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Community-wide mesocarnivore response to partial ungulate migration

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Summary

1. Mesocarnivores have been found to increase in numbers and geographic ranges in human-disturbed ecosystems with cascading negative impact on biodiversity. To mitigate such impacts it is essential to identify the proximate causes of such mesocarnivore releases. Here we assess to what extent increased partial migration in semi-domesticated tundra reindeer induce a response in boreal and arctic mesocarnivores.
2. We used a large-scale and multi-year quasi-experimental study design with camera traps deployed on coastal tundra peninsulas in northern Norway to estimate area occupancy of the whole carnivore community. These peninsulas represent summer pastures for separate semi-domestic reindeer herds that, owing to different degrees of partial migration, now display spatially and temporally variable densities of year-round resident reindeer. We estimated resident reindeer density by means of aerial surveys.
3. Area occupancy of all the recorded carnivore species increased strongly when resident reindeer densities exceeded 1.5 deer per km^2.
4. Most of the increasing carnivore species were typical boreal forest species, implying range expansions into tundra when provided with stable food resources (prey and carrion) in terms of resident reindeer.
5. **Synthesis and application**. We found that boreal mesocarnivores, known to negatively impact the productivity of reindeer and arctic wildlife of conservation concern, steeply increased in tundra areas with many year-round resident reindeer due to increased partial migration. To avoid such negative impacts actions should be taken to minimize residency in tundra reindeer.

Key-words: arctic tundra, corvids, eagles, mesopredators, semi-domestication, reindeer, red fox, wolverine.

Introduction

Increased abundance and range expansions of medium-sized carnivores (mesopredators; sensu Soulé et al. 1988) often become the unintended consequences of human interventions in ecosystems, with potentially negative cascading impacts on biodiversity (Prugh et al. 2009; Ritchie & Johnson 2009). While population declines and range contractions of apex predators are the most highlighted proximate causes of such mesocarnivore increase, through relaxed top-down regulation (Estes et al. 2011), also increased resource levels may provide bottom-up boosts of mesopredator populations (Crooks & Soule 1999; Larivière 2004; Elmhagen & Rushton 2007). When both top-down and bottom-up constraints on mesocarnivore populations become relaxed simultaneously, the setting is expected to maximize mesocarnivore outbreaks (Prugh et al. 2009). Rarely, however, are the effects of factors that may cause mesocarnivore outbreaks and range expansion explicitly quantified (Prugh et al. 2009), especially considering the entire community of carnivores that may respond (Sutherland et al. 2011). A community approach is important because different species with different bottom-up and top-down constraints and/or functions in the food web may be involved (DeVault et al. 2003; Finke & Denno 2004; Finke & Denno 2005; Wilson & Wolkovich 2011).

Ungulates constitute important food resource in terms of prey for large predators, but also as carrion for scavengers of all sizes (Selva et al. 2003; Wilmers et al. 2003a; Wilmers et al. 2003b). Ungulates are also important resources for humans. This leads to various management strategies, including removal of competing large carnivores and ungulate domestication. For instance, in large parts of the Arctic herds of tundra reindeer (*Rangifer tarandus*) – the numerically dominant and most widespread northern ungulate - have been semi-domesticated by native people (Jernsletten & Klokov 2002; Forbes & Kumpula 2009; Forbes 2010). Semi-domestication of reindeer impacts many aspect of their ecology including range use patterns and reindeer-predator interactions (Forbes & Kumpula 2009) and together with the removal of apex predators this has led to increased reindeer abundance (Hausner et al. 2011; Næss & Bårdsen 2013). Large carnivores preying on reindeer are persecuted and often severely suppressed in regions with reindeer herding (Ims & Ehrich 2013). Moreover, the original ranges and movement patterns of the herds have become increasingly constrained by human infrastructure (Forbes 2010; Degteva & Nellemann 2013).

Throughout their circumpolar range most populations of *Rangifer* travel between boreal forests in winter to coastal calving grounds in tundra in the summer (Gunn & Miller 1986; Fauchald et al. 2007). These migrations represent some of the longest, and ecologically most important, migrations documented for terrestrial mammals (Fancy et al. 1989). Generally, Fryxell & Sinclair (1988) argued that animal migration causes resident predators to depend on alternative resident prey for most of the year and are therefore less able to respond numerically to the temporary superabundance of migratory prey. Hence, migration is expected to limit carnivore abundance.

In northern Fennoscandia the original seasonal coast-inland migration pattern of wild reindeer became altered already when the herds were semi-domesticated 3-400 years ago (Muga 1986). The migration became further restricted by closure of the borders between Norway and Russia, Finland and Sweden from the mid 1800's (NOU 1984; Jernsletten & Klokov 2002), preventing the use of the historical winter pastures in the northern boreal coniferous forest in Russia and Finland (NOU 1984). More recently, the migration has become increasingly affected by modern anthropogenic infra-structure causing migration barriers (Forbes 2010) as well as malfunctioning governmental policies (Hausner et al. 2011). Finally, reindeer migration patterns are likely to be affected by on-going climate change that alters the length of seasons (Tveraa et al.

2013) and limits the access to winter pastures due to more ice-crusted snow (Bartsch et al. 2010). Altogether, the cumulative effect of such emergent pressures on reindeer ranges may have contributed to more partial migration (*sensu* Lack 1943), whereby a fraction of the population do not migrate and become year-round resident in the summer habitat. Generally, global envirnomental change is predicted to cause more partial migrations among animal species (Chapman et al. 2011). In turn, a more partial migration (i.e. an increasing fraction of non-migrant individuals) can have propagating ecological impacts, in particular, when the migrant species are trophically important in food webs (Brodersen et al. 2008). Yet very few studies have adressed the ecological consequences of such emergent partial migration patterns (Chapman et al. 2011).

