

## **Selectivity of eurasian lynx *Lynx lynx* and recreational hunters for age, sex and body condition in roe deer *Capreolus capreolus***

Authors: Andersen, Reidar, Karlsen, Jørn, Austmo, Lars Bendik, Odden, John, Linnell, John D. C., et al.

Source: Wildlife Biology, 13(4) : 467-474

Published By: Nordic Board for Wildlife Research

URL: [https://doi.org/10.2981/0909-6396\(2007\)13\[467:SOELLL\]2.0.CO;2](https://doi.org/10.2981/0909-6396(2007)13[467:SOELLL]2.0.CO;2)

---

BioOne Complete ([complete.BioOne.org](https://complete.BioOne.org)) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at [www.bioone.org/terms-of-use](https://www.bioone.org/terms-of-use).

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

---

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

# Selectivity of Eurasian lynx *Lynx lynx* and recreational hunters for age, sex and body condition in roe deer *Capreolus capreolus*

Reidar Andersen, Jørn Karlsen, Lars Bendik Austmo, John Odden, John D.C. Linnell & Jean-Michel Gaillard

Andersen, R., Karlsen, J., Austmo, L.B., Odden, J., Linnell, J.D.C. & Gaillard, J-M. 2007: Selectivity of Eurasian lynx *Lynx lynx* and recreational hunters for age, sex and condition in roe deer *Capreolus capreolus*. - Wildl. Biol. 13: 467-474.

Data on the age, sex and condition of roe deer *Capreolus capreolus* killed by Eurasian lynx *Lynx lynx* and human hunters were collected in two study areas in the counties of Nord-Trøndelag and Hedmark in central and southeastern Norway, respectively. Data on the age and sex structure of the standing population were also collected. No differences in the age or sex structure of roe deer killed by lynx were found between the two study areas or between years with differing snow depths which was expected to affect age-class vulnerability. The profile of 151 lynx-killed roe deer (24% adult males, 44% adult females, 11% male fawns and 21% female fawns) was not statistically different from that of the standing population. In contrast, hunters killed a significantly larger proportion of adult animals, especially males (44% adult males, 28% adult females, 15% male fawns and 13% female fawns). The detailed age structure of lynx killed and hunter killed animals was not different within the adult age class. The body condition of roe deer declined during late winter (more so for males than for females), however, there was no difference in the condition of roe deer killed by lynx or hunters during early winter (the hunting season ends on 24 December). The overall picture is typical of a stalking predator that has few options to select individuals based on condition, age or sex in a prey species with no sexual dimorphism and which is relatively small in relation to the size of the predator (lynx are 50-70% the size of an adult roe deer). Human hunters, on the other hand, are clearly harvesting a non-random section of the population. The result is that hunting does not replicate natural predation, although lynx predation is likely to have a higher *per capita* impact on roe deer growth rates.

**Key words:** Eurasian lynx, harvest, hunting technique, predation, roe deer, selectivity

Reidar Andersen\*, Laboratoire Comportement et Ecologie de la Faune Sauvage de l'Institut National de la Recherche Agronomique, Chemin de Borde Rouge-Auzeville, B.P. 27, 31326 Castanet-Tolosan Cedex, France - e-mail: reidar.andersen@ym.ntnu.no

Jørn Karlsen, County Governor in Oppland, N-2626 Lillehammer, Norway - e-mail: jka@fmop.no

Lars Bendik Austmo, County Governor in Nord-Trøndelag, Environmental Protection Unit, N-7734 Steinkjer, Norway - e-mail: lau@fmnt.no

John Odden & John D.C. Linnell, Norwegian Institute for Nature Research, NINA, Tungasletta 2, N-7485 Trondheim, Norway - e-mail addresses: john.odden@nina.no (John Odden); john.linnell@nina.no (John D. C. Linnell)

Jean-Michel Gaillard, UMR CNRS 5558, Université Claude Bernard Lyon 1, F-69622 Villeurbanne Cedex, France - e-mail: gaillard@biomserv.univ-lyon1.fr

\*Present address: Norwegian University of Science and Technology, Museum of Natural History and Archaeology, N-7491 Trondheim, Norway

Corresponding author: Reidar Andersen

Received 28 January 2005, accepted 16 August 2005

Associate Editor: Henryk Okarma

Predation is one of the key factors potentially influencing the structuring components (e.g. age, sex and individual quality) in natural populations (Sih 1987, Lima & Dill 1990, Stearns 1992, Huggard 1993). Although two very different predator species may be functionally identical, it is important to know the specific effect on prey for each predator, as earlier studies (Sih et al. 1998, and references therein) have demonstrated that multiple predators have effects that cannot be predicted simply by summing the effects of each predator species. While it has long been assumed that predators select 'the old, weak and sick' members of prey populations (Mech 1970, Curio 1976) and that the degree of selection depends on the predators' hunting technique (Schaller 1972), modern day recreational hunters often select large trophy animals. Despite the fact that humans are the dominant ungulate predator in most temperate ecosystems, there have been few attempts to compare their selectivity with that of mammalian carnivores within the same ecosystem (see Ginsberg & Milner-Gulland 1994 for a tropical example).

