Risk taking by Eurasian lynx (*Lynx lynx*) in a human-dominated landscape: effects of sex and reproductive status

N. Bunnefeld[1], J. D. C. Linnell[2], J. Odden[2], M. A. J. van Duijn[3] & R. Andersen[4]

1 Animal Ecology Group, University of Groningen, The Netherlands
2 Norwegian Institute for Nature Research, Trondheim, Norway
3 Department of Sociology/Statistics & Measurement Theory, University of Groningen, The Netherlands
4 Department of Biology, Norwegian University of Science and Technology, Trondheim, Norway

Abstract

This study aimed to test how the sex and reproductive status of Eurasian lynx influenced their use of 'attractive sinks' – habitats with high prey density and high mortality risks. Locations of 24 Eurasian lynx *Lynx lynx* were obtained by radio-telemetry in a mixed forest and agricultural habitat in south-eastern Norway. Roe deer, the major food source of lynx in the study area, occurred at higher densities closer to areas of human activity and infrastructure. Proximity of lynx locations to human activity and infrastructure was used as a risk index because the most common causes of death among Scandinavian lynx were of anthropogenic origin. This study shows that distances from lynx locations to human activity were significantly greater for females with newborn kittens than for males, but this decreased with kitten age. The data suggest that this response to human activity is influenced by the reproductive strategies of males and females, and might explain male-biased human-induced mortality in this study and in carnivores more generally.

Introduction

The distribution and abundance of prey has an important influence on carnivore spatial distribution (Sunquist & Sunquist, 1989). Prey may be distributed randomly, evenly or clumped, and this affects the spatial decisions made by carnivores (Davies & Houston, 1984). Habitat choice is likely to be influenced by mortality risk as well as prey abundance and distribution. Interspecific killing among mammalian carnivores has been reported in felids, canids and mustelids (Palomares & Caro, 1999). To decrease the chance of becoming prey, carnivores may avoid habitats with high densities of larger predators. For example, European genets *Genetta genetta* and European mongooses *Herpestes ichneumon* avoid suitable habitats where Iberian lynx *Lynx pardinus* are common (Palomares *et al*., 1996). From the point of view of large carnivores in the modern world, humans represent by far the most dangerous intraguild predators. People are generally the most common cause of death among large carnivores both inside and outside protected areas (Woodroffe & Ginsberg, 1998). From the point of view of reducing mortality risk, large carnivores should avoid areas of high human activity.

However, avoiding mortality risk must be balanced against foraging efficiency. In some systems (such as tropical forests), the density of prey may be greatly reduced close to areas of human activity (Robinson & Bennett, 2000). In such a setting, there should be no trade-off between mortality risk and prey availability. However, in Europe and North America some cervid species, which are the main prey of large carnivores, may occur at higher density in areas where humans have modified the habitat, or provide supplementary food (McShea, Underwood & Rappole, 1997). In such cases there may be a clear trade-off between mortality risk and foraging efficiency, and areas associated with human activity may represent 'attractive sinks' (*sensu* Delibes, Goana & Ferreras, 2001). From the theory of sexual selection, males are expected to take greater risks than females in polygynous and dimorphic species (Trivers, 1985). Theory and data indicate that variation in lifetime reproductive success is greater among males than among females, with high numbers of offspring sired by a few males and no offspring for most of the males (Payne, 1979; Clutton-Brock, Guiness & Albon, 1982). Variation in reproductive success among males can be due to differences in body size or condition, and any deficiency in physical condition can have negative effects on their reproductive success (Clutton-Brock, Albon & Guinness, 1988). Studies on large mammals, including carnivores, have also shown that males are more likely to get into conflict with people (Sukumar, 1991; Linnell *et al*., 1999; Odden *et al*., 2002). However, the high

costs of feeding dependent young (Oftedal & Gittleman, 1989), both during lactation and especially during the period when the young's energy demands increase but predatory skills are not developed, are likely to attract females to areas of higher foraging efficiency. Thus, sex and reproductive status are likely to influence the trade-offs that an individual faces.

