Otter *Lutra lutra* predation on farmed and free-living salmonids in boreal freshwater habitats

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Ludwig, G.X., Hokka, V., Sulkava, R. & Ylönen, H. 2002: Otter *Lutra lutra* predation on farmed and free-living salmonids in boreal freshwater habitats. - Wildl. Biol. 8: 193-199.

In this paper we aim to define whether fish farms or stocked trout streams substantially contribute to the diet of otters *Lutra lutra* living in freshwater habitats of Mid-Finland. Diet was assessed using spraint analysis. We especially focused on areas with fish farms and stocked trout *Salmo trutta* streams (salmonid-rich habitat) and used 'normal' (salmonid-poor) habitats as control. Frequency of salmonid remains in spraints was significantly higher in salmonid-rich habitats than elsewhere in all seasons, the difference increasing from summer to winter. In salmonid-rich habitats, however, salmonid consumption was not strongly seasonal. Data from spraint collection indicated a shift in activity towards salmonid-rich habitats in winter. Otters therefore seem to switch prey seasonally, due to seasonal variation in the availability of other prey categories, by choosing to forage in particular, predictable habitats. Furthermore, our results suggest that, in salmonid-rich habitats, the increase in salmonid frequency is to a larger extent due to the presence of fish farms than that of trout streams. Fish farms, and to a lesser extent stocked streams, may therefore constitute seasonally important feeding grounds for otters.

Key words: diet, fish farms, Lutra lutra, otter, predation, salmonids, spraint analysis

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Received 4 April 2001, accepted 17 December 2001

Associate Editor: Miguel Delibes

The European otter *Lutra lutra* is an endangered species in many European countries (Mason & Macdonald 1986), although signs of recovery are evident (Kranz 2000). However, in Finland the otter is currently widespread and the population trend was positive in most parts of the country, at least during 1980-1995 (Sulkava & Liukko 1999).

The potential negative impact of otter predation on fish stocks of both economical and recreational value is a problem in some regions of Europe. Substantial work has therefore been devoted to the quantification of otter damage on commercially valuable fish populations in artificial ponds or natural waters. Carss, Kruuk & Conroy (1990) report increased predation on salmon *Salmo salar* during spawning time in a river in Scotland, and Roche (1998) concludes that economically important carp *Cyprinus carpio* in South Bohemia is an important source of food during winter, when other fish prey is limited. These and other findings (Kemenes & Nechay 1990, Bodner 1993, Durbin 1997, Bodner 1998, Kucerova 1998, O'Neill, Day & Paterson 1998) suggest that the impact of otter on commercially valuable fish species may depend on the availability of alternative prey. Furthermore, spatial and temporal heterogeneity in the relative availability of different prey is likely to affect patterns in habitat use.

Within the Finnish lake district, fish farmers have been complaining about increasing damage caused by otters at both commercial fish ponds and in stocked trout *Salmo trutta* streams. The most important farmed and stocked species are trout, rainbow trout *Oncorhynchus mykiss* and salmon, and to a lesser extent grayling *Thymallus thymallus* and whitefish *Coregonus* sp. These salmonid species generally represent a minor proportion of the natural fish fauna in most Finnish freshwaters, where fish communities are mainly dominated by cyprinids, percids, pike *Esox lucius* and burbot *Lota lota*. Hence, results of previous dietary investigations in eastern (Skarén 1992) and central Finland (Sulkava 1996) may not be representative for areas with high densities of salmonids, such as fish farms or stocked trout streams.

In this paper, we investigate the extent to which fish farms or stocked trout streams affect i) the composition of otter diet and ii) the patterns in the use of habitats at any time of the year.

