

Influence of food availability and reproductive status on the diet and body condition of the European lynx in Finland

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The carcasses of the 497 European lynx *Lynx lynx* (Linnaeus, 1758) killed in two areas in Finland in the 1980s were sexed, the nutritional status and diet of the lynx determined and the breeding stage of the females checked. There was no significant deviation in the sex ratio from 50:50 in any of ten hunting seasons. Fifty-three percent of the females over 1 year of age had given birth the previous spring, the mean litter size from the last pregnancy being 2.33 ± 0.73 ($\bar{x} \pm SD$, $n = 82$). In E Finland 86.2% of the winter diet consisted of hares, whereas in SW Finland the lynx consumed hares and white-tailed deer equally. There was no difference in diet between the sexes or age categories in E Finland, but in the white-tailed deer area of SW Finland the male lynx consumed more deer and hares less frequently than the females ($p < 0.05$). The lynx in SW Finland were on average, in a much better nutritional condition than those of E Finland. The male lynx in both areas had gained more depot fat than the females, on average a difference arising primarily from the smaller amount of fat in the female lynx which had given birth the previous spring. There were positive correlations in E Finland in all the age and sex categories between hare density and mesentery-omentum fat whereas snow depth produced negative correlation coefficients with the mesentery-omentum fat showing a significance of 90% in the adult females.

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Introduction

The primary prey of the European lynx *Lynx lynx* (Linnaeus, 1758) is the roe deer *Capreolus capreolus* when it is available, and its large body size is an adaptation to the use of roe deer as a main food supply (Pulliainen 1981). The smaller body size of three other lynx species, *L. rufus*, *L. pardinus* and *L. canadensis*, could thus be an adaptation for hare-sized prey. In the southern half of Finland, however, the area recently recolonized by the lynx, there are practically no roe deer available. In the western half of this area the lynx can choose between hares and white-tailed deer *Odocoileus virginianus*, introduced from North America over 50 years ago, as their main food items, while in its eastern half the choice is between hares and other small game (Pulliainen and Hyypiä 1975,

Pulliainen 1981, 1990). In addition to these regional differences in the situations of food availability, there have also been considerable fluctuations in hare densities during the 1980s.

The aims of this paper were to investigate (1) the choice of prey by the lynx in different food availability situations, (2) the influence of food availability and snow depth on the physical condition of the lynx in different sex and age categories, and (3) the demography of the Finnish lynx populations on the basis of kill statistics. This information is needed in the management of the species and for a deeper understanding of the different adaptations existing in the European lynx.

Material and methods

General

In 1968 the lynx was declared to be protected in Finland throughout the year by law. The Ministry of Agriculture and Forestry has granted special licences for hunting in areas where local populations are deemed to permit this. The regulations attached to the special licences oblige the hunters to weigh and measure the lynx killed, and since the winter of 1980/81 to send the carcasses to the Department of Zoology, University of Oulu, for examination. All of the carcasses received had been skinned, and in some cases the heads had been removed. In addition, the hunters were asked to describe the hunting event by filling in the appropriate form.

The yearly kill numbers increased three fold during the 1980s (Table 1). At the beginning of the decade almost all the kills took place in southeastern Finland (SE Finland), close to the border with Soviet Karelia, but in the later years hunting extended northwards from this core area of SE Finland to Northern Karelia and Kainuu and northwest into northern Savo. This created a wide, continuous hunting area which we will call here eastern Finland (E Finland) (Fig. 1).

Table 1. Sex distributions of lynx studied in open seasons in E Finland and SW Finland, and the percentages of the special licences which have resulted in a kill in the country (kill %, could be ascertained from the open season of 1983/84 onwards).

Open season	E Finland		SW Finland		Total	Kill (%)
	Males	Females	Males	Females		
1980/81	5	6	—	—	11	—
1981/82	5	11	—	—	16	—
1982/83	10	8	—	—	1	—
1983/84	11	17	—	—	28	55
1984/85	21	21	—	—	42	59
1985/86	23	32	5	3	63	57
1986/87	34	30	13	11	88	55
1987/88	25	22	9	8	64	71
1988/89	23	22	15	14	74	52
1989/90	34	30	15	14	93	51
Total	191	199	57	50	497	$\bar{x} = 56$

performance of the females was based on corpora lutea and placental scars (Saunders 1961, Nava 1970). The female reproductive tracts were removed and washed, the uterine horns were slit and stretched over a light source, and placental scars were counted using a magnifying glass or trans-lucence microscope.

