

1 Title: Risk-taking by Eurasian lynx in a human-dominated landscape: effects of sex and  
2 reproductive status

3 Short title: Risk-taking by Eurasian lynx

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24

1 ABSTRACT

2

3 This study aimed to test how the sex and reproductive status of Eurasian lynx influenced  
4 their use of "attractive sinks" - habitats with high prey density and high mortality risks.

5 Locations of 24 Eurasian lynx (*Lynx lynx*) were obtained by radio-telemetry in a mixed  
6 forest and agricultural habitat in southeastern Norway. Roe deer, the major food source  
7 of lynx in the study area, occurred at higher densities closer to areas of human activity  
8 and infrastructure. Proximity of lynx locations to human activity and infrastructure was  
9 used as a risk index since the most common causes of death among Scandinavian lynx  
10 were of anthropogenic origin. This study shows that distances from lynx locations to  
11 human activity was significantly greater for females with newborn kittens than for  
12 males, but this decreased with kitten age. The data suggest that this response to human  
13 activity is influenced by the reproductive strategies of males and females, and might  
14 explain male biased human-induced mortality in this study and in carnivores more  
15 generally.

16 Key words: Eurasian lynx, risk-taking, human-dominated landscape, reproductive  
17 status, attractive sinks

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1 INTRODUCTION

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3 The distribution and abundance of prey has an important influence on carnivore spatial  
4 distribution (Sunquist & Sunquist, 1989). Prey may be distributed randomly, evenly, or  
5 clumped and this affects the spatial decisions made by carnivores (Davies & Houston,  
6 1984). Habitat choice is likely to be influenced by mortality risk as well as prey  
7 abundance and distribution. Interspecific killing among mammalian carnivores has been  
8 reported in felids, canids and mustelids (Palomares & Caro, 1999). To decrease the  
9 chance of becoming prey, carnivores may avoid habitats with high densities of larger  
10 predators. For example, European genets (*Genetta genetta*), and European mongooses  
11 (*Herpestes ichneumon*) avoid suitable habitats where Iberian lynx (*Lynx pardinus*) are  
12 common (Palomares *et al.*, 1996). From the point of view of large carnivores in the  
13 modern world, humans represent by far the most dangerous intraguild predators. People  
14 are generally the most common cause of death among large carnivores both inside and  
15 outside protected areas (Woodroffe & Ginsberg, 1998). From the point of view of  
16 reducing mortality risk large carnivores should avoid areas of high human activity.

17

18 However, avoiding mortality risk must be balanced against foraging efficiency. In some  
19 systems (such as tropical forests), the density of prey may be greatly reduced close to  
20 areas of human activity (Robinson & Bennett, 2000). In such a setting, there should be  
21 no trade-off between mortality risk and prey availability. However, in Europe and North  
22 America some cervid species, which are the main prey of large carnivores, may occur at  
23 higher density in areas where humans have modified the habitat, or provide  
24 supplementary food (McShea, Underwood & Rappole, 1997). In such cases there may

1 be a clear trade-off between mortality risk and foraging efficiency, and areas associated  
2 with human activity may represent "attractive sinks" (sensu Delibes, Goana & Ferreras,  
3 2001). From the theory of sexual selection, males are expected to take greater risks than  
4 females in polygynous and dimorphic species (Trivers 1985). Theory and data indicate  
5 that variation in lifetime reproductive success is greater amongst males than amongst  
6 females, with high numbers of offspring sired by a few males and no offspring for most  
7 of the males (Clutton-Brock *et al.*, 1982; Payne 1979). Variation in reproductive success  
8 among males can be due to differences in body size or condition, and any deficiency in  
9 physical condition can have negative effects on their reproductive success (Clutton-  
10 Brock *et al.*, 1988). Studies on large mammals, including carnivores, have also shown  
11 that males are more likely to get in conflict with people (Linnell *et al.*, 1999; Odden *et*  
12 *al.*, 2002; Sukumar, 1991). However, the high costs of feeding dependent young  
13 (Oftedal & Gittleman, 1998), both during lactation and especially during the period  
14 when the young's energy demands increase but predatory skills are not developed, is  
15 likely to attract females to areas of higher foraging efficiency. Thus, sex and  
16 reproductive status are likely to influence the trade-offs that an individual faces.

