

Prey spectrum, prey preference and consumption rates of Eurasian lynx in the Swiss Jura Mountains

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We examined 617 kills made by radio-tracked Eurasian lynx *Lynx lynx* (Linnaeus, 1758) from March 1988 to May 1998 to assess prey spectrum, preference, and food consumption rates in the Swiss Jura Mountains. Roe deer *Capreolus capreolus* and chamois *Rupicapra rupicapra* were the main prey (69 and 22%, respectively), followed by red fox *Vulpes vulpes*, brown hare *Lepus europaeus*, domestic cat *Felis catus*, wild cat *Felis silvestris*, marmot *Marmota marmota*, pine marten *Martes martes*, capercaillie *Tetrao urogallus*, and badger *Meles meles*. Lynx fed on an ungulate prey from 1 to 7 days, depending on the prey category. The consumption rates of males, of females alone, and of females with kittens varied from 3.2 to 4.9 kg per night, with an increasing trend as the kittens grew older. Including the days when lynx had no kill (searching time) lynx consumed 2 ± 0.9 kg per night. The mean searching time was 1.5–2 days for females, depending on the season and the number of kittens, and 2.5 days for males. The mean interval between consecutive kills was 5.9 for males and 5.2 days for females, respectively. At 38% of carcasses the presence of one or several scavengers (red fox, raven *Corvus corax* or both) was detected. Although 69% of the kills were roe deer and only 22% chamois, we hypothesise that in the forests of the Jura Mountains chamois are more vulnerable to lynx predation than roe deer, as chamois had a slightly higher preference index (0.59) than roe deer (0.41), based on rough estimates of the two ungulate populations in the study area.

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Introduction

The species of the genus *Lynx* are believed to have evolved to prey on lagomorphs (Kurten 1968), what is still true for 3 of the 4 extant species. The preferred prey of Eurasian lynx *Lynx lynx* (Linnaeus, 1758), however, is the roe deer *Capreolus capreolus*, as studies in the Swiss Alps (Breitenmoser and Haller 1987, 1993, Haller 1992), in Poland (Okarma *et al.* 1997), and in Norway (Linnell *et al.* 1996) have shown. In Finland, however, where roe deer are not present in lynx habitat, the main prey of lynx are hares *Lepus* sp. or introduced white-tailed deer *Odocoileus*

virginianus (Pulliainen *et al.* 1995). Knowledge about the food habits of Eurasian lynx is incomplete. Most authors analysed stomach contents (Sunde and Kvam 1997) or scats (Jędrzejewski *et al.* 1993). Using these methods, however, the daily food requirement cannot be estimated. Furthermore, most studies are confined to the winter months because of the timing of the hunting season and the advantage of snow and lynx tracks to find the scats. Only recent studies used radio-telemetry to find fresh kills; but these studies were confined to small sample sizes (in the Swiss Alps – Breitenmoser and Haller 1987, Haller 1992; in Poland – Okarma *et al.* 1997). Knowledge of the prey spectrum, prey preference and consumption rates of lynx in different regions can help to understand how lynx can influence ungulate communities.

We studied the food habits of lynx by means of year-round radio-tracking of lynx and direct finding of kills in the Jura Mountains. We present data of a long-term study of the prey spectrum, prey utilisation, consumption rate and prey preference of lynx.

Study area

The study was conducted in the Jura Mountains, a secondary chain of limestone mountains forming the north-western border of Switzerland with France. The altitude ranges from 372 m (Lake Geneva) to 1679 m a.s.l. (summit of Mont Tendre). Over 60% of the study area lies above 1000 m a.s.l. Snow depth during winter varies from 0 to over 100 cm depending on elevation, exposure and year. The main study area was confined to the northern part (Jura Mountains) of the canton of Vaud (VD) covering 680 km². Lynx were also followed in the adjoining areas of the canton of Neuchâtel (NE) and in France, the total area being approx. 3000 km². Deciduous forests along the slopes and coniferous forests on the ridges cover 58% of the highlands. The forest is commercially managed through shelter-wood cutting. These mixed forests, with the main tree species beech *Fagus sylvatica*, spruce *Picea abies* and white spruce *Abies alba*, and the adjoining open areas offer high quality habitat for ungulates. The proportion of trees with less than 12 cm diameter at a height of 130 cm (regrowth, 80% deciduous species) is estimated at 7% of the forested area (Eidgenössische Anstalt für forstliches Versuchswesen 1988). The ungulate community consists of roe deer, chamois *Rupicapra rupicapra*, red deer *Cervus elaphus*, and wild boar *Sus scrofa*. Chamois occur locally in the rocky areas of the Jura Mountains and red deer occur in low numbers. Roe deer are hunted during 18 days a year in autumn and chamois and red deer during 8 and 4 days, respectively, in early winter. Wild boar are hunted from October to March and are considered abundant. The roe deer hunting bag showed an increasing trend during the last 10 years with a mean harvest of 570 roe deer, which corresponds to 1.4 roe deer harvested per 100 ha forest. Wild ungulates are not fed during winter. During summer, the open areas are used as pastures for cattle. Sheep are rare in the Swiss part of the Jura Mountains.

