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Lynx *Lynx lynx* hunting in Norway is regulated through regional quotas according to the magnitude of predation on semi-domesticated reindeer *Rangifer tarandus* and domestic sheep *Oves aries*. Lynxes and semi-domesticated reindeer were studied using telemetry in an area in Nord-Trøndelag County, Norway, with high lynx predation on reindeer and domestic sheep and a high hunting pressure on lynxes. The probability of an ungulate killed by lynxes being livestock as opposed to a roe deer (the only alternative wild ungulate) increased with increasing distance from fields ($P < 0.0001$) and roads ($P < 0.0001$). Hunting was the only mortality cause found for radio-collared lynxes. The culling of lynxes was biased towards the vicinity of roads and cultivated fields compared with the general distribution of radio-collared lynxes ($P < 0.001$) and radio-collared semi-domesticated reindeer killed by lynxes ($P < 0.001$). Because of the easy location in rural areas due to the well-developed road system, lynxes suffered the highest hunting mortality in habitats where the proportion of livestock in the diet was lowest, whereas lynxes inhabiting alpine areas more than 3 km from the nearest road escaped hunting. The hunters' preference for hunting lynxes near roads leads to a risk of selective reduction in regions and habitats where lynxes do little harm, whereas numbers in remote areas with high predation on livestock may remain unaltered.

Key words: Lynx lynx, hunting, management, livestock, habitat, roads

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The Eurasian lynx *Lynx lynx* is widespread in northern Asia (Heptner & Sludskij 1972), but in Europe, outside Russia and Fennoscandia, it is divided into a number of relatively small, discrete populations (Nowell & Jackson 1996). The species is classified as vulnerable in Europe by IUCN (Nowell & Jackson 1996), so special consideration should be expressed in the management of the remnant populations in Europe. A factor complicating this management is that lynxes may be a pest to livestock. This may lead to regional or national political pressure for a reduction of lynx populations, e.g. as in Norway and Sweden, where lynx predation on semi-domesticated reindeer *Rangifer tarandus* has been an increasing problem for the native reindeer husbandry (Bjärvall, Franzén, Nordkvist & Åhman 1990, Kvam, Nybakk,

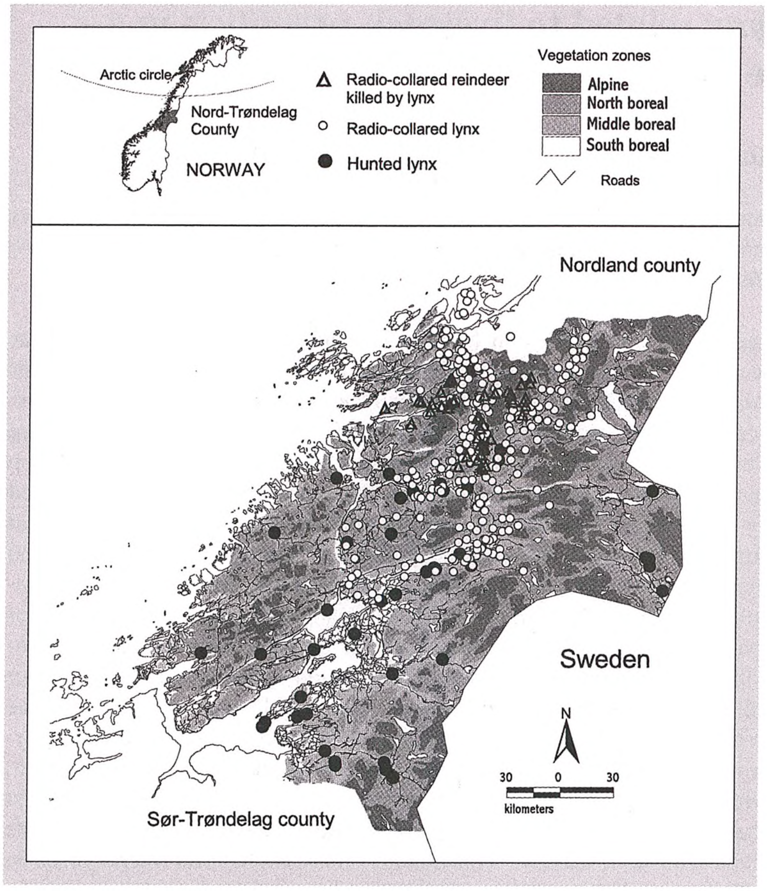

Figure 1. Nord-Trøndelag County with the spatial distribution of the radio-collared lynxes (only fixes obtained from fixed-wing aircraft from March 1994 through February 1997), the killings of lynxes in the hunting seasons 1996 and 1997 and the 49 radio-tagged reindeer killed by lynxes from May 1995 through December 1996. Almost all agricultural areas are found in the south boreal vegetation zone. Many of the dead-ending roads into northern boreal and alpine areas are closed by snow in winter when lynxes are hunted.