17

18 In this study we investigated the extent to which the forest and farmland matrix habitats  
19 of southeastern Norway represent an attractive sink for Eurasian lynx (*L. lynx*), and how  
20 sex and reproductive status influence lynx decision making in relation to mortality risk.  
21 Research in Scandinavia has shown that the most common cause of death among radio-  
22 collared Eurasian lynx is of anthropogenic origin (legal harvest, poaching, vehicle  
23 collisions) (Andersen *et al.*, 2003; Andrén *et al.* submitted) and earlier studies from  
24 central Norway indicate that this mortality is closely linked to lynx proximity to areas of

1 human activity (Sunde, Overskaug & Kvam, 1998a). Roe deer (*Capreolus capreolus*)  
2 represent the main prey of lynx in southern Norway (Birkeland & Myrberget, 1980;  
3 Andersen *et al.*, 1998) and are closely associated with human modified landscapes and  
4 the presence of agricultural land (Mysterud, Bjørnsen & Østbye, 1997; Mysterud 1999;  
5 Sunde *et al.* 2000).

6 In this analysis we investigate the hypotheses that:

- 7 (1) High roe deer densities are related to areas of human activity,
- 8 (2) Lynx mortality is closely related to areas of human activity,
- 9 (3) Sex and reproductive status influence habitat use by lynx in a human-modified  
10 environment, where males are found closer to human activity than females, especially  
11 when followed by vulnerable young and
- 12 (4) Females with dependent young decrease distances to human activity when family  
13 food demand increases, whereas males do not alter their spatial strategy over the year.

14

## 15 MATERIALS AND METHODS

16

### 17 Study Area

18

19 The study was conducted in south-eastern Norway in the counties of Hedmark,  
20 Akershus and Østfold between 1995 and 2002. The study area (14,000 km<sup>2</sup>) ranges  
21 between 0m and 300m above sea level in the southern part and along north-south  
22 running valleys with hills (200m up to 900m above sea level) further north. The study  
23 area is dominated by boreal forest, mainly Norwegian spruce (*Picea abies*) and Scots  
24 pine (*Pinus sylvestris*), and is intensively managed for timber and pulp. Agricultural

1 land is confined to strips along valley bottoms and constitutes less than 5% of the total  
2 area (Fig.1). In south-eastern Norway lynx diet is mainly based on roe deer (*Capreolus*  
3 *capreolus*), but mountain hares (*Lepus timidus*) and various species of birds are also  
4 eaten (Birkeland & Myrberget, 1980; Andersen *et al.*, 1998). Population density in the  
5 study area, measured on the 1<sup>st</sup> January 2002, was between seven people per km<sup>2</sup> in  
6 remote areas and 104 people per km<sup>2</sup> closer to the city of Oslo (Statistics Norway, 2002,  
7 [www.ssb.no](http://www.ssb.no)). Lynx are subject to a quota-regulated harvest throughout the study area  
8 within an annual season from 1<sup>st</sup> February to 30<sup>th</sup> April. Harvest is mainly based on  
9 hunting teams tracking and circling lynx – with most hunts beginning from where a lynx  
10 track is detected in the snow, usually close to a house or when crossing a road. In some  
11 cases box-traps, usually located close to houses or roads are used. In addition to legal  
12 harvest poaching is widespread, peaking in the late summer and autumn (Andrén *et al.*  
13 submitted).

14

#### 15 Roe Deer Distribution

16

17 Although pellet group counts of ungulates have been criticized for giving imprecise  
18 results of abundance estimates (e.g. Smart, Ward & White, 2004), this technique has  
19 been used successfully to estimate the distribution and relative abundance of ungulates  
20 (Borkowski, 2004) and has been shown to obtain good quality results to describe habitat  
21 use when compared with radio-telemetry data (Guillet *et al.*, 1995). The pellet group  
22 counts mainly reflect autumn-winter-spring distribution of roe deer (outside the growing  
23 and decomposition seasons). Some roe deer in all areas showed small scale seasonal  
24 movements (based on unpublished telemetry data) such that the summer distribution

1 may have been slightly more dispersed than the winter picture indicates, however we  
2 assume that the overall pattern is representative of spatial variation in density over the  
3 year.