Material and methods

From April 1988 to June 1998, we captured 29 lynx with foot snares close to fresh kills, or in large double-door live traps on narrow paths (Breitenmoser *et al.* 1993). Lynx were immobilised with 0.1–0.15 mg/kg Medetomidin (Domitor®, Farnos, Finland) and 0.8–1 mg/kg Ketaminum (Ketasol, Graub, Switzerland) and fitted with radio collars (200 g; K. Wagener, Germany). As antagonist we used 0.5–0.75 mg/kg Atipamezol (Antisedan®, Farnos, Finland). Radio-marked lynx were subsequently relocated from the ground to a precision of 1 km² or 1 ha. To find kills, we monitored the movements of individual lynx daily. Lynx usually fed for several days on a kill, hiding during the day and returning to

the carcass each evening. If lynx stayed for more than half an hour in one place at dusk, we located it precisely by approaching it to a distance of about 50–200 m. The next day, this area was scanned with a Bavarian bloodhound. We found signs of kills in about 90% of our searching attempts. The species of each kill was recorded. If the kill was complete enough, ie not more than approx. 3 kg eaten, we recorded the part of the body the lynx started to feed on and the life weight of the prey was estimated. Common prey were classified into seven weight categories: male chamois, female chamois, male roe deer, female roe deer, juvenile chamois, juvenile roe deer, and fox. Chamois and roe deer were defined as juvenile from birth to the end of next May.

To estimate the consumption rates, only kills weighed at least twice and of which the intestinal tract was weighed separately were considered. The presence of scavengers at carcasses of ungulates killed by lynx was read from signs and tracks on snow whenever possible. To account for different needs of single lynx and family groups (females with kittens), we divided the year into two-month-periods: (1) April/May: the female is pregnant; it is also the time between the separation from last year's kittens and the birth of the new ones; (2) June/July: the female remains roughly stationary with the new-born kittens; (3) August/September: the small kittens venture out of the den (kittens already follow the mother to the kill, A. Jobin *et al.*, pers. obs.); (4) October/November: the kittens stop drinking milk, and grow permanent teeth (Lindemann 1955); (5) December/January: the kittens probably eat as much as an adult lynx; and (6) February/March: the rutting season, where some kittens may still accompany the female.

To compute lynx' preference for roe deer or chamois, we compared the proportions of these two ungulates killed by lynx to the proportions of the spring population estimates of these two species, calculated as a mean of the last five years. The density of roe deer was estimated from the total known loss, which consisted of hunting bag, dead roe deer found, and lynx predation (Jobin 1998), multiplied by a factor of three. In chamois, the total known loss was multiplied by a factor of five. If the populations are assumed to be neither increasing nor decreasing, the annual recruitment of roe deer and chamois can be estimated at one third and one fifth, respectively of the whole population. Therefore these factors take account of the possible harvest without a reduction of the population (Salzmann 1977, Blant 1987, Onderscheka *et al.* 1990). We used the index suggested by Chesson (1978) for measuring selectivity. The values of this index range from 0 to 1, with higher values implying higher selectivity. Chesson's selection index for prey in the *i*th category is formulated as:

$$\alpha_i = (r_i/n_i) / \Sigma(r_j/n_j)$$

where α_i – preference index for prey type *i*, r_i , r_j – proportion of prey type *i* or *j* in the diet, and n_i , n_j – proportion of prey type *i* or *j* in the environment.

