Hedmark University College

Eurasian lynx (*Lynx lynx*) and wolverine (*Gulo gulo*) response to seasonal variation in prey availability: influences on space use, seasonal site fidelity and reproduction

Zea Walton

Faculty of Applied Ecology and Agricultural Sciences

Master in Applied Ecology

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Abstract

In systems with migratory prey, resource availability varies seasonally and can modify the spatial organization of carnivores. Predators within these systems must therefore adopt a strategy to deal with prey movements when resources are seasonally unavailable. The seasonal migration of semi-domesticated reindeer (*Rangifer tarandus*) in northern Norway creates large temporal variation in prey availability for carnivores in this area. In this study, I investigate the response of Eurasian lynx (*Lynx lynx*) and wolverine (*Gulo gulo*) to seasonal reindeer migration in Finnmark and Troms counties, Norway. I examine the space use of these solitary carnivores in two areas: one with migratory reindeer (Finnmark) and another with seasonally stable reindeer availability (Troms). I use GPS data to examine seasonal home range overlap and centroid shift distances to investigate how temporally changing prey abundance influences carnivore space use. I further investigate the influence of reindeer availability on lynx reproduction and recruitment rates. Lynx and wolverine largely maintained stable residency, even within a system of migratory prey. Mean proportion of seasonal home range overlap for lynx and wolverine was >50% for all individuals. Male lynx showed a higher degree of home range stability than females while wolverines showed no intersexual differences. When reindeer were not seasonally available, most individuals exhibited directional home range overlap suggesting that winter home range expansion is necessary to obtain adequate food resources. In both species, females exhibited greater winter home range expansion and shift distances. Contrary to expectations, some carnivores that overlapped winter reindeer grazing areas showed less stability than either those that were completely lacking winter reindeer or those that had stable reindeer presence year around. This was evident in both lynx and wolverine. Female lynx showed restricted range use in summer, related to denning behavior, while reproduction increased winter home range expansion in females. However, reproduction was not influenced by winter reindeer availability. Recruitment was lower in areas without winter reindeer presence (20%) than in areas with reindeer (47%) indicating that winter reindeer availability may influence kitten survival. The results of this study indicate that the decreased lynx recruitment seen may be related to the costs of living within a system with seasonally marginal resources. Further research is needed investigating a link between foraging behavior and demographic processes in lynx. Overall, my findings suggest that the space use of carnivores in areas of predictable reindeer presence is more stable than carnivores with seasonal variation in prey availability. It may be important to consider the effect of seasonal resource distribution on carnivore demography and overall spatial stability in population management planning as well.

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Introduction

Resource acquisition is an important factor affecting animal distribution and movement patterns (Sandell, 1996) and changes in resource availability in both time and space modulate the spatial organization of animals (Powell, 2012). Movement patterns may vary seasonally, with ungulates undertaking seasonal migrations in search of suitable grazing lands or for predator avoidance (Fryxell and Sinclair, 1988; Hebblewhite and Merrill, 2007) while carnivore movements are largely influenced by their seasonally migrating prey (Ballard et al 1997; Walton et al 2001; Nelson et al 2012; Powell, 2012). In ecosystems with large carnivores and migratory prey, carnivores often face challenges securing a regular supply of food, especially when prey migration creates large temporal variation in resource availability between seasons (Schmidt 2008; Nelson et al. 2012; Gervasi et al. 2013; Henden et al 2014). Carnivores must therefore adopt a strategy to deal with spatially changing resource availability. These adaptations may include remaining residents, retaining fidelity to home ranges while subsisting on alternative prey. Alternatively, they may involve expanding or completely shifting their ranges, following the seasonal movements of migratory prey.

Current theory predicts that when prey availability is high, animals utilize the smallest amount of space possible to meet their energetic needs. If faced with temporally variable prey resources however, a home range must become large enough to support an animal during periods of lowest prey abundance (Sandell, 1989; Powell, 2000; Powell, 2012). This implies an inverse correlation between home range size and the availability of resources (Powell, 2000; Herfindahl et al 2005). Increasing home range size in combination with the ability of an animal to effectively search for and capture prey during periods of resource scarcity may have individual fitness and reproductive consequences (Pulliainen et al 1999; Persson 2005). Alternatively, pursuing migratory prey may be detrimental to territorial animals as the risk of losing an established territory may incur reproductive costs as well as potentially increasing intraspecific and interspecific competition. Furthermore, the ability of carnivores to retain area specific knowledge of the distribution of resources, as acquired through site fidelity over time, is thought to benefit individuals by increasing fitness, lowering mortality and increasing reproduction through increased spatial memory related to resource availability (Eide et al 2004; Van Moorter et al 2009; Janmaart et al 2012; Powell, 2012).

Previous studies have shown variation in adaptations in space use by carnivores in response to migratory prey (Apps, 2000; Walton et al 2001; Danell et al 2006; Valiex et al 2012; Elbroch et al 2013, Henden et al 2014) with some carnivores following the migratory movements of prey (wolves, Ballard et al 1997; mountain lions, Pierce, 1999) while others remain stable territory holders (tigers, Hojnowski et al 2012; mountain lions, Elbroch et al 2013; Eurasian lynx, Danell et al 2006; lions, Valiex et al 2012; wolverines, Persson et al 2010). However, there has been limited research on the temporal effects of prey migration on the spatial response of carnivores. Even fewer studies have examined how seasonally absent or pulsed resources influence carnivore reproduction. Mech (1995) found that wolves decreased reproduction following a seasonal decline in main food and Canadian lynx reproduction was found to decline with cyclic hare density declines (Mowatt et al 1996, Apps, 2000). Additionally, resource subsidy is believed to improve reproduction through either artificial food supplementation (Angerbjörn et al 1991; Persson, 2005) or seasonal influx of resources (Giroux et al 2012).

In Scandinavia, Eurasian lynx (*Lynx lynx*) and wolverine (*Gulo gulo*) largely overlap with the distribution of free ranging semi-domesticated reindeer (*Rangifer tarandus*) which represent an important ungulate prey for both of these solitary carnivores (Haglund, 1966; Pederson et al. 1999; Sunde et al. 2000; Nybakk et al. 2002; van Djik et al. 2008; Mattisson et al. 2011a+b; Tveraa et al. 2014). Wolverines are medium sized carnivores functioning as opportunistic predators and scavengers (Lofroth et al. 2007; van Dijk et al. 2008; Persson et al 2010; Inman et al. 2012a) and often utilize caching behavior to provision carrion during periods of resource scarcity (Inman et al. 2012). Eurasian lynx are obligate predators, specialized on medium sized ungulates, regularly preying upon roe deer and reindeer (Pedersen et al. 1999; Nybakk et al 2002; Odden et al 2006; Mattisson et al 2011b).

Within northern Norway, reindeer are intensively managed by indigenous Sami' husbandry practices and distribution varies both spatially and temporally due to anthropogenically influenced seasonal migration and regional environmental conditions (Tveraa et al. 2014). In some regions, migration between grazing areas is minimal, such that both winter and summer reindeer seasonal ranges are often included within a lynx/wolverine home range.

This equates to reindeer providing a relatively consistent food resource throughout the year within this area, whilst in other regions, reindeer move up to 200 km away from summer grazing pastures to winter grazing areas. The availability of food for lynx and wolverine in these latter regions is presumably dependent on movements of migrating semi-domesticated reindeer (Bjärvall et al. 1990) with reindeer availability patchily distributed and of varying abundance within an animal's home range or not present at all in winter (Haglund, 1966; Mattisson et al 2011b). These northernmost regions also exhibits very low productivity, providing few alternative prey species, which may compound the effects of limited resource availability. This results in large seasonal fluctuations in resource availability and low resource predictability in northern areas in winter (Haglund, 1966; Pedersen et al 1999; Danell et al. 2006).

Given the unpredictability of reindeer distribution throughout the winter, the ability of female lynx and wolverine to acquire prey may be of great importance to reproduction rates and successful recruitment. There is a strong relationship between food availability and reproduction in mammals and subsidization or seasonal pulses in local resources have been shown to positively influence reproductive rates in carnivores (Angerbjörn et al 2001; Persson, 2005; Giroux et al 2008). It is therefore possible that a lack of seasonal resource availability creates an inverse response. Persson (2005) found that reproduction in female wolverines is limited by winter food availability.

