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## Diet of Eurasian lynx, *Lynx lynx*, in the boreal forest of southeastern Norway: the relative importance of livestock and hares at low roe deer density

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**Abstract** The year-round food habits of lynx were studied using radio-telemetry and snow-tracking in the boreal forest of southeastern Norway. The main objectives of the study were to clarify the importance of domestic sheep and small prey species in the diet of lynx in an area with a very low density of roe deer. During the period 1995–1999, we found 193 scats and 358 kills made by lynx. Our results indicate that roe deer were the most common prey species (contributing to 83 and 34% of the biomass consumed in winter and summer, respectively), although a wide range of other species were also found, including mountain hares, tetranoids, red foxes, domestic sheep, wild reindeer, and even moose. Most of the diet was obtained by predation, although we did document several cases of scavenging. Roe deer were more important in the diet in winter than in summer, perhaps because they were easier to locate in winter as they clustered around feeding sites. In summer, domestic sheep and small prey increased in importance. Despite the very low density of roe deer in this study area, lynx seemed to still specialise on them, although domestic sheep did constitute a significant amount to their diet,

especially for males and yearlings. However, the contribution of sheep to summer diet was far from that expected if their relative density was considered.

**Keywords** Carnivore-livestock conflicts · Sheep · *Capreolus capreolus* · Lynx · Norway

### Introduction

The Eurasian lynx is distributed from the Atlantic coast of Western Europe to the Pacific Ocean in the Russian Far East (von Arx et al. 2004). While the genus *Lynx* is generally specialised on lagomorphs (Werdelin 1981), more than 30 species have been found in the diet of Eurasian lynx. Current information on the feeding behaviour of Eurasian lynx suggests that they may be termed opportunistic generalist predators that have specialised on small ungulates in many parts of their range (Jedrzejewski et al. 1993). The interaction between lynx and their prey have been extensively studied in the forested ecosystems of central Europe (Breitenmoser and Haller 1993; Okarma et al. 1997; Jobin et al. 2000) where roe deer (*Capreolus capreolus*) and chamois (*Rupicapra rupicapra*) dominate the diet, and in northern Russia (Matyushkin and Vaisfeld 2003) where birds and hares dominate. It is not clear what the lower threshold of wild ungulate density is below which lynx switch to a diet dominated by small prey. In the boreal forest of Fennoscandia, roe deer are present but occur at very low densities—thus providing an opportunity to study lynx diet in an area with conditions that lie between those of continental Europe and Siberia.

In Western Europe, lynx also prey on domestic sheep (Stahl et al. 2001; Odden et al. 2002; Herfindal et al. 2005a,b). Depredation on sheep is a major obstacle for successful conservation of lynx in the multi-use landscapes of Europe, and the conflict is far higher in Norway compared to any other European country (Kaczensky 1996). Every year more than 2 million sheep and lambs are grazed in forest and mountain habitats from May to September (Statistics Norway 2005). Sheep are generally allowed to graze freely,

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with little supervision from the owner, and during the last 10 years between 5,462 and 9,862 sheep have been compensated as being killed by lynx annually (Norwegian Directorate for Nature Management 2005).

The conflict between carnivores and livestock occurs when carnivores kill domestic animals instead of non-domestic, wild prey. One important question concerning depredation ecology is whether carnivores regard livestock as prey, or if carnivores just kill livestock that are encountered by chance during movements associated with hunting wild prey and territory maintenance (Odden et al. 2002; Moa et al. 2006). Free-ranging and unguarded sheep represent a predictable and easily killed prey that lack most anti-predator behaviours. If sheep are being actively hunted as prey, we should expect that sheep feature prominently in lynx diet, especially in an area with a low density of wild ungulates.

