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Abstract: Prey class selection and kill rates by lynx were studied in the Swiss Jura Mountains from March 1988 until May 1998 to evaluate the significance of lynx predation for roe deer and chamois. We found clear differences in the kill rates and prey class selection between lynx of different age, sex and breeding status. Male lynx killed more chamois than female lynx, and chamois was never found in kill series of subadult lynx. Family groups had the highest kill rate. They killed an ungulate every 5.0 days, compared to an average of 6.2 - 6.6 days for single lynx. During our 10-year study, the density of independent lynx was rather stable, ranging within 0.94 - 1.01 individuals/100 km². Based on the observed kill rates and the estimated lynx population structure we calculated that lynx killed 354 ± 13 roe deer and 87 ± 13 chamois annually in the 710 km² study area. The magnitude of lynx predation on roe deer and chamois was primarily shaped by lynx population structure. A decline in the number of resident male lynx reduced the number of chamois killed in the study area by ¼ of the previous number due to the difference in prey selection of male and female lynx. There was a difference in the most frequently killed age and sex classes between roe deer and chamois: lynx killed more male chamois (39%) than females or fawns, whereas in roe deer, does (38%) were most often killed. By altering adult survival, lynx predation has a significant impact on prey population dynamics. Lynx killed a maximum of 9% of the roe deer and 11% of the chamois spring population. Considering the differences in the recruitment potential of the two prey species, lynx has a greater impact on chamois than on roe deer.

Significance of lynx *Lynx lynx* predation for roe deer *Capreolus capreolus* and chamois *Rupicapra rupicapra* mortality in the Swiss Jura Mountains

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Prey class selection and kill rates by lynx *Lynx lynx* were studied in the Swiss Jura Mountains from March 1988 until May 1998 to evaluate the significance of lynx predation for roe deer *Capreolus capreolus* and chamois *Rupicapra rupicapra*. We found clear differences in the kill rates and prey class selection between lynx of different age, sex and breeding status. Male lynx killed more chamois than female lynx, and chamois was never found in kill series of subadult lynx. Family groups had the highest kill rate. They killed an ungulate every 5.0 days, compared to an average of 6.2-6.6 days for single lynx. During our 10-year study, the density of independent lynx was rather stable, ranging within 0.94-1.01 individuals/100 km². Based on the observed kill rates and the estimated lynx population structure we calculated that lynx killed 354 ± 13 roe deer and 87 ± 13 chamois annually in the 710 km² study area. The magnitude of lynx predation on roe deer and chamois was primarily shaped by the lynx population structure. A decline in the number of resident male lynx reduced the number of chamois killed in the study area by ¼ of the previous number due to the difference in prey selection of male and female lynx. There was a difference in the most frequently killed age and sex classes between roe deer and chamois: lynx killed more male chamois (39%) than females or fawns, whereas in roe deer, does (38%) were most often killed. By altering adult survival, lynx predation has a significant impact on prey population dynamics. Lynx killed a maximum of 9% of the roe deer and 11% of the chamois spring population. Considering the differences in the recruitment potential of the two prey species, lynx has a greater impact on chamois than on roe deer.

Key words: *Capreolus capreolus*, kill rate, *Lynx lynx*, predation, *Rupicapra rupicapra*

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The effect of large predators on ungulate populations has received much interest in Africa, North America and the former Soviet Union (e.g. Filonov 1980, Sinclair 1985, Van Ballenberghe 1987), where both predator and ungulate populations are relatively well preserved. In Western Europe, however, where large predators have mostly been exterminated (Breitenmoser 1998), predation on ungulates has received little attention because these large predator/ungulate prey systems are rare.