Since wolverines utilize caching and scavenging strategies, they may be less reliant on predation to secure food resources during times of low resource availability (Inman et al 2012). Lynx, an obligate predator, are presumed more susceptible to temporal changes in prey resources (Mowatt et al 1996; Apps et al 2000). As an adaptation to the migratory nature of their prey, lynx in northern Sweden were found to adopt larger annual ranges to increase the encounter likelihood of remaining reindeer (Danell et al. 2006). This has not been investigated for wolverines but it is believed that the scavenging and caching behavior of wolverines can offset periods of low prey availability by prolonging food resources during periods of resource scarcity. This dependency on cached food resources is likely to increase territoriality and site fidelity in wolverines with decreasing resource predictability (Maher and Lott, 2000; Eide et al 2004).

Both of these sympatric carnivores (Mattisson et al 2011a) have been shown to remain stable territory holders despite low prey densities in other systems (Herfindahl et al 2005; Danell et al. 2006; Breintenmoser-Wursten et al. 2007; Persson et al. 2010). However, within this system, carnivores that reside in areas with seasonal reindeer migration are almost completely devoid of the only ungulate species available as prey. This extreme temporal variability in resources may serve to modify animal space use patterns compared to other systems. I therefore expect three possible scenarios: (1) stable seasonal home ranges (i.e. high overlap between winter and summer home ranges) (2) home range expansion/retraction (some overlap) or (3) complete home range shift (no overlap) following migratory prey. Carnivores that remain stable residents, despite migratory prey, are expected to show some degree of seasonal shift in space use in response to lower prey encounter rates and increased movement distances than those in areas without migratory prey. Furthermore, retaining high degrees of fidelity despite low prey densities is anticipated to have fitness consequences. Limited prey availability and long search distances to obtain prey for provisioning cubs is likely to be costly and is therefore expected to be associated with lowered reproduction and recruitment as well.

Using resident adult lynx and wolverine of both sexes, I examined the space use of these solitary carnivores in two areas: one with migratory prey and another with seasonally stable prey resources. I examined seasonal home range overlap estimates and shifts in home range centroids as measures of home range stability and seasonal site fidelity, to investigate how temporally changing prey abundance influences species space use. I further investigated a link between foraging behavior and demographic processes in lynx, examining the effect of these differing areas on reproductive and recruitment rates.

Methods

Study Area

I conducted the study in Finnmark (70˚10´N, 24˚70´E) and Troms (69˚00´N, 19˚90´E) counties in northern Norway (Fig. 1; Mattisson et al. 2011b). The area is predominantly alpine tundra with a tortuous coastline characterized by a coastal alpine climate while the interior is composed of large plateaus above tree line. The area is usually snow covered from November to March. At lower elevations, mountain birch (Betula pubescens) is the most common tree species with occasional stands of scots pine (Pinus sylvestris). Semi-domesticated reindeer is the dominant ungulate species present, while mountain hares (Lepus timidus), tetraonids (Lagopus spp., Tetrao spp.), red foxes (Vulpes vulpes), and small rodents (Clethrionomys spp., Microtus spp. and Lemmus lemmus) are present as alternative prey species for lynx and wolverines residing in these areas (Danell et al. 2006; van Dijk et al. 2008; Mattisson et al. 2011b; Koskela et al 2013).

Within the study area, reindeer availability is highly variable exhibiting strong latitudinal and seasonal variation among different management areas and reindeer districts (Mattisson et al. 2011b; Henden et al 2014; Tveraa et al 2014). In the southern portion of the study area (Troms), reindeer availability is seasonally stable with reindeer residing annually in the area while in the north (Finnmark) carnivores experience dramatic changes in prey availability as the reindeer herds migrate seasonally from their summer grazing areas to overwintering pastures (Mattisson et al. 2011b). This creates a marked absence of reindeer in winter for those carnivores residing in the summer grazing areas within Finnmark. However, during some years, groups of reindeer may remain in their summer grazing areas during winter, either intentionally left there for the winter or 'lost' during migration.

Carnivore Data Collection

This study utilized telemetry data from GPS-collared lynx (n = 27) and wolverine (n = 21), monitored during 2007-2013 within Troms and Finnmark. The data was collected as part of a long-term research collaboration of the Norwegian and Swedish lynx projects, Scandlynx (http://scandlynx.nina.no/). Capture and handling of study animals occurred during the
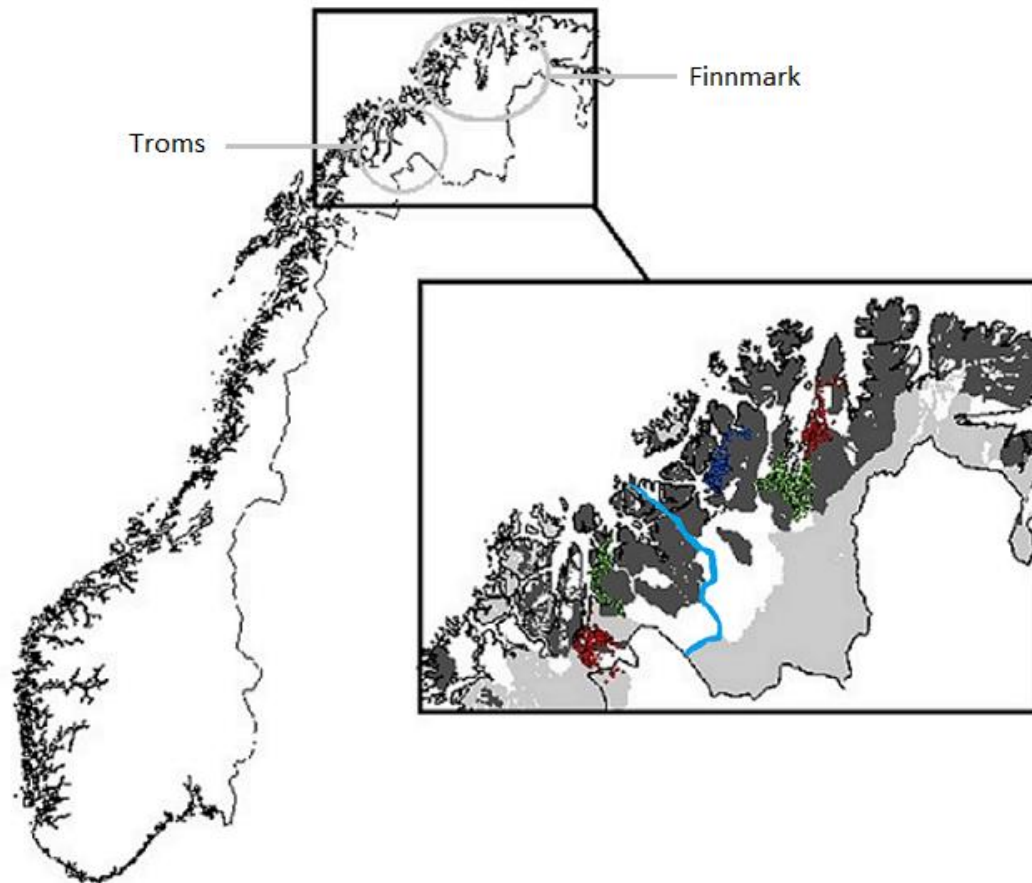
Figure 1. Overview of study area and locations of study animals in Troms and Finnmark Counties, Norway illustrated by the gray circles. Dark gray areas in the inset represent summer reindeer grazing areas. Light gray areas highlight the winter grazing areas and the blue line denotes the county border between Troms and Finnmark. The colored points are a sample of five female lynx GPS positions within the two study areas.

winter via chemical immobilization from helicopter following procedures outlined by Arnemo et al (2012). The Norwegian animal research ethics committee and the wildlife management authority approved all research. In total, ~63 000 GPS locations for lynx and ~32 000 GPS positions for wolverine were available for this study. There was high variation in number of locations per animal as a result of different programming schedules and duration of monitoring period. In general, GPS-collars were programmed to take between 1-48 locations per day. Positions that were deemed inaccurate due to poor position quality (n=37 lynx; n=114 wolverine) were removed from analysis. Additionally, only those individuals considered resident (i.e. > 20 months of age) were used for further analysis.