By means of a large-scale study conducted over three years in coastal tundra of northernmost Norway, our aim was to assess how the community of carnivores responded to spatio-temporal variation in the degree of partial reindeer migrations across different management districts. Partial reindeer migration implies that a fraction of the herd stays in their summer pastures also in winter. In northern Norway the degree of partial migration varies among different reindeer management districts and years, presumably owing to differences in management/herding practices, range restrictions and climatic conditions. This particular setting provided an opportunity to employ a quasi-experimental approach (cf. Ims et al. 2007) in which spatio-temporal variation in density of resident reindeer in tundra was exploited to estimate the response in the associated community of carnivores. If, as hypothesised by Fryxell & Sinclair (1988), carnivore populations in coastal tundra are limited by access to reindeer prey or carrion during winter, we predict that they will respond by increased species-level presence (i.e. area occupancy) to increasing density of resident reindeer. Furthermore, we expected that such a response would be strong (i.e. unconstrained) as the grey wolf (*Canis lupus*) – which was the natural apex predator in low-arctic tundra - have been exterminated from the entire reindeer herding region of northern Fennoscandia (Elmhagen & Rushton 2007; Hobbs et al. 2012). The extant carnivore assemblage in the study region consists of species with widely different ecological niches (Killengreen et al. 2012). They range from small-sized scavengers that never prey on reindeer (e.g. corvids) to predators of calves (e.g. red fox *Vulpes vulpes* and golden eagle *Aquila chrysaetos*) and adult reindeer (e.g. wolverine *Gulo gulo*). The various species in the carnivore assemblage also differ with respect to ecosystem affinity (i.e. to which degree they have strongholds in the boreal forest or the tundra), their mobility (e.g. birds and mammals) and use of alternative prey. Thus we also aimed to assess whether the individual species within such a functionally diverse community responded similarly or differently to increased residency of reindeer in coastal tundra.

Material and methods

STUDY AREA

The study was carried out from 2009 to 2011 on four peninsulas along the coast of Finnmark, northern Norway (Fig. 1); i.e. the peninsulas of Varanger (70–71º N and 28–31º E), Nordkinn (70-71º N, 27-28º E), Sværholt (70º N, 25-26º E) and Porsanger (69-70º N, 24º E). The northernmost parts of the four peninsulas are within the low arctic bioclimatic tundra zone (Walker et al. 2005). The vegetated tundra areas are dominated by dwarf shrub heaths (Oksanen & Virtanen 1995; Ims et al. 2007; Killengreen et al. 2007).

SAMPLING DESIGN

Carnivore monitoring at the two easternmost peninsulas (i.e. Varanger and Nordkinn) has been conducted yearly since 2005, in relation to a conservation project on the regionally endangered arctic fox (*Vulpes lagopus*) (Killengreen et al. 2012), while the monitoring at the two western peninsulas (Porsanger and Nordkinn) was initiated in 2009 and continued through 2011 in connection with the present study. Within all four peninsulas, two-three study blocks were selected (Fig. 1) in order to cover an anticipated spatial variation in the number of resident (i.e. non-migrating) reindeer during winter based on their belonging to different herding districts with different management practices (Ims et al. 2007). In each study block we selected 5 - 8 study sites. The linear distance between two adjacent study sites within a block was minimum 4.5 km with an average nearest distance of 5.8 km (SD = 0.88 km). At each study site we placed one wildlife camera trap baited with a 15-20 kg block of frozen reindeer slaughter remains approximately 3 m in front of the camera. Obviously the bait of these traps was intended to function as a local carnivore attractant. However, as we here focus on analysing large-scale variation in carnivore presence in relation to the density of resident reindeer among the study blocks with the same baiting of traps, the use of bait is not expected to affect our results. The cameras (Reconyx PC85/PC800 – Reconyx Inc., Wisconsin, USA) were set in a time-laps mode with images taken at regular intervals of 10 min on Varanger and Nordkinn and at intervals of 15 min on Sværholt and Porsanger. On Sværholt and Porsanger the cameras was in use in 30-39 days (i.e. 28th of March to 26th of April in 2009, 25th of February to 25th of March in 2010 and 17th of February to 21st of March in 2011) and the bait was never replaced during this period. On Varanger and Nordkinn the cameras were in use for between 53-64 days (i.e. 10th of March to 27th of April in 2009, 1st of March to 3rd of Mai in 2010 and 4th of March to 9th of April in 2011) and the bait was replaced 2-3 times at each study site each year. The difference in camera settings and bait maintenance was due to different logistic constraints in the two main regions (i.e. pairs of peninsulas). However, the set-up was within the range of frequencies and duration of recordings suggested by Hamel et al. (2013a). Moreover, the different bait-replacement schemes are also taken into account in the statistical analysis (see below). The season in which the recordings were made is bio-climatically the winter season at these high latitudes, with close to 100% snow cover, and before the return of migratory wildlife from their wintering areas further south. It is important to note, however, that the sampling periods coincide with the period when the carnivore species have established territories (e.g. corvids and eagles), are pregnant (e.g. foxes) or have already given birth to young (e.g. wolverine) (Englund 1970; Persson 2005). Hence, we expected that our recordings to a large degree reflect those carnivores that reside in these areas year-round.

COUNTS OF RESIDENT REINDEER

The numbers of resident reindeer were counted annually during February and March in each study block by aerial surveys. The surveys were thus conducted before migrants returned to the summer pastures towards the end of April**.** The aerial surveys were conducted according to a strip transect sampling design (Buckland et al. 2001), with one dedicated and experienced observer counting reindeer on both sides of the aeroplane. The area covered by the aerial surveys was constant over years within the blocks, but varied between blocks due to variation in the spatial extent of the tundra habitat within the blocks (range = 250 - 600 km^2, mean = 398.5, SD = 156.1, Table 1).

