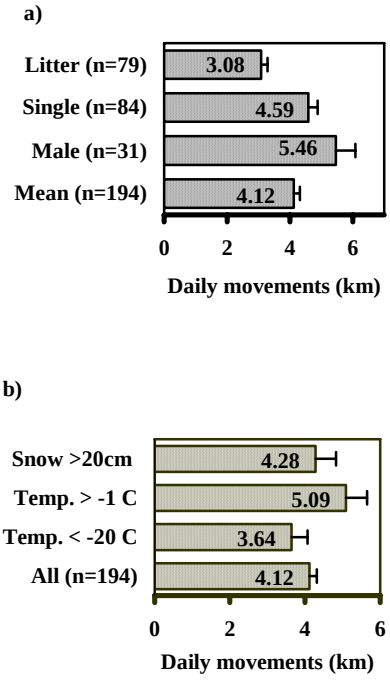

Figure 2. The daily movements of otters (a) and the effects of some weather conditions on the movement of otters (b) in central Finland in winter (mean length ±SE). Single = female or young lone individual. The female with cubs moved less than other otters (ANOVA: $F = 12.5$, $p < 0.001$, paired T-test, df = 1; litter-male: $p = 0.0009$ and litter-single: $p < 0.0001$). Otters also moved more in mild than in very cold weather (T-test, $T = 2.1$, $p = 0.04$). Only loose snow, in which an otter sinks, has been taken into account in the thickness of snow cover. N = the number of days. Total length of routes was 798.4 km. Animals without known sex or age are included in the mean length of movements.

2.2 Snow-tracking methods and the estimates of otter population

In Finland, the long winter with permanent snow cover and ice on lakes, creates an excellent opportunity to study animal movements. Moving on snow is natural for otters when they are searching for new feeding areas. Between November and April only few rapids and some outlets of big lakes remain unfrozen. Between these ice-free areas, all lakes and ponds are totally covered by ice, and ice covers most of the flowing rivers, too. It is therefore possible in these conditions to see nearly all movements of an animal by their tracks in the snow.

2.2.1 Home range mapping method, segment method and one-visit census

In the home range mapping method (later called HMM), the estimation of the total number of otters living in an area is started by identifying all separate river and lake systems (I). All waterfalls, rapids and other places that are not covered by ice were studied carefully, during suitable ice and snow conditions, as well as all waters with potential tunnels below the ice. Different otter individuals were identified on the basis of footprint (or trail) size, age, direction of the trails and areas without tracks between trails (I, II, III). After the first survey there were often signs of

individuals that had not been counted in the first time, and therefore open rapids and other possible areas were studied again two or three days later, and again some days later. After these two checks, it was highly likely that all otters along one river system had been found (I). It was possible to estimate the otter population of a larger area when the census advanced systematically from one river system to another (I, II). The same or nearly the same method has been used in Sweden (Erlinge 1967a and 1968a, Aronson 1995), Poland (Sidorowich et al. 1996), Belarus (Sidorovich 1997) and the Czech Republic (Simek & Springer 1998).

In order to test the reliability of a population estimate carried out by HMM, the otter population was also estimated in 1998-99 by another method (I), previously used by Reid et al. (1987). In this segment method (later SM), all shorelines of rivers and streamlets were divided into numbered, 500 metre-long segments. I did not include the shorelines of lakes, because these are totally covered by ice in winter, and lakes do not offer feeding areas for otters in my study area in winter (I, III, IV). A total of 1522 segments were numbered. A random sample of numbered segments, 205 segments, was selected for the survey (I). Each segment was searched for the tracks of otters, which were estimated to be either less than or more than 24 hours old. The ages of the tracks were estimated using snowfall, hoar frost and non-frozen scats. Only fresh ($\leq$ 24 h.) tracks were used in estimating the population. Individuals were distinguished from one another by the age, size and direction of the tracks. The population estimate is the mean number of animals or the mean number of positive segments, determined from observed fresh signs in the sampled segments, extrapolated across all segments in the study area (I).

In the late 1980s I also started to develop a faster and easier way to estimate the population of otters. In this one-visit census method (later OVC), the entire study area can be investigated in two or three days. It is impossible to find all otters in the area in such a short time, but if the same proportion of the total study area was checked every time, the size of the total population possibly can be estimated.

In the OVC method, 111 permanent study sites were selected all over the study area (I, II). All sites were combined into three groups, and each group, i.e. 30-40 study sites, was investigated in one day. The distance between the study sites varied between one and five kilometres in each watercourse. At each study site 20-600 metres of river or lake banks were searched for otter tracks. The length of the search depended on the ice cover and other physical characteristics of the watercourse at the site. For example, a longer

distance had to be examined at a site that was situated in ice-free rapids than at an inlet that was totally covered by ice.

Because field investigations were carried out within two to four days after the last snowfall, it was possible to estimate the age of the tracks exactly. Individuals could be distinguished from each other by identifying the empty areas between individuals, or by the age, size and direction of tracks (I, II). For instance, if tracks were found in two streams separated by a lake without tracks, the traces were most probably left by two individuals. Because the distance travelled per 24 h. by an individual otter (excluding males) did not usually exceed 6 km (Fig. 2a) (I), tracks were classified as being left by two different individuals if two positive sites were in different water systems, or if the distance between sites with fresh tracks was more than 10 km.

Because at least one OVC investigation had been carried out every winter after 1990 (I), and the total population was known by HMM, it was possible to compare how different conditions affect the proportion of otters found in one sampling.

2.2.2 Monitoring of otters

In 1994, the environmental authorities in Finland decided to carry out a pilot study of otter monitoring (II). The study was carried out using the OVC method, which was developed and tested in the early 1990s in central and eastern Finland (e.g. Sulkava 1993 and 1995, Sulkava & Liukko 1999, Sulkava & Storrank unpublished, I, II). I acted as the head of this project. The Finnish monitoring pilot project was designed to test whether such a field method carried out during the winter is feasible, to assess how well it can be applied by various organisations, and to see how useful it is in the monitoring of Finland's otter populations (Sulkava 1995, Sulkava & Liukko 1999, II). The survey was also expected to provide new data about the status of the otter in Finland.

The Finnish monitoring system covers 16 study areas, comprising 37 000 km^2 of Finnish river and lake landscapes (about 10% of the area of the country) (Fig. 1 in II). About 100 permanent survey sites were established in each of the study areas. During the three study winters, the total numbers of sites examined were 1466, 1589 and 1213 (II). All the study areas and sites were selected by uniform criteria beforehand by myself (Sulkava & Liukko 1999, II). Field investigations were carried out between November and April, and always two to four days after a snowfall (II). All the observations were compiled in a database hosted by the Finnish Environment Institute. Field workers made the first estimates of the number of otters, and I made second critical examination, and the final estimates of the

number of otters in all the areas (II). Maps of the survey areas with the positive and negative sites, and the field data with the information on the criteria used by the field workers in separating different otter individuals, were all of great importance in this second examination (Sulkava & Liukko 1999, Storrank et al. 2002, II).

