The cost of migratory prey: Seasonal changes in semi-domestic reindeer distribution influences breeding success of Eurasian lynx in northern Norway

Running title: Reproductive cost of migratory prey

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Abstract

Migratory prey is a widespread phenomenon that has implications for predator – prey interactions. By creating large temporal variation in resource availability between seasons it becomes challenging for carnivores to secure a regular year-round supply of food. Some predators may respond by following their migratory prey, however, most predators are sedentary and experience strong seasonal variation in resource availability. Increased predation on alternative prey may dampen such seasonal resource fluctuations, but reduced reproduction rates in predators is a predicted consequence of migratory primary prey behavior that has received little empirical attention. We used data from 23 GPS collared Eurasian lynx (*Lynx lynx*) monitored during 2007-2013 in northern Norway, to examine how spatio-temporal variation in the migratory behavior of semi-domestic reindeer (*Rangifer tarandus*) influences lynx spatial organization and reproductive success using estimates of seasonal home range overlap and breeding success. We found that lynx of both sexes maintained seasonally stable home ranges and exhibited site fidelity across years, independent of whether they had access to reindeer throughout the year or experienced a scarcity of reindeer in winter due to migration. However, lynx without access to reindeer in winter showed a decreased probability of reproducing and a tendency for lowered kitten survival into their first winter, when compared to female lynx with reindeer available year around. This supports the hypothesis that sedentary predators experience demographic costs in systems with migratory primary prey. Changes in the migratory behavior of ungulates, including disrupted migrations, is therefore likely to have bottom-up effects on the population dynamics of sedentary predators as well as the previously documented consequences for ungulate population dynamics.

Introduction

Seasonally migratory prey is a widespread phenomenon (Fryxell and Sinclair 1988, Hebblewhite and Merrill 2007) that creates large temporal variation in resource availability between seasons making it challenging for predators to secure a regular year-round supply of food (Schmidt 2008, Nelson et al. 2012, Henden et al. 2014). In response to this challenge, large carnivores have adopted various space use strategies. Some large carnivores follow the migratory movements of prey (arctic wolves *Canis Lupus*, mountain lions *Puma concolor*: Ballard et al. 1997, Pierce et al. 1999, Walton et al. 2001) while others remain stable territory holders (tigers *Panthera tigris*, mountain lions: Hojnowski et al. 2012, Elbroch et al. 2013) or exhibit seasonal range expansion (Eurasian lynx *Lynx lynx*, lions *Panthera leo*: Danell et al. 2006, Valeix et al. 2012).

   Pursuing migratory prey increases access to primary prey throughout the year, but there are several reasons why not all predators choose this strategy. Seasonal movement out of an established territory may increase the risk of losing the territory and thereby the advantages associated with prior residence (Hoem et al. 2007) and local knowledge of resource availability in space and time (Eide et al. 2004), knowledge that may have fitness consequences (Eide et al. 2004, Janmaat et al. 2009, Van Moorter et al. 2009). Furthermore, physical limitations set by offspring movement rates (Martin et al. 2013) and elevated exposure of offspring to predation risk outside an established home range (Persson et al. 2003) may inhibit long distance movements in individuals that care for offspring. Finally, there may be alternative prey of sufficient abundance available locally to allow the carnivore to remain resident. In such cases, an adjustment of home range size may be a sufficient response to the seasonal reduction in primary prey abundance (Sandell 1989, Powell 2000, Powell 2012). The choice of space use strategy in response to migratory prey may therefore depend on biological attributes of the carnivore as well as the local abundance of alternative

3

prey. However, we may expect specialist predators with a narrow diet breadth, carnivores living in areas with limited alternative prey, and reproducing females to be affected more profoundly by changes in resource availability.

A strong relationship between resource availability and both reproductive success and survival is well documented in carnivores (Brand and Keith 1979, Angerbjörn et al. 1991, Hofer and East 1995, Fuller and Sievert 2001, Giroux et al. 2012, Rauset et al. 2015). The seasonal reduction in food availability caused by migratory prey is therefore expected to limit predator population growth (Fryxell and Sinclair 1988). Accordingly, low alternative prey availability in the season when fluctuating prey are absent has been documented to have negative effects on predator populations (Angerbjörn et al. 1991, Eide et al. 2004). Loss of prey migratory behavior (Berger 2004) or a decrease in the proportion of the prey population that migrates (partial migration: Chapman et al. 2011, Middleton et al. 2013) can therefore be expected to increase predator population growth. However, so far there has been little focus on the consequences of variation in prey migratory behavior on predator population dynamics and abundances (Henden et al. 2014).

In this study, we examined how seasonal variation in prey availability influences space use and reproductive success in a specialist predator, the Eurasion lynx. Eurasian lynx, the only large felid in Europe, are a primary predator of medium sized ungulates (Odden et al. 2006, Molinari-Jobin et al. 2007) and are in general stable territory holders even during periods of low prey density (Ward and Krebs 1985, Breitenmoser-Wursten et al. 2007, Schmidt 2008). In northern Scandinavia, Eurasian lynx largely overlap with the distribution of migratory semi-domestic reindeer (*Rangifer tarandus*), which in this area represent the only ungulate prey available for this solitary carnivore (Pedersen et al. 1999, Mattisson et al. 2011, Tveraa et al. 2014). Annual migration between summer and winter grazing areas occurs throughout the area, although migration distances and the occurrence of partial migration, varies greatly

(Mattisson et al. 2011, Henden et al. 2014). This variation creates a situation where some lynx may experience reindeer as available prey throughout the year, while others experience an almost complete lack of ungulate prey during the winter season.