The European roe deer *Capreolus capreolus* is the most widespread wild ungulate in Europe today, and it occurs mainly in areas where large mammalian predators are presently absent. However, in an increasing number of areas of sympatry predator-prey interactions between the Eurasian lynx *Lynx lynx* and the European roe deer are common. Although > 30 species are found in the diet of lynx (Jędrzejewska & Jędrzejewski 1998), roe deer constitutes up to 90% of the biomass in lynx diet (Jędrzejewski et al. 1993), and each lynx is estimated to kill 30-70 roe deer annually (Jobin et al. 2000; R. Andersen, unpubl. data). Earlier studies in Switzerland (Molinari-Jobin et al. 2002) indicated that roe deer does were most often killed, while studies in Poland (Okarma et al. 1997) indicated that roe deer

fawns and adults were killed in proportion to their occurrence in the population. In the latter study, the body condition of lynx-killed roe deer (measured as marrow fat content in 70 animals) was described as normal, indicating no selection for undernourished prey.

In our study we compare the age, sex and condition of roe deer killed by lynx and recreational hunters, and relate this to estimates of the status of the standing population. More specifically we predict that roe deer killed by lynx will represent a random section of the population (i.e. age, sex and body condition of prey will not be different from that of the standing population), whereas hunters will select adult males, i.e. a non-random section of the population.

## Material and methods

### Study areas

Data were collected from 13 different municipalities in two lynx study areas, situated in the counties of Nord-Trøndelag (64°N, 12°E) and Hedmark (61°N, 12°E), in central and southeastern Norway, respectively (see Sunde et al. 2000 and Odden et al. 2002 for detailed descriptions). All municipalities are situated within the boreal zone (Påhlsson 1984), with Norway spruce *Picea abies* dominating on areas of high productivity, and Scots pine *Pinus sylvestris* on areas of lower productivity. Both study areas have continental climates with warm summers and cold winters; average monthly temperatures ranging between 13°C and 19°C in July, and between -5°C and -11°C in January. Although snow depth varies annually, snow covers the ground from October/November to early May in both areas, reaching the maximum depth in March. Due to the relatively harsh winters, high harvest quotas,

and heavy predation pressure from lynx and red fox *Vulpes vulpes*, both study areas have relatively low densities of roe deer. Moose *Alces alces* occur at high densities and red deer *Cervus elaphus* occur in scattered populations in both areas. Semi-domestic (Nord-Trøndelag) and wild (Hedmark) reindeer *Rangifer tarandus* are found at higher elevations. In addition to roe deer, natural prey for lynx like mountain hare *Lepus timidus*, capercaillie *Tetrao urogallus*, black grouse *T. tetrix* and willow grouse *Lagopus lagopus* are found in all subareas.

Lynx have been continually present in both study areas, and the local populations were at the highest levels for almost a century during the study years (Brøseth et al. 2003). Both study areas are open to roe deer hunting. From mid-August until 25 September, hunting is restricted to bucks, but after 25 September hunting for all age classes is open. The season closes on 24 December. There is a quota limit on the total number of animals that can be killed, but generally not on either age or sex. Because of the broad similarities between both areas, various data sets from the two study areas were pooled for the current analysis.

### **Standing age and sex distribution of the roe deer population**

To assess the degree of hunter/predator selectivity we needed to estimate the age and sex structure of the standing roe deer population. In both study areas there is a high degree of seasonality, and roe deer show large seasonal variation in grouping behaviour and spatial distribution. During the snow-free season roe deer are spread out and maintain territories (bucks) and dispersed summer home ranges (does). In contrast, during winter roe deer often form groups (Holand et al. 1998) utilising artificial feeding sites or restricted habitats characterised by reduced snow accumulation (Mysterud et al. 1997). During this period it is possible to count the total number, age and sex of animals present. In the Hedmark study area Eide (1995) surveyed a total of 117 km of transects on skies, and showed that 82% of all roe deer tracks were < 800 m from an artificial feeding site. Furthermore, in the Hedmark study area almost all radio-collared roe deer ( $N > 100$ ) wintered at artificial feeding sites which allowed us to assume that the animals seen at feeding sites constituted the vast majority of the available animals, and therefore could be regarded as the best available estimate of the standing age and sex structure.