Diet and food availability

The food of the lynx was determined from remains in the gastrointestinal tracts. The contents of the stomach and intestines were washed over a finemeshed sieve, weighed and the percentage of each food item by volume estimated visually to the nearest 20% (Brand and Keith 1979). Food items were identified by comparison with skeletal (i.e. bones, claws, teeth, jaws), hair and feather reference material in the Zoological Museum of the University of Oulu. Although varying amounts of lynx hairs were quite commonly found in the stomach, no assumption was made that the animals fed on other lynx. Some lynx had food items such as the plastic skins of sausages and the remains of fish and domestic animals in their gastrointestinal tracts, indicating that they had occasionally fed on dungheaps or rubbish dumps. Trapping and the use of carrion or bait in hunting are forbidden in Finland.

Data on fluctuations in the populations of the two Finnish hare species, the mountain hare *Lepus timidus* and the brown hare *L. capensis*, and of tetraonid birds are based on questionnaires administered seasonally by the Finnish Game Research Institute and the Hunters' Central Organization in which a random sample of sportsmen provide annual figures on their catches of the different game species. When examining the possible effect of the prevailing snow conditions on hunting success, and thus on the physical condition of the lynx, we calculated the yearly index of snow depth recorded in E Finland from data reported by three meteorological observation stations located in different parts of the region concerning the mean snow depth in December–January each winter.

Body condition

A number of indices to describe the physical and nutritional status of the lynx was measured. The data on body weights of the lynx studied were based on the obligatory reports attached to the special licences of the hunters. The mesentery and omentum together with the fat attached to the folds of these organs were removed and weighed (see Parker *et al.* 1983). The mesentery-omentum fat index was calculated for each lynx according to the formula:

$$\frac{\text{weight of mesentery-omentum fat}}{\text{body weight}} \times 100$$

The fat deposits situated dorsally and ventrally in the body cavity (ie the fattening rate of the body cavity) was evaluated visually on a scale 0 (none) to 5 (very abundant). The renal fat deposits, ie the percentage of the surface of the kidneys (*Capsula fibrosa*) covered by depot fat was estimated in accuracy of 5% (Riney 1955). The mean coverage of fat for both kidneys was used in comparisons. The renal fat deposits could not be estimated from 7% of carcasses because of shooting damages of the kidneys.

Student's *t*-test was used when comparing the body weights and mesentery-omentum fat indices between the two areas and different sex and age categories of the lynx. Differences in the distribution of the fattening rate values of the body cavity and the renal fat deposits were tested by using χ^2 -test. Spearman rank correlation test was used when studying the influence of hare density and snow depth on the amount of mesentery-omentum fat.

Results

Population numbers

Observations on the numbers of the lynx made by the Finnish Border Patrol Establishment in the areas adjacent to Russia and also other scattered records indicate a clear expansion of lynx to the north and northwest from the core area (the areas 1 and 2 in Fig. 2) in SE Finland and possibly from Russia during the past 20 years (Fig. 2). The numbers of lynx in southern parts of SE Finland have remained quite stable during the past twenty years showing at most only a slight increase (Fig. 2), while in recent years populations in some northern parts of SE

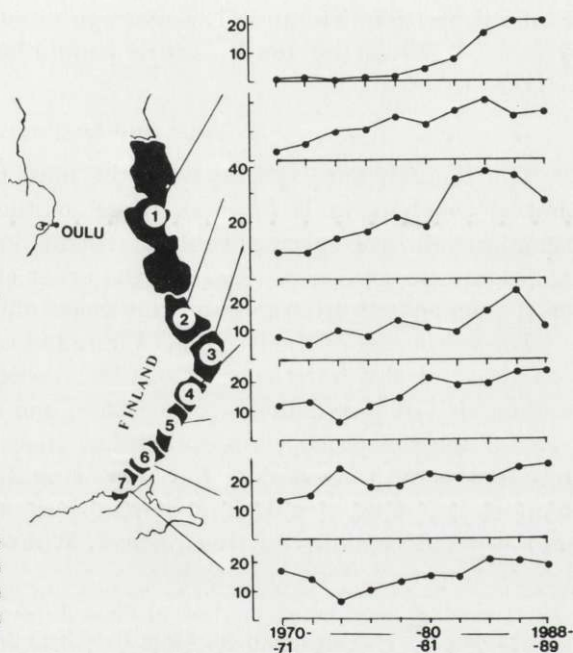


Fig. 2. Numbers of lynx reported by the Finnish Border Patrol Establishment in the vicinity of the Finnish-Soviet frontier in the years 1970/71–1988/89 (calculated as means for two-year periods).

