Eurasian lynx habitat selection in human-modified landscape in Norway: Effects of different human habitat modifications and behavioral states

Yaëlle Bouyer [a,b,*], Gilles San Martin [c], Pascal Poncin [a], Roseline C. Beudels-Jamar [b], John Odden [d], John D.C. Linnell [d]

[a] Unité de Biologie du Comportement, Université de Liège, Quai Van Beneden 22, 4000 Liège, Belgium
[b] Conservation Biology Unit, D.O. Nature, Royal Institute of Natural Sciences of Belgium, Rue Vautier 29, 1000 Brussels, Belgium
[c] Plant Protection and Ecotoxicology Unit, Life Sciences Department, Walloon Agricultural Research Centre, Chemin de Liroux 2, 5030 Gembloux, Belgium
[d] Norwegian Institute for Nature Research, PO Box 5685 Sluppen, 7485 Trondheim, Norway

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ABSTRACT

Eurasian lynx are often regarded as being particularly sensitive to human land-use. However, in the European context where human influence is pervasive, the conservation of lynx requires that they be integrated into the human-dominated landscape. Although previous studies have looked at how lynx respond to human land-use in a broad sense, they have failed to examine the details of how different types of human induced impacts (forest fragmentation, human density, different types of transport infrastructure) influence distinct lynx behaviors. Furthermore, they have not examined the extent to which lynx modify their fine scaled avoidance behavior of anthropogenic landscape features according to the specific behaviors (resting sites, kill sites, movement) in which they are engaged and how these relationships are modified by prey density or the sex of the lynx. We used Resource Selection Functions to examine how 19 GPS-marked lynx in southeastern Norway responded to an index of cumulative human habitat modification while engaged in different activities. We found that lynx select for areas with medium levels of human modification, avoiding both the very highly modified and the areas with low degrees of modification. Females in general appear to be less tolerant of human modification than males, especially when it comes to resting sites. Terrain (ruggedness and elevation) appears to be important in permitting lynx to exploit heavily modified areas. Our study demonstrates that lynx show a nuanced response to human habitat modification, which offers hope for their conservation in Europe.

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1. Introduction

Most of the planet is now impacted by human activities (Sanderson et al., 2002), with an ever increasing conversion and fragmentation of natural habitats. Transport infrastructure, forest-related activities and forest conversion to agriculture continually fragment and disturb habitats, and can affect species behavior, abundance and survival (Vos and Chardon, 1998; Kramer-Schadt et al., 2004; Northrup et al., 2012; Fahrig and Rytwinski, 2009; Trombulak and Frissell, 2000; Baldwin et al., 2004). Human density and related infrastructure, above some thresholds, are often linked to avoidance behavior (Basille et al., 2009). Of all the species negatively affected by human developments and activities, large carnivores are generally considered as particularly sensitive because of their large spatial requirements and low densities (Fahrig and

Rytwinski, 2009; Cohen and Newman, 1991; Crooks, 2002). These spatial requirements imply that large carnivore conservation, especially in crowded areas like some parts of Western Europe, require their integration into human-dominated landscapes because protected areas are too small (Chapron et al., 2014). In addition to their indirect effects (habitat fragmentation, development of road networks, loss of prey availability, Huck et al., 2010; Putman and Staines, 2004; Milner et al., 2007), humans are considered as the most dangerous intra-guild predators for large carnivores (Woodroffe and Ginsberg, 1998; Treves and Karanth, 2003) directly causing mortality through hunting, poaching and vehicle collisions (Lindsey et al., 2007; Packer et al., 2009; Andrén et al., 2006; Kaczensky et al., 2003).

The response of large carnivores to human activity is conceptually similar to a prey species' response to predation risk (Frid and Lawrence, 2002). For example, large carnivores will adjust their habitat use to avoid human hunting (Ordiz et al., 2012; Theuerkauf et al., 2003) or human encounters (Ordiz et al., 2013; Wam et al., 2012; Valeix et al., 2012). To reduce mortality risk, large carnivores should then avoid areas with high densities of humans and select areas with perceived low mortality risk. However, in Europe, the ungulates that are the main prey of

* Corresponding author at: Conservation Biology Unit, D.O. Nature, Royal Institute of Natural Sciences of Belgium, Rue Vautier 29, 1000 Brussels, Belgium.
E-mail addresses: yaellebouyer@gmail.com (Y. Bouyer), roseline.beudels@naturalsciences.be (R.C. Beudels-Jamar), john.linnell@nina.no, john.odden@nina.no (J.D.C. Linnell).

large carnivores often occur at higher densities close to artificial feeding sites and human modified landscapes (Mysterud et al., 1997; Bunnefeld et al., 2006; Torres et al., 2011). This distribution of prey can induce potential trade-offs between risk avoidance and prey access (Bunnefeld et al., 2006). Therefore, individual predators should balance their choices between access to resources and mortality risks induced by human proximity (Valeix et al., 2012). Complex species like large carnivores should have the ability to make these trade-offs in a very fine-scaled and differentiated manner. To date, there have been many broad scale studies of how a diversity of large carnivores respond to human habitat modification, activities and structures (e.g. Jedrzejewski et al., 2004; Blanco et al., 2005; Niedziałkowska et al., 2006; Ordiz et al., 2013). However, these studies have not been able to explore the way the species adapt to human-modified landscapes at fine scales.

