Research

What shapes Eurasian lynx distribution in human dominated landscapes: selecting prey or avoiding people?

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In the multi-use landscape of southern Norway, the distribution of lynx is likely to be determined both by the abundance of their favoured prey – the roe deer – and the risk associated with the presence of humans because most lynx mortalities are caused by humans (recreational harvest, poaching, vehicle collisions). We described the distribution of the reproductive portion of the lynx population based on snow-track observations of females with dependent kittens collected over 10 yr (1997–2006) in southern Norway. We used the ecological-niche factor analysis to examine how lynx distribution was influenced by roe deer, human activity, habitat type, environmental productivity and elevation. Our first prediction that lynx should be found in areas of relatively high roe deer abundance was supported. However, our second prediction that lynx should avoid human activity was rejected, and lynx instead occupied areas more disturbed in average than those available (with the exception of the most densely occupied areas). Lynx, however, avoided the most disturbed areas and our third prediction of a trade-off between abundance of prey and avoidance of human activity was supported. On the one hand, roe deer in the most disturbed areas benefit to a large extent from current human land use practices, potentially allowing them to escape predation from lynx. On the other hand, the situation is not so favourable for the predators who are restricted in competition refuges with medium to low prey densities. The consequence is that lynx conservation will have to be achieved in a human modifed environment where the potential for a range of conflicts and high human-caused mortality will remain a constant threat.

Large mammalian carnivores typically occupy the upper trophic level in terrestrial ecosystems. They often have a keystone role, as they are strongly interactive species. Their absence usually coincides with marked changes in structure and composition, resilience to disturbance, or species diversity of ecosystems (Jędrzejewska and Jędrzejewski 2005, Soulé et al. 2005), although this role may be limited in some situations (Andersen et al. 2006). Large carnivores also cause severe conflicts with human interests, through competition for prey and depredation on livestock, which in the past often led to extermination campaigns that have seriously reduced their distribution and numbers (Breitenmoser 1998). In the absence of large carnivores, humans have usurped the role of top-predator, in addition to modifying the original habitat through agriculture and infrastructure development. The last three decades have

seen a global reversal of carnivore policy with the passing of conservation legislation. As a result, and through both natural expansion and reintroduction, a widespread increase in the abundance and distribution of large carnivores is currently taking place in most European countries. However, after a long period of continuous human development, the landscape which large carnivores are returning to is very different from the landscape they left one or two centuries ago. There has been much debate about both the ability of large carnivores to persist in human dominated landscapes (Woodroffe 2000, Linnell et al. 2001b) and the ecological role that they will play in these new, highly modified ecosystems (Linnell et al. 2005, Andersen et al. 2006). For instance Woodroffe (2000) found a positive relationship between historical patterns of large carnivore extinction probability and human population density. However, in the

presence of favourable legislation, large carnivores can usually recover much of their past range despite the presence of high human densities (Linnell et al. 2001b).

Eurasian lynx *Lynx lynx* in Norway have followed the general temporal pattern of large carnivore abundance and distribution in Europe. Subject to a state sponsored bounty program from 1846, they were nearly exterminated by the mid 20th century, persisting in one or two remnant populations in southeastern and central Norway. However, under increasingly restrictive hunting legislation lynx expanded during the late 20th century and are now widespread throughout the whole country with the exception of the southwest. In response to conflicts with sheep farmers (depredation on domestic sheep; Odden et al. 2002) and hunters (competition for game species; Odden et al. 2006), Norwegian lynx populations are managed as a game species and objectives have been set for limiting their density and distribution (Ministry of the Environment 2004). When planning for the conservation of large carnivores in human-dominated landscapes, one needs reliable information about their range of habitat tolerance (Linnell et al. 2005, May et al. 2008). Lynx habitat tolerance is likely to be shaped by two main factors: access to food and mortality risk. In Europe, the major prey item for Eurasian lynx are roe deer *Capreolus capreolus* (Odden et al. 2006), although they can survive on alternative prey such as hares *Lepus* sp., grouse and other small ungulates. In most cases, lynx mortality is human-caused (hunting, poaching, vehicle collisions; Andrén et al. 2006), and lynx, although attracted at a large scale to human-dominated areas (Bunnefeld et al. 2006), actively avoid humans at a smaller scale (e.g. when resting, Sunde et al. 1998), especially females with new born kittens (Bunnefeld et al. 2006). However, high roe deer densities often occur in fragmented and disturbed areas associated with high human activity. Lynx may thus have to balance selection for prey density against mortality risk from humans. Habitat selection should then reflect the response of animals to the trade-off between food availability and mortality risk.

