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Eurasian lynx natal den site and maternal home-range selection in multi-use landscapes of Norway

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Introduction

For many carnivore species with altricial offspring, securing suitable den sites with associated early maternal home ranges may be essential for reproduction (Gittleman & Thompson, 1988; Laurenson, 1994), especially for those that do not excavate their own shelters (Ross et al., 2010). The use of natal dens protects vulnerable newborn offspring against predation and inclement weather (Magoun & Copeland, 1998; Fernández & Palomares, 2000). Understanding natal den site selection is thus essential to ensure that these habitats are conserved, especially in human-dominated landscapes, as successful reproduction in carnivores may be negatively affected by human disturbance (Linnell et al., 2000) and female carnivores face significant energetic demands during this period. At present there is a dearth of information concerning the denning behaviours of wild felids, such as the pattern of breeding den use after parturition and during the early rearing of kittens.

The Eurasian lynx *Lynx lynx* is a solitary felid that breeds seasonally, producing litters of two to four kittens (Gaillard *et al.*, 2013). Kittens have a 50% survival rate over their first year (Breitenmoser-Würsten *et al.*, 2007) with mortality highest during the first 3–4 months (Schmidt, 1998).

Abstract

In carnivores, securing suitable den sites with associated early maternal home ranges is important for successful reproduction, and understanding natal den site selection is essential to ensure that these habitats are protected from human disturbance. This study investigated Eurasian lynx Lynx lynx natal den site selection across multiple use landscapes in Norway and explores whether the selection of early maternal home ranges across southern Norway involved a trade-off of security for access to their preferred prey species, roe deer *Capreolus capreolus*. The characteristics of natal dens and home ranges from 33 reproductive events were quantified across south-eastern and northern Norway. Natal dens were located in terrain further from the most accessible and disturbed areas (public roads) and in terrain more rugged than generally available. Early maternal home ranges were characterized by low human and low road density in rugged terrain and a selection for areas associated with higher or lower roe deer densities was not important in our analysis. Humans are the dominant cause of lynx mortality throughout Norway and our findings suggest that female lynx primarily chose areas that limited their interaction with people during the denning period.

> Although more research is required on early kitten mortality, natural causes such as starvation and disease are thought to play a role, and in Norway intra-guild predation is not considered an important factor (Andrén et al., 2006). Only two detailed studies, undertaken in Poland (Schmidt, 1998) and Switzerland (Boutros et al., 2007), have described Eurasian lynx denning behaviours, with both studies reporting that secure and well-camouflaged den sites are a prerequisite for kitten survival. No published data exist from northern Europe, where climatic conditions are especially challenging and where there are important differences in lynx management practices that may influence patterns of habitat selection. For instance, northern lynx populations are harvested annually in an attempt to mitigate conflicts with various livestock husbandry practices (Linnell et al., 2010). As a consequence, anthropogenic actions are responsible for almost 90% of mortality events reported in Scandinavian lynx, due to legal hunting in addition to poaching and road traffic incidents (Andrén et al., 2006). Additionally, poaching is the primary cause of lynx mortality across Norway and is considered a threat across all European lynx populations (von Arx et al., 2004).

> Research investigating lynx spatiotemporal distributions across central and southern Norway (Basille *et al.*, 2009) has

revealed a preference for habitat in rural lowland areas associated with higher human activity than average, as these areas support high densities of roe deer (Torres *et al.*, 2011), the preferred prey of lynx in this area. Human-dominated areas may therefore constitute population sinks for lynx (Bunnefeld *et al.*, 2006), as an abundance of roe deer attracts lynx and mortality risk increases due to a closer proximity to human activity (Basille *et al.*, 2009, 2013). This spatiotemporal strategy is however modified by both sex and reproductive status, and females with dependent young avoid risky habitats in the early kitten rearing phase by selecting day lairs and kill sites further from areas of human activity than males (Bunnefeld *et al.*, 2006).

This study investigated the landscape characteristics associated with lynx natal dens and maternal home ranges in relation to the annual home ranges of individual female lynx throughout Norway. Based on the above, we were interested in investigating to what extent female lynx select for remote and rugged terrain during this period to minimize disturbance and provide maximum security, and across southern Norway where data on prey densities were available, if this selection came at a cost in terms of reducing their access to prey.

