Environmental variation as a driver of predator-prey interactions

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Abstract.   Animals often face the trade-off of optimizing foraging while limiting predation. In variable and seasonal environments the availability of resources changes spatially and temporally, forcing animals to adapt their spatial foraging patterns over time and, thus, to modify their exposure to predation. Previous research has mostly dealt with the causes and consequences of animal spatial patterns separately, with studies either examining how changes in the environment influence habitat selection, or determining the effects of habitat use on vulnerability to predation. Here we combine these aspects through an examination of how weather conditions affect predation risk by modifying the spatial behavior of the prey. We used reindeer calves (*Rangifer tarandus*) in Norway to investigate (1) the environmental causes and (2) the survival consequences of habitat use. We further examined how those relationships varied temporally and according to the body mass of calves. We found that deep snow and ice conditions led reindeer to shift from their usually preferred high-elevation pastures to lowland forested areas. This increase in forest use was associated with lower calf survival, mostly due to elevated lynx (*Lynx lynx*) predation rates. Golden eagles (*Aquila chrysaetos*) and wolverines (*Gulo gulo*) also preyed on calves but their effect was much smaller and not associated with a specific habitat type. The link between climatic conditions, habitat use, and predation changed over the winter season and depended on the body weights of the calves. The effect of harsh weather conditions on reindeer use of forested habitats was stronger towards the end of the winter, which coincides with more deteriorated body conditions and lower food availability on high-elevation pastures, and predation probabilities were higher for smaller individuals. Our study demonstrates that environmental variation importantly affects predator-prey interactions.

Key words: ecological trade-off; habitat use; Norwegian semidomestic reindeer; predation rates; predator-prey dynamics; *Rangifer tarandus*; seasonal environments; ungulate foraging ecology; weather variability.

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Introduction

Animals are faced with the trade-off of maximizing energy intake while minimizing predation risk (Lima et al. 1985, Houston et al. 1993). To increase their fitness, they need to select areas within the available landscape where they can optimize foraging while avoiding predators (Gilliam and Fraser 1987, Brooker et al. 2013). In variable and seasonal environments, the areas optimal for foraging will change through time (Lucht et al. 2002, Rowhani et al. 2011). Indeed, temporal variations in temperature and precipitation will alter the spatial pattern of resource availability by modifying plant productivity, vegetation structure and accessibility (Nemani et al. 2003, Cornelius et al. 2012). In such a dynamic environment, herbivore species must

move throughout the landscape to track changes in food availability, within and between habitats, and forage efficiently (Wilmshurst et al. 1999, Searle et al. 2005).

These changes in spatial behavior of herbivores may, in turn, affect the rate and type of predator encounters, since predator species' composition and predator densities are not homogeneously distributed across habitats (Connell and Kingsford 1998, McKenzie 2006, Basille et al. 2012). Thus, even though species can perceive spatial variation in predation risk and avoid areas with higher probability of predation (Valeix et al. 2009, Laundré et al. 2010, Robinson et al. 2010), weather-driven resource limitations in safer areas may force animals to use 'high risk' areas. The effect of environmental conditions on habitat use is not expected to be constant through time, or to be the same for all animals since temporal and individual variations in motivation and vulnerability may modulate the relationships between climatic variables, habitat use and predation probability (Bunnefeld et al. 2011, Mysterud et al. 2011). That is, individuals in which body condition is low, or deteriorating, might end up having riskier behaviors than those with less energetic constraints. (Bachman 1993, Godin and Crossman 1994, Beale and Monaghan 2004).

Previous studies have mostly examined the weather-spatial behavior and the spatial behavior-predation risk relations separately. Several determinants of habitat use and selection have received attention, for example, resource heterogeneity (Mysterud et al. 1999, Pellerin et al. 2010, Darmon et al. 2012), climatic variables (Bjornn 1971, Kumpula and Colpaert 2007, Stahlschmidt et al. 2011), season (Wiktander et al. 2001, Milakovic et al. 2012) and intrinsic characteristics (e.g., sex or age; Johnson and Bayliss 1981, Hillen et al. 2011). Other studies have examined how demographic parameters such as reproduction and survival vary across space and time (Hebblewhite et al. 2002, Kauffman et al. 2007, Ågren et al. 2008, Andruskiw et al. 2008, Teo et al. 2009). Here, we use a combined approach to explore both of these processes and connect the causes and consequences of spatial behavior (Fig. 1). The main objective of this study was to investigate how spatio-temporal variation in environmental conditions causes shifts in herbivore habitat use and to estimate the changes in predation risk associated with these changes in habitat use.