ANALYSES

For all the analyses we reduced the large sample of camera records (e.g. 33686 animal records/pictures in Varanger/Nordkinn in 2009) of individual species each year to simple ‘‘detection/nondetection’’ (1/0) for each day and site in the study. For the analysis of species-specific occupancy and community richness we adopted a slightly modified version of the multispecies hierarchical model presented in Zipkin et al. (2010). This modelling framework allows true absence to be distinguished from non-detection by incorporating presence-absence and detection-nondetection as two distinct components in the statistical model (MacKenzie et al. 2002; Kéry et al. 2009; Zipkin et al. 2010). Due to different length of the camera surveys and the bait shifting regimes in the study blocks in the peninsulas of Varanger/Nordkinn and Sværholt/Porsanger, respectively, we conducted separate analyses for these two regions (which then were represented by 5 and 6 study blocks each (cf. Table 1). Moreover, we analysed each year separately as the time of camera initiation varied between years as well as the length of the recording period. We modelled the occurrence probability for species *i* at study site *l* by incorporating site-specific covariates (c.f. Zipkin et al. 2010). We incorporated reindeer density (i.e. count/survey area) in the occupancy estimates by assuming that the logit transform of the occurrence probability (ψ) was a linear combination of a species effect (i) and the site-specific reindeer density (l) as follows:

$$logit(\psi_{i,l}) = u_i + \alpha_{1i} * ReindeerDensity_{l,}$$

Reindeer density was standardized (mean = 0, SD = 1), meaning that the inverse-logit of u_i is the occurrence probability for species i in study sites with average reindeer density. Moreover, the α_{li} is the slope parameter for the effect of reindeer density for species i. It is important to note that models of species occupancy assume a closed system, i.e. that the occupancy of species does not change over the time of the survey within a year. As this assumption is likely to be violated in open systems like ours, with long surveys of highly mobile species inhabiting large home ranges, occupancy should be interpreted as the proportion of sites used by the species in a given time period (MacKenzie et al. 2004). Also note that the hooded crow was removed from the analysis of the carnivore assemblage in Porsanger/Sværholt in 2010 because it was not recorded.

The detection probability (p) for species i was assumed to vary based on slightly different variables for the study sites in the different peninsulas. This was done to account for the potential temporal heterogeneity in detection due to the bait replacements conducted on Varanger /Nordkinn. In both analyses we included reindeer density to account for the possibility that camera baits were used less when the density of reindeer and possibly the access to natural carcasses in an area was high. Finally, we included “day-of-the-year”, and its squared value, to account for seasonal changes in detection probabilities caused by changes in day length and predator activity levels. Thus for Varanger/Nordkinn:

$$logit(p_{i,l}) = v_i + \beta_{1i}*ReindeerDensity_l + \beta_{2i}*DayOfTheYear_l + \beta_{3i}*BaitReplacement_l + \beta_{4i}*DayOfTheYear^2_l \quad ,$$

while for Sværholt/Porsanger:

$$logit(p_{i,l}) = v_i + \beta_{1i}*ReindeerDensity_l + \beta_{2i}*DayOfTheYear_l + \beta_{3i}*DayOfTheYear^2_l \quad ,$$

where v_i denote the detection probability for average values of the covariates. As for the occupancy compartment of the model, all predictors for detection probability were standardized (mean = 0, SD = 1). Our analysis was performed using WinBUGS 1.4.3 (Spiegelhalter et al. 2003), which uses Markov Chain Monte Carlo (MCMC) simulations to estimate posterior probability distributions. We estimated the model parameters by using naïve prior distributions for all the parameters in the model (Appendix B; WinBUGS model) (cf. Zipkin et al. 2010). We ran two parallel chains of length 25000 from random starting values, discarded the first 5000 as burn-in, and retained 1 in 10 updates. Model convergence was assessed by the convergence factor Rhat for each parameter in the model, where Rhat values close to 1 implies convergence (Gelman & Rubin 1992).

RESULTS

REINDEER COUNTS

Reindeer aerial counts showed that the number of resident reindeer, and hence the degree of partial migration, varied considerably among years, regions and blocks (Table 1). Resident reindeer were more abundant in the first year (2009) of the study (reindeer presence in 9 out of 11 blocks) than in the two later years (5 blocks in 2010 and 4 blocks in 2011). Moreover, Porsanger/Sværholt tended to have blocks with higher reindeer numbers than Varanger/Nordkinn, except in year 2011 when there were no block with high reindeer numbers in either of the two regions. Also among the blocks within a given year and region the counts exhibited large spatial variation, often with neighbouring blocks having highly contrasting numbers (Table 1). This provided a powerful setting for the quasi-experimental study design and statistical analysis, in particular for those region and year combinations with the largest range in reindeer densities.

CARNIVORE AREA OCCUPANCY

Seven small to medium-sized carnivore species, with very different average levels and spatio-temporal variation in estimated area occupancy, were present (Fig. 2). The raven (*Corvus* *corax)* was by far the most common and least variable species, followed by the red fox. The regionally endangered arctic fox was the least common species and only present on the Varanger Peninsula. Although generally low for most species (< 0.5: Appendix A), the estimated mean detection probability showed substantial variation. Reindeer density, day-of-the-year and bait replacement (the latter only for the Varanger/Nordkinn region) were all important for the probability of detection of the carnivore species and therefor important to take into account in the detection compartment of the model in order to obtain unbiased estimates of area occupancy rates (Appendix A).