Materials and methods

Study sites

This study investigated den site selection for lynx populations situated in southern and northern Norway (Fig. 1). Data were obtained from individual VHF and GPS-collared females between 1996 and 2012 from multifaceted projects investigating lynx ecology. In Southern Norway, data from female lynx (n = 22) were collected over a large study area encompassing the six counties of Hedmark, Buskerud, Akershus/Østfold,



Figure 1 Location of both study sites in Norway and the distribution of Eurasian lynx annual home ranges (n = 33) (Purple polygons). All green dots represent natal den sites, as determined by observers or interpreted from telemetry data. Red lines represent public roads. (To view the colours on the figure, please visit the online version of the paper on Wiley Online Library).

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Vestfold and Telemark between c. 58 and 63°N (Fig. 1) and in Northern Norway (n = 11) from the counties of Troms and Finnmark between c. 68 and 70°N (Fig. 1). For a description of both study sites refer to Herfindal *et al.* (2005) and Mattisson *et al.* (2011). In short, both study sites are subject to intensive management of wildlife populations and habitat, becoming increasingly human modified further south.

Lynx movement data

Female lynx were equipped with either VHF or GPS collars as part of the large-scale Scandlynx research project (http:// scandlynx.nina.no/) and following standard handling protocols approved by the Norwegian Experimental Animal Ethics Committee. Details on lynx capture can be found elsewhere (Herfindal et al., 2005). For female lynx that experienced reproductive events, 11 individuals were equipped with VHF collars (Telonics MOD-335, Telonics Inc., Mesa, AZ, USA), with two individuals fitted with store-on-board GPS collars (Lotek 3300SL, Lotek Wireless Inc., Ontario, Canada; Televilt Posrec 300, Followit AB, Lindesberg, Sweden) and 13 individuals fitted with GPS-GSM collars (Tellus 1C, Followit AB and Vectronic GPS PLUS, Vectronic Aerospace GmbH, Berlin, Germany). Primarily using aircraft, at least two to four locations per month were recorded for each VHF-collared lynx. On the ground search effort was also implemented, which varied in intensity, but increased dramatically during the denning period. The accuracy of locations for VHFcollared lynx was considered to be within 500 m of the estimated location, based on observer experience, while GPS locations were more accurate and within a few meters, and positioning schedules varied from a basis of three to four per day to every hour.

Consistent with other studies comparing use to availability (Kaartinen, Luoto & Kojola, 2010; May et al., 2012), we used 95% minimum convex polygons (MCPs) to determine the maximum probable home range from each breeding female (Ranges 8; Kenward et al., 2008). A prerequisite of at least 20 locations over a minimum of 6 months were required to calculate the annual home range for individual lynx, reducing potential autocorrelation (Herfindal et al., 2005; Basille et al., 2013). In our analysis, however, all lynx had annual home ranges constructed with >40 locations, with a northern mean of 1092 points [±335.84 standard deviation (SD)] and a southern mean of 363.54 (±293.26 SD). A minimum of 14 locations calculated from locations up to 8 weeks after parturition were used to define the maternal home range (Linnell et al., 2001). Only three lynx in this study were close to this low threshold and when we tested the effect of removing these individuals from the analysis we found no change in results, so we included these individuals. The remaining maternal home ranges were constructed using >30 locations with a northern maternal range mean of 329.45 points (±283.89 SD) and a southern maternal home range mean of 106.45 (±86.69 SD). Ninety-five per cent MCPs were also used for estimating the maternal home range, peeled around the harmonic mean centre (Spencer & Barrett, 1984).

Den site monitoring

Female lynx adopt a central place foraging behaviour centred around the natal den for the first 6–8 weeks after parturition in May and June (Schmidt, 1998). Repeated revisits to any one location by a female lynx during this time frame indicated a possible den site and suspected natal dens were generally visited when kittens were between 2 and 6 weeks of age to confirm parturition, accurately locate natal dens and record kitten demographic parameters.

Environmental covariates

A total of 33 reproductive events from 26 individual lynx were used in the analysis. Explanatory covariates considered likely to be important in influencing the denning behaviour of female lynx (Table 1) were extracted from GIS-based digital maps using ArcGIS 9.3.1 (Environmental Systems Research Institute (ESRI), 2009). For den sites, the value extracted was that closest to the locality, depending on the resolution of the data (Table 1). For annual and maternal ranges, mean values were calculated based on all values falling within the respective ranges.