Seasonal Home Ranges

To test if lynx and wolverine remain stationary across seasons or expand their ranges in response to reindeer movements, I quantified summer and winter seasonal home ranges for

each individual using 95% minimum convex polygon (MCP) estimates (Mohr, 1947) using the package 'adehabitat' (Calenge, 2006) in R 3.1.1 (R Development Core Team, 2013). 95% contours were selected in order to minimize the influence of extra-territorial movements and outliers, which could artificially inflate home range estimates (White and Garrott, 1990; Getz et al. 2007). I limited available GPS positions to two seasonal periods, 'winter' (1 February - 30 April) and 'summer' (1 June – 30 August) to detect temporal changes in movement patterns of lynx and wolverine in response to reindeer movements. By assigning a temporal period to seasonal home range estimates (White and Garrott, 1990; Fieberg and Börger, 2012), I standardized the sampling duration across individuals, which allowed for comparisons of space use patterns. Additionally, using multiple MCP home range estimates over time in combination with mixed effects models can be helpful when looking at variables that vary temporally (Börger et al. 2006; Fieberg and Börger, 2012). MCP estimation was chosen as the most parsimonious method for examining temporally changing space use patterns because it is a good measure of the restricted outer bounds of an individual's range. By combining static MCP home range analysis across biologically meaningful periods (ie. seasonal periods with and without reindeer presence), allows me to examine overlap estimates of range use change over time (Fieberg and Kochanny, 2005). It also allows larger effective sample sizes within individuals, while being highly comparable to other spatial carnivore studies (Fieberg and Börger, 2012). I based these seasonal periods upon semi-domesticated reindeer migration events in order to restrict analysis to periods when reindeer presence was accounted for. Typically, semi-domestic reindeer migrate from summer to winter pastures between September - November and return April - May (www.Reindrift.no). I calculated the number of days a location was acquired per individual within a given season/year. I excluded all individual seasonal home ranges with less than 29 days of data within each three month period (n = 3 lynx and n = 5 wolverine) in order to prevent underestimation of home range areas. Lynx positions averaged 73 ± 3.9 and 75 ± 2.2 and wolverines 71 ± 6.9 and 68 ± 5.7 location days per three-month seasonal period for males and females respectively.

Home Range Overlap/Stability

Home range overlap indices and seasonal shifts in home range center points are useful for measuring the degree of site fidelity for an individual (Kernohan et al. 2001; Fieberg and

Kochanny, 2005). These seasonal shifts in home range size or location may indicate that carnivores follow migratory movements of prey or undergo range expansion or retraction (Apps, 2000; Hojnowski et al 2012; Elbroch et al 2014). Therefore, to test if lynx and wolverine remain stationary across seasons or exhibit seasonal shifts in home range area in relation to the availability of reindeer, I examined two-dimensional spatial overlap of seasonal home ranges of lynx and wolverines using Ranges8 version 2.16 (Kenward et al 2008). Only animals with seasonal data available for both winter and summer periods within the same year were examined for territorial stability and range expansion or contraction. However, wolverine data was limited to nine individuals (female = 4, male = 5) having both summer and winter seasonal data available within the same year. In comparison, 23 lynx (female = 17, male = 5) were available for seasonal analysis. Overlap matrices were calculated as the proportion (%) of area of the summer home range (HR_S) overlapped by the winter home range (HR_W) = HR_{S-W}, and the area of the winter home range (HR_W) overlapped by the summer home range (HR_S) = HR_{W-S}. To test for site fidelity I measured the mean overlap (MeanOV) between seasonal home ranges to examine if individuals have completely separate seasonal ranges (no overlap 0%), did not change range use between seasons (high overlap >50%) or expanded their ranges directionally between seasons (some overlap 0-50%). All individuals that had seasonal home range overlap >50% were considered stable territory holders (Hojnowski et al. 2011). To differentiate partial changes in range use (some overlap) ie. those individuals expanding one seasonal home range from those which spatially switch home range use during one season, I looked at proportional differences between seasons (DiffOV) in combination with area measurements and determined seasonal directionality of the range expansion. Difference in overlap values were scaled between 0-1 using the equation:

$$x' = \frac{x - \min(x)}{\max(x) - \min(x)}$$

(Eq. 1)

I estimated the distance between the home range centroids to test for range shifts as a measure of fidelity (White and Garrott, 1990; Kernohan et al 2001; Janmaat et al 2009). Home range centroids were identified using the recalculated arithmetic mean center using Ranges8. For individuals that had multiple years of seasonal home range estimates available, summer and winter site fidelity was measured using mean overlap of each individual's

summer and winter ranges averaged across all years. Three male and six female lynx had only one year of data available preventing comparison across years. Three female and two male wolverine were similarly excluded.

Reindeer availability

Within the northern portion of the study area, the seasonal migration of reindeer from summer grazing pastures to overwintering grounds creates a sudden absence of reindeer in these summer areas in winter. For those carnivores whose home ranges overlap with reindeer summer grazing areas their access to reindeer in winter is greatly reduced, possibly creating the need to expand or completely shift their home ranges to aid in including areas with increased reindeer availability. However, some reindeer may be sporadically present in their summer ranges in winter (ie. some remain after migration) owing to incomplete/partial migration or becoming 'lost' every year (Haglund, 1966; Mattisson et al 2011b; Henden et al. 2014). These could be single animals or small groups of scattered animals left behind during winter migrations, possibly providing limited hunting opportunities to carnivores which reside there (Haglund, 1966; Danell et al. 2006). Furthermore, some reindeer grazing districts may choose to overwinter their reindeer in the summer pastures rather than moving them to different wintering areas. Therefore, reindeer may still be present over winter even when they are believed to be largely absent (Mattisson et al 2011b; Henden et al 2014).

To determine the presence/absence of reindeer I first examined spatial overlap of carnivore home ranges with seasonal grazing areas. Spatial data describing reindeer grazing areas was obtained from GIS-layers compiled by the reindeer husbandry administration of Norway (https://kart.reindrift.no/reinkart/). Each home range was given a seasonal reindeer (1 = presence, 0 = absence) estimate (Rein_Seas) to determine which individuals overlapped with which seasonal grazing areas.

Those carnivores that were assessed a zero for reindeer availability in the winter were further analyzed using a winter reindeer estimate (Rein_Win) in order to quantify if they actually had access to "remaining" reindeer. A winter reindeer estimate of (0) represents a few sporadically scattered reindeer (almost zero) that remain in the summer grazing areas when the main herd is moved to winter grazing areas. A winter reindeer value of (1) equals entire

reindeer herds that remain in their summer grazing ranges during winter because the reindeer districts elected to do so.

I did this by utilizing multiple reindeer data sources in combination with spatial data describing reindeer grazing areas to quantify a measure of reindeer availability for both summer and winter seasons within different management areas. Each seasonal carnivore home range was intersected with each layer of reindeer data using ArcGIS version 10.1 (ESRI, 2012) and was ranked as 0 or 1 where 0= no (few) reindeer and 1= reindeer present. Only reindeer data matching the specific year of a seasonal home range were used.

I used reindeer count data from aerial winter line transect blocks and camera stations (from Henden et al. 2014) to quantify numbers of reindeer within summer grazing areas that remained present in winter. A study block consisted of lines transects spaced 1.7 km apart and 5-8 camera study sites spaced on average 5.8 km from each other (Henden et al 2014). I created polygons connecting outer locations of line transect blocks and camera station locations and added a buffer of 1.7 km (= distance between transect lines within each block). I then intersected each seasonal home range with these polygons in ArcGIS and summarized the number of reindeer counted in each block that overlapped within the home range. I summarized a count of reindeer in pictures for all sites that intersected with a home range.

Indirect measures of reindeer presence were also calculated based on identification and confirmation of reindeer killed by monitored lynx during predation studies (Mattisson et al. 2011b) and lynx and wolverine killed reindeer carcasses registered in a national database for carnivore monitoring and management (http://www.rovbase.no/). When a predation study was conducted within a matching home range period, the total number of reindeer killed were summarized as a measure of reindeer presence. The total number of reindeer carcasses documented in Rovbase during the specified winter season were similarly summarized. As the number of kills will be highly dependent on area of the home range I also divided number of kills with the area of the home range to estimate kills/100km^2. A final measure, based on observations of reindeer in winter herds per grazing cooperative, across the administrative areas used by radio-collared lynx and wolverine, was obtained via personnel communication with personnel at the State Nature Inspectorate (Statens Naturoppsyn, SNO).

