Prey density, environmental productivity and home-range size in the Eurasian lynx (*Lynx lynx*)

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Abstract

Variation in size of home range is among the most important parameters required for effective conservation and management of a species. However, the fact that home ranges can vary widely within a species makes data transfer between study areas difficult. Home ranges of Eurasian lynx *Lynx lynx* vary by a factor of 10 between different study areas in Europe. This study aims to try and explain this variation in terms of readily available indices of prey density and environmental productivity. On an individual scale we related the sizes of 52 home ranges, derived from 23 (9:14 male:female) individual resident lynx obtained from south-eastern Norway, with an index of density of roe deer *Capreolus capreolus*. This index was obtained from the density of harvested roe deer within the municipalities covered by the lynx home ranges. We found a significant negative relationship between harvest density and home-range size for both sexes. On a European level we related the sizes of 111 lynx (48:63 male: female) from 10 study sites to estimates derived from remote sensing of environmental productivity and seasonality. A multiple linear regression model indicated that productivity of the study site had a clear negative relationship with home-range size. At both scales, sex emerged as a significant explanatory variable with males having larger home ranges than females. In addition, the size of male home-ranges increased faster with decreasing prey density than for females. These analyses support widely held predictions that variation in home-range size is due to variation in prey density.

Key words: Eurasian lynx, *Lynx lynx*, home-range size, prey density, environmental productivity

INTRODUCTION

Home-range size is among the most basic of ecological parameters that is regularly described for a given species. The analysis of factors influencing home-range size has received constant attention from the point of view of theoretical ecology (life-history variation, allometry, energetics) during the last quarter of a century (Harestad & Bunnell, 1979; Gittleman & Harvey, 1982; Grant, Chapman & Richardson, 1992; McLoughlin & Ferguson, 2000; Kelt & Van Vuren, 2001; Haskell, Ritchie & Olff 2002). However, the importance of the use of space for management and conservation has been realized for far longer (Burt, 1943; Woodroffe & Ginsberg, 2000).

An understanding of the requirements for use of space is vital in management and conservation in order to scale the size of management units to the species they are designed to manage (Knick, 1990; Woodroffe & Ginsberg, 2000). This concerns both the design of harvesting units and protected areas (Schwartz, 1999). Furthermore, home-range sizes are often used when producing population estimates, either through the application of formal distance rules or when extrapolating from surveys of species distribution to potential population size (Rabinowitz, 1993; Gros, Kelly & Caro, 1996). Finally, with respect to conservation planning and species recovery programmes, it is important to know how much space individuals need when estimating potential carrying capacities for recovery areas. In all these circumstances, using the wrong information about space requirements could have major consequences for the outcome of conservation strategies.

One major problem lies in the fact that home-range sizes vary greatly between species. While some of the interspecific variation in home-range size can be explained in terms of body mass and feeding style (e.g. Gittleman & Harvey, 1982; Guarino, 2002) there are many species with patterns of space use that deviate dramatically from predicted values (Ferguson *et al*., 1999). Furthermore, there is substantial variation within species where populations can vary by factors of from 10 to 1000 (Gompper & Gittleman, 1991). Variation in food/prey availability is often identified as an important factor in explaining intraspecific variation in home-range size (Sandell, 1989;

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Table 1. Details on study sites used in the analyses of home-range size. Numbers before location names refer to the map in Fig. 1

Study site	No. of animals		100% MCP home-range size (km^2)		Reference
	Male	Female	Male	Female	
1 Sarek, Sweden	8	21	709	407	Linnell *et al.*, 2001
2 Nord-Trøndelag, Norway	3	2	1515	561	Linnell *et al.*, 2001
3 Hedmark, Norway	7	10	1456	832	This study
4 Akershus, Norway	2	2	812	350	This study
5 Bergslagen, Sweden	4	1	632	307	Linnell *et al.*, 2001
6 Bialowieza Primeval forest, Poland	5	3	248	133	Schmidt *et al.*, 1997
7 Swiss Jura, Switzerland	3	5	264	168	Breitenmoser *et al.*, 1993
8 Northwestern Alps, Switzerland	11	12	159	106	Breitenmoser-Würsten *et al.*, 2001
9 French Jura, France	3	5	258	150	Stahl *et al.*, 2002
10 Kocevje, Slovenia	2	2	200	177	Huber *et al.*, 1995

Powell, Zimmermann & Seaman, 1997; Grigione *et al.*, 2002) and density (Carbone & Gittleman, 2002). However, estimating the density of food and prey can be both difficult and expensive in the field and it is desirable to evaluate indirect methods that could explain some of the existing variation in home-range size.