Results

Prey spectrum and preference

From March 1988 to May 1998, a total of 617 kills were found. Roe deer were the main prey (69%), followed by chamois (22%), red fox (6%) and brown hare (2%). All other prey species were of little importance (Table 1). Of all ungulate species available, lynx clearly preferred the small species, roe deer and chamois, whereas small game like foxes and brown hares were rarely killed. Red deer and wild boar killed by lynx were never found.

The mean spring population density of the last five years was 4890 ± 810 roe deer and 1060 ± 260 chamois, which corresponds to 6–9 roe deer/km² and 1.2–1.9 chamois/km² (Jobin 1998). Therefore, roe deer were four times as abundant as chamois, whereas lynx killed roe deer only three times as often as chamois (Table 1). The preference index for roe deer was $\alpha = 0.410$, and for chamois $\alpha = 0.590$. If feeding is non-selective, the preference index should equal 0.500. Consequently,

Table 1. Number of lynx kills found from March 1988 to May 1998 in the Jura Mountains.

Prey species	Number of kills found	Percentage of prey items
Roe deer <i>Capreolus capreolus</i>	428	69.3
Chamois <i>Rupicapra rupicapra</i>	133	21.5
Red fox <i>Vulpes vulpes</i>	37	6.0
Brown hare <i>Lepus europaeus</i>	13	2.0
Domestic cat <i>Felis catus</i>	1	0.2
Wild cat <i>Felis sylvestris</i>	1	0.2
Alpine marmot <i>Marmota marmota</i>	1	0.2
Pine marten <i>Martes martes</i>	1	0.2
Capercaillie <i>Tetrao urogallus</i>	1	0.2
Badger <i>Meles meles</i>	1	0.2
Total	617	100

lynx in the Jura Mountains preyed on roe deer and chamois according to their abundance, with a slight preference for chamois.

Prey utilization

Lynx fed on an ungulate prey from less than one day to up to a week, depending on the prey category. Adult chamois lasted for 4.6 days and male and female roe deer for 4.3 and 4.0 days, respectively. Generally, consumption time by lynx grew logarithmically with prey weight (Fig. 1). Lynx ate all muscles, body fat and

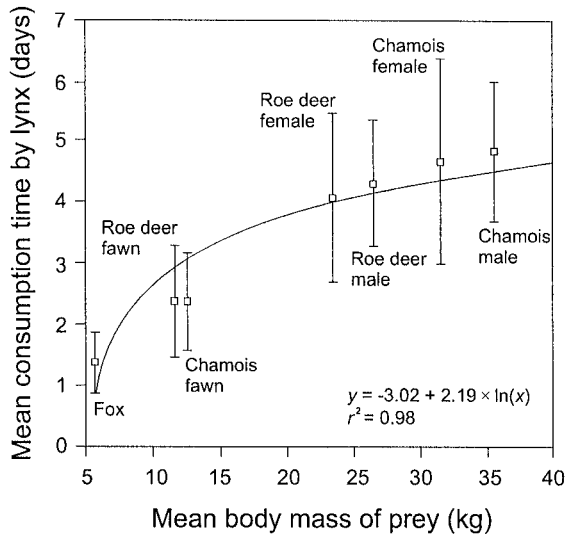


Fig. 1. Mean (\pm SD) consumption times by lynx in relation to the mean body mass of prey.