Throughout Europe and Siberia, the Eurasian lynx *Lynx lynx* is associated primarily with forested areas that have well established ungulate populations (Nowell & Jackson 1996), and its main prey is roe deer *Capreolus capreolus* (Breitenmoser & Haller 1987, Okarma, Jedrzejewski, Schmidt, Kowalczyk & Jedrzejewska 1997). In the Swiss Alps and the Jura Mountains, the main alternative prey is chamois *Rupicapra rupicapra* (Breitenmoser & Haller 1993, Jobin, Molinari & Breitenmoser 2000). The impact of lynx on prey populations, however, is not fully understood. It depends on many factors, of which the most obvious ones are the density of predators and prey, and the kill rate. So far, the predation rate of lynx has been studied in the Swiss Alps and in Poland by means of radio telemetry. Breitenmoser & Haller (1987) estimated the annual mortality due to lynx predation for roe deer to be 6-9% of the spring population and for chamois 2-3% of the population in their study area in the northwestern Alps. In the Central Swiss Alps, in contrast, the roe deer disappeared from the Turtmantal after the colonisation of this area by lynx, and chamois numbers declined by 50% from 800 to 400. There was a clear timely correlation between the disappearance of the roe deer, the decline in chamois numbers and the arrival of the lynx (Haller 1992, Breitenmoser & Haller 1993). In the Bialowieza Primeval Forest, Poland, one of the largest remaining tracts of ancient mixed deciduous forests in the lowlands of Europe, lynx predation was reported to be the main cause of mortality. Roe deer erupted after lynx extermination and declined again after the return of the predator (Jedrzejewska, Jedrzejewski, Bunevich, Milkowski & Krasinski 1997). In recent years, lynx have once again been reported to be the main mortality factor of roe deer, killing a mean of 26% of the summer (seasonally highest) numbers of roe deer (Okarma et al. 1997). Because of these varying results it is clearly of interest to obtain data on the impact of lynx predation from a variety of contrasting sites.

In this study, we assessed the significance of lynx predation for roe deer and chamois mortality in the Swiss Jura Mountains by estimating lynx density and kill rates. Since predation on juveniles has a different impact on roe deer population dynamics than predation on adults - and predation on males is different from that on females (Gaillard, Festa-Bianchet & Yoccoz 1998) - we differentiated for age and sex classes of the prey. Finally, we compared the mortality caused by lynx predation with other known mortalities of roe deer and chamois.

Study area

Our study was conducted in the Jura Mountains, a secondary chain of limestone mountains forming the northwestern border between Switzerland and France. The main study area was confined to the wildlife management unit 'Jura' of the canton of Vaud (VD) which covers 710 km². Lynx and prey density estimates refer to this area. Lynx were also studied in the adjoining areas of the canton of Neuchâtel (NE) and in France. The altitude ranges from 372 m (Lake Geneva) to 1,679 m a.s.l. (summit of Mont Tendre), and more than 60% of the study area lies above 1,000 m a.s.l. Mean monthly temperatures ranged from -6°C in January to 15°C in July. Snow depth during winter varies from 0 to over 100 cm depending on elevation, exposure and year. Deciduous forests along the slopes and coniferous forests on the ridges cover 53% of the study area. The forest is commercially managed through shelter-wood cutting. The mixed forests with the main tree species beech *Fagus sylvatica*, spruce *Picea abies* and white spruce *Abies alba*, and the adjoining meadows offer high-quality habitat for wild ungulates. The ungulate community consists of red deer *Cervus elaphus*, roe deer, chamois and wild boar *Sus scrofa*. From 1988 to 1997, 5 ± 4 red deer, 571 ± 193 roe deer, 58 ± 27 chamois and 144 ± 70 wild boar were hunted annually in the main study area. The ungulate management policy was to reduce forest damage while maintaining high yields. In both roe deer and chamois, males and females were hunted in equal proportions. 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. Lynx were the only large predator in the study area as wolves *Canis lupus* and brown bears

Ursus arctos were exterminated in the 18th and 19th centuries, respectively (Breitenmoser 1998).

Methods

From March 1988 to May 1998, 29 different lynx were live-trapped and radio-collared following the procedures described in Jobin et al. (2000). Radio-marked lynx were subsequently relocated from the ground. Locations were assigned to one of three accuracy levels (1 km², 1 ha or direct observation) depending on bearing distance, activity of lynx, and additional observations. To find kills, we monitored the movements of individual lynx daily. Lynx usually fed for several days on a kill, lying up at a distance 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 searched, usually with a Bavarian bloodhound or a Rhodesian ridgeback. Both dogs were trained to follow lynx tracks: we therefore did not depend on snow cover to find kills. With the aid of the dogs, we were also able to find kills that were consumed in less than two days, i.e. red foxes *Vulpes vulpes*, brown hares *Lepus europaeus*, roe deer and chamois fawns killed during their first two months of life. Using this method, we tried to minimise the bias towards finding only large kills on which lynx feed for several days. In this way, we found a total of 617 prey items, of which 561 were ungulates (Jobin et al. 2000). Ungulate prey was classified into six categories: male, female and juvenile chamois, and male, female and juvenile roe deer. Chamois and roe deer were defined as juvenile from birth to end of May the next year.