Overskaug, Sørensen & Brøndbo 1995). The Norwegian government has recently allowed a more liberal culling policy to control lynx predation on livestock, but has been met with international criticism (e.g. MacKenzie 1996).

Where lynx conservation through sustaining viable population sizes is to be optimised against the demands for population control, a sound management regime would be, whenever possible, to remove the economically most harmful individuals from a population. This paper presents data on lynx predation on livestock in a heterogeneous landscape and evaluates the efficiency of the present lynx management policy based on hunting quotas. First, we analyse in which habitats lynxes rely most on livestock as prey. Then, the impact of hunting pressure on the mortality is assessed from data on survival and death-causes of radio-tagged lynxes. Finally, we evaluate whether the lynxes are killed in the places where they generally occur or prey on livestock. In this context, special emphasis is placed on the occurrence of roads and habitation, since roads make lynxes accessible for hunters.

Study area

The study was carried out in Nord-Trøndelag County, Central Norway. Lynxes and semi-domesticated reindeer were studied using telemetry in the northern part of the county, with the centre of field activities located at 64°30'N, 12°20'W (Fig. 1). The total area, regularly used by the radio-collared lynxes during the three-year study (1994-1997), covered approximately 8,000 km^2 (see Fig. 1).

The topography is dominated by hills, reaching from the sea shore to a maximum elevation of 1,160 m a. s. l. The tree line is situated 300-400 m a. s. l. Permanent snow cover is usually present in the lowlands from the middle of November to the beginning of May. This period will, in the following, be referred to as the 'winter season'. The county is sparsely populated (6.1 persons per km^2). Cultivated fields cover 4.4% and coniferous woodland 32% of the total land area (data from the Norwegian Yearbook of Statistics 1993); the remaining land is primarily covered by alpine or subalpine vegetation. A well-developed grid of permanently open roads exists in the populated and cultivated areas, whereas most of the more elevated and less exploited areas are only sparsely intersected by roads (see Fig. 1) of which many are closed in winter.

Approximately $^3/_4$ of the lynx diet in this area consisted of ungulates: roe deer *Capreolus capreolus*, semi-domesticated reindeer and domestic sheep *Ovis aries*, independently of habitat and season (Sunde 1996). The roe deer expanded into the region in the 1940s (Østbye & Bjørnsen 1990) and are now abundant, though always associated with cultivated land.

Semi-domesticated reindeer range freely, primarily above the tree line, but seasonal migrations are controlled by the owners, the native Sami people. In summer, domestic sheep graze freely in the forests and lower alpine zones from the beginning of June to mid-September.

The density of lynxes was estimated to be 5.3 individuals per 1,000 km^2 in January 1996, or a total of 120 individuals in the county (Knutsen & Kjørstad 1996). Extensive and increasing losses of semi-domesticated reindeer and domestic sheep to lynxes were documented in the area (Knutsen & Kjørstad 1996, Kjelvik 1997). Accordingly, the county governor has permitted increased hunting quotas in an attempt to control this damage. Hence, the numbers of lynxes shot each year from 1994 through 1997 were 8, 12, 31 and 39. The hunting season is February and March, and hunting is free until the regional quotas are filled.

Material and methods

Collection of data

Data on free ranging lynxes were obtained from a telemetry study in the northern part of Nord-Trøndelag county, central Norway (see Fig. 1), lasting from January 1994 through March 1997. The study included 11 independently moving lynxes (Table 1), that were monitored regularly, daily whenever possible. Because the lynxes were much easier to locate with telemetry when occurring near roads than when residing in remote areas, only fixes obtained from tracking with fixed-wing aircraft were used to ensure an unbiased sample for the habitat use description. Ten radio-tagged lynxes contributed sufficient data (≥6 aerial fixes) to be included in the analysis.