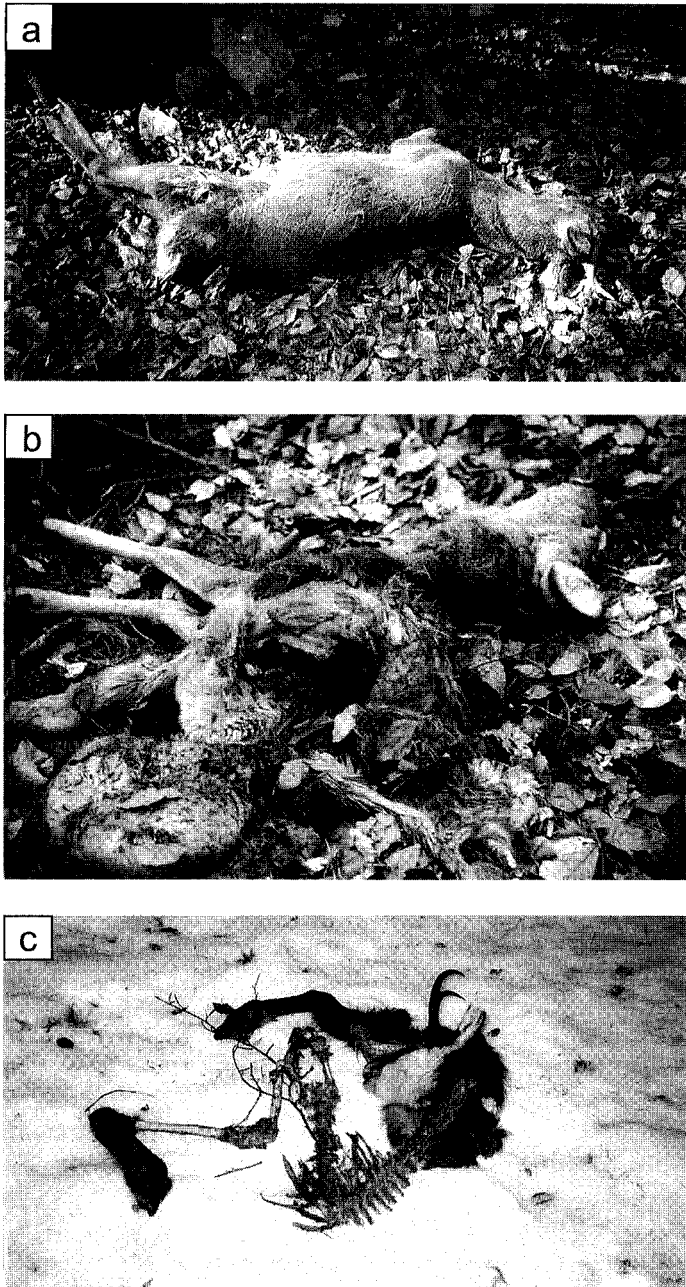


Fig. 2. Prey utilisation of lynx. (a) Male roe deer after one meal, where feeding started at hind quarters. (b) Female roe deer, where internal organs were already eaten except for the stomach and intestines. (c) Remains of a female chamois completely consumed by lynx.

internal organs except the digestive tract. Feeding started on the hind quarters in 70% of all cases (Fig. 2a), around the anus and on the shoulders in 14 and 16%, respectively ($n = 43$). For 359 kills, we collected data on the consumption of the kill by lynx. The stomach and the intestines were never eaten (Fig. 2b). Remains of a kill were the hide, the head, larger bones, the stomach and the intestinal tract (Fig. 2c). Unlike those of adult ungulates, lynx consumed the digestive tract of fawns up to two weeks of age completely, as they contained only milk. In 90% of all analyzed cases, the "edible" parts (muscles, heart, kidneys, lungs, spleen, liver) of the kills were consumed completely ($n = 351$). Humans removed 2% of the kills, the other 8% were abandoned by lynx for unknown reasons. Male lynx were twice observed to interrupt the consumption of their kills. They left the kill for more than 10 km, and returned to feed at the prey only two or more nights later.

Male lynx consumed an average of 3.4 kg per night, females 3.2 kg, and family groups 3.2–4.9 kg, with an increasing trend as kittens grew older (Table 2). Family groups consumed more than single lynx (one-tailed t -test: $p < 0.05$), and significantly increased their food intake from October to March compared to the time period from June to September (two-tailed t -test: $p < 0.05$). In Feb/March the consumption rates of family groups were lower than in Dec/Jan. Occasionally, lynx demonstrated a remarkable food intake and an irregular consumption: On 25 July 1996, we found the remains of a fox killed by the male M12. Two days later, the lynx killed a male chamois of an estimated weight of 36 kg 21 km from this site. He consumed this kill completely within three nights, eating as much as 9 kg in the night before he left. Only six days later he killed the next prey, a roe deer fawn. However, it cannot be excluded that M12 shared his chamois prey with an unknown lynx.