Our objective was to detect two or more consecutive kills made by individual lynx ('kill series'). We always started a kill series with the first day a kill was made and then located this lynx every consecutive day. If the daybeds of females and subadults were within a radius of 1 km for two consecutive days, and we failed to find prey remains, we assumed that the lynx had actually killed an ungulate prey and that we were unsuccessful in finding it (Okarma et al. 1997). We then interrupted this kill series to start a new one. As male lynx move around much more when they have a kill (Swiss Lynx Project, unpubl. data), we used a different definition for kill series of males: we interrupted the kill series when we failed to find prey remains even though male lynx returned within two days to within a radius of 1.5 km. The daybeds were within the defined radius for 88% of all kills found. Lynx sometimes had their daybeds fur-

ther apart 1) during the rutting season (4%), 2) when they killed a fox or brown hare (3%), 3) when they killed a roe deer or chamois fawn which was less than two months old (2%), or 4) for unknown reasons.

The length of a kill series was estimated by summing up the days from when the first kill was made to the day of total consumption of the last kill in the series, and by adding a mean searching time of 2.5 days for males, 1.8 days for subadults, single females and females with kittens in June/July, 1.5 days for females with kittens in August/September, 1.9 days in October/November, 2.4 days in December/January, and 1.5 days for females with kittens in February/March (Jobin et al. 2000).

The kill rate, i.e. the number of roe deer and chamois per age and sex class, red foxes, and brown hares killed by a lynx per year, was estimated separately for males, single females, family groups (females with kittens) and subadults. For each of these lynx categories, the number of prey items killed during the kill series was calculated for two-month periods to account for seasonal differences in prey availability and then summed up to obtain the total number of prey per category and year.

For the calculation of the predation rate by the lynx in the study area, we used lynx densities and population structure estimated based on home range size, the proportion of individual home ranges within the study area and knowledge of the presence of untagged individuals (Breitenmoser, Kaczensky, Dötterer, Breitenmoser-Würsten, Capt, Bernhart & Liberek 1993) for three different periods according to the development of the lynx population: 1988-1991, 1992-1994 and 1995-1997. The number of males, females (assuming that each year one female did not have kittens or lost them at a very early stage; Swiss Lynx Project, unpubl. data) and subadult lynx in the study area were multiplied by the annual kill rate of the respective category. We assumed that 0.25 subadults per female and year were present in the study area, and that the immigration rate of young dispersing lynx was the same as the emigration rate (Breitenmoser et al. 1993). Other roe deer and chamois mortalities were based on the mean number of individ-

Table 1. Number of kill series, kills and duration of kill series recorded for males, single females, family groups and subadult lynx in the Swiss Jura Mountains during 1988-1997.

| Lynx category | No of kill series | No of kills | No of days |
|----------------|-------------------|-------------|------------|
| Males | 27 | 58 | 350 |
| Single females | 12 | 28 | 159 |
| Family groups | 45 | 124 | 559 |
| Subadults | 8 | 17 | 88 |
| Total | 92 | 227 | 1136 |

Table 2. Annual numbers of prey items killed and estimated annual kill rates per lynx category in the Swiss Jura Mountains during 1988-1997.