Within ranges, potential human impact was measured as both road density and human (resident) density. Road density (public and private roads) was calculated as the total length of roads within each home-range type divided by the area of the relevant home range. Public roads are high traffic roads, ranging from municipal roads to national highways, while private roads are characterized by little traffic in connection to farming, logging or recreational areas. We divided roads into these two categories to account for different levels of potential disturbance (May et al., 2012). An index of roe deer density, based on extrapolation from pellet group count techniques within lynx home ranges, was inferred from a separate study investigating density patterns of large carnivore prey species in southern Norway (Bouyer et al., 2015). Human density was calculated as the mean density within the home-range type, based on available data of residential addresses (Table 1). Human accessibility to lynx habitat was calculated by estimating the distances between den sites and the nearest private and public roads as well as human settlement. Mean values of elevation, Terrain Ruggedness Index (TRI; Riley, DeGloria & Elliot, 1999) and Slope–Aspect Index (SAI; a common topoclimatic index that assigns highest values to steep, east-facing slopes) were calculated based on those raster cells that fell within the respective home-range areas.

Statistical analysis

Comparison of environmental covariates between ranges

Paired *t*-tests were used to compare mean environmental covariates between maternal and annual home ranges. When required, data were log transformed to achieve normality. Northern and southern study sites were investigated separately and statistical analysis was performed using R 3.1.1 (R Development Core Team, 2014).

Habitat selection at den sites and across ranges

Based on existing knowledge from other studies of this species and related felids, biologically meaningful models a priori determined as likely to influence den site selection were constructed to compare den sites against environmental conditions across the maternal and annual home ranges. Models were evaluated using conditional logistic regression to identify possible relationships between den site selection and environmental covariates (Manly et al., 2002). Values recorded at each den site were compared with those recorded at 40 random points within each corresponding home range (maternal or annual), thus employing a used (den locations) and available (random locations) design to create resource selection functions (Manly et al., 2002). For analyses, all covariates were separated between northern and southern lynx. Model selection using the roe deer index covariable was performed with a reduced sample size (n = 22) encompassing lynx home ranges in southern Norway only. Mean values of environmental covariates were also compared between maternal and annual home ranges using standard logistic regression. All non-normally distributed covariates were log transformed prior to analysis.

Table 1 Environmental variables used in analysis and source of data

Environmental variable	Data source and scale/resolution
Elevation	Obtained from the Norwegian State Mapping Authority. Derived from a raster digital elevation model (DEM) with a spatial resolution of 100 m ² .
Terrain Ruggedness Index (TRI)	Measured by taking the square root of the sum of squared differences in elevation of each pixel in a 100-m DEM to its eight neighbours (May <i>et al.</i> , 2012).
Slope–Aspect Index (SAI)	SAI (May <i>et al.</i> , 2012) assigns highest values to east-facing areas with steep slopes. Slope and aspect derived from a 100 m ² resolution DEM.
Public/private road and settlement distances	Calculated from digital 1:50 000 topographic maps obtained from the Norwegian Mapping Authority.
Human density	The number of individuals per square kilometre. Spatial resolution of 1 km ² . Obtained from Statistics Norway (Takle, 2002).
Index of roe deer density	Obtained through pellet group counts from Bouyer <i>et al.</i> (2015). Spatial resolution of roe deer raster dataset was 1 km ² .

Table 2 Comparison of mean values of environmental covariables between lynx maternal and annual home ranges in different parts of Norway

	Maternal home	Annual home range				
Variable	range (mean \pm SD)	(mean ± SD)	<i>t</i> -value	d.f.	Р	
Northern Norway						
Human density (people per km ²)	0.88 ± 2.12	1.4 ± 1.5	1.495	10	0.166	
Public road density (km/km ²)	0.061 ± 0.098	0.075 ± 0.053	0.509	10	0.622	
Private road density (km/km ²)	0.072 ± 0.154	0.092 ± 0.057	0.857	10	0.411	
TRI	632.42 ± 559.72	443.56 ± 401.78	3.709	10	0.004	
Elevation (m.a.s.l.) 374.76 ± 255.93		423.71 ± 204.55	0.835	10 10	0.4	
SAI	SAI 5.20 ± 7.70		2.731		0.021	
Southern Norway						
Human density ^a (people per km ²)	2.38 ± 4.59	12.70 ± 16.90	6.038	21	<0.0001	
Public road density (km/km ²)	0.114 ± 0.156	0.375 ± 0.228	8.273	21	<0.0001	
Private road density (km/km ²)	0.970 ± 0.530	1.009 ± 0.214	0.951	21	0.353	
TRIª	218.96 ± 210.83	145.51 ± 132.25	2.487	21	0.021	
Elevation (m.a.s.l.)	361.17 ± 194.03	425.08 ± 175.06	2.506	21	0.021	
SAI	10.75 ± 10.31	13.26 ± 6.70	1.378	21	0.182	
Roe deer index ^a	0.88 ± 0.98	1.09 ± 0.86	2.734	21	0.012	