In this study, we investigated the extent to which the forest and farmland matrix habitats of south-eastern Norway represent an attractive sink for Eurasian lynx *L. lynx*, and how sex and reproductive status influence lynx decision making in relation to mortality risk. Research in Scandinavia has shown that the most common cause of death among radio-collared Eurasian lynx is of anthropogenic origin (legal harvest, poaching, vehicle collisions; Andersen *et al.*, 2003; Andrén *et al.*, 2006), and earlier studies from central Norway indicate that this mortality is closely linked to lynx proximity to areas of human activity (Sunde, Overskaug & Kvam, 1998*a*). Roe deer *Capreolus capreolus* represent the main prey of lynx in southern Norway (Birkeland & Myrberget, 1980; Andersen *et al.*, 1998) and are closely associated with human modified landscapes and the presence of agricultural land (Mysterud, Bjørnsen & Østbye, 1997; Mysterud, 1999; Sunde *et al.*, 2000).

In this analysis we investigate the hypotheses that
(1) high roe deer densities are related to areas of human activity,
(2) lynx mortality is closely related to areas of human activity,
(3) sex and reproductive status influence habitat use by lynx in a human-modified environment, where males are found closer to human activity than females, especially when followed by vulnerable young, and
(4) females with dependent young decrease distances to human activity when family food demand increases, whereas males do not alter their spatial strategy over the year.

Materials and methods

Study area

The study was conducted in south-eastern Norway in the counties of Hedmark, Akershus and Østfold between 1995 and 2002. The study area (14 000 km^2) ranges between 0 and 300 m above sea level in the southern part and along north–south running valleys with hills (200 up to 900 m above sea level) further north. The study area is dominated by boreal forest, mainly Norwegian spruce *Picea abies* and Scots pine *Pinus sylvestris*, and is intensively managed for timber and pulp. Agricultural land is confined to strips along valley bottoms and constitutes less than 5% of the total area (Fig. 1). In south-eastern Norway, lynx diet is mainly based on roe deer *C. capreolus*, but mountain hares *Lepus timidus* and various species of birds are also eaten (Birkeland & Myrberget, 1980; Andersen *et al.*, 1998). Population density in the study area, measured on 1 January 2002, was between 7 people km^{-2} in remote areas and 104 people km^{-2} closer to the city of Oslo (Statistics Norway, 2002, www.ssb.no). Lynx are subject to a quota-regulated harvest throughout the study area within an annual season from 1 February to 30 April. Harvest is mainly based on hunting teams tracking and circling lynx – with most hunts beginning from where a lynx track is detected in the snow, usually close to a house or when crossing a road. In some cases box traps, usually located close to houses or roads, are used. In addition to legal harvest, poaching is widespread, peaking in the late summer and autumn (Andrén *et al.*, 2006).

Roe deer distribution

Although pellet group counts of ungulates have been criticized for giving imprecise results of abundance estimates (e.g. Smart, Ward & White, 2004), this technique has been used successfully to estimate the distribution and relative
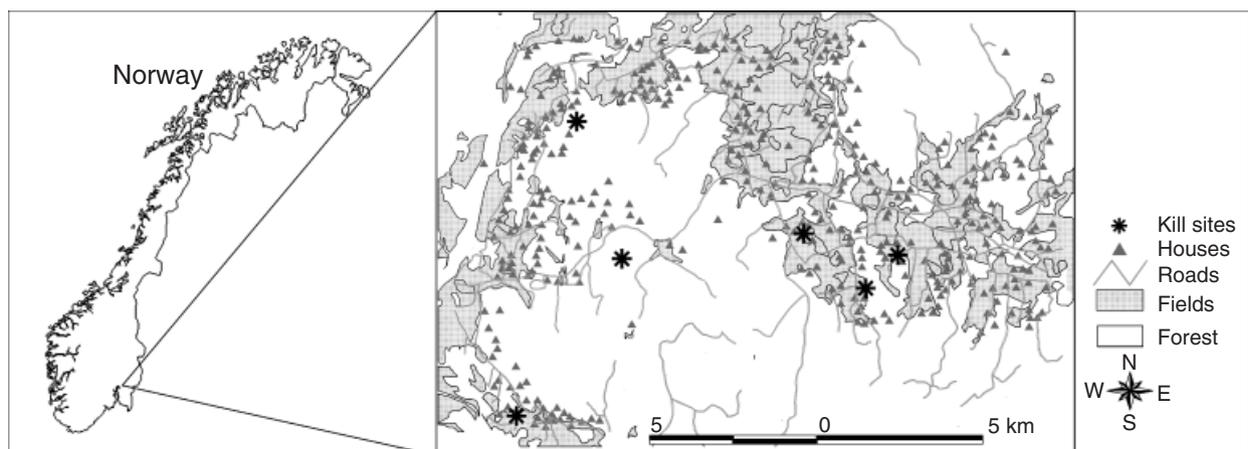