A sample of killed roe deer and livestock (reindeer and sheep), found through radio-tracking and snow-tracking of lynxes, was used for comparison with the distribution of shot lynxes and for estimation of the roe deer/livestock ratio in the lynx diet. The detectability of carcasses in the field was probably equal among the three ungulate species, but the sampling suffered the same bias as did the telemetry data for lynxes in the vicinity of roads. Roe deer, however, occurred so close to farmland and roads that it is unlikely that the habitat distribution of carcasses led to serious biases. An unbiased sample of reindeer killed by lynxes was obtained in 49 reindeer (with mortality sensor transmitters) that were killed independently of each other from May 1995 through December 1996. The 49 reindeer originated from a telemetry study on reindeer mortality in the same area where the lynxes were studied (see Fig. 1). No unbiased sample existed for sheep, but the presumed bias would act conservatively against the null-hypothesis when tested against the distribution of shot lynxes.

The following parameters were used in the habitat/landscape analyses: distances from the nearest

Table 1. Periods of surveys and fates of radio-collared lynxes (M = male, F = female). Transmitter years are not calculated for juveniles (italics) accompanying adult females. Status: Juv = Juveniles, S.ad = Subadults, Ad = Adults (≥2 years.). Cause of termination: Technical = failure of radio transmitter, + = intact radio-transmitter by the end of the study.

Lynx	Status	Period of survey From	to	Transmitter years	Cause of termination	Fate
F1	Ad	16.01.94	11.04.94	0.81	Technical	Alive (Nov.1996)
		21.09.95[1]	19.04.96		Cub left[2]	
F2	S.ad	24.01.94	25.02.95	1.08	Technical	Shot (23.03.96)
F3	Ad	09.02.94	29.11.95	0.80	Technical	Shot (12.02.96)
M1	Ad	02.04.94	25.09.94	0.48	Shot	Shot illegally
F4	Ad	07.04.94	06.10.96	1.50	Technical	Alive (May 1996)
F5	S.ad/Ad	21.04.94	11.02.96	1.81	Shot	Shot
F6	S.ad/Ad	02.03.95	01.04.97	2.09	+	Alive (Apr. 1997)
M2	Ad	18.03.95	01.04.97	2.04	+	Alive (Apr. 1997)
M3	Ad	11.04.95	25.02.96	0.88	Shot	Shot
F7	*Juv*[3]	*14.09.95*	*11.02.96*	-	*Shot*	*Shot*
M4	*Juv*[3]	*14.09.95*	*11.02.96*	-	*Shot*	*Shot*
M5	S. ad[4]	21.09.95	03.03.97	0.87	Shot	Shot
M6	S. ad	04.05.96	01.02.97	0.75	Shot	Shot
M7	*Juv*[5]	*15.07.96*	*01.04.97*	-	+	*Alive (Apr. 1997)*

[1] An accompanying cub (M5) was radio-collared, whereby the adult lynx (defect transmitter) was monitored.
[2] Left its radio-collared cub (M5).
[3] Radio-collared cub in company with F5.
[4] Radio-collared cub in company with F1 from 21.09.95 to 19.04.96, after which it was left on its own.
[5] Radio-collared cub in company with F6.

cultivated field (DF) and permanently open road (DR), measured on 1:50,000 scale maps (M711 series: Statens Kartverk), and four broad vegetation zones, recorded with a Geographic Information System (GIS) (Arc Info ver. 2.1). The biome categories in the GIS-application were: 1) South boreal (spruce forest with some hardwood species), 2) Middle boreal (coniferous forest), 3) North boreal (low and open forest and shrub vegetation with birch and conifers) and 4) Alpine vegetation (subalpine shrub vegetation and alpine tundra). Agricultural land was primarily found in the south boreal vegetation zone, but was also represented in the middle boreal zone.

Analyses of data

The probability that a killed ungulate at a certain distance from cultivated fields or roads would be livestock (reindeer or sheep) vs a wild ungulate (roe deer) was modelled using logistic regression (Norusis 1994).

The mean survival of radio-collared lynxes, from radio-tagging until they were shot or censored, i.e. transmitter failure or study termination (see Table 1), was estimated with Kaplan-Meier analysis (Kaplan & Meier 1958, Norusis 1994). The possible effect of the median DR (Table 2) on lynx survival was tested using a Cox regression model (forward stepwise selection procedure, Norusis 1994).

The distributions of DR of shot lynxes versus reindeer killed by lynxes were tested using a two-sample randomisation test, where the difference between median values of the two distributions ($Diff_{median}$ = $Median_{reindeer}$ - $Median_{shot\ lynx}$) was used as test statistic, with P = 2 × the proportion of the randomised $Diff_{median}$ that was smaller than 0 (Manly 1997). To test whether lynxes were shot closer to roads than the general distribution of radio-collared individuals would indicate, a more conservative subset was made, where the distribution of the shot lynxes was tested against 5,000 re-sampled distributions, to which each of the 10 lynxes contributed with one randomly selected fix.