In January 1995 and 1996, we counted 123 and 101 animals, respectively, on 63 different feeding places in Hedmark. Of these 211 were sexed and 124 were divided into two age groups; fawns (< 1 year old) and adults (> 1 year old). The snow conditions varied substantially between the two winters. Data from three meteorological stations in the area (The Norwegian Institute of Meteorology) showed that in January 1995 the snow depth varied between 62 and 70 cm, whereas in January 1996 snow depth varied between 20 and 30 cm at the three stations. Such large annual variation in snow depth could potentially cause variation in habitat use among the various sex and age groups. However, as there was no evidence of between-year variation in sex and age distribution at the feeding places ( $\chi^2 = 0.258$ ,  $df = 3$ ,  $P = 0.968$ ) we pooled the data. Unfortunately it was not possible to collect such data from the Nord-Trøndelag study area.

### **Estimation of age and body condition of predated and harvested animals**

Lynx-killed roe deer were found by either 1) snow-tracking unmarked lynx until a roe deer kill was located, or 2) radio-tracking lynx until the movement pattern indicated that a kill had been made. The kills by radio-tracked lynx were not approached until the lynx had left, so as not to disturb the lynx. Only animals located during autumn and winter were used in the present analysis. Lynx-killed roe deer were collected in both the Hedmark and Nord-Trøndelag study areas. A total of 153 roe deer killed by lynx was found between September 1994 and May 1996. Of these, 151 could be aged (< 1 year old or > 1 year old) and sexed. In order to determine the exact age class of roe deer that were > 1 year old, we sectioned the incisors (Reimers & Nordby 1968) in 44 roe deer killed by lynx (during 1994-1996) and 53 roe deer killed by hunters (in 1995 only).

The femur was collected from 79 lynx-killed roe deer. From 23 of these animals we also collected the lower jaw. A portion of the bone marrow was removed from the white portion of the femur, avoiding the haemopoietic end arts of bones. Body condition was expressed as percentage fat and was analysed volumetrically using the Babcock method (Helrich 1990). As has previously been found for moose (Bergstrøm et al. 1986) and semi-domestic reindeer (Kjelvik 1997), we also found a close correlation between bone marrow fat content in the lower jaw and the femur in 23 lynx-killed animals

( $F = 52.92$ ,  $df = 1, 21$ ,  $P < 0.001$ ,  $R^2 = 0.72$ ). Consequently, we transformed values of fat content from the lower jaw in 46 animals harvested between October and December 1996, to femur values using the formula:

$$\text{Femur fat} = 0.682 * \text{lower jaw fat} + 19.83 \quad (1).$$

Age and sex structure of hunter-killed animals was collected from two sources. First, we collected harvest bag statistics from all the municipalities within both study areas. From these we were able to sex and age 6,074 roe deer shot during 1988-1997. In addition, jawbones were collected from hunter-shot animals so we could accurately age animals  $> 1$  year old for a more detailed look at age structure. These jawbones were collected from both the Hedmark and Nord-Trøndelag study areas.

## Results

### Temporal and spatial variation in prey selection

Despite the fact that environmental conditions varied considerably between the winters of 1995 and 1996, there was no evidence of between-year variation in sex and age distribution of lynx-killed animals ( $\chi^2 = 5$ ,  $df = 3$ ,  $P = 0.171$ ). There was also no significant difference in sex and age distribution of lynx-killed roe deer between the Nord-Trøndelag and Hedmark study areas ( $\chi^2 = 8$ ,  $df = 6$ ,  $P = 0.238$ ). Consequently, we pooled the data from both years and from both study areas for further analysis.

### Effect of age and sex

The age and sex structure of lynx-killed roe deer had a non-significant tendency to differ from that observed in the standing population ( $\chi^2 = 7.333$ ,  $df = 3$ ,  $P = 0.062$ ; Table 1). The minor discrepancy

in the structure could be ascribed, entirely, to a larger proportion of juvenile females (20.5 vs 11.4% in the standing population) and, to a lesser extent, to a smaller proportion of adult males (23.8 vs 32.7% in the standing population) in the lynx-killed sample.