Finland seem to have decreased, probably due to overkilling. There has been a clear, recent increase in the lynx population of Kainuu (areas 1–2 in Fig. 2), the most comprehensive track censuses carried out so far in Finland by the local Game Management authorities in the winters of 1988/89 and 1989/90 setting its numbers at 50 and 51 for these two years. Of all the special licences granted, only 56% has resulted in a kill in the open seasons of 1983/84–1989/90 showing quite a little year-to-year variation (Table 1).

Population structure

The sex ratio of the lynx killed was 49:51 (191 males/199 females) in E Finland and 53:47 (57/50) in SW Finland, the overall ratio among the 497 lynx thus being

50:50 (Table 1). Similarly, there was no significant deviation from the 50:50 ratio in any of the ten hunting seasons. Fifty three percent of the females over 1 year of age had given birth the previous spring in both areas. The proportion of the females over 1 year of age having been pregnant did not show any trend over the winters. When the kill numbers of the female lynx annually exceeded 10 specimens in E Finland, the proportions of pregnant females were at highest in the winters of 1986/87 (64%) and 1987/88 (61%), and at lowest 1985/86 and 1989/90 (43% in both winters). Kittens made up only 13% of the total catch.

The numbers of placental scars of the previous pregnancy could be ascertained from 82 females. The litter sizes were 10×1 , 38×2 , 31×3 and 3×4 , the mean \pm SD being 2.33 ± 0.73 ($n = 82$). The reproductive rate did not differ between E Finland and SW Finland. The average numbers of placental scars were 2.46 ± 0.84 ($n = 22$) in the southwestern population, and 2.27 ± 0.67 ($n = 60$) in the eastern ($t = 0.40$, ns).

Diet and food availability

The Finnish hare species were the most prominent component of the winter diet of the lynx in E Finland, 86.2% of the gastrointestinal tracts containing remnants of these species (Table 2). Tetraonids were second in abundance (12.8%) and domestic cats third (3.9%) in the order of predominance. There were no sex- or age-dependent differences in the choice of food made by the lynx in E Finland.

The mean diet of the lynx in SW Finland consisted equally of white-tailed deer (43.0%) and the hare species (42.1%, Table 2). Other major food items were tetraonids (10.3%), domestic cats (7.5%) and microtids (12.1%). Male lynx over 1 year of age consumed white-tailed deer more often than females, and hares less frequently, the ratio of deer to hares being 27:15 for the males and 16:25 for the females ($\chi^2 = 5.30$, $p < 0.05$), whereas there was no difference between the adult and subadult females in this respect. White-tailed deer constituted 60% of the

Table 2. Winter diet of the lynx in Finland (percentages of gastrointestinal tracts containing the prey species in question). Data from the seasons 1967/68–1979/80, Pulliainen (1981). n – number of tracts analysed.

Prey	SE Finland	E Finland	SW Finland
	1967/68– –1979/80	1980/81– –1989/90	1985/86– –1989/90
Hares, <i>Lepus timidus</i> and <i>L. europaeus</i>	79.5	86.2	42.1
White-tailed deer <i>Odocoileus virginianus</i>	–	–	43.0
Tetraonids	6.6	12.8	10.3
Microtids	1.6	3.1	12.1
Domestic cat <i>Felis catus</i>	4.1	3.9	7.5
Red fox <i>Vulpes vulpes</i>	0.8	2.1	0.9
Raccoon dog <i>Nyctereutes procyonoides</i>	–	1.8	4.7
n	88	390	107

Table 3. Total catch numbers of hares and tetraonids, snow depth index (calculated from data reported by three meteorological observation stations located in different parts of the region concerning the mean snow depth in December–January each winter), the seasonal means for the mesentery-omentum fat index (see Material and methods), and body weight in adult male and female lynx in E Finland (see text for further details).