4

5 The distribution and relative abundance of roe deer were determined by conducting 16  
6 transect counts for pellet groups in spring 2002 in southern Norway (counties Akershus  
7 and Østfold). Faecal pellet groups were counted by walking a 2 km long and 1m wide  
8 transect line in a right angle away from an agricultural field. A pellet group was defined  
9 as 3 or more pellets from the same defecation. The number of pellet groups per 250m  
10 was recorded. The number of pellet groups for the first 250m were compared with the  
11 number of pellet groups found between 251m and 2000m. The data were analysed with  
12 an Analysis of Variance with distance to the field, observer and transect number as  
13 fixed factors.

14

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

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

4

## 5 Capturing Lynx

6

7 In connection with a long term and multi-faceted project on lynx ecology, lynx were  
8 captured and equipped with radio-collars (<150 g, or less than 1% of an adult female)  
9 using a variety of techniques between 1995 and 2002. Adult lynx were trapped with box  
10 traps constructed in wood or metal mesh and with spring-loaded wire foot-snares  
11 (Nybakk *et al.*, 1996). Animals were often recaptured using the same techniques, with  
12 trained dogs or darting from a car or helicopter. All adult animals were immobilized  
13 using a mixture of ketamine (100 mg) and medetomidine (4 mg), reversed with  
14 atipamezole (5 mg); juveniles received a half dose. All drugs were provided intra-  
15 muscularly by hand, blow-pipe or gas-powered darting rifle. Neonatal kittens were also  
16 captured (by hand) at natal lairs and were equipped with implanted transmitters  
17 (Arnemo *et al.*, 1999). All procedures were approved by the Norwegian Experimental  
18 Animal Ethics Committee, and permits for wild animal capture were obtained from the  
19 Directorate for Nature Management. Only 3 mortalities occurred because of capture.  
20 Two of these were through trauma associated with the use of leg-snares and the 1 darted  
21 from a vehicle suffered a reaction to the drugs. No complications were ever detected as  
22 a result of collaring or implanting. Capture techniques and animal handling are  
23 described in more detail in Herfindal *et al.* (2005). Radio-collars were not removed,  
24 because, (1) most lynx in Norway, including our study animals die within a few years of

1 initial capture through legal or illegal hunting, and (2) wherever possible animals are  
2 recollared when needed and maintained within the study which is still ongoing.

3

#### 4 Radio-tracking

5

6 Positions of radio-collared lynx were determined by radio tracking from the ground and  
7 air. All positions tracked between 9am and 5pm with a location error of 100m or less  
8 were classified as day-lairs. Lynx day-lairs are generally not more than three kilometres  
9 from the kill if they return the next night (Øvrum 2000). After five consecutive nights  
10 the carcass is usually finished and the lynx move on. To avoid possible dependence  
11 between day-lairs from the same kill, we used only day-lairs that were at least 5 days or  
12 >3 kilometres apart. Therefore, all of the 349 day-lairs used in the analysis can be  
13 regarded as being independent from each other for analysis of spatial patterns.

14

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

22

23 The reproductive status of a female was determined by the presence of dependent  
24 young. At the end of May/beginning of June lynx females give birth to 1-3 kittens. The

1 den was localised by directly approaching the radio-collared female and the location  
2 where kittens were observed was determined as the den site.

3

#### 4 Lynx Distance Analysis

5

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

10

11 Shortest, straight-line, distances from roe deer kill-sites and day-lairs to various indices  
12 of human development were calculated using ESRI ArcView, extension Nearest feature  
13 v.3.6c (Jenness, 2003). For every day-lair and kill-site, the distance to the nearest  
14 occupied house, agricultural field, and daily-used road was calculated using maps with a  
15 scale of 1:250 000. Roads included highways, municipal roads, and private roads.