We used a semi-domestic Norwegian reindeer herd (*Rangifer tarandus*) as our study system. Reindeer is an ungulate species inhabiting high northern latitudes, where the distribution of resources is greatly influenced by strong seasonality and harsh winter conditions (Klein 1999, Tveraa et al. 2007). Except during round-ups twice a year, our study herd ranges freely within a defined natural pasture area and can thus move freely between habitats with different levels of food resources and predation risk. As for other long-lived ungulate species, reindeer are most vulnerable to environmental variation and predation as juveniles (Gaillard et al. 2000, Tveraa et al. 2003). We therefore focus on calves in this study. In cold climates, herbivore access to vegetation may become severely restricted by deep or poor snow conditions in winter, particularly by presence of ice layers (Aars and Ims 2002, Stien et al. 2010, Hansen et al. 2011). Thus, we hypothesized that winter snow and ice accumulation would force reindeer to move from their preferred open tundra habitats at high elevations (Kumpula and Colpaert 2007, Vistnes et al. 2008) to low-elevation forested habitats, because a thinner snow cover in the forest (Tappeiner et al. 2001, Kumpula and Colpaert 2007) facilitates access to ground vegetation. In addition reindeer take advantage of lichens growing on trees as a food resource (Helle and Tarvainen 1984, Kumpula 2001).

Such weather-driven changes in habitat use are, in turn, expected to lead to changes in predation rates, given the uneven distribution of predators across space. The dominant predator of reindeer in our study system is the Eurasian lynx (*Lynx lynx*) (Pedersen et al. 1999, Nybakk et al. 2002, Mattisson et al. 2011). The lynx stay mostly in forested habitats and use an ambush strategy to attack ungulate prey such as roe deer (*Capreolus capreolus*) and reindeer (Sunde et al. 2000*a*, *b*, von Arx et al. 2004). In our study system, overall predation rate and predation events due to lynx are therefore expected to be higher in the forest than in the tundra. Wolverine (*Gulo gulo*), red fox (*Vulpes vulpes*) and golden eagle (*Aquila chrysaetos*) are also predators of reindeer in our study system (Nybakk et al. 1999, 2002). These predators use a broader variety of
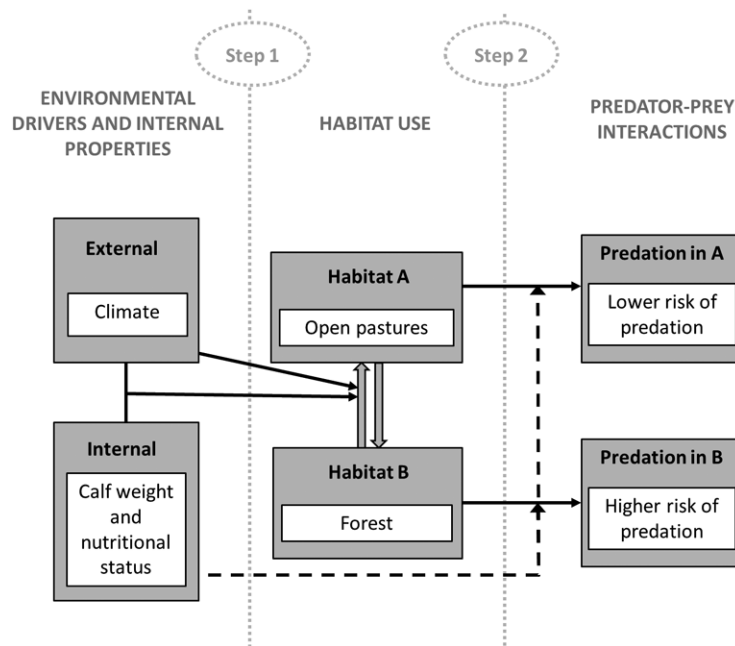
Fig. 1. Conceptual scheme showing the association between causes and consequences of reindeer space use. Solid arrows represent habitat-mediated associations of environmental and internal drivers with the demographic parameters (i.e., type and probability of predation), while dashed arrows represent potential direct effects.

habitats, and their predation pressure is therefore less related to the forested habitats (Watson 1997, Landa et al. 1999, May 2007, Pagel et al. 2010). It might even be skewed towards the tundra habitat in the case of the golden eagle (Nybakk et al. 1999, Nieminen et al. 2011). Finally, we examined whether nutritional status (measured by body mass and time into the winter season) influenced the foraging-predation risk trade-off decisions by testing whether habitat use patterns and predation rates changed through time and with body mass.