Previous studies at the landscape scale have focused on modelling lynx tolerance to habitat fragmentation and human infrastructure in central and eastern Europe. In historical areas of lynx presence (Niedzialkowska et al. 2006), the habitat of autochtonous lynx populations was characterized by a higher proportion of forest and a lower fragmentation than observed nowadays. Conversely, lynx occurrence was negatively associated with human settlements and transportation infrastructure. Zimmermann and Breitenmoser (2002) also provided support for the influence of forest and roads on lynx distribution from a reintroduced population in Switzerland: lynx recolonised areas with high elevation and slope, and to a lesser extent areas with large forests and few roads. Due to human activities in this area, both the presence of forest and the absence of roads were highly correlated with elevation and slope, which underlines their functional importance on lynx habitat selection. Guisan and Zimmermann (2000) stated that such area-specific models should only be applied to regions and situations similar to those where the basic data were originally gathered. Schadt et al. (2002) however extended a habitat suitability model based on data obtained from lynx in the French and Swiss Jura Mountains to design

a Germany-wide conservation plan, and found that the critical factor was the connectivity of forested and non-forested semi-natural areas. Using the natural recovery of lynx in southern Norway, where both the level of fragmentation and the degree of human infrastructure development are much lower than elsewhere in Europe, we aimed to assess how lynx distribution at the population scale (i.e. southern Norway) relates to a range of environmental characteristics including an index of prey abundance, different habitat types, and human impact using recent developments of the ecological-niche factor analysis approach (ENFA; Basille et al. 2008). We expected that 1) lynx should select areas with high prey abundance and therefore the habitat of the lynx should be associated with relatively high roe deer abundance; 2) lynx should avoid areas of high human activity and therefore the habitat of lynx should be associated with a relatively low level of human activity; 3) potentially as a consequence of these two patterns lynx may have to trade searching for food against avoiding humans: as roe deer abundance and human activities should co-vary positively to some extent because roe deer take advantage of human transformation of the landscape, some optimal combination between roe deer abundance and human disturbance should occur.

Material and methods

Study area

The study took place in southern Norway, between ca 58°N and 63°N (Fig. 1). The study area (ca 100 000 km²) was defined as the 8 southern counties with a permanent lynx presence and where roe deer are the main prey. We did not include the county of Oslo that is too densely populated to
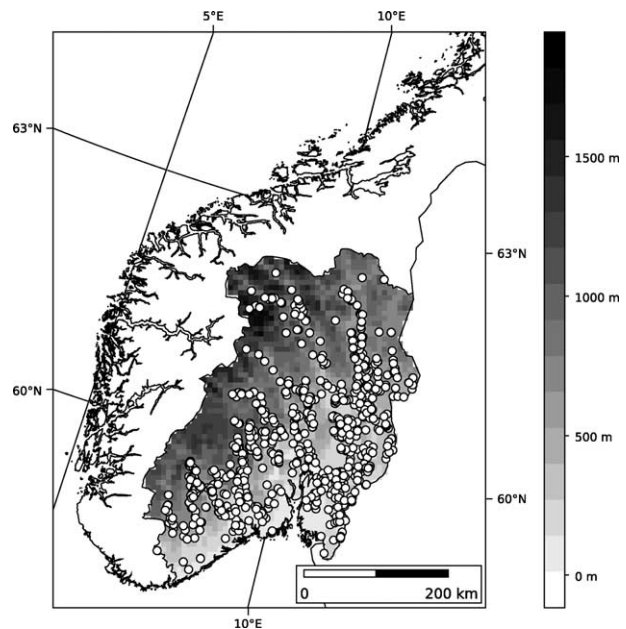

Figure 1. The study area situated in southern Norway. Family group observations are represented by white dots. Elevation is represented by the gray scale.

provide reliable estimates of both lynx and roe deer densities.

The study area covers a gradient from highlands covered with alpine tundra in the north and west to lowlands covered with a matrix of boreal forest and farmland in the southeast. The proportion of forest that has been converted to farmland or given over to human infrastructure increases close to the coast. For the analysis, the study area was divided into a grid of 7×7 km^2 cells (ca 50 km^2 per cell which is about 10% of a female lynx home range in Norway, Linnell et al. 2001a, Herfindal et al. 2005).

Lynx distribution data

Since 1996, lynx have been monitored using a standard methodology based on non-replicated counts of family groups (i.e. a female with dependent young of the year). Records of tracks in the snow are collected by hunters, game wardens and the public, and verified by game wardens (Linnell et al. 2007a). Outside the mating season (March and April), observations of 2 or more lynx together are attributed to a family group. As most of our data were collected during winter, we used these data to measure lynx distribution during wintertime: the occurrence of a family group indicates that reproductive lynx are resident in the area. We pooled 10 yr of data, from 1997 to 2006 (911 observations).

As adult females lynx are territorial (Breitenmoser et al. 1993), several observations in the same pixel from one year are likely to be from the same female. We therefore used as an index of distribution the number of years of monitoring during which lynx reproduction was observed within a given pixel. Thus, the distribution variable varied from 0 (pixels with no observation of lynx during the ten years) to 10 (pixels with at least 1 observation of a family group every year).