Lynx diet has been studied in Scandinavia, but it was mainly focussed on winter time (Dunker 1988; Haglund

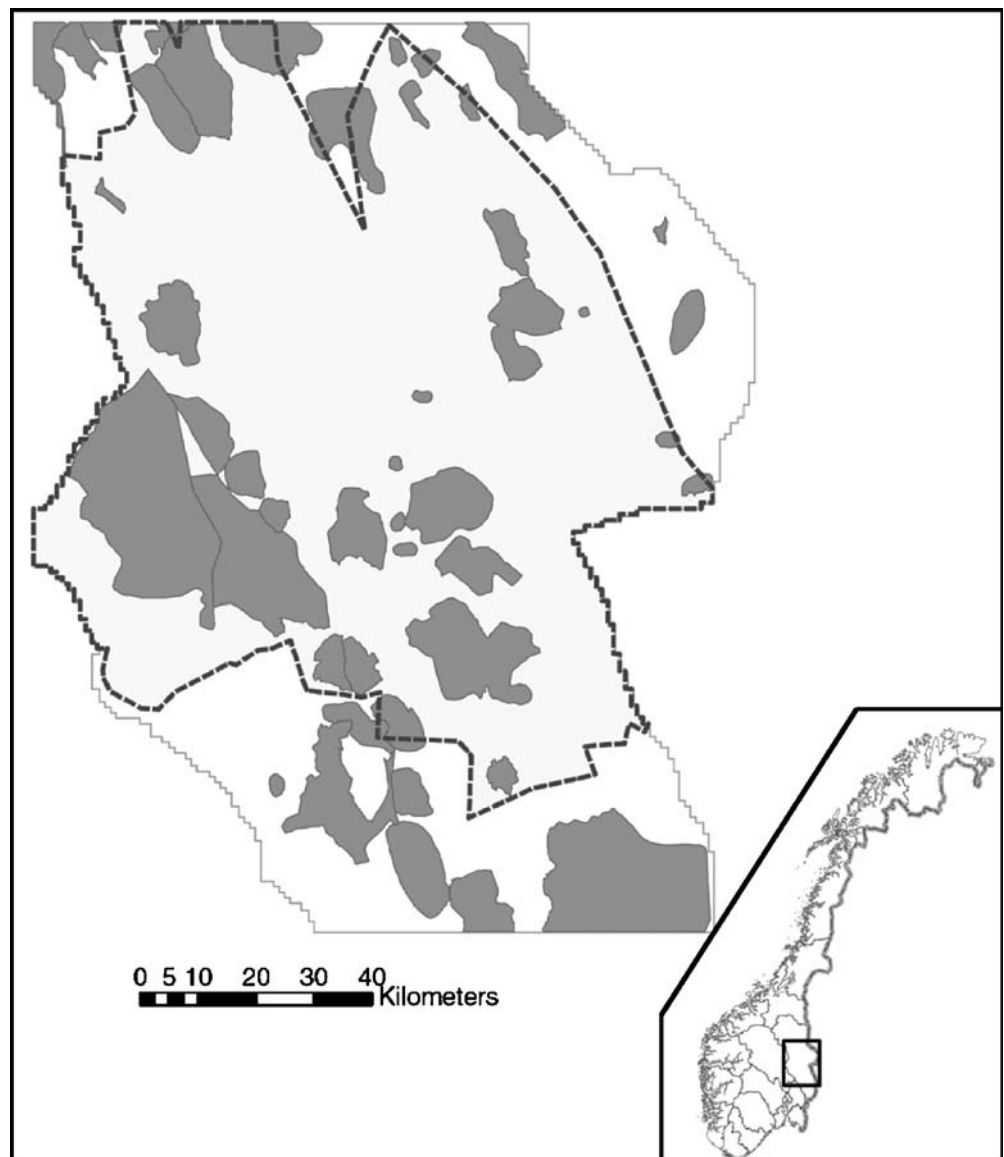
1966; Birkeland and Myrberget 1980; Pulliainen et al. 1995; Pedersen et al. 1999) and/or on areas where semi-domestic reindeer are available (e.g. Haglund 1966; Pedersen et al. 1999; Sunde et al. 2000). In this study, we examined the year-round food habits of lynx of different age and sex classes in a boreal forest in Hedmark county, southeastern Norway. The main objectives of the study were to clarify the importance of domestic sheep vs other small prey species in the diet of lynx in an area with low density of roe deer.