Figure 1 Representative part of the study area in south-eastern Norway illustrating the distribution of lynx kill sites within the human-dominated landscape, including occupied houses, agricultural fields, daily-used roads and forest.

abundance of ungulates (Borkowski, 2004) and has been shown to obtain good quality results to describe habitat use when compared with radio-telemetry data (Guillet *et al.*, 1995). The pellet group counts mainly reflect autumn–winter–spring distribution of roe deer (outside the growing and decomposition seasons). Some roe deer in all areas showed small-scale seasonal movements (based on unpublished telemetry data) such that the summer distribution may have been slightly more dispersed than the winter picture indicates; however, we assume that the overall pattern is representative of spatial variation in density over the year.

The distribution and relative abundance of roe deer were determined by conducting 16 transect counts for pellet groups in spring 2002 in southern Norway (counties Akershus and Østfold). Faecal pellet groups were counted by walking a 2 km long and 1 m wide transect line in a right angle away from an agricultural field. A pellet group was defined as three or more pellets from the same defecation. The number of pellet groups per 250 m was recorded. The number of pellet groups for the first 250 m was compared with the number of pellet groups found between 251 and 2000 m. The data were analysed with an analysis of variance, with distance to the field, observer and transect number as fixed factors.

A further faecal pellet group count was conducted in spring 2000 in the county of Hedmark. We distributed a series of fifty-eight 1 km^2 sample areas along the main valley systems. Within each sample area, forty 10 m^2 plots were searched for all roe deer pellet groups which were summed to represent the 1 km^2 sample area, for which a number of parameters were estimated, including the distance to the nearest agricultural field, percentage of fields within the sample area, number of houses and number of artificial feeding sites within the sample area. In a multiple regression analysis the effects of these parameters were investigated, identifying those providing most explanatory power in a backward selection procedure.

A square root transformation of all roe deer pellet count data was carried out as suggested by Zar (1999). All roe deer data were analysed using the computer package R (R Development Core Team, 2004).

Capturing lynx

In connection with a long-term and multifaceted project on lynx ecology, lynx were captured and equipped with radio-collars (<150 g, or less than 1% of an adult female) using a variety of techniques between 1995 and 2002. Adult lynx were trapped with box traps constructed in wood or metal mesh and with spring-loaded wire foot snares (Nybakk *et al.*, 1996). Animals were often recaptured using the same techniques, with trained dogs or darting from a car or helicopter. All adult animals were immobilized using a mixture of ketamine (100 mg) and medetomidine (4 mg), reversed with atipamezole (5 mg); juveniles received a half dose. All drugs were provided intramuscularly by hand, blow-pipe or gas-powered darting rifle. Neonatal kittens were also captured (by hand) at natal lairs and were

equipped with implanted transmitters (Arnemo *et al.*, 1999). All procedures were approved by the Norwegian Experimental Animal Ethics Committee, and permits for wild animal capture were obtained from the Directorate for Nature Management. Only three mortalities occurred because of capture. Two of these were through trauma associated with the use of leg snares and the one darted from a vehicle suffered a reaction to the drugs. No complications were ever detected as a result of collaring or implanting. Capture techniques and animal handling are described in more detail in Herfindal *et al.* (2005). Radio-collars were not removed, because (1) most lynx in Norway, including our study animals, die within a few years of initial capture through legal or illegal hunting, and (2) wherever possible animals are recollared when needed and maintained within the study, which is still ongoing.

Radio-tracking

Positions of radio-collared lynx were determined by radio-tracking from the ground and air. All positions tracked between 9:00 and 17:00 h with a location error of 100 m or less were classified as day lairs. Lynx day lairs are generally not more than 3 km from the kill if they return the next night (Øvrum, 2000). After five consecutive nights, the carcass is usually finished and the lynx move on. To avoid possible dependence between day lairs from the same kill, we used only day lairs that were at least 5 days or >3 km apart. Therefore, all of the 349 day lairs used in the analysis can be regarded as being independent from each other for analysis of spatial patterns.