Material and methods

Study area

The main study area is situated in the region of Jyväskylä in Mid-Finland (62°14'N, 25°45'E), consisting of several subcatchments of the Kymijoki watershed. The area is characterised by a dense network of small and medium-sized, usually short streams and rivers that flow through a patchwork of farm land, woods and drainage land, thereby feeding a large number of lakes. The entire study area covers an area of 2,800 km^2. Within the area, we distinguished between two main types of habitat, i.e. natural habitat, characterised by low average salmonid abundance (hereafter called 'poor'), and habitat characterised by the presence of fish farms and/or stocked trout streams (hereafter called 'rich'). For the former type, 65 sampling sites were chosen such that the distance between sites, and therefore independence of spraints (Carss & Parkinson 1996), was maximised. For rich habitats, we chose four areas of fish production and/or intensive stocking. Two of them were fish farms, the Korholankoski fish farm, a hatchery producing trout, rainbow trout and salmon, and the Siikakoski fish farm, producing only rainbow trout. Both farms were unfenced and situated adjacent to a lake outlet stream, stocked with trout, rainbow trout and grayling. The third area was the research fish farm of the Finnish Game and Fishery Research Institute in Laukaa, producing trout, rainbow trout, whitefish, grayling and carp. This farm was fenced and not situated adjacent to any trout stream. The fourth rich habitat study area was the stocked lake-outlet stream of Liunankoski near Joroinen, about 140 km to the east of the main study area. This stream was not situated in the vicinity of any fish farm. It is annually stocked with trout, rainbow trout and grayling. Stocked trout streams in central Finland are characterised by their short length, usually being only a short section of rapids of several hundred metres, to which most stocked salmonids remain confined. Both fish farms and trout streams remain accessible throughout the winter, whereas access to poor habitats is restricted, as lakes, and to a large extent also streams and slow rivers, freeze over for periods of up to five months.

Collection of spraints and habitat use

Spraints were collected monthly over one year from June 1998 to May 1999. At the three fish farms, the entire farm area was searched for spraints as were much of the surroundings. The lake-outlet streams next to the fish farms of Siikataimen and Korholankoski, as well as a total of 1,000 m of the in- and outflow stream of the Laukaa fish farm were carefully searched, too. The Liunankoski stream was investigated on a stretch of 1,000 m. At poor sites, searching occurred at and near the centre of the selected site only. All sites were cleaned of spraints one month before the first sampling session. Spraints were assigned to nordic seasons as described in Sulkava (1996): spring (April-May), summer (June-August) autumn (September-October) and winter (November-March). Seasonal changes in patterns in habitat use were approximated by comparing (using χ^2-test) the seasonal ratios of spraints found at poor sites to those found at rich sites.

Diet analysis

After collection, spraints were preserved in polyethylene bags and stored at -20°C until further treatment. In the laboratory, spraints were soaked in a solution of washing powder for 24 hours, rinsed through a sieve (mesh size: 0.5 mm) and dried at 50°C for another 24 hours.

Fish prey was identified to species level, whenever possible, on the basis of undigested prey remains. A reference collection of key bones and scales of all important species was used in addition to common keys including

Libois & Hallet-Libois (1988), Conroy, Watt, Webb & Jones (1993) and Knolleisen (1996). Trout and rainbow trout were grouped because often it was not possible to discriminate between the two species. Occurrence of perch *Perca fluviatilis* was not included in the analyses if scales were the only remains (see Carss & Parkinson 1996). Mammals, amphibians, birds and crayfish were not identified to species level. Composition of diet was expressed as frequency of occurrence (percentage frequency; the proportion of spraints containing a particular prey item). The problems associated with faecal analysis and frequency of occurrence have been discussed elsewhere (e.g. Carss & Parkinson 1996, Jacobsen & Hansen 1996). It is generally accepted that frequency of occurrence gives a relatively poor estimate of the true proportions of various prey groups, but it is a good indicator of the rank order of prey categories in the diet. We concluded that frequency is the easiest and most appropriate method when assessing seasonal variation in diet and when testing for differences in diet between different habitats. Cross-tabulation χ^2-tests (Zar 1999) were performed to test for differences in prey composition between habitats and seasons. Although independence of spraints has been maximised, it is not necessarily always guaranteed; therefore we used a stricter significance level of 0.01.