Open season	Number of catches		Snow depth index (cm)	Fat index		Body weight (kg)	
	Hares	Tetraonids		Ad males	Ad females	Ad males	Ad females
1982/83	284000	126000	27	2.27	2.32	18.6	15.3
1983/84	235000	110000	54	2.08	1.61	16.7	15.3
1984/85	199000	103000	21	2.88	2.37	17.9	15.5
1985/86	139000	81000	35	1.72	1.53	15.4	15.7
1986/87	116000	120000	24.5	1.90	1.31	17.9	14.2
1987/88	92000	105000	42	1.96	1.81	17.1	15.2
1988/89	187000	240000	50	1.88	1.13	16.3	14.9
1989/90	169000	224000	20.5	1.85	1.44	16.8	15.6

prey animals in the winters of 1985/86–1986/87, when hunting commenced in the core area of SW Finland, an area with an abundant deer population, but later on when the hunting area was widened the proportion of white-tailed deer in the diet of the lynx decreased markedly.

Yearly changes in the populations of the two hare species and tetraonid birds in E Finland could be ascertained from the winter of 1982/83 onwards. The total catch of hares was at its highest during that winter; its numbers declined steadily until the smallest catch was recorded in the winter of 1987/88, representing only a third of the 1982/83 catch (Table 3). Catches of tetraonids, the other notable prey of the lynx, remained quite stable but at a low level in the winters of 1982/83–1987/88, while numbers increased markedly in the winter of 1988/89 to about 2.5 times the mean for the previous years (Table 3). The growth in populations of the tetraonids was not reflected in an increasing proportion of these species in the diet of the lynx. The mean yearly index of snow depth determined for E Finland was highest in the winters of 1983/84 (54 cm) and 1988/89 (50 cm) and lowest in 1989/90 (20.5 cm) and 1984/85 (21 cm) (Table 3).

Body condition

There were positive correlation coefficients in E Finland in all the age and sex categories studied between the hare population and the mesentery-omentum fat index describing the physical condition of the lynx killed (Table 4). By comparison, the yearly index of snow depth produced negative correlation coefficients with the mesentery-omentum fat index showing a significance of 90% in the adult females (Table 4).

Measurements of the physical and nutritional condition of the lynx showed the animals in SW Finland to have been in better physical condition on average than

Table 4. Coefficients of correlation (Spearman rank correlation) between the mesentery-omentum fat of the lynx and the abundance of hares and snow depth index in E Finland in the open seasons of 1982/83–1989/90. o – $p < 0.10$, ns – $p > 0.10$.

Correlation	Ad males $n = 159$	Ad females $n = 95$	Subad females $n = 70$
Fat index/abundance of hares	+0.130 ns	+0.118 ns	+0.084 ns
Fat index/snow depth index	-0.105 ns	-0.169 o	-0.032 ns

Table 5. Body weights (kg, $\bar{x} \pm SD$) of lynx killed in the open season of 1985/86–1989/90 in E Finland and SW Finland (numbers of individuals in parentheses). In comparisons, males/females over 1 year of age, the differences in the body weights in both areas were highly significant. *T*-test: *** – $p < 0.001$, ** – $p < 0.01$, ns – $p > 0.10$.

Region	Ad males	Ad females	Subad females
E Finland	16.8 ± 3.8 (125)	15.1 ± 2.1 (63)	12.4 ± 2.1 (50)
SW Finland	19.2 ± 4.0 (51)	16.6 ± 2.3 (24)	13.0 ± 1.9 (19)

Significance markers: *** between E and SW Ad males; *** between E and SW Ad females; ns between E and SW Subad females; ** between E and SW Ad females; *** between E and SW Subad females.

Table 6. Mesentery-omentum fat indices ($\bar{x} \pm SD$) of lynx killed in the open seasons of 1985/86–1989/90. *T*-test: *** – $p < 0.001$, ** – $p < 0.01$.