Roe deer killed by the radio-collared lynx were found during intensive radio-tracking periods (Odden *et al.*, 2002). We located kills using telemetry points where lynx were stationary for more than 1 h. To avoid disturbance, we searched for kills after the lynx had left the area and spent at least one night and one day in another part of its home range. The exact positions of 153 carcasses killed by radio-collared lynx were determined by means of GPS. All these kills can be regarded as being independent from each other for analysis of spatial patterns as we had no cases of multiple killing.

The reproductive status of a female was determined by the presence of dependent young. At the end of May/beginning of June, lynx females give birth to one to three kittens. The den was localized by directly approaching the radio-collared female and the location where kittens were observed was determined as the den site.

Lynx distance analysis

We have used two indices of lynx habitat use. Firstly, we used the location of day lairs where lynx typically remain inactive during the daylight hours. Secondly, we used the locations of roe deer that have been killed by lynx. A roe deer kill is usually consumed over 3–5 days, and is normally visited for 1–2 h in the evening.

Shortest, straight-line, distances from roe deer kill sites and day lairs to various indices of human development were calculated using ESRI ArcView, extension nearest feature v.3.6c (Jenness, 2003). For every day lair and kill site, the distance to the nearest occupied house, agricultural field and daily-used road was calculated using maps with a scale of 1:250 000. Roads included highways, municipal roads and private roads. The effects of sex and reproductive status on distances to human development were analysed using multi-level modelling (computer package MLwiN v.1.10.0007 by Rasbash *et al.*, 2001). Multilevel models consider the nested structure of the data: distance measurements made at various times during the reproductive year (level 1) are nested within individual lynx (level 2). An important advantage of the multilevel approach is that incomplete and unbalanced data sets of repeated measures can be analysed. In this case, the number of observations and the time period for which they were recorded varied with individual lynx. The resulting model is also known as a mixed model, where sex and reproductive status are fixed factors and the individual lynx is a random factor. Because data were collected over an 8-year period, data were also nested within years, resulting in a more complex cross-nested model of observations belonging to both lynx and years. Because in such a cross-nested model no significant effect was found for the variance associated with years and only small changes in the estimates of the parameters of interest (the same was found in a two-level model with fixed year effects), year was not included in the final model. Thus, a straightforward two-level model with main effects and interaction effects was used for testing the effects of sex and reproductive status. The significance of differences in distances at the beginning of the reproductive year between males, females without kittens and females with kittens was tested with a likelihood ratio or deviance test. Such a test compares the full model with different parameters for the three groups and a reduced model where parameters have been set equal for all groups or for two of the three groups. The difference in deviance (a relative fit measure) between both models is equivalent to a likelihood ratio test statistic following a χ^2 distribution with the number of restricted parameters as the degrees of freedom. The significance of the effect of distance for the groups of males, females with kittens and females without kittens was tested with a two-tailed *t*-test. The significance of differences between the effects of distance per reproductive group was compared using a deviance test as described before.

The present data set includes 153 locations of roe deer carcasses killed by adult (>2 years) radio-collared lynx, this group comprising eight individual males and 11 individual females (Table 1). The data set also includes 349 temporally independent day lairs from 10 individual males and 14 individual females (Table 1). Only adult lynx (>2 years) were used in the analysis. The start of the reproductive year for the model was set at 20 May, when the first females give birth.

Adult lynx shot during the yearly quota hunt between 1995 and 2002 were recorded for the study area. The

Table 1 Number of kill sites and day lairs for individual males [M1–10 (a)] and females [F1–14 (b)]

(a) Id/#	Kill site	Day lair
M1	3	20
M2	4	8
M3	16	28
M4	–	5
M5	4	13
M6	3	17
M7	4	10
M8	5	21
M9	5	15
M10	–	2

(b) Id/#	Kill site (–)	Kill site (+)	Day lair (–)	Day lair (+)
F1	8	1	1	–
F2	8	–	11	2
F3	0	12	2	10
F4	1	11	–	24
F5	–	–	9	3
F6	6	11	12	31
F7	3	7	6	32
F8	–	4	2	3
F9	10	3	3	13
F10	–	–	6	5
F11	–	–	1	–
F12	9	7	4	15
F13	3	–	4	–
F14	1	4	2	9

For females the total number of kill sites and day lairs is also broken down by reproductive status: without kittens (–) and with kittens (+).

distances between locations where 40 females and 64 males were shot and the nearest house, field or road were calculated with ArcView as described above for the calculation of kill sites and day lairs. Additionally, we used ArcView to calculate distances between 1000 random locations within the study area and occupied houses, agricultural fields and daily-used roads.