Table 1. Reindeer presence/absence during winter (Rein_Win) in Finnmark, Norway where 0 equals no reindeer present and 1 signifies reindeer presence. Reindeer index values are summarized as 0 = no reindeer in winter in their summer or winter ranges, 1 = no reindeer in their summer range in winter but reindeer in their winter range in winter, 2 = reindeer in winter in summer range and in winter in winter range (i.e. reindeer year around).

REINDEER PRESENCE IN WINTER			
REINDEER INDEX	Summer Home Range	Winter Home Range	Explanation
0	0	0	No winter reindeer in either seasonal carnivore home range
1	0	1	Winter reindeer only present in winter carnivore home range
2	1	1	Winter reindeer in both summer and winter carnivore ranges

Combination of these different estimation methods allowed me to assess reindeer presence in areas with no winter grazing, where reindeer are supposedly absent, but with clear indications of reindeer presence. However, these remaining reindeer could consist of large herds that overwintered in their summer grazing areas or only a few in number and patchy in distribution (Haglund, 1966; Mattisson et al 2011b; Henden et al 2014) within certain areas of a home range or certain periods within the season and I lacked the necessary fine-scaled spatio-temporal data to quantify a density estimate of reindeer.

These Rein_Win values of winter reindeer presence/absence in both summer and winter carnivore home ranges were then combined into a reindeer index (Table 1) of annual reindeer availability. This was done by summing the presence of winter reindeer in each carnivore seasonal home range. Reindeer index values are summarized as 0 = no reindeer in winter in carnivore summer or winter ranges, 1 = no reindeer in carnivore summer range in winter but reindeer in carnivore winter range in winter, 2 = reindeer in winter in carnivore summer range and in winter in carnivore winter range (i.e. reindeer year around). All carnivores had access to reindeer in summer in their summer ranges.

Reproduction

Female lynx in northern Norway typically give birth in June and denning females have restricted area use during their summer seasons (Samelius et al 2012; van Dalum 2013). I analyzed female lynx data separately to test for the effect of reproductive status on summer home range area and subsequent overlap indices. To do this I quantified those females that were determined to have given birth in the summer period (summer control of kittens,

observed with kittens, etc. Nilsen et al. 2012) from those that had successful recruitment (ie. those females which have successfully reared kittens) as several females known to have given birth were subsequently found not to have surviving kittens (Nilsen et al 2012; van Dalum, 2013). Females whose kitten survival could not be determined were excluded from recruitment analysis. The mean size of summer home ranges between denning females and those that did not give birth were compared. Mean summer home range size of reproductive females (238 ± 53.7 km^2) differed significantly (t-test; t = 2.352, p = 0.033) from those without kittens (473 ± 84.1 km^2) showing a negative correlation with summer home range size. To account for this I included status (male (M), female (F), or family group (FA)) as a covariate in my final models.

Data Analysis

All analyses were run using R 3.1.1 (R Development Core Team, 2013). I evaluated seasonal and gender specific differences in home range sizes for both lynx and wolverine using t-tests. To examine if the presence of reindeer during the winter had any effect on lynx reproduction and recruitment success I analyzed reindeer availability based on the reindeer index with reproduction and recruitment estimates using Fisher's exact tests. I excluded those lynx with a reindeer availability index of 1 (Table 1) as the sample size (n = 2) was too small for comparison. Due to a lack of available reproduction data, status could not be assessed for the wolverines included in this study, and only intersexual home range and overlap differences were analyzed.

For lynx, I utilized generalized linear mixed models (GLMMs) using the lme4 package (Bates et al 2012) to test for differences in spatial behaviors between sexes and access to reindeer. Individual lynx (LynxID) were included as random intercept to allow for individual variation and avoid the effects of pseudo-replication among individuals. Response variables used were mean home range overlap (MeanOV), the difference in overlap between summer and winter ranges (DiffOVLP) and centroid shift (Cent_Shift). Covariates included Status (M, F, FA), Area (Finnmark, Troms) and seasonal reindeer availability (Reindeer Index (0,1,2) and Rein presence/absence (0,1)) as predictors. The two reindeer variables were each tested separately but there was limited data for all three class types using the Reindeer Index. Therefore, the lynx that had a reindeer index value of 1 (n = 2) were removed from analysis. The remaining classes were analyzed as a simple presence absence variable, Rein. As the

overlap response variables were proportional between 0 and 1, a binomial distribution was chosen and modeling was done using the logit link function. For the centroid shift a Poisson distribution was used. For each of the dependent variables, I utilized a small sample size corrected version of Akaike Information Criteria (AICc) using the R package MuMin (Barton, 2103) to select the most parsimonious model for interpretation. To assess the relative support for each model among candidate models, I also computed Akaike weights. Those models with ΔAIC ≤ 2 were considered to be equally supported by the data (Table 5). Final models were tested for overdispersion and model residuals plotted to examine distribution to assess goodness of fit. Due to the small sample size (n = 15) of wolverine data multivariable modelling was not possible. Instead, comparison of each of the overlap indices and the shift in home range centroid with the reindeer index were made using ANOVA and a post hoc calculation of Tukey's Honest Significance Difference test (Tukey's HSD) to compare the differences between means.

Results

Seasonal Home Range Estimates

Lynx

A total of 106 seasonal home ranges for 23 lynx (female = 17, male = 5) were calculated between 2007-2013. Average male home ranges were found to be significantly larger than female home ranges (t test; t = -4.32, df = 42, p<0.001). There was also seasonal variation in home range size depending on sex (Females; t = -2.30, df = 30, p = 0.029; Males: t = 0.59, df = 12, p = 0.565; Fig. 2; Table 2). Male home ranges did not change between summer and winter while female summer home ranges were, on average, 263 km^2 smaller than winter home ranges. Winter home range sizes did not differ between reproductive versus non-reproductive female lynx (p = 0.352). However, intrasexual summer home range size differences were found to be negatively correlated with both reproduction ($F_{(1,26)}$ = 4.03, β = -232.6 ± 115.9, p = 0.055, R^2 = 0.10,) and to an even greater extent, recruitment ($F_{(1,26)}$ = 6.14, β = -230.1 ± 92.9, p = 0.020, R^2 = 0.16). Reindeer presence did not have an effect on mean home range sizes of lynx in winter for either sex (ANOVA; Female: $F_{(1,27)}$ = 0.26, p = 0.616; Male: $F_{(1,10)}$ = 0.29, p = 0.610; Table 3). All lynx had access to reindeer in the summer.

Wolverine

30 seasonal home ranges for nine wolverines (female = 4, male = 5) were calculated between 2010-2013. There were no detectable differences between male and female home range sizes in summer (t = -0.56, df = 7, p = 0.590) or winter (t = -0.20, df = 10, p = 0.845; Table 2).

Table 2. Average home range areas (km^2) based on 95% MCP estimates of summer and winter seasonal home ranges (n=44) for lynx and (n=15) for wolverine. Range of minimum and maximum area values given in parenthesis.

	Home Range Area (km2)			
	Summer		**Winter**	
Lynx	Mean ± SE	Range	Mean ± SE	Range
Female (n=31)	307 ± 48.6	(22-1050)	570 ± 106.7	(73-3000)
Male (n=13)	1200 ± 179.2	(385-2911)	1093 ± 237.6	(144-3005)
Wolverine				
Female (n=4)	510 ± 185.0	(162-1043)	622 ± 175.6	(163-963)
Male (n=5)	617± 161.8	(325-1248)	663 ± 170.0	(300-1174)

Sample size (n) represents the number of seasonal home ranges per sex.

Table 3. Mean home range area estimates (km^2) in relation to the presence (1) or absence (0) of reindeer for both lynx and wolverine.