METHODS

Study area and data collection

The study was conducted in the Skjækerfjell reindeer district (63°56′ N 12°02′ E) which is located in the Nord-Trøndelag County in Central Norway. The district covers an area of about 2350 km² with an abundance of 1911 reindeer (estimated before calving in 2009). The animals are not given supplementary food and are held within the district borders by herding and natural borders such as lakes and mountain ranges. Within the district, the reindeer range freely except during round-ups that last a few days, twice a year: once during summer, when young calves are marked, and once during autumn/winter, when animals are slaughtered. The topography of the area varies between sea level and 1100 m. Tree line lies at about 700 m above sea level. Below that, vegetation belongs to the northern boreal forest type, with conifers dominating lower lands and birch forest towards higher elevations. Above the tree line the habitat is heath-dominated alpine tundra vegetation. Climate is sub-arctic, with a strong oceanic influence resulting in an average annual precipitation of 1560 mm and cool summers (12°C of average temperature). The average winter temperature is −3.6°C, and snow cover lasts from late November to April. However, weather conditions vary in the study area, depending mainly on latitude/longitude and elevation (Tveito et al. 1997, Tveito et al. 2000, Tveraa et al. 2007). This creates a spatial heterogeneity in snow cover and, thus, in resource availability for reindeer (Kumpula and Colpaert 2007).

One hundred calves were equipped on the 13 November of 2009 and another hundred calves on the 13 November and 6 December of 2010, giving a total of 200 female reindeer calves equipped with global positioning system (GPS) collars (Telespor, www.telespor.no). Body weight of the individuals was recorded to the nearest 0.2 kg using an electronic balance (Avery Berkel, Birmingham, UK) during the marking process. The collars had GSM-GPS technology and activity sensors and sent updates on the location and survival of the animals once per day over the whole wintering season (from 13 November 2009 to 9 May 2010 and from 15 November 2010 to 8 May 2011). Eleven of these calves were excluded from analyses due to scarcity and bad quality of the collected data. When a mortality event occurred, the location of the carcass was promptly visited, and autopsy was carried out to determine the cause of death. Different predators have different killing techniques, and autopsy combined with other traces can separate kills from different predator species (Tveraa et al. 2003, Norberg et al. 2006). The habitat characteristics (forested vs. open habitats) of each location visited by the GPS collared animals was assigned using a satellite-derived vegetation map for the area (http://kartkatalog.miljodirektoratet.no/map_catalog_dataset.asp?datasetid=15&download=yes&language=EN).

Daily weather data were obtained from meteorological stations of the Nord-Trøndelag County (http://eklima.met.no). Weekly average snow depth (*snow* in cm) and number of days with icing (*icedays*) were calculated using the available data. As direct observations of ice were not available for the study area, the number of days with presence of ice (*icedays*) was calculated from available records of rainfall, snow depth and air temperatures. We inspired ourselves from related indexes such as that of Solberg et al. (2001) and considered that ice was present (index = 1), as opposed to absent (index = 0) in days when one of the following scenarios occurred: (1) rainfall and average daily temperature <1°C, which would lead to freezing rain; (2) presence of snow on the ground and mean temperature between −1° and 1°C, which would result in melting and refreezing; (3) mean temperatures below −1°C when previous day was subject to melting (average temperature > 1°C) or icing.

Statistical approach and models

Given the complexity of the system, with potential direct and indirect interactions among individual characteristics (body mass), climatic variables, habitat type and predator species, we used a sequential approach for our analyses (Fig. 1). First, we determined which factors were driving changes in habitat use (measured as time spent in forested or open habitats, step 1; Fig. 1). Second, we examined the effect of habitat use on the probability for reindeer to be killed by predators (step 2; Fig. 1). To reduce potential problems of multicollinearity, we made sure that there were no substantial correlation between predictor variables used in the models (Pearson correlation coefficients $< |0.45|$).

In the analysis of habitat use (step 1; Fig. 1), we used a generalized linear mixed model (GLMMs) to analyze weekly data on the proportion of time spent in forested habitats (*prop_forest*). The models were fitted assuming a binomial error distribution (for the number of observed locations in the forest out of all observations in the week) and a logit link function (Table 1, model 1). Weekly average snow depth (*snow*) and number of days with icing (*icedays*) were used as predictor variables. Since the availability of intrinsic energetic reserves may buffer against resource limitation and reduce the motivation to change habitats, we also introduced in the model an interaction between the climatic variables and two variables describing reindeer body condition: individual weight at marking (*weight;* in kg) and time into the winter season (*timing,* number of weeks passed since the first of November of each year), as a surrogate of nutritional deterioration throughout the winter months.