Eurasian lynx mate in late March-April and typically give birth annually to two kittens in late May/early June (Gaillard et al., 2014). Kittens are dependent on their mothers until the following spring (Nilsen et al. 2012, Samelius et al. 2012). As both income breeders and obligate predators, lynx do not rely on stored body reserves (Jönsson 1997) to meet the increased energetic demands of late gestation-early lactation, but must instead rely on currently available resources to maintain body condition and rear kittens (Gaillard et al., 2014). Consequently, their demographic rates are susceptible to temporal changes in prey resources (Mowat et al. 1996, Apps 2000, Mattisson et al. 2011). Lack of ungulate prey in winter creates the need to subsist on alternative prey, both at a time when female lynx need to build up reserves for subsequent reproduction, as well as provision their kittens. The exclusion of ungulates from the diet of lynx has been found to decrease body condition and fat stores (Pulliainen et al. 1995) potentially reducing reproduction and kitten growth and survival.

Based on the hypothesis that the costs associated with following migratory prey are higher than the costs of remaining resident and living off less preferred prey, we predict that lynx will maintain stable year-round home ranges, despite being dependent on migratory reindeer. By remaining resident, lynx can retain territorial borders allowing for increased spatial knowledge of resources and valuable summer areas for breeding, and potentially increasing encounter rates with overlapping lynx during mating season. However, not following migratory reindeer will require prey switching for survival. Prey switching to smaller alternative prey is likely to provide less energetic value than ungulates, making it harder for lynx to meet their energetic needs during winter. Additionally, these northernmost sub-arctic

regions exhibit low productivity, providing few alternative prey species, all of low biomass (<10 kg; Mattisson et al. 2011), which may further compound effects of seasonality in the availability of reindeer as prey (Pulliainen et al. 1995). Because this is anticipated to have demographic costs, we further predict that reproductive output will be lower for female lynx that remain resident, due to the seasonal scarcity of their main prey.

Methods

Study Area

The study was conducted in Finnmark (70˚10´N, 24˚70´E) and Troms (69˚00´N, 19˚90´E) counties in northern Norway (Fig. 1). The area is predominantly alpine tundra characterized by a coastal alpine climate while the interior is composed of large plateaus above tree line. The area is usually snow covered from October/November to April/May. At lower elevations, mountain birch (*Betula pubescens*) is the most common tree species with occasional stands of Scots pine (*Pinus sylvestris*). Semi-domestic reindeer are 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 residing in these areas (Mattisson et al. 2011). Free ranging domestic sheep (*Ovis aris*) are also available in summer (Mattisson et al. 2014).

Carnivore Data Collection

Telemetry data was collected from GPS collared lynx monitored during 2007-2013 (n=27 lynx, totaling 44 lynx-years of data) as part of a long-term research project: Scandlynx (http://scandlynx.nina.no/). Capture and handling of study animals occurred during winter via chemical immobilization from helicopter following procedures outlined by Arnemo et al.

6

(2012). The Norwegian Animal Research Ethics Committee and the Norwegian Environment

Agency approved all research. In total, ~63 000 GPS locations were available for this study.

Only non-dispersing individuals of breeding age (i.e. > 20 months of age) were used for

analysis (n=23: female=17, male=6). Juvenile lynx residing within a mother's home range

(pre-dispersal) or individuals traveling broadly without a clear home range

(dispersal/transients) were excluded from analysis (n=4). GPS locations deemed inaccurate

during manual screening (n=37) were removed.

Female lynx adopt a central place foraging behavior around the natal lair for 6-8 weeks

after the birth of kittens (Nilsen et al 2012; White et al. 2015). To confirm reproductive

events, female lynx were therefore checked for movement patterns consistent with this pattern

of birth and post-natal behavior during summer (late May to mid-June) with a subsequent

"kitten check" in the field at 20-37 days (mean=26) after presumed birth of kittens (Nilsen et

al. 2012, White et al. 2015). Lynx kittens are dependent on their mother for ≥ 9 months

(Samelius et al. 2012) thus recruitment, i.e. successful rearing of kittens, was determined

between November and January by snow tracking or visual observation of kittens in company

with their marked mother (Gaillard et al. 2014). In some years we did not manage to secure

data on whether females had live kittens in summer (n=4 observations missing) or the

subsequent winter (n=1). In total, we had data from 17 individual females for analysis of the

influence of reindeer availability on the proportion of female lynx with kittens in summer

(n=38 lynx-years of data) and the proportion of females with kittens in summer that still had

recruits in winter (n=27 lynx-years of data).