Results

Roe deer distribution

The transect counts conducted in southern Norway showed that roe deer were clumped around agricultural fields (Fig. 2). Pellet density was highest close to agricultural fields (<250 m) and was lower further away from agricultural fields (250–2000 m) ($F = 37.513$, d.f. $= 1$, $P<0.001$). There was no effect of observer ($F = 0.3864$, d.f. $= 2$, $P>0.5$) in a first model approach. Observer was then excluded; transect was included in the model, but transect also had no significant effect on the roe deer pellet distribution ($F = 0.796$, d.f. $= 15$, $P>0.5$).

The faecal pellet count in Hedmark showed that the number of roe deer pellets increased with percentage cover of fields ($t = 3.326$, d.f. $= 55$, $P<0.01$) and number of artificial feeding sites ($t = 2.586$, d.f. $= 55$, $P<0.05$) in the
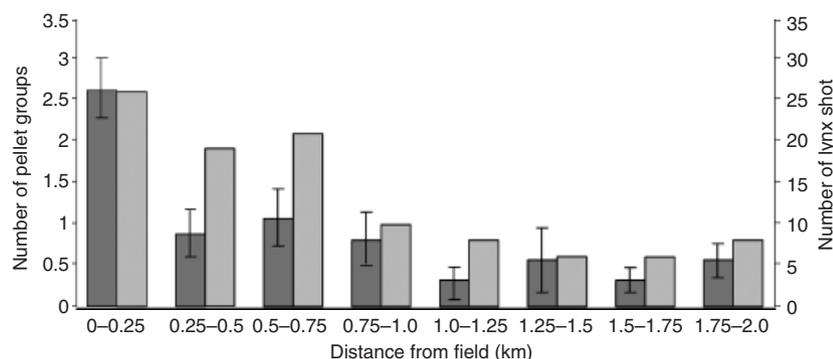
Figure 2 Faecal pellet groups were counted by walking a 2 km long and 1 m wide transect line in a right angle away from an agricultural field. The numbers of pellet groups are shown per 0.25 km transect (dark grey). The number of lynx shot and the distance per 0.25 km to the next agricultural field is shown as well (light grey).

Table 2 Estimates, with standard error (SE), of the mean distances in metres at the beginning of the reproductive year, between kill sites and indices of human development: occupied houses, agricultural fields and daily-used roads

Fixed effect	Occupied houses		Agricultural fields		Daily-used roads	
	Estimate	SE	Estimate	SE	Estimate	SE
Males	633	282	377	174	272	80
Females without kittens	1503	245	1067	150	210	69
Females with kittens	1643	302	1194	187	249	85
Males × day number	−0.642	1.08	1.132	0.669	−0.083	0.302
Females without kittens × day number	−3.383	0.991	−1.138	0.615	0.211	0.275
Females with kittens × day number	−4.694	1.215	−1.683	0.758	0.096	0.336

Estimates are shown for three groups: males, females without kittens and females with kittens. Also shown: interaction of distance with the number of days from the start of the reproductive year (day number; May 20 being counted as day 0).

sampling area. The number of houses within the study area ($t = 0.38$, d.f. $= 53$, $P = 0.7$) and the distance to the next field ($t = -0.653$, d.f. $= 54$, $P = 0.5$) were not significant and were excluded from the model. The final regression model had significant explanatory power ($r^2 = 0.2137$, $F_{2,55} = 7.47$, $P < 0.01$) and suggested that agricultural activity increases roe deer density.