Eurasian lynx *Lynx lynx* populations are recovering in many areas of Europe (Breitenmoser *et al.*, 2000). Lynx are often subject to active management because of their depredation on livestock, their status as a game animal in many countries, and the fact that their conservation in Europe mainly occurs in multi-use landscapes rather than protected areas (Linnell *et al.*, 2001). Throughout their range in Europe home-range sizes of lynx vary by a factor of 10 (Linnell *et al.*, 2001; Jedrzejewski *et al.*, 2002) making it hard to transfer data from one study area to another. We aimed to test the hypothesis that home-range size (at two geographic scales) varies inversely with indices of prey density. On the individual level we examined if variation in prey density (indexed from hunting statistics of the main prey of lynx) explains differences in home-range size of lynx living along an environmental gradient in south-eastern Norway. On a population level we relate the mean home-range sizes of lynx from 10 European populations to satellite derived indices of environmental productivity and seasonality.

MATERIALS AND METHODS

Study areas: Norway

Data on the home ranges of lynx were collected in 2 discrete study areas in 5 counties (Hedmark, Akershus, Østfold, Buskerud and Oppland) in south-eastern Norway. The Hedmark study area has been described elsewhere (Linnell *et al.*, 2001; Odden *et al.*, 2002), but basically it consists of boreal forest interspersed with farmland along valley bottoms. The southern study area is broadly similiar, however, there is a clear gradient (increasing snow fall, decreasing proportion of farmland and decreasing human density) as you move from the

southern study area to Hedmark. In both these areas, roe deer *Capreolus capreolus* are the major prey of lynx.

Study areas: Europe

The European study areas from which we have extracted published data are described in detail in their original publications (Table 1). Basically, all consist of forested habitat surrounded by, or interspersed with farmland. In all areas roe deer are the main prey, with the exception of Sarek (where semi-domestic reindeer dominate the diet; Pedersen *et al.*, 1999), North-Trøndelag (where semi-domestic reindeer *Rangifer tarandus* and roe deer are consumed in approximate equal amounts; Sunde *et al.*, 2000), and the 2 Swiss study areas (where chamois *Rupicapra rupicapra* are a frequent compliment to roe deer as prey; Breitenmoser & Haller, 1993; Jobin, Molinari & Breitenmoser, 2000). Red deer also constitute a secondary prey in the Bialowieza study area (Okarma *et al.*, 1997). The Scandinavian study sites were subject to hunter harvest, while all are exposed to illegal poaching to various degrees.

Home-range analyses

For the individual level (Norway), we used lynx radio-tracking fixes, collected from 1995 to 2002 (Linnell *et al.*, 2001). Using a variety of techniques, 56 lynx were captured 95 times between 1995 and 2000, and were equipped with radio-transmitters in the 2 study areas (Nybakk *et al.*, 1996). Walk-through box-traps constructed in wood or metal mesh and baited with lynx urine were placed on known lynx trails. Box traps were checked twice per day. Spring-loaded foot-snares were placed where lynx-killed prey were found by chance, by snow-tracking or by monitoring radio-collared prey. These snares were continually monitored using radio-alarms, and reaction time was usually less than 15 min. Neonatal kittens were also captured (by hand) at natal lairs and were equipped with implanted transmitters (Arnemo