Reindeer Availability

Within northern Scandinavia, free ranging reindeer are intensively managed by indigenous

Sami husbandry practices and controlled by management regulations enforcing seasonal

migrations (Tveraa et al. 2014). Our study area overlaps the three northernmost reindeer herding regions in Norway: Troms, West Finnmark, and East Finnmark (Tveraa et al. 2014). Reindeer availability in Troms is, to a certain extent, seasonally stable as districts here only conduct short distance reindeer migrations between summer and winter grazing pastures. This equates to reindeer being available as a food resource within lynx summer home ranges throughout the year and thus a predictable winter resource in this region. In the two regions in Finnmark, many reindeer herds move up to several hundred kilometers away from summer grazing pastures on the coast to inland overwintering pastures. This creates a marked absence of reindeer in winter for carnivores residing within summer grazing areas in Finnmark. However, some reindeer may become lost during these migrations and are sporadically present as single animals or small groups of scattered animals during winter. These remaining reindeer may provide limited hunting opportunities to carnivores that reside in these areas (Mattisson et al. 2011). Additionally, during the years of this study, partial migration occurred in some herds in parts of both West and East Finnmark (Henden et al. 2014), with several reindeer grazing districts defying regulations and choosing to overwinter their entire reindeer herds, or parts of them, in summer pastures rather than moving them to the wintering areas. As partial migration events occurred in both West and East Finnmark, they were combined as Finnmark in analyses to represent an area of low predictability of winter resources while Troms represents a region of relatively high winter resource predictability.

As the magnitude and distribution of reindeer migration varied between years, we could not solely rely on the designated seasonal grazing areas to quantify reindeer availability in winter. Therefore, we assessed reindeer presence in winter annually, by first overlapping each lynx winter home ranges (see below, n=44 lynx-years of data) with the designated reindeer winter grazing areas based on a GIS-layer compiled by the reindeer husbandry administration of Norway (https://kart.reindrift.no/reinkart/) using ArcGIS version 10.1 (ESRI). Lynx with

winter home ranges that overlapped reindeer winter grazing areas were characterized as having reindeer available as prey throughout the winter (n=17 lynx-years). As Eurasian lynx specialize on ungulates and can retain high kill rates on ungulates even at low prey density (Nilsen et al. 2009), we here assume that prey switching does not occur in winter if reindeer are available (Appendix 1, Table A1; Mattisson et al. 2011). We then evaluated access to reindeer for individuals with winter home ranges that did not overlap winter grazing areas (n=27 lynx-years) using a combination of different data sources: 1) Reindeer count data from winter line transect blocks and camera stations (for details see Henden et al. 2014). 2) Kill rate estimates of monitored lynx during the winter period (for details see Mattisson et al. 2011). If lynx retained high kill rates on reindeer during winter (≥ 3 reindeer/ month), we assumed that there was adequate reindeer presence to sustain lynx throughout winter. 3) Personal communication with personnel at the State Nature Inspectorate (Statens Naturoppsyn, SNO: Mattisson et al. 2011). There is a legal requirement for herders to move reindeer from their summer ranges to winter ranges and any reindeer remaining are controversial and likely to be reported and investigated by SNO.

The approaches used to evaluate the availability of reindeer to lynx each winter did not allow quantification of the density of reindeer within a lynx winter home range but did allow us to create a binary index of winter reindeer availability for lynx (0/1). A winter reindeer index of zero represents none or only a few sporadically scattered reindeer (close to zero), while a winter reindeer index of one denotes a substantial number of reindeer present. We characterized both summer and winter home ranges with respect to the reindeer index to evaluate whether lynx shifted range use between seasons in order to access reindeer (Appendix 1, Table A2).

Assessing annual variations in availability of reindeer across a large spatial scale including several districts, managers and herders has inherent challenges. In general, transect and

camera data were only available in areas where incomplete migration was expected to occur, thus lacking for some lynx which had no reindeer in winter. However, in these areas we could confirm the lack of reindeer via predation studies. In addition to these estimates, we further confirm our index using the knowledge of the SNO rangers that work in these areas, finding 100% agreement between ranger knowledge and predation/transect/camera data.

We acknowledge that our decision to assign reindeer presence is somewhat arbitrary. However, we are still confident that this mixture of quantitative and qualitative data provides an acceptable broad scale measure of reindeer presence/absence in lynx seasonal ranges.

Home Range Stability

Home range overlap indices and seasonal shifts in home range center points are useful for measuring the degree of site fidelity of an individual (Kernohan et al. 2001, Fieberg and Kochanny 2005, Janmaat et al. 2009). Furthermore, seasonal shifts in home range size or location can indicate that carnivores follow migratory movements of prey or undergo range expansion or retraction (Breitenmoser-Wursten et al. 2007, Hojnowski et al. 2012, Valeix et al. 2012). Therefore, to test if lynx remain stationary across seasons or exhibit seasonal shifts in home range use in relation to the availability of reindeer, we examined two-dimensional spatial overlap of seasonal home ranges.