Environmental variables

A range of environmental variables were used as potential habitat variables. We included information on habitat type, elevation and environmental productivity, as well as roe deer density and human activity (Table 1, see below).

Environmental phenology derived from NDVI

The normalised difference vegetation index is an index based on the difference in reflectance between the red and near-infrared wavelengths. NDVI is closely related to photosynthetic activity and plant productivity (Reed et al. 1994). Thus, by using annual curves of NDVI for a specific area, it is possible to calculate several indices that can be interpreted as the change in plant productivity, or environmental phenology, through the year (Pettorelli et al. 2005). We used the GIMMS (Global Inventory Modelling and Mapping Studies) data set, which gives the maximum value NDVI composite for 15-d periods, to calculate four parameters of environmental phenology: the onset of spring measured as the date when the green-up of the vegetation starts, the derived NDVI corresponding to the rate of change in NDVI at this date, the peak value representing the highest NDVI-value reached during the season, and the

integrated NDVI calculated as the sum of NDVI-values throughout the growing season. The NDVI dataset we used in this study had a spatial resolution of ca 7×7 km^2 (Karlsen et al. 2006), and this resolution therefore determined the spatial resolution of our analyses, henceforth referred to as the grand pixel resolution. The GIMMS dataset was available from summer 1981 to 2003 (Tucker et al. 2005). To avoid calibration problems, we used the GIMMS dataseries only based on average phenological values. We justify the use of environmental phenology covering only 60% of our study period (1997–2006) with the rather small change in climatic conditions during the study period.

Habitat type

We used the habitat typology based on the Global Land Cover 2000 database (Bartholomé et al. 2002). This dataset has a spatial resolution of ca 1×1 km^2 in our study area and consists of 23 different habitats types. We redistributed these habitats types into five main classes: urban areas, agricultural areas, forest, alpine tundra, and bare rock-gravel. We then calculated the proportion of each of these classes per grand pixel (7×7 km^2). Based on the composition of habitat types inside each grand pixel, we calculated the Simpson's index of diversity as $L = \Sigma_{i=1}^{s} p_i^2$, where p_i is the proportion of habitat type i inside the grand pixel. This index goes from low values when there are many different habitat types in low proportion, to high values when there are a few dominating habitat types.

Elevation measures

The elevation data were obtained from the Norwegian Mapping Authority as a raster digital elevation model (DEM) with a spatial resolution of 100×100 m^2. We then calculated, for each grand pixel, the mean elevation and

Table 1. Environmental variables used in the analysis. See details in the text.

Name	Description
Agri	Proportion of agricultural areas
Alpine	Proportion of alpine areas
Bare	Proportion of bare ground
DEM	Mean elevation
DEMslope	Mean slope
DEMstd	Standard deviation of the elevation
Forest	Proportion of forest
Human	Mean value of human density
NDVIderived	Derived of the annual NDVI-curve at the onset of spring
NDVIint	Integrated NDVI between spring and autumn
NVDIpeak	Peak of the annual NDVI-curve
NDVIspring	The week number in spring when NDVI-values reach levels corresponding to leaf burst on birch
PublR	Total length (km) of public roads (paved roads, ranging from municipality roads to national highways) km^{-2}
PrivR	Total length (km) of private roads (roads in connection to farming and logging or some recreational resorts) km^{-2}
Roe	Mean number of roe deer shoot by legal hunting from 1997 to 2005
Simpson	Simpson's index of habitat type diversity
Urban	Proportion of urban areas

slope, as well as the standard deviation in elevations in order to get a measure of the variation within each grand pixel.

Measure of roe deer abundance

An index of roe deer abundance was calculated from the Norwegian hunting statistics on a municipality basis (Herfindal et al. 2005). In each grand pixel, the roe deer hunting data from 1997 to 2005 of the underlying municipalities were averaged to match the data of lynx family groups. All but 3 municipalities (n = 157) had data for at least 7 yr. For the three missing municipalities, we used the mean of roe deer abundance of the neighbouring municipalities. Given the rather low proportion of the quota that is actually harvested (mean = 28% with only 2.4% of the cases with >70% of the hunting quota harvested), we assumed that the harvesting is not quota-limited and reflects to a large extent regional variation in actual population size. Grøtan et al. (2005) showed that annual variation of the hunting statistics was highly correlated with the variation of three other estimates of roe deer abundance: 1) number of roe deer killed in car accidents, 2) mean number of sightings at feeding sites, 3) reconstructed fluctuations in the size of the population at the island of Ytterøya, Levanger, central Norway. At the broad scale of our study (one pixel for 50 km^2), we considered that this index was sufficient to detect broad patterns of variation in density across the study area.

Human impact

We measured human impact as road density and human density. Data on road density were obtained from the Norwegian Mapping Authority. Road density was calculated as the total length of roads (km) within each grand pixel for private and public roads separately. The human density map was obtained from Statistics Norway (Takle 2002), and corresponded to the number of inhabitants per square kilometre, with a spatial resolution of 1×1 km^2. These data were re-sampled to the grand pixels by summing the values of the 1×1 km^2 pixels within each grand pixel.