Lynx mortality

Lynx were shot closer to roads (females: $340\,\text{m} \pm 46$ SE; males: $377\,\text{m} \pm 35$ SE), fields (females: $751\,\text{m} \pm 89$ SE; males: $709\,\text{m} \pm 78$ SE) and houses (females: $935\,\text{m} \pm 133$ SE; males: $866\,\text{m} \pm 107$ SE) than would be expected from a random distribution [roads: $858\,\text{m} \pm 69$ (95% confidence interval (CI), $n = 1000$); fields: $1267\,\text{m} \pm 92$ (95% CI, $n = 1000$); houses: $2216\,\text{m} \pm 159$ (95% CI, $n = 1000$)]. No sex differences were detected in the locations where animals were shot (roads: $F = 0.4067$, d.f. $= 1$, $P > 0.5$; fields: $F = 0.1209$, d.f. $= 1$, $P > 0.7$; houses: $F = 0.1643$, d.f. $= 1$, $P > 0.6$).

Distances between lynx locations and human activity

The estimates (with standard error) of the multilevel model for distances between the nearest occupied house, agricultural field and daily-used road and locations where lynx killed roe deer and chose day lairs are shown in Tables 2 and 3, respectively. An overview of the comparisons of the three

groups (males, females with kittens and females without kittens) is given in Table 4 for the intercepts and in Table 5 for the slopes.

At the beginning of the reproductive year (20 May), roe deer kill sites from females with dependent kittens were further away from occupied houses (χ^2 test: $\chi^2 = 5.973$, d.f. $= 1$, $P = 0.01$; see also Fig. 3) and agricultural fields (χ^2 test: $\chi^2 = 10.225$, d.f. $= 1$, $P = 0.001$) than locations where males killed roe deer. Also females without dependent young killed further from occupied houses (χ^2 test: $\chi^2 = 5.436$, d.f. $= 1$, $P = 0.02$) and agricultural fields (χ^2 test: $\chi^2 = 9.012$, d.f. $= 1$, $P = 0.003$) than males.

Females with kittens also chose day lairs further away from houses than males (χ^2 test: $\chi^2 = 14.747$, d.f. $= 1$, $P < 0.001$) and females without kittens (χ^2 test: $\chi^2 = 11.11$, d.f. $= 1$, $P < 0.001$; see also Fig. 4) and chose day lairs further away from fields and roads than males (χ^2 test: $\chi^2 = 13.234$, d.f. $= 1$, $P < 0.001$ and χ^2 test: $\chi^2 = 6.065$, d.f. $= 1$, $P = 0.01$, respectively).

Distances between houses and kill sites decreased for females with kittens throughout the year with a steeper slope than males (χ^2 test: $\chi^2 = 6.214$, d.f. $= 1$, $P = 0.01$; see also Fig. 3). Females with kittens changed distance from day lairs to houses and fields over time more than did males (houses: χ^2 test: $\chi^2 = 7.481$, d.f. $= 1$, $P = 0.006$; fields: χ^2 test: $\chi^2 = 10.772$, d.f. $= 1$, $P = 0.001$). Therefore similar distances at the end of the reproductive year occurred for males and females with dependent young relative to houses (Fig. 4) and fields.

Table 3 Estimates, with standard error (SE), of the mean distances in metres at the beginning of the reproductive year, between day lairs and indices of human development: occupied houses, agricultural fields and daily-used roads

Fixed effect	Occupied houses		Agricultural fields		Daily-used roads	
	Estimate	SE	Estimate	SE	Estimate	SE
Males	1181	172	970	104	267	48
Females without kittens	1186	226	1231	137	328	63
Females with kittens	2135	180	1518	109	438	50
Males × day number	−1.728	0.726	−0.464	0.442	−0.071	0.207
Females without kittens × day number	−2.508	1.013	−1.92	0.616	−0.101	0.288
Females with kittens × day number	−4.748	0.832	−2.669	0.507	−0.651	0.237

Estimates are shown for three groups: males, females without kittens and females with kittens. Also shown: interaction of distance with the number of days from the start of the reproductive year (day number; May 20 being counted as day 0).

Table 4 Intercepts of males, females without kittens (−) and females with kittens (+) are compared for kill sites and day lairs and occupied houses, agricultural fields and daily-used roads using a χ^2 test (d.f. = 1)

	Intercept					
	Kill sites			Day lairs		
	Houses	Fields	Roads	Houses	Fields	Roads
Males/females (+)	*	**	NS	***	***	*
Males/females (−)	*	**	NS	NS	NS	NS
Females (−)/(+)	NS	NS	NS	***	NS	NS

*Significant at $P < 0.05$.
**Significant at $P < 0.01$.
***Significant at $P < 0.001$.
NS, not significant.