Available GPS locations were limited to two distinct periods, 'winter' (HR_W: 1 February - 30 April) and 'summer' (HR_S: 1 June – 30 August). These periods limit analyses to intervals when reindeer presence could be accounted for (see above). Typically, semi-domestic reindeer migrate from summer to winter pastures between September - November and return April - May (www.Reindrift.no). To maximize sample size, the winter period was not set to start until February as most lynx captures occurred between mid- January and March. Seasonal home ranges were estimated annually for each individual using 95% minimum

10

convex polygon (MCP) estimates using R- package 'adehabitat' (Calenge 2006) in R (R

Development Core Team, 2013). 95% contours minimize the influence of extra-territorial

movements and outliers which can artificially inflate home range estimates (White and Garrot

1990, Getz et al. 2007). The choice of a broad estimator such as MCP, which focuses on

changes of the peripheral boundaries of range use by season, and is not sensitive to variation

in number of GPS locations per animal (2-48 locations/day), was most complementary to our

binary reindeer index for examining whether lynx shifted, expanded or contracted home range

boundaries in response to migrating reindeer. We did not have fine scale spatial data available

for reindeer to examine use of core areas within home ranges. By assigning a fixed period to

the seasonal home range estimates (White and Garrot 1990, Fieberg and Borger 2012), the

sampling duration was standardized across individuals, allowing for comparison of space use

patterns. Number of location days per range averaged 78 ± 1.8 SE per three-month seasonal

period.

To test for within year stability and range expansion or contraction, we calculated the

overlap between summer and winter ranges and vice versa, only including individuals where

data on both winter and summer periods were available within the same year. We then

estimated mean proportion of overlap between seasonal ranges ([Overlap HR_{S-W} + Overlap

HR_{W-S}] /2) using Ranges8 (Anatrack Ltd.). All individuals that had seasonal home range

overlaps >50% were considered stable territory holders (Hojnowski et al. 2012, Richard et al.

2014). For individuals (n=13) with multiple years of seasonal home range estimates available,

site fidelity was further measured using mean proportion of overlap of an individual's summer

and winter ranges averaged across all years. To determine whether lynx expanded or retracted

ranges in winter in response to a lack of reindeer we estimated the difference in the proportion

of overlap between seasonal home ranges. This identified lynx that expanded one of their

ranges (high differences, approaching 1 for winter expansion or -1 for summer expansion)

from lynx that either did not change range use or shifted ranges without changing area use (low differences approaching zero). As a further indicator of lynx following migrating prey we estimated the distance between seasonal home range centroids, using the arithmetic mean, to test for long distance shifts in range use (White and Garrot 1990, Kernohan et al. 2001, Janmaat et al. 2009).

Statistical Analysis

To examine the effect of reindeer availability in winter on lynx space use, we used generalized linear mixed models (GLMMs) with a logit-link beta distribution (R-package glmmADMB; Skaug et al. 2014) for analyses of mean home range overlap (i.e. proportional data). In addition to the reindeer availability index (0: no reindeer in winter, 1: reindeer in winter) we further included a three level variable of reindeer district (Troms[1], Finnmark[1] and Finnmark[0]) to examine the influence of reindeer predictability on lynx space use compared to actual reindeer availability. Troms[1] represents a region of relatively high winter resource predictability where reindeer are available in winter and predictable between years. Partial migration events in areas of Finnmark create unpredictable winter resources certain years where reindeer may be either available in winter but not predictable (i.e. Finnmark[1]), or not available in winter due to complete migration (i.e. Finnmark[0]). Reproducing females had smaller ranges in summer than non-reproducing females (see results) creating a lower mean overlap for family groups. Therefore, lynx status (females, females with kittens, males) and individual lynx (to avoid the effects of pseudo-replication among individuals) were included as random intercepts in the models. For each of the dependent variables, corrected Akaike Information Criteria (AICc) was used for comparison between models. To assess the relative support for each model we computed Akaike weights.

Reproductive Success

The influence of reindeer availability on the proportion of female lynx that had kittens in summer and proportion of females with kittens in summer that had surviving recruits the subsequent winter were analyzed separately using GLMMs with a binomial error distribution and a logit link function. As lynx have been found to have a common optimal litter size of two kittens, which varies little depending on study area, female body condition, or whether they were wild or captive lynx (Gaillard et al 2014), we did not test for variation in litter size or survival of individual lynx kittens. The reindeer availability index (0: no reindeer in winter, 1: reindeer in winter) for the preceding winter was used as a predictor in the analyses of presence of kittens in summer, while the reindeer index for the subsequent winter was used in the analysis of recruit survival into their first winter. Two year old lynx have previously been documented to have lower reproductive rates than adult lynx (Nilsen et al. 2012). Among the available observations, three were associated with two year old females, three were from females of unknown age while the remaining observations were associated with mothers greater than two years of age. We excluded the observations with unknown age and included the two level factor (2 yrs, >2yrs) as a fixed effect in the model for kitten presence in summer. For the analysis of kitten survival, observations from two year olds were excluded as only one observation was available. Individual lynx ID was fitted as a random intercept in both models.