Recreational hunters, on the other hand, shot a higher proportion of males (58.5%) and of adults (72.9%) than available in the population (45.0 and 69.4%, respectively;  $\chi^2 = 16.98$ ,  $df = 1$ ,  $P < 0.001$  and  $\chi^2 = 8.82$ ,  $df = 1$ ,  $P = 0.003$ , respectively). This was an effect of the fact that most animals were shot during the buck-only season, as the proportion of males shot during the ordinary hunting period was not significantly different from the standing sex distribution ( $\chi^2 = 0.86$ ,  $df = 1$ ,  $P = 0.354$ ). Among  $> 1$ -year-old animals for which exact ages were available there were no significant differences in age distribution between those killed by lynx and

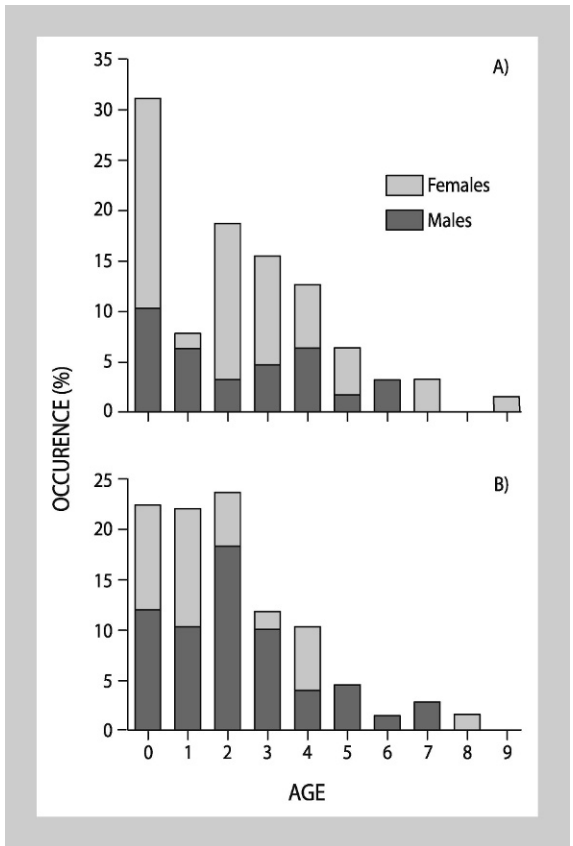


Figure 1. Sex and age distribution of roe deer killed by lynx (A; during the winters of 1994/95 and 1995/96) and hunters (B; in autumn 1995). Eighty roe deer killed by lynx were classified as fawns or adults, and 44 adults could be classified to exact age classes. The proportion of fawns killed by hunters was calculated from hunting records from the study area ( $N = 153$ ), whereas the age distribution of adults was calculated from samples sent in by hunters from the study area ( $N = 53$ ).

Table 1. Standing age and sex distribution of roe deer revealed by proportions seen on artificial feeding places during November-April ( $N = 246$ ; in addition there were 21 juveniles which could not be sexed), and proportion killed by lynx ( $N = 148$ ) and hunters ( $N = 6,074$ ) in 13 municipalities in central and south-eastern Norway.

	Juveniles		Adults	
	Males	Females	Males	Females
Standing age and sex distribution	0.123	0.114	0.327	0.436
Killed by lynx	0.113	0.205	0.238	0.444
Killed by hunters	0.145	0.127	0.441	0.288

those killed by hunters (Kolmogorov-Smirnov 2-sample test:  $Z = 0.973$ ,  $P = 0.30$ ; Fig. 1).

### Effect of body condition

There was no difference in femur fat content between juveniles (57.5%) and adults (60.9%;  $t = -0.907$ ,  $df = 114$ ,  $P = 0.366$ ). In roe deer killed by lynx there were significant interacting effects of month and sex; the femur fat content decreased from early (November) to late (April) winter at a much higher rate in males than in females (slope of  $-1.022$  and  $-0.057$  on an arcsine scale in males and females, respectively;  $t = 2.03$ ,  $P = 0.045$ ). From early November to the end of February, the femur fat content was quite constant and was not influenced by sex (between-sex difference of  $0.362$ ;  $t = 1.04$ ,  $P = 0.303$ ) or month (slope of  $-0.023$ ;  $t = 0.45$ ,  $P = 0.655$ ).