To deal with autocorrelation of the GPS data, we incorporated three random effects in our mixed model: *year* (i.e., year of study start, 2009 or 2010) to account for inter-annual variability; *individual,* to consider the non-independency of data within individuals; and *group* (within which *individual* was nested), to control for correlations between animals moving together. The latter variable was built by grouping animals that spent more than 40% of their time (i.e., GPS fixes) at less than 500 m of distance from one another. Preliminary analyses showed poor model convergence. This problem appeared because most of the groups consisted of a single animal, and

Table 1. Results of the generalized linear mixed models used to analyze the causes of habitat use of reindeer calves (step 1) and the consequences of their space use for predation risk (step 2). We present the estimated effect of each explanatory variable, and a measure of variance explained by each model (R^2, approximated by Nakagawa and Schielzeth's (2013) method). Larger absolute values of standardized coefficients (SCoef) indicate higher relative importance of each effect. In model 2b the relative influence of each variable is shown by the standardized odds ratios in Fig. 4.

| | Step 1 | | | | Step 2 | | | | |
| | Model 1: Use of forested habitats† | | | | Model 2a: Survival probability† | | | Model 2b: Cause of mortality (predation type)† | |
Effects	Estimate±SE	p	SCoef	Effects	Estimate±SE	p	SCoef	Estimate±SE	p
Intercept	−1.341			Intercept	1.821				
Snow	−0.018 ± 0.021	ns	−18.70	by lynx				−2.598	
Icedays	−0.105 ± 0.150	ns	−12.77	by other				−1.534	
Snow × weight	0.0004 ± 0.0005	ns	17.11	Weight	0.106 ± 0.055	0.055	24.19		
Iceday × weight	0.0007 ± 0.004	ns	3.50	by lynx				−0.094 ± 0.066	ns
Snow × timing	0.001 ± 0.0003	<0.0001	29.89	by other				−0.152 ± 0.101	ns
Iceday × timing	0.009 ± 0.0017	<0.0001	20.98	Prop_forest	−1.104 ± 0.533	0.038	−25.84		
				by lynx				1.631 ± 0.661	0.014
				by other				−0.328 ± 0.950	ns
				Timing	−0.0292 ± 0.029	ns	−13.34		
				by lynx				0.008 ± 0.036	ns
				by other				0.081 ± 0.050	ns

Notes: Models 1 and 2a: binomial distribution (link = logit); random factors = year + group. Model 2b: multinomial distribution (link = generalized logit); random factors = year + group.

† For model 1: use of forested habitats, $R^2 = 0.400$. For model 2a: survival probability, $R^2 = 0.104$. R^2 values must be cautiously interpreted because their use in multilevel models has not yet been widely tested. Besides, since our aim was not to predict, but to test for the effect of specific variables, the number of predictors used is low. R^2 could not be estimated for the multinomial model.

the *individual* random factor was largely accounted for by the *group* random factor. To improve model convergence, we therefore removed the *individual* random factor from the analyses.

In the second step, we used logistic mixed models to test for the impact of habitat use (*prop_forest*) on the weekly probability of being preyed upon (Fig. 1; Table 1, model 2a). The binary response variable describing the weekly *mortalitystatus* of the calves was assumed to follow a binomial distribution. That is, at the end of each week, every animal was coded as zero if it was still alive or one if it had died within the week. To disentangle the effect of the different predator species, we used a multinomial GLMM to model the probability for reindeer to be killed by each predator species (Fig. 1; Table 1, model 2b). In the latter model, predation events by golden eagles and wolverines were merged because each caused only a low number of mortalities, and both were expected to be habitat generalists. The dependent variable (*mortality-cause*) in the multinomial GLMMs therefore contained 3 classes: alive, killed by lynx or killed by other predators. In addition to the effect of habitat use (*prop_forest*), we also included *weight* and *timing* in both predation models to account for the effect of body condition on mortality probability. As in the analyses of habitat use, we included *year* and *group* as random factors in the predation models to control for autocorrelation in the data. Direct effects of weather conditions on predation risk were not included to avoid multicollinearity problems that could have aroused due to the previously mentioned association between habitat use and climatic variables (Fig. 1).