When the OVC method was tested, about 50% of otters were found in every survey conducted in central Finland (Sulkava 1995, Sulkava & Liukko 1999, I, II). Based on this probability of finding otters, the total population size could be estimated. When the total number of otters in Finland was evaluated, the abundance of otters outside the study areas was estimated with help of data from a Finnish wildlife triangle scheme (e.g. Lindén et al. 1996, Helle et al. 1998). The wildlife triangle scheme gives the relative abundance of otters throughout the country. It thus enabled us to evaluate that how large area around of our OVC study areas the density of otters was approximately the same as inside of our study areas (I).

2.3 Breeding

The size of snow tracks of a female (wide of a footprint in most often 55-65 mm) and cubs (40-54 mm) are different at the beginning of winter, between October and December (Sulkava 2006a and 2006b) in central Finland. This is because all known litters are born between May and September in the study area (Sulkava 2006b), and the female and cubs stay together over the following winter (III). The situation is similar in other areas in the same latitudes, as in Sweden (Erlinge 1967a) and in Shetland (Kruuk 1995). However, identifying of a litter is also possible later in winter, if it is possible to see a group or to follow it for a couple of days (e.g. Sulkava 1993). In my study area the number of litters and cubs was studied by snow-tracking in autumn and early winter (I, III).

It was not possible to know the actual date of birth in this study. I calculated the date of birth using the first snow tracks measured in snow in autumn or early winter (Sulkava 2006b). I had one reference collection of footprint size made by a young captive female otter at different ages and size. I also compared this data with larger data for weight and length of otter cubs in captivity (Reuther 1999), and the size of feet measured from dead individuals (Hellsten 2004, Sulkava, unpublished). However, it is uncertain how reliable this method was, as otters in the wild may not develop as rapidly as in captivity, and measurements made on dead animals are not exactly the same as footprints in nature. I therefore did not try to find out exact date of birth.

Thanks to the exact data I had on the number of otters living in one lake and river system, and the number of cubs in these well

defined living areas, it was possible to study differences in cub production between river systems. Because the population growth curve was S-shaped, i.e. first the density increased and then become asymptotic, I could find out the local carrying capacity, and analyse possible density-dependence in the reproduction of the otter population.

2.4 Diet of otters

A total of 1506 spraints (scats) was collected in different parts of the study area from 1988 to 1993 (IV). The spraints were collected every month throughout these years. The year was divided into four seasons: spring (April and May); summer (June to August); autumn (September and October); and winter (November to March). The spraints were dried and the remains were identified according to the keys of Eloranta (1975), Webb (1976), Steimmetz & Muller (1988), and using the reference collections of skeletons and scales of fish and other taxa. The size of the fish was estimated according to the method of Jenkins et al. (1979) and Wise (1980).

The composition of the otter diet has been presented (IV) as percentage frequency (PF), as relative frequency (RF) and as bulk percentages (BP). Percentage frequency records the percentage of spraints containing a particular prey item. Relative frequency is the number of occurrences of an item, expressed as a percentage of the total number of occurrences of all items in the samples (sum is 100). Bulk percentage is the percentage where the importance of a particular item in a spraint has been scored visually. The value for each item in each spraint is summed and expressed as the bulk percentage (see, Wise et al.1981, Mason & Macdonald 1986). The diet of otters in different seasons and in different areas was compared.

3 RESULTS AND DISCUSSION

3.1 Movements of otters within their home range

In summer the spraint marking intensity of otters increased towards autumn in all kinds of waters in central Finland (Kruskal-Wallis test, $\chi = 53.9$, df = 5, $p < 0.0001$) (Fig. 3). Most possibly the increasing sprainting activity towards autumn was due to the greater need of individuals to scent mark (i.e. reserve) their home range for winter, a period of very limited food resources (III, IV). Between June and August there were no statistical differences in the monthly sprainting activity of otters between different waters, i.e. in small streamlets, rivers and areas near lakes (measured by positive sprainting sites) (Kruskal-Wallis test, in all cases $p > 0.1$). This means, for example, that otters moved in all kinds of waters in their home range in summer.

However, the areas near lakes, i.e. estuaries and outflows, were the most intensively marked in spring (in May, Kruskal-Wallis test, χ^2 = 9.23, df = 2, p = 0.01) and in autumn (September, χ^2 = 6.75, df = 2, p = 0.03). The reason for this was most probably the same as in the case of increasing activity towards autumn, the greater need to reserve a home range for winter. Estuaries and outflows are places where all individuals enter an area, and most probably find the markings of other individuals.

A different pattern of seasonal sprainting activity has been found in many other areas, too. Most spraints were found between winter and spring in Scotland and Shetland (Mason & Macdonald 1986, Conroy & French 1987, Macdonald & Mason 1987, Kruuk 1992). On the other hand, in Spain most spraints found during winter or summer, depending on the area studied (Lopez-Nieves & Hernando 1984, IUCN 2000). In Austria, the Czech Republic and Germany, two peaks were found, one in autumn and another in spring (IUCN 2000, Roche 2001). At least in some parts of Portugal, most spraints were found in autumn (IUCN 2000). Erlinge (1968b and 1969) did not find any seasonality in the sprainting of otters in southern Sweden.

At the beginning of the study period, in the period of snow cover, between November and April, the probability of finding fresh otter tracks increased towards spring (Kruskal-Wallis test, χ^2 = 11.76, df = 5, p = 0.04) (Fig. 4a). Today, however, it seems to decrease towards spring (Kruskal-Wallis test, χ^2 = 18.65, df = 5, p = 0.002) (Fig. 4b). However, there is no decrease before February (November to January), and between February and April (both, p > 0.05). The possible decrease could be due to mortality and lack of births in the population of otters in the study area in winter. If mortality rate is at the same level every month in my study area as it was in south and central

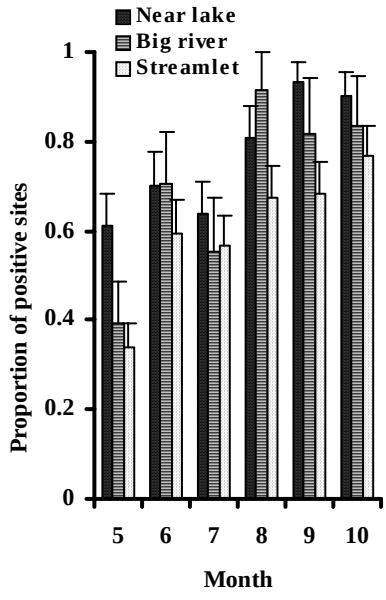

Figure 3. Proportion of positive sprainting sites in different months and areas. The number of sites studied: May 151, June 101, July 123, August 89, September 85, October 85, and total 634.