The estimated effect of the reindeer density on species-specific carnivore area occupancy rates differed between years and study regions both in terms of strength (Fig. 3) and precision (see Appendix A for estimates of model parameters and their credibility intervals). However, the sign and strength of the estimated effect (i.e. the slope parameter α_1) depended on the range of reindeer densities within regions and years (Fig. 3, Table 1). Specifically, all slope estimates were consistently positive for the three year and region combinations where the range in reindeer densities exceeded 1.5 deer per km^2 (Porsanger/Sværholt 2009 and 2010, Varanger/Nordkinn 2009; Fig. 4), indicating a community wide carnivore response to reindeer residency above some threshold density. The responses were weaker and much less consistent for densities less than 0.5 deer per km^2, although the majority of the slope estimates were still positive (Fig. 4). This strong community response was also evident with respect to estimated species richness, with a significantly higher estimated species richness in areas of high vs. low reindeer density in years where the range in reindeer densities was large and exceeded 1.5 deer per km^2 (Appendix B; Fig. B1).

Discussion

During the long Arctic winter the tundra is climatically hostile and biologically unproductive; an ecosystem where plants and invertebrates are dormant under a thick and hard snow cover and where most mobile vertebrate prey species have escaped by migrating to lower latitudes. This must, almost as a virtue of necessity, have "knock-on" effects on higher trophic levels in terms of an impoverished carnivore community, in particular with few carnivores that feed on large herbivores (Krebs et al. 2003). Increased residency of large herbivores is thus expected to cause increased residency of carnivore species that would otherwise not find subsistence in tundra. However, whether carnivores originating from other ecosystems actually will increase in tundra also depends on their tolerance to other attributes of the tundra environment, like open habitats without vegetation cover and harsh climatic conditions. Thus the expectation of an increased presence of such carnivores is in need of an empirical test.

By using a large-scale study design that included samples of different reindeer herds over three years, we found that carnivore area occupancy rates in tundra increased distinctly with increasing density of non-migrating reindeer. This is, to our knowledge, the first empirical confirmation of the expectation that increased tendency for partial ungulate migration may induce a strong bottom-up boost in the mesocarnivore community, especially when the native apex predator has been removed. It is notable how similar the response to high reindeer density was in different carnivore species despite their different ecosystem origins. Several of the species found to respond most strongly typically belong to neighbouring ecosystems. The hooded crow (*Corvus corone*), red fox and the golden eagle are all mainly associated with forest ecosystems at high latitudes, while the white-tailed eagle (*Haliaeetus albicilla*) mainly belongs to the marine food web (Killengreen et al. 2012). This indicates that the increased presence of these predators is due to an influx from neighbouring ecosystems and thus represents range expansions. This inference is corroborated by the recent large-scale tendency for northwards expansion of boreal carnivores and omnivores that are able to exploit increased amount of human-induced subsidies in the arctic tundra (Ims & Ehrich 2013). On the other hand, forest-dwelling species such as the European lynx (*Lynx lynx*) and the pine marten (*Martes martes*), which is known to inhabit the boreal forest in the study region, was not recorded in tundra in this study. The lack of response in these species may be due to smaller propensity for scavenging or stronger avoidance of open tundra habitats than the boreal species we actually recorded by the camera traps baited with carrion.

The mammalian carnivores that prevailed in tundra in this study, as well as the eagles and raven, start their breeding season already in February-March (Englund 1970; Persson 2005), prior to the return of migrating reindeer in late April and early May. This suggests that increased residency of reindeer may allow such carnivore species to reside and breed. The increased presence of resident wolverine, golden eagle and red fox on reindeer calving grounds, all which are important predators of new born calves (Fauchald et al. 2004; Norberg et al. 2006; Johnsen et al. 2007; Nieminen 2010; Mattisson et al. 2011; Nieminen et al. 2011) is expected to negatively affect the reindeer populations and cause significant losses to the owners of the herds (Hobbs et al. 2012). Moreover, many of the carnivores that are subsidized by reindeer carrion in the critical winter period (Killengreen et al. 2011) are also generalists predators (e.g. corvids and foxes) that may negatively impact other species in the tundra food web, such as ground-nesting birds in the spring (Fletcher et al. 2010). A recent study of nest predation rates in the study region showed that corvids and red fox were the most influential nest predators on ground-breeding birds (Ims et al. 2013). Notably, a high nest predation rate in the lesser white-fronted goose (*Anser erythopus*) in the study region appears to be a key factor for its present red-listed status as critically endangered in Norway (DN 2011). Finally, a species-enriched carnivore community may cause intensified intra-guild interaction. Henden et al. (2010) showed how increased densities of the red fox, due to increased access to reindeer carrion during the limiting winter period (Killengreen et al. 2011), could negatively impact the subdominant and threatened artic fox in Fennoscandia (see also Angerbjörn et al. 2013; Hamel et al. 2013b). Hence, while partial migration patterns are likely to feedback on the reindeer herds themselves through increased predation rates, increased residency of reindeer may also work as a catalyst for many impacts that affects arctic biodiversity negatively.

MANAGEMENT IMPLICATION

In light of increasing human impact on ecosystems through e.g. overharvesting, anthropogenic barriers, climate change, removal of apex predators, habitat loss and degradation, it is expected that the phenomenon of disrupted migration of many animal species will be accentuated (Berger 2004; Berger et al. 2008; Bolger et al. 2008; Wilcove 2008; Wilcove & Wikelski 2008). While this problem has also been raised earlier in the case of tundra reindeer (e.g. Jernsletten & Klokov 2002), the present study is the first to present actual numbers that quantifies the degree of partial migration for a sample of reindeer herds and management districts at a regional scale in northern Fennoscandia. The implications of our study are, however, likely so be substantially broader as there are in total 2.2 million semi-domestic reindeer distributed over wide expanses of the Eurasian tundra (Huntington 2013).