All models were fitted using SAS proc glimmix (version 9.4; SAS Institute, Cary, NC, USA), and their goodness of fit was evaluated through the ratio of the obtained generalized chi-square to the degrees of freedom (Fernandez et al. 2010). We provide the standardized coefficients for models 1 and 2a, as a measure of the relative

importance of each predictor. For model 2b, the relative importance of each predictor is better described by the standardized odds ratios. These ratios correspond to the multiplication factor of the odds of being predated by each type of predator, given an increase of one standard deviation in the value of the explanatory variables.

RESULTS

Analysis of reindeer habitat use

Snow and ice conditions had significant effects on the propensity of reindeer calves to use forested areas in winter. Those effects increased as season progressed as showed by the interactions between *timing* and both *snow* and *icedays* (Table 1, model 1; Figs. 2, 3B). In early winter, the reindeer calves tended to remain on open pastures even when there was snow and ice on the ground; whereas they tended to use more forested areas when icing and deep snow occurred later in the season (Fig. 2). The weather effects on habitat use did not depend on the body mass of the calves, as indicated by the absence of significant interactions between weather variables and calf body weight (Table 1).

Analysis of reindeer mortality

Overall, 14.3% of marked calves were predated during our study (27 out of 189). The probability of dying due to predation was positively related to the use of forest and tended to be negatively related to the body weight of the calf (Table 1, model 2a). There was no additional effect of time within the winter season (i.e., *timing*) on mortality probabilities (Table 1). Lynx were responsible for most of the mortality among the reindeer calves (n = 19 out of 27), while golden eagles and wolverines were responsible for the other mortality events (n = 6 and n = 2 out of 27, respectively). As expected, the probability of being killed by a lynx increased significantly in the forest (Table 1, model 2b; Fig. 4). The risk of being preyed upon by golden eagles and wolverines, however, did not seem to be associated with habitat use. Predation by eagles and wolverines, but not by lynx, tended to increase over the winter season (*timing*), although this relationship was not significant (Table 1, model 2b; Fig. 4). As in the models for overall mortality,

there was a tendency towards higher predation rates on animals with smaller body weights, but this effect was not statistically significant in the multinomial analysis (Fig. 4; Table 1, model 2b).

DISCUSSION

By using an integrative approach that takes into account both the causes and consequences of animal space use, we were able to demonstrate the importance of snow and ice conditions as drivers in the predator-prey relationship between lynx and reindeer. While previous studies have usually dealt with determining the effect of climatic conditions on habitat selection (Dussault et al. 2005, Hansen et al. 2010, Stahlschmidt et al. 2011) or, directly, on vulnerability to be predated (Stenseth et al. 2004, Wikenros et al. 2009, Mabille et al. 2010), our approach allowed us to get a better insight into the behavioral mechanism indirectly linking environmental drivers to predation risk.

We show that winter weather conditions, as described by snow depth and icing events, determined forest use of reindeer calves in winter. During summers or periods of little or no snow, reindeer prefer open tundra habitats at high elevations, which offer better pasture conditions and lower insect densities (Hagemoen and Reimers 2002, Skarin 2006, Vistnes et al. 2008). During colder months however, the presence of ice and snow cover reduces the quality and accessibility of ground food resources for reindeer (Skogland 1978, Hansen et al. 2010). Although reindeer are well adapted and able to dig in deep and hard snow conditions (Helle 1984, Helle and Tarvainen 1984, Kumpula et al. 2004), this practice is energetically expensive (Fancy and White 1985, Collins and Smith 1991). The foraging costs thus increase as ice and snow build up, and reindeer may be forced to move to lower elevations to find a thinner snowpack and to complement the decrease of ground vegetation with arboreal lichens (Helle and Tarvainen 1984, Tappeiner et al. 2001, Kumpula and Colpaert 2007).