There was no significant difference in femur fat content between roe deer killed by lynx and roe deer shot by hunters in the period October-December ( $62.9 \pm 5.5$  ( $N = 10$ ) and  $63.4 \pm 9.1$  ( $N = 42$ ) for lynx-killed and hunter-killed roe deer, respectively;  $t = 0.16$ ,  $df = 50$ ,  $P = 0.88$ ).

## Discussion

According to our predictions we found that lynx killed a random section of the prey population. There was no selection of any sex or age category, and the body condition of lynx-killed and hunter-killed roe deer did not differ. Furthermore, among adult animals, specific age did not differ between roe deer killed by lynx and roe deer killed by hunters, however, hunters killed a disproportionately large proportion of adults, especially males.

Despite large environmental variation (e.g. snow depth), there was no temporal variation in prey selectivity. The mobility of roe deer is affected by snow depths of  $> 40$ - $50$  cm (Mysterud et al. 1997), but roe deer in the Hedmark study area did not change their habitat use, despite large annual variation in snow depth. Artificial feeding sites were heavily used in both years by all sex and age groups. Although roe deer reach about 70% of adult body size during their first winter (Andersen et al. 1998), we would expect the mobility of the youngest age class to be most affected by high snow accumulation. Although it is hypothesised that predators preferentially select young animals because they are less able to escape predation (Mech 1970, Curio 1976, Vitale 1989,

Karanth & Sunquist 1995), optimal foraging theory predicts that predators ought to choose the most profitable prey (MacArthur & Pianka 1966, Charnov 1976). For large predators the most profitable prey type would be the largest available prey that can safely be killed (Sunquist & Sunquist 1989). All adult lynx can safely kill any age and sex class of roe deer. Hence, if lynx were able to select specific categories of roe deer, adult animals would be over-represented. However, we will hypothesise that a stalking lynx will select its prey based on the actual position of the animal (e.g. lynx try to shorten the distance to the prey before attacking), and do not have time to pick out a particularly vulnerable animal like coursing predators (Fuller 1989, Bowyer 1987). This can explain why there was no temporal variation in prey selectivity (i.e. no difference between the years with different snow depth).

The age and sex structure of lynx prey was quite similar to the standing age and sex distribution (except for a higher occurrence of female fawns in lynx-killed roe deer), and the body condition did not differ between animals killed by lynx and animals killed by hunters. As it is unlikely that hunters will be able to judge the body condition of an individual animal, we expect that lynx select a random sample of animals within each sex and age group. The fact that there was no significant difference in the actual age of animals killed by lynx and hunters supports this conclusion. In contrast, in predator-prey studies involving coursing predators like wolves *Canis lupus*, it has been shown that the median ages for adult male and female prey were somewhat greater than for hunter-killed deer (Fuller 1989). The lack of such selectivity in this study can be attributed both to the fact that lynx is a stalking predator, i.e. select the prey that could be most easily approached, and to the facts that there are neither body size dimorphism or further age-related increases in body size in roe deer  $> 2$  years old (Andersen et al. 1998), making it impossible to select on either age or sex of animals based on body size alone. Thus, the pattern of lynx predation found in our study is broadly similar to those from the Jura mountains in Switzerland (Molinari-Jobin et al. 2002) and from Białowieża in Poland (Okarma et al. 1997).

Male biased predation has been found in several predation studies (e.g. Karanth & Sunquist 1995, Fitzgibbon 1990, Fitzgibbon & Fanshawe 1989, Poulle et al. 1993). Several explanations for the observed pattern are presented. Males are often soli-

tary, i.e. no group-shared vigilance (Taylor 1984), or in species that group specific spacing behaviours of the males may render them more vulnerable to predators, as observed in gazelles (Fitzgibbon 1990), even though the overrepresentation of male gazelles in the diet of African wild dogs *Lyacon pictus* was hypothesised to be caused by lower flight distances (Fitzgibbon & Fanshawe 1989). Furthermore, males roam widely during the rut, which increases the risk of encountering predators, or males may be hampered during escape because of their antlers or may suffer from intra-specific aggression-related injuries or post-rutting loss of condition (Karanth & Sunquist 1995). During winter, roe deer bucks are included in groups of animals surrounding artificial feeding places, where often matrilineal groups are developed (Holand et al. 1998), moreover, bucks have no antlers in winter. Consequently, bucks do not roam, are not solitary and share the same group vigilance as other animals. Furthermore, the highest level of territorial aggression in roe deer is in May; thus, aggression-related injuries in winter are less likely to affect escape from predators. This may explain the lack of male-biased predation in our study.