^aData were log transformed to achieve normality for analysis. d.f., degrees of freedom; SAI, Slope–Aspect Index; SD, standard deviation; TRI, Terrain Ruggedness Index.

Model selection was performed based on the corrected Akaike information criterion (AIC_c) score and Akaike weights (Burnham & Anderson, 2002). In cases where a single model did not have strong support (model weight >0.7), model averaging was employed to obtain final parameter estimates. Models with a ΔAiC_c value of <3 were used to synthesize the parameters of the final model. Because of the repeated reproductive events for some individuals (n = 8), alternative models were constructed, firstly with and without a random term to account for potential effects of repeated measurements from individual lynx and secondly using a single randomly chosen reproductive event for each individual. In all cases parameter estimates for models did not differ significantly; therefore, results reported are for models with all reproductive events included.

Validation of site selection functions

The models derived from the earlier analyses represent den site resource selection functions at different spatial scales. In order to evaluate the predictive strength of these models, the K-fold cross-validation procedure of Boyce *et al.* (2002) was employed, based on Spearman rank correlation between ranked resource selection values (divided into 10 equal interval classes or bins) and area-adjusted den site frequencies. The dataset was divided into four separate 'folds' for evaluation.

Results

Maternal home-range selection: univariate comparisons

Comparison of habitat features associated with the location of early maternal home ranges against those of annual home ranges revealed that maternal home ranges were situated in areas with higher terrain ruggedness values in both northern (P < 0.05) and southern study sites (<0.01) (Table 2). Mean elevation values for early maternal home ranges were also lower than annual home-range sites (P < 0.01) for southern ranges only. Human density in the northern regions of Norway displayed no significant difference between homerange types with an average of 1.4 people per km² (± 1.5 SD) within the annual home-range sites and 0.8 people per km² $(\pm 2.1 \text{ SD})$ in early maternal home-range sites (Table 2). In southern Norway, human density within annual home ranges (12.7 people per km² ±17 SD) was significantly higher (P < 0.001) than human densities recorded within early maternal home ranges (2.4 people per $\text{km}^2 \pm 4.6 \text{ SD}$). Roe deer densities (southern areas only) showed a slight, but significant, difference after log transformation of data (P < 0.05) between annual and maternal home ranges, with annual areas (1.10 roe deer per km² ± 0.8 SD) having higher densities of roe deer than maternal areas (0.8 roe deer per $\text{km}^2 \pm 0.9 \text{ SD}$).

Maternal home-range selection: multivariate models

At a home-range scale, in northern Norway (eight models fitted), no single model had strong support, but three models had a $\Delta AIC_c < 3$ (Table 3) and were used to derive an averaged model. The models suggested that northern maternal home ranges were in areas of lower elevation, lower human density and higher terrain ruggedness relative to annual home ranges. The averaged model also included Slope–Aspect Index, and suggested selection for more west-facing and lower sloped areas. For southern lynx populations, the maternal home ranges were also associated with more rugged terrain than annual ranges, and in areas with lower public and private road density than available. The averaged model also included selection for areas with lower human density and

 Table 3
 Summary of variables included in averaged models assessing selection of maternal home ranges relative to environmental conditions in annual home ranges using logistic regression

				Public	Private				
		Human		road	road				
Model	Elevation	density	TRI	density	density	SAI	AICc	ΔAIC_{c}	AIC_{c} w
Maternal versus annual (Northern populations)									
1	х	Х	Х				30.27	0.00	0.366
2	х					Х	33.01	2.73	0.193
3		Х					33.15	2.88	0.117
Averaged coefficient	-0.012	-2.692	3.135			-0.081			
Standard error	0.005	1.663	1.442			0.059			
Summed weights	0.559	0.483	0.366			0.193			
Maternal versus annual (Southern populations)									
1				х			43.51	0.00	0.339
2			Х	х	Х		44.53	1.01	0.204
3		Х		х			45.78	2.27	0.109
4	х			х	Х		46.21	2.70	0.088
Averaged coefficient	-0.004	-0.151	0.541	-14.601	-3.198				
Standard error	0.003	0.075	0.289	5.754	2.241				
Summed weights	0.088	0.109	0.204	0.740	0.292				

Models shown here had ΔAIC_c values of <3 and were therefore included in averaged model.