16 Effects of sex and reproductive status on distances to human development were  
17 analysed using multilevel modelling (computer package MLwiN v.1.10.0007 by Rasbash  
18 *et al.*, 2001). Multilevel models consider the nested structure of the data: distance  
19 measurements made at various times during the reproductive year (level 1) are nested  
20 within individual lynx (level 2). An important advantage of the multilevel approach is  
21 that incomplete and unbalanced data sets of repeated measures can be analysed. In this  
22 case: the number of observations and the time period for which they were recorded  
23 varied with individual lynx. The resulting model is also known as a mixed model where  
24 sex and reproductive status are fixed factors and the individual lynx is a random factor.

1 Since data were collected over an eight-year period, data were also nested within years,  
2 resulting in a more complex cross-nested model of observations belonging to both lynx  
3 and years. Because in such a cross-nested model no significant effect was found for the  
4 variance associated with years and only small changes in the estimates of the parameters  
5 of interest (the same was found in a two-level model with fixed year effects), year was  
6 not included in the final model. Thus, a straightforward two-level model with main  
7 effects and interaction effects was used for testing the effects of sex and reproductive  
8 status. The significance of differences in distances at the beginning of the reproductive  
9 year between males, females without kittens and females with kittens was tested with a  
10 Likelihood Ratio or deviance test. Such a test compares the full model with different  
11 parameters for the three groups and a reduced model where parameters have been set  
12 equal for all groups or for two of the three groups. The difference in deviance (a relative  
13 fit measure) between both models is equivalent to a Likelihood Ratio test statistic  
14 following a chi-square distribution with the number of restricted parameters as the  
15 degrees of freedom. The significance of the effect of distance for the groups of males,  
16 females with kittens and females without kittens was tested with a two-tailed t-test. The  
17 significance of differences between the effects of distance per reproductive group was  
18 compared using a deviance test as described before.

19 The present data set includes 153 locations of roe deer carcasses killed by adult (>2  
20 years) radio-collared lynx, this group comprising eight individual males and eleven  
21 individual females (Table 1). The data set also includes 349 temporally independent  
22 day-lairs from ten individual males and 14 individual females (Table 1). Only adult lynx

1 (>2 years) were used in the analysis. The start of the reproductive year for the model  
2 was set 20<sup>th</sup> May, when the first females give birth.

3  
4 Adult lynx shot during the yearly quota hunt between 1995 and 2002 were recorded for  
5 the study area. The distances between locations where 40 females and 64 males were  
6 shot and the nearest house, field or road were calculated with ArcView as described  
7 above for the calculation of kill-sites and day-lairs. Additionally, we used ArcView to  
8 calculate distances between 1000 random locations within the study area and occupied  
9 houses, agricultural fields and daily-used roads.

10

11

## 12 RESULTS

13

### 14 Roe Deer Distribution

15

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

23

1 The faecal pellet count in Hedmark showed that the number of roe deer pellets increased  
2 with percentage cover of fields ( $t= 3.326$ ,  $df=55$ ,  $P<0.01$ ) and number of artificial  
3 feeding sites ( $t=2.586$ ,  $df=55$ ,  $P<0.05$ ) in the sampling area. The number of houses  
4 within the study area ( $t=0.38$ ,  $df=53$ ,  $P=0.7$ ) and the distance to the next field ( $t=-0.653$   
5  $df=54$ ,  $P=0.5$ ) were not significant and were excluded from the model. The final  
6 regression model had significant explanatory power ( $r^2=0.2137$ ,  $F_{2,55}=7.47$ ,  $P< 0.01$ )  
7 and suggested that agricultural activity increases roe deer density.

8

### 9 Lynx Mortality

10

11 Lynx were shot closer to roads (females:  $340m \pm 46$  SE; males:  $377m \pm 35$  SE), fields  
12 (females:  $751m \pm 89$  SE; males:  $709m \pm 78$  SE) and houses (females:  $935m \pm 133$  SE;  
13 males:  $866m \pm 107$  SE) than would be expected from a random distribution (roads:  
14  $858m \pm 69$  (95% C.I.,  $n=1000$ ); fields:  $1267m \pm 92$  (95% C.I.,  $n=1000$ ); houses:  $2216m$   
15  $\pm 159$  (95% C.I.,  $n=1000$ ). No sex differences were detected in the locations where  
16 animals were shot (roads:  $F=0.4067$ ,  $df= 1$ ,  $P>0.5$ ; fields:  $F=0.1209$ ,  $df= 1$ ,  $P>0.7$ ;  
17 houses:  $F=0.1643$ ,  $df= 1$ ,  $P>0.6$ ).