et al., 1999). Animals were often recaptured using the same or different techniques. Trained dogs were also used to recapture animals. These dogs were released close to radio-located lynx and chased the lynx until it either escaped or climbed a tree. Once lynx were in a tree they were darted and caught in a net if they fell. Finally, a single animal was darted from a vehicle and 4 were darted from a helicopter. All animals were immobilized using a mixture of ketamine and medetomidine, reversed with atipamezole. All procedures were approved by the Norwegian Experimental Animal Ethics Committee. Only 3 mortalities occurred because of capture. Two of these were through trauma associated with the use of leg-snares and the 1 darted from a vehicle suffered a reaction to the drugs. Most animals were equipped with radio-collars, apart from neonatal kittens and a few 6-month-old kittens that received implant transmitters. No complications were ever detected as a result of collaring or implanting. As the collars were not self-releasing, most lynx were recaptured every 2 years to change the collar until the animals died or were killed by hunters or poachers.

The radio-collared lynx were relocated at least twice per month as a minimum sample. Aircraft were used mainly for this regular work to reduce any possible biases due to the animal's location with respect to roads. Additionally more intensive radio-tracking from both the ground (in some cases round the clock) and the air (daily) was carried out during different periods. Based on general experience, and specific trials, the accuracy of locations was considered to be within at least 500 m of the estimated location. Field methods in the other study sites were broadly similar, and are described in the original publications.

We used annual 95% minimum convex polygons (MCP), peeled around the kernel centre (RANGES V; Kenward & Hodder, 1996). A lynx year was defined as stretching from June 1 to May 31, and we calculated annual home ranges for several years for each lynx, if data were available. Only resident adult lynx with stable territories were used in the analyses. No home range was calculated with less than 20 locations. For the study area analyses, we used mean home-ranges size for males and females from studies listed in Table 1. Since these studies all used 100% MCP, we calculated this for our 2 study areas as well. The sum of all home-ranges in a study was used as the size of the study area.

The density index map for roe deer

The number of roe deer shot within each municipality was recorded for a 3-year period (1998–2000; H. Brøseth, pers. comm.), while the area of forest habitat was calculated from data provided by the Norwegian Mapping Authority. From these data sets, we created a roe deer density map where we distributed the annual average number of reported shot roe deer in each municipality across the forested areas, and calculated a roe deer density index based on killed roe deer per km^2 of forest in each

municipality. We assumed that harvest density reflected population density, and because of the way the Norwegian hunting system is organized this assumption appears to be valid (Solberg *et al.*, 1999).

Each lynx home range was overlaid with this roe deer density map. An average roe deer density within the lynx home range was calculated, weighted by the proportion of home range within each municipality. Lynx typically overlapped with 2–5 municipalities.

The global productivity map

Monthly global 4×4 km MODIS FPAR data sets were downloaded from NASA MODIS home page (http://modis-land.gsfc.nasa.gov), covering October 2000 through October 2002. FPAR is an expression for the fraction of photosynthetical absorbed radiation, and is a measure of the percentage of radiation, available for photosynthesis, that is absorbed (Knyazikhin *et al.*, 1998, Myneni *et al.*, 2002). Due to atmospheric conditions, cloud cover and long nights north of the Arctic Circle, values were not available for all areas in all months. This was especially true for northern Scandinavia during winter. We therefore used the mean value for each month for the 2 years if values for both years existed and used the value for 1 year if 1 year was missing values. Since the FPAR during winter in northern Scandinavia is close or equal to 0, we used this for areas where data were missing for both years. This was only relevant for some areas north of the Arctic Circle.

From the monthly data sets, we then created 2 new data sets, 1 representing the mean FPAR through a year, the other representing standard deviation of the 12 monthly values for each pixel. The annual mean FPAR will be high in areas with high productivity, and decrease with the proportion of mountain or other non-productive areas. The standard deviation of FPAR represents seasonality, where areas with high seasonality will have higher values than areas with more stable environments throughout the year.