	Season	Reindeer Presence	
		0	1
Lynx	Summer	511 km^2	591km^2
	Winter	603km^2	678 km^2
Wolverine	Summer	491 km^2	554 km^2
	Winter	1048 km^2	491 km^2

Neither male nor female summer home ranges were significantly different in size from their winter home ranges (Female: t = -1.21, df = 4, p = 0.293; Male: t = -0.35, df = 9, p = 0.733). Wolverine winter home range sizes varied significantly in relation to reindeer presence however ($F_{(1,10)}$ = 6.70, β = -557.4 ± 215.3 SE, p = 0.027, R^2 = 0.34; Table 3), with male home ranges decreasing significantly in area with presence of reindeer ($F_{(1,6)}$ = 44.32, β = -879.9 ± 132.2, p = 0.001, R^2 = 0.86) while females showed no variation ($F_{(1,2)}$= 0.03, p=0.882). It should be noted that the sample size of wolverines without access to reindeer in the winter was limited to three so caution should be used with this interpretation. Summer home ranges showed little variation between study areas ($F_{(1,10)}$ = 0.25, p = 0.630, R^2 = -0.07) while winter home ranges were significantly larger for wolverines residing in Finnmark ($F_{(1,10)}$ = 20.83, p = 0.001, R^2 = 0.64).

Spatial Overlap Estimates

Lynx

The calculated lynx home ranges provided sufficient data for 44 overlap indices to measure directional home range expansion and seasonal home range fidelity. Pooled overlap amongst lynx was 56 ± 3.2%, indicating a high degree of home range stability. However, there was high variation among individuals with seasonal overlap values ranging from 0% to 100% indicating that both male and female lynx exhibit varying degrees of site fidelity across seasons (Table 4). There was no significant difference in the proportion of overlap between summer and winter home ranges (HR_{S-W}) amongst males and females (t = 0.22, df = 28 p = 0.831). However, the proportion of overlap of winter ranges with summer ranges (HR_{W-S}) differed significantly between sexes (t = -3.74, df = 36, p<0.001) with males having a higher proportion of overlap than females. Seasonal site fidelity, measured for individuals with multiple years of seasonal home ranges (F = 10, M = 3), was 51% ± 0.05 SE for females and

63% ± 0.09 SE for males with an overall overlap of 54% ± 0.04 SE indicating spatial stability across years.

Wolverine

Of the 30 wolverine seasonal home range estimates, 15 paired ranges were used to calculate seasonal home range overlap. Wolverines showed no significant intersexual differences in mean seasonal home range overlap values (Summer: t = -0.12, df =7, p = 0.908; Winter: t = -0.73, df = 7, p = 0.486; Table 4). There was also no difference between seasons (t = -0.45, df = 14, p = 0.660). However, seasonal overlap estimates differed per study area. Looking at study area differences showed individuals in Finnmark having a significantly lower degree of mean overlap (46% ± 1.3) than Troms (77% ± 7.6; Fig. 3). Female wolverines had an overall site fidelity of 48% ± 12.7 SE and males averaged 66% ± 11.5 SE with total seasonal site fidelity measured as 57% ± 9.3 SE for wolverines supporting territoriality and home range stability.

Home Range Centroid Shift (Range Expansion/Retraction)

Lynx

Migratory animals or those moving long distances in search of prey would not show residence in the same areas but large shifts in area use between seasons. Therefore, in addition to overlap measurements, I also measured the difference in home range center points from one season to the next to further illustrate potential shifts in space use. Lynx showed mean centroid shifts of 11 ± 1.3 km. There were no differences between sexes (t = -0.39, df = 14, p = 0.705) with mean centroid shifts of 12 ± 1.3 km and 11 ± 3.2 km for male and female lynx respectively. However, when related to home range size, male home ranges averaged 1147 km^2 and females 438 km^2 showing that male lynx exhibit much more stable range use than females. I further examined those home ranges that showed very low seasonal overlap measurements. Only four home ranges had mean home range overlap values ≤ 20%, and of these, the shift in home range centroid was relatively high (15 - 21 km) showing seasonal shifts in area of use. The largest centroid shift calculated was 43 km. This was for a male lynx which occupied an extremely large home range across seasons (summer = 2911 km^2, winter = 2431 km^2) thus, this value should not be considered a large shift in range use relative to the total home range area.

Table 4. Proportion of overlap (%) between seasonal home ranges of male and female Eurasian lynx (n=44) and wolverine (n=15) based on 95% MCP estimates. Overlap estimates calculated as the proportion of the area of the summer home range overlapped by the winter home range and vice versa within a single year per individual. Overlap values of greater than 50% represent stable home ranges and site fidelity.

	Proportion of Home Range Overlap (%)					
	Summer- Winter		Winter-Summer		Combined Overlap Index	
Lynx	Mean ± SE	Range	Mean ± SE	Range	Mean ± SE	Overlap Range
Females (n=31)	62 ± 5.6	(0-100)	42 ± 5.8	(0 -99)	52 ± 5.3	(0-100)
Males (n=13)	60 ± 6.8	(17-100)	73 ± 6.1	(43 -100)	67 ± 6.9	(17-100)
Wolverine						
Females (n=5)	59 ± 19.7	(0-86)	47 ± 21.7	(0-93)	53 ± 20.2	(0-93)
Males (n=10)	62 ± 10.8	(35-91)	62 ± 12.8	(29-92)	62 ± 8.9	(29-92)

Sample size (n) represents the number of seasonal home ranges per sex.

Wolverine

Wolverine showed stability to home ranges with no intersexual differences in centroid shift distances. Males averaged 15 km and females 13 km and both showed identical value ranges (1.5 km – 28 km). The one exception was a male outlier who shifted home range completely in winter 2012 showing the farthest shift distance, 38.7 km. In contrast, a female wolverine in Finnmark, with a home range area of 1043 km^2 in summer and 963 km^2 in winter, shifted centroid 5 km, showing strong site fidelity.

Seasonal Home Range Overlap and Reindeer Presence

Lynx

Reindeer presence/absence, reproduction, and study area were the most influential factors affecting mean home range overlap for lynx as indicated by model selection (Table 5). Reproduction was negatively correlated with mean overlap (β = -1.64 ± 0.99 SE, p = 0.100, Fig. 2) while study area had the most significant influence on mean overlap values, showing an increase in overlap for home ranges in Troms compared with Finnmark (β = 3.03 ± 1.21 SE, p = 0.012, R^2 = 0.32, Fig. 2). Reindeer presence in the winter had negligible influence on the spatial stability of lynx ($F_{(1,41)}$ = 2.05, β = 1.58 ± 0.96 SE, p = 0.100, Fig.2). Overall, the second ranked model was determined to be the most explanatory, however, it explained less than half (R^2 = 0.40) of the variation observed. Individual lynx showed minimal variation within the effect of these variables.
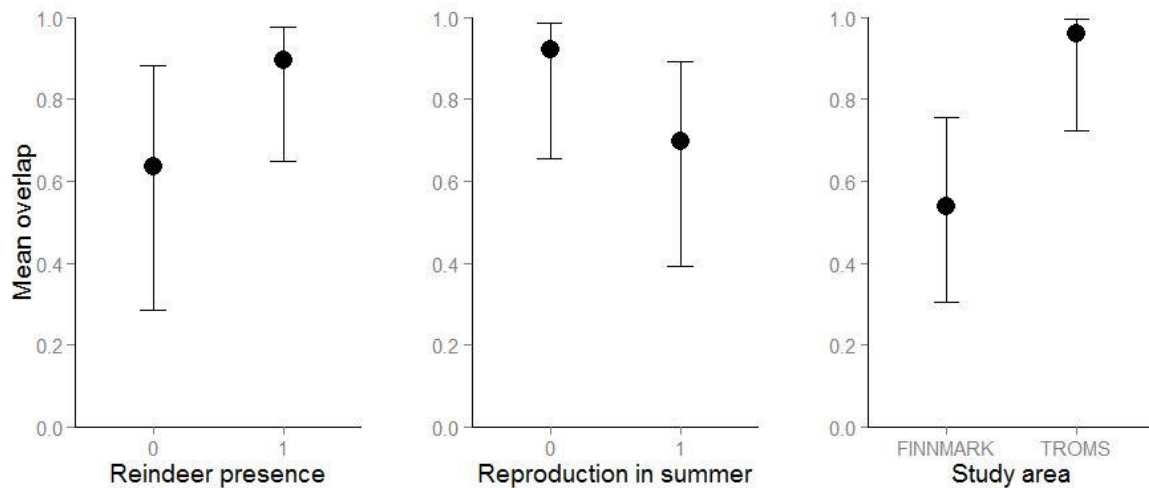
Figure 2. The effect of reindeer presence, reproduction and study area on mean home range overlap for lynx. The plots are showing fitted values with 95% confidence limits.