Results

Within the lynx-reindeer system in northern Norway, lynx maintained consistent, seasonally stable home ranges. Male seasonal ranges ($1146 \text{ km}^2 \pm 146$ SE, n=26) were in general larger than females ($438 \text{ km}^2 \pm 61$ SE, n=62) and reproducing females had, because of maternal behavior being centered around a natal lair (White et al. 2015), smaller ranges in summer ($238 \text{ km}^2 \pm 54$, n=22) than non-reproducing females ($473 \text{ km}^2 \pm 84$, n=9). Mean proportion of

13

overlap amongst seasonal lynx home ranges was 56% (SE=3%), indicating a relatively high

degree of home range stability (Table 1). Inter-annual site fidelity, measured for individuals

with multiple years of data, was 51% (SE=5%) for females and 63% (SE=9%) for males

indicating spatial stability across years as well. With the exception of one outlier, lynx of both

sexes showed short mean centroid shift distances (11 km, SE = 1.3, with outlier excluded).

The outlier was a male lynx with a high proportion of seasonal overlap (78%), but with very

large home ranges in both seasons (summer = 2911 km^2, winter = 2431 km^2). Therefore, in

this case as well, the centroid shift distance (43 km) did not reflect a large shift in range use.

Centroid shift distances for all lynx were within the radius of an average seasonal range (M:

19 km, F: 12 km) and relatively short compared to reindeer migration distances.

Influence of reindeer availability on lynx space use

In the dataset, 13 lynx-year observations were categorized as without access to reindeer

during winter, while 31 had reindeer available during both winter and summer (Appendix

1, Table A2.). All but one of these lynx had overlapping summer and winter home

ranges, indicating that none of the collared lynx followed reindeer on their long distance

migration. The single lynx not exhibiting overlap between summer and winter ranges did not

have access to reindeer in its new winter range, so the range shift was not because it followed

migrating reindeer. Furthermore, we found no influence of reindeer availability on the

proportion of seasonal home range overlap (Table 2) and did not observe expansion of range

use in winter as a response to migrating reindeer (Fig. 2). Winter range size did not change

depending on reindeer presence or absence (t.test males: t=0.77, p=0.5, females: t=0.21,

p=0.8). This suggests that the presence or absence of reindeer in winter had little influence on

lynx space use in winter. We note, however, that there was a tendency for higher overlap

between seasonal home ranges within the Troms reindeer district (β=0.6, SE=0.30), where

14

reindeer availability in winter is more predictable, than within the Finnmark reindeer districts. This suggests that the predictability of reindeer presence may influence lynx space use more than actual reindeer presence within a given year. Both individual lynx and status accounted for some of the variation in the models (random effect estimates for individual = 0.21, 0.46 SD, status = 0.06, 0.24 SD).

Reproductive output and reindeer availability

Reindeer availability in winter increased the probability of lynx reproducing in the subsequent summer from 0.49 to 0.85 (Fig. 3; logistic regression coefficient $\beta=1.8$, SE=0.9, P=0.04). There was no significant effect of reindeer availability in winter on the probability of kitten survival into the subsequent winter (logistic regression coefficient $\beta=1.2$, SE=1.2, P<0.49). However, the trend was in the same direction with point estimates of survival being 0.59 for lynx without winter reindeer and 0.82 for lynx with winter reindeer availability. Consistent with previous findings, there was also a trend towards a lower probability for two-year-old lynx to reproduce (logistic regression coefficient $\beta=-2.0$, SE=1.4, P<0.16) when compared to older female lynx.

Discussion

We found no evidence that Eurasian lynx followed their main prey, semi-domestic reindeer, on their migrations. Lynx predominantly maintained their home ranges across seasons, independent of reindeer availability and with no trend towards range expansion. These findings support the theory that the costs associated with following migratory prey are higher than the costs of remaining resident and living off less preferred prey (Valeix et al. 2012). We document, however, that the reproductive cost of remaining resident when the reindeer migrate is still substantial. On average, only half of the female lynx managed to produce

kittens in areas without reindeer the previous winter, while 85% produced kittens when reindeer were present. In addition, kitten survival the subsequent winter also tended to be lower when reindeer were scarce. In contrast, northern lynx with access to reindeer had similar reproduction rates to lynx in areas of high roe deer density in southern Norway (Nilsen et al. 2012). However, lynx without access to reindeer had much lower reproductive rates than lynx in areas of low roe deer density (Nilsen et al. 2012). Thus, for lynx without access to winter reindeer, resource availability is likely too low for females to maintain fitness for subsequent reproduction and to provide for their young over winter (Jedrzejewski et al. 1996, Schmidt 2008).

Generally, sub-arctic ecosystems consist of short food chains and low productivity. Accordingly, the density of alternative prey is found to decrease with latitude (Simpson 1964). While adult lynx without access to reindeer in winter manage to survive on alternative prey, the inclusion of meso-predators such as red fox and domestic cats in winter lynx diets further indicates that more preferred alternative prey (Appendix 1, Table A1; Mattisson et al. 2011) are scarce in the system in winter. Our results emphasize the importance of ungulate prey for Eurasian lynx population dynamics, and that resource availability is important for breeding success (Rauset et al 2015, Laaksonen et al. 2002, Tavecchia et al. 2005, Scheel and Packer, 1995). It further corroborates previous documentation of the importance of ungulates for lynx body condition and fat stores (Pulliainen et al. 1995). Towards the northern limit of their distribution, resource availability in winter appears to limit reproductive success in lynx without access to reindeer, and suggests a role for bottom-up regulation of lynx populations in this northern ecosystem.