Statistical analyses

On the individual level, we fitted a mixed linear model with restricted maximum likelihood estimation (Pinheiro & Bates, 2000), with log(home-range size) as dependent, and roe deer density and lynx sex as explanatory variables. The home-range size was log-transformed in order to get a more constant variation over the range of the roe deer density index (Sokal & Rohlf, 2000). In addition, we used the interaction between the 2 explanatory variables in the global model. Individual identity was used as a random factor in the model, in order to account for between-year variation within an individual lynx.

On the study area level, we used mean FPAR and standard deviation of FPAR as measures of habitat productivity and seasonality, respectively. For each study site,

Table 2. AICc-values for models on individual and study area level. For study area level, only those with AICc less than 40 is listed

	Model	K	AICc
Study area level	[Sex] + [Productivity] * [Seasonality]	6	36.471
n = 20	[Sex] + [Productivity]	4	37.443
	[Sex] + [Productivity] + [Seasonality]	5	39.453
Individual level	[Sex] + [Roe deer index]	5	56.383
n = 52	[Sex] * [Roe deer index]	6	58.599
	[Roe deer index]	4	59.794
	[Sex]	4	62.261

we drew a circle with area equal to the study area size, defined as the sum of all lynx home ranges in the specific study site. We then calculated mean FPAR and standard deviation of FPAR within this circle, excluding water and urban areas from the calculations. However, these mean and standard deviation values were highly negatively correlated, so we used the standardized residuals from a linear regression with standard deviation of FPAR as dependent and mean FPAR as explanatory variable, as a measure for seasonality. We wanted to investigate the effect of mean FPAR in an interaction with seasonality, therefore, the standardized mean FPAR as the explanatory variable 'productivity' was used for a more easy interpretation of the effects. Mean home-range size within a study area was used as the dependent variable, where we separated between sexes, and used sex as a covariate in the model. Home-range size was log-transformed in order to get a more constant variation over the range of the explanatory variables (Sokal & Rohlf, 2000). The global model included the full interaction between seasonality, productivity and sex.

The most parsimonious model was chosen by both a backward stepwise procedure with alpha-levels set at 0.05, and using AIC_c due to rather small sample sizes both on the individual and study area level (Burnham & Anderson, 1998). All statistics were run in R version 1.6.2 (Anon, 2003). Log-ratio for the linear mixed model was calculated with restricted maximum likelihood to avoid bias in the parameter estimates (Pinheiro & Bates, 2000).

RESULTS

Individual level

A total of 52 annual home ranges of lynx was used in the analyses, from nine males and 14 females. Of these, three males and four females were from the southern study area. Mean annual home-ranges size (95% MCP) was 917 km^2 and 560 km^2 for males and females respectively (SD = 580 km^2 and 205 km^2).

The model selection based on AICc for the individual home-range size excluded the interaction between roe deer density and sex, resulting in a model with roe deer density and an additive effect of sex (Table 2; model $r^2 = 0.523$, $F = 9.31$, df = 2,17, $P = 0.002$). Also, a backward stepwise procedure resulted in the same

model (roe deer index: $F = 8.019$, df = 1, $P = 0.011$, sex: $F = 12.210$, df = 1, $P = 0.003$). There was a significant decrease in home-range size with increasing roe deer density ($\beta = -0.781$, df = 28, $t = -3.434$, $P = 0.002$), and male lynx had larger home ranges than female lynx irrespective of roe deer density (male–female: $\beta = -0.474$, df = 21, $t = -3.049$, $P = 0.006$). The effect of sex, when re-transforming the log (home-range size) will be multiplicative, i.e. the actual difference (in km^2) in home-range size between male and female lynx will decrease with increasing roe deer density (see Table 3; Fig. 2).

Study area level

A total of 10 study sites was used, with 48 male and 63 female home ranges (Table 1; Fig. 1). Mean home-range size (100% MCP) was 625 km^2 (SD = 509 km^2) for males and 319 km^2 (SD = 231 km^2) for females.