Quantification of species–habitat relationships can be done through habitat selection modeling. Habitat selection can vary depending on behavioral state since access to a diversity of resources is essential for survival and reproduction. Finding, killing and consuming prey, territory defense, mating, raising offspring and avoiding mortality are necessary parts of an individual's daily or annual life cycle (Wilmers et al., 2013). Spatial segregation of the resources for different behaviors can theoretically induce specific behavioral differences in habitat selection (Owen-Smith et al., 2010; Roever et al., 2014). Quantifying habitat selection from pooled data (including different behavioral states) can have important implications for conservation and management (Roever et al., 2014). Indeed, one major effect of pooling data is the risk of reducing the inference obtained from statistical models used to understand species ecology and habitat selection. Roever et al. (2014) identified pitfalls in the statistical quantification of habitat selection when behaviors are pooled: (1) Opposing patterns of habitat selection between behaviors may lead to an overall failure to detect selection; (2) An underestimation of the strength of selection and failure to recognize the importance of some habitats, and (3) The shape of the selection curve is likely to be sensitive to behavior and thus can express different forms from one behavior to another.

Our previous studies of Eurasian lynx (*Lynx lynx*) habitat selection in Norway have focused on a coarse spatial scale — approximately related to the distribution and alignment of lynx home ranges (Basille et al., 2009, 2013; Bouyer et al., 2015). A home range necessarily contains all the diverse resources needed for individual survival and reproduction. These studies have shown that lynx can live in relative close proximity to human-modified areas, often selecting for areas with medium levels of human modification. However, these studies have not explored the behavioral mechanisms by which lynx manage to integrate themselves into these landscapes. In this study, we use GPS telemetry data on lynx in southeastern Norway to explore lynx habitat selection in a human-dominated landscape. We differentiate between the sexes and between three broad behaviors (resting sites, kill sites, movement) in our attempt to understand how lynx respond to different degrees of human impacts (Riffell et al., 1996). In addition, we examine how prey density and topography modulate these patterns.

Contrary to previous studies on lynx habitat selection in Norway, we were interested in the cumulative effects of different types of human modifications to the landscape. We considered that effects were cumulative when the joint effects of features in close proximity were greater or lesser than the influence of the features alone (Riffell et al., 1996). An animal's response may depend on the intensity of human pressure (Harriman and Noble, 2008; Semeniuk et al., 2014). For example, an agricultural field surrounded by forest may not represent an area of high human pressure for a carnivore and may even have a positive effect as it can attract prey such as large herbivores. In contrast, an agricultural field surrounded by houses and a road may represent too great a risk of mortality and disturbance to be worth the potential benefits.

For this reason, we expected that lynx would select for areas with medium human modification, and avoid areas of both very low and very high cumulative land-uses. Taking into consideration the

evolutionary significance of the different behaviors (Krebs and Davies, 1981), we predicted that resting sites would show a stronger selection for less disturbed areas, and kill sites would occur in areas with higher human pressures due to the presence of prey (Basille et al., 2009). We also expected that females would show a stronger avoidance of human dominated landscapes than males. Finally, we predicted that a complex topography (based on ruggedness and slope) would increase lynx tolerance of human land uses because of the variability in cover and security provided.

2. Material and methods

2.1. Study site

The study was conducted in southeastern Norway across seven counties (Telemark, Vestfold, Østfold, Buskerud, Oslo, Akershus and Oppland) between 58°N and 63°N. This includes the most populated areas in Norway, including the urban conglomeration around the capital city, Oslo. The area contains a gradient of environmental conditions with highly fragmented urban, suburban and agricultural areas in the southeast (Oslo, Østfold, Akershus) and southwest (Vestfold) to forest dominated areas in the north (Oppland) and northwest (Telemark, Buskerud). The topography goes from flat or hilly areas in the south and east to higher altitudes with steep slopes in the north and west. Overall, the forests are intensively exploited through clear cutting and regrowth, and are mainly composed of Norwegian spruce (*Picea abies*), Scots pine (*Pinus sylvestris*), hoary alder (*Alnus incana*) and birch (*Betula pubescens*). Agriculture mainly consists of the production of grass and grain, with some production of crops like potatoes, turnips and strawberries. For more information on the study site, see Basille et al. (2009).

2.2. Animal capture

Between 2008 and 2013, 19 individual lynx (8 females and 11 males) were captured, as part of a Scandinavian project on lynx, following pre-established protocols. We used GPS-collars that transferred data via the GSM network (GPS plus mini, Vectronic Aerospace GmbH, Berlin, Germany). Lynx were trapped in wooden walk-through box-traps and foot snares. Box traps were equipped with two SMS-alarms that permitted access to the box by fieldworkers within an average of 5 h. Foot snares were continually monitored using radio-alarms which permitted a reaction time always less than 15 min. Animals were darted with an initial dose of 4 mg medetomidine + 100 mg ketamine per animal using a remote drug delivery system (Dan-Inject). In adults captured in box traps (calm animals), the doses were reduced to 2 mg medetomidine + 50 mg ketamine. For reversal of immobilization, 5 mg of atipamezole (Antisedan®) per mg of medetomidine was administered. All procedures were approved by the Norwegian Experimental Animal Ethics Committee, and permits for wild animal capture were obtained from the Norwegian Environment Agency. No complications were detected as a result of collaring among these animals.