Our results illustrate that the change in habitat use towards use of forested areas was associated with an increase in the probability of being killed by Eurasian lynx. The lynx is an important predator of reindeer calves as shown by this
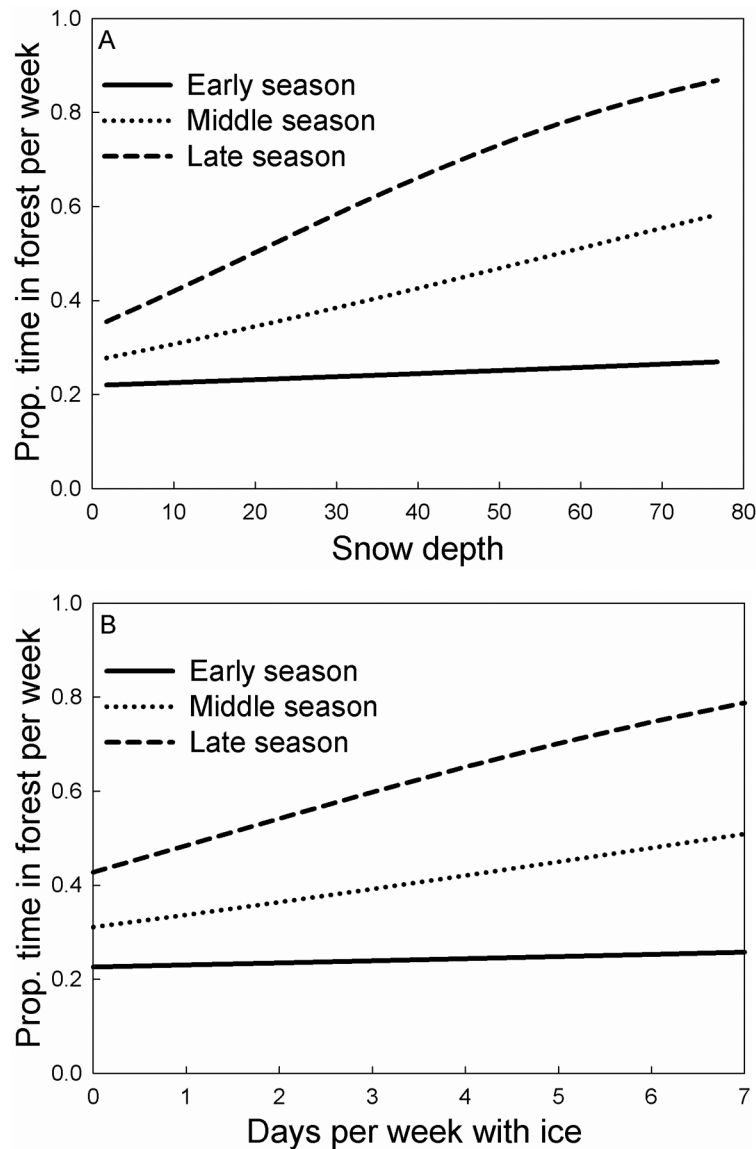
Fig. 2. Determinants of reindeer habitat use. (A) The relationship between snow depth and use of forested habitat according to the time into the winter season. (B) The relationship between number of days with ice on the ground and use of forested habitat according to the time into the winter season. Season levels chosen for this representation are: Early season = up until third week of November, Middle season = up until third week of January and Late season = up until third week of April.

and other studies (Pedersen et al. 1999, Nybakk et al. 2002, Graham et al. 2005). Due to their hunting strategies entailing stalking and ambushing their prey, their preferred habitats are forested areas (Murray et al. 1995, Hetherington and Gorman 2007). In contrast, predation by golden eagles and wolverines was lower and not found to differ between habitats. This agrees with their more generalist use of habitats, and the fact that both are facultative scavengers as opposed to the lynx, which is an obligate predator (Watson 1997, Landa et al. 1999, May 2007, Pagel et al. 2010).
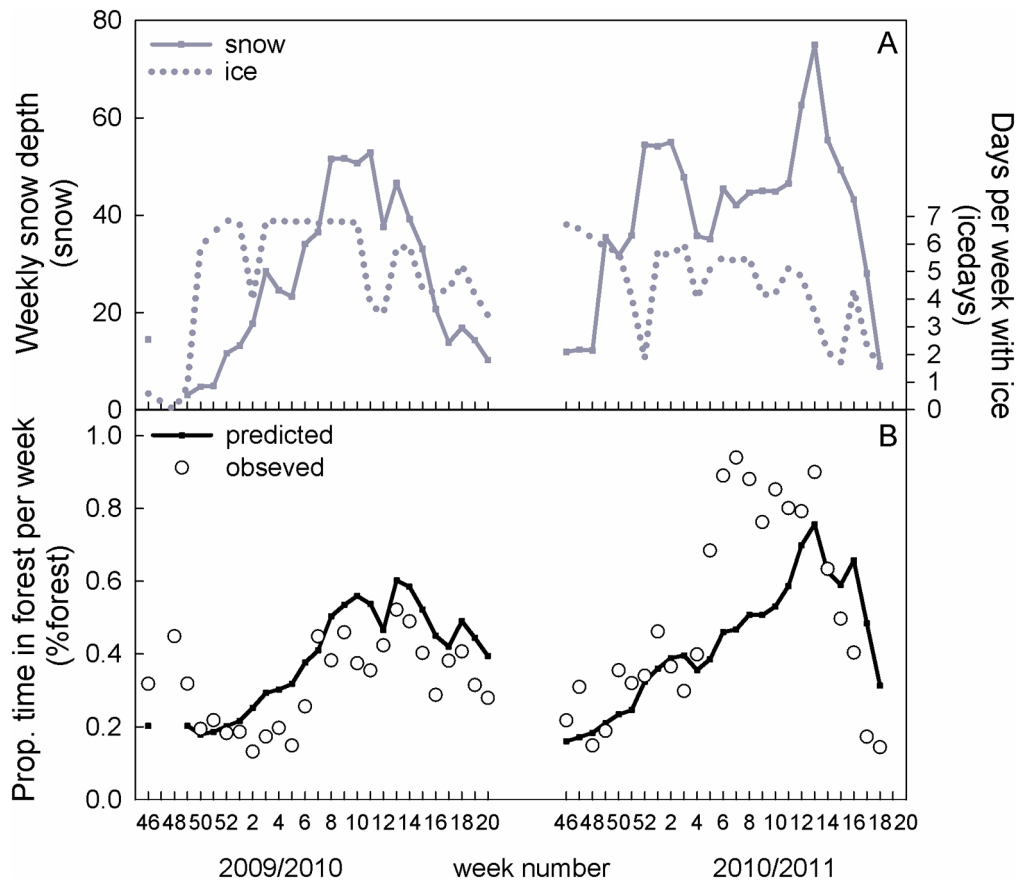
The effect of snow cover and icing on reindeer