Results from studies of large carnivores reporting body condition of their prey are varied. Indications of heavy predation on old animals and animals in poor physical condition have been observed in some studies, e.g. African wild dogs preying on impala *Aepyceros melampus* (Pole et al. 2003), lynx preying on red deer fawns (Okarma 1984), or coyotes *Canis latrans* preying on mule deer *Odocoileus hemionus* and white-tailed deer *O. virginianus* (O'Gara & Harris 1988). In contrast, Poulle et al. (1993) found that coyote killed deer > 6 years old, however, most deer killed were in good physical condition. Mountain lions *Puma concolor* preying on mule deer and white-tailed deer often killed individuals in prime condition (O'Gara & Harris 1988, Huseman et al. 2003).

The relative vulnerability of ungulate prey species to solitary stalking predators may depend both on prey anti-predator behaviours and on prey size (Temple 1987). It is not surprising that a stalking predator like the mountain lion, nearly as large as its prey, can kill prey in good physical condition (Pierce et al. 2000), whereas lynx in Poland, being  $\frac{1}{3}$  the body size of red deer, select substandard individuals. At the same time, cooperative hunting, such as e.g. in coyotes, makes predators able to select animals in good body condition (Pierce et al. 2000).

Hence, the size of the stalking predator relative to its prey, and cooperative hunting in many coursing predators, may reverse the general patterns usually found in coursing and stalking predators.

In contrast to lynx, recreational hunters in our study showed clear selectivity for adult animals, especially males. This is in accordance with a study by Lentle et al. (2000), reporting that recreational red deer hunters in New Zealand shot a larger proportion of males (most bucks in the rutting season) and harvested a significantly greater number of older males, than compared to a random sample. Under most environmental conditions, both the mean and the variance of fitness components greatly differ among age and sex classes in populations of large herbivores (Gaillard et al. 2000), and the components most potentially influential for changing population growth show buffered temporal variation (Gaillard & Yoccoz 2003). While most populations can sustain quite high predation rates on juveniles, those populations decline quite rapidly when the annual survival rate of prime-age animals, especially females, decreases substantially (e.g. Kinley & Apps 2001, McLoughlin & Owen-Smith 2003). This indicates that recreational hunters could have the potential to affect population growth *per se* more than lynx, although their focus on males may buffer this impact. While extremely skewed sex ratios (low male percentage) have been shown to affect the reproduction of female moose (Sæther et al. 2003), there is no evidence that these effects occur in roe deer under the existing sex ratios. Given the current preference of recreational hunters to shoot trophy males it is actually lynx which kill the highest proportion of adult females (see also Molinari-Jobin et al. 2002). The fact that both lynx and recreational hunters selected animals in good physical condition, indicate that their effect on roe deer mortality is likely to be additive, i.e. increasing their potential effect on population growth rate. Because predator avoidance can potentially be costly, the manner in which roe deer make space use decisions to balance the relative risks of hunter versus lynx predation is an additional issue deserving attention before we can truly evaluate the relative numerical and selection impacts of lynx and hunters.

*Acknowledgements* - the data reported in this publication have been collected under the auspices of projects financed by the Norwegian Research Council, the Norwegian Directorate for Nature Management, the Norwegian Institute for Nature Research, the Offices of Envi-

ronmental Affairs from the counties of Nord-Trøndelag and Hedmark, the Norwegian Ministry of Defence and Hedmark University College, Evenstad, Norway. The authors are grateful to the many field workers who have assisted in data collection.