Results

Consumption of salmonids and other prey categories

During the sampling period, a total of 1,772 spraints was collected and analysed; of these 1,235 (70%) came from poor and 537 (30%) from rich habitats. The annual frequencies of all important prey groups are listed in Table 1. Fish was the most important prey category for all habitats and seasons combined, occurring in 84% of all spraints. Amphibians occurred especially frequently in poor habitats. In general, mammals, birds and freshwater crayfish occurred less frequently. When all seasons were combined, frequencies of the dominant prey groups differed significantly between rich and poor habitats. Salmonids, percids, burbot and bullhead *Cottus gobio* were more important in the former, whereas cyprinids, pike, amphibians and mammals dominated in the latter.

Salmonids were the dominating fish prey in rich habitats, occurring with a frequency of 37.2%. Variation between the different sites, however, was large; annual salmonid frequencies in otter diet at the four rich sites ranged from as low as 3.7% at Liunankoski (N = 108) to 58% at Korholankoski (N = 181). The corresponding frequencies for Laukaa (N = 88) and Siikakoski (N = 160) were 53.6 and 39.8%, respectively. Other important prey categories were burbot, percids (mainly perch) and cyprinids (mainly roach *Rutilus rutilus* and bream *Abramis brama*).

Table 1. Percentage frequencies of the dominant prey groups and comparisons (χ^2) of percentage frequencies of the main prey groups in the diet of otter in both habitats at all seasons. NS: non significant; *: significantly different at 0.01 > P > 0.001; **: significantly different at P < 0.001.

	Salmonid-rich	Salmonid-poor	χ^2	P
Sample size (N)	537	1235		
Summer	67	337		
Autumn	66	330		
Winter	319	318		
Spring	85	250		
Seasonality	χ^2 = 340.7; P < 0.001	χ^2 = 15.5; P < 0.01		
Fish	94.0	80.3	53.71	**
Salmonidae	37.2	6.8	257.71	**
Percidae	31.8	26.3	5.67	NS
Cyprinidae	21.4	38.6	49.81	**
Esox lucius	14.2	23.3	19.27	**
Lota lota	35.8	22.5	33.69	**
Cottus gobio	13.6	4.0	54.10	**
Mammals	2.8	6.4	9.67	*
Birds	4.5	7.0	3.99	NS
Amphibians	15.1	30.4	45.72	**
Crustaceans	0.7	3.8	12.54	**

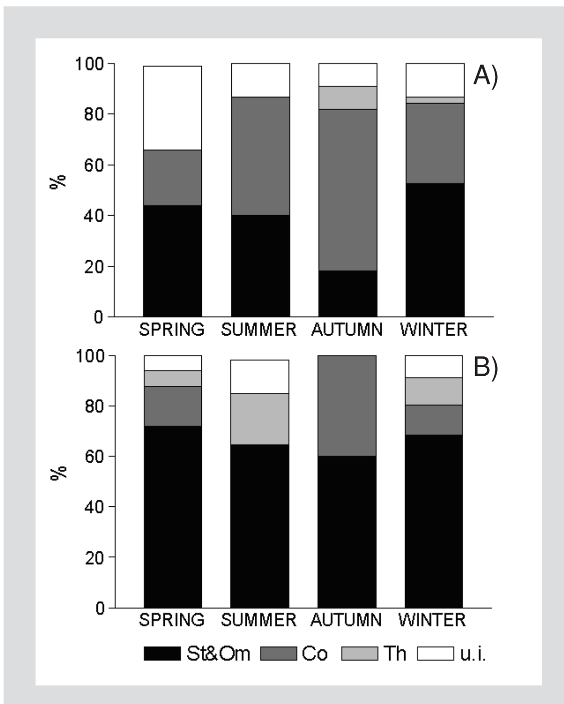

Figure 1. Seasonal composition of salmonid prey species (St & Om = trout and rainbow trout; Co = whitefish; Th = grayling; u.i. = unidentified) expressed as proportions (in %) of all salmonid presences in A) salmonid-poor and B) salmonid-rich habitats.