Habitat selection

We had data on observations of lynx throughout the study area, based on a presence-only design (Pearce and Boyce 2006). The ecological-niche factor analysis (ENFA; Hirzel et al. 2002) is a factorial analysis designed for presence-only data that summarizes the habitat selection into two components, the marginality and the specialization, to distinguish the habitat used from the availability. The marginality measures the position of the habitat within the environment (i.e. deviation of the average conditions in the habitat used from the average conditions available in the environment). The specialization measures the dispersion of the habitat within the available environment (i.e. tolerance of the species according to characteristics of its environment). The ENFA is like a principal component analysis (PCA); however, it is based on two components with well-defined a priori biological meaning to assess the position of the habitat within the environment. Using the ENFA we first extracted one axis of marginality, followed by several

uncorrelated axes of specialization which successively account for the maximum of the specialization until the number of initial variables have been exhausted. The number of axes of specialization to keep was defined using the broken-stick method (Jackson 1993). The ENFA can be used to build factorial maps of the habitat (Basille et al. 2008) with a projection of the environmental variables on the marginality and specialization axes. Such factorial maps provide an optimal (in terms of distinction between marginality and specialization) and undistorted representation of the habitat within the environment. A Monte-Carlo procedure was used to assess the significance of both marginality and specialization axes. The same number of localisations as observed were randomly distributed 1000 times over the study area and an ENFA was run at each step. A comparison of the 1000 sets of marginality and first eigenvalues of specialization with the observed values provides the significance of each component, expressed as the proportion of random values higher than the observed value.
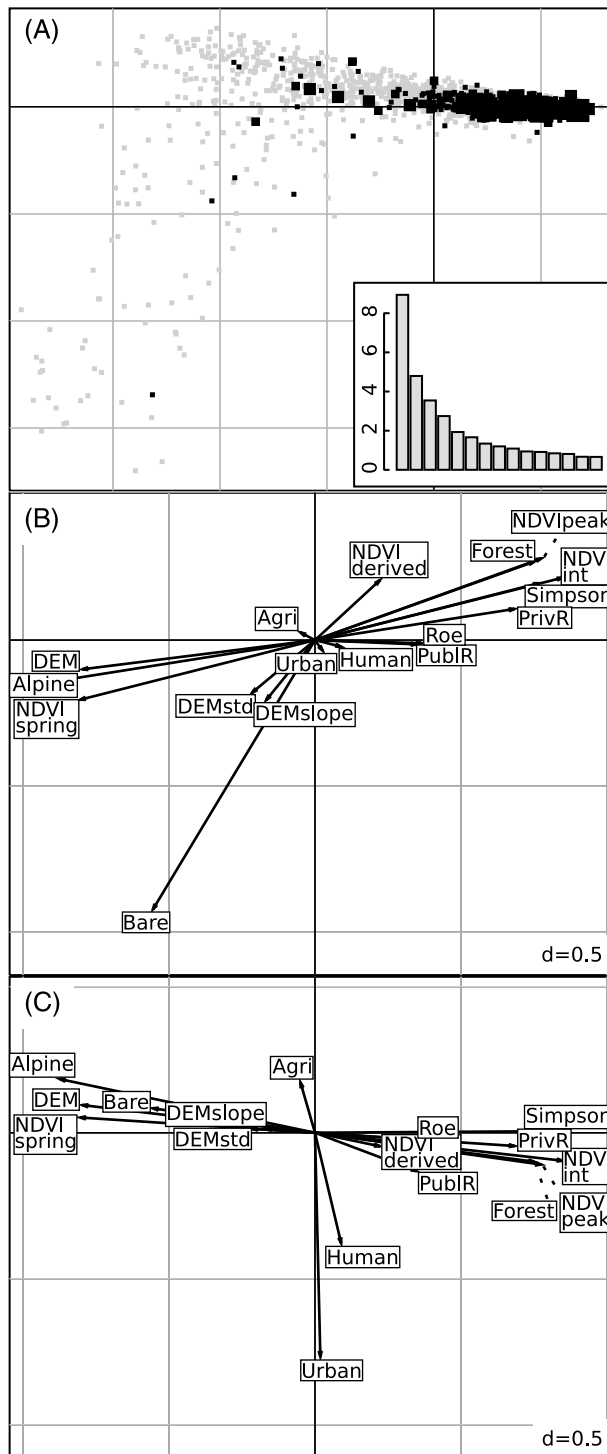
The ENFA is an exploratory tool that allows the variables responsible for the position and the shape of the habitat to be identified. These analyses allowed us to test our two first predictions. For the last prediction, we compared lynx space use, roe deer abundance and human-related variables. This was done in two steps, firstly from a lynx perspective and secondly from a roe deer perspective. To test the use of roe deer abundance and human-related variables by the lynx over their whole range, we divided each of the variables into a few classes in order to get approximately equal numbers of pixels in each class, and to avoid empty classes. Roe deer abundance and public road density were square root transformed, and human density was log-transformed to get approximately equal bin sizes. When the ratios of density of used pixels over density of available pixels per class was >1, the class was more used than expected by chance (selection), whereas when it was <1, the class was less used than expected by chance (avoidance). We then created 1000 random distributions with the same number of available pixels per class and the same overall number of used pixels. At each step, we again computed the ratios so that we obtained a distribution of 1000 random ratios. The comparison of the observed value to the 95% confidence interval of the random distribution gave us an assessment of the significance of the selection for each class.