Difference in seasonal home range overlap values were scaled from zero to one with values close to one indicative of expansion of winter home ranges while those values close to zero indicate summer home range expansion. Reproduction was found to be the most important factor explaining differences in overlap values and was significantly correlated with larger overlap values. This indicates a positive correlation between winter home range expansion and reproductive individuals ($F_{(1,41)}$ = 4.168, β = 1.39 ± 0.68 SE , p = 0.041, Fig. 3; Table 5).

According to AICc model selection, differences in centroid shift distance are best explained by the interaction between study area and reindeer with reproduction accounting for only a small degree of observed variation (Table 5). Home range centroids showed greater shift distances in Finnmark than in Troms ($F_{(1,39)}$ = 14.91, p<0.001, R^2 = 0.26) for lynx. This indicates higher home range stability in Troms seasonally. The interaction between area and reindeer presence illustrates that with an absence of reindeer in both areas lynx exhibit similar, relatively short distance shifts but when reindeer are present in both areas the shift in centroid distance is more than twice as high in Finnmark than in Troms (Fig. 4). Reindeer, however, only accounted for a small portion (R^2<0.05%) of the variation in centroid distances and testing the model without area showed the null model as highest ranked with individual lynx explaining some residual variation.

Table 5. Evaluation of GLMM-models to assess the effect of reindeer availability (rein), area (Finnmark, Troms), and reproduction (Repro) on lynx seasonal space use as measured by two overlap indices: proportion of home range overlap (MeanOV) and differences between seasonal specific overlap (DiffOVLP) and the centroid shift between seasonal home ranges (Cent_Shift). Models were fitted with a binomial (logit) distribution except Cent_shift, which was poisson, distributed and all models included individual lynx (LynxID) as a random intercept. Reindeer estimates were separated into presence (1)/absence (0). Only models with ΔAIC < 4 are shown.

MeanOV	df	R^2	AICc	ΔAIC	weight
Area	3	0.32	43.65	0.00	0.28
Area + Rein + Repro	5	0.40	43.74	0.09	0.27
Area + Repro	4	0.35	44.12	0.47	0.22
Area + Rein	4	0.35	44.31	0.66	0.20
Null[1]	*2*	*0.07*	*53.89*	*10.23*	*0.00*

DiffOVLP	df	R^2	AICc	ΔAIC	weight
Repro	3	0.13	57.82	0.00	0.40
Area + Repro	4	0.14	59.62	1.80	0.16
Rein + Repro	4	0.13	59.93	2.11	0.14
Null	2	0.03	59.95	2.13	0.14
Area	3	0.04	61.61	3.79	0.06

Cent_Shift	df	R^2	AICc	ΔAIC	weight
Area * Rein + Repro	6	0.96	292.9	0.00	0.46
Area * Rein	5	0.96	292.9	0.01	0.45
Null[1]	*2*	*0.92*	*313.0*	*20.1*	*0.00*

Note: [1] null models included for comparison if Delta AIC >2

Wolverine

Most wolverine had access to reindeer during both summer and winter (10 out of 15) and the ones that did not have access to reindeer during winter remained resident (3/15) with high home range overlap and small shift distances between seasons. Wolverines that included winter grazing areas in their winter home range but not in their summer range (reindeer index 1; 2/15) completely moved their ranges showing no overlap and long shifts of 30-40 km. This relationship between reindeer and mean home range overlap showed a significant difference between those individuals that overlapped with winter reindeer grazing areas (reindeer index 1) and the other two reindeer index classes ($F_{(2,12)}$ = 12.46, p = 0.001; Fig. 5). However the difference between wolverines with and without access to reindeer was not significant (Tukey's HSD, p = 0.955, Fig. 5A).
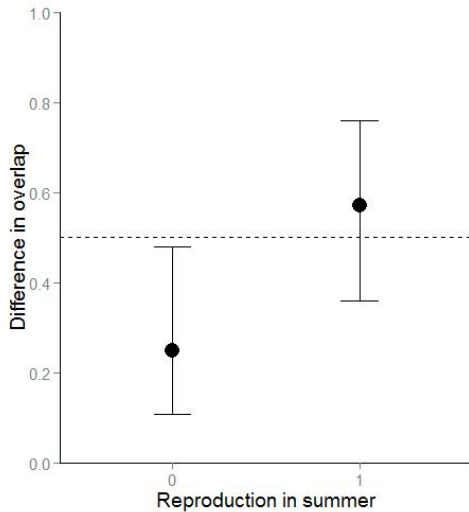
Figure 3. Effect of reproduction on the difference in seasonal home range overlap values for lynx showing the role that reproduction has on increasing home range stability in summer for reproductive lynx. Values close to one indicate winter home range expansion and values close to zero indicate summer home range expansion. The dotted midline at 0.5 roughly separates when summer home range overlap is larger than winter home range overlap.

Difference in overlap values also showed a significant difference between those wolverines that had access to reindeer and those that did not ($F_{(2,12)}$ = 4.83, p = 0.029, Fig. 5B). Wolverines without access to reindeer in the winter had larger winter home ranges compared to summer ranges while those with access to reindeer showed bidirectional range expansion. Centroid shift distances also showed this response with wolverines that overlapped winter reindeer grazing areas shifting significantly farther distances (Tuckey's HSD, p = 0.011, Fig. 5C). Both wolverines with winter access to reindeer than those without any reindeer showed similar home range stability (p = 0.87).
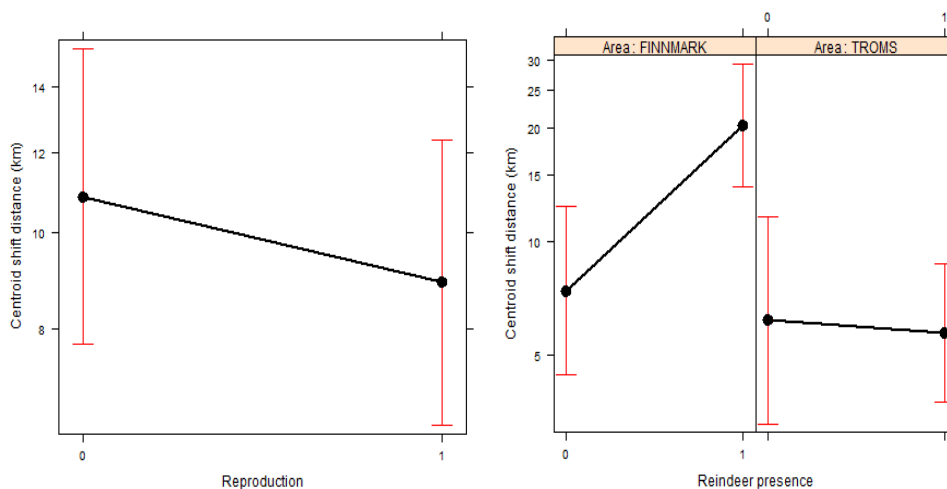

Figure 4. Effect of the interaction of study area (Finnmark and Troms) and reindeer availability on the centroid shift distances (km) in lynx. Reproduction further showed a positive effect on site fidelity.
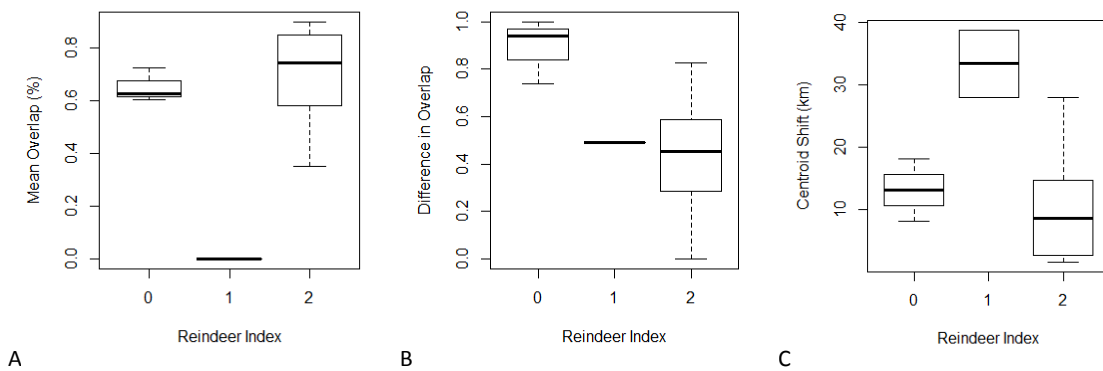
Figure 5. Relationship between reindeer availability to wolverines and mean home range overlap (A), difference in seasonal home range overlap (B) and shift in home range centroid (C). Reindeer availability is measured by the reindeer index (table 1) where the different reindeer availability categories are 0 = no reindeer, 1 = access to reindeer during winter as reindeer remaining in summer grazing areas in winter and 2 = year around access to reindeer (i.e. overlap with both winter and summer reindeer grazing areas). Mean overlap is the proportion of home range overlap averaged across seasons. Difference in overlap is scaled from zero to one with values close to one indicative of expansion of winter home ranges while those values close to zero indicate summer home range expansion. Shift in home range centroid shows site fidelity between seasonal ranges.