Otter diet in rich and poor habitats was significantly different. In poor habitat fish dominated on an overall basis, but to a significantly lesser degree than in rich habitats. Salmonids were significantly less preyed upon in poor habitat, the frequency for all sites and for the entire study period being only 6.8%. Instead, the diet was dominated by cyprinids, amphibians, percids, pike and burbot (see Table 1 for details).

The species composition of salmonid remains differed between habitats (Fig.1). Trout and rainbow trout were the most important salmonids at all rich sites, overall making up 69% of all salmonids present. In poor habitats, whitefish (42%) was apparently as important as trout/rainbow trout.

Seasonal variation in sprainting activity

The seasonality of spraints recovered was very strong in rich habitat, where almost 60% of all spraints were found in winter (see Table 1). Seasonality was less evident, though significant, in poor habitat. Correspondingly, the ratio of the number of spraints found in poor habitats to that found in rich habitats was also highly seasonal ($\chi^2 = 192.7$, df = 3, $P < 0.001$).

Seasonal variation in diet

The frequencies of all main prey categories for each season are presented in Figure 2. Salmonid predation varied seasonally in both rich and poor habitats ($\chi^2 = 24.4$ and 20.3, respectively; df = 3, $P < 0.001$). In rich habitats, predation on salmonids reached a peak during the