Snowtracking allowed a record of scavenging by other animals at lynx kills. At 37.9% of the carcasses, the presence of a scavenger was detected ($n = 161$). The most common scavenger was red fox (50.8%), followed by ravens *Corvus corax* and other corvids (39.3%) and, very occasionally, dogs *Canis familiaris*, cats and wild boar. Foxes only "scavenged" on ungulates killed by lynx after the lynx had

Table 2. Mean (\pm SD) nightly consumption rates of single lynx and family groups during the different time periods ($n = 166$) and number of days between two consecutive kills (searching time, $n = 172$). The number of kittens at the beginning of June averaged 1.8 per adult female.

Parameter	Consumption rates (kg)	Searching time (days)
Males (whole year)	3.4 \pm 1.7 ($n = 67$)	2.5 \pm 1.9 ($n = 65$)
Single females (whole year)	3.2 \pm 1.2 ($n = 32$)	1.8 \pm 1.9 ($n = 45$)
Family groups:		
June/July	3.2 \pm 1.3 ($n = 10$)	1.8 \pm 1.0 ($n = 12$)
August/September	3.4 \pm 1.4 ($n = 19$)	1.5 \pm 1.7 ($n = 32$)
October/November	3.7 \pm 1.3 ($n = 10$)	1.9 \pm 1.8 ($n = 22$)
December/January	4.9 \pm 1.2 ($n = 7$)	2.4 \pm 2.0 ($n = 15$)
February/March	3.6 \pm 0.9 ($n = 11$)	1.5 \pm 1.6 ($n = 39$)

abandoned the kill ($n = 31, \chi^2 = 14.2, df = 1, p < 0.001$), whereas corvids scavenged while lynx were still utilizing the kill ($n = 24, \chi^2 = 4.2, df = 1, p < 0.05$). Twice, we found a fox killed by a lynx within 100 m of an ungulate kill.

The time lynx spent feeding on a kill (consumption time) is followed by the searching time, the time span from leaving a kill to making a new kill (Table 2). The searching time for females was shorter than for males (t -test: $p < 0.01$), with a mean of 1.5–2 days versus 2.5 days. When summing consumption time and searching time, male lynx made a kill every 5.9 ± 1.5 days, and females every 5.2 ± 1.4 days, respectively.

Discussion

The lynx population of the Jura Mountains was re-introduced in the early 1970s, as was the population of the Swiss Alps (Breitenmoser 1983). In regard to the lynx's diet, our data from the Jura Mountains confirm the findings from the Alps: The most important prey species for lynx were the roe deer and chamois (90% in the Jura Mountains; 88.5% in the northern Alps, Breitenmoser and Haller 1987; 85% in the central Alps, Haller 1992). There were some differences in regard to occasional prey species, and most prominent in the extent of lynx predation on livestock. In the Alps, lynx killed sheep and, occasionally, goats (Breitenmoser and Haller 1987, Haller 1992). In our study area, none of the radio-tracked lynx preyed on livestock. This is most likely due to the fact that sheep are very rare, whereas wild prey is abundant. In other parts of the Jura Mountains, predation by lynx on sheep has temporarily been a problem (Vandel *et al.* 1992). All non-ungulate prey was obviously of minor importance for the diet of lynx in the Jura Mountains. However, smaller prey, such as foxes and hares, may have a certain significance for the survival of subadult, inexperienced lynx, or for females taking care of kittens (Okarma *et al.* 1997, F. Zimmermann, unpub.).

Even though roe deer were the main prey (69% of prey killed), they may not be the preferred prey of lynx in the Swiss Jura Mountains. The true population sizes of roe deer and chamois in the study area are unknown. Density estimates of ungulates in forest areas are highly speculative and populations are usually highly underestimated. If roe deer and chamois populations are assumed to remain stable, then the total known loss can be multiplied by a factor of three and five, respectively, to give a rough population estimate. The higher factor in chamois can be explained by the fact that the annual recruitment in chamois is lower than in roe deer. From these rough population estimates, we concluded that lynx in the Jura Mountains preferred chamois slightly over roe deer. However, a review of prey preference of lynx by Jędrzejewski *et al.* (1993) showed that wherever roe deer are available, they are the preferred ungulate species. Our different finding could be due to a higher vulnerability of chamois to lynx predation in the Jura Mountains. Since the highest peak of the Swiss Jura Mountains reaches only an altitude of 1679 m, and in summer the deforested parts are used as pastures for cattle, chamois are

forced into the forests. We hypothesise that the difference in prey preference was caused through a higher vulnerability of chamois in forests, compared to roe deer. For successful anti-predator behaviour, chamois require rugged areas with high visibility (Nerl *et al.* 1995). In the Jura Mountains, these areas are hardly available to chamois. Predators are reported to hunt chamois more successfully where they have easier access than in steep rocky areas (Knaus and Schröder 1983). Ungulates are more vulnerable to predation outside their prime habitat. Hornocker (1970) described a similar situation where increasing numbers of elk *Cervus canadensis* used marginal habitats where they were more vulnerable to mountain lion *Felis concolor* predation.