Region	Ad males	Ad females	Subad females
E Finland	1.87 ± 0.78 (125)	1.43 ± 0.60 (63)	2.09 ± 0.79 (50)
SW Finland	2.76 ± 0.87 (51)	2.18 ± 0.59 (24)	2.87 ± 0.86 (19)

Significance markers: *** between E and SW Ad males; *** between E and SW Ad females; *** between E and SW Subad females; ** between E and SW Subad females.

those in E Finland. The males over 1 year of age and the adult females killed in SW Finland were heavier than those killed in E Finland (Table 5). Only in the category of the subadult females was the difference not significant (Table 5). The lynx from SW Finland, both the sexes and all age categories, had more depot fat attached to their mesentery and omentum than those from E Finland (Table 6). Similarly, the lynx of all the sex and age categories from SW Finland had more depot fat in their body cavities than those from E Finland (Figs 3 and 4, Table 7).

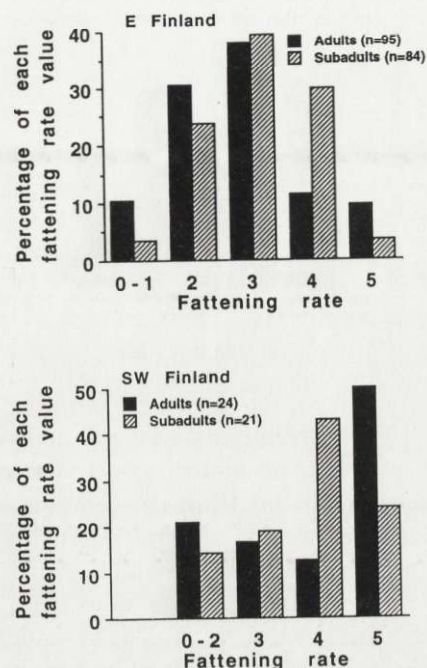
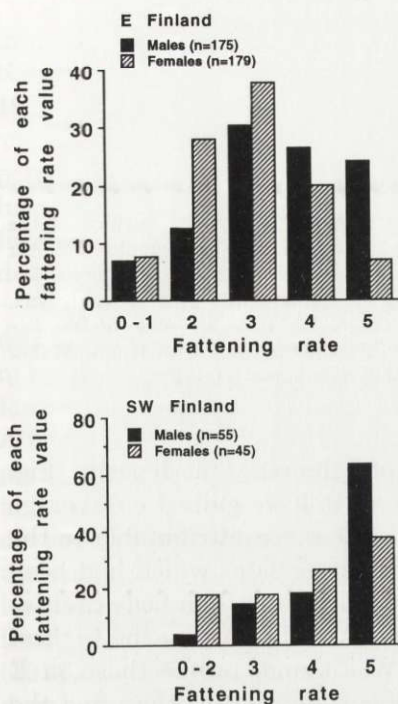


Fig. 3. Occurrence of depot fat in the body cavities of male and female lynx over 1 year of age killed in E Finland and SW Finland. Percentages of each fattening rate value recorded are presented. The amount of depot fat in the body cavity is estimated visually on a scale of 0 (none) to 5 (very abundant). For statistical significances, see Table 7.

Fig. 4. Occurrence of depot fat in the body cavities of adult and subadult female lynx killed in E Finland and SW Finland. Percentages of each fattening rate value recorded are presented. For statistical significances, see Table 7.

Table 7. χ^2 -values and statistical significances in the distributions of the fattening rate values for the body cavity between and inside the study areas for male and female lynx over 1 year of age, and adult (having been pregnant) and subadult (no pregnancy) female lynx. *** - $p < 0.001$, ** - $p < 0.01$, * - $p < 0.05$, ns - $p > 0.05$. For further details, see the text.

Comparisons	Categories			
	Males	Females	Ad females	Subad females
E Finland/SW Finland	31.34***	35.32***	18.92***	13.04**
	E Finland		SW Finland	
Males/Females	30.25***		9.10*	
Ad females/Subad females	13.37**		5.60 ns	

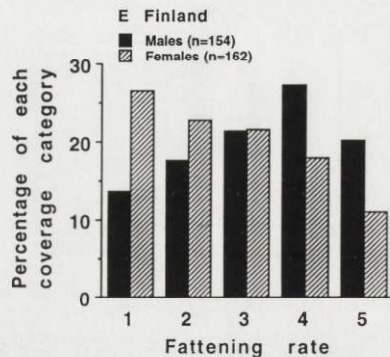


Fig. 5. Coverage of depot fat on the surface of the kidneys (*Capsula fibrosa*) in male and female lynx over 1 year of age in E Finland, estimated in accuracy of 5%. The mean of both the kidneys was used for each lynx. Categories of coverage: 1 – 40%, 2 – 42.5–55.0%, 3 – 57.5–70.0%, 4 – 72.5–85.0%, and 5 – 87.5%. Males/females, $\chi^2 = 14.82$, $df = 4$, $p = 0.0051^{**}$.