Lynx Reproduction and Reindeer availability

Of the 28 female years for which reproduction and recruitment data were available, 22 lynx reproductive events occurred within the study period (Table 6). Reproduction was not influenced by winter reindeer availability (Fisher's Exact Test, p = 0.390) with the proportion of females giving birth being relatively similar regardless of reindeer presence. Recruitment was lower in areas without winter reindeer presence (20%) than in areas with reindeer (47%) indicating that winter reindeer availability may influence kitten survival, although this difference was not significant (Fisher's Exact Test, p = 0.234; Fig. 6; Table 6).

Table 6. Measure of the effect of reindeer availability on reproduction and recruitment of Eurasian lynx. Successful female reproduction and recruitment calculated as the proportion of successfully breeding females within the different reindeer availability categories where 0 = no reindeer, 1 = access to reindeer during winter as reindeer remaining in summer grazing areas in winter and 2 = year around access to reindeer (i.e. overlap with both winter and summer reindeer grazing areas).

Reindeer Availability Index	Number of Females	Number of Reproductions	Number of Recruitments	Proportion (%) Reproduction	Proportion (%) Recruitment
0	10	6	2	0.60	0.20
1	2	1	1	*	*
2	19	15	9	0.79	0.47
Total	31	22	12	0.71	0.39

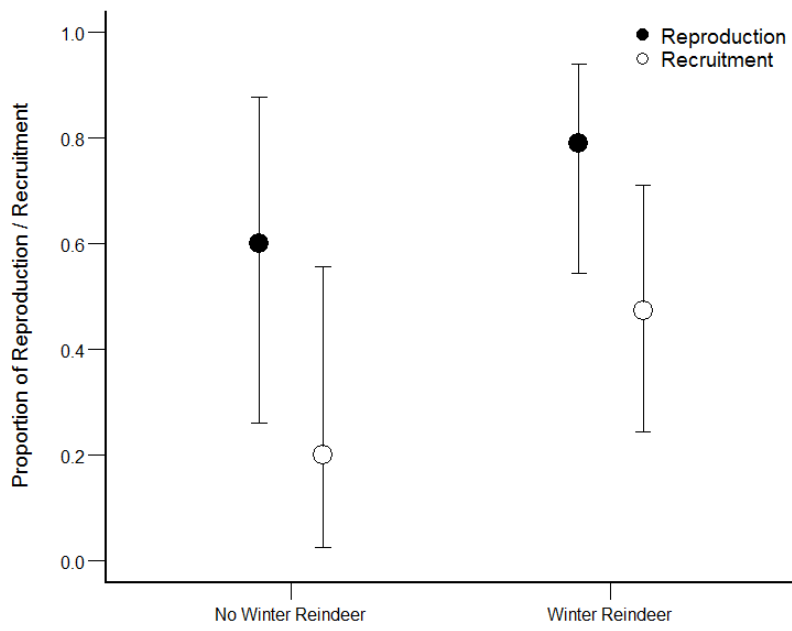*Sample sizes too small and removed from comparative analysis

Figure 6. Proportion of female lynx reproduction and recruitment in response to winter reindeer availability. All lynx had access to reindeer in summer. Error bars are Clopper–Pearson 95% confidence intervals (CIs).

Discussion

My study suggests that, even within a system of migratory prey, lynx and wolverine largely maintain stable residency. This stability was considered relatively fixed (mean overlap for lynx and wolverine was >50% for all individuals) but a few individuals (wolverine= 2, lynx= 2) showed complete seasonal home range shifts. These cases of secondary dispersal; moving short distances into a neighboring or unoccupied territory, can create substantial changes in space use between seasons and years.

The largest shift in space use was by a male wolverine who, in 2010 and 2011, occupied a home range that contained no reindeer in winter. He showed strong seasonal stability with mean overlap values of 72% and 63% for 2010 and 2011 respectively. In 2012, he shifted home range centroid 39 km away to a completely new area having 0.01% overlap with his former home ranges. This new area had access to winter reindeer but it is presumed that the shift resulted from a new territory becoming available, not in response to reindeer migration, due to the stability he showed within his former home ranges the previous years. The stability of these carnivores is therefore likely to be related in part to prior occupancy where carnivore residency limits both density and space use through intraspecific interactions.

For lynx, one female (F248) occupied a home range in 2009 that did not have access to winter reindeer showing a tenfold expansion of her range use between summer and winter ($275km^2$ to 3000 km^2). Part of her large range expansion may be related to increased search distances necessary to find the few reindeer that may remain. Data is lacking from 2010 as she was not successfully recollared that year, but in 2011 and 2012 she shifted home range to an area with winter reindeer presence. She maintained high seasonal overlap both years, but not across years. Each year she shifted her home range approximately 20 km while still overlapping with winter reindeer. She also overlapped reindeer presence with another female (F268) and two males (M269, M266) (Fig. 8) indicating that when present, winter reindeer may exist as a spatially clumped resource of sufficient abundance to allow multiple individuals to exploit it. In this case, year around access to reindeer in combination with area occupancy may have influenced her space use patterns and caused her annual shifts.

When reindeer were not seasonally available, most individuals exhibited directional home range overlap that suggests winter home range expansion is necessary to obtain adequate food resources. In general, both species showed more extensive space use in winter than in summer, particularly for females. Male lynx had a higher proportion of home range overlap than females indicating greater stability within home ranges and limited home range expansion. This intersexual difference was not seen in wolverines. In both species however, females exhibited greater winter home range expansion and shift distances. This follows the predictions made by Sandell (1989) saying that female space use patterns reflect the distribution of resources, whereas males conform their distribution to females.

Lynx have been found to expand their home ranges in response to declines in prey in other studies as well (Ward and Krebs, 1985; Breitenmoser-Wursten et al 2007). Valiex et al (2012) examined resident lion response to ungulate migrations and found that most showed shifts in space use related to alternative prey switching and increased home range sizes hypothesizing that the costs associated with following migratory prey are likely to be higher than the cost of shifting to other less preferred prey. Similarly, Danell et al (2006) found that lynx in Sweden do not follow the migratory movements of their preferred prey, reindeer, but showed home range expansion in response to alternative prey densities. These findings support my assertion that lynx remain resident and must rely on resident prey in the absence of migratory prey.

Contrary to expectations, some carnivores that overlapped winter reindeer grazing areas showed less stability than either those that were completely lacking winter reindeer or had a stable reindeer presence year around. This was evident for both lynx and wolverine. In Finnmark, lynx with access to winter reindeer moved twice as far as those residing in Troms, while lynx without access to reindeer showed similar stability in both areas. Similarly, wolverines that resided in an area with winter reindeer availability shifted home range centroids greater distances, showing very little site fidelity. This indicates that in the absence of reindeer, carnivores remain stable territory holders, switching to alternative prey but when their primary prey is present to varying degrees, they may need to expand their space use to include reindeer in their diet. This also suggests that lynx remain specialized on their preferred prey species, reindeer, even in times of extremely low availability and with great

variation in resource distribution (Pedersen et al 1999; Herfindahl et al 2005; Danell et al 2006; Odden et al 2006). Kill rate studies of lynx in these areas showed that although reindeer predation rates were greatly reduced when reindeer were largely absent from the system, lynx still maintained reindeer as a dietary component, which supports this conclusion (Mattisson et al 2011b). The presence of alternative prey may therefore be a critical resource especially for those lynx that must rely on alternative prey species to supplement diet and ultimately, may help to offset the fitness costs of remaining a stable territory holder despite variation in available prey seasonally (Danell et al 2006).