| Prey category | Lynx category | | | |
|--------------------|---------------|----------------|---------------|-----------|
| | Males | Single females | Family groups | Subadults |
| Chamois male | 8.3 | 7.7 | 3.6 | - |
| Chamois female | 7.3 | 1.0 | 4.3 | - |
| Chamois juvenile | 8.3 | - | 3.2 | - |
| Roe deer male | 13.9 | 9.9 | 21.0 | 6.1 |
| Roe deer female | 7.8 | 23.8 | 20.5 | 32.8 |
| Roe deer juvenile | 10.1 | 16.3 | 19.7 | 18.3 |
| Fox | 2.3 | 1.5 | 6.1 | 13.3 |
| Brown hare | - | 9.1 | 1.0 | - |
| Total | 58.6 | 69.3 | 79.4 | 70.5 |
| Days/kill | 6.2 | 5.3 | 4.6 | 5.2 |
| Total ungulates | 55.7 | 58.7 | 72.3 | 57.2 |
| Days/ungulate kill | 6.6 | 6.2 | 5.0 | 6.4 |

uals harvested during the three periods as well as roe deer/chamois-car collisions and other known mortalities (official statistics of the canton of Vaud). The data collection of perished ungulates was done using the same method throughout the study.

Results

Kill rate

We recorded 92 kill series with 227 kills representing a total of 1,156 lynx days (Table 1). The mean kill series length was 13 days (range: 5-36 days). The numbers of kills in a series averaged 2.5 (range: 2-8). This implies that lynx annually killed 58.6-79.4 prey items, depending on their social status (Table 2). Male lynx killed more chamois than any other lynx category ($G = 59.9$, $df = 3$, $P < 0.001$). When preying upon roe deer, they killed more bucks than does or fawns, whereas single females and subadults killed more roe deer does ($G = 35.1$, $df = 2$, $P < 0.001$). Females with kittens preyed on all roe deer age and sex classes equally. We never found chamois in a kill series of subadult lynx. As an alternative to roe deer subadults preyed on red fox, which was the next smaller available prey. Subadults killed more foxes than adult lynx ($G = 16.7$, $df = 3$, $P < 0.001$). Family groups had the highest kill rate. They killed an ungulate every 5.0 days, compared to an average of 6.2-6.6 days for single lynx.

Lynx population

Except for the period 1992-1994, more than two males and almost four females were resident in the study area as well as an average of one transient (Table 3). The density of independent lynx was estimated at 1.01 individuals/100 km² during 1988-1991 and 0.96 individuals/100 km² during 1995-1997. However, at the beginning of the second period two males were poached and therefore only one male was present during 1992-1994. During this time, the male increased his home range from 360 km² during 1988-1991 to 912 km² (100% convex polygon). This indicates that no other male lynx was present in the study area. However, the lynx density declined only to 0.94 individuals/100 km², as the number of females and subadults increased (see Table 3). Despite the decline and later increase in the number of males present, the overall lynx density remained fairly constant over the whole study period.

Lynx predation

The change in the lynx sex ratio in the three periods had an influence on the total number of chamois and roe deer killed by the lynx population in the study area. During the first period (1988-1991), we estimated that lynx killed on average 99 chamois annually, whereas in the second period (1992-1994), when only one male lynx was present, 73 chamois were killed (Table 4). In the third period (1995-1997), male density increased, and 89 chamois were killed annually. However, due to the presence of an increased number of females and suba-

Table 3. Number of lynx present in the study area (710 km²) in the Jura Mountains of the canton of Vaud during 1988-1991, 1992-1994 and 1995-1997. N indicates the number of individuals that were radio-collared during the respective period for more than one year (except subadults) and had at least part of their home range within the study area.

| Lynx category | 1988 - 1991 | | 1992 - 1994 | | 1995 - 1997 | |
|---------------|-------------|----|-------------|---|-------------|----|
| | | N | | N | | N |
| Males | 2.49 | 3 | 0.99 | 1 | 2.12 | 3 |
| Females | 3.79 | 4 | 4.57 | 4 | 3.77 | 5 |
| Subadults | 0.95 | 6 | 1.14 | 2 | 0.94 | 7 |
| Total | 7.23 | 13 | 6.70 | 7 | 6.83 | 15 |

Table 4. Estimated number of chamois and roe deer killed annually by lynx during the three periods. The prey are classified according to sex and age. Animals referred as male and female are adults only.