By conducting aerial surveys we found that a substantial number of reindeer did not migrate from their summer pastures and moreover that these numbers differed among herds and years. Future studies should attempt to unravel the underlying cause of this variability in order to identify management actions that could minimise the number of reindeer that reside in the summer pastures during winter. Potential management actions could involve new herding practices, mitigation of migration barriers, regulation of herd sizes and adjustments of management district borders. Minimising residency on summer pastures, ought to provide a win-win situation by being beneficial for the productivity of the herding industry which presently struggles with high losses (Tveraa et al. 2003; Forbes & Kumpula 2009; Hobbs et al. 2012), for the management of tundra small game species which show declining populations (Ehrich et al. 2011; Henden et al. 2011), for the restoration of threatened arctic fox populations (Henden et al. 2010) and for conservation of arctic ground nesting birds that experiences high nest losses (McKinnon et al. 2010; Ims et al. 2013). Indeed, a common denominator of these issues may be boreal mesocarnivores that expand into vulnerable tundra ecosystems (Ims & Ehrich 2013).

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Tables:

Table 1. Reindeer counts (# individuals) and area covered (km^2) during aerial surveys in 2009-2011 in each block and peninsula.

Peninsula	Block	Survey Area (km^2)	Count 2009	Count 2010	Count 2011
Porsanger	North	252	32	0	0
Porsanger	Middle	290	2	0	0
Porsanger	South	614	27	0	180
Sværholt	North	266	128	93	0
Sværholt	Middle	358	44	88	0
Sværholt	South	555	1585	1356	88
Nordkinn	North	283	289	0	0
Nordkinn	South	253	0	52	141
Varanger	North	318	0	35	42
Varanger	South-East	581	1102	0	0
Varanger	South-West	613	61	0	0

Figures:

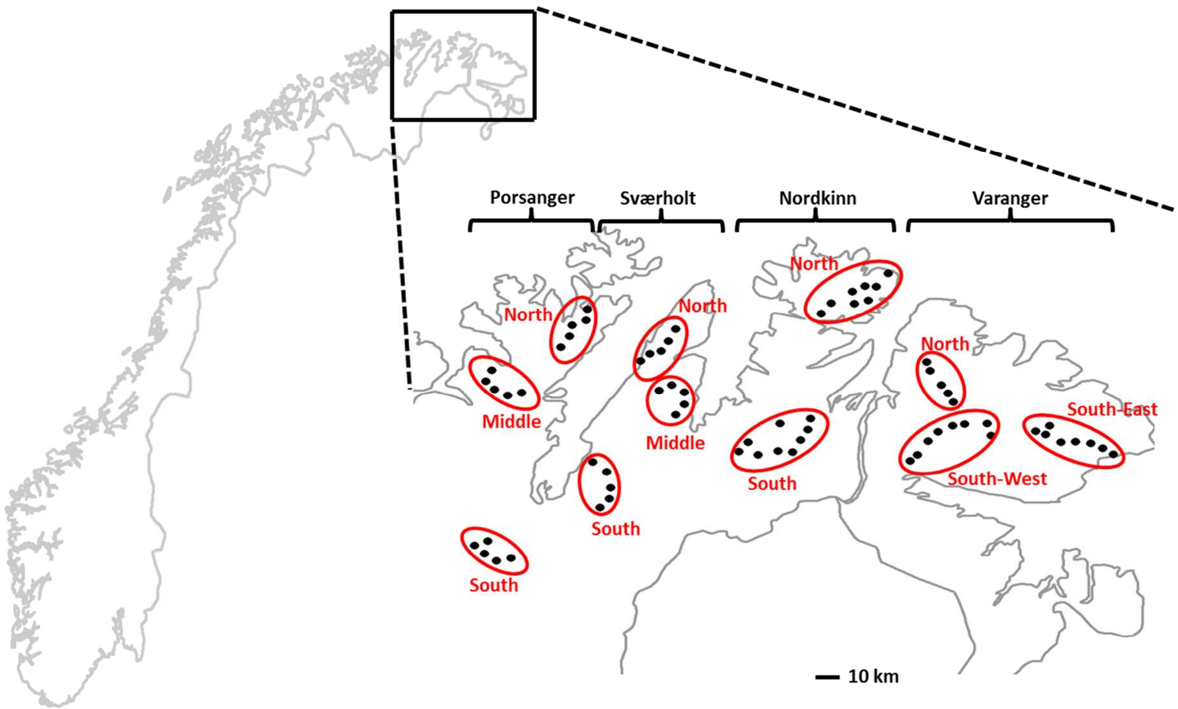

Fig. 1. Map giving the location of the four peninsulas (Porsanger, Sværholt, Nordkinn and Varanger) in Finnmark County, northern Norway. Red circles enclosing black dots depict the different blocks within each peninsula and the selected study sites within blocks, respectively. Note the scale of the inserted map.