The fattening rate for the body cavities (Fig. 3) and the renal fat deposits (Fig. 5) showed the males over 1 year of age in E Finland to have gained on average more depot fat than the females (Figs 3 and 5), a difference attributable to the smaller amount of depot fat in the body cavities of the females which had been pregnant (Fig. 4). The males in SW Finland also had more fat in their body cavities on average than the females (Fig. 3), two-thirds of the males having the highest fat index value of 5. The subadult females in SW Finland, unlike those in E Finland, had not gained any more depot fat in their body cavities than had the adults (Fig. 4). Half of the adult females had gained the highest fattening rate value in SW Finland (Fig. 4), which indicates very advantageous food availability in that area.

There were significant differences between the adult and subadult females in their mesentery-omentum fat deposits in both areas, the subadults having more fat than the adults (Table 6), but the fattening rate for the body cavity deviated significantly between adult and subadult females only in E Finland (Table 7).

Discussion

The size of the European lynx is an adaptation to the use of roe deer as its main food (Pulliainen 1981), ie roe deer is an optimal-sized prey for the lynx. The study by Jędrzejewski *et al.* (1993) provided the further evidence for the reliability of this hypothesis. The lynx in Poland did not select roe deer by sex or age but preferred juvenile red deer *Cervus elaphus* and totally avoided adult stags (Jędrzejewski *et al.* 1993).

Our previous research has shown (Pulliainen and Hyypiä 1975, Pulliainen 1981, 1990) that the lynx of SE Finland which could not hunt on roe deer preyed upon hares, so that ca 70–80% of their diet consisted of these hares, the remainder comprising other small game, tetraonids and various mammalian species. Thus, the composition of the winter diet of these European lynx resembled very closely

that of the Canadian lynx *Lynx canadensis* in Canada and Alaska (Elton and Nicholson 1942, Keith 1963, Saunders 1963, van Zyll de Jong 1966, Nellis *et al.* 1972, Brand *et al.* 1976, Brand and Keith 1979, Parker *et al.* 1983), for which snowshoe hares *Lepus americanus* constituted the stable food regardless of the population cycle stages of the predator and the prey. The further data collected here from SE Finland confirmed the earlier finding that hares constitute the stable food of the lynx in that area (Table 2), even though their availability does vary due to natural population fluctuations (Table 3).

Brand and Keith (1979) studied the demography of the Canadian lynx in relation to a decline in snowshoe hare densities in Alberta, Canada, a work closer in scope to the present investigation than any other. Brand *et al.* (1976) had already found that the Canadian lynx responded to changing hare densities in central Alberta by shifting to alternative food sources to some extent, and more importantly by varying its food consumption rates. Later Brand and Keith (1979) indicated that similar dietary responses occurred among lynx throughout Alberta during the decline in 1971–1976. Body fat indices increased significantly between the early and late winter when snowshoe hares were at intermediate or abundant levels but decreased significantly during years of hare scarcity, suggesting that the lynx suffered a negative energy balance (Brand and Keith 1979). Brand *et al.* (1976) concluded that during years of hare scarcity average consumption by lynx dropped about 20% below that required to maintain body weight. This resulted in lowered pregnancy rates and litter sizes and increased postpartum mortality among kittens. Parker *et al.* (1983) noted that the decline in pregnancy rates with a decrease in snowshoe hare densities could be seen especially clearly in the yearling cohort, accompanied by increased mortality among kittens during the first six months of life. Sadleir (1969) suggested that those kittens that survived through the winter at times of low hare populations may have experienced a nutritive stress that could have delayed sexual maturity, thereby reducing conception rates among young females.