Finally, to assess the relationship between roe deer abundance and human-related variables, we fitted a generalized linear model with a negative binomial error and a log link function to handle overdispersed count data (Ver Hoef and Boveng 2007). The roe deer abundance at the municipality level was the response variable with the human-related variables as explanatory variable, and the municipality area as offset variable (Venables and Ripley 2002). We tested the influence of the different explanatory variables using likelihood ratio tests. We computed Monte-Carlo simulation to derive confidence intervals of the conditional mean and the optimal value.

All statistical analyses were conducted using R 2.7.1 (R Development Core Team 2008) and the R-package ''adehabitat'' (Calenge 2006).

Results

Using the ENFA we found a clear structure in the selection of the habitat by lynx (Fig. 2); both marginality and specialization were highly significant (p < 0.001). The specialization was very strong on the first axis of specialization (variance ratio of 8.9, which means that the distribution of used pixels was almost nine times narrower on this axis compared to what was available), and to a lesser extent on the following three axes (variance ratios of 4.8, 3.5 and 2.7 respectively),

Figure 2. Results of the ENFA. (A) Display of the habitat in the plane formed by the marginality axis (x axis) and the first specialization axis (y axis). The grey squares represent the available pixels, whereas the black squares represent the used pixels, with a side proportional to the frequency of lynx observations. This graph shows both the position and the shape of lynx habitat within the environment. The lower-right insert presents the eigenvalues of specialization from the analysis. (B) Graph of the correlations between the environmental variables and the marginality axis (x axis) and the first specialization axis (y axis). The projection of the arrows on the axes give the contribution of each variable to the definition of the axes. Compared to the horizontal axis, long arrows towards the right (respectively the left) indicate that the habitat is characterized by high (respectively low) values on these variables. Compared to the vertical axis, long arrows indicate that the habitat is restricted on some characteristics of the variable, regardless of the direction (the sign of the specialization is not important). (C) Graph of the correlations between the environmental variables and the marginality axis (x axis) and the second specialization axis (y axis).

which were retained from our analysis (Fig. 2A). The position of the used habitat was clearly distinct from the available habitat on the scatterplot (Fig. 2A) enabling us to interpret the correlations of the variables with the axes of the analysis (Table 2). Using the marginality axis we identified the preferred habitat of the lynx as including a higher plant productivity (during the whole year and at the most productive time, corresponding to high value of integrated NDVI and NDVI peak, respectively), a larger proportion of forest, a higher habitat diversity (Simpson's index), a lower proportion of alpine areas, an earlier onset of spring and a lower elevation than what was available on average, with absolute values of correlations ranging from 0.75 to 0.87 (Table 2; Fig. 2B). The habitat of lynx also included higher roe deer abundance than what was generally available (correlation of 0.37), therefore validating our first prediction. However, contrary to our second prediction, the density of private and public roads were positively associated with the lynx distribution (correlations of 0.68 and 0.35, respectively). Of the variables associated with human presence only agricultural areas seemed to be slightly avoided in comparison to what was available on average (correlation of −0.05). The lynx distribution was, however, restricted to a narrow niche regarding the proportion of urban areas and human density, as indicated by high correlations with the second specialization axis (correlations of −0.77 and −0.38, respectively, Table 2; Fig. 2C). Indeed, lynx used intermediate values of human occupancy, and were rarely detected far from this optimum. Note that the high specialization on the first axis against the proportion of bare ground (correlation of −0.92, Fig. 2B) simply corresponded to the fact that lynx were almost never found at medium to high proportion of bare ground which corresponds to glaciers and rocky areas at high elevation, and were therefore strongly restricted on areas with a small proportion of bare ground.

Additionally, there was a marked selection of areas characterized by intermediate values of roe deer abundance, whereas areas with very low or very high abundance were used less than expected (Fig. 3a). The same pattern also occurred for the public road density (with an optimum

Table 2. Correlations of the environmental variables with the axes of the ENFA, given for the marginality axis (Mar) and the first four axes of specialization (respectively Spe1, Spe2, Spe3 and Spe4). Note that the sign of the specialization is not important. For variables description, see Table 1.