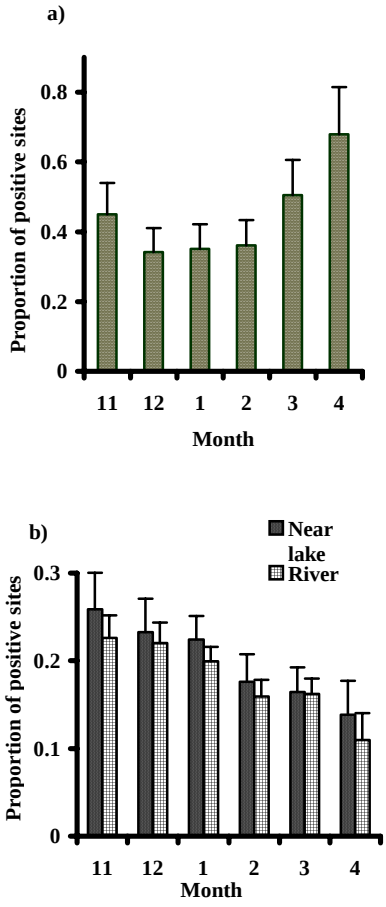

Figure 4. Monthly proportion of areas with otter tracks in all snow-trackings during the years 1986-1993 (a), and in one-visit censuses (OVC) during the years 1990-2004 (b). The total number of sites studied in the years 1986-1993 was 2216 (monthly: November 363, December 427, January 797, February 508, March 610 and April 155), and in 1990-2004 n = 2860.

Finland in studies of otters found dead (Rudbäck & Stjernberg 1999, Hellsten 2004), mortality could explain about half of this decline. However, individuals killed by traffic accidents or other accidents caused by humans, are found more easily and fall into the hands of museums more often than individuals that have died of starvation or predation.

Because the food shortage is much more serious in winter than in other seasons, nowadays the actual death rate probably is higher in winter than in other seasons (see also Fig. 9). Higher mortality rate in winter could explain most of the observed decrease in monthly probability of finding tracks in the field (Fig. 4b).

The otters moved about in their home range throughout the year in central Finland (I, III, IV, this thesis). Spraints and tracks were found in all kinds of waters the year round. Even the smallest streamlets (less than 2 metres wide) had been utilized in all seasons.

In studies using the OVC method, most of the otters were usually found in small rivers and streamlets in winter, but the frequency of observed otters per study sites was higher in larger rivers (Fig. 5). However, this is most probably due to the large amount of small watercourses.

In winter, spraints were recorded more often in areas near lakes (Fig. 6). Otters clearly spend more time in areas near lakes, i.e. near possible good feeding areas.

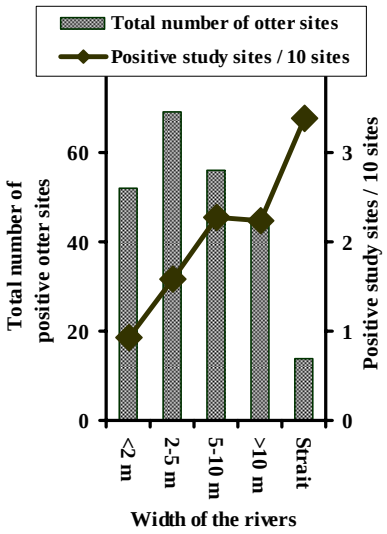

Figure 5. The number of observed positive otter sites in different habitats during the Finnish otter monitoring pilot project in 1995-98 (Sulkava & Liukko 1999, II).

3.1.1 Home range size

There was great variation in the sizes of home ranges in central Finland, and the demand for forage determined the size of home range. For example, one small home range lay in a large estuary, where one otter or one family group lived almost the whole winter. They only moved a distance of six to ten kilometres in winter. Correspondingly, a typical large home range consisted of only smaller waters, and included very few open waters in winter. Males moved longer distances, and often in more than one lake and river system. Typical home range size was 20-50 km of main watercourse (Fig. 7a) (I, III).

The size of home ranges varied greatly also in Sweden (Erlinge 1967a), as in my study area. Erlinge (1967a) found that the diameter of the home range of an otter family group was about 7 km, and for an adult male about

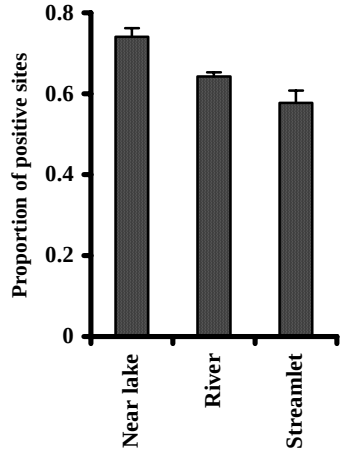

Figure 6. The proportion of positive otter sites in different waters between November and April in the years 1990-2004 (n = 2860) (Kruskal Wallis test, χ = 14.02, df = 2, $p < 0.0001$).