## Materials and methods

### Study area

The 8,600-km<sup>2</sup> study area was situated in Hedmark county in the southeastern part of Norway (61°15' N, 11°30' W) (Fig. 1). The region's vegetation is predominantly boreal

**Fig. 1** The study area in Hedmark County, Norway (*small map*). The *bold dashed line* represents a union of all the lynx home ranges used in the analyses. *Gray areas* are sheep grazing areas



coniferous forest, and 72% of the study area is covered with forest. Scots pine (*Pinus sylvestris*) and Norwegian spruce (*Picea abies*) dominate the forest. Birch (*Betula* sp.) may also be well represented, especially in the forest–alpine tundra interface and along rivers. Most of the coniferous forest has been felled and replanted at least once during the last centuries, resulting in a mosaic of even aged stands. Non-forest habitats consist mainly of bogs, and alpine-tundra above treeline. Agricultural lands make up less than 5% of the area, and occur mainly in valley bottoms. The topography consists of several parallel river valleys running from north to south at about 200–500 m above sea level, separated by hills ranging from 600–900 m a.s.l. Generally, the terrain is steeper in the western and northern parts of the area.

A wide range of wild mammal and bird species are available as potential prey for the lynx. Roe deer are available in most parts of the study area, but at very low densities (0.3 per km<sup>2</sup>, this paper). In winter, roe deer are clustered in valley bottoms and close to supplemental feeding sites, but in summer they can be found anywhere in the forested part of the study area. Wild reindeer (*Rangifer tarandus*) are found in the northwestern part of the area during summer, while red deer (*Cervus elaphus*) occur sporadically and at extremely low density. Moose (*Alces alces*) occur in high numbers. A wide range of small prey species are also available. The most important are hare (*Lepus timidus*), red fox (*Vulpes vulpes*), capercaillie (*Tetrao urogallus*) and black grouse (*Tetrao tetrix*). The distribution of domestic sheep within the area is widespread but patchy, although any potential lynx home range would contain at least some grazing sheep, and sheep density is highest in the western and northern parts. Sheep are grazed in the forest, without fences or supervision from June until September.

The density of lynx inside the study area has been estimated to be 0.34 per 100 km<sup>2</sup> including dependent offspring (Odden et al. 2000). The lynx population is subject to an annual recreational harvest, such that numbers were more or less stable during the study period. The climate is continental with warm summers and cold winters. Average January and July temperatures are –10 and 15°C, respectively. Average annual precipitation amounts to 500–1,000 mm. Snow conditions vary, but usually the ground is covered with snow from November until April. The midwinter snow depths typically vary from 50 to more than 200 cm.

### Lynx capture and data collection

Between 1995 and 1999 a total of 42 lynx were captured and equipped with radio-transmitters using a variety of techniques. Walk-through box traps constructed in wood or metal mesh and baited with lynx urine were placed on known lynx trails. Radio-alarms on the box traps were checked twice per day. Spring-loaded foot snares were placed at lynx-killed prey. These snares were continually monitored using radio-alarms, and reaction time was less

than 15 min. Neonatal kittens were also captured (by hand) at natal lairs and were equipped with implanted transmitters (Arnemo et al. 1999, 2006). Animals were often recaptured using the same or different techniques. Trained dogs were also used to recapture animals. These dogs were released close to radio-located lynx and chased the lynx until it escaped, climbed a tree, or sought refuge under rocks. Once a lynx was in a tree, they were darted and caught in a net if they fell. Finally, a few animals were darted from car and helicopter.

All adult animals were immobilised using a mixture of ketamine (100 mg) and medetomidine (4 mg), reversed with atipamezole (5 mg); juveniles received a half dose. All drugs were provided intra-muscularly by hand, blow-pipe or gas-powered darting rifle. All procedures were approved by the Norwegian Experimental Animal Ethics Committee, and permits for wild animal capture were obtained from the Directorate for Nature Management. Most animals were equipped with radio-collars, apart from neonatal kittens and some few 6-month-old kittens that received free-floating intraperitoneal implant transmitters (Arnemo et al. 1999, 2006). No complications were ever detected as a result of collaring or implanting, although two animals died during capture-related activities (Arnemo et al. 2006). Collars weighed 120 g or less than 1% of an adult female's body weight (Telonics).