2.3. Behavior identification

We selected data collected during periods of intensive location collection (up to 19 locations per day; 570 lynx days: 431 for females and 239 for males) in order to identify the behavior related to each GPS point. Only resident individuals with stable home range were selected for this analysis. For reproductive females, we removed GPS locations obtained between the beginning of June and the end of August, which correspond to the three first months of offspring when their movement was constrained while the kittens remained within a natal lair. Differentiation between behaviors was first made based on travel speed, and reinforced by field visits to locations. Field data were collected between November and April in winter, and between May and

September in summer. Animals were fitted with GPS-GSM collars that allowed us to easily detect a potential kill site directly after the animal had left the area due to the presence of several lynx locations a few hundred meters apart in the same area and over a short term period (2–3 days). This method has given good detection results in similar Scandinavian studies (Gervasi et al., 2014; Mattisson et al., 2011). Potential kill sites were defined as a set of at least two locations within 100 m and were visited to search for prey remains (Mattisson et al., 2011). The prey species and, whenever possible, its sex and age class were identified when a carcass was found. For small prey items (hares and birds), underestimation of their presence is most likely probable as they are more difficult to find, may not persist long, and may be so small that no clusters are formed when they are killed and completely consumed. However, lynx diet in south Norway is heavily dominated by wild ungulates, mainly roe deer (Gervasi et al., 2014; Odden et al., 2006). These kill sites are easy to find because lynx typically spend several days consuming them. In this study we only focused on large ungulate kills. Such field visits also helped confirm some locations as resting sites (based on signs in snow during winter and compressed vegetation in summer). A threshold of 135 m/h was obtained by calculating the mean speed between two consecutive confirmed resting sites. When the speed between two consecutives locations was less than 135 m/h and no kill was recorded at this location, the location was considered as a resting site. Kills were defined when the speed between two consecutives locations was less than 135 m/h and when the presence of prey was confirmed. Movements were defined when the speed between two points was more than 135 m/h and when no kill was recorded. Because lynx are not ambush hunters, there was little risk of confusing resting sites with hunting sites.

To reduce autocorrelation, we systematically selected points with at least 2 h differences for the movements. Since points of resting and killing sites tended to be clustered over several days, only one point representative of the cluster was kept for the analysis and considered as a kill or resting site.

2.4. Statistical analysis

2.4.1. Habitat covariates

We included environmental, topographic and anthropogenic covariates in our models. All these covariates were available in a raster format at a 1 km² spatial resolution. Topographic variables included elevation and terrain ruggedness (Terrain Ruggedness Index, Riley et al., 1999) as a previous study showed that these variables may have an important effect on lynx habitat selection (White et al. submitted). Elevation was obtained from the Norwegian Mapping Authority as a raster digital elevation model (DEM). An index representative of roe deer abundance based on extrapolation from pellet-group count techniques within lynx home ranges (Bouyer et al., 2015) and proportion of forest were also included as predictor variables. In addition, sex was taken into consideration to test for potential differences in lynx habitat selection between males and females.

Anthropogenic covariates were represented as a habitat modification index (Fig. 1). Our interest was in the additive effect of the main anthropogenic variables expected to have an impact on lynx habitat selection. Home ranges encompassed different values of the index, with some individuals living in more human-disturbed areas than others. To create this index, we used digital maps representative of the density of fields (Global Land Cover 2000 database), forest roads, public roads (Norwegian Mapping Authority) and human residential density (Takle 2002) inside 1km²pixels in an area large enough to include the home ranges of all our study lynx. The default situation (index value 1) consists of semi-natural habitats (mainly exploited boreal forest, bogs, or rarely alpine tundra) but without habitat conversion (to fields or built-up areas), infrastructure (roads) or resident people. We then ranked other pixels according to the extent to which this situation was modified (Table 1). With each additional anthropogenic variable, the index was ranked higher. Road presence was considered as an increase in disturbance on lynx use of the landscape. In Norway, forest roads are associated with activities such as farming, logging and hunting
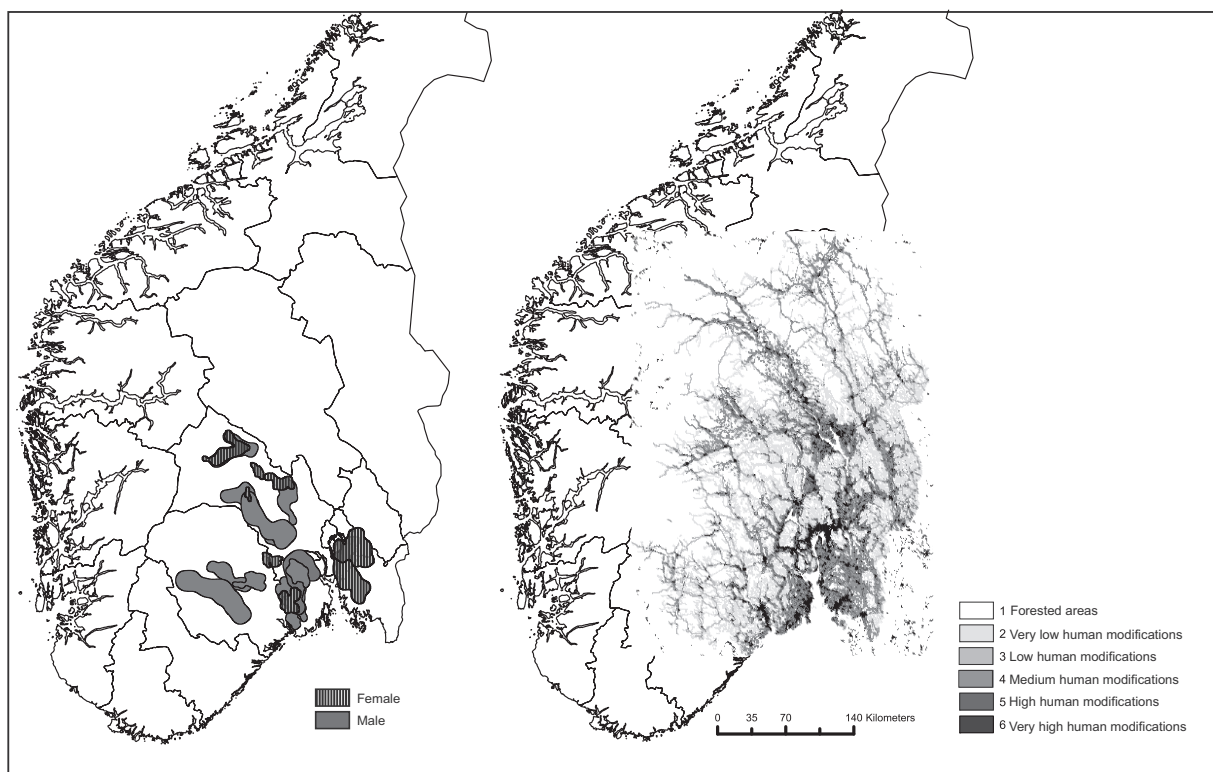