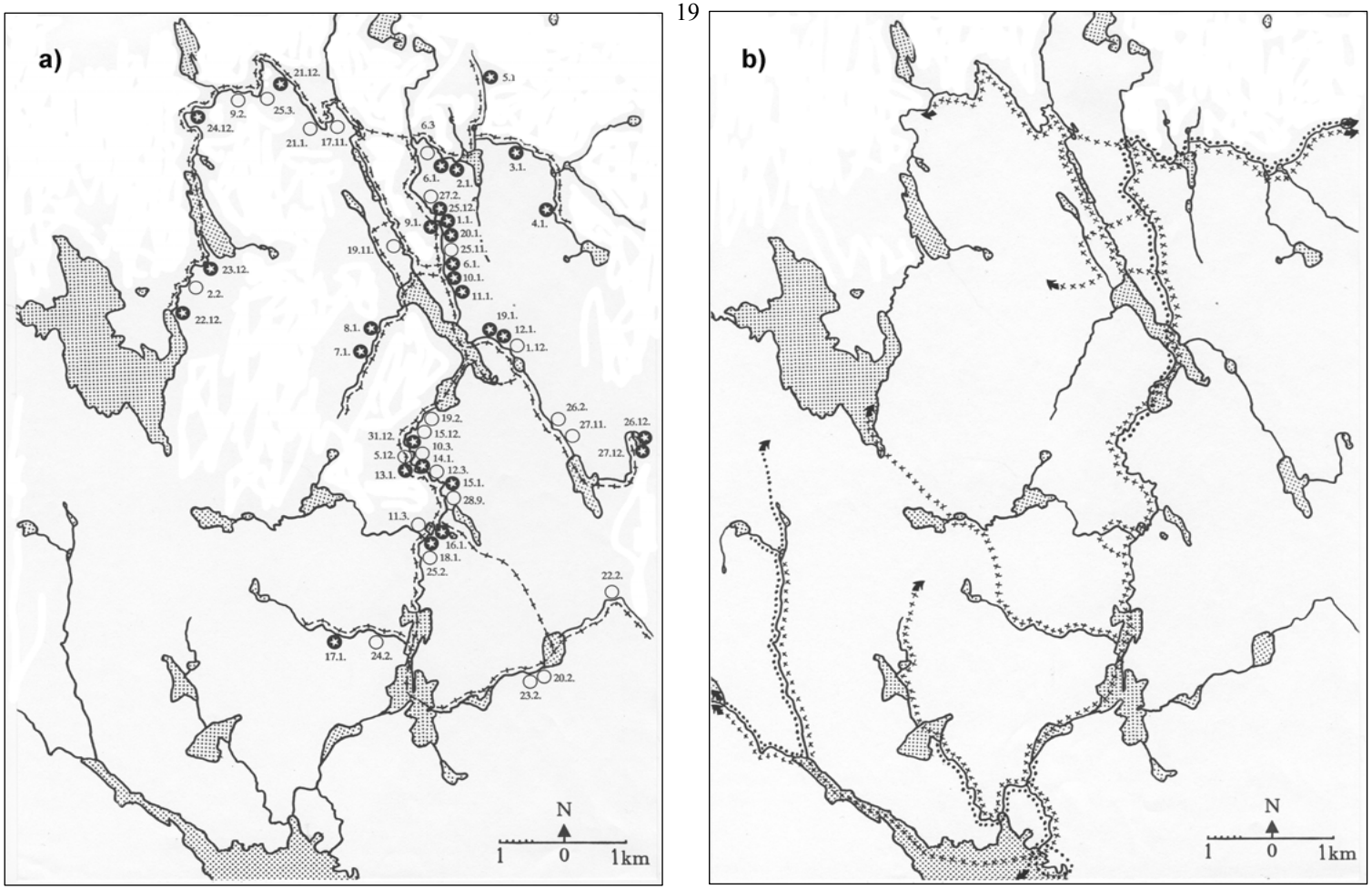

Figure 7. The movement of the otter litter (female and one cub) based on snow-tracking in winter 1990-91 (a), and movements of other otters (b) in the home range of studied litter at the same time (area number 1 in Fig. 1). In a: = moving of the litter, = exact site of the litter (date), ○ = litter near the site (impossible to know exact site). In b: = moving of the one male otter, and = other single otters.

15 km in southern Sweden. Later the home ranges of otters have been studied using radio tracking. The mean length of rivers and streams used by otters in central (Jenkins 1980, Green et al. 1984) and northern Scotland (Kruuk et al. 1993, Durbin 1996 and 1998), was between 19 and 85 km for males and 16 to 25 km for females. The mean area of water utilized by males was 63 ha, and by females 20 ha in Scotland, and the average number of otters in streams was approximately one individual per 15 km (Kruuk et al. 1993). There were great variations between the sizes of the areas utilized. The water area in the smallest home ranges was only 6.2 ha and in the biggest 78.7 ha (Durbin 1996). In marine coastal conditions the home ranges of otters were smaller than those in inland waters, and social behaviour is also different. Most probably the large amount of prey in marine habitats allows very different social behaviour in these areas. For example, on the coast of Shetland, the otters live in groups, and the group utilizes an area between 4 and 14 km of seacoast (Kruuk & Moorhause 1991, Kruuk 1995). Coastal otters use a wider strip of water than is possible for otters in most rivers or tributaries. Kruuk et al. (1989) found that otters use water as far as 100 metres offshore, and estimated that there is about one animal per km living on the seacoast of Shetland.

Otters utilized all kinds of waters inside their home range, but the core area of the home range was usually the biggest river (Fig. 7a). Only few otters lived in the same lake and river system in wintertime in central Finland (Fig. 7b) (I, III). To find two litters or two males in the same river was extremely unusual. Probably the heaviest competition takes place in summer and autumn, when the boundaries of home ranges are established. Otters divide the resources for winter, and high marking intensity in autumn indicates another individual that the river is already occupied. This system could notably reduce the need for aggression in winter, when the demand for food is greater and its availability lower than in summer.

3.2 Methods and the size of population

3.2.1 Snow-tracking versus other methods

Snow-tracking was found to give more accurate estimates than other large-scale field methods for the density of otter populations. The main problems involved in the standard method include the seasonality of sprainting activity. In central Finland I found distinct seasonality of summertime sprainting activity, with its peak in autumn (Fig. 3). Together with the short summer and other possible errors, this does not provide a good opportunity to study otter populations by the standard method in Finland.

Methodological problems of the standard and other methods have been widely discussed earlier (e.g. Jenkins & Burrows 1980, Kruuk et al. 1986, Kruuk & Conroy 1987, Mason & Macdonald 1987, Conroy & French 1991, Mason & Macdonald 1991, Romanowski et al. 1996, Romanowski & Brezezinski 1997, Carss et al. 1998, IUCN 2000, Ruiz-Olmo et al. 2001b). It is evident that there is much variation in sprainting activity between seasons and areas, and possibly also between different age and sex groups (e.g. Mason & Macdonald 1986, Sulkava & Sulkava 1989, Kruuk 1995, IUCN 2000). Other possible methodological problems include differences between field workers (e.g. Sulkava & Storrank 1993), bank-side vegetation (e.g. Elmeros & Bussenius 2002) and the presence of spraintable bridges (IUCN 2000).

Snow-tracking gives more information on the populations of otters than spraints and footprints in summer (Sulkava & Storrank 1993, Sulkava 2006a, I, II, III). For example, it is possible to estimate the total population of otters in the study area (I, II, III). Snow-tracking has been used in otter studies earlier in Sweden (e.g. Erlinge 1968a, Kjellander & Mortensen 1985, Aronson 1995), in Canada (Reid et al. 1987), Finland (Skaren & Kumpulainen 1986, Skaren & Jäderholm 1987, Sulkava & Sulkava 1989, Kauhala 1996, Sulkava & Liukko 1999, Storrank et al. 2002), Belarus (Sidorovich 1991 and 1997, Sidorovich & Lauzhel 1992), Germany (Klenke 1996 and 2002, Hertweck et al. 2002), Poland (Sidorovich et al. 1996), the Czech Republic (Simek 1996 and 1997, Simek & Springer 1998), Austria (Kranz & Knollseisen 1998, Kranz et al. 2002) and Slovakia (Kadlecik & Urban 2002).

All techniques for estimating otter populations are time consuming and difficult, involving highly specialized investigators. In snow-tracking methods, for example, the investigators may miss otters that have not left tracks at a study site. It is also possible that distinguishing different individuals from one another may cause problems. However, the general visibility of snow tracks is good, and compared to spraints they are very easy to identify.

Comparison of two different snow-tracking methods, HMM and SM in 1998-99, gave a similar picture of the local otter population (I). In the SM method, twelve otter individuals and eight positive segments (with fresh tracks) were found in the studied 0.5-km intervals. This means either 0.059 or 0.039 otters per segment respectively, and a total population estimate of 89 or 59 otters. The population estimate made by the number of positive segments (59 otters) was almost the same as the estimate by the HMM method, in which I estimate that 51 otters lived in the study area (I).