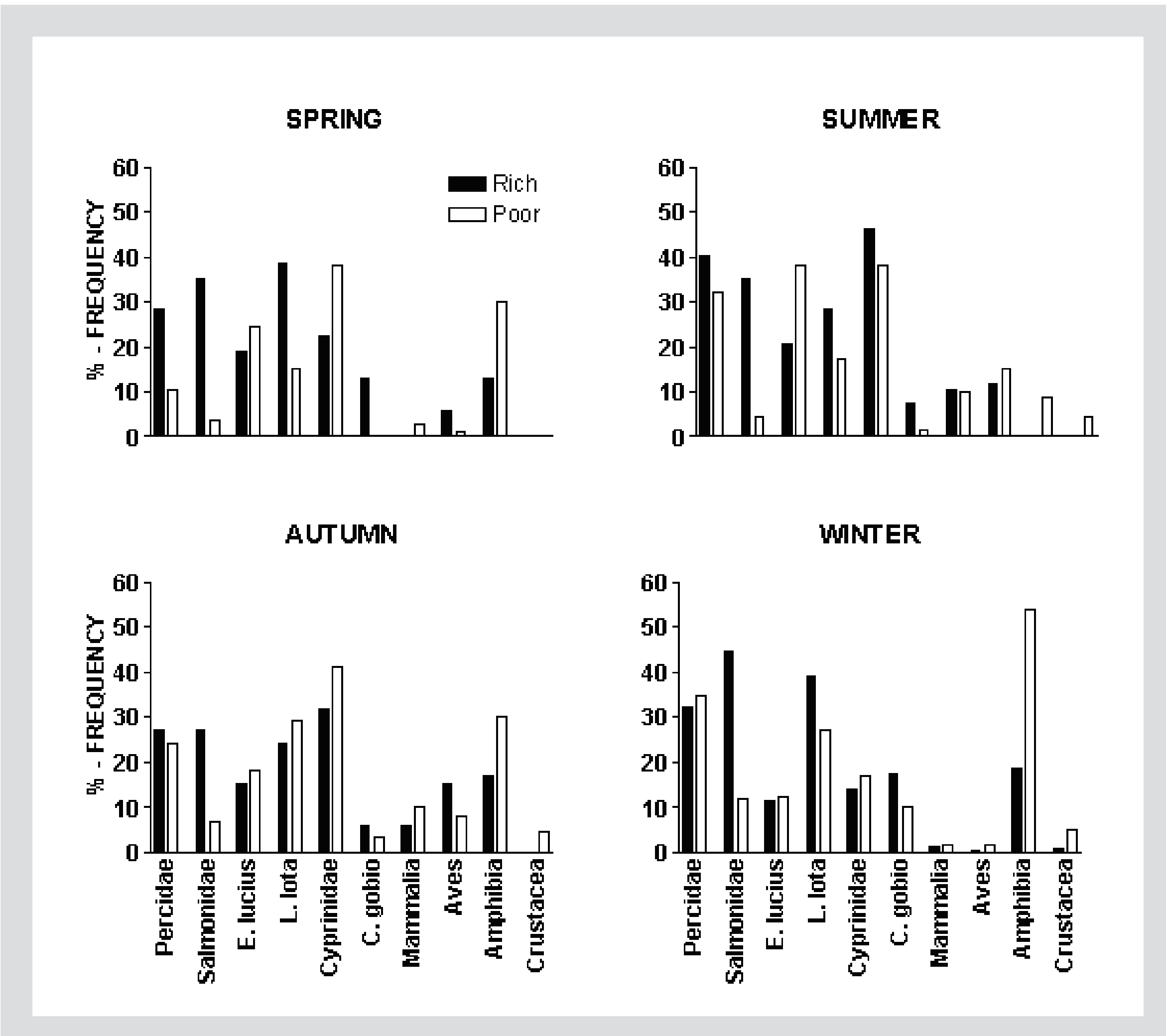

Figure 2. Seasonal composition of otter diet in salmonid-rich (■) and salmonid-poor (□) habitats during spring, autumn, summer and winter, with prey groups expressed as %-frequency.

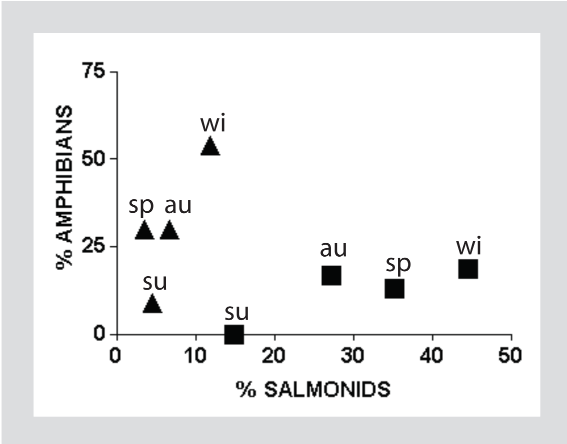

Figure 3. Relationship between salmonid and amphibian frequency (in %) during spring (sp), autumn (au), summer (su) and winter (wi) for salmonid-poor (▲) and salmonid-rich (■) habitats.

winter and spring and was lowest in summer. In contrast, in salmonid poor habitats salmonids were preyed upon most during winter and autumn and least during spring. The difference in salmonid frequency in otter diet between rich and poor habitats was significant in all seasons. Amphibians were the most important prey in poor habitats during the winter season. The relationship between amphibian and salmonid frequency in the two main types of habitat is shown in Figure 3.

Discussion

Frequency of prey remains in rich and poor habitats differed significantly, most strikingly in salmonids. While our results from poor habitats support those of former studies (Skarén 1992, Sulkava 1996), we clearly demonstrated that otters, according to the assumptions of the optimal foraging approach to patch use (Begon, Harper & Townsend 1986), may respond to increased availability of certain species; salmonids were significantly more preyed upon in rich habitats throughout the study period than they were in poor habitats, but to a higher degree during winter and spring, i.e. during the time of ice cover, than during summer and autumn.