The four biome categories were ranked according to a north-south gradient, and the distribution of killed lynxes was tested with Mann-Whitney's U-test against the distributions of 1) radio-collared reindeer, 2) reindeer, 3) sheep and 4) roe deer found through the tracking of lynxes.

The conventional statistics were conducted with $SPSS_{WiN}$ ver. 6.2. The randomisation statistics were conducted with spreadsheet macros.

Results

Influence of habitat on the proportion of ungulates killed by lynxes

Fifty independent kills of roe deer, 19 of reindeer and 15 of domestic sheep were found when tracking the radio-collared lynxes. Roe deer were found much closer to cultivated fields (median distance = 88 m) and roads (median = 200 m) than were reindeer (DF; median = 1,100 m, DR; median = 1,500 m) and sheep (DF; median = 1,620 m, DR; median = 1,350 m) registered using the same methods.

The logistic regression equations of the probability that a killed cervid at a certain distance from fields or roads would be a reindeer vs a roe deer ($P_{reindeer}$) were Z_{DF} = 3.620(DF) - 2.847 (P = 0.0009) and Z_{DR} = 3.674(DR) - 3.668 (P = 0.0002), where $P_{reindeer} = e^Z : (e^Z + 1)$. The models correctly classified 88% (DF) and 90% (DR) of the observations to species. The effects of DR and DF on distribution of prey species

Table 2. Distribution of radio-collared lynx in relation to nearest cultivated field and nearest road as revealed by aerial tracking. Distances are also shown for the killing sites for six of the 10 lynxes that were shot later. N = number of aerial fixes.

		Distance from nearest field (km)				Distance from nearest road (km)			
			90 percentile				90 percentile		
Lynx	N	Median	Lower	Upper	Shot	Median	Lower	Upper	Shot
F1	29	0.3	0.1	2.3	-	0.6	0.4	2.8	-
F2	24	0.3	0.2	3.8	0.0	0.8	0.6	5.1	0.0
F3	31	1.5	0.4	3.5	0.5	0.9	0.4	4.2	0.5
M1	16	0.6	0.2	4.3	0.0	1.2	0.3	4.4	0.1
F4	34	3.6	0.4	9.6	-	3.6	0.1	9.8	-
F5	45	1.8	0.1	7.1	0.7	1.7	0.1	7.5	0.7
F6	32	0.7	0.1	3.5	-	1.1	0.1	3.9	-
M2	34	3.2	0.5	8.2	-	3.9	0.1	8.5	-
M3	28	0.6	0.1	3.0	0.8	0.7	0.1	2.7	0.8
M5	6	1.3	0.0[1]	2.8[1]	0.5	1.8	0.3[1]	3.3[1]	0.5

[1] Extreme values are given

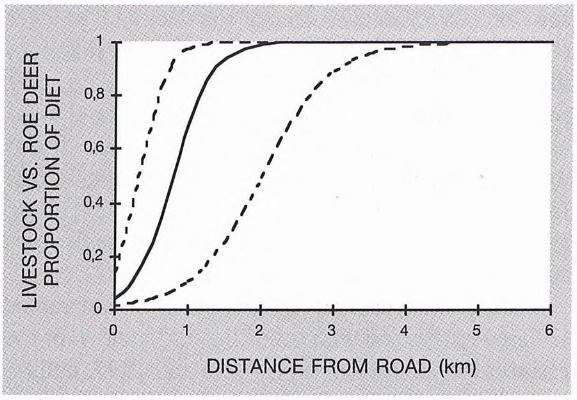

Figure 2. Logistic regression model of the probability that an ungulate killed by a lynx is livestock vs a roe deer (the only wild ungulate in the area preyed upon by lynxes) as a function of the distance to the nearest road. All carcasses where found by radio-tracking and/or snow tracking of lynxes. The thin dashed lines indicate the 95% confidence limits of the model estimate.

were highly interdependent; if both factors were entered in a forward selection procedure, the second factor had no additive effect on prey type ($P = 0.39$). The livestock (also including sheep) vs roe deer model further improved the significance of the effect of DF on prey type ($Z_{DF} = 4.436(DF) - 3.020$, $P < 0.0001$) and of DR ($Z_{DR} = 3.876(DR) - 3.052$, $P < 0.0001$) (Fig. 2).