Space is not used homogenously within an animal's home range however. Some shifts in space use are naturally expected as reindeer are less likely to utilize the same areas within their seasonal ranges but will move based on habitat features, environmental conditions and grazing opportunities. Habitat features can structure the distribution and abundance (single, clumped, grouped) of prey. Local environmental conditions vary year to year with each migration event and may influence the number of remaining reindeer and their distribution as well (Henden et al 2014).

Those reindeer that should be absent but have remained overwinter in their summer pastures may be at extremely low numbers but they may be spatially predictable to lynx, finding shelter in particular areas in a lynx' home range. They may also presumably be in poorer condition as they are overwintering in areas that are not favorable to winter grazing (Haglund, 1966). Henden et al (2014) found that these partial ungulate migrations supported mesocarnivore residency and they likely provide an important winter resource to large carnivores as well.

It may also be necessary for carnivores living in Finnmark to expand or shift home ranges more to include reindeer and alternative prey in both summer and winter. Arctic ecosystems consist of a limited food chain with low environmental productivity and the density of alternative prey species is generally found to decrease with northern latitudes (Simpson, 1964). In southern Norway, the relative abundance of alternative prey species within a lynx' home range was found to modulate the proportion of alternative prey killed (Gervasi et al 2013). So, in areas where alternative prey species exist at low densities, altering trophic

interactions with anthropogenically enforced reindeer migration may have a more critical impact on these northern populations than at southern latitudes (Ims and Fuglei, 2005).

According to Von Schantz (1984), "An individual who experiences resource fluctuation over a prolonged period should maintain a territory size sufficient to meet its' needs during years of resource scarcity." Lynx that show stability to areas with limited seasonal resource availability and low resource productivity, such as those in Finnmark, are therefore expected to maintain very large home ranges. Indeed, lynx home ranges in northern Norway may conform to this "obstinate strategy" as Eurasian lynx in Scandinavia have been found to have some of the largest home ranges recorded in the world (Linnell et al 2001; Herfindahl et al 2005). Home ranges of lynx and wolverine were extremely large within both areas indicating that both species and sexes used space extensively regardless of season. The extremely large home range sizes of lynx in northern Norway may be partially attributable to seasonally and spatially variable food resources and corresponded to other estimates in Norway with males using space more extensively than females (Sandell, 1989).

This study also found lynx females showed restricted range use in summer related to denning behavior, while reproduction increased winter home range expansion in females. Intersexual differences in home range size seen in summer are related to female reproduction during this time of year, which restricts their daily movement distances and therefore their overall home range size during these periods (McNutt, 2013). Danell et al (2006) found a similar trend in Sweden, with family groups using substantially smaller areas in summer than non reproductive females and my results also support this.

Lynx have been shown to utilize alternative prey species when primary prey densities are low (Brietenmoser-Wursten et al 2007; Mattisson et al 2011b; Grevasi et al 2013). Given that lynx exhibit year around residency, it is likely that alternative prey switching plays an important role in lynx overwintering survival. Lower prey biomass and increased search and hunting frequency associated with prey switching may have fitness consequences to lynx. In North America, lynx that switch to alternative prey species during crash phases of their cyclic primary prey, hare, have been shown to have reproductive and recruitment consequences (Mowatt et al 1996; Apps, 2000). Similar results have been found for Eurasian lynx in Finland

having access only to hare as their primary prey instead of having an ungulate component in their diet (Pulliainen et al 1995). This study showed a similar trend, with lower recruitment in areas without winter reindeer although this decrease was not significant due to low sample size.

Range expansion can be costly as search time and movement distances must increase when prey is scarce. There are also likely to be costs associated with a lack of spatial knowledge of available food resources. Site fidelity can increase resource predictability as an animal's local knowledge of resource availability over space and time is improved (Eide et al 2004). In an anthropogenically influenced migratory system primary prey predictability may be an important factor to reproductive success (Angerbjörn et al 1999; Giroux et al 2013). Therefore, retaining territoriality and site fidelity may be of great benefit to lynx in times of low resource availability. This would apply to spatial awareness of alternative prey resources as well.

Another important aspect of carnivore space use that this study highlights is that females reacted more strongly to prey shortages than did males, showing less stability in winter. The distribution and abundance of prey in space and time is difficult to measure and the predictability of food resources may have a pronounced effect on the spacing behavior. As female reproductive success is dependent on food resources, their space use may be strongly influenced by the predictability of resources. It is beneficial for females to maintain a stable home range large enough to provide adequate resources to support reproduction. Additionally, increasing landscape familiarity can enhance hunting and, consequently, reproductive success (Pierce, et al 2000; Eide et al 2004; Van Moorter et al 2012). The results of this study indicate that decreased lynx recruitment may be tied to the costs of living within a system with seasonally marginal resources. The lack of recruitment among study animals is consistent with studies of other northern lynx populations in response to hare density declines (Poole, 1995, Mowat et al 1996; Apps, 2000). Evidence of breeding, illustrated by the similar birth rates within the two areas, is consistent with the suggestion of Mowatt et al (1996) that breeding and implantation continue to occur regardless of prey densities but that recruitment of kittens is affected by low prey densities.

In systems with migratory prey, resource availability may be too narrow for females to adequately provide for their young over winter or for juveniles to survive to the following winter (Jêdrzejewska and Jêdrzejewski, 1998; Schmidt 2008). This may be especially true for young females that are reproducing for the first time or newly dispersed individuals with limited local knowledge. Mowatt et al (1996) additionally found that yearling female Canadian lynx reproduction almost ceased during the first year of a decline in cyclic hare populations while adult females still managed to recruit offspring, though at a rate lower than in peak hare years. Similar results were found with young lynx in Scandinavia (Pulliainen et al 1995). Anthropogenic migration of reindeer may contribute to keeping lynx populations at a lower level than predicted by resource availability through decreased kitten/juvenile survival (Ballard et al 1997). Alternative prey may therefore become important to the reproductive success of lynx in these areas with prey switching behavior being the mechanism that maintains recruitment in this system. Further research is needed investigating a link between foraging behavior and demographic processes in lynx.

Management Implications

Local reindeer husbandry incurs heavy predation from both wolverines and lynx (Haglund 1966; Landa et al 1997; Pedersen et al 1999; Nybakk et al. 2002; van Dijk et al. 2008; Andrén et al 2011; Mattisson et al. 2011a+b; Koskela et al. 2013). As a result, management in Norway largely focuses on lethal control to manage carnivore population densities to help mitigate human conflicts. Management plans targeting reduced carnivore densities can have the unintended consequences of reducing population stability and altering space use patterns however. Lower carnivore density creates unoccupied territories which would potentially allow for greater home range expansion to occur or the ability to shift longer distances without interacting with territorial neighbors which could increase encounter rates with reindeer, increasing conflict in these areas (Maletzke et al 2014). This disruption of territoriality can also create an influx of immigrant males further affecting space use patterns.

High levels of human caused mortality, including both legal management and illegal hunting, have a large influence on carnivore population dynamics in northern Scandinavia (Andrén et al 2006) and serve to keep carnivore population densities below environmental carrying

capacity (Herfindal et al 2005). This study illustrates that a proportion of northern lynx populations maybe seasonally bottom up regulated through limited prey availability during winter months lowering recruitment. It is likely that migratory prey has an effect on subadult dispersal and survival as well. Coupled with low recruitment rates, populations in these systems could experience high turnover. The combination of bilateral population regulation of these carnivores could have severe demographic consequences.

Understanding carnivore response to ungulate migrations can aid in understanding population dynamics and the impact of these predators on both their primary and alternative prey. This can be beneficial for conservation and management planning purposes as this information may prove useful for understanding impact carnivores have in these regions. In order to manage populations and the communities effectively, it is also necessary to have an understanding of what drives animal space use patterns and how reproductive response affects the population dynamics of predators in these systems. Therefore, it may be important to consider the effect of temporal resource distribution on carnivore demography as well as the overall spatial stability of a population in management planning as well.

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Let the adventure continue….

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