The results of the OVC method were weakly dependent on weather or the thickness of snow cover. Only very cold weather affected negatively the moving activity of otters (Fig. 2b, I). During the period of high population level (after the year 1993 in the study area), the high death rate in winter most probably leads to decreasing probability of finding otter tracks towards spring (Fig. 4b). It seems that the OVC method (I) is a reliable way of estimating the total number of otters. However, it is important to do the field work as early as possible, i.e. when the population is at its highest at the beginning of winter. When the OVC-method is used to monitor the population, the field work should be done at the same time in winter every year.

3.2.2 Monitoring project

A national OVC study on the monitoring of otters was carried out in 1995-98 (Liukko 1999). Otter tracks were found in all study areas during all the field periods (II). Fresh otter tracks were found at 169 sites in the first year (11.5% of the sites were positive), at 141 sites in the second year (8.9%) and at 120 sites in the third year (9.9%).

The estimated minimum number of otters in the study areas was 121 in the first winter (8.3 individuals per 100 sites), 112 in the second winter (7.0) and 101 in the third winter (8.3). The otter population was most abundant in the central part of the country (II). This result is supported by other studies as well (e.g. Stjernberg & Hagner-Wahlsten 1991 and 1994, Wikman 1996, Helle et al. 1998).

The evaluated OVC method was developed for the monitoring of otter populations (I, II). Because of the short monitoring period, only three years, it was not possible to detect any significant change in the size and distribution of the otter population. The pilot study produced new information on the status of the otter populations, and this can be used if the survey is repeated in the future. The track index (the number of positive sites per 100 study sites) or otter index (the number of otters per 100 sites) of the areas can be used as abundance index in monitoring (II). These results also provided an opportunity to estimate the abundance of otter populations in the study areas and to generalize it for the whole country.

In the OVC pilot project the studied areas together made up about 10% of the area of Finland, and the estimated minimum number of otters was 1116 individuals in the years of the monitoring project. The OVC method was developed and tested in central Finland (I, II, III), where about 50% of all otters were found in all samplings (Sulkava 1993, 1995 and 2006a, Sulkava & Liukko 1999, I, II). Based only on these results, the population might be about 2200 individuals. However, it was possible to estimate this result

more accurately with help of the indices of relative abundance of otters produced by the Finnish wildlife triangle scheme (Lindén et al. 1996, Helle et al. 1998). The final estimate of the Finnish otter population was 2000-2550.

Knowledge from Finnish wildlife triangle scheme (Lindén et al. 1996), regional studies (see citations in Sulkava & Liukko 1999 and II) and from this study (II), indicate that probably more than 50% of Finnish otters lived in a central region of Finland, and more than 80% in the area where the OVC method works its best (area with enough snow and ice in winter). For this reason I believe that the estimated densities of the Finnish otter population during the years of the project were reliable.

The pilot project indicated that the OVC method was reliable and its costs were relatively low, at least compared to the standard method (Sulkava & Liukko 1999, IUCN 2000, II). The otter's behaviour and the prevailing climatic conditions make the monitoring of otters by snow-tracking possible in Finland (I, II, III, Sulkava 2006a). The conclusion drawn from the study was that the OVC method works well on a national scale and gives useful results. It could therefore also be a useful tool for monitoring otter populations in other large northerly areas (II).

3.3 Density of otters

The otter population in the study area increased significantly between 1985 (20 animals) and 2002 (I, III). In winter 2002-2003 there were 52 otters living in the study area, and at least 20 other individuals in the nearest surrounding area. The mean density of otters was 1.2 per 100 km^2 (in area of all river systems, in Fig. 1) in 1985-86 and 3.2 per 100 km^2 in 2002-03. In rivers and streamlets, the density of otters was 0.3 otters per 10 km of river (0.11 individuals per river hectare) in 1985-86 and 0.7 per 10 km (0.28 per ha) in 2002-03. The otter population increased rapidly from 1985 to 1993. Since then, the population has varied between 40 and 50 individuals.

Growth of the otter population in the study area followed the sigmoidal model of population increase (III). Population growth at its most rapid phase (1985-93) was 143%. This represents on average 17.9% per year (III). Population growth was equal in all kind of waters, when calculated by individuals per river hectare or per river kilometre.

At present, in central Finland, the otter population is dense and probably fully saturated at a low local carrying capacity. The density of otters (0.7 individuals per 10 km of river) was more or less equal to that in the same latitudes in Scotland (0.7) (Kruuk et al. 1993) and in Russian Karelia (0.6-1.3)

(Tumanov 2002), but the carrying capacity of those areas is not known. In southern latitudes or on marine coasts, most waters are more productive, and there is more food available for otters than in northern rivers and lakes. For this reason the southern and marine otter populations can be denser. For example, in Belarus the otter density varied between 1.7 and 5.9 individuals per 10 km of watercourse (3.7-10.7 individuals per 100km^2), depending on the size and type of river (Sidorovich 1997, Sidorovich & Pikulik 2002). The density of otters was 2.2 individuals per 10 km in Poland (Sidorovich et al. 1996) and 1.5-3.1 in Latvia (Ozolins & Rantins 1992a and 1992b). In a fishpond area in the Czech Republic the density was as high as 48-62 individual per 100 km^2 (Simek & Springer 1998). On the coast of Shetland, one animal per kilometre of shoreline was found (Kruuk et al. 1989, Kruuk & Moorhause 1991). In the 1960s, the density of otters was one adult per 4-6 km of river in southern Sweden (Erlinge 1967a and 1968a).

Comparing the density of otters in different areas is complicated. The otter population in central Finland was low when all shores of lakes and rivers were included (0.24 individuals per 10 km of shoreline), while the density per available feeding areas in winter (5.2 individuals per 10 km) was, in fact, even higher than in more southerly populations, where all waters are ice-free most or all of the year. In central Finland nearly all waters (also most of the flowing rivers) are totally covered by ice in winter. For this reason the differences in food availability between southern and northern latitudes are extremely pronounced in winter.

3.4 Reproduction and the carrying capacity of the study area

3.4.1 Reproduction

It was not possible to know the actual date of birth in this study. Determination of birth seasons was, however, possible. Occasionally, it was also possible to determine the time of birth at one or two month's intervals (Fig. 8).

Seasonality in the timing of otter reproduction increases towards the northern and continental areas, and non-seasonal reproduction has been found only in marine populations. Seasonal breeding was typical for otter populations in Sweden (Erlinge 1967a), Shetland (Kruuk et al. 1993, Kruuk 1995), Norway (Heggberget & Christensen 1994), Denmark (Elmeros & Madsen 1999) and Russia (Tumanov 2002). Some breeding seasonality has been found also in the Netherlands (Wijngaarden & Peppel 1970), Germany (Reuther& Festetics 1980), Portugal (Beja 1996) and Belarus (Sidorovich 1997). In England, Mason & Macdonald (1986) did

not find seasonality in the breeding of otters. This was probably due to the marine climate conditions and the small differences between the seasons in England. However, later surveys have found possible seasonality in England, too (Liles 2003). There are more than enough good feeding habitats and food for otters in summer in central Finland. However, only those cubs that were born in summer and had grown sufficiently before winter were able to survive the winter following their birth, and all known litters were born between May and September (Fig. 8) (Sulkava 2006b).