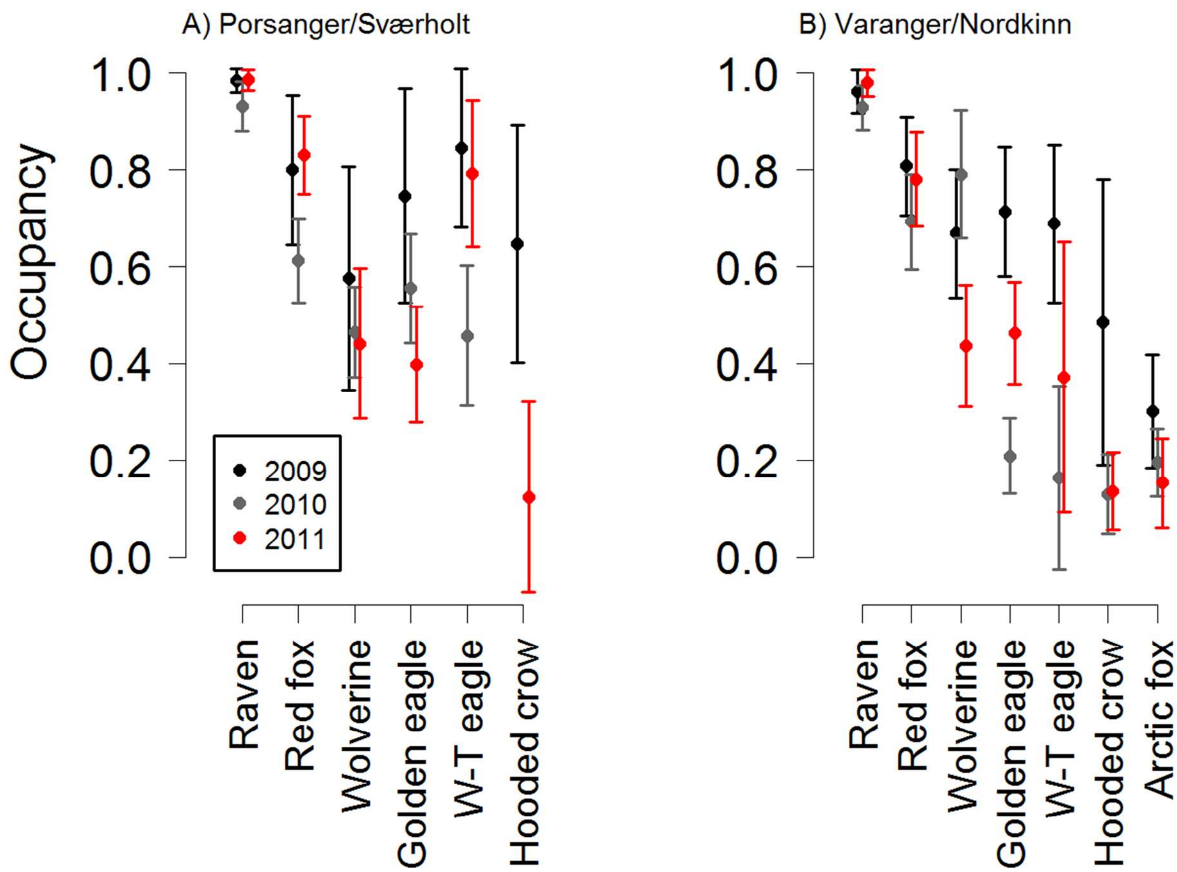

Fig. 2. Mean area occupancy rates with standard deviation for the different carnivore species over the three years of the study and the two pairs of peninsulas (panel A and B) with somewhat different sampling designs. Note that hooded crows are absent from the Porsanger and Sværholt peninsula in 2010 (no recordings).