The model with lowest AICc included sex and the interaction between seasonality and productivity (Table 2). However, the model with sex and productivity alone had an AICc indicating that the model was equal in explaining the variation in home-range size (Burnham & Anderson, 1998). Despite this, we chose the model with interaction as the final model, since the interaction term was significantly contributing to the model when using a backward stepwise removal of terms (sex: $F = 8.821$, df = 1, $P = 0.010$, productivity: $F = 30.699$, df = 1, $P < 0.001$, seasonality: $F = 1.798$, df = 1, $P = 0.200$, the interaction [productivity * seasonality]; $F = 6.454$, df = 1, $P = 0.023$). Male lynx had larger home ranges than females (male–female: $\beta = -0.582$, df = 15, $t = -2.970$, $P = 0.010$), irrespective of the productivity or seasonality. Furthermore, the home-range size decreased with increasing productivity ($\beta = -0.800$, df = 15, $t = -5.765$, $P < 0.001$), and this decrease was steeper when seasonality was above the mean of all study sites, and flattened out when seasonality was below the mean of all study sites (productivity * seasonality, $\beta = -0.315$, df = 15, $t = -2.541$, $P = 0.023$). Home range was not significantly affected by seasonality alone ($\beta = 0.018$, df = 15, $t = 0.158$, $P = 0.876$). As on the individual level, the effect of sex, when re-transforming the log (home-range size) will be multiplicative, i.e. the actual difference in home-range size between male and female lynx will decrease with increasing productivity and decreasing seasonality (Table 3; Fig. 3a,b).

DISCUSSION

The sizes of home ranges give valuable insights into how lynx are influenced by their environment, and as predicted this study has shown that variation in the size of their home ranges is linked to relatively simple indices of prey density and environmental productivity on both a regional and a continental scale. This relationship has been predicted by many authors (Sandell, 1989; Gompper &
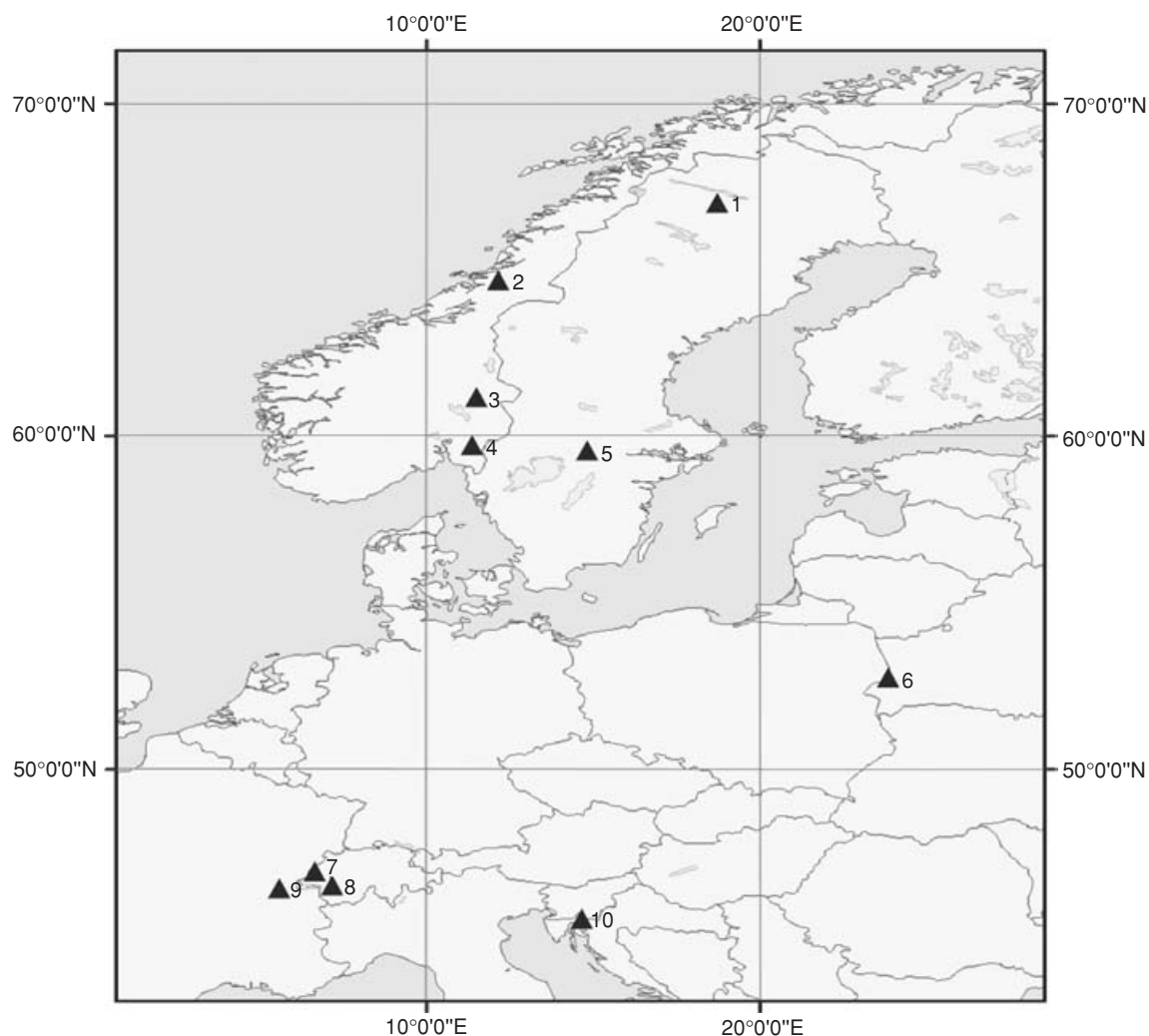
Fig. 1. Location of the study sites. Numbers refer to the numbers in Table 1. The study sites 3 and 4 were used merged in the individual analyses.