18

### 19 Distances between Lynx Locations and Human Activity

20

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

1 females without kittens) is given in Table 4 for the intercepts and in Table 5 for the  
2 slopes.

3  
4 At the beginning of the reproductive year (20<sup>th</sup> May) roe deer kill-sites from females  
5 with dependent kittens were further away from occupied houses (Chi-square test:  
6  $\chi^2=5.973$ ,  $df=1$ ,  $P=0.01$ ) (see also Fig. 3) and agricultural fields (Chi-square test:  
7  $\chi^2=10.225$ ,  $df=1$ ,  $P=0.001$ ) than locations where males killed roe deer. Also females  
8 without dependent young killed further from occupied houses (Chi-square test:  
9  $\chi^2=5.436$ ,  $df=1$ ,  $P=0.02$ ) and agricultural fields (Chi-square test:  $\chi^2=9.012$ ,  $df=1$ ,  
10  $P=0.003$ ) than males.

11  
12 Females with kittens also chose day-lairs further away from houses than males (Chi-  
13 square test:  $\chi^2=14.747$ ,  $df=1$ ,  $P<0.001$ ) and females without kittens (Chi-square test:  
14  $\chi^2=11.11$ ,  $df=1$ ,  $P<0.001$ ) (see also Fig. 4) and chose day-lairs further away from fields  
15 and roads than males (Chi-square test:  $\chi^2=13.234$ ,  $df=1$ ,  $P<0.001$  and Chi-square test:  
16  $\chi^2=6.065$ ,  $df=1$ ,  $P=0.01$  respectively).

17  
18 Distances between houses and kill-sites decreased for females with kittens throughout  
19 the year with a steeper slope than males (Chi-square test:  $\chi^2=6.214$ ,  $df=1$ ,  $P=0.01$ ) (see  
20 also Fig 3). Females with kittens changed distance from day-lairs to houses and fields  
21 over time more than did males (houses: Chi-square test:  $\chi^2=7.481$ ,  $df=1$ ,  $P=0.006$ ;  
22 fields: Chi-square test:  $\chi^2=10.772$ ,  $df=1$ ,  $P=0.001$ ). Therefore similar distances at the

1 end of the reproductive year occurred for males and females with dependent young  
2 relative to houses (Fig 4) and fields.

3  
4 Distances between 1000 random locations and occupied houses ( $2216\text{m} \pm 159$  (95%  
5 C.I.,  $n=1000$ )), agricultural fields ( $1267\text{m} \pm 92$  (95% C.I.,  $n=1000$ )) and daily-used roads  
6 ( $858\text{m} \pm 69$  (95% C.I.,  $n=1000$ )) suggest that males and females without kittens killed  
7 roe deer and chose day-lairs closer to human activity than the random distribution. Only  
8 distances between females with kittens and houses and fields (Fig 3, Fig 4) fell within  
9 the 95% confidence intervals of distances to random locations.

10

11

## 12 DISCUSSION

13

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

23

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

13

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

20

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

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

8

9 For the last few hundred years, humans have been the main predators on large  
10 carnivores throughout Eurasia. Centuries of persecution peaked in the 19<sup>th</sup> and early 20<sup>th</sup>  
11 centuries with state bounty payments and highly organised extermination programs.  
12 This led to a global reduction in large carnivore populations. In Scandinavia, there was  
13 an all time low in the mid 20<sup>th</sup> century when lynx were almost exterminated. Although  
14 populations have rebounded in recent decades following the introduction of favourable  
15 management practices, human activity remains the main source of mortality. Sunde *et*  
16 *al.* (1998a) have shown that lynx are harvested close to roads, with all lynx shot within  
17 3km from a road. Similar distances (<1.5km) between harvest locations and roads have  
18 been found in this study. Sunde, Stener & Kvam (1998b) approached resting lynx  
19 during daytime and found that the tolerance distance to humans is strongly correlated  
20 with horizontal visibility and forest maturation stage. Their study showed that lynx fled  
21 from approaching people in open forest and on open land at distances of 50m and 250m  
22 respectively. Thus lynx avoid humans actively on a smaller scale but our study suggests  
23 that lynx are attracted to human-dominated areas at a larger scale. There is also a

1 temporal component to this since kill-sites are used at night when humans are less  
2 active.