| Number of ungulates killed by lynx annually. | | | | | | | |
|----------------------------------------------|---------------|------|---------------|------|---------------|------|-------------------|
| Prey category | 1988-1991 (%) | | 1992-1994 (%) | | 1995-1997 (%) | | Mean \pm SD (%) |
| Chamois male | 38 | (38) | 29 | (40) | 35 | (39) | 34 \pm 5 (39) |
| Chamois female | 31 | (31) | 24 | (33) | 28 | (32) | 28 \pm 3 (32) |
| Chamois fawn | 30 | (31) | 20 | (27) | 26 | (29) | 25 \pm 5 (29) |
| Total chamois | 99 | | 73 | | 89 | | 87 \pm 13 |
| Roe deer male | 109 | (31) | 106 | (29) | 103 | (30) | 106 \pm 3 (30) |
| Roe deer female | 132 | (37) | 142 | (39) | 128 | (38) | 134 \pm 7 (38) |
| Roe deer fawn | 114 | (32) | 118 | (32) | 109 | (32) | 114 \pm 4 (32) |
| Total roe deer | 355 | | 366 | | 340 | | 354 \pm 13 |

adults during 1992-1994, presumably more roe deer were killed than during the other years. Overall, we estimated that 87 ± 13 chamois and 354 ± 13 roe deer were killed by lynx annually. This corresponds to an average of 1 roe deer/2 km² and 1 chamois/8 km².

Roe deer and chamois differed in the age and sex class that was most often killed: lynx killed more male chamois (39%) than females or fawns, whereas in roe deer, does (38%) were most often killed (see Table 4).

Ungulate mortalities

Hunting was the most important documented mortality factor for roe deer in all three periods (Table 5). It almost tripled within 10 years, from 373 roe deer harvested in 1989 to 1,033 roe deer harvested in 1997. This increase was due to the fact that foresters complained about browsing damage caused by roe deer. The number of roe deer that perished on roads showed an increasing trend, too. Lynx predation accounted for 24-37% of all known roe deer mortalities. In chamois, lynx predation was three times as high as the hunting mortality during the first period. During 1992-1997, mortality caused by lynx predation was only slightly higher than hunting mortality (see Table 5).

Discussion

We studied lynx density, kill rates and prey class selection in the Swiss Jura Mountains to evaluate the significance of lynx predation for roe deer and chamois mortality and found clear differences in the kill rates between lynx of different age, sex and breeding status. The kill rates found in the Swiss Jura Mountains do not differ from kill rates in the Swiss Alps (Breitenmoser & Haller 1993), but are slightly lower than kill rates found in Poland, where the main prey species of lynx were roe deer and red deer (5.4 days/deer for single lynx, 3.1 days/deer for females with two kittens; Okarma et al. 1997). This difference might be due to the fact that in Poland lynx were frequently displaced by scavengers, especially by wild boar, which forced the lynx to kill more frequently. If lynx prey mainly on ungulates, we can conclude that kill rates show little variation. But a high presence of scavengers can lead to a significant increase in kill rates.

During our 10-year study the abundance of independent lynx was rather constant, ranging within 0.94-1.01 individuals/100 km². Therefore, the magnitude of lynx predation on roe deer and chamois was primarily shaped by the lynx population structure. The impact of lynx on chamois varied according to the number of male lynx

Table 5. Mortality factors of roe deer and chamois in the Swiss Jura Mountains during the periods 1988-1991, 1992-1994 and 1995-1997 in which the composition of the lynx population varied. ? indicates that no data were available.

| | Mean number killed during 1988-1991 | Mean number killed during 1992-1994 | Mean number killed during 1995-1997 |
|----------------------------------|-------------------------------------|-------------------------------------|-------------------------------------|
| Roe deer mortality factor | | | |
| Hunting harvest | 432 \pm 51 (45%) | 524 \pm 22 (46%) | 802 \pm 200 (56%) |
| Road kills | 133 \pm 29 (14%) | 187 \pm 28 (17%) | 236 \pm 8 (17%) |
| Other mortalities | 41 \pm 3 (4%) | 55 \pm 14 (5%) | 48 \pm 7 (3%) |
| Estimated lynx predation | 355 (37%) | 366 (32%) | 340 (24%) |
| Total | 961 \pm 29 (100%) | 1132 \pm 34 (100%) | 1426 \pm 205 (100%) |
| Chamois mortality factor | | | |
| Hunting harvest | 33 \pm 8 (25%) | 66 \pm 28 (43%) | 83 \pm 8 (43%) |
| Road kills | ? | 4 \pm 3 (3%) | 7 \pm 1 (4%) |
| Other mortalities | ? | 11 \pm 2 (7%) | 11 \pm 4 (6%) |
| Estimated lynx predation | 99 (75%) | 73 (47%) | 89 (47%) |
| Total | 132 \pm 8 (100%) | 154 \pm 34 (100%) | 190 \pm 5 (100%) |