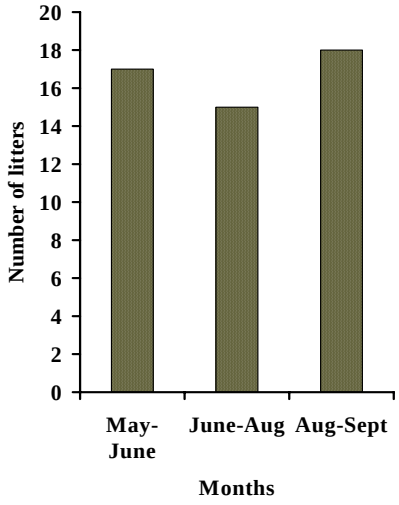

Figure 8. Approximately birth-time of 50 litters in Central Finland in 1985-2002. All litters (total of 119 litters), found in the study area in 1985-2002, were born between the beginning of May and the end of September.

The female and cubs stayed together for more than eight months; at least over most of following winter in central Finland (Sulkava 2006a and 2006b, I, III). The time offspring is dependent on their mother seems to be approximately of the same length as in other areas in the same latitudes. In Shetland the cubs stay with their mother for 9-13 months (Kruuk et al. 1991), in Sweden for about one year (Erlinge 1967a) and in Scotland for about 16 months (Kruuk 1995). How long the offspring is dependent on their mother in more southern populations is not known.

Several litters were born in most years in my study area, indicating a healthy and vital otter population (I, III). In central Finland the mean number of cubs with a female was 1.51 (III). This is a typical fecundity for populations in similar latitudes, but lower than that of more southerly populations. On the sea coast of Scotland the number of cubs was 1.55 and in Shetland 1.86 (Kruuk et al. 1987 and 1991). In lower latitudes the number of cubs seems to be higher; in Holland 2.8 (Wijngaarden & Peppel 1970), in Poland 2.4 (Wlodek 1980) and in England 2.5 (Mason & Macdonald 1986). In Belarus Sidorovich (1991 and 1997) found the litter size to be 2.7 from embryos, 2.6 at the age of one month, and 2.1 cubs after leaving the den. On the sea coast of Norway the mean litter size of otters was 2.5 during pregnancy,

but only 2.0 after the cubs became mobile outside the breeding den (Heggberget & Christensen 1994). The mortality of cubs was 0.63 (total of 2.75 embryos per pregnancy) before the young left the den (2.12 cubs with a female) in Germany (Ansorge et al. 1996).

Most probably the small number of cubs and clear seasonality of breeding in central Finland, as in other northern areas, is an adaptation to the highly seasonal availability of prey (food). The cubs were born in summer, but the mating season was in spring. In the spring the female otters may not have been in very good condition, due to the harsh climate conditions and shortage of food and feeding areas in winter. The fact that only females overwintering in river systems with large lakes (which maintain ice-free outflows) could produce cubs (III), also points out to the conclusion of food shortage during winter.

3.4.2 Density-dependence and carrying capacity

The mean litter size decreased in the study period with increasing density of the population (III). The density-dependence of offspring production indicates intraspecific competition in the population of otters. In 1993 the otter population most probably reached the local carrying capacity of the study area (Fig. 3 in I, and Fig. 3 in III). After 1993 population size oscillated up and down (was typically "saw-like"), indicating intraspecific competition between otters (Royama 1992, III). Although there is abundant water in the study area, the carrying capacity is low. The limiting factor is the time when waters are open, i.e. competition for food intensifies when nearly all waters are covered by ice in winter. When the population density increased shortage of winter food became evident, and the litter size decreased. The shortage of food could also be seen in cub production in different river systems. Only females living in the river systems with large open waters in winter could produce many offspring (III). The increased competition could also be seen in the number of death otters as the population density increased (Fig. 9).

Kruuk et al. (1991) and Kruuk & Conroy (1991) found a strong correlation between numbers of cubs and numbers of prey in Shetland. They also observed that females can deliberately reduce litter size by neglecting their offspring. A female will only abandon a cub if there is shortage of food (Kruuk 1995). Also in Spain, a clear connection between fish abundance and otter populations was found (Ruiz-Olmo et al. 2001a). This may be the case in central Finland, too. I counted the number of cubs in late autumn or early winter, but I do not have data on the litter size at birth. Hypothetically litter size might be the same, but the number of cubs

in winter decreased during the study period.

3.5. Source-sink dynamics and spatial organization of otters

There was clear source-sink dynamics between the habitats occupied by otter populations. Otters in a few river systems produced most cubs, which then occupied the secondary habitats, allowing the total otter density to increase in all the river systems in the study area. The five most productive river systems (altogether 16 river systems) produced 72% (111 cubs) of all the juveniles in the study area during the years 1985-2003 (total of 154 cubs) (III). Otters in the secondary habitats did not reproduce (Table 1) (III).

It was also likely that immigration was not an important factor for population growth in the study area. Earlier studies revealed that population density increased simultaneously both inside the study area and its surroundings (personal observations, Mäkelä & Rajala 1995, Helle et al. 1998, Sulkava & Liukko 1999, Ludvig et al. 2002). The birth rate was also higher than population growth rate (Fig. 9b), and so there were more young otters than could be sustained inside the area. This could be seen also in the increasing number of death individuals (Fig. 9a). The high birth rate and limited possibilities for finding a free home range outside the study area indicate that the population growth in sink river systems was due to births in source river systems close by. This phenomenon was not known earlier in otters.

To find out why some river systems were more productive than others, I studied the size of rivers, riverbed and lakeshore lengths, lake areas of otters and possible feeding areas in winter, and examined the relationships between the population density or cub production and the characteristics of habitats.

More litters and cubs were born in river systems with large lake surface area than those of small lake area (Table 1) (III). Seven river systems with large lake surface areas produced 84% (129 cubs) of the juveniles (areas 1, 3, 4, 6, 10, 11 and 15 in Fig. 1). Three of these river systems were large and four medium-sized, classified by the mean width of the main river. There were also more large and medium-sized lakes in the river systems that produced most of the litters and cubs (Table 1) (III).

Riverbed length or size of water areas in rivers (ha) did not correlate with the number of cubs (III). Neither did riverbed length correlate with the number of litters. Large lakes were important for otters in winter even though all the lakes themselves were totally ice covered, since large lakes maintain ice-free outflows, and these were important feeding areas for otters (Fig. 6).

Table 1. The number of cubs born in river systems with large (first seven) and small lakes in the study area in 1985-2003, and the number and surface area of lakes in all river systems. In a few cases it was not clear whether there were one or two cubs in one litter. These cases were measured as 1.5 cubs per litter.