The diet of lynx of different age and sex classes was studied by collecting scats and remains of killed prey from radio-marked and unmarked lynx from 1995 to 1999. The diet composition in winter, defined in this paper as the period between November 1st and May 1st, was estimated through faecal analysis and by collecting prey remains. Prey remains and scats were found by following lynx tracks in the snow between sequential, daily radio locations. To avoid disturbing the lynx, suspected kill sites were only examined after the lynx had left the area. We also followed tracks from unmarked lynx. In summer, prey remains were found by following radio-marked lynx intensively in periods from 1 to 20 nights (mean number of nights=5.6, ±3.4SD). During an intensive tracking period, lynx were located at least every half an hour in either a full 24-h cycle or during the active period at night. To find kills, lynx were located precisely whenever they remained active at the same point for at least 1 h. Searches for kills, often with dogs, were made after we were sure the lynx had left the area to minimise disturbance (Odden et al. 2002).

### Analysis of diet composition

Prey remains were identified through comparison with reference collections of hair, feathers and bones following Sunde (1996). Multiple scats deposited by the same lynx or family group in 1 day (i.e. scats coming from the same meal or kill) were pooled and treated as one sample to avoid serially dependent data. Winter diet was also estimated as the frequency of occurrence of different prey items found during systematic snow-tracking. We calculated the ingested mass from prey remains using representative

live weights for small prey species and winter slaughter weights of ungulate species, because skin and guts of large ungulates are rarely eaten by lynx, whereas small prey species in general are completely eaten (J. Odden, unpublished data). Difference in the proportion of roe deer vs small species between different age and sex classes were tested using Pearson Chi-square.

The intensive tracking periods in summer were used to estimate the individual meat intake of different prey categories. Only individuals tracked for more than five nights during a summer were included in the analysis. A Mann–Whitney *U* test was used to compare intake of meat between different age and sex classes.

We calculated an index of change in roe deer density between years, based on the changes in mean average number of roe deer recorded annually at feeding sites in a central part of the study area. Roe deer in this area show seasonal variation in distribution and space use, occupying restricted home ranges in winter confined to the proximity of artificial feeding sites (Eide 1995). The feeding sites are voluntarily established by local people to offer additional winter forage to the local roe deer population.

In summer, a more even distribution is found when roe deer spread out and maintain territories and home ranges nearly four times the size of their winter areas (Linnell, Odden and Andersen, unpublished data). Determining the

exact density of roe deer is normally difficult; however, extensive use of census lines during periods with snow-covered ground revealed that all tracks from roe deer were found less than 700 m away from a known artificial feeding site, indicating that most animals are confined to habitats surrounding such feeding sites. Consequently, the mean average number of animals recorded annually at 23–58 different feeding sites could be used as a reliable index of changes in roe deer density. In addition, we used the number of roe deer shot per area of forest per municipality as an index of roe deer density.

Logistic regression was used to identify factors influencing the probability of lynx killing a roe deer vs another prey species (Homer and Lemeshow 2000). Parameters were evaluated and retained in a forward stepwise manner, whereby the individual contribution of each new variable was evaluated using a Wald test (*W*). The parameters entered included season (summer or winter), month, the roe deer density index, number of roe deer shot per area, single animal or family group and lynx sex and age class. The final model was tested with the Hosmer and Lemeshow goodness-of-fit test statistic (H-L Stat) to ensure model fit (Homer and Lemeshow 2000). All statistical analyses were carried out using the SPSS for Windows computer package.