present. A decline in the number of males reduced the number of chamois killed in the study area by $\frac{1}{4}$ of the previous number. During our study, both roe deer and chamois populations showed an increasing trend; we therefore would have expected to observe an increase in lynx numbers as well. However, two males were poached, so we were unable to witness a numerical response. It is interesting to note that when male density was at its lowest, the density of females slightly increased (see Table 3). We assume that lynx in the Jura Mountains were primarily shaped by 'human mortality', as 18% of adult radio-collared lynx were known to be poached ($N = 17$), and we suspect that three other adult lynx were poached, too, even though their carcasses were never found (Swiss Lynx Project, unpubl. data).

To evaluate the significance of lynx predation on roe deer and chamois populations we need to know roe deer and chamois densities. But roe deer are known to be difficult to census. Therefore, we face serious risks of underestimation in roe deer counts (Gaillard 1988). In the Jura Mountains, the same applies for chamois. They are forced to live in forested habitats, as most deforested areas are used for cattle grazing during summer. Roe deer, and especially chamois, show a clustered distribution in the Jura Mountains (Blant 1987, Salzmann 1975). Drive counts conducted from 1988 to 1991 resulted in roe deer densities of 1-22 individuals/km², depending on region and year (Durand 1992). Berlie (1997) reported a mean chamois density of 25 individuals/km² in a favourable area of 3 km². However, the average chamois density is much lower. By considering the total known mortality and recruitment potential of roe deer and chamois, we estimated roe deer and chamois densities to range within 6-9 and 1.2-1.9 individuals/km², respectively (Jobin et al. 2000). Liberek (1992) estimated the chamois density in the same area at 1.5 chamois/km². These densities have to be considered to be minimal densities. Lynx would therefore kill a maximum of 9% of the roe deer and 11% of the chamois spring population.

Sound data on prey population dynamics are still lacking for predation-influenced populations in Europe. However, predation on adults, especially females, will have a stronger effect on the population growth rate than predation on juveniles, as they are the segment of the population that can most quickly be replaced. A change in adult survival should have about three times as high an impact on the population growth rate than the equivalent change in recruitment, which is determined by juvenile survival (Gaillard et al. 1998). By lowering the survival of adult ungulates, predation can therefore have a great influence on prey population dynamics. Lynx

killed slightly more roe deer does than bucks and fawns, whereas in chamois, males were killed more frequently. But the capacity of a prey population to sustain lynx predation depends on the magnitude of the predation losses, compared to the potential annual increment that the prey would produce in the absence of lynx. The possible increment of roe deer and chamois differ: Loison (1995) observed growth rates of only $\lambda = 1.14$ in an Alpine chamois population that was expanding after a keratoconjunctivitis epizootic, whereas in roe deer growth rates of up to $\lambda = 1.37$ were observed (Gaillard, Boutin, Delorme, VanLaere, Duncan & Lebreton 1997). On the island of Storfosna in Norway, the roe deer population growth rate was even higher as the population doubled in 1.7 years (Andersen & Linnell 2000). The estimated maximum impact of lynx on roe deer (9%) in the Jura Mountains lies well within the range that can easily be supported by the population. But lynx predation may have the potential to prevent the chamois population from increasing, as lynx may 'absorb' the annual recruitment. Chamois might be more vulnerable to lynx predation than roe deer in the highly forested areas of the Jura Mountains due to habitat features (Jobin et al. 2000). But the mechanisms underlying lynx predation on ungulate populations, especially numerical and functional response of lynx to changing prey densities, require that lynx-prey relations be more fully studied.

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