Table 5 Slopes of males, females without kittens (−) and females with kittens (+) are compared for kill sites and day lairs and occupied houses, agricultural fields and daily-used roads using a χ^2 test (d.f. = 1)

	Slope					
	Kill sites			Day lairs		
	Houses	Fields	Roads	Houses	Fields	Roads
Males/females (+)	*	NS	NS	*	**	NS
Males/females (−)	NS	NS	NS	NS	NS	NS
Females (−)/(+)	NS	NS	NS	NS	NS	NS

*Significant at $P < 0.05$.
**Significant at $P < 0.01$.
NS, not significant.

Distances between 1000 random locations and occupied houses [2216 m ± 159 (95% CI, $n = 1000$)], agricultural fields [1267 m ± 92 (95% CI, $n = 1000$)] and daily-used roads [858 m ± 69 (95% CI, $n = 1000$)] suggest that males and females without kittens killed roe deer and chose day lairs closer to human activity than the random distribution. Only distances between females with kittens and houses and fields (Figs 3 and 4) fell within the 95% CIs of distances to random locations.

Discussion

Our results suggest that (1) areas associated with human activity represent 'attractive sinks' for lynx (potentially high mortality and high prey density, Fig. 2) and (2) both sex and reproductive status modify lynx response to this trade-off. The presence of dependent and vulnerable young is especially important, particularly at the beginning of the reproductive year. At this time, when the kittens are newborn, females with dependent young chose day lairs and kill sites further away from areas of human activity than did males. Additionally, we have shown that females with dependent young decreased distances from roe deer kill sites and day lairs to human activity with kitten age.

The Eurasian lynx is a seasonally breeding, solitary felid for whom the reproductive success of females is expected to be closely related to the amount of energy they can allocate to reproduction (Sandell, 1989). Females rear the kittens by themselves, and our study suggests that they face a trade-off between foraging in areas of high roe deer densities close to human activity and hunting in areas with low human densities but less abundant roe deer. Over the course of time, the kittens gain weight and show higher activity levels, so energetic demands of the kittens and therefore family group consumption rates increase (Jobin, Molinari & Breitenmoser, 2000). During the same period, kittens also become less vulnerable to predation because of increasing physical strength and coordination. Maternal females might maximize their reproductive success by minimizing risk during the most critical period of the year and hunting in risky but high-quality habitats later in the year.

The greater concentration of prey in winter, combined with the increasing food demand of the family, might explain why maternal females chose similar distances from kill sites to occupied houses and agricultural fields as males and females without kittens during winter (end of the reproductive year). Roe deer are more concentrated around people during winter, because of less snow at low elevations (Mysterud, 1999) and the presence of artificial feeding sites.

The spatial distribution of lynx kill sites and day lairs is more affected by the presence of occupied houses than by agricultural fields and daily-used roads. That these findings were not consistent with our expectations is likely to be due to differences in human activity throughout the year. Agricultural fields are likely to show variation in usage levels by
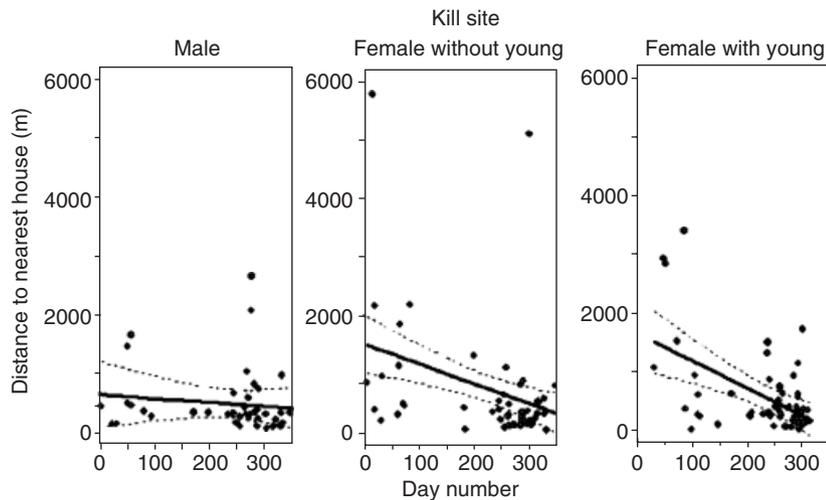
Kill site