**Table 1** Winter diet of Eurasian lynx in Hedmark estimated from prey items found in scats and during systematic snow-tracking from 1995 to 1999

| Species                                   | Scats     |      | Snow-tracking |      |
|---|-----------|------|---------------|------|
|   | FO % (n)  | BM % | FO % (n)      | BM % |
| <i>Capreolus capreolus</i>                | 40.7 (57) | 74.6 | 63.8 (81)     | 82.7 |
| <i>Alces alces</i>                        | 2.9 (4)   | 2.6  | 0.8 (1)       | 6.1  |
| Unidentified cervid                       | 2.9 (4)   | 0.8  |               |      |
| <i>Ovis aries</i> <sup>1</sup>            |           |      | 0.8 (1)       | 1.4  |
| <i>Lepus timidus</i>                      | 22.9 (32) | 17.4 | 15.7 (20)     | 4.6  |
| <i>Oryctolagus cuniculus</i> <sup>2</sup> |           |      | 0.8 (1)       | 0.2  |
| <i>Tetrao sp</i>                          | 1.4 (2)   | 0.8  | 5.5 (7)       | 1.3  |
| <i>Pica pica</i>                          |           |      | 0.8 (1)       | 0.0  |
| Unidentified birds                        | 9.3 (13)  | 0.3  |               |      |
| <i>Vulpes vulpes</i>                      | 2.1 (3)   | 2.6  | 3.9 (5)       | 1.9  |
| <i>Mustela vison</i>                      | 0.7 (1)   | 0    |               |      |
| Unidentified carnivores                   | 2.9 (4)   | 0.3  |               |      |
| <i>Sciurus vulgaris</i>                   | 2.1 (3)   | 0.1  | 3.9 (5)       | 0.1  |
| <i>Lemmus lemmus</i>                      |           |      | 0.8 (1)       | 0.0  |
| <i>Rattus norvegicus</i>                  |           |      | 0.8 (1)       | 0.0  |
| Unidentified rodents                      | 6.4 (9)   | 0.3  |               |      |
| <i>Sorex araneus</i>                      |           |      | 0.8 (1)       | 0.0  |
| Unidentified species                      | 5.7 (8)   |      |               |      |
| Other <sup>3</sup>                        |           |      | 1.6 (2)       | 1.6  |

<sup>1</sup>Domestic sheep free-ranging, killed in November

<sup>2</sup>Domestic rabbit, killed inside fence

<sup>3</sup>One moose killed by car and bait put out by hunters to shoot foxes

Diet is expressed as frequency of occurrence (FO) and percentage of ingested biomass (BM %). All sex and age classes and marked and unmarked lynx are pooled



## Results

In total, 193 scats from marked and unmarked (99 samples from 15 different marked individuals and 94 samples from unmarked individuals) lynx were collected and analysed during winter. In addition, 24 radio-collared lynx were followed intensively for 410 nights during four summers from 1995 to 1999. At least nine species of prey were identified in the lynx scats and a total of 358 prey remains from 19 different prey species were found killed by marked and unmarked lynx during the study period. In an additional eight cases, the lynx fed on carrion or on baits put out by hunters to attract red foxes.

Roe deer was the most frequent prey item found in the lynx scats (41%) followed by hares (23%) (Table 1). We found no difference in the proportion of scats containing roe deer between single animals and family groups ( $\chi^2=0.128$ ,  $P=0.720$ ,  $df=1$ ,  $n=110$ ) or between males and females ( $\chi^2=0.632$ ,  $P=0.427$ ,  $df=1$ ,  $n=53$ ).

Roe deer were also the most frequent prey item found during systematic snow-tracking (64%,  $n=81$ ) followed by hares (16%) (Table 1). Roe deer and hares contributed to 83 and 5%, respectively, of the ingested biomass in the lynx diet estimated from the kills. The proportion of roe deer vs small species found during snow-tracking did not differ between single animals and family groups ( $\chi^2=0.128$ ,  $P=0.720$ ,  $df=1$ ,  $n=110$ ), between males and females ( $\chi^2=1.870$ ,  $P=0.171$ ,  $df=1$ ,  $n=80$ ) or between yearling and adult lynx ( $\chi^2=2.604$ ,  $P=0.107$ ,  $df=1$ ,  $n=120$ ).

A total of 114 kills from 13 species were found during 410 intensive tracking nights during the summers from 1995 to 1999 (Table 2). Domestic sheep and goats were the most frequently killed prey (39%). Because sheep and goat kills in most cases were not fully utilised, their meat comprised only 29% of the biomass in summer diet. Wild ungulates contributed to 51% of the biomass ingested during summer, and different small prey species contributed to 19% of the biomass of summer diet.