1 Forested areas
2 Very low human modifications
3 Low human modifications
4 Medium human modifications
5 High human modifications
6 Very high human modifications

Female
Male

0   35   70   140 Kilometers

Fig. 1. Location of the 19 lynx home ranges used in the study area (left map) and the habitat modification index with the 6 modification classes (right map).

Table 1
Presentation of the human habitat modification categories. The index is intended to represent increasing levels of human habitat modification, levels of infrastructure and potential for disturbance. The map-based criteria that we used to classify the 1×1 km pixels are presented, along with an interpretation of what landscape type this represents. The column "% of presence" quantifies the percentage of pixels of the related index value present in the study area.

Class	Classification criteria	Interpretation	% of presence
1	Semi-natural habitats with no fields and no roads	"Forested" areas of semi-natural habitat with no infrastructure or habitat conversion (although all forest is exploited)	59%
2	Presence of agricultural fields and/or forest road	Rural landscape (low human modification)	20%
3	Presence of both forest roads and public roads, but no fields	Rural landscape (low human modification, but with public road access)	9%
4	Presence of fields, forest roads and public roads	Rural landscape (medium human modification)	7%
5	Human density ≥ 20 and < 100 inhabitants per km^2	Rural landscape (medium to high human modification and substantial number of residents)	3%
6	>100 inhabitants per km^2	Rural–urban interface (periurban/suburban/urban)	2%

of both ungulates and lynx. Hunters use snow tracks to locate lynx and are responsible for 43% of lynx deaths in Scandinavia (Andrén et al., 2006). Presence of public roads at high density also have a negative effect on lynx habitat selection both at large and at fine scale (Bunnefeld et al., 2006; Andrén et al., 2006; Basille et al., 2013). To account for the negative effect of human density, we selected a threshold of 20 inhabitants/km^2 based on a previous study conducted in the same area (Bouyer et al., 2015) Lynx were deterred by a density of 20 inhabitants/km2 or more in a rural landscape. To account for the presence of an urban (built-up) area, a threshold of 100 inhabitants/km^2 was chosen based on visual examination of spatial variation in population density and known presence of built up areas.

2.4.2. Use of resource selection functions

We used resource selection functions (RSFs) to assess habitat selection under a use-availability design (Manly et al., 2002) for the three different behavior types. RSFs compare habitats that are used (animal points) with those that are available (or unused) to predict a relative probability of use. RSFs equations often take the form:

$$w(x) = \exp(\beta_1 x_1 + \dots + \beta_n x_n),$$

where $w(x)$ is the relative probability of use, β_n are the estimated coefficients, and x_n are habitat variables.

To define available habitat characteristics, we generated random 'available' locations within home ranges. For each individual lynx we used a different number of random locations equal to the number of locations of the most common behavior.

To account for different responses between different animals to similar availabilities of habitat, we added individual identity as a random effect to our model (Hebblewhite and Merrill, 2008). It allowed for conditional inferences about individuals lynx as well as marginal inferences about the population and accounted for different sample sizes between individuals (Gillies et al., 2006; Wilmers et al., 2013). To obtain individual estimates of selection on the Index covariate, we added a random coefficient to the model. The generalized linear two-level mixed-effects binomial model for location i and lynx j, with a random coefficient is given by:

$$\text{Logit}(y_{ij}) = \beta_0 + \beta_1 x_{1ij} + \beta_2 x_{2ij} + \dots + \beta_n x_{nij} + \gamma_{1j} x_{1j} + \gamma_{0j},$$

where $\beta 0$ is the fixed-effect intercept, γ_{0j} is the random intercept (i.e., the difference between the mean intercept $\beta 0$ for all lynx and the intercept for lynx j), and γ_{1j} is the random coefficient of covariate $\times 1$ for lynx j (i.e., the difference between the mean coefficient $\beta 1$ for all lynx and the coefficient for lynx j) (Mabille et al., 2012).

To improve model convergence and to facilitate comparison of model coefficients among covariates, we z-transformed all the covariates such as $(\frac{x - \bar{x}}{std(x)})$. For each behavior, models were fitted with multiple and all possible combinations of covariates and the best models retained were the ones minimizing the AIC.

All analyses were conducted using the package *lme4* in R. We checked for correlation among variables using the Variance Inflation

Factor (VIF; realized on GLMs) in the package car and made sure than no variables had a VIF higher than 3. GLMMs did not exhibit any signs of spatial autocorrelation based on the semi-variograms.