3  
4 The combination of survival and reproduction, described in a two-dimensional model  
5 with high human-caused mortality in otherwise high quality habitats has been found to  
6 capture the source-sink dynamics of a brown bear (*Ursus arctos*) population (Naves *et*  
7 *al.*, 2003). In areas with high human activity, mortality is mostly human-caused whereas  
8 reproduction is determined by the availability and distribution of natural prey. Refuge  
9 areas for resting and breeding with low human activity and low mortality risks might  
10 therefore ensure the persistence of large carnivores, including lynx in Scandinavia. This  
11 study suggests that the trade-off between high costs of rearing kittens and the  
12 vulnerability of new born kittens is addressed by a spatio-temporal strategy of avoiding  
13 risky habitats in the early phase of kitten rearing and hunting in areas with abundant  
14 prey but higher risk at a later stage. Therefore, the combination of refuge areas and  
15 areas with high food abundance is likely to be important for Eurasian lynx in general.

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17

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9

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24

1 TABLES

2

3 Table 1: Number of kill-sites and day-lairs for individual males (M1-10 (a)) and females  
4 (F1-14 (b)) are shown. For females the total number of kill-sites and day-lairs is also  
5 broken down by reproductive status: without kittens (-), and with kittens (+).

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(a)

Id/#	killsite	daylair
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

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(b)	killsite	killsite	daylair	daylair
Id/#	(-)	(+)	(-)	(+)
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

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1 Table 2. Estimates, with standard error (SE), of the mean distances in metres at the  
 2 beginning of the reproductive year, between kill-sites and indices of human  
 3 development: occupied houses, agricultural fields, and daily-used roads. Estimates are  
 4 shown for three groups: males, females without kittens, and females with kittens. Also  
 5 shown: interaction of distance with the number of days from the start of the  
 6 reproductive year (day number; May 20<sup>th</sup> being counted as Day 0).

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 nr.	-0.642	1.08	1.132	0.669	-0.083	0.302
Females without kittens*day nr.	-3.383	0.991	-1.138	0.615	0.211	0.275
Females with kittens*day nr.	-4.694	1.215	-1.683	0.758	0.096	0.336

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1 Table 3. Estimates, with standard error (SE), of the mean distances in metres at the  
 2 beginning of the reproductive year, between day-lairs and indices of human  
 3 development: occupied houses, agricultural fields, and daily-used roads. Estimates are  
 4 shown for three groups: males, females without kittens, and females with kittens. Also  
 5 shown: interaction of distance with the number of days from the start of the  
 6 reproductive year (day number; May 20<sup>th</sup> being counted as Day 0).

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 nr.	-1.728	0.726	-0.464	0.442	-0.071	0.207
Females without kittens*day nr.	-2.508	1.013	-1.92	0.616	-0.101	0.288
Females with kittens*day nr.	-4.748	0.832	-2.669	0.507	-0.651	0.237

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1 Table 4: Intercepts of males, females without kittens (-) and females with kittens (+) are  
 2 compared for kill-sites and day-lairs and occupied houses, agricultural fields and daily-  
 3 used roads using a Chi-square test (df=1). The significance is shown as: \* <0.05, \*\*  
 4 <0.01, \*\*\* <0.001.

	Intercept					
	killsites			daylairs		
	houses	fields	roads	houses	fields	roads
Males/Females (+)	*	**	ns	***	***	*
Males/Females (-)	*	**	ns	ns	ns	ns
Females(-)/(+)	ns	ns	ns	***	ns	ns

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8 Table 5: Slopes of males, females without kittens (-) and females with kittens (+) are  
 9 compared for kill-sites and day-lairs and occupied houses, agricultural fields and daily-  
 10 used roads using a Chi-square test (df=1). The significance is shown as: \* <0.05, \*\*  
 11 <0.01, \*\*\* <0.001.