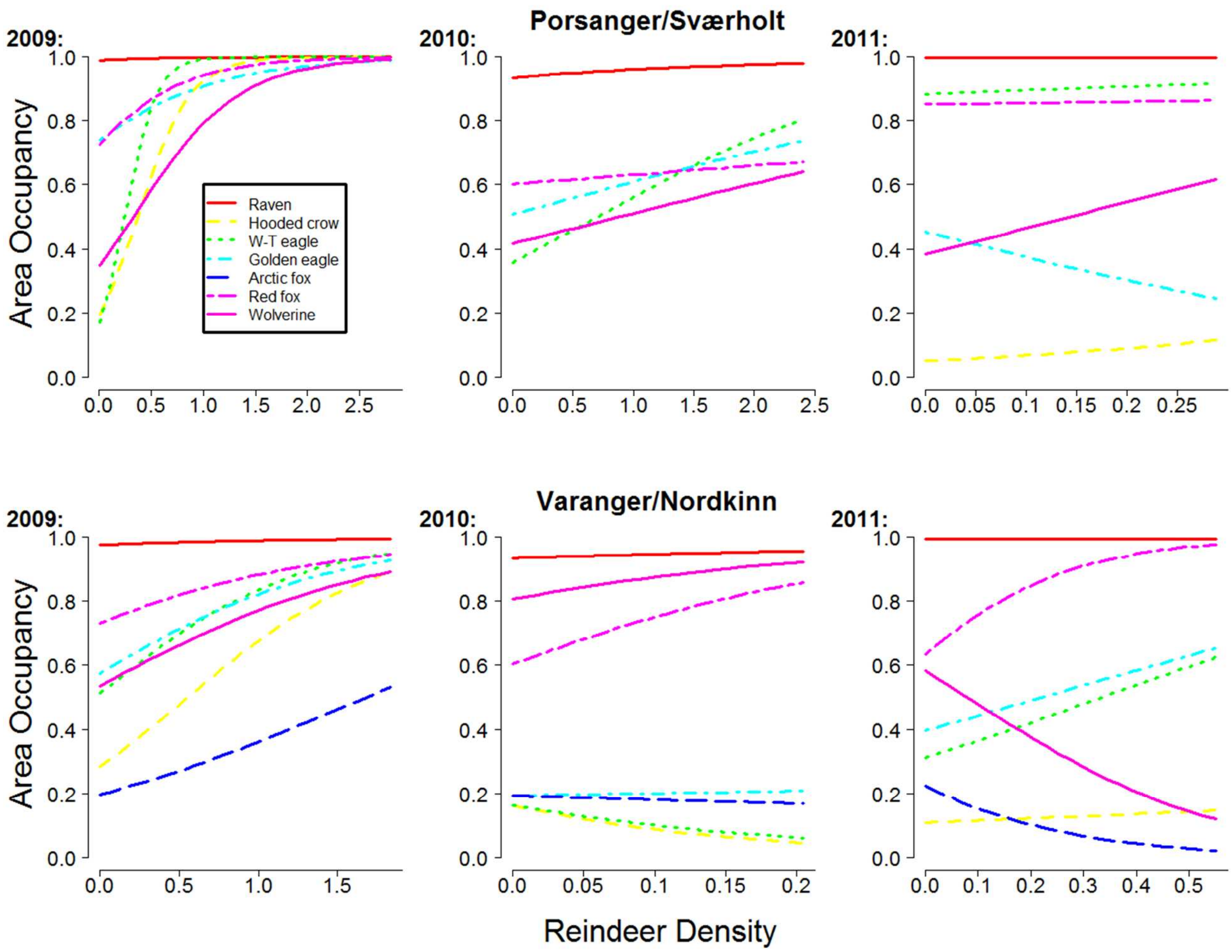

Fig. 3. Estimated species-specific area occupancy rates as a function of reindeer density for the two regions and the three years. Note that arctic foxes (blue stippled lines) are only present on Varanger Peninsula (right panel), that hooded crows are absent from the Porsanger/Sværholt region in 2010 (no recordings) and the distinctly different scale on the x-axes (i.e. reindeer density=animals per km^2).

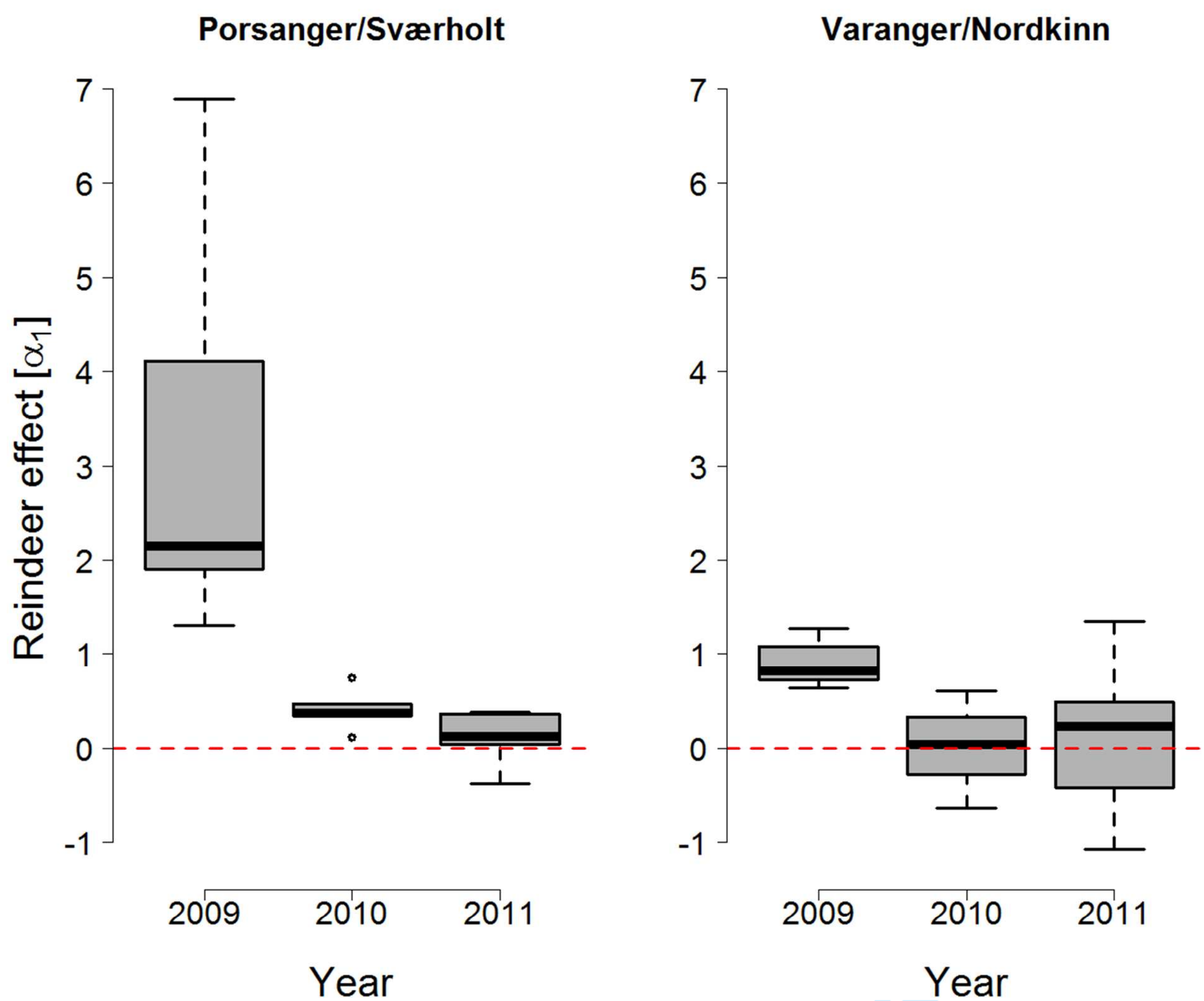

Fig. 4. Distribution (boxplots) of reindeer density effects (i.e. slope estimates [α_1]; Appendix A) on carnivore species-specific area occupancy for the two regions over the three years.

Appendix B.