Predators with migratory ungulate prey in African ecosystems modify their resident behavior to cope with migratory prey movements and increase access to their seasonally variable prey (commuting: spotted hyenas *Crocuta crocuta*; seasonal shifting, expanding:

lions (Hofer and East, 1995; Scheel and Packer, 1995, Valiex et al 2012)). Both Canadian and Eurasian lynx have been found to expand their home ranges in response to prey declines elsewhere (Ward and Krebs 1985, Danell et al. 2006, Breitenmoser-Wursten et al. 2007). In contrast, we found no strong evidence of winter range expansion for lynx that experienced an absence of reindeer in winter. Lynx may, rather than balancing the high energy tradeoff of long distance searching for migratory ungulate prey or expanding their ranges to access them, switch to smaller, resident alternative prey species that are more predictable or seasonally available than migratory reindeer (Breitenmoser-Wursten et al. 2007, Mattisson et al. 2011, Gervasi et al. 2014). Whether this prey switching is forced (due to a complete lack of reindeer) or elective (rather use areas of high small prey abundance than expand area use in search for sporadic reindeer) is difficult to determine.

We estimate the seasonal (3 months) home ranges of lynx in northern Norway to be large, and of similar size to annual (12 months) home ranges in more southern areas of Norway with low ungulate prey densities (Herfindal et al. 2005). However, in the area where availability of reindeer was predictable between years (i.e. Troms), lynx had both smaller home ranges and a higher within year spatial stability. This indicates that the predictability of reindeer presence may be more influential on lynx space use than actual reindeer presence within a given year. Von Schantz (1984) suggested that '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'. Accordingly, lynx in areas with limited seasonal resource availability and low resource predictability are expected to maintain very large home ranges as a strategy to deal with seasonal variation. It may be that the home range size of lynx in areas with low predictability of reindeer presence is adjusted according to expected needs in poor winters.

While the cost of remaining resident was lowered reproductive success when reindeer became seasonally scarce, following migratory prey is likely related to even higher costs. This

supports the theory that loss of territory and associated landscape familiarity may have great fitness consequences to individuals (Pierce et al. 1999, Eide et al. 2004, Van Moorter et al. 2009). Interestingly, kill rate studies of lynx in these areas (Mattisson et al. 2011) have shown that lynx maintain reindeer as a dietary component even when reindeer are largely absent from their home range, though to a much lesser degree (decreasing from 86% to 15% of prey items in winters with low reindeer availability). This suggests that occasional/sporadic individuals that remain after migration allow lynx to exploit their preferred prey, reindeer, even in times of extremely low availability and with great variation in resource distribution (Mattisson et al. 2011). While these remaining reindeer may be at extremely low numbers, they may be spatially predictable within a lynx' home range, exploiting certain areas for shelter or food. Thus, retaining territoriality and its' associated spatial knowledge may be crucial for lynx in their search and exploitation of such a seasonally scattered food source.

In northern Norway, our findings have direct implications for the management of reindeer and lynx. Local reindeer husbandry incurs heavy depredation from lynx (Swenson and Andrén 2005, Mattisson et al. 2011). As lynx do not follow the reindeer migration, depredation impacts will be higher in areas where reindeer remain year around than in areas with migrating reindeer. Enforcing long distance reindeer migration may therefore act as a mitigating measure with respect to losses of reindeer. Furthermore, the effect of migratory behavior on lynx population dynamics suggest that less effort should be needed to constrain lynx population sizes (for example through recreational hunting; Linnell et al. 2010) in areas with migratory reindeer than in areas where reindeer reside throughout the year due to partial or only short distance seasonal migration.

There has been considerable focus on what causes disruption of ungulate migrations, as well as partial migration, and associated consequences for ungulate populations (Berger 2004, Bolger et al. 2008, Cagnacci et al. 2011, Middleton et al. 2013). Less focus has been on the

ecosystem consequences of such changes (Henden et al. 2014). Our study finds support for the hypothesis that changes in the migratory behavior of ungulates can have bottom-up effects on the population dynamics of predators (Fryxell and Sinclair 1988), and we expect this to be a common phenomenon. Changes in the distribution or timing of ungulate movements, whether from climate driven changes to migration patterns, herding management or other anthropogenic influences like habitat fragmentation, is likely to negatively affect the reproductive success of sedentary carnivores (Scheel and Packer 1995, Hofer and East, 1995). Given the reduced abundance of alternative prey at increasing latitudes, we suggest that alterations in migratory behavior of ungulates may be more critical for predator population dynamics at higher rather than lower latitudes, however, this hypothesis remains to be tested. Clearly, knowledge regarding the consequences of changes in ungulate migrations for predator and prey dynamics has both management and species conservation implications and should be explored further in other systems as well.