3. Results

Average home range size using the 95% kernel method was 912 km^2 (± 485 km^2) for males and 535 km^2 (± 481 km^2) for females. We recorded 709 resting site locations for 19 individuals (a mean of 30 (± 30 SE) per individual), 194 kill-sites for 16 individuals (a mean of 11 (± 4) per individual) and 3905 movement locations for 19 individuals (mean of 205 (± 70) per individual) (Table 2).

The RSFs analysis results revealed that lynx selection of landscape was dependent on the degree of human modification (Table 3). Plots of the relative sensitivities of each behavior to human modification revealed that the pattern of response to human impact was similar between the behaviors (Fig. 2). For all three behaviors, lynx seem to select rural areas of medium to high human modification and avoid unmodified semi-natural habitats and rural–urban interface areas. Some individuals responded slightly differently from the population mean for the different behaviors, but no distinct pattern was found. Due to the low number of kills at the urban–rural interface (N = 2), results or kill-sites in such areas are not presented (see Fig. 2).

3.1. Effect of ruggedness

For all the three behaviors considered, lynx selected rugged areas. Resting sites and kill-sites are present in rugged areas for all the classes of human habitat modification except for the rural–urban interface (Fig. 3). Lynx clearly select for, and move, in rugged areas for all the different classes of human habitat modification.

3.2. Effect of sex and elevation

Lynx response to elevation varied by sex and behavior. Males and females show different responses for resting sites but similar responses for kill-sites and movement. For resting sites, females selected high elevation for all modification classes except for the rural–urban interface. In contrast, males selected for low elevation for all modification classes. Lynx killed at low elevation when in landscapes with low human modification, while they killed at much higher elevation in rural landscapes with medium to high human modification. Kills did not occur in the rural–urban interface. Lynx moved at low elevations in forested areas and in rural landscapes with low human modification, but they moved at higher elevation when they were in rural landscapes with medium to high human modification.

3.3. Effect of sex and forest density

Resting sites, kill sites and movements all occurred where patches of forest were present. The probability of observing resting sites for females was higher in rural landscapes of medium human modification but lower in unmodified areas and in the rural–urban interface. The

Table 2
Number of locations observed for each behavior within the different classes of the habitat modification index for males (M) and females (F).

Index classes	1		2		3		4		5		6		Total
Sex	M	F	M	F	M	F	M	F	M	F	M	F	
Resting sites	46	31	93	67	61	18	83	170	37	84	4	15	709
Kill-sites	26	6	32	25	18	3	38	27	10	7	2	0	194
Movements	319	182	699	369	368	84	579	675	239	298	32	61	3905

probability to observe resting sites for males was higher in medium to high human modification rural landscapes and the rural–urban interface. The probability to observe a kill, both for males and females, increased with forest density and human modifications.

3.4. Effect of sex and roe deer density

The differential behavioral response of both males and females to roe deer density was not constant across behaviors: it was similar for kill-sites and movements, but different for resting sites. Females used resting sites at low roe deer density in heavily forested areas and rural landscapes with low human modification. Female's resting sites were also observed at medium roe deer density in rural landscapes of medium to high human modification, and in the rural–urban interface. Males avoided high roe deer density and selected for low roe deer density for their resting sites in all categories of human land-use

modification. Kills were located at relatively low roe deer density for all the classes of human habitat modification. Lynx moved in low roe deer density areas when they were in heavily forested areas and in rural landscapes of low human modification. They moved at medium to high roe deer density when they were present in rural landscapes of medium to high human modification and in the rural–urban interface.

4. Discussion

Our study explored how Eurasian lynx in Norway adjust their patterns of habitat selection associated with specific behavioral states (resting sites, kill sites and movement) in response to the cumulative impact of various anthropogenic modifications to the landscape. Our results reveal that lynx actually select for areas with medium degrees of human modification, preferring to use rural areas with various

Table 3
Results for the best RSFs presented for each behavioral state. Binomial mixed models with z-transformed explanatory variables.

