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Lynx prey selection for age and sex classes of roe deer varies with season

T. Mejlgaard[1], L. E. Loe[1], J. Odden[2], J. D. C. Linnell[2] & E. B. Nilsen[2]

1 The Department of Ecology and Natural Resource Management, Norwegian University of Life Sciences, Aas, Norway
2 Norwegian Institute for Nature Research, Trondheim, Norway

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Correspondence
Leif Egil Loe, Department of Ecology and Natural Resource Management, Norwegian University of Life Sciences, P.O. Box 5003, Zip. No. 1432, Aas, Norway. Tel: +47 64 96 58 05; +47 64 96 58 01
Email: leif.egil.loe@umb.no

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Abstract

Predator selectivity for age and sex classes has large implications for their impact on prey populations. We examined whether the Eurasian lynx *Lynx lynx* selects specific sex and age categories of roe deer *Capreolus capreolus*, and if this selection pattern differs between summer and winter. Data on sex and age of 194 roe deer killed by 44 VHF- and GPS-marked lynx were collected in southern Norway from 1995 to 2010. The sex and age distribution of the roe deer population was estimated using demographic parameters estimated from radio-collared roe deer in the study area. We found that lynx selection differed between summer and winter. In both seasons, lynx selected adult roe deer of both sexes. In summer, there was a clear selection against yearlings, but in winter, lynx selected male yearlings. Compared with the availability, fawns of both sexes were under-represented during summer. Male and female lynx did not differ in their prey selection, but yearling lynx tended to kill a larger proportion of roe deer fawns than older lynx. We argue that seasonal differences in behaviour, activity and habitat use by roe deer may explain this variation in lynx selection patterns, supporting the view that prey selection is affected by the life cycle stage of both the predators and the prey.

Introduction

Predation by large carnivores can potentially exert a strong top-down control on the demography of wild ungulates (Festa-Bianchet *et al*., 2006; Nilsen *et al*., 2009*a*). However, the strength of top-down control varies, and understanding inter- and intraspecific patterns of prey selection shown by predators is thus important (Cooper, Pettorelli & Durant, 2007; Gervasi *et al*., 2012).

The hunting technique, social system and body size of the predator relative to the prey are expected to be particularly influential in determining the age and sex distribution of predated animals. Group living, coursing predators often capture prey larger than their own body size and have the opportunity to actively select prey within a group during the chase (Fitzgibbon & Fanshawe, 1989; Hayward *et al*., 2006*b*). At the interspecific level, stalking predators have been shown to prefer prey species close to their own body size (Hayward *et al*., 2006*a*; Hayward, Jędrzejewski & Jêdrzejewska, 2012). At the intraspecific level, solitary stalking predators not limited by prey body size are expected to select age and sex classes of a prey proportional to their availability (Kleiman & Eisenberg, 1973). Success depends on ambushing from a short distance. In each hunting situation, selection is expected to be strongly limited by access to cover and the location of each individual prey in the group, particularly in species with small group sizes and little sexual dimorphism (Aanes *et al*., 1998).

In addition to the effect of abundance and body mass, prey availability is affected by temporal and spatial distribution, habitat use, activity patterns and anti-predator behaviour (Sunquist & Sunquist, 1989). Vulnerability may thereby differ among sex, age classes and seasons (Owen-Smith, 2008). Young individuals in the exploration or dispersal phase may behave less predictably and thus experience lower predation rates (Mitchell & Lima, 2002). In addition, energetic expenditure and conspicuous behaviour may render adults of both sexes more vulnerable to predation during periods of heavy reproductive investment (e.g. Karanth & Sunquist, 1995; Owen-Smith, 2008).

The European roe deer *Capreolus capreolus* is the most abundant and widespread ungulate species in Europe (Andersen *et al*., 2007). Roe deer are often the main food source for the Eurasian lynx *Lynx lynx* in areas where the two species are sympatric (e.g. Jedrzejewski *et al*., 1993; Odden, Linnell & Andersen, 2006), and lynx predation is frequently the main natural cause of roe deer mortality (e.g. Jedrzejewski *et al*., 1993; Okarma *et al*., 1997). Lynx are solitary hunters that stalk prey using concealment from vegetation cover (Haglund, 1964). Because of the relatively small body size of roe deer in relation to lynx and the low sexual dimorphism in roe deer, lynx can potentially kill roe deer in all sex and age classes (Aanes *et al.*, 1998; Andersen *et al.*, 2007). From optimal foraging theory (Charnov, 1976), the lynx would therefore be predicted to select adult individuals due to their larger body mass. Nonetheless, because of their hunting technique, the low sexual dimorphism and small group sizes of roe deer, lynx may be expected to kill age and sex classes proportional to their availability in the standing population (Jedrzejewski *et al.*, 1993; Okarma *et al.*, 1997; Aanes *et al.*, 1998; Andersen *et al.*, 2007).

Few studies have examined whether lynx selection patterns for sex and age in roe deer vary between seasons. During summer, adult roe deer of both sexes allocate resources to reproduction, through territory establishment and lactation, respectively (Andersen *et al.*, 2000; Melis *et al.*, 2005). Hence, adult roe deer probably face a trade-off between reproductive activities and anti-predator behaviour (Lind & Cresswell, 2005) and may therefore have increased predation risk in summer (Owen-Smith, 2008). Furthermore, as lynx prefer to hunt in habitats of high roe deer suitability (Odden *et al.*, 2008), roe deer spending most time in less suitable habitats may have lower risks of predation. A particularly important component of the seasonal prey abundance is the recruitment of new calves in early summer, resulting in a numerical increase in prey and a prey category with small body size and a rapidly changing behaviour (Panzacchi *et al.*, 2008).

This study builds on the study of Andersen *et al.* (2007), but adds 12 more years of data from two more study sites. This large expansion of the dataset allows us for the first time to address life cycle effects in how Scandinavian lynx select roe deer. We examined whether lynx select different sex and age categories of roe deer, and if this pattern varies with season. We compared the sex and age structure of roe deer killed by lynx during summer and winter with the standing summer and winter population, respectively. Finally, we examined whether sex, age and reproductive status of lynx affect which sex and age classes they kill.

Material and methods

Study area

The data were collected in eight counties in south-eastern Norway (Fig. 1). The total study area was approximately 57 000 km^2, encompassing a north-south gradient in topography, habitat structure, climatic conditions and density of roe deer and lynx (see Nilsen *et al.*, 2009*a*,*b* for a habitat description). Lynx, red foxes *Vulpes vulpes* and humans are the main predators of roe deer throughout the study area. Using harvest rates as a proxy, roe deer occur in very low densities (0.005–0.6 shot per km^2 annually) in the north and with medium densities (<2.5 shot per km^2 annually) in the south (Nilsen *et al.*, 2009*b*; Statistics Norway, 2011). Lynx density is broadly constant across the study area and harvested in an annual hunt (Nilsen *et al.*, 2012). For the lynx in the study area, roe deer are the main food source, in addition to domestic sheep *Ovis aries* that are only available in summer (Odden *et al.*, 2006).

Figure 1 The study area in Hedmark, Oslo, Akershus, Østfold, Telemark, Buskerud, Oppland and Vestfold (57 000 km^2). The black points are locations of the 106 VHF- and GPS-collared lynx tracked from 1995 to 2010.

Collection of data

A total of 44 lynx were captured and equipped with VHF collars (Telonics Inc., E. Impala Avenue Mesa, AZ, USA) or GPS collars (Followit, Lindesberg, Sweden and Aerospace GmbH, Berlin, Germany) between 1995 and 2010. For further details regarding capture, immobilization and marking of lynx, see Arnemo *et al.* (2011). Searches for prey killed by VHF-marked lynx (n = 100) were carried out through intensive radio-tacking of focal lynx over a 10-day period (Nilsen *et al.*, 2009*b*). Kills by GPS-marked lynx (n = 54) were detected using the cluster method (Sand *et al.*, 2005; Mattisson *et al.*, 2010). During winter, we also made searches for kills by following tracks from unmarked lynx (Odden *et al.*, 2006).

A total of 244 roe deer carcasses were found in the study area between 1995 and 2010. Of these, 194 could be sexed and aged by tooth sectioning (Reimers & Nordby, 1968) and tooth eruption patterns. Of the 194 sexed and aged carcasses, kill date was known for 163 carcasses. Of these, 36 and 127 were killed during summer (01.06–30.11) and winter (01.12–31.05), respectively. Our definition of season was made based on the date of birth in roe deer, which is late May to early June in the study area (Linnell & Andersen, 1998; Panzacchi *et al.*, 2008). A total of 90 lynx-killed roe deer were found by following tracks from unmarked lynx. The remaining 154 carcasses (all with known sex) were killed by the 44 marked lynx. The date of the kills was known in 148 of these 154 kill incidents.

The lynx were categorized as juvenile (<2 years old) and adult (≥2 years old). The reproductive status at the time of the kill was defined as females with and without kittens. Kittens leave their mother around 30 March (20 February–1 May, n =

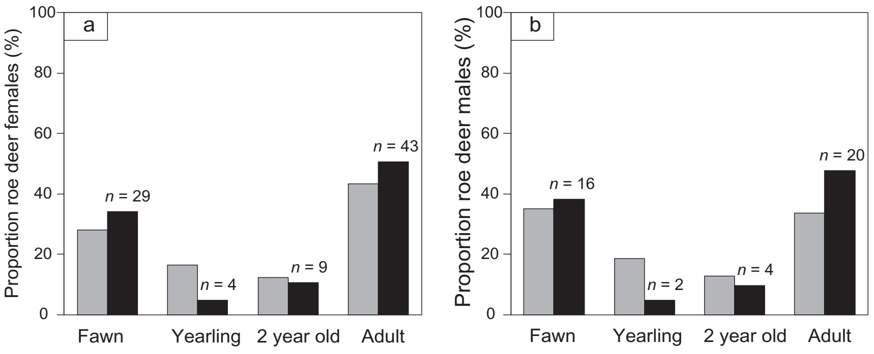

Figure 2 (a) Age distribution of female roe deer in the standing winter population (grey bars) and of female roe deer killed by lynx during winter, $n = 85$ (black bars). Number of killed females in each age category is given by *n* above the black bars. (b) Age distribution of male roe deer in the standing winter population (grey bars) and of male roe deer killed by lynx during winter, $n = 42$ (black bars). Number of killed males in each age category is given by *n* above the black bars.

21; Samelius *et al*., 2012). Accordingly, all female lynx that killed roe deer in April and May were defined as females without kittens.

Estimating the age and sex structure of the standing roe deer population

Demographic parameters used to estimate the standing sex and age distribution were based on survival and reproduction data from 300 VHF-marked roe deer in Hedmark, Akershus and Østfold (J. D. C. Linnell, unpubl. data). We assume that these animals are representative for the entire population because most individuals will visit winter feeding sites (our capture sites) after heavy snow fall. Survival rates were estimated for females and males in the age categories fawn, yearling, 2 years old and adult (>2 years old). In addition, fertility rates for females in the respective age categories were estimated from field controls of numbers of fawns born. The reason for pooling all age classes older than 2 years was due not only to limitations in the data but also that the survival and fertility rates of 2–8-year-old roe deer are relatively similar (Gaillard *et al*., 1993; Festa-Bianchet, Gaillard & Cote, 2003). We assumed a 1:1 sex ratio at birth. Based on the estimated survival and fertility rates, we constructed a post-breeding Lefkovitch matrix model using the population model $\mathbf{n}(t + 1) = \mathbf{A} \times \mathbf{n}(t)$ (Caswell, 2001). The standing sex and age distributions were calculated as a mean for the entire year: summer (01.06–30.11) and winter (01.12–31.05). The population in the beginning of the year was assumed to be given by the eigenvector w of the matrix, which gives the stable age distribution. We assumed no further births later in the year, so that the stable sex and age structure in each season could be projected from the structure of the spring population based on the estimated mortality rate for each sex and age category.

Statistical analyses

We analysed whether the lynx preys selectively on roe deer by comparing the sex and age distribution of lynx-killed roe deer with that of the standing population, using chi-square tests. By using lynx kill data on the sex and age categories of roe deer, we also examined whether the predation pattern was dependent on lynx sex, age and reproductive status. To do this, generalized linear models with Poisson distributions were fitted (McCullagh & Nelder, 1989). The analyses were performed using a backward elimination procedure (Crawley, 2007). Because of a relatively small dataset, we never fitted models with more than three variables. Both of the two variables – roe deer sex and age – were always included in the saturated models. To test whether the interactions were significant, we used analysis of variance and chi-square test (Crawley, 2007). We iteratively removed one two-way interaction from the saturated model. The model without the two-way interaction was then tested against the model containing all of the two-way interactions using likelihood ratio tests, as recommended by Crawley (2007, pp. 554–556). All matrix calculations and statistical analyses were performed in R 2.12.1 (R Development Core Team, 2010).

Results

Selection relative to the standing population of roe deer

Lynx predated selectively with respect to roe deer sex and age. Overall, they selected females over males [$\chi^2 = 6.41$, degrees of freedom (d.f.) = 1, $P = 0.011$] and adults rather than younger individuals ($\chi^2 = 33.13$, d.f. = 3, $P < 0.01$). Separate analyses for the summer and winter seasons showed that this pattern was dependent on season. During winter, lynx selected fawns and adults of both sexes. On the contrary, yearlings of both sexes were under-represented in the lynx-killed sample compared with their availability in the standing winter population [females: $\chi^2 = 9.54$, d.f. = 3, $P = 0.023$ (Fig. 2a); males: $\chi^2 = 7.28$, d.f. = 3, $P = 0.064$ (Fig. 2b)].

During summer, as in winter, lynx selected adults of both sexes. Contrary to winter, lynx selected yearling males, even to a greater extent than adult males in summer. Fawns of both sexes were under-represented in the lynx-killed sample compared with the availability of these during summer, in contrast to winter [females: $\chi^2 = 9.79$, d.f. = 3, $P = 0.020$ (Fig. 3a); males: $\chi^2 = 8.21$, d.f. = 3, $P = 0.042$ (Fig. 3b)].

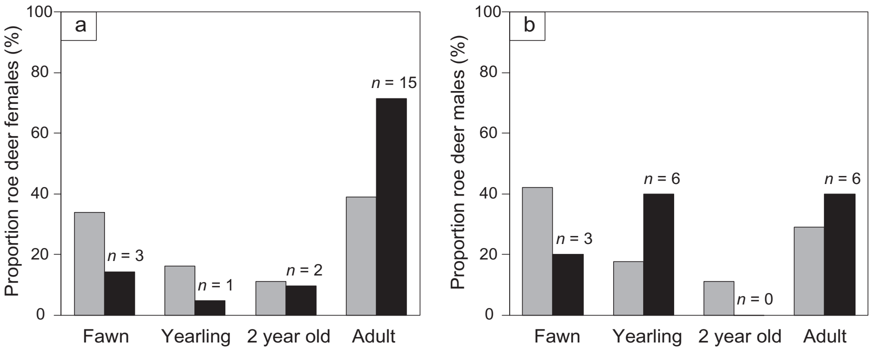

Figure 3 (a) Age distribution of female roe deer in the standing summer population (grey bars) and of female roe deer killed by lynx during summer, *n* = 21 (black bars). Number of killed females in each age category is given by *n* above the black bars. (b) Age distribution of male roe deer in the standing summer population (grey bars) and of male roe deer killed by lynx during summer, *n* = 15 (black bars). Number of killed males in each age category is given by *n* above the black bars.

Effect of lynx sex, age and reproductive status on roe deer kill rate

The predation pattern of male lynx in relation to roe deer sex and age was not different from that of female lynx (roe deer sex × roe deer age × lynx sex, $P = 0.130$). Neither was the predation pattern between the lynx sexes different when considering roe deer sex (roe deer sex × lynx sex, $P = 0.515$) and age (roe deer age × lynx sex, $P = 0.235$) separately. No difference was found in predation patterns between juvenile and adult lynx regarding both sex and age (roe deer sex × roe deer age × lynx age, $P = 0.998$) or only sex of roe deer (roe deer sex × lynx age, $P = 0.507$), although juvenile lynx tended to kill fawns and 2 year olds to a greater extent than adult lynx (roe deer age × lynx age, $P = 0.079$). Female lynx with and without kittens did not predate differently upon roe deer of different sex and age (roe deer sex × roe deer age × lynx reproductive status, $P = 0.249$). However, lynx without kittens tended to kill a larger proportion of females (roe deer sex × lynx reproductive status, $P = 0.074$) and a smaller proportion of adults (roe deer age × lynx reproductive status, $P = 0.083$) than lynx with kittens.

Discussion

Here, we demonstrate that lynx select roe deer of certain age and sex categories and that this pattern is dependent on season. Lynx selected fawns and adults of both sexes in winter, whereas yearlings of both sexes were selected against. During summer, adults of both sexes and yearling males were selected. The strong seasonal patterns in prey selection suggest that subtle mechanisms influencing variable encounter rates and vulnerability are involved. Here, we explore the potential causative mechanisms for these seasonal and life cycle-dependent patterns.

Yearling roe deer may be less predictable prey

According to optimal foraging theory, the most profitable prey would be the largest available that can safely be killed, all else being equal (Sunquist & Sunquist, 1989; Hayward *et al.*, 2006*a*, 2012). Lynx can safely kill roe deer in all sex and age classes (Aanes *et al.*, 1998; Andersen *et al.*, 2007), suggesting that they should select adult males and females year-round. We found that the lynx-killed roe deer of both sexes and all age classes and with a seasonal variation not predicted from optimal foraging theory. The most likely reasons for the observed selection pattern are therefore through differences in habitat use or behaviour of the different sex and age classes of roe deer (Molinari-Jobin *et al.*, 2004).

Young individuals were selected to a lower degree than adults and their accompanying calves in winter. The probability of lynx encounters, and consequently predation risk, is likely to be high on winter feeding sites (Holand *et al.*, 1998) and in habitats with high roe deer suitability (Odden *et al.*, 2008). Yearlings have a more explorative behaviour than older individuals (Van Moorter *et al.*, 2008) and may be expelled from winter feeding sites and high-quality roe deer habitats by older individuals (Espmark, 1974), resulting in lower encounter rates with lynx compared with adults and fawns.

Seasonality in the predation risk of fawns and male yearlings

Roe deer fawns lie hidden in vegetation and are relatively inactive during the first weeks of life (Linnell, Wahlstrøm & Gaillard, 1998). As lynx mainly hunt using sight and hearing (Kleiman & Eisenberg, 1973), the hiding strategy is probably an efficient anti-predator behaviour against lynx simply because the lynx has difficulty finding them. The fact that fawns often hide in open habitats such as meadows (Panzacchi *et al.*, 2010) may also discourage lynx from spending time in these areas while searching.

During the second summer of life, male roe deer either range widely in large home ranges or disperse from natal area (Wahlstrøm, 1994), driven by aggression from older males and a lack of ability to establish a territory (Wahlstrøm, 1994). Although we have argued that movements may reduce winter predation, these summer movements tend to be on such a scale that it takes the young male roe deer outside areas with which they are familiar; a factor known to be associated with increased predation risk (Clarke *et al.,* 1993), whereas the winter movements tend to be bounded within a more limited area (Andersen, Duncan & Linnell, 1998). Furthermore, roe deer are more dispersed during summer due to inclusion of high elevation areas (Mysterud, 1999). Lynx may therefore be expected to search for roe deer in a wider area during summer than winter. Hence, yearling movements may also increase the likelihood of being detected and encountered by lynx (Lima, 1998).

Adult roe deer may be more vulnerable in their reproductive season

In accordance with previous predation studies (e.g. Karanth & Sunquist, 1995; Owen-Smith, 2008), the selection of adults during summer may be due to reproductive activities. When defending territories and during the mating period, male adult roe deer have an increased level of activity and distraction (Hewison, Vincent & Reby, 1998). At the same time, they are highly spatially stable within their territories (Bideau *et al*., 1993). During summer, male adult roe deer may thus be both predictable and vulnerable when lynx are in close proximity. Equivalent to males, adult females have a stable use of area (Bideau *et al*., 1993). In addition, reproducing females go through an energy-demanding lactation period (Andersen *et al*., 2000), which may force them to adopt more risky tactics while feeding during summer. Increased vulnerability due to investment in reproduction may thus contribute to explain why adults are selected during summer.

Young lynx tend to kill more young roe deer – an effect of mutual inexperience?

We found that juvenile lynx tended to kill more fawns and female roe deer. Lynx may be less adept at capturing roe deer during their first phase of independence (Okarma *et al*., 1997). In that case, the lower ability of fawns to escape might be one explanation for the higher proportion of fawns killed by juvenile than adult lynx.

The results of this study suggest that lynx predate selectively on roe deer, and that the pattern is seasonal. This introduces a greater degree of subtly to our earlier results (Andersen *et al*., 2007) and may highlight the importance of considering seasonality and life cycles in studies of intraspecific prey selection patterns shown by such predators. Our explanations for these findings are rather speculative, but further studies of habitat selection and vulnerability of roe deer of different age and sex classes may add further light on the validity of these explanations.

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