Chamois is one of the best alternative prey for lynx. About 1/3 heavier than roe deer (Fig. 1), a chamois can still easily be killed by a single lynx. In the northern Alps, with chamois and roe deer populations of comparable size, lynx preferred roe deer, as chamois were living at higher altitudes and in more rugged terrain (Breitenmoser and Haller 1987). But where chamois are much more abundant than roe deer and are also available in the forests, lynx can almost completely switch to chamois, as Haller (1992) reported from the central Swiss Alps. Nevertheless, the significance of alternative prey and of prey switching in lynx is not yet understood and should be the subject of further investigation.

Lynx are very well adapted to a food regime of feast and famine. Lynx return to a kill for several consecutive nights, depending on the kill's weight. The consumption rates depended on sex and season, and ranged from 1 to, exceptionally, 9 kg per night. This feast is followed by the searching time, the time span from leaving a kill until they make a new kill. In lynx, the females alone care for kittens. We found that females killed more prey than males, with a mean searching time of 1.5–2.0 days, whereas males had on average 2.5 days without a kill. In the Jura Mountains, lynx returned to a kill and fed for 3.4 (± 1.1) days. Similar results were obtained by Okarma *et al.* (1997) in Poland, where lynx fed on an ungulate prey for 3.2 days.

Single females had the lowest consumption rate of 3.2 kg/day. The consumption rate of family groups increased with the growing demands of kittens, up to a mean of 4.9 kg/day during December/January. The decreased consumption rate during February/March could be explained by the fact that the family groups decrease due to dispersal of some of the young lynx and/or anecdotal observations indicated that females reinforced their hunting effort and made parallel kills that were not found. According to Okarma *et al.* (1997), a normal meal of a lynx consists of about 2 kg of meat, ranging from 1.6–3.6 kg. This corresponds well to the consumption rates of single lynx (2 ± 0.9 kg) recorded in this study, when we add the searching time.

The kill rate of lynx was investigated earlier by Breitenmoser and Haller (1993) in the Swiss Alps. The mean time interval between consecutive kills did not differ: 5.0 and 5.1 days for the Alps, as in the Jura the mean time interval was 5.9 and 5.2 days for males and females, respectively. An obvious difference between the Alps and the Jura was the average consumption of kills. In the Alps, surplus killing (killing of prey without eating anything of the kill, Kruuk 1972) was observed 10

times, and lynx consumed only half or less of the kills of over 30% of the ungulates killed, whereas in the Jura, 90% of the kills were entirely consumed. This difference could be due to higher human disturbance and/or better availability of ungulates in the Alps (eg during the recolonization of lynx; Breitenmoser and Haller 1993).

The role of scavengers is not yet understood. The most common scavenger was red fox, followed by *Corvidae*. Lynx often hide or camouflage their kills, and this can restrain scavenging by birds, but not by mammals. In contrast to corvids, foxes only "scavenged" at lynx kills after the lynx had abandoned the kill. Whether they avoided lynx kills because of the danger of getting killed themselves or because of the scent of humans at lynx kills, we do not know.