River system (numbers in Fig. 1)	Total production of cubs in 1985-2003	Cubs / 100 ha of lake surface	Number of large lakes (more than 100 ha)	Number of medium size lakes (20-99.9 ha)	Total surface area of lakes (ha)	Total number of lakes and ponds
Large lakes						
1	23	2.47	1	10	931	40
3	23.5	1.34	4	7	1752	29
4	14	0.44	4	4	3156	24
6	15	0.75	6	11	2013	42
10	17.5	1.50	2	10	1166	27
11	32	0.95	2	0	3353	9
15	4	0.28	3	6	1428	22
Subtotal	129	0.93	22	48	13799	193
Small lakes						
2	3	0.86	1	2	347	22
5	1	0.31	1	1	327	27
7	3	0.58	1	3	515	10
8	7	3.54	0	4	198	6
9	3	1.63	0	3	184	10
12	1	0.19	1	3	526	27
13	2	0.38	3	6	526	33
14	3	0.90	1	2	334	20
16	2	0.65	1	2	310	5
Subtotal	29	0.89	9	26	3267	160
Total	154	0.90	31	74	17066	353

Although the litter size decreased in the study period, the annual number of litters increased at the same time. This was especially clear in the river systems with small lake surface areas (ANOVAR, df=1, F=19.00, p=0.002) (Table 1). Most probably the reason was that all river systems with large lake areas (good habitats for overwintering) were occupied, and when young individuals came to reproductive age, they had to breed in secondary habitats. There was less food available in these habitats, and females were younger than other areas. For these two reasons litters were smaller in secondary habitats, and also the possibilities of cubs surviving over the next winter diminished.

3.6 Mortality

A decreasing birth rate and/or an increasing death rate could explain the S-shaped growth curve of the population (Becon et al. 1990). Mortality for otters is difficult to estimate. In the study area, dead otters are found occasionally in the field, but I do not know how many otters actually died per year. However, since the density of the population was at about the same level inside of my study area than the surrounding areas, it is not likely that many individuals emigrated (or immigrated) from the study area to surrounding areas. The fluctuating population ("saw-like" shape of dynamics) (Fig 9a) (III), also indicate that possible migration was not an important factor in population dynamics. Therefore I calculated the number of dying individuals by subtraction:

Number of dying = Total number of otters in year $_t$ ─ *the number of adult otters in year* $_{t+1}$

This calculation is, of course, confused by possible immigration and emigration, but is after all highly indicative.

Birth rate is calculated:

Birth rate = Number of cubs in year $_t$ */ number of adults in year* $_t$

There were less dying individuals in the period of increasing population than after it (Fig. 9a). Before the year 1993, the mean growth rate of the population was 0.11 per year, and after that 0.02 per year (Fig. 9b). The calculated annual number of deaths (4.43) was lower than the number of births (7.75) before the year 1993. After that, population growth stopped, and the number of births (10.00) and deaths (11.00) seems to be equal (Mann-Whitney Test, $p > 0.05$) (Fig. 9a).

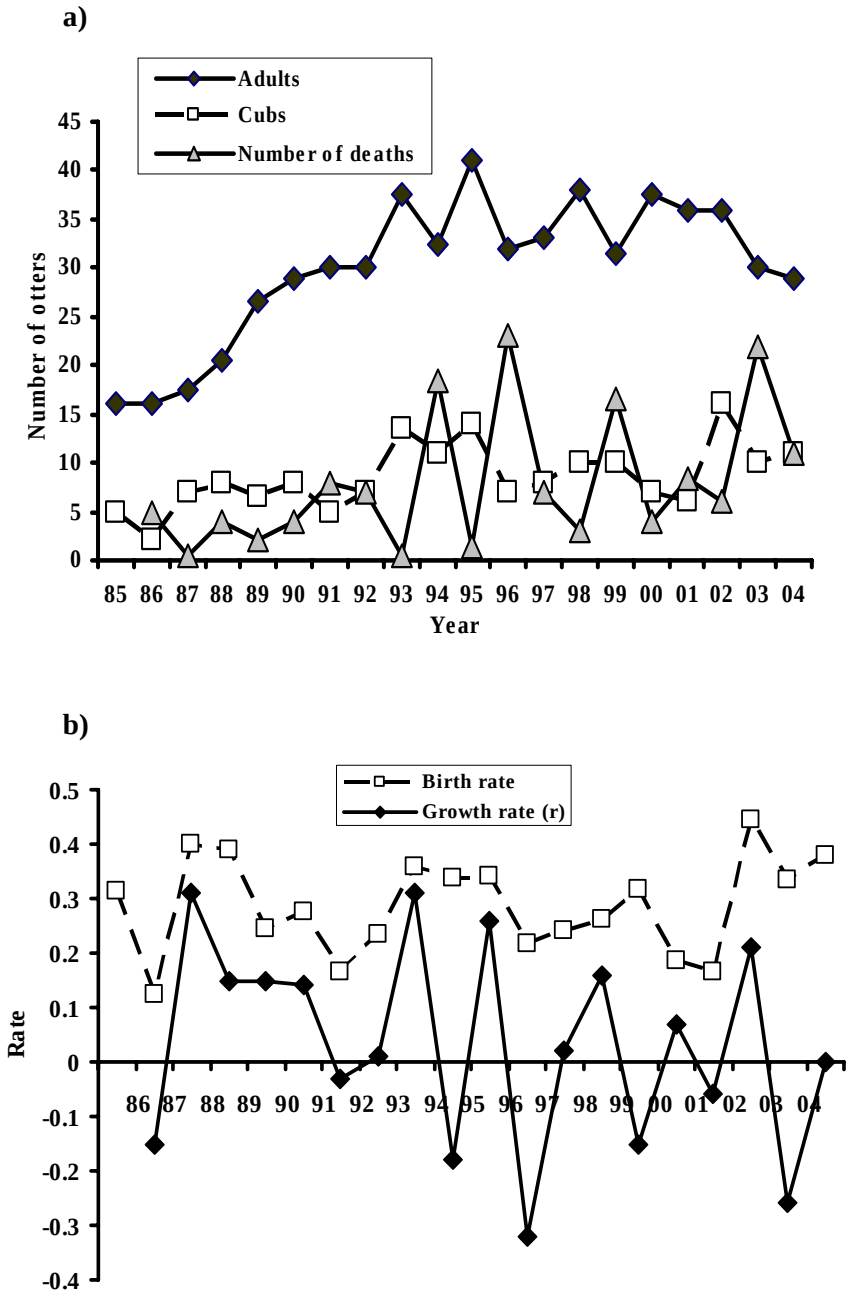

Figure 9. The annual number of cubs and adult otters, and the estimated number of dead otters in the study area (a). There were more deaths after saturation of the population in 1993 (Mann-Whitney Test, U = 18.5, p = 0.03). The birth rate and the growth rate (r) of the population (b).