| Fixed effects	Resting sites		Kill sites		Movements	
	Coefficients	Std. Error	Coefficients	Sdt. Error	Coefficients	Std. Error
Roe density	0.528	0.087	− 13.303	2.455	− 2.468	0.336
SexM	− 0.096	0.496	1.148	1.467	0.016	0.161
Index2	0.581	0.259	5.779	1.790	1.066	0.195
Index3	1.015	0.449	5.294	2.158	1.271	0.273
Index4	1.301	0.336	7.086	1.845	1.785	0.216
Index5	1.116	0.467	6.162	1.943	1.981	0.232
Index6	− 2.525	0.844	− 30.182	1289.505	2.044	0.407
Forest density	0.731	0.112	− 0.023	0.365	0.419	0.055
Ruggedness	0.685	0.054	0.283	0.071	0.579	0.064
Elevation	0.919	0.097	− 4.860	0.770	− 1.264	0.109
SexM × Elevation	− 2.241	0.165	− 0.611	0.251	− 0.106	0.070
SexM × Index2	− 0.824	0.345	− 1.474	1.373	/	/
SexM × Index3	− 0.719	0.572	0.288	1.878	/	/
SexM × Index4	− 0.797	0.461	− 0.704	1.585	/	/
SexM × Index5	− 0.334	0.637	− 0.234	1.757	/	/
SexM × Index6	2.910	1.278	29.065	1289.222	/	/
SexM × Forest density	0.399	0.186			0.122	0.071
SexM × Roe density	− 1.394	0.293	/	/	/	/
SexM × Ruggedness	/	/	/	/	0.227	0.083
Index2 × Forest	/	/	0.983	0.584	/	/
Index3 × Forest	/	/	0.629	0.551	/	/
Index4 × Forest	/	/	0.724	0.452	/	/
Index5 × Forest	/	/	1.146	0.681	/	/
Index6 × Forest	/	/	14.309	18.681	/	/
Index2 × Elevation	/	/	4.189	0.785	0.830	0.117
Index3 × Elevation	/	/	5.082	0.902	1.505	0.156
Index4 × Elevation	/	/	5.446	0.788	1.787	0.115
Index5 × Elevation	/	/	6.086	0.863	2.151	0.142
Index6 × Elevation	/	/	9.797	4.804	4.037	0.372
Index2 × Roe	/	/	10.915	2.520	2.372	0.355
Index3 × Roe	/	/	12.195	2.816	2.052	0.470
Index4 × Roe	/	/	13.046	2.486	2.885	0.344
Index5 × Roe	/	/	13.071	2.563	2.718	0.340
Index6 × Roe	/	/	23.936	14.283	2.723	0.378
Random effects	**Variance**		**Variance**		**Variance**	
Index2	0.027		3.641		0.155	
Index3	0.538		8.311		0.463	
Index4	0.365		6.207		0.330	
Index5	0.973		6.971		0.344	
Index6	3.396		11.316		0.882	
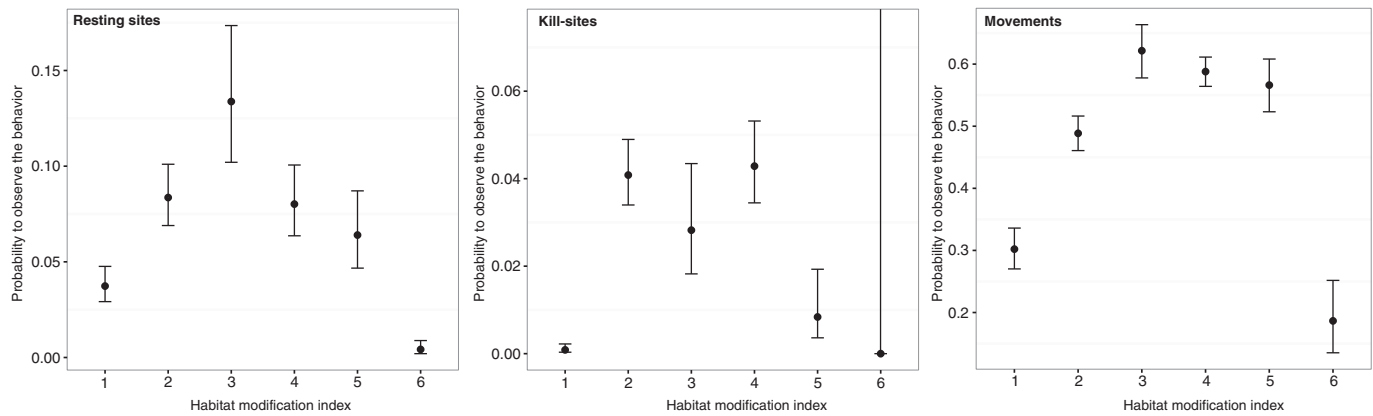
Fig. 2. Lynx habitat selection for the three behaviors (resting, killing and moving) presented for six levels of increasing habitat modification (with the other covariates maintained at their mean for each index category). The standard error of the prediction is very high for kill-sites and land-use modification index 6 because there were very few observations of this behavior in these conditions (N = 2).

degrees of modifications with a mix of forest and agriculture that are often associated with the presence of human settlements and transport infrastructure. Unmodified areas of semi-natural habitat and partly urbanized areas were less preferred. Habitat selection of resting sites differed between males and females, with females selecting for more secure landscapes than males. These results confirmed previous observations on lynx habitat selection in human dominated landscapes in the same study area (Bunnefeld et al., 2006; Basille et al., 2009).

4.1. Impact of prey distribution on lynx habitat selection

The selection by lynx for rural landscapes where human habitat modification is present with regard to unmodified areas of semi-natural habitat is probably a direct consequence of roe deer presence. Roe deer represent the main prey species for lynx in this study area (Odden et al., 2006; Gervasi et al., 2014). Roe deer occur at highest densities in fragmented landscapes where human activities provide improved forage through opening forest canopy, agricultural crops, and supplementary feeding sites during winter (Basille et al., 2009; Torres et al., 2011). The data used in our studies also indicate the same pattern, with a predicted pellet density (Bouyer et al., 2015) increasing from 0.34 pellets/km^2 for class 1 of the anthropogenic index, to 2.65 pellets/km^2 for class 6 (Fig. 4). However, our study also reveals that lynx avoid the most modified landscapes (rural–urban interface) even if roe deer density is highest in such landscapes. This fine-scale avoidance of the most modified landscapes confirms the trade-off between roe deer density and human disturbance previously described at a coarser scale (Basille et al., 2009). In contrast, lynx avoidance of relatively unmodified and heavily forested landscapes is probably due to the associated increased energetic costs of hunting roe deer in areas where they occur at very lower density, and with less predictable distribution.