For the Laukaa farm and the Liunankoski stream, there was no doubt about where the salmonids had been preyed upon, as they do not occur in the near surroundings. At Siikakoski and Korholankoski, however, the situation is more confusing, as salmonids occur both within the farm and in the adjacent streams. Our results nevertheless suggest that otters preferably take salmonids from farms rather than from streams; salmonid frequencies were high in Laukaa (no trout stream) but very low at Liunankoski (no fish farm). Carss, Nelson, Bacon & Kruuk (1998b) pointed out that availability of prey is more critical to otters than mere abundance. Whatever the density or abundance of prey, access to prey is highly variable, as it changes with e.g. time of day, season, habitat or prey type. In stocked trout streams, therefore, high abundance of salmonids is not necessarily equal to high availability. However, in unnatural habitats like fish farms, where fish are crowded in ponds, availability can be seen as a function of abundance, i.e. it is always high.

The comparatively low seasonal variation in the percentage frequency of salmonids at Siikakoski and Korholanoski indicates that availability remains rather constant throughout the year. In contrast, O'Neill et al. (1998) reported percentage frequency of salmon at a salmon hatchery and its adjacent salmon stream in Ireland to be highly seasonal. They argued that salmonids become more vulnerable to predation in winter because of reduction in swimming performance induced by lowered water temperature (Heggenes, Krog, Lindas, Dokk & Bremnes 1993). Again, this should actually apply to stocked populations, but not necessarily to crowded populations kept in small ponds. Therefore, we should expect a higher degree of seasonality if the fish were taken mainly from the stream rather than from the farm. This does not seem to be the case in our study.

Concerning other prey groups, our results support the investigations by Skarén (1992) and Sulkava (1996) by underlining the importance of percids, cyprinids, pike, burbot and amphibians. The observed difference between poor and rich habitats in most prey groups most certainly reflects differences in the availability of prey, and are probably neither positively nor negatively correlated with the presence of salmonids. Amphibians might be an exception. Though amphibian frequency slightly increased with salmonid frequency within rich habitats, it was always significantly lower than in poor habitats. Weber (1991) argued that seasonal exploitation of amphibians by otters in northeastern Scotland may have resulted from a decrease in availability of other important prey. Cyprinids, the main prey of the otter in poor habitat from spring to autumn, migrate to deeper strata of lakes during winter, and this is indeed reflected by a decrease in both cyprinid and overall fish frequency. Amphibians may then be the most profitable alternative prey. The observed relationship between amphibian and salmonid frequency in both habitat types supports the hypothesis that in rich habitat, there is no need to switch to less profitable prey.

Our study suggests that prey switching may occur in otters as a result of seasonal changes in the relative availability of prey groups, and that it is mainly the relative availability of alternative prey that determines the frequency at which otters visit fish farms, as salmonid consumption in summer is lower than could be expected. Similarly, Roche (1998) concluded that carps in a fish pond area in southern Bohemia might actually be underselected during times of high availability of alternative prey, becoming important only at times of food shortage.

The seasonality of the proportion of spraints found in poor and rich habitats further indicates that otter activity becomes more directed towards rich food patches during winter. A possible outcome could be an increase in home range overlap at sites with high availability of food during the time of food shortage. Carss et al. (1998) pointed out that even though otters generally take prey in accordance with their abundance in any one habitat, it may be possible that they do select for particular prey types, by selecting to forage in habitats with particular, predictable fish communities. We therefore conclude that areas with such fish communities, i.e. fish farms, and to a lesser extent stocked trout streams, may constitute substantial feeding grounds for otters during times of food shortage. We do accentuate, however, that fish farms and stocked populations are not necessarily vital components of otter habitats at the population level. Further research is needed to assess the proportion of otters that actually do forage at fish farms and to evaluate the extent to which these otters rely on these rich and predictable food sources.

Acknowledgements - we would like to thank Dr Miguel Delibes, Dr Jana Eccard and an anonymous referere for their comments on the manuscript. This study was part of a project investigating the ecology of otters near fish farms in central Finland and was financed by the Ministry of Agriculture and Forestry.

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