Kvam (1990) did not find any significant differences amongst different years in Norway in the ovulation rates of the female lynx older than 2 years of age although the availability of different prey species changed annually. The food availability situation in Norway is very different, however, as compared to E Finland or Alberta, Canada. The lynx in Norway can choose between three main alternative foods, reindeer, roe deer and mountain hares (Birkeland and Myrberget 1980), whereas the lynx in E Finland and also in Alberta, Canada, have in fact only one species as its main food source.

Most female Canadian lynx reach reproductive maturity by their second breeding season (22 months), but the reproductive success of these yearlings appeared to be closely correlated with the abundance of snowshoe hares (Parker *et al.* 1983). Kvam (1991) found in Norway that most female lynx were normally fertile in the second spring of life but half of the females were sexually mature already at 3/4 years of age and tended to come into heat at the very end of the

reproductive season. Kvam (1991) in any case doubted the ability of 1-year-old females to raise their young very shortly after their mothers have weaned them.

In our material of lynx killed mostly at times of quite low population levels in the hare species (see Tables 1 and 3) only 53% of the females over 1 year of age had given birth the previous spring. Thus, it is obvious that female yearlings regularly fail to breed in Finland at least during declines in hare populations, whilst the older females often do so. The small proportion of kittens in the catch (13%) is actually an indication of the low reproductive rate of the Finnish lynx. On the other hand, conclusions on the demographic aspects made on the basis of hunting statistics may be to some extent biased because the hunters may prefer large-sized animals.

The Canadian lynx of both sexes studied in Alberta and the European lynx studied here in SE Finland had winter diets of similar composition. If this were not so, it would reduce in transpecific competition, as suggested by Brown and Lasiewski (1972). This is really relevant, since the home ranges of an adult male and a female with kittens may partly or totally overlap (Carbyn and Patriquin 1983, Haller and Breitenmoser 1986, Zachariae *et al.* 1987).

Unlike the situation in E Finland, the lynx in SW Finland are able to choose white-tailed deer for their prey as well. The frequency of occurrence of white-tailed deer was higher in the diet of the male lynx than in that of the females, just as Breitenmoser and Haller (1987) described a case in which a male and a female lynx hunting in the same area showed different preferences for killing roe deer and chamois *Rupicapra rupicapra* (12:14 and 21:7, respectively). The mean weights of male and female lynx over 1 year of age in SW Finland were 19.2 and 15.0 kg, respectively (Table 5), and the difference between the sexes in consuming white-tailed deer may be partly explained by this difference in body size, since female lynx may not always be strong enough to capture such large prey. On the other hand, the sexual dimorphism in body weight might also be a result of the prey items chosen. The fact that the weight difference between sexes was greater in SW Finland where the lynx could prey on white-tailed deer, favours this hypothesis (see Table 5).

It is characteristic for lynx in Finland to kill in winter a new prey every night (see Pulliainen and Hyypiä 1975). Killing a deer in wintertime does not necessarily make it easier for a female lynx followed by two or three kittens to manage for several days without any more kills since the carcass of a large prey animal which has remained partly uneaten may freeze at low temperatures and the teeth and jaws of the lynx are not the best tools for dealing with such food. However, Jędrzejewski *et al.* (1993) reported the lynx in Poland feeding on average during 3–4 days on a killed deer in wintertime (see also Kossak 1989).

The soft snow may be a critical factor for the lynx effecting on the hunting success of the species especially in early winter (December–January). Later on in the winter, usually in February but at the latest in March, the low night temperatures followed by high daily temperatures may condense the snow and

produce a hard layer on its surface, which forms a firm support for the final jump that the lynx makes when capturing its prey. Thus the snow depth itself in middle and late winter does not relate the actual truth about snow conditions from the standpoint of the lynx.

The European lynx weighs twice as much as the Canadian lynx, which indicates that it consumes more energy, although the idea of Bergmann's Rule reduces this difference. It also means that the former exerts greater pressure on the surface of the snow when chasing a hare. Pulliainen and Hyypiä (1975) showed that the prevailing snow conditions may have a very marked effect on hunting success, since soft snow aids the hares in escaping. Haglund (1966) also noticed in Sweden that the most common reason for unsuccessful hunting in winter was the consistency of the snow. The success of the Canadian lynx in capturing snowshoe hares in Alberta, Canada, was significantly lower in the winter when the bearing strength of the snow was definitely less (Nellis and Keith 1968). In addition to this, the depth of the snow cover may also be relevant.