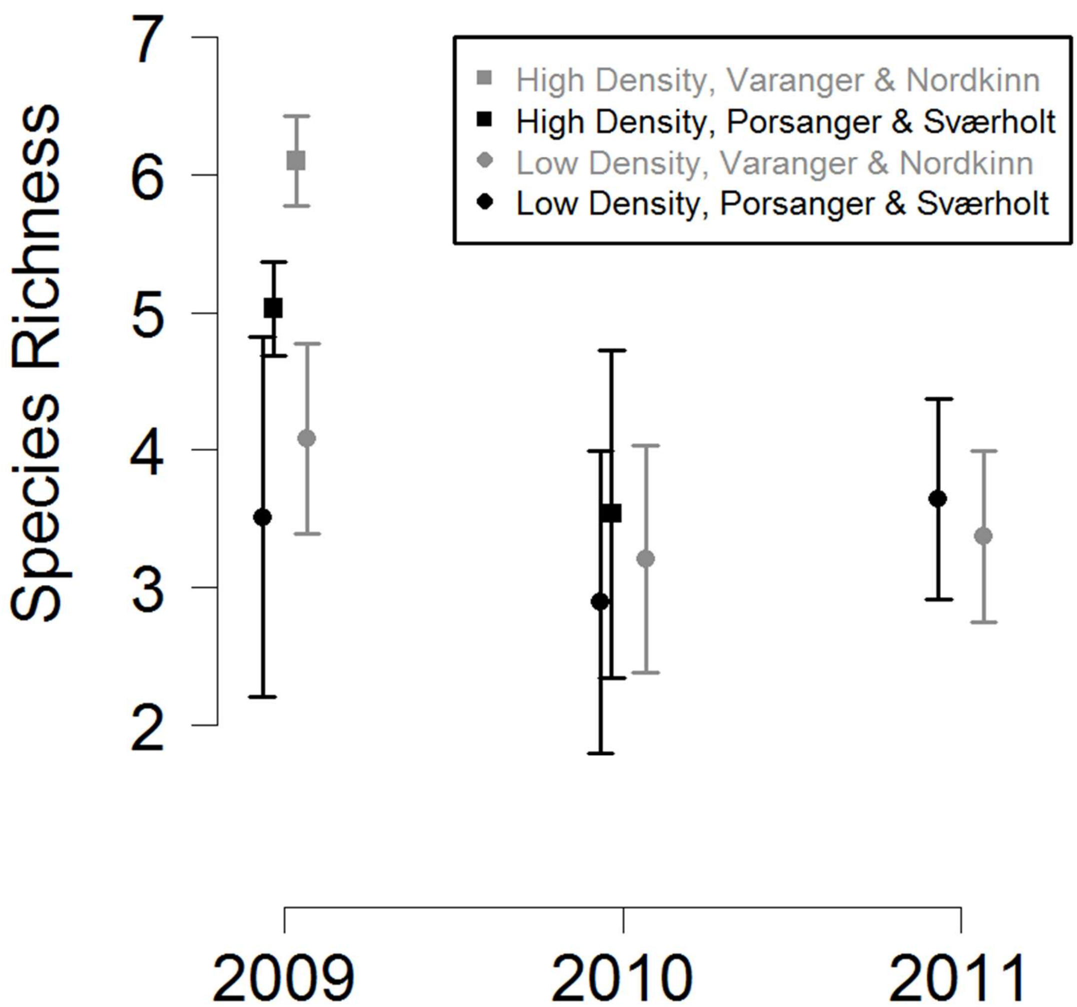

Fig. B1. Estimated mean site-specific species richness with standard error bars in relation to low and high reindeer density for the three years and two regions of the study. High density: >1.5 reindeer/km^2 and Low density: < 0.5 reindeer/km^2. Note that species richness at a specific site is a derived quantity in the model and represents the sum of occupancy rates for the different species estimated to be present (cf. WinBUGS model below).

*WinBUGS model: (model structure for the Porsanger/Sværholt analyses.)

```
  model{
## Prior distributions for community-level parameters
omega ~ dunif(0,1)
v.mean ~ dunif(0,1)                 ### Detection
mu.v <- log(v.mean) - log(1-v.mean)
u.mean ~ dunif(0,1)                 ### Occupancy
mu.u <- log(u.mean) - log(1-u.mean)
tau.u ~ dgamma(0.1,0.1)
tau.v ~ dgamma(0.1,0.1)

mua1 ~ dnorm(0, 0.001)
mub1 ~ dnorm(0, 0.001)
mub2 ~ dnorm(0, 0.001)
mub3 ~ dnorm(0, 0.001)
tau.a1 ~ dgamma(0.1,0.1)
tau.b1 ~ dgamma(0.1,0.1)
tau.b2 ~ dgamma(0.1,0.1)
tau.b3 ~ dgamma(0.1,0.1)

## Create priors for species i from the community level prior distributions
for (i in 1:(n+nzeroes)) {
   w[i] ~ dbern(omega)              ## whether it belongs to the detected species or not
   u[i] ~ dnorm(mu.u, tau.u)        ## Occupancy
   v[i] ~ dnorm(mu.v, tau.v)        ## species-specific detection
   a1[i] ~ dnorm(mua1, tau.a1)      ## parameter for covariate of occupancy
```

```
   b1[i] ~ dnorm(mub1, tau.b1)            ## parameters for covariates of detection:
   b2[i] ~ dnorm(mub2, tau.b2)
   b3[i] ~ dnorm(mub3, tau.b3)


## Create a loop to estimate the Z matrix (true occurrence for species i at site j.
for (j in 1:J) {
     logit(psi[j,i]) <- u[i]+ a1[i]*Reinab1[j]
  mu.psi[j,i] <- psi[j,i]*w[i]
  Z[j,i] ~ dbern(mu.psi[j,i])
## Create a loop to estimate detection for species i at point k during sampling period/replicate k.
for (k in 1:K[j]) {
   logit(p[j,k,i]) <-  v[i] + b1[i]*date1[j,k]  + b2[i]*Reinabdet[j,k] + b3[i]*date2[j,k]
     mu.p[j,k,i] <- p[j,k,i]*Z[j,i]
     X[j,k,i] ~ dbern(mu.p[j,k,i])
}   }}
## Derived quantities: ##
## Total estimated richness
n0 <- sum(w[(n+1):(n+nzeroes)])
N <- n + n0
## Site level richness estimates for the whole community.
for(j in 1:J){
Nsite[j]<- inprod(Z[j,1:(n+nzeroes)],w[1:(n+nzeroes)])
}
} Model end
```