Figure 3 Distances (in metres) between kill sites of males, females with young and females without young and occupied houses are shown with 95% confidence intervals (dotted lines). Data are shown throughout the year with day zero set at 20 May, the beginning of the reproductive year, when the first females give birth.
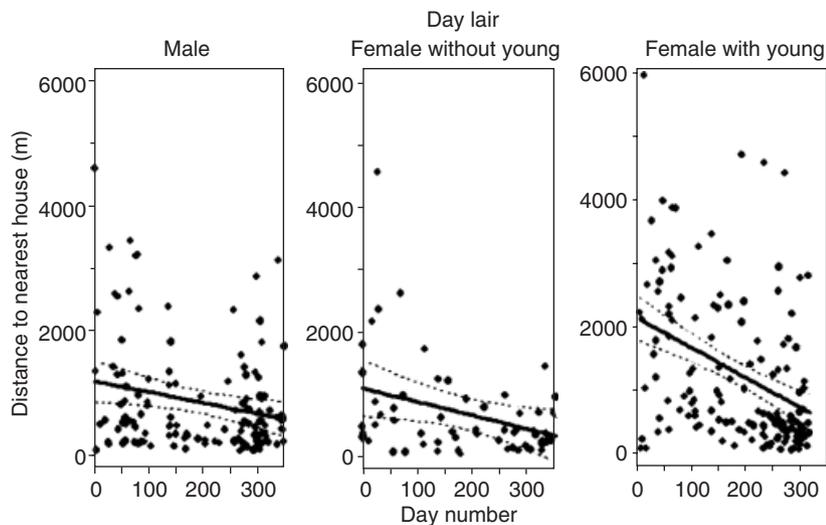
Day lair

Figure 4 Distances (in metres) between day lairs of males, females with young and females without young and occupied houses are shown with 95% confidence intervals (dotted lines). Data are shown throughout the year with day zero set at 20 May, the beginning of the reproductive year, when the first females give birth.

humans over the year, with high activity levels occurring during late spring and summer, and less activity occurring during autumn and winter. Roads might have been a less predictable site of human activity in the sparsely populated study area. Furthermore, most human activity associated with roads is in the form of vehicles, which may not be perceived as being as risky as humans per se (Andersen, Linnell & Langvatn, 1996). Among these sites, occupied houses are the most consistent source of human activity and show the clearest results in our study.

For the last few hundred years, humans have been the main predators on large carnivores throughout Eurasia. Centuries of persecution peaked in the 19th and early 20th centuries with state bounty payments and highly organized extermination programs. This led to a global reduction in large carnivore populations. In Scandinavia, there was an all-time low in the mid 20th century when lynx were almost exterminated. Although populations have rebounded in recent decades following the introduction of favourable

management practices, human activity remains the main source of mortality. Sunde *et al.* (1998*a*) have shown that lynx are harvested close to roads, with all lynx shot within 3 km from a road. Similar distances (<1.5 km) between harvest locations and roads have been found in this study. Sunde, Stener & Kvam (1998*b*) approached resting lynx during daytime and found that the tolerance distance to humans is strongly correlated with horizontal visibility and forest maturation stage. Their study showed that lynx fled from approaching people in open forest and on open land at distances of 50 and 250 m, respectively. Thus lynx avoid humans actively on a smaller scale, but our study suggests that lynx are attracted to human-dominated areas at a larger scale. There is also a temporal component to this as kill sites are used at night when humans are less active.

The combination of survival and reproduction, described in a two-dimensional model with high human-caused mortality in otherwise high-quality habitats, has been found to capture the source–sink dynamics of a brown bear *Ursus*

arctos population (Naves *et al.*, 2003). In areas with high human activity, mortality is mostly human caused, whereas reproduction is determined by the availability and distribution of natural prey. Refuge areas for resting and breeding with low human activity and low mortality risks might therefore ensure the persistence of large carnivores, including lynx in Scandinavia. This study suggests that the trade-off between high costs of rearing kittens and the vulnerability of newborn kittens is addressed by a spatio-temporal strategy of avoiding risky habitats in the early phase of kitten rearing and hunting in areas with abundant prey but higher risk at a later stage. Therefore, the combination of refuge areas and areas with high food abundance is likely to be important for Eurasian lynx in general.

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