There were significant differences between the adult and subadult females in their mesentery-omentum fat deposits in both areas, the adults having less fat than the subadults (Table 6), but the fattening rate for the body cavity deviated significantly between adult and subadult females only in E Finland (Table 7). Thus, it is obvious that the amount of fat attached to the mesentery and omentum responds more sensitively to a change in food availability and reproductive status than does that in the body cavity. In areas with relatively good prevailing food availability, the reproductive status of the mother lynx is not reflected in the fattening rate of the body cavity, but rather the lynx seems to react to the situation of a negative energy balance by first utilizing primarily the fat reserves attached to the mesentery and omentum, organs with rich blood vessels and a high metabolism rate.

The kittens of both the Canadian and European lynx grow very slowly. Mortality among the kittens of the former species occurs even during the summer and early autumn, when they are entirely dependent on their mother for food (Brand and Keith 1979). In the Swiss Jura Mountains half of the kittens died during the first 10–11 months of life while still living with the mother, the remaining young studied died after leaving their mothers, the oldest one reaching nineteen months of age (Kaczensky *et al.* 1991). In Sweden (Johnsson 1986) and in Finland (Pulliainen 1974, 1981) kittens which have lost their mother in January or early February may die of starvation, since they are unable to hunt effectively enough in snow conditions (they are often found in the yards of houses or in hay barns before death). Eighteen percent of the kittens studied here were clearly starving, whereas only four such cases were recorded amongst the adults (0.9%). Recorded injuries to the skull or other parts of the skeleton of the kittens also suggest that mortality must be fairly high. Pulliainen (1974) recorded a case of cannibalism in this species, the victim being a kitten.

We have now two ecologically separate populations of the lynx in southern Finland (Fig. 1), the western one of which has an opportunity to feed on white-tailed deer. This originally introduced deer population is artificially fed in many areas, thus eliminating natural population fluctuations due to snow conditions. This white-tailed deer population provides an exceptionally good food basis for the local lynx population. The first hunting licences were granted in the core area of this deer population at a time at which deer constituted over 60% of the diet of the lynx (Pulliainen 1990). When the hunting area was expanded, the corresponding proportion decreased to about 40%. Hares now make up an equal proportion of the diet. Thus, there is a significant alternative prey to deer and vice versa. No corresponding alternative is available for the eastern ecological population.

The fundamental differences in the food basis of the lynx between the western and eastern populations are reflected in the body parameters used to measure the individual success of the lynx, the western adult males being on average 2.4 kg heavier than their eastern conspecifics (Table 5), with a corresponding difference of 1.1 kg between the females over 1 year of age. It can be surmised that muscles and the skeleton of the individuals of the western population were in excellent condition, but the difference in weight between the two populations was apparently mainly due to depot fats. The mesentery and omentum of the western lynx weighed more in all age and both sex categories (see Table 3), and the differences in the fattening rate of the body cavity were correspondingly statistically significant (Figs 4 and 5). When the hunting area of the western population was expanded into counties outside the white-tailed deer area, this was immediately reflected in a decrease in the fat index.

Although there appeared to be significant differences in mean condition between the two ecological populations, some indicators gave similar results. A balanced sex ratio can be regarded as being natural in a lynx population (Brand and Keith 1979, Parker *et al.* 1983), and the sex ratio of the lynx catch did not differ significantly from the 50:50 distribution in either of the present areas (Table 1). The reproductive rate also seemed to be the same in both populations.

Finally, one fundamental difference in role between the sexes in a lynx population is, from the standpoint of the population, the male has only one task, to copulate in late winter, whilst the female has to take care of the kittens, which – as stated above – grow very slowly. The male and the female are segregated (see Mech 1980), and while a kill of one hare is enough for an adult male, an adult female followed by two or three kittens has to kill at least two hares every day (Pulliainen 1981). Both pregnancy and taking care of the kittens (including feeding them) result in physical pressure on the females, and this must be visible in the physical condition of the animals involved. The present data shows that this is indeed the case (Tables 3 and 6, Figs 3 and 5) for the females which had produced offspring during winter. They were in a worse condition than the adult males killed in the same area at the same time. It must be emphasized that all these

comparisons must be projected separately on each occasion, which for practical purposes means that the females constitute indicators of the status of the lynx population in this respect as well.

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