Name	Mar	Spe1	Spe2	Spe3	Spe4
Agri	−0.050	0.026	0.173	−0.167	0.237
Alpine	−0.874	−0.139	0.184	−0.641	−0.192
Bare	−0.555	−0.922	0.084	−0.170	−0.175
DEM	−0.796	−0.100	0.095	0.625	−0.000
DEMslope	−0.167	−0.205	0.013	−0.220	0.175
DEMstd	−0.215	−0.180	0.013	0.478	0.097
Forest	0.751	0.268	−0.099	0.017	−0.346
Human	0.090	−0.022	−0.378	0.010	−0.177
NDVIderived	0.222	0.205	−0.046	−0.067	−0.213
NDVIint	0.848	0.214	−0.096	0.043	−0.043
NDVIpeak	0.775	0.280	−0.109	−0.014	−0.085
NDVIspring	−0.804	−0.204	0.052	0.135	−0.261
PublR	0.348	−0.014	−0.131	0.194	−0.326
PrivR	0.683	0.107	−0.045	−0.129	0.265
Roe	0.366	−0.011	−0.025	−0.086	0.337
Simpson	0.766	0.195	0.005	0.059	0.045
Urban	0.018	−0.026	−0.767	−0.070	0.502

between 0.39 and 0.6 km of roads km^{-2}, Fig. 3b) and human density (with an optimum between 2.3 and 6.5 inhabitants km^{-2}, Fig. 3c), therefore lending strong support for our third prediction. Lynx used areas with extremely low and extremely high values of both roe deer abundance and human disturbance less than expected, whereas areas with intermediate values were selected for, indicating that a trade-off occurred between these two variables. This trade-off was furthermore supported by similar findings for roe deer, however with higher optima. Indeed, roe deer abundance was strongly related to both public road density and human density, both simple and quadratic terms being highly significant in both cases ($\chi^2_{Roads} = 1947.6$, DF = 1, p < 0.001; $\chi^2_{Roads^2} = 490.9$, DF = 1, p < 0.001; $\chi^2_{Human} = 1474.6$, DF = 1, p < 0.001; $\chi^2_{Human^2} = 369.6$, DF = 1, p < 0.001). There was an optimum of 1 km of public roads km^{-2} (with 95% confidence interval ranging from 0.97 to 1.02, Fig. 4a), and an optimum of 136 inhabitants km^{-2} (with 95% confidence interval ranging from 115 to 163, Fig. 4b), both optima being higher than for lynx (about twice and 30 times, respectively).

Discussion

We found that 1) lynx were found in areas with a higher roe deer density than generally available in the study area, therefore validating our first prediction; 2) lynx occupied areas with more human activity (relatively to roads primarily) than generally available, therefore rejecting our second prediction; 3) there was a clear trade-off in lynx habitat selection so that an optimal combination of intermediate roe deer abundance and intermediate human disturbance occurred because lynx avoided the areas with maximum roe deer densities, due to the association with high road and human densities.

The distribution range of lynx in southern Norway is characterized by a high proportion of forests, which correspond to productive areas with an early green-up of the vegetation and a low elevation, and by a relatively high roe deer abundance. This supports previous studies in Poland (Niedziałkowska et al. 2006), in Switzerland (Zimmermann and Breitenmoser 2002) and in France (Basille et al. 2008). Forest can indeed be considered as the main habitat for lynx, with roe deer as the main prey species.

On the other hand, lynx habitat was characterized by very low values of proportion of bare ground and alpine tundra. This selection against mountainous areas is potentially a side effect of the absence of a suitable main prey species at high elevation in Norway. For instance, in the Alps of central Europe, chamois *Rupicapra rupicapra* can constitute a significant proportion of lynx diet (up to 22% of lynx kills, Molinari-Jobin et al. 2004).

Contrary to our second prediction, lynx were found in areas with slightly more human activity than generally available. Such findings support previous results reported by Bunnefeld et al. (2006) who found that even if their mortality risk is higher close to roads, houses and fields, lynx are attracted by human-dominated areas. Additionally, lynx could tolerate human activity provided that there is a high density of forested areas (Sunde et al. 1998).

Family group data are collected by hunters, game wardens and the public, and are therefore potentially influenced by the accessibility of the habitat. If this was the case in our study, we would have expected to find more signs of lynx presence in areas close to roads and the results would have been biased towards areas of high disturbance. Norway's forests and mountains are highly accessible, networked by many public and private roads (including logging roads). On the coarse scale of our analysis, it is highly unlikely that many pixels would have been without road access. To ensure that our data set was unbiased, there was a minimum effort in the sampling with 1819 transects (3 km long) distributed among the different counties. As a result, 81% of the collared lynx were detected during two censuses in Hedmark county (16 collared lynx), among which all females with kittens were detected (Linnell et al. 2007b).