4.2. Habitat components relevant to lynx use of human-modified landscapes

Even though lynx select for areas with medium degrees of human modification, our study reveals that they still respond to other environmental characteristics of the landscape. In our analyses, lynx selected for areas with greater degrees of forest cover, and with more rugged terrain, for all the behaviors considered. These results confirm previous studies conducted on lynx habitat selection (Basille et al., 2009; May et al., 2008; Niedziałkowska et al., 2006; Zimmermann and Breitenmoser, 2002; Sunde et al., 1998). Forest represents habitat cover that is known to provide security. Sunde et al. (1998) reported that lynx were tolerant of human proximity when the density of forested areas was high, i.e. when good shelter was available. It is likely that presence of forest, even in relatively small patches, provides sufficient shelter for lynx to avoid

being disturbed by humans even at high human densities. Lynx preference for rugged areas can also be associated with shelter and an attempt to avoid disturbance by humans. Lynx are known to select for steep areas in heavily disturbed landscapes as steepness is associated with a low level of human activity (Basille et al., 2008). By contrast, the strength of selection for ruggedness was lower in less modified landscapes (Basille et al., 2009). Terrain ruggedness has not received much focus as a habitat characteristic before, but there is a growing body of literature that indicates how important this landscape characteristic can be at facilitating carnivore use of human dominated landscapes (Nellemann et al., 2007; Petram et al., 2004).

4.3. Importance of behaviors in habitat selection

Because humans are the major cause of large carnivore mortality in most landscapes (Woodroffe, 2000; Woodroffe and Ginsberg, 1998; Treves and Karanth, 2003), understanding their behavioral response to human presence is important in a context where large carnivores have to share landscapes with humans. Thus, behavioral responses to human-induced environmental changes can help determine the capacity of a species to adapt to environmental changes and human presence (Tuomainen and Candolin, 2011; Sih et al., 2011, 2012). Use of specific behavioral data instead of unclassified location data in our study has provided valuable nuanced insights for understanding lynx habitat selection within human modified landscapes in Norway, as their relative selection for, and avoidance of human modification was dependent on the specifics of the behavior. In general, lynx showed an ability to move through areas that were much more modified than areas where they would consume a kill or rest. Lynx movements are considered the most important indicator of lynx activity as it is often unequivocally related to hunting behavior (Jędrzejewski et al., 1993; Schmidt, 1999). However, in our study we did not look at the actual path used by lynx, the distance covered or the period of the day when the movements occurred. To better understand the effects of human disturbance on lynx movement, it would be interesting to take into account these information as they seem to have a high impact on other large carnivores. For example, European brown bears and wolves, which are primarily diurnal (Mech, 1992), seem to avoid humans by shifting their activity to twilight and night time (Theuerkauf et al., 2003; Ordiz et al., 2012; Ciucci et al., 1997).

Although selection of habitat was mostly similar between the sexes for movements and kill sites, resting males and females did not select for the same habitats. Females selected for rugged areas at high elevation, with medium roe deer density and high forest cover, while males selected for lower elevations and lower roe deer densities. Sexual selection theory indicates that males are more likely to take greater risks
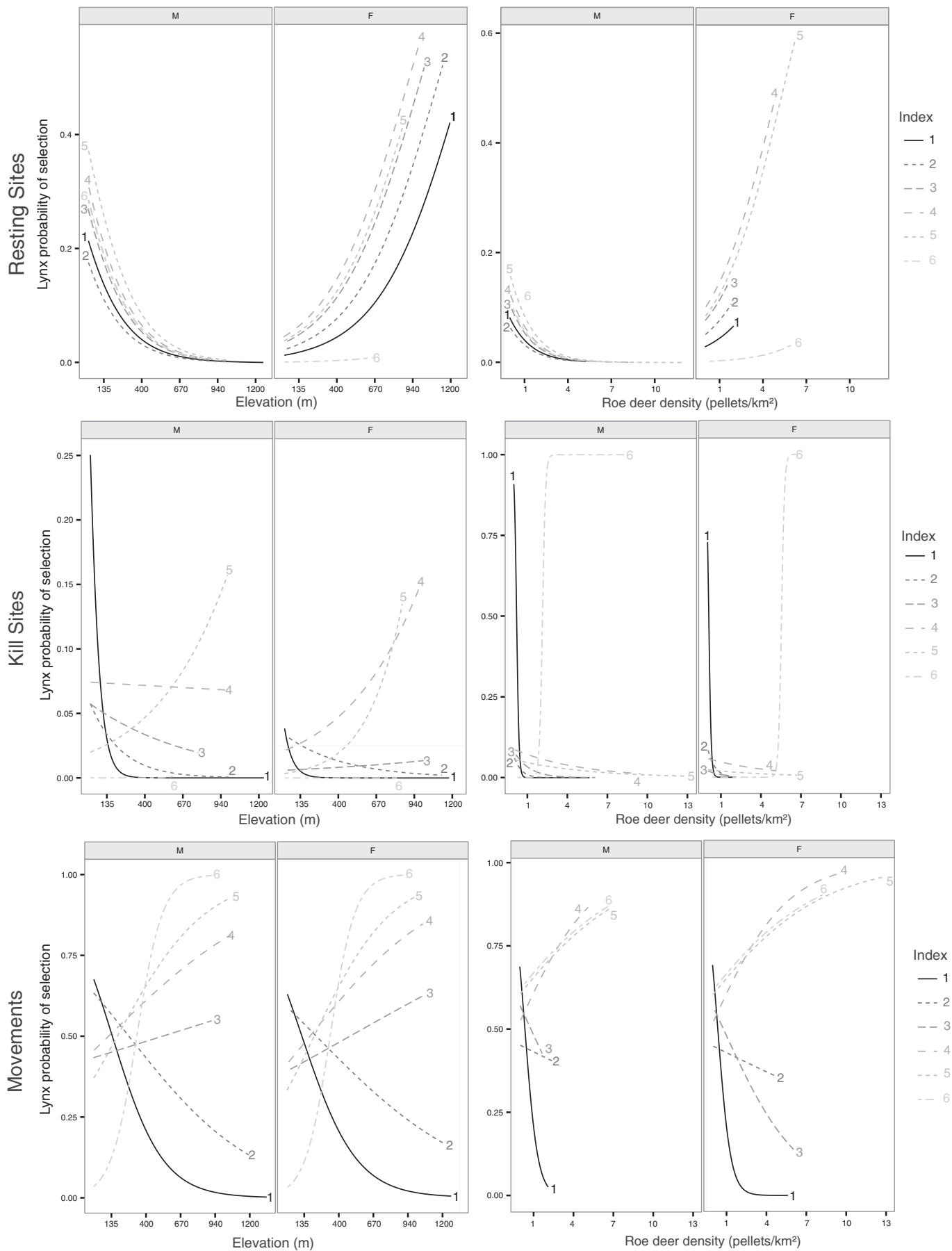
Fig. 3. Estimated relationship between the probability of lynx selection and elevation and roe deer density (with the other covariates maintained at their mean levels).
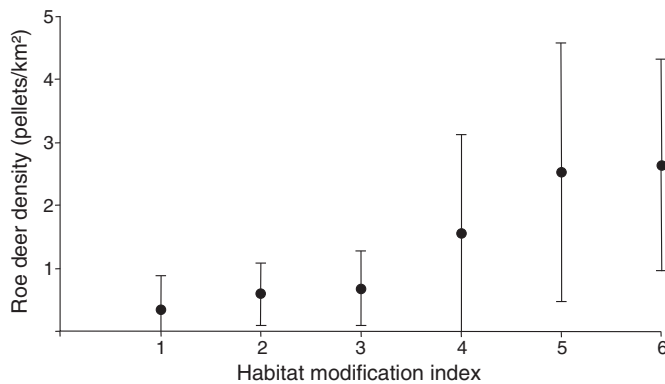
Fig. 4. Average roe deer density (pellets/km²) for each of the habitat modification categories.