12

	Slope					
	killsites			daylairs		
	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

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1 Figure 1: The map shows a representative part of the study area in south-eastern  
2 Norway to illustrate the distribution of lynx kill-sites within the human dominated  
3 landscape, including occupied houses, agricultural fields, daily-used roads, and forest.

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5 Figure 2: Faecal pellet groups were counted by walking a 2 km long and 1m wide  
6 transect line in a right angle away from an agricultural field. The numbers of pellet  
7 groups are shown per 0.25 km transect (dark grey). The number of lynx shot and the  
8 distance per 0.25 km to the next agricultural field is shown as well (light grey).

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10 Figure 3: Distances (in meters) between kill-sites of males, females with young and  
11 females without young and occupied houses are shown with 95% confidence intervals  
12 (dotted lines). Data are shown throughout the year with day zero set 20<sup>th</sup> May, the  
13 beginning of the reproductive year, when the first females give birth.

14

15 Figure 4: Distances (in meters) between day-lairs of males, females with young and  
16 females without young and occupied houses are shown with 95% confidence intervals  
17 (dotted lines). Data are shown throughout the year with day zero set 20<sup>th</sup> May, the  
18 beginning of the reproductive year, when the first females give birth.

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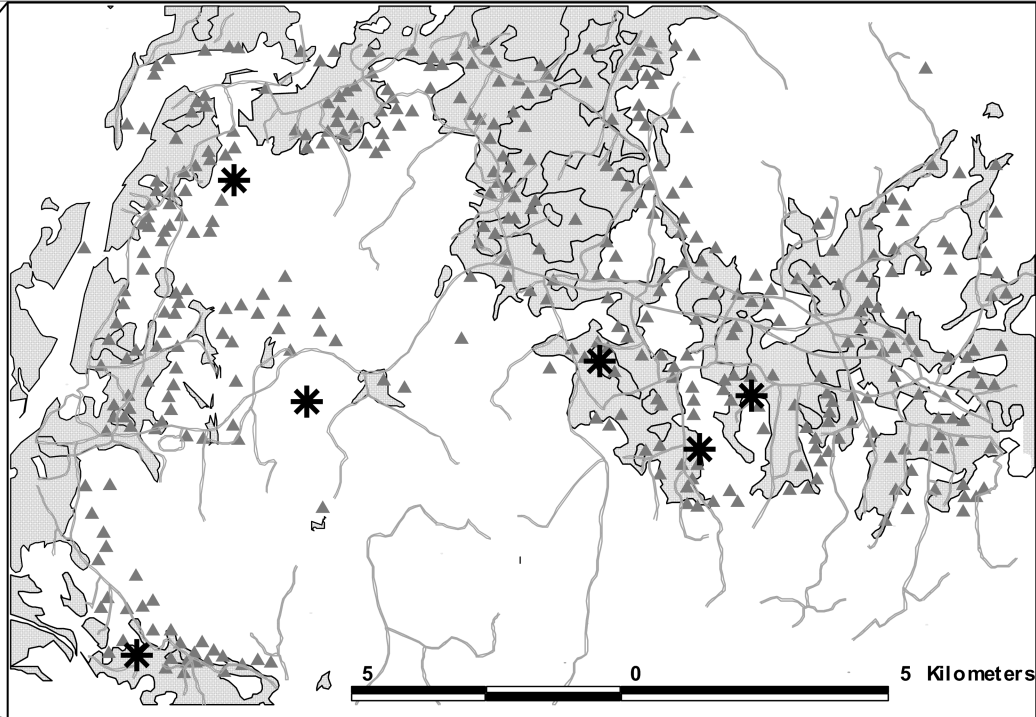
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Norway