AIC_c, corrected Akaike information criterion; SAI, Slope-Aspect Index; SD, standard deviation; TRI, Terrain Ruggedness Index.

lower elevation. These effects were broadly consistent with the *t*-test analyses, although there was some evidence of different preferences between northern and southern populations in the *t*-tests, which may be linked to overall differences in topography and landscape between different regions. When the roe deer covariate was introduced to model selection for the southern population (15 models fitted), no strong support for any single model was observed and the roe deer index did not feature in the top models. The models included in averaging did not incorporate the roe deer index variable suggesting that this is not a strong determinant of maternal-range selection. Other variables included were largely consistent with the combined analysis, although SAI was not included.

Den site selection

Across northern Norway, at the den site scale (22 models fitted), the most parsimonious model for the location of den sites in both home-range types identified den site locations in areas characterized by complex and rugged terrain and at lower elevation than available ($AIC_c = 64.83$, w = 0.35 for best-supported maternal model and $AIC_c = 58.36$, w = 0.26 for best-supported annual model) (Tables 4 and 5). All models included in the averaging contained the elevation and TRI covariates at both scales. Models including the Slope-Aspect Index were also important for the location of den sites at both home-range scales with a summed AIC_cw of 0.28 for maternal site models and 0.38 for annual site models (Tables 4 and 5). Den sites were located in areas of lower elevation than available in both home-range types, possibly indicating a trade-off between elevation and ruggedness. Selecting den sites in areas further from public and private roads and settlements was less important in the northern study area at both scales.

In southern Norway (29 models fitted), selection for den sites in more rugged terrain than available was also consistently selected for, and dens were also found to be further away from private roads at both scales ($AIC_c = 137.12$, w = 0.39 for best-supported maternal model and $AIC_c = 131.37$, w = 0.15for best-supported annual model). Selecting den sites in areas further from public roads was also important across the southern annual home ranges (summed AIC_c w of 0.56) but not important in maternal-home ranges. Plots of the predicted den site selection relative to different environmental covariables at the two scales considered are shown in Figs 2–5.

Validation of resource selection functions

For both den site analyses (comparison with maternal and annual ranges), the resource selection functions derived from the averaged models effectively predicted locations chosen (northern maternal range, mean $r_s = 0.795$, P < 0.01, annual range, mean $r_s = 0.801$, P < 0.01, annual range, mean $r_s = 0.801$, P < 0.01, annual range, mean $r_s = 0.801$, P < 0.01, annual range, mean $r_s = 0.813$, P < 0.01).

Discussion

Similar to other carnivore den site studies (Laurenson, 1994; May *et al.*, 2012), lynx den sites were located in areas that offer greater protection to newborn kittens than averagely available, which minimized interaction with humans, their primary predator and source of disturbance (Andrén *et al.*, 2006). Our findings support the suggestions of Bunnefeld *et al.* (2006) that female lynx in Norway avoid risky habitats in the early phase of rearing vulnerable kittens.

			Distance to	Distance to				
Model	Elevation	TRI	public road	private road	SAI	AICc	ΔAIC_{c}	AIC _c w
Northern populations								
1	х	х				64.83	0.00	0.358
2	х	х			х	66.49	1.66	0.156
3	х	х	х			66.58	1.75	0.149
4		х		Х	х	66.82	1.99	0.132
Averaged coefficient	-0.005	1.113	0.217	0.095	-0.002			
Standard error	0.002	0.376	0.144	0.051	0.003			
Summed weights	0.663	0.795	0.149	0.132	0.288			
Southern populations								
1		х		Х	х	137.12	0.00	0.394
2		х		Х		138.89	2.77	0.098
3	х	х			х	138.99	2.88	0.029
Averaged coefficient	-0.004	0.801		0.463	-0.005			
Standard error	0.002	0.228		0.218	0.002			
Summed weights	0.029	0.521		0.492	0.423			

Table 4	Summary of variables	included in averaged	models assessing l	ynx den site selection	at the maternal ra	ange scale across Norway
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Models shown here had ΔAIC_c values of <3 and were therefore included in averaged model.