Impact of hunting on lynx mortality

Five of 11 independently moving radio-collared lynxes died while their radio-collars were still in function (see Table 1). All deaths were due to hunting. Under the assumption that the five cases of mortality were representative for the rest of the population, hunting was responsible for at least 55% of mortality (one-tailed lower 95% confidence limit of a binomial expression for five cases of mortality by hunting vs zero cases of other mortality causes).

The annual survival rate of independently moving, radio-collared lynxes (N = 11) (see Table 1) was estimated to be 0.63 (95% confidence limits: 0.53-0.69) with Kaplan-Meier analysis. In a Cox regression equation, the effect of median DR (see Table 2) on survival time was not significant (one-tailed $P = 0.16$, $N = 10$). However, the test was weak due to the small sample size.

Locations of lynx hunts

Of 46 successful hunts, 44 were communally organised, while two of the lynxes were shot opportunistically, when observed near urban areas. The median linear distance between the spotting of the lynxes or lynx tracks and the location of the killing was 270 m for organised hunts. All hunted lynxes were located and shot within 3 km of the nearest road (Fig. 3).

The distribution of hunted lynxes was much more truncated towards roads than was the distribution of semi-domesticated reindeer killed by lynx ($Diff_{median} = 2.2$ km, $P \ll 0.001$) and the distribution of radio-collared lynxes (median $Diff_{median} = 1.2$ km, $P < 0.001$): a

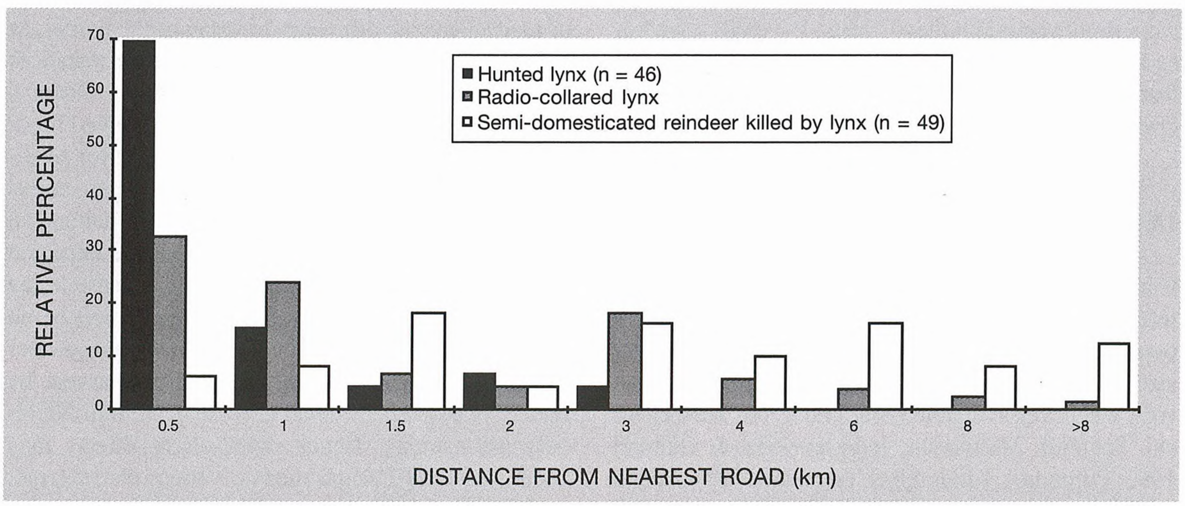

Figure 3. Percentage distribution related to distance between nearest road and location of track encounter of legal shootings of lynxes (N = 46), mean values of 5,000 subsamples of 122 aerial telemetry fixes from 10 radio-collared lynxes during the winter season (16 Nov. - 15 May) and radio-collared semi-domesticated reindeer (N = 49) killed by lynx. Each lynx contributed with one randomly selected fix to each subsample.