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References

- Blant M. 1987. Dynamique de population, condition et constitution du chevreuil (*Capreolus capreolus* L., 1758) dans les cantons de Neuchâtel et Vaud (ouest de la Suisse). Ph D thesis, University of Neuchâtel, Neuchâtel: 1-160.
- Breitenmoser U. 1983. Zur Wiedereinbürgerung und Ausbreitung des Luchses *Lynx lynx* in der Schweiz. Schweizerische Zeitung für Forstwesen 134: 207-222.
- Breitenmoser U. and Haller H. 1987. Zur Nahrungsökologie des Luchses *Lynx lynx* in den schweizerischen Nordalpen. Zeitschrift für Säugetierkunde 52: 135-144.
- Breitenmoser U. and Haller H. 1993. Patterns of predation of reintroduced European lynx in the Swiss Alps. Journal of Wildlife Management 57: 135-144.
- Breitenmoser U., Kaczensky P., Dötterer M., Breitenmoser-Würsten C., Capt S., Bernhart F. and Liberek M. 1993. Spatial organisation and recruitment of lynx (*Lynx lynx*) in a reintroduced population in the Swiss Jura Mountains. Journal of Zoology, London 231: 449-464.
- Chesson J. 1978. Measuring preference in selective predation. Ecology 59: 211-215.
- Eidgenössische Anstalt für forstliches Versuchswesen 1988. Schweizerisches Landesforstinventar: Ergebnisse der Erstaufnahme 1982-1986. Berichte Nr. 305, Birmensdorf: 1-375.
- Haller H. 1992. Zur Ökologie des Luchses im Verlauf seiner Wiederansiedlung in den Walliser Alpen. Mammalia depicta: 1-62.
- Hornocker M. G. 1970. An analysis of mountain lion predation upon mule deer and elk in the Idaho Primitive Area. Wildlife Monographs 21: 1-39.
- Jędrzejewski W., Schmidt K., Miłkowski L., Jędrzejewska B. and Okarma H. 1993. Foraging by lynx and its role in ungulate mortality: the local (Białowieża Forest) and the Palaearctic viewpoints. Acta Theriologica 38: 385-403.
- Jobin A. 1998. Predation patterns of Eurasian lynx in the Swiss Jura Mountains. Ph D thesis, University of Bern, Bern: 1-75.

- Knaus W. and Schröder W. 1983. Das Gamswild: Naturgeschichte, Verhalten, Ökologie, Hege und Jagd, Krankheiten. Verlag Paul Parey, Hamburg, Berlin: 1-232.
- Kruuk H. 1972. Surplus killing by carnivores. *Journal of Zoology*, London 166: 233-244.
- Kurten B. 1968. Pleistocene mammals of Europe. Weidenfels and Nicolson, London: 1-317.
- Lindemann W. 1955. Über die Jugendentwicklung beim Luchs (*Lynx lynx* Kerr.) und bei der Wildkatze (*Felis s. silvestris* Schreb.). *Behavior* 7: 1-44.
- Linnell J. D. C., Stoen O. G., Odden J., Ness E., Gangas L., Karlsen J., Eide N. and Andersen R. 1996. Lynx and roe deer in eastern Hedmark. NINA Oppdragsmelding 414: 1-36.
- Nerl W., Messner L. and Schab P. 1995. Das grosse Gamsbuch. Hubertusverlag, Klosterneuburg: 1-292.
- Okarma H., Jędrzejewski W., Schmidt K., Kowalczyk R. and Jędrzejewska B. 1997. Predation of Eurasian lynx on roe deer and red deer in Białowieża Primeval Forest, Poland. *Acta Theriologica* 42: 203-224.
- Underscheda K., Reimoser F., Tataruch F., Steineck T., Klansek E., Völk F., Willing R. and Zandl J. 1990. Integrale Schalenwildbewirtschaftung im Fürstentum Liechtenstein unter besonderer Berücksichtigung landschaftsökologischer Zusammenhänge. *Naturkundliche Forschung im Fürstentum Liechtenstein*, Band 11. Vaduz: 1-265.
- Pulliaainen E., Lindgren E. and Tunkkari P. S. 1995. Influence of food availability and reproductive status on the diet and body condition of the European lynx in Finland. *Acta Theriologica* 40: 181-196.
- Salzmann H. C. 1977. Untersuchungen zur Fortpflanzungsbiologie der Gamsen im Schweizerischen Jura. *Zeitschrift für Säugetierkunde* 42: 180-189.
- Sunde P. and Kvam T. 1997. Diet patterns of Eurasian lynx *Lynx lynx*: what causes sexually determined prey size segregation? *Acta Theriologica* 42: 189-201.
- Vandel J. M., Stahl P. and Migot P. 1992. Prédation du lynx sur le cheptel domestique dans le massif du Jura. *Bulletin mensuel, Office National de la Chasse* 166: 28-43.

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