than females in polygynous and dimorphic species (Trivers, 1985). Using another dataset from an adjoining study area, Bunnefeld et al. (2006) showed than female lynx with newborn kittens displayed a greater avoidance of humans than males, but that this avoidance behavior tended to decrease with kitten age. Even if most of the data on females used in this analysis do not correspond to the period when their kittens are very small, it seems that females showed a greater avoidance of risks than males. Sleeping is a period of great vulnerability because of a decrease in sensory awareness (Cristescu et al., 2013). Selection of resting sites is therefore important to minimize the risk of detection and maximize the benefits of the sleep period (Lima et al., 2005). Selection of higher areas by females would lead to a reduction of the risk of detection since human activity is more important in the valleys (Zimmermann and Breitenmoser, 2002). Females also selected for areas with higher predicted roe deer density, which indicates that they select resting sites where availability of food is important. All these results suggest that anti-predator behavior is more developed with females than males as shown by their systematic avoidance of areas of very high human modification. Similar results have been observed in jaguars (Conde et al., 2010).

Lynx generally consume all of a roe deer where they kill it, requiring that they return to the carcass multiple times over several consecutive days and nights (Jobin et al., 2000). Based on our data, we observed that when a carcass was available and the lynx was not eating, it sometimes slept several hundred meters away from the dead prey, changing the location of resting sites from day to day. Belotti (2012) reported that when a kill was close to human trails, lynx tend to move further away from the kill during the day. Even if we did not take into account the distance between kill sites and resting sites in relation to sources of human disturbance, it is clear in our results that lynx select different habitats for resting than for killing. Resting sites were located in areas where disturbance is more likely to be lower than at kill sites, which suggests that they select resting sites to minimize the risk of disturbance and kill sites to increase the chance of prey encounters. The fact that kill-sites and associated resting sites can be spatially disconnected implies that lynx can exploit prey in riskier habitats than they otherwise spend time in.

4.4. Conclusion and management implications

Overall, our results indicate that as long as prey are present, lynx are able to use a range of habitats with medium to high levels of human modification. Furthermore, we showed that lynx actively select for areas with medium levels of disturbance, only avoiding areas that are in immediate proximity to urban areas. Although these results come from Norway, which has relatively high forest cover and low human densities, these results are highly promising in the context of lynx recovery in continental Europe (Chapron et al., 2014). Today, most of

Europe is a mosaic of small forest patches and agricultural habitats crisscrossed by roads and with high human densities. Our results demonstrate that the presence of people, roads and fields are not automatically an obstacle to lynx presence as long as there is some cover (forest and terrain) and prey. Just because lynx can use an area does not automatically imply that their population has a positive or stable trend (Stapleton et al., 2014), and indeed our earlier work has shown that lynx are more vulnerable to being shot in areas with higher road densities (Basille et al., 2013). However, most lynx mortality in Norway is due to legal hunter harvest (Andrén et al., 2006) which is regulated within an adaptive management system with annual monitoring and quota setting (Linnell et al., 2010; Nilsen et al., 2012) implying that the fate of lynx in the study region is amenable to management control. Results such as these are important to frame the large carnivore conservation discourse (Linnell et al., 2015) because they show that there is no automatic connection between lynx and wilderness (Boitani and Linnell, 2015). This is good news for lynx conservation, as it implies that lynx conservation can potentially be achieved across vast areas of the European landscape, and not just in some few pockets of relatively unmodified habitat. Only once the potential is realized is it possible to begin taking steps to realizing it.

Acknowledgments

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