Fig. 3. Temporal patterns in climate and associated use of the forest habitat. (A) Temporal variation in snow and icing conditions. (B) Comparison between average forest use predicted by our habitat model (model 1; random factors are not taken into account in the predictions) with real observed data (averaged for all individuals).

habitat use to was not constant through time. Individuals reacted more strongly to climatic conditions as the winter season progressed. This trend could be attributed, at least partially, to the temporal variation in the nutritional status through the cold months (Kumpula 2001, Fauchald et al. 2004). At northern latitudes, ungulates tend to become weaker during winter due to: (1) the extra energy costs associated with snow digging in search for ground vegetation and with locomotion in snowy conditions (Fancy and White 1985, 1987, Parker and Robbins 1985) and (2) the seasonal decrease in the availability and quality of food resources (Skogland 1978, Heggberget et al. 2002, Hansen et al. 2010). Thus, although animals in the beginning of the winter might be willing to invest more energy to avoid

woodlands, the tolerance to forage in icy conditions will decrease later in the winter season, as energetic reserves, body condition, and food availability decline (Helle and Tarvainen 1984, Kumpula and Colpaert 2007).

The deterioration of body condition throughout the winter may also explain the weak positive effect of time (*timing*) on the probability to be killed by golden eagle or wolverine. This interpretation is supported by previous studies showing that these predators tend to prey on the weaker and smaller individuals (Tjernberg 1983, Nybakk et al. 1999, Mattisson et al. 2011, Nieminen et al. 2011). More wolverine and eagle predation at the end of winter may therefore suggest that their inflicted calf mortality to some degree could be compensatory. That is, calves
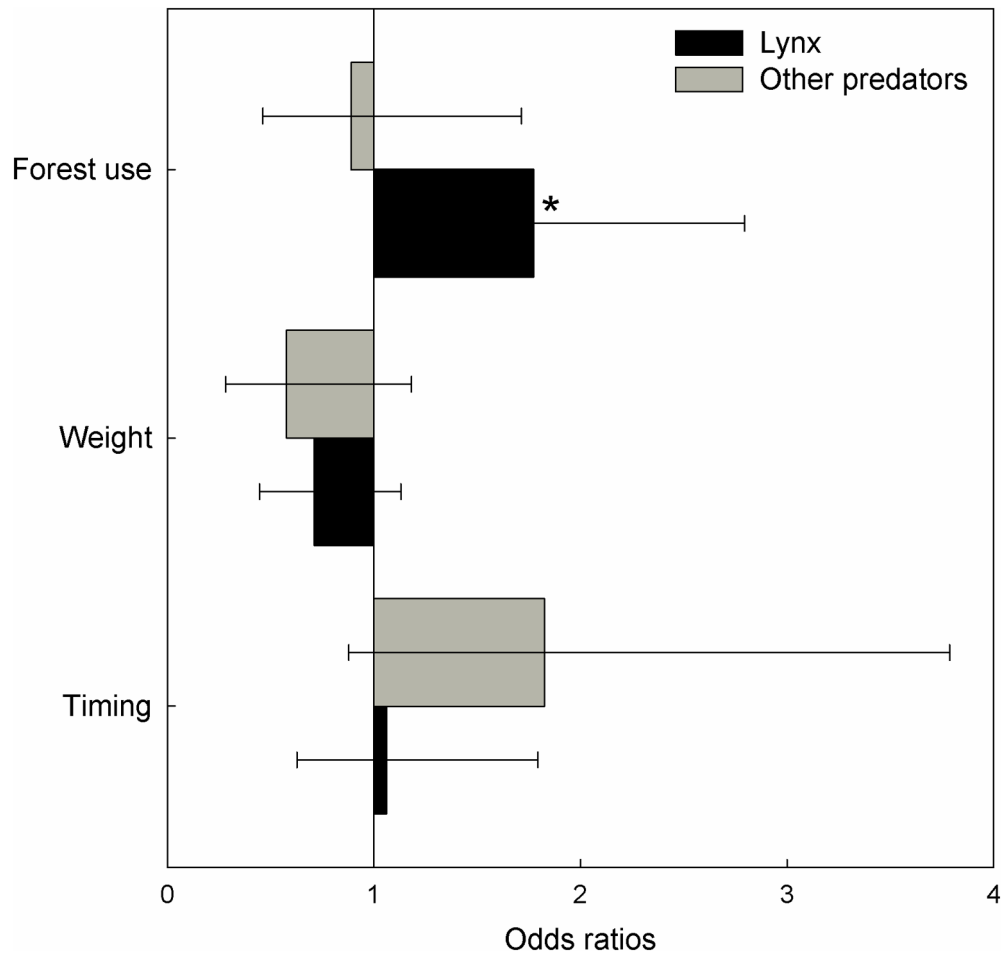
Fig. 4. Factors affecting risk of predation by different predator types on reindeer calves. Odds ratios greater than one indicate that predation probabilities are positively related to those variables, while values lower than one denote a negative effect. Confidence intervals (95% CI) overlapping the value one indicate no statistical significant effect of the predictor, while asterisks (*) denote significant factors.