AIC_c, corrected Akaike information criterion; SAI, Slope–Aspect Index; TRI, Terrain Ruggedness Index.

Table 5	Summary of	f variables included in	averaged models	assessing lynx den	n selection at the a	annual range across N	Vorway
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		Distance		Distance to	Distance to				
Model	Elevation	to urban	TRI	public road	private road	SAI	AICc	ΔAIC_{c}	AIC_{c} w
Northern populations									
1	х		х				58.36	0.00	0.26
2	х	х	х			Х	58.82	0.46	0.21
3	х		х	х			59.59	1.24	0.14
4	х		Х		х		59.63	1.27	0.13
5	х		Х		х	х	60.36	2.01	0.09
6		х	Х	х		х	60.86	2.50	0.08
Averaged coefficient	-0.006	0.962	1.152	0.202	0.339	-0.004			
Standard error	0.002	0.601	0.317	0.178	0.178	0.003			
Summed weights	0.830	0.290	0.910	0.220	0.220	0.380			
Southern populations									
1			Х	х	х		131.37	0.00	0.15
2			Х	х			131.54	0.17	0.14
3			Х	Х		х	131.79	0.41	0.13
4			Х		х		132.07	0.70	0.11
5	х		Х	Х	Х	х	132.54	1.16	0.09
6	х		Х	х			133.51	2.13	0.05
7			Х				133.51	2.14	0.05
8	х		Х			х	133.65	2.28	0.05
Averaged coefficient	-0.002		0.822	0.483	0.388	-0.004			
Standard error	0.002		0.196	0.103	0.265	0.002			
Summed weights	0.190		0.770	0.560	0.350	0.270			

Models shown here had ΔAIC_c values of <3 and were therefore included in averaged model.

AIC_c, corrected Akaike information criterion; SAI, Slope-Aspect Index; TRI, Terrain Ruggedness Index.

Den site placement

The most consistent feature that lynx selected for across Norway was den sites that were associated with more rugged terrain than available, similar to denning lynx elsewhere in Europe (Boutros *et al.*, 2007; Krofel, Skrbinšek & Kos, 2012). Rugged terrain potentially reduces disturbance and mortality risk by limiting human access (Magoun & Copeland, 1998; Ross *et al.*, 2010) and likely shelters lynx kittens from the elements (Boutros *et al.*, 2007). Considering the retrospective nature of this study, microstructural features of each natal den site were not investigated, but rocky outcrops that offer shelter



Figure 2 Plots of the predicted den site selection relative to different environmental covariables across annual ranges for the northern population.

and dense vegetation at the den also likely influence den selection across Norway.

The Norwegian landscape is highly accessible, with many public and private roads penetrating even the remotest areas (Basille *et al.*, 2009; c.f. Fig. 1). Even so, when compared with overall availability (annual home range), across southern Norway, den sites were also located further from frequently used public roads, as also noted for denning brown bears *Ursus arctos* (Linnell *et al.*, 2000; Sahlén, Støen & Swenson, 2011), wolves *Canis lupus* (Kaartinen *et al.*, 2010; Ahmadi, López-Bao & Kaboli, 2014) and wolverines *Gulo gulo* (May *et al.*, 2012) where the level of human activity was determined to be the primary factor for avoidance. A lack of importance in selecting den sites further from public roads in the maternal home range is most likely due to this selection already occurring at the larger annual home-range scale in southern Norway.

Although the kitten-raising period does not overlap with the hunting season, female lynx that choose dens further from frequently used roads may still reduce mortality risk. Poaching is a primary cause of lynx mortality across Norway (Andrén *et al.*, 2006). The presence of roads increases human accessibility and directly relate to mortality risk as harvested lynx in Norway are predominately killed within 3 km of a road (Basille *et al.*, 2013). This pattern of avoiding areas that are easily accessible for humans has been found in other felid species (Ross *et al.*, 2010).