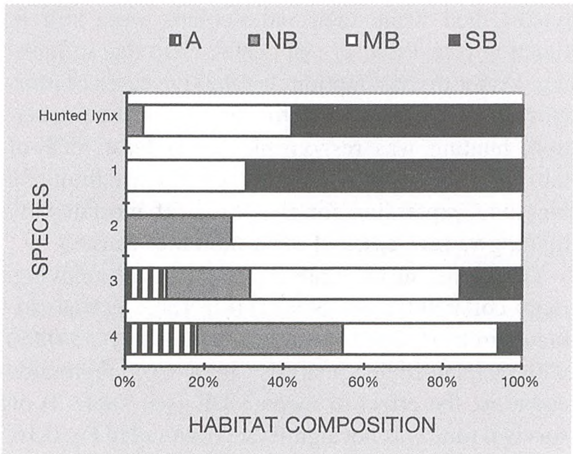

Figure 4. Vegetation zones of the sites where lynxes were shot (N = 46) compared with vegetation zones of killed 1) roe deer (N = 50), 2) domestic sheep (N = 16), 3) semi-domesticated reindeer (N = 19), all found by snow-tracking and radio-tracking lynxes and 4) radio-collared reindeer killed by lynxes (N = 49). The habitat distribution of hunted lynx is similar to the distribution of roe deer killed by lynxes (Mann-Whitney U-test, P = 0.202), but significantly different from the distributions of sheep and reindeer (Mann-Whitney U-tests, P < 0.001). Abbreviations for vegetation zones; A) alpine and subalpine vegetation, NB) north boreal vegetation, MB) middle boreal vegetation, SB) south boreal vegetation.

lynx faced a risk of being shot approximately 2.1 times higher than average within 1/2 km from a road, whereas it escaped hunting if it was more than 3 km from the nearest road (see Fig. 3).

When ranking the habitat according to biome category (Fig. 4), both sheep and reindeer were generally found in more 'northern' zones than where lynxes were shot (Mann-Whitney U-tests; P < 0.001), whereas habitat distribution of roe deer was equal to the distribution of hunted lynxes (Mann-Whitney U-test; P = 0.202).

Discussion

Currently, the economic losses due to predators are introduced into management strategies of carnivore population sizes (Boman 1995). Small or medium-sized ungulates form the base prey for the European lynx whenever available (Haglund 1966, Jedrzejewski, Schmidt, Milkowski, Jedrzrejewska & Okarma 1993, Pulliainen, Lindgren & Tunkkari 1995) and the ungulate-to-small-game proportion of the lynx diet has been found to be the same between different habitats within the study area (Sunde 1996) and between different regions in Norway and Sweden, in spite of varying occurrences of roe deer and reindeer (Haglund 1966, Sunde & Kvam 1997). It is therefore likely that the daily consumption of ungulate meat per lynx is the same in all habitats. An optimal management strategy to limit livestock losses should therefore be, whenever possible, to remove lynxes from the remote pastures, where no wild ungulates are available rather than from cultivated landscapes where roe deer form the stable prey.

With hunting causing all known deaths of radio-collared lynxes and with the killing of 1/4 and 1/3 of the estimated lynx population in 1996 and 1997, culling was undoubtedly the most important factor controlling population density during the study period. Hence, the annual survival obtained from hunting statistics was lower than previously estimated (0.71) for Norwegian lynx populations (Kvam 1990), even though radio-collared individuals were spared by hunters on several occasions and therefore survived better than untagged lynxes in the same habitats. No significant effect on survival was found of the median distance to roads, but the test had low power due to the very small sample size.

The finding of increased man-induced mortality in carnivores in the vicinity of roads is not new (e.g. McLelland & Shackleton 1988, Mech 1989, Ferreras, Aldama, Beltrán & Delibes 1992, see also Weaver, Paquet & Ruggiero 1996). In this case, however, a high hunting pressure was permitted in order to control lynx predation on livestock. Hunters locate lynxes by patrolling the accessible roads by car for crossing tracks. Areas with a well-developed system of roads therefore offer easy locating of the lynxes, as also indicated by the generally short linear distances between the spotting and shooting points. From a management point of view, this habitat-skewed hunting is unfortunate, because it entails a risk for selective culling of the 'wrong' animals. If the open quotas are increased to reduce the general level of damage to reindeer husbandry, it is furthermore to be expected that the general hunting pressure will increase in the habitats adjacent to roads, whereas there will be no effect in the remote areas. The possible consequences to lynx occurrence of this unbalanced harvest by habitat will depend upon the flow of individuals between habitats. Hence, inexpedient effects may occur, if the landscape mosaic varies over a larger scale than does the home range size of reproducing females, or if single individuals develop specific habitat preferences. It is therefore recommended that the hunting mortality of individuals occupying different habitats be targeted by future studies of lynx populations in heterogeneous landscapes. If management authorities adopt a culling policy based on an open quota system in heterogeneous landscapes, local differences in road access and livestock damage should be considered. Accordingly, the effect of hunting on lynx numbers in different areas and habitats should be monitored.

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