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Table 1. Proportion of overlap (%) between seasonal home ranges of Eurasian lynx males, females, and females with kittens (n=44 lynx-years) based on 95% MCP estimates. Seasonal home range overlaps estimates >50% were considered stable, however, reproducing females had smaller ranges in summer than non-reproducing females due to central place foraging behavior around the natal lair, creating a lower mean overlap for family groups.

	Proportion of Home Range Overlap (%)		
	Summer-Winter	**Winter-Summer**	**Mean Overlap**
	Mean ± SE	Mean ± SE	Mean ± SE
Males (n=13)	60 ± 7%	73 ± 6%	67 ± 4%
Females (n=9)	66 ± 10%	56 ± 10%	61 ± 6%
Females with kittens (n=22)	61 ± 7%	37 ± 7%	49 ± 5%
All lynx (n=44)	**62 ± 4%**	**51 ± 5%**	**56 ± 3%**

Note: Sample size (n) represents the number of seasonal home ranges each year.

Table 2. GLMM-models to assess the effect of reindeer availability (Rein), reindeer district (District) or district in combination with reindeer availability (District_Rein) on seasonal range overlap in Eurasian lynx. Models were fitted with a logit-link beta error distribution and lynx status (female (F), female with kittens (FA), male (M)) and lynx ID were included as a random intercept in all models.

	d.f.	AICc	ΔAIC	AICω
District	5	-23.9	0	0.48
Null	*4*	*-22.6*	*1.3*	*0.25*
Rein	5	-21.5	2.4	0.14
District_Rein[1]	6	-21.4	2.5	0.13

[1]Three level categorical variable. Two reindeer districts: Troms and Finnmark and presence (1) / absence (0) of reindeer combined; Troms[1], Finnmark[1], Finnmark[0]. As Troms did not have any reindeer=(0) interactions were not possible.
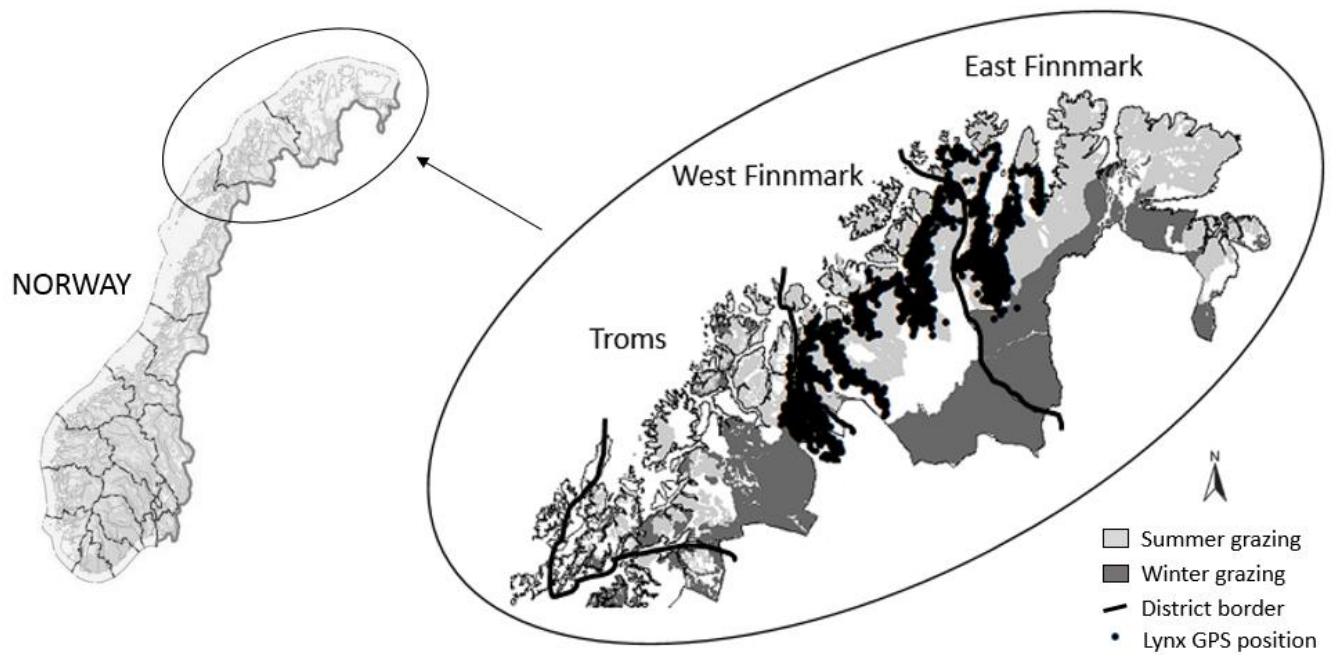
Figure 1. Overview of the study area in northern Norway. Light and dark grey areas in the

enlargement represent summer and winter reindeer grazing areas, respectively. The black

lines denote borders between Troms, Finnmark West and Finnmark East reindeer herding