Contrary to other carnivore-denning studies (Boutros et al., 2007; May et al., 2012), lynx in the northern study site



preferentially selected den sites at lower, rather than higher, elevations. Other authors (Petram, Knauer & Kaczensky, 2004) have suggested dens at higher elevations reduce encounters with humans. However, dens in this study were already located in areas that were relatively inaccessible to humans, so denning females may be less inclined to occupy higher elevations as an avoidance strategy as long as they can access rugged terrain at lower elevation. Moreover, the structure of the Norwegian landscape is such that most steep slopes occur at low to intermediate elevation where forest cover is densest. At higher elevations, the terrain is less steep and less forested with lower prey densities. Although data on prey densities were not available for the northern study site, semi-domestic reindeer dominate the ungulate community here and are highly mobile and migrate seasonally (Mattisson *et al.*, 2011). Figure 3 Plots of the predicted den site selection relative to different environmental covariables across maternal ranges for the northern population.

This results in large spatiotemporal variation in the density of this species, making it difficult to determine if selection against higher elevations in Northern Norway potentially reflects an absence of suitable prey, although it could certainly be a factor.

Denning at the home-range scale

Early maternal home ranges in northern Norway were located in rugged terrain in areas at lower elevation and lower human density than available. Southern populations preferentially selected for lower public road density. The absence of importance in a selection for lower public road densities in the northern study sites likely reflects the general low level of infrastructure in this region. When the prey density covariate



Figure 4 Plots of the predicted den site selection relative to different environmental covariables across annual ranges for the southern population.

was added (southern populations only), it was surprisingly not important in model selection. Because lynx are central place foragers in the early kitten-raising period (Orians & Pearson, 1979; Krofel *et al.*, 2012), we speculated that the selection of natal dens could be influenced by feeding optimization (Stephens & Krebs, 1986) to meet the higher energetic demands imposed upon lactating females (Gittleman & Thompson, 1988). Female lynx in Norway may select for secure denning habitat over access to food, at least during the early weeks of the kittens' life, although further investigation into other prey densities merits investigation. Nonetheless, previous research investigating lynx space use in central and southern Norway found that females with dependant young employ a spatiotemporal strategy of avoiding risky habitats with higher densities of roe deer during the early kitten rearing phase (Bunnefeld *et al.*, 2006). As the kittens gain weight and exhibit greater energetic demands, maternal females subsequently return to these riskier high-prey density habitats later in the year (Bunnefeld *et al.*, 2006; Basille *et al.*, 2009).

Disrupting reproductive behaviours represents a greater evolutionary cost than disrupting feeding behaviour (Wilmers *et al.*, 2013). Thus, reducing mortality risk may be the most important factor during the early phase of denning. Despite poor support in our analysis for the selection of denning habitat associated with high- or low-prey densities, other carnivore species (Van der Meer *et al.*, 2013), including denning



Figure 5 Plots of the predicted den site selection relative to different environmental covariables across maternal ranges for the

felids (Durant, 2000; Fernández & Palomares, 2000; Wilmers *et al.*, 2013), have been shown to select secure denning habitat over access to food. The energetic effect of the use of areas with less prey may not be costly, however, as Eurasian lynx are extremely effective hunters and are adept at catching roe deer even at very low densities (Nilsen *et al.*, 2009).

Conclusions and recommendations

Across Norway, the selection of natal den sites and early maternal home ranges by Eurasian lynx appears to be influenced by a combination of landscape features and the impacts of human activity. The sympatric occurrence of humans and large carnivores can induce behavioural changes in a species, as humans are the primary cause of mortality for many carnivore species in the modern world (Andrén et al., 2006). Human disturbance has already been shown to stimulate den relocation for Lynx species (Olson et al., 2011), yet what cost disturbance incurs remains unclear. Despite a high mortality risk associated with selecting habitat within humandominated landscapes (Bunnefeld et al., 2006; Basille et al., 2009), lynx can persist in these areas by making behavioural changes that favour their survival during different life stages (Basille et al., 2013), such as denning in inaccessible terrain that reduce their interactions with humans. Few carnivore studies to date have focused on the selection of isolated rugged terrain to reduce mortality risk (Linnell et al., 2000) and overall our study emphasizes the importance of quantifying

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the impacts of human disturbance on denning carnivores, especially in human-dominated landscapes (Ciuti *et al.*, 2012; Ahmadi *et al.*, 2014).

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