preyed upon by golden eagles and wolverines may otherwise have been prone to die from malnutrition or disease, due to winter food limitation (Bartmann et al. 1992, Tveraa et al. 2003). Alternatively, their increased predation pressure on reindeer towards the end of the winter may be associated with the higher nutritional needs of predators around the period (March–April) when young are born (Tjernberg 1981, Persson 2005).

Finally, we found no strong evidence for an effect of reindeer body size, as measured by their body mass at the onset of the winter, on habitat selection. This may be a consequence of the grouping behavior of this species (Burch 1972,

Skarin et al. 2008). Indeed, we found calves with up to 6 kg difference in body mass (i.e., with approximately 15% difference in mass) moving together in the same group. Still, the overall probability of being predated tended to decrease with increasing body weight. This result is consistent with previous studies showing a negative relationship between calf weight and predation probability (Nybakk et al. 1999, Tveraa et al. 2003, Nieminen et al. 2011).

In conclusion, by investigating drivers of animal habitat use together with determinants of the probability of being killed by a given predator species, we have been able to identify the importance of weather-driven space use in

the dynamics of predator-prey interactions. Future studies should aim to jointly examine the behaviour of the predator and prey species involved in the interaction. Such studies will help us to understand the mechanisms driving multi-species interactions and, thereby, to better anticipate the response of ecosystems to major drivers such as global climate change and habitat fragmentation.

Acknowledgments

Literature Cited

Aars, J., and R. A. Ims. 2002. Intrinsic and climatic determinants of population demography: the winter dynamics of tundra voles. Ecology 83:3449–3456.

Ågren, J., J. Ehrlén, and C. Solbreck. 2008. Spatio-temporal variation in fruit production and seed predation in a perennial herb influenced by habitat quality and population size. Journal of Ecology 96:334–345.

Andruskiw, M., J. M. Fryxell, I. D. Thompson, and J. A. Baker. 2008. Habitat-mediated variation in predation risk by the American marten. Ecology 89:2273–2280.

Bachman, G. C. 1993. The effect of body condition on the trade-off between vigilance and foraging in Belding's ground squirrels. Animal Behaviour 46:233–244.

Bartmann, R. M., G. C. White, and L. H. Carpenter. 1992. Compensatory mortality in a Colorado mule deer population. Wildlife Monographs 121:3–39.

Basille, M., D. Fortin, C. Dussault, J.-P. Ouellet