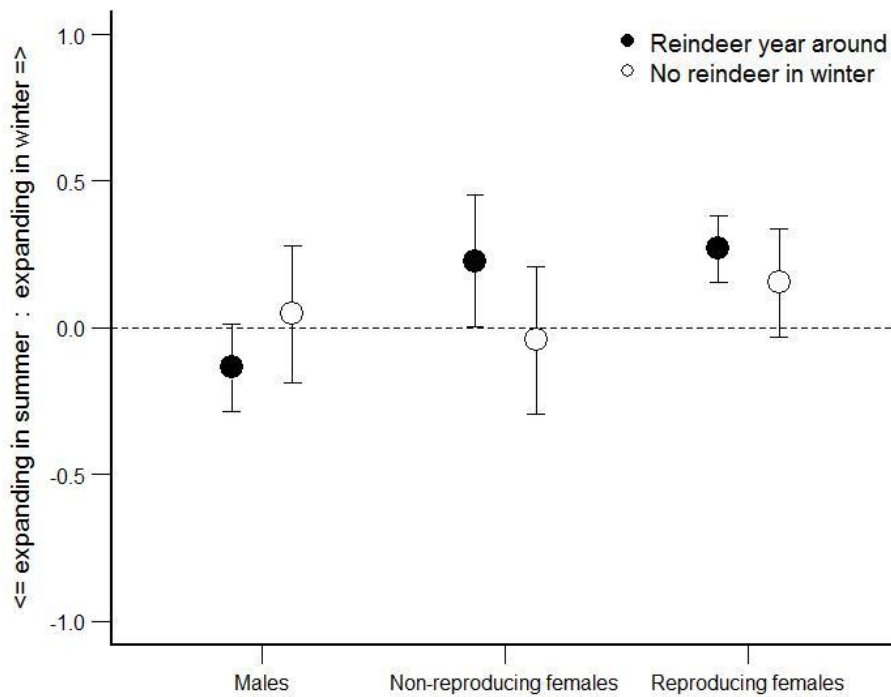regions. GPS locations for lynx are shown as black points.

Figure 2. Changes in seasonal range use by Eurasian lynx in response to migrating prey. Expansion (y-axis>0), or retraction (<0) of range use in winter compared to summer in areas with constant prey availability during the year (Reindeer: black circles) and in areas where prey migrate out of lynx ranges in winter (No reindeer: white circles), separated by lynx sex and reproductive status. Values and SE were estimated with a generalized linear (mixed) effect model for each group where lynx ID was included as random intercept.
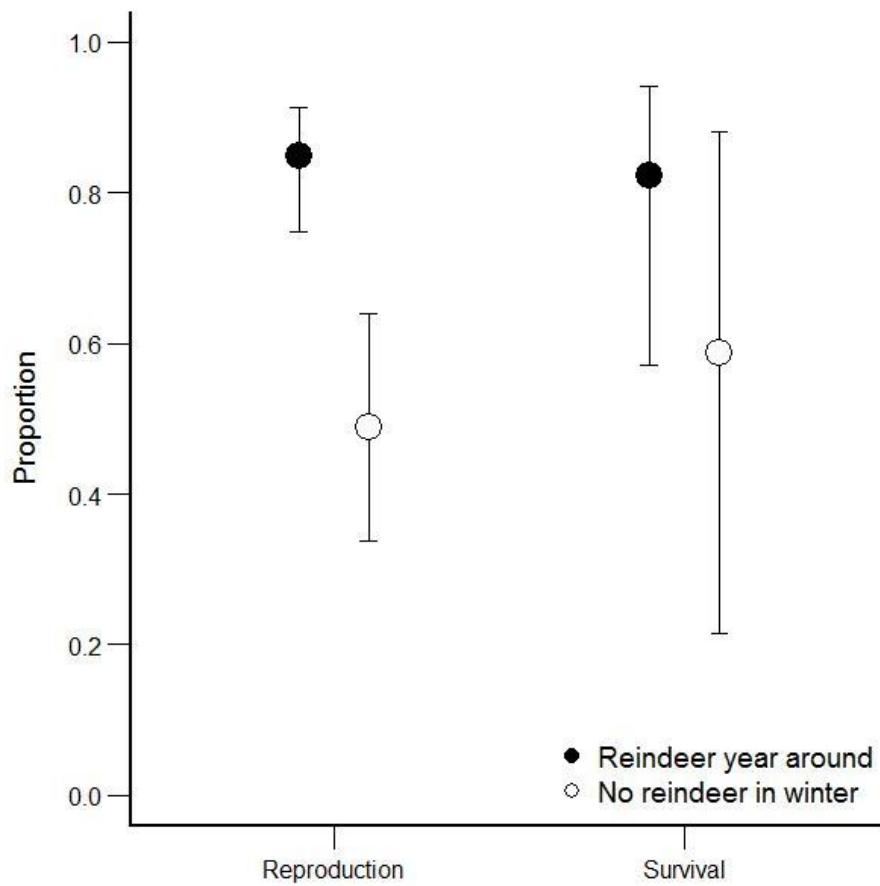
Figure 3. Proportion of female lynx that 1) give birth in summer (reproduction) and 2) successfully have at least one kitten still alive in winter (survival) depending on the availability of reindeer, the main prey of the lynx (black circles: reindeer year around, open circles: no reindeer in winter). Proportions and SE were estimated with generalized linear (mixed) effect models where lynx ID was included as random intercept.