## References

- Andersen, R., Gaillard, J-M. & San José, C. 1998: Variation in life history parameters. - In: Andersen, R., Duncan, P. & Linnell, J.D.C. (Eds.); *The European Roe Deer. The biology of success*. Scandinavian University Press, pp. 285-307.
- Bergström, R.J., Cederlund, G.M., Stålfelt, F.V. & Dannel, K. 1986: Variability in mandible marrow fat in 3 moose populations in Sweden. - *Journal of Wildlife Management* 50: 719-726.
- Bowyer, R.T. 1987: Coyote group size relative to predation on mule deer. - *Journal of mammalogy* 51: 515-526.
- Brøseth, H., Odden, J. & Linnell, J. 2003: Minimum number of family groups, population estimate and population development in Norway 1996-2002. - Norwegian Institute for Nature Research Oppdragsmelding 777: 1-29.
- Charnov, E.L. 1976: Optimal foraging: The marginal value theorem. - *Theoretical Population Biology* 9: 129-136.
- Curio, E. 1976: The ethology of predation. - Springer Verlag, Berlin, 205 pp.
- Eide, N. 1995: Ecological factors affecting the spatial distribution of mountain hare, red fox, pine marten and roe deer in a southern boreal forest during winter. - M.Sc. thesis, Agricultural University of Norway, Ås, 46 pp.
- Fitzgibbon, C.D. 1990: Why do hunting cheetahs prefer male gazelles? - *Animal behaviour* 40: 837-845.
- Fitzgibbon, C.D. & Fanshawe, J.H. 1989: The condition and age of Thomson's gazelles killed by cheetahs and wild dogs. - *Journal of Zoology London* 218: 99-107.
- Fuller, T.K. 1989: Population dynamics of wolves in north-central Minnesota. - *Wildlife Monograph* 105: 1-41.
- Gaillard, J-M., Festa-Bianchet, M., Yoccoz, N.G., Loison, A. & Toïgo, C. 2000: Temporal variation in fitness components and population dynamics of large herbivores. - *Annual Review of Ecology and Systematics* 31: 367-393.
- Gaillard, J-M. & Yoccoz, N.G. 2003: Temporal variation in survival of mammals: a case of environmental canalization? - *Ecology* 84: 3294-3306.
- Ginsberg, J.R. & Milner-Gulland, E.J. 1994: Sex-biased harvesting and population dynamics in ungulates: implications for conservation and sustainable use. - *Conservation Biology* 8(1): 157-166.
- Helrich, K. 1990: Official methods of analysis of the Association of Official Analytic Chemists. Fifteenth edition. - AOAC, Inc., Arlington, Virginia, USA, 32 pp.
- Holand, Ø., Mysterud, A., Wannag, A. & Linnell, J.D.C. 1998: Roe deer in northern environments: physiology and behaviour. - In: Andersen, R., Duncan, P. & Linnell, J.D.C. (Eds.); *The European roe deer: the biology of success*. - Scandinavian University Press, pp. 117-138.
- Huggard, D.J. 1993: Prey selectivity of wolves in Banff National Park. II. Age, sex and condition of elk. - *Canadian Journal of Zoology* 71: 140-147.
- Husseman, J.S., Murray, D.L., Power, G., Mack, C., Wenger, C.R. & Quigley, H. 2003: Assessing differential prey selection patterns between two sympatric large carnivores. - *Oikos* 101: 591-601.
- Jędrzejewska, B. & Jędrzejewski, W. 1998: Predation in vertebrate communities: the Białowieża Primeval Forest as a case study. - Springer Verlag, Berlin, 450 pp.
- Jędrzejewski, W., Schmidt, K., Milkowski, L., Jędrzejewska, B. & Okarma, H. 1993: Foraging by lynx and its role in ungulate mortality: the local (Białowieża Forest) and the Palaearctic viewpoint. - *Acta Theriologica* 38: 385-403.
- Jobin, A., Molinari, P. & Breitenmoser, U. 2000: Prey spectrum, prey preference and consumption rates of Eurasian lynx in the Swiss Jura Mountains. - *Acta Theriologica* 45: 243-252.
- Karanth, K.U. & Sunquist, M.E. 1995: Prey selection by tiger, leopard and dhole in tropical forests. - *Journal of Animal Ecology* 64: 439-450.
- Kinley, T.A. & Apps, C.D. 2001: Mortality patterns in a subpopulation of endangered mountain caribou. - *Wildlife Society Bulletin* 29: 158-164.
- Kjølvik, O. 1997: Overlevelse og mortalitet av tamrein i et rovviltområde. (In Norwegian with an English summary: Survival and mortality in domestic reindeer in a large carnivore area). - Cand. Scient. thesis, Department of Zoology, Norwegian University of Science and Technology, Trondheim, 52 pp.
- Lentle, P.G., Stafford, K.J., Potter, M.A., Springett, B.P. & Dunning, D.W. 2000: An analysis of a recreational hunter's red deer tallies in the Tararua Ranges, North Island, New Zealand. - *New Zealand Journal of Ecology* 24: 11-18.
- Lima, S.L. & Dill, L.M. 1990: Behavioral decisions made under the risk of predation: a review and prospectus. - *Canadian Journal of Ecology* 68: 619-640.
- MacArthur, R.H. & Pianka, E.R. 1966: On the optimal use of patchy environment. - *American Naturalist* 100: 603-609.
- McLoughlin, C.A. & Owen-Smith, N. 2003: Viability of a diminishing roan antelope population: predation is the threat. - *Animal Conservation* 6: 231-236.
- Mech, L.D. 1970: The wolf - ecology and behavior of an endangered species. - Garden City, NY Natural History Press, 384 pp.