Kill sites



Houses



Roads



Fields



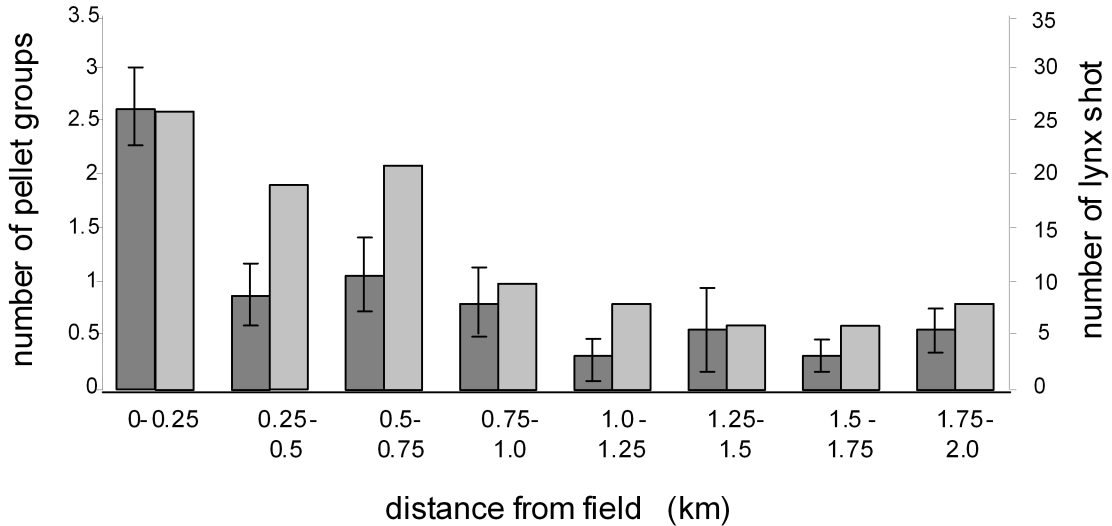
Forest



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5 Kilometers

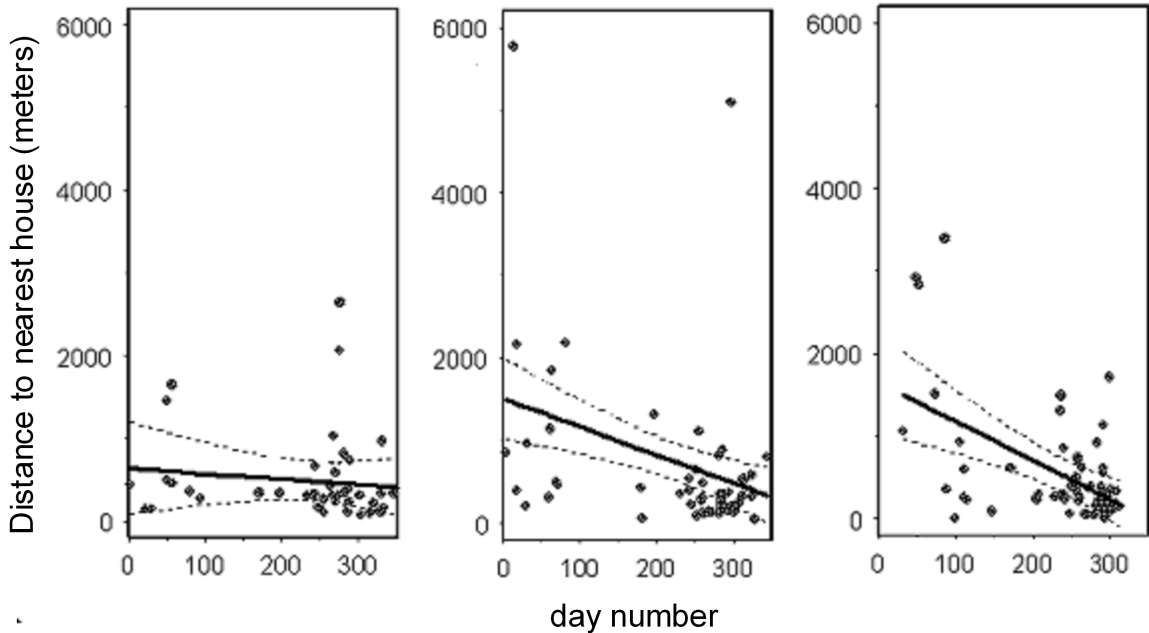


## killsite

male

female without young

female with young



## daylair

male

female without young

female with young