Gittleman, 1991) but has rarely been demonstrated through quantification of prey density within home ranges for a carnivore species. Instead many studies have used indirect indices of prey density, such as habitat, obtained through field surveys to establish a relationship between individual home-range size and predicted prey density (bobcats *Lynx rufus*, Litvaitis, Sherburne & Bissonette, 1986; badger *Meles meles*, da Silva, Woodroffe & MacDonald, 1993; red fox *Vulpes vulpes*, Lucherini & Lovari, 1996; stone marten *Martes foina*, Genovesi, Sinibaldi & Boitani, 1997). McLoughlin *et al.* (2003) have provided an alternative approach by using remote sensing to categorize habitat types for grizzly bears *Ursus arctos* in northern Canada, and were able to explain inter-individual variation in home-range size in terms of area of forest and bedrock within the ranges. In contrast, a range of other studies has also failed to find this habitat – home-range size relationship (striped skunk *Mephitis mephitis*, Bixler & Gittleman, 2000; African wild dog *Lycaon pictus*, Creel & Creel, 2002; lions *Panthera leo*, Spong, 2002). This implies that simple habitat classification is

Table 3. List of parameter estimates for the two final models

Variable	Beta	*SE*	*t*-value	df	*P*
Individual level					
Sex (female–male)	− 0.474	0.155	− 3.049	21	0.006
Roe deer index	− 0.781	0.227	− 3.434	28	0.002
Study area level					
Sex (female–male)	− 0.582	0.196	− 2.970	15	0.010
Productivity	− 0.800	0.139	− 5.765	15	< 0.001
Seasonality	0.018	0.111	0.158	15	0.876
Productivity * Seasonality	− 0.315	0.124	− 2.542	15	0.023