The meat intakes of different prey categories by lynx of different age and sex are given in Table 3. The estimated

total meat intake per 100 days during summer did not differ between adult males and adult females (Mann–Whitney,  $U=59.0$ ,  $n=23$ ,  $P=0.801$ ), adult males and juveniles (Mann–Whitney,  $U=35.0$ ,  $n=17$ ,  $P=0.923$ ) or adult females and juveniles (Mann–Whitney,  $U=47.0$ ,  $n=22$ ,  $P=0.539$ ). The amount of wild ungulate meat in the summer diet did not differ between adult males and adult females (Mann–Whitney,  $U=90.5$ ,  $n=23$ ,  $P=0.979$ ), but adult lynx had significantly more wild ungulate meat compared to juveniles (Mann–Whitney,  $U=61.5$ ,  $n=31$ ,  $P=0.043$ ).

Adult males ate more sheep meat compared to female lynx (Mann–Whitney,  $U=21.0$ ,  $n=23$ ,  $P=0.002$ ), but there was no difference between adult males and yearlings (Mann–Whitney,  $U=27.0$ ,  $n=17$ ,  $P=0.370$ ). Also yearlings tended to eat more sheep meat than females (Mann–Whitney,  $U=38.5$ ,  $n=22$ ,  $P=0.076$ ).

Adult females tended to eat more meat of small prey species compared to adult males, but the difference was not significant (Mann–Whitney,  $U=38.5$ ,  $n=23$ ,  $P=0.117$ ). There was no difference in the amount of small prey species in the diet between adult males and yearlings (Mann–Whitney,  $U=36.0$ ,  $n=17$ ,  $P=1.000$ ) or adult females and yearlings (Mann–Whitney,  $U=37.5$ ,  $n=22$ ,  $P=0.202$ ).

Adult females with kittens tended to eat more small prey species compared to single adult females, but the difference was not significant (Mann–Whitney,  $U=14.0$ ,  $n=14$ ,  $P=0.195$ ). No difference between the two groups were found with respect to total meat intake (Mann–Whitney,  $U=20.0$ ,  $n=14$ ,  $P=0.606$ ), the amount of wild diet (Mann–Whitney,  $U=20.0$ ,  $n=14$ ,  $P=0.591$ ) nor the amount of sheep in the diet (Mann–Whitney,  $U=21.0$ ,  $n=14$ ,  $P=0.396$ ).

In the logistic regression model, the only variables that could explain the variation in preference of roe deer vs other prey were season and the roe deer index. (Table 4). The odds of a lynx killing roe deer were highest in winter and higher in the initial years with higher density of roe deer. The variables family group, age and sex of lynx and the number of roe deer shot per area were not included in the model.

**Table 2** Summer diet of lynx as estimated from kills found during intensive tracking of lynx of all age and sex categories (summer 1995–1999) presented as frequency of occurrence (FO) and percentage of ingested body mass (BM%)

| Prey species               | <i>N</i> | FO (%) | Total ingested body mass (kg) | BM (%) |
|----------------------------|----------|--------|-------------------------------|--------|
| <i>Capreolus capreolus</i> | 18       | 15.8   | 187.8                         | 34.2   |
| <i>Alces alces</i>         | 1        | 0.9    | 6.0                           | 1.1    |
| <i>Rangifer tarandus</i>   | 4        | 3.5    | 87.3                          | 15.9   |
| <i>Ovis aries</i>          | 41       | 36.0   | 144.4                         | 26.3   |
| <i>Capra hircus</i>        | 3        | 2.6    | 18.0                          | 3.3    |
| <i>Lepus timidus</i>       | 22       | 19.3   | 57.6                          | 10.5   |
| <i>Tetrao urogallus</i>    | 16       | 14.0   | 43.0                          | 7.8    |
| <i>Tetrao tetrax</i>       | 3        | 2.6    | 1.8                           | 0.3    |
| <i>Columba sp.</i>         | 2        | 1.8    | 1.0                           | 0.2    |
| <i>Anthus sp.</i>          | 1        | 0.9    | 0.1                           | 0      |
| <i>Vulpes vulpes</i>       | 1        | 0.9    | 1.0                           | 0.2    |
| <i>Martes martes</i>       | 1        | 0.9    | 0.9                           | 0.2    |
| <i>Rattus norvegicus</i>   | 1        | 0.9    | 0                             | 0      |