Finally, lynx avoided areas with the highest human and road densities, which matched closely with an avoidance of the highest roe deer abundance. At the same time, roe deer
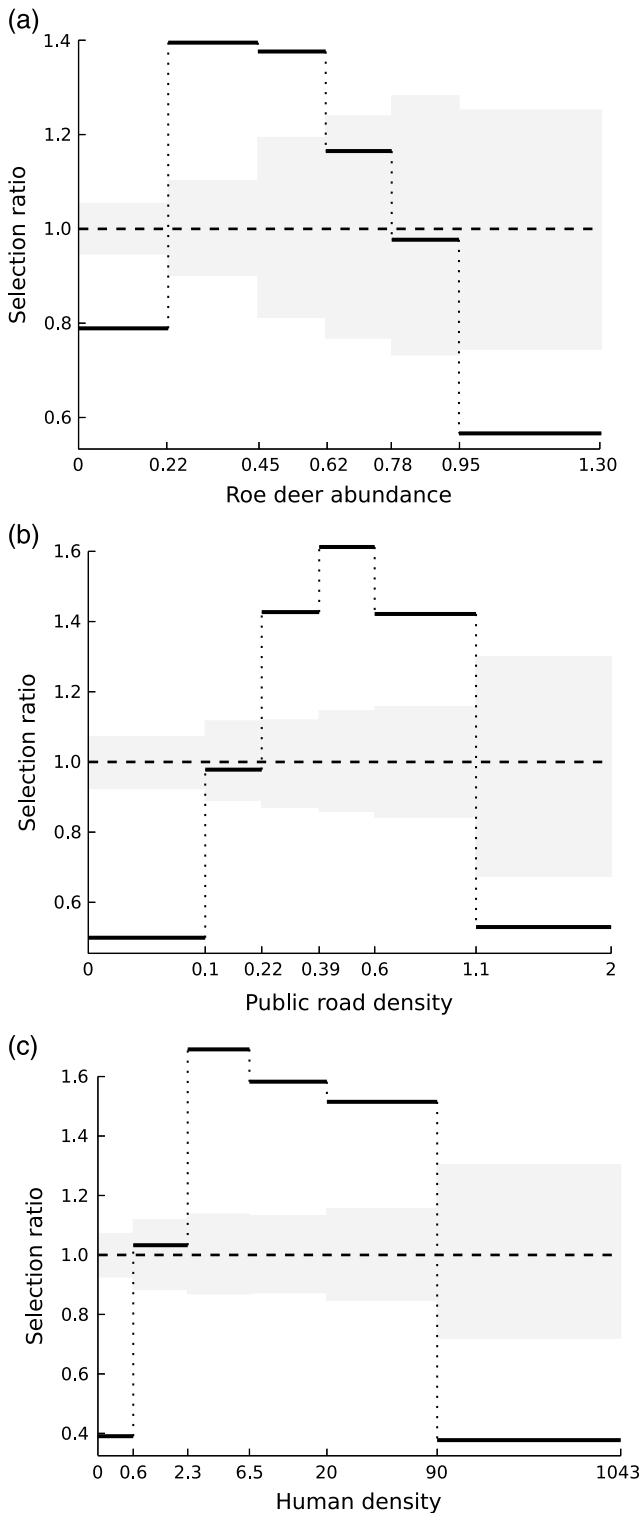
Figure 3. Ratios of density of used pixels over density of available pixels for different environmental variables. The observed ratio is represented by a thick line and should be compared to the random distribution with its 95% confidence interval in grey. The horizontal line at y = 1 indicates a null selection. (a) Roe deer abundance. (b) Public road density. (c) Human density. For reading convenience, the x axis has been square root transformed for (a) and (b) and log-transformed for (c).