not always a good predictor of prey density. A range of other studies have documented a relationship between year to year variation in home-range size within a study site and annual variation in prey/food density (e.g. black bear *Ursus americanus*, Powell *et al.*, 1997; American marten *Martes americana*, Thompson & Colgan, 1987). In common for all these studies has been the need to conduct original field work to assess prey or habitat.
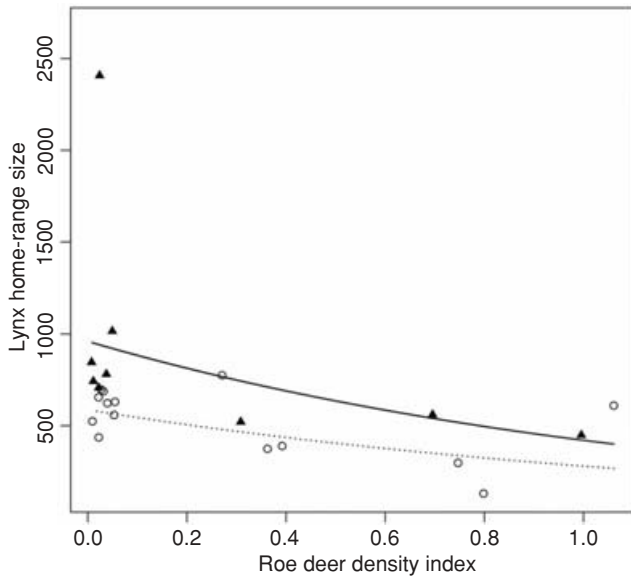
Fig. 2. Observed home-range size and roe deer *Capreolus capreolus* density for males (filled triangles) and females (open circles), and predicted relationship from the multivariate linear mixed model (filled line, males; dashed line, females). The models are calculated from all 52 annual home ranges, whereas the symbols are illustrative and reflect an average value for each of the 23 individual lynx *Lynx lynx*.

Our use of hunting statistics as an index of variation in prey density is a novel approach; it rests on the assumption that inter-municipality variation in harvest density reflects the variation in actual population density. Management of Norwegian wildlife is relatively homogenous in terms of objectives, with the provision of hunting opportunities and the desire for landowners to earn from the sale of hunting licences motivating relatively high harvests. Quotas are also set by municipal game boards, and follow perceived changes in the population size. Studies of moose *Alces alces* in Norway have shown a good relationship between harvest density and population density over time (Solberg *et al.*, 1999), and for red deer *Cervus elaphus* it has been widely assumed that harvest reflects population density (Langvatn *et al.*, 1996). Although we have no direct test of this assumption for roe deer we believe that it is likely that there is a general relationship between these two parameters, especially when the very large variations in densities are considered. However, because different countries have very different hunting traditions we did not feel that it was appropriate to use hunting statistics to explain patterns in home-range variation outside Norway.

FPAR is an index that reflects the fraction of incident photosynthetical absorbed radiation absorbed by the green leaves in the canopy and has been used as a measure of net primary production (Sellers *et al.*, 1997). It is closely related to the Normalized Different Vegetation Index (NDVI) (Myneni *et al.*, 2002). Although this type of data has not been used very much in explaining ecological patterns, it has been suggested that remote sensing derived FPAR, rather than NDVI, should be used in ecosystem
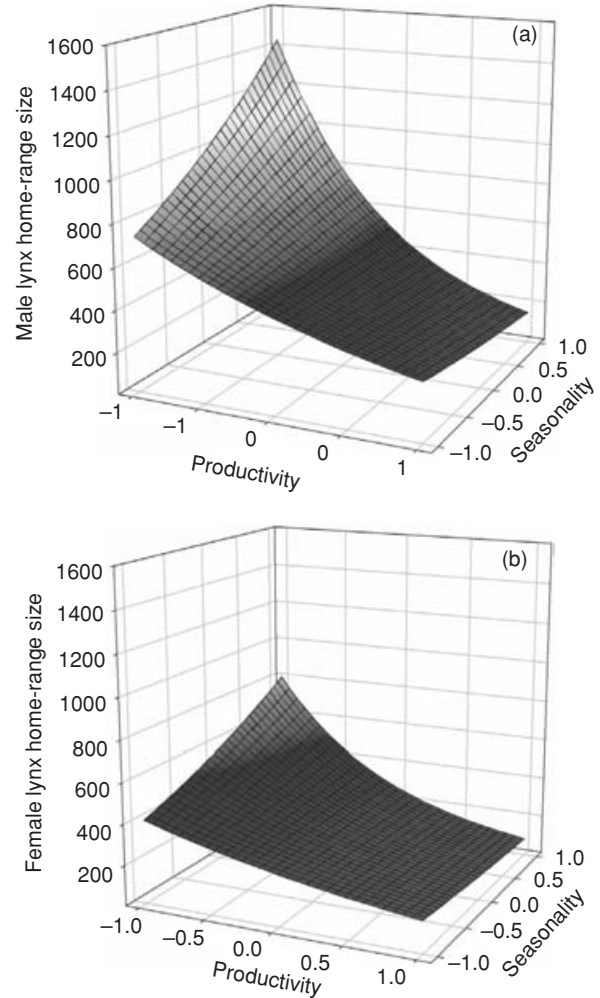