All sex and age classes are pooled

**Table 3** Summer diet of lynx of different age and sex classes as estimated as mean meat intake rates (kg per 100 days) of different groups of prey

| Age/sex category | Number of lynx | Number of nights | Meat intake (kg per 100 days) |                 |                 |
|------------------|----------------|------------------|-------------------------------|-----------------|-----------------|
|                  |                |                  | Wild ungulates                | Small prey      | Sheep           |
| Adult males      | 9              | 155              | 70.4 kg (49.9%)               | 18.7 kg (13.3%) | 51.9 kg (36.8%) |
| Adult females    | 10             | 189              | 87.8 kg (57.5%)               | 32.5 kg (21.3%) | 32.3 kg (21.2%) |
| Yearlings        | 8              | 66               | 9.1 kg (14.3%)                | 22.7 kg (35.8%) | 31.7 kg (49.9%) |

All individuals and years pooled

## Discussion

Lynx killed prey species ranging in size from mice to moose, but this study clearly demonstrates that roe deer remained the most important prey even in an area with a very low density of roe deer. The amount of roe deer in the lynx diet in this study varied with season. Roe deer in this area show seasonal changes in distribution and space use. In winter, roe deer occupy restricted home ranges confined to the proximity of artificial feeding sites. In summer, a more even distribution is found (Linnell, Odden and Andersen, unpublished data). This seasonal change from a dispersed to a clumped distribution may facilitate a reduction in search time, and thus explain the high proportion of roe deer in winter diet. However, even in summer, roe deer remained the single most important contribution to lynx diet, indicating that lynx are effective at searching for, and killing roe deer, even when they occur at low density. The feeding ecology of lynx in this snow-rich northern boreal forest is remarkably similar to the more productive habitats in central Europe with far higher roe deer densities (Jedrzejewski et al. 1993). This is also reflected in published data on the kill rates of lynx collected from across Europe. Even though densities of roe deer vary with a factor of 30 (from 0.3 roe/km<sup>2</sup> in this study to approximately 11 roe/km<sup>2</sup> in Switzerland and Poland), the kill rates only vary with a factor of 2.5 (from 72 animals/year in Switzerland to 28 animals/year in Hedmark) (Andersen, Linnell and Odden, unpublished data). Although small prey items were frequently killed and made up a reasonable proportion of the number of prey items, their contribution to biomass consumption was low.

In winter, data were collected through snow-tracking, and most prey should be expected to be found. However, in

summertime data were collected through intensive radio tracking, and prey species smaller than hares might have been under-represented because they are consumed quickly and, therefore, are more difficult to find. The fact that we found a large number of small prey items, down to the size of rats, provides an indication that our tracking was accurate. The use of dogs to find kills was very successful in this respect. Furthermore, our estimates of daily meat intake rates (~1.5 kg/day) do not differ much from previous estimates (Jobin et al. 2000), which indicate that any prey items that we did not detect could not have been of much nutritional importance. An additional problem concerns prey items killed, but not eaten, as we would not have searched at locations where the lynx did not stop. This mainly concerns sheep, where we have earlier documented a high degree of surplus killing, especially by male lynx (Odden et al. 2002). The problem is not so important for estimating lynx diet as the important parameter in this study is the kills which are consumed; however, it should be borne in mind that the predation impact of lynx on sheep can be greater than that revealed by their contribution to lynx diet.