3.7 Diet

Fish and amphibians were the main components in the diet of otters in central Finland (IV). Small cyprinids (mainly *Rutilus rutilus, Alburnus alburnus, Leuciscus idus* and *Acerina cernua*), perch (*Perca fluviatilis* and *Acerina cernua*) and pike (*Esox lucius*) were the most important fish for otters in central Finland (IV). The food composition varied seasonally. Amphibians (*Rana* sp. and *Bufo bufo*) were the most important prey in winter (BP used in all percents), (33.2% of food). Perch, pike and cyprinids were important in all seasons, but in winter small sculpins (*Cottus cottus*) (9.8% of food) and burbots (*Lota lota*) (8.9%) were also important food sources for otters. Cyprinids were the most important prey in spring (38.7% of food). Amphibians were important especially in the smallest streamlets (in winter; 68.4% of food). The otters also ate toads. In some river systems, crayfish (*Astacus* sp.) and mammals were commonly consumed, but salmonids, birds, reptiles, insects, molluscs and plants were used only occasionally by most otters in the study area. Most of the otters lived in small forest rivers, and therefore amphibians and sculpins played a critical role in the diets of most otters in winter (IV). These results are also supported by later studies (Ludwig et al. 2002). Although the otter is more a specialist than a generalist like the mink (Bonesi & Macdonald 2004), it is obvious that otters take the most abundant food and prey easiest to catch on most foraging occasions (e.g. Clavero et al. 2004, IV). In Finnish conditions there are few possibilities to favour certain prey items over others in winter (I, III, IV). Several studies have shown that fish dominate the diet of otters, but there was also significant temporal and spatial variation in the diet (e.g. Erlinge 1969, Fairley 1972, Jenkins et al. 1979, Chanin 1981, Kemenes 1989, Mortensen 1989, Carss et al. 1990, Brzezinski et al. 1993, Kucerova 1998, Roche 1998, Ludwig et al. 2002, Clavero et al. 2004). Variation in the diet of different areas also indicates that the foraging habits and diet of otters is still incompletely known. The diet of otters in central Finland appears to be very different from that found in most other areas (e.g. Erlinge 1967b and 1972, Webb 1975, Kruuk & Hewson 1978, Jenkins & Harper 1980, Wise et al. 1981, Kruuk & Moorhouse 1990, Beja 1991, Bodner 1998, Taaström & Jakobsen 1999). Most of the otters lived in small rivers or streamlets in central Finland in winter, and fed mainly on amphibians. A few earlier studies have reported that otters eat remarkable amounts of amphibians (Fairley 1972, Macdonald & Mason 1982, Skaren & Kumpulainen 1986, Adrian & Delibes 1987, Laanetu 1989, Sulkava & Sulkava 1989, Weber 1990, Ozolins & Rantins

1992a, Skaren 1992a, Sidorovich 1997).

CONCLUDING REMARKS

In this study the long-term trend and clear increase in otter population were documented for the first time by total annual counting of otters (I, III). Finding a clear sigmoidal model for the increasing densities of otter population made it possible to determine the local environmental carrying capacity for the study area (III). Otters in a few river systems produced most of the cubs, creating a source-sink habitat structure in studied river systems (III). The density-dependent offspring production of the population of otters was also documented first time (III). The density-dependence of offspring production, together with typical the saw-like shape of the growth curve and increasing number of deaths when the population density increased, indicate that intraspecific competition in the otter population was the main factor regulating population size. Aggression between individuals may occur in summer, although the reason for competition, lack of food, is evident in winter, when most feeding areas are covered by ice (I, III, IV).

Local characteristics, such as the presence of amphibians in the otter's diet in Finland, have now been discovered (IV). Other typical features such as the very large home ranges and long distances moved by the otters are now also known (I, III, this thesis). Evaluating the monitoring of otter numbers using the new OVC method developed, shown that the method works well in Finnish conditions, and that the Finnish otter population in the years 1995-1998 comprised 2000-2250 individuals (I, II).

More studies are needed to investigate the role of different water systems and possible seasonal territoriality of otters during winter. Home range studies of male otters are still needed. Possible changes in diet after the saturation point of the otter population have not yet been studied. The lack of real monitoring system of otters in Finland needs to be urgently fixed.

ACKNOWLEDGEMENTS

I should like to thank all those people who worked with me and made this study possible. I am especially grateful to my father Pertti Sulkava, who has done more work in the field than others. I should also like to thank all the other field assistants for their great help in the field investigations. I thank you Ari, Esa and Matti Aalto, Pauli Arppe, Eero Heinonen, Jouni and Teijo Kaijanmäki, Jouni Kalmari, Juhani Kiltinen, Lauri Laitinen, Jouni Lamminmäki, Kari and Tarmo Myntti, Antero Mäkelä, Marko Mäkinen, Ossi Nokelainen, Jouko Pihlainen, Ari Sillanpää, Kimmo Sipiläinen, Bo Storrank, Jaana, Pekka and Raija Sulkava and Tuomas Syrjä. I hope that I have not forgotten any of you. Many other peoples have also informed me of otter tracks, otters, litters, dead otters or other otter-related matters during all these years. My thanks go to them!

I wish to thank Prof. Heikki Hyvärinen, Prof. Heikki Roininen and Prof. Jorma Tahvanainen, my supervisors from the University of Joensuu. Jaana Höglund, Ulla-Maija Liukko, Gilbert Ludwig, Torsten Stjernberg, Bo Storrank, Pekka Sulkava and Hannu Ylönen, I thank you, too, for your excellent co-operation. My thanks are also due to Prof. Seppo Sulkava for his comments and inspiration, and Pekka Sulkava, Heikki Roininen and Hannu Huuskonen for their help with the statistical analyses.

The Finnish Environment Institute, the Finnish Ministry of the Environment, The Regional Environment Centres, the regional administration of the Forest and Park Service, the Finnish Museum of Natural History, the Finnish Game and Fisheries Research Institute, the Memoranda Society, WWF Finland, the Finnish Association for Nature Conservation, Natur och Miljö rf, Keurusseudun Luonnonystävät ry and Ranua Zoo, have all supported some part of this study either financially or in some other way. My thanks also go to those 60 people who worked in the field or with data during the pilot study of the Finnish otter monitoring. Rosemary Mackenzie corrected the English language of this paper.

I also wish to thank my friends Tuula & Ari, Päivi & Hannu, Airi & Jouni and others: some moments of life are happy. Thanks also go to all my friends in the Finnish Association for Nature Conservation, BirdLife Finland, Suomenselän Lintutieteellinen Yhdistys, Keurusseudun Luonnonystävät, the Finnish Flying Squirrel Association and other co-operating conservationists: It sometimes seems hard work, but is sometimes also rewarding.

Finally I should like to thank and intensively kiss my wife Jaana: perhaps it is a miracle, but after these twenty years of study we still love each other. Our children, Erika and Carita, have been splendid, too.

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