Fig. 3. The relationship between home-range size, and productivity and seasonality for (a) male and (b) female lynx for 10 study sites throughout Europe.

models, due to the manner in which it responds to the limiting factors of phytomass accumulation (Veroustraete, Patyn & Myneni, 1996). It is therefore a good measure of the primary productivity of an area, which is also known to influence the entire food web (McNaughton *et al.*, 1989).

Previous attempts to compare home-range size between populations have generally used latitude as a simple measure of variation in environmental productivity (e.g. Buskirk & McDonald, 1989; Gompper & Gittleman, 1991). However, latitude can be a very poor indicator of productivity as it does not take the effects of altitude and oceanic influence into account – both factors are crucial in the context of Europe where the Gulf Stream has a huge regional influence on local climate. The ready availability of remote sensing data that directly estimates productivity provides a far more accurate measure to compare regions. Our results indicated a clear relationship between home-range size and study area productivity. Although we have no independent data that relates productivity directly to prey density, it is a reasonable assumption that such a relationship exists. McLoughlin *et al.* (1999) and McLoughlin, Ferguson & Messier (2001)

have shown a similar relationship of declining home-range size with increased productivity and decreased seasonality for North American brown bears, although they estimated productivity from weather station data.

The analyses showed that for a given prey density/productivity males had larger home ranges than females. This is an almost universal finding among mammalian carnivore home-range studies (Sandell, 1989; Powell, 1994; McLoughlin & Ferguson, 2000) and probably reflects both the larger body size of male lynx (they are *c*. 25% larger) and the predicted sex differences in reproductive strategies of the two sexes (Sandell, 1989). It is of interest that in both analyses the size of male home ranges increased more rapidly than female home-range size with decreasing productivity/prey density. This is actually in accordance with predictions made by Sandell (1989) that female home-range size should closely follow prey density, but that at some point male home-range size should increase more rapidly due to a change in mating tactics. He predicted that at lower female density (resulting from lower prey density) males should abandon territoriality and adopt a roaming mating system. This pattern is also predicted in red foxes (Goszczynski, 2002). Although our data show that the male lynx were still more or less territorial at low density, there may be some subtle changes in the nature of their space use that reflects this process.

Although, these simple indices explained general patterns of variation in home-range size (by factors of 5–10) there is clearly much variation that can never be explained by such rough indices. McLoughlin & Ferguson (2000) present a hierarchical overview of factors influencing home-range size, and the factors that we cannot account for include body weight (see Grigione *et al*., 2002 for mountain lions), landscape structure, topography (Powell & Mitchell, 1998), social structure and local variation in prey density. These parameters can only be quantified by original field work in the different areas.

Our results support widely held predictions that variation in home-range size is at least partly explained by variation in prey density and environmental productivity, and in Eurasian lynx, go a long way towards supporting the predictions made by Linnell *et al*. (2001). Apart from the ecological interest of confirming this pattern our results have a number of implications for management and further studies of carnivore use of space. Successful conservation and management requires scaling protected areas or management units to the biological scales in which species function. Because of the huge amount of both inter- and intra-specific variation in home-range size there are clear risks associated with transferring data from one study area to another, or from one species to another. Clearly conducting site specific telemetry studies is not possible for all possible sites, and even conducting site-specific estimates of prey density would prove to be difficult in many areas. Our results indicate that simple indices of prey density or environmental productivity may improve extrapolation of space use when direct site-specific data are not available.

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