in Norway are well known to occur in fragmented and disturbed areas (Mysterud 1999). Indeed, in our study area, roe deer abundance positively correlated with human density and roads density up to very high thresholds. Concerning road density, the optimum for roe deer was about two times higher than for lynx (corresponding to 0.4–0.6 and 1 km of roads km^{-2} for lynx and roe deer, respectively). Even more important, the human density optimum was about 30 times higher for roe deer than for lynx (corresponding to 2.3–6.5 and 136 inhabitants km^{-2} for lynx and roe deer, respectively). Roe deer were therefore much more tolerant of human disturbance than lynx, and could therefore sustain themselves in most converted areas. These results supported our third prediction and suggest that some areas used by lynx could potentially function as ''attractive sinks'' (sensu Delibes et al. 2001); attractive due to the presence of abundant roe deer, but sinks because of mortality risks caused by the proximity of people. Despite
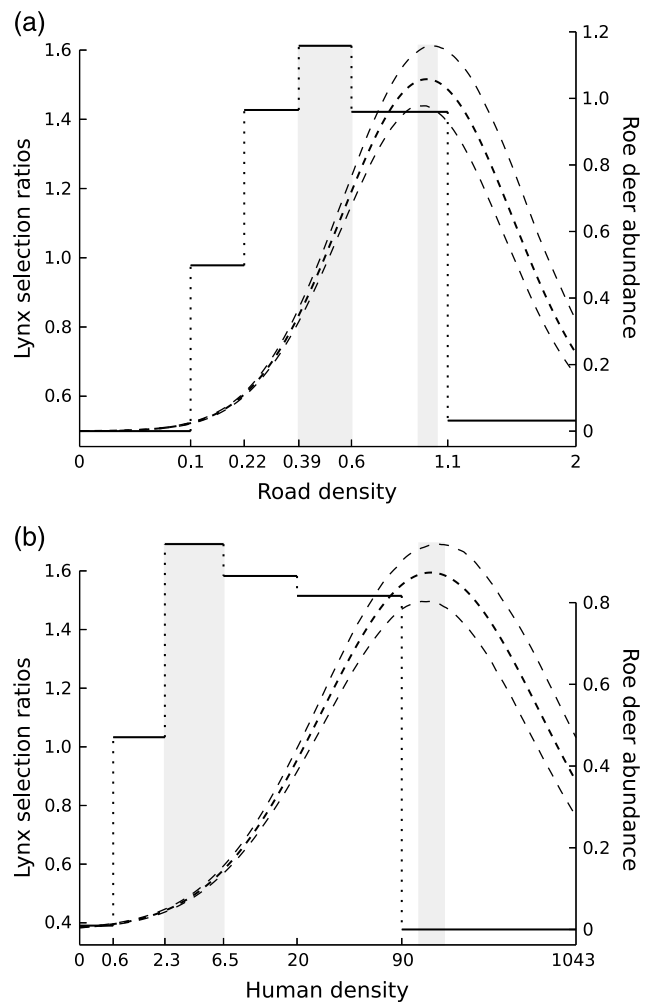

Figure 4. Lynx selection ratios (thick lines) and roe deer abundance (dashed lines) for (a) public road density, and (b) human density. For roe deer abundance, 95% confidence intervals of the predictions are provided. The grey bins indicate lynx and roe deer optima. The x axis has been transformed prior the analysis to match the scale transformation of Fig. 3, i.e. with a square root function for (a) and a log function for (b).

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these mortality risks, maladaptive behaviors tend to the selection of these areas where the species is unable to replace itself without immigration. While the whole lynx population is not currently threatened and is still expanding in southern Norway, such attractive sinks could lead to local population reductions. However, lynx seemed to select against these risky areas and therefore perceive them as unsuitable. In our study area, an additional analysis using locations where lynx are shot provided no additional information because of the crude resolution. Further analyses at a finer scale, including the exact locations where lynx are killed and fitness proxies, are needed to test this hypothesis.

Optimal foraging theory (Stephens and Krebs 1986) predicts that animals should balance both energy intake and predation risk, which often grow concurrently (Houston et al. 1993), leading to a necessary trade-off. Whereas the theory is well developed for herbivores, with a particular emphasis on modelling (Lima and Bednekoff 1999), there has been little empirical evidence of this mechanism for large carnivores. Cheetahs *Acinonyx jubatus* in the Serengeti National Park in Tanzania have low competitive ability compared with their principal competitors, hyenas and lions, which are directly responsible for their low density (Durant 1998). In response to that, cheetahs actively avoid lions and hyenas, and are therefore restricted in areas with lower prey density, which become "competition refuges" (Durant 2000). Our results suggest that the same mechanism could occur in southern Norway where lynx face "competition" for space with humans: areas with the highest prey potential correspond to areas favourable for human activity, including hunting. In this context, their low "competitive" ability compared with humans created both "competition" refuges at low to moderate roe deer density and potential attractive sinks at high prey density. This result, however, might be specific to southern Norway where the gradient in the environment allow roe deer abundance and human activity to grow concurrently to some extent. In other areas such as central Europe, a negative association between roe deer and human may generally result in both a high roe deer abundance and a low human activity in the areas selected by lynx (Zimmermann and Breitenmoser 2002, Niedziałkowska et al. 2006).

Lynx and roe deer in southern Norway share a similar pattern of space use regarding to human impact, using areas with intermediate levels of disturbance more than areas that are either undisturbed or highly disturbed. On the one hand, roe deer benefit to a large extent from current human land use practices, which results potentially in a decreased predation pressure from lynx as a side-effect. On the other hand, the situation was not so favourable for the predators that are restricted in competition refuges at medium to low prey density. However, lynx are very efficient predators even at low roe deer density and in addition can survive by preying on several alternative prey species including mountain hares, forest grouse, red foxes, domestic sheep, red deer, wild reindeer, and even moose (Odden et al. 2006). As a consequence, roe deer were trapped between humans (through hunting) and lynx (through predation). In terms of lynx conservation this study confirms the ability of lynx to live in relatively human-modified habitats, but this also implies that lynx conservation is going to occur mainly in areas with high potential interaction rates between humans and lynx as the lynx avoid the "wilderness" areas with little human activity. This implies that human caused mortality rates are going to remain high and that lynx management will need to involve constant monitoring to ensure that populations persist.

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