Despite the fact that the density of free-ranging sheep was eight times that of roe deer, sheep were not the most important source of food for lynx during summer. Sheep only constituted about 29% of the digestible biomass in lynx diet during summer estimated from the frequency of lynx kills made during summer and the relative consumption of each kill. A study of the foraging behaviour of lynx in central Norway also showed low preference for sheep (Sunde et al. 2000). Stahl et al. (2002), studying lynx in the French Jura Mountains, also found that lynx spent less than 3% of their nights on sheep kills, during which time, it was assumed, they were consuming sheep meat. Likewise, from

**Table 4** Logistic regression models of variables found to be significant in predicting likelihood of a kill being a roe deer vs another prey species (145 kills)

| Variables | $\beta$           | SE     | $W$   | $P$    | Exp( $\beta$ ) | Nagelkerke $r^2$ | Hosmer and Lemeshow test |
|-----------|-------------------|--------|-------|--------|----------------|------------------|--------------------------|
| Step 1    | Season (winter)   | 1.226  | 0.348 | 12.393 | 0.000          | 3.407            |                          |
|           | Constant          | -0.693 | 0.250 | 7.687  | 0.006          | 0.500            | 0.114                    |
| Step 2    | Roe density index | 0.413  | 0.171 | 5.810  | 0.016          | 1.512            |                          |
|           | Season (winter)   | 1.217  | 0.356 | 11.654 | 0.001          | 3.376            |                          |
|           | Constant          | -1.902 | 0.571 | 11.108 | 0.001          | 0.149            | 0.166                    |

All individuals were pooled.  $\beta$  is the estimated coefficient, with standard error SE;  $W$  is the Wald test statistic; Exp( $\beta$ ) is the predicted change in odds for a unit increase in the predictor (Odds ratio). The final models were tested with the Hosmer and Lemeshow goodness-of-fit test statistic (H-L stat)

the neighbouring Swiss Jura Mountains, sheep have been shown to constitute an insignificant portion of lynx diet (Weber and Weissbrodt 1999; Jobin et al. 2000; Molinari-Jobin et al. 2002), although sheep were not so widespread in this portion of the Jura Mountains.

Male lynx killed sheep more frequently than female lynx. This can partly be explained by the fact that males use bigger home ranges than females (Linnell et al. 2001; Herfindal et al. 2005a,b), and thereby encounter sheep more often. Males also seem to be less susceptible to human disturbance compared to females (Bunnefeld et al. 2006). However, males also kill more sheep per killing event (Odden et al. 2002). This pattern conforms to other studies of depredation by carnivores (see Linnell et al. 1999 for a review). Even though males were responsible for all multiple killings of sheep, and they generally utilised each carcass to a lesser degree compared to females, sheep represented a more important dietary component for adult males and yearlings compared to females, as sheep meat was the second most important prey item for these lynx categories. Female lynx in this area give birth to kittens around June 1st, just after the sheep have been released unguarded in forest and mountain habitats. However, female lynx with kittens killed far less sheep than might be expected from their high energetic needs. Several females gave birth to kittens within areas of high sheep densities, but they virtually ignored this abundant resource. Instead of killing sheep, which were only a few hundred meters away, females often travelled more than 10 km from the kittens to kill a hare or a roe deer.

Lynx depredation on sheep clearly seems to be more due to chance encounters between lynx and sheep rather than the result of lynx actively seeking sheep as prey. Studies of lynx foraging patch selection also have shown that the probability of a lynx using an area increase with increasing roe deer density, and that lynx do not select patches with sheep (Odden et al. 2006 Submitted; Moa et al. 2006). The avoidance of abundant free-ranging sheep seems to reflect some intrinsic aversion to sheep (Odden et al. 2002; Moa et al. 2006), indicating that depredation on livestock and predation on wild prey are based on different processes. It has previously been a speculated phenomenon that this might be rooted in the ontogeny of search image and prey recognition, inasmuch as sheep are unavailable when kittens begin hunting with their mothers during their first winter (Odden et al. 2002). That being said, this is the study area that has documented the greatest dietary dependence of lynx on livestock anywhere in Eurasia. It, therefore, appears that the high rates of depredation on sheep in our study area are at least in part a response to the low densities of roe deer, although the degree of 'switching' is far lower than would be expected from their relative densities.

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