- Molinari-Jobin, A., Molinari, P., Breitenmoser-Würsten, C. & Breitenmoser, U. 2002: Significance of lynx *Lynx lynx* predation for roe deer *Capreolus capreolus* and chamois *Rupicapra rupicapra* mortality in the Swiss Jura Mountains. - *Wildlife Biology* 8(2): 109-116.
- Mysterud, A., Bjørnson, B.H. & Østbye, E. 1997: Effects of snow depth on food and habitat selection by roe deer *Capreolus capreolus* along an altitudinal gradient in south-central Norway. - *Wildlife Biology* 3(1): 27-33.
- Odden, J., Linnell, J.D.C., Moa, P.F., Herfindal, I., Kvam, T. & Andersen, R. 2002: Lynx depredation on domestic sheep in Norway. - *Journal of Wildlife Management* 66(1): 98-105.
- O'Gara, B.W. & Harris, R.B. 1988: Age and condition of deer killed by predators and automobiles. - *Journal of Wildlife Management* 52: 316-320.
- Okarma, H. 1984: The physical condition of red deer falling prey to the wolf and lynx and harvested in the Carpathian Mountains. - *Acta Theriologica* 29: 283-290.
- Okarma, H., Jędrzejewski, W., Schmidt, K., Kowalczyk, R. & Jędrzejewska, B. 1997: Predation of Eurasian lynx on roe deer and red deer in Białowieża Primeval Forest, Poland. - *Acta Theriologica* 42: 203-224.
- Påhlsson, L. 1984: Naturgeografisk regioninndeling av Norden. - Nordiska ministerrådet, Sweden, 510 pp. (In Swedish)
- Pierce, B.M., Bleich, V.C. & Bowyer, R.T. 2000: Selection of mule deer by mountain lions and coyotes; effects of hunting style, body size, and reproductive status. - *Journal of Mammalogy* 81: 462-472.
- Pole, A., Gordon, I.J. & Gorman, M.L. 2003: African wild dogs test the "survival of the fittest" paradigm. - *Proceedings of the Royal Society of London B* (Suppl), 270, S57.
- Pouille, M.L., Crête, M., Huot, J. & Lemieux, R. 1993: Prédation exercée par le Coyote (*Canis latrans*) sur le Cerf de Virginie, *Odocoileus virginianus*, dans un ravin en déclin de l'Est du Québec. - *Canadian Field Naturalist* 107: 177-185. (In French).
- Reimers, E. & Nordby, O. 1968: Relationship between age and tooth cementum layers in Norwegian reindeer. - *Journal of Wildlife Management* 32: 957-961.
- Roff, D.A. 1992: The evolution of life histories. Theory and analysis. - Chapman & Hall, 535 pp.
- Sæther, B.-E., Solberg, E.J. & Heim, M. 2003: Effects of altering sex ratio structure on the demography of an isolated moose population. - *Journal of Wildlife Management* 67(3): 455-466.
- Schaller, G.B. 1972: The serengeti lion: a study of predator-prey relations. - Chicago, University of Chicago Press, 480 pp.
- Sih, A. 1987: Predators and prey lifestyles: an evolutionary and ecological overview. - In: Keerlot, W.C. & Sih, A. (Eds.); *Predation: Direct and indirect impacts on aquatic communities*. - University Press of New England, pp. 203-223.
- Sih, A., Englund, G. & Woster, D. 1998: Emergent impacts of multiple predators on prey. - *Trends in Ecology and Evolution* 13: 350-355.
- Stearns, S.C. 1992: The evolution of life histories. - Oxford University Press, 249 pp.
- Sunde, P., Kvam, T., Bolstad, J.P. & Bromdal, M. 2000: Foraging of lynxes in a managed boreal-alpine environment. - *Ecography* 23: 291-298.
- Sunquist, M. & Sunquist, F. 1989: Ecological constraints on predation by large felids. - In: Gittleman, J.L. (Ed.); *Carnivore behavior, ecology, and evolution*. Cornell University Press, New York, pp. 283-301.
- Taylor, R.J. 1984: *Predation*. - Chapman and Hall, London, 166 pp.
- Temple, S.A. 1987: Do predators always capture standard individuals disproportionately from prey populations? - *Ecology* 68: 669-674.
- Vitale, A.F. 1989: Changes in the anti-predator responses of wild rabbits, *Oryctolagus cuniculus* (L.) with age and experience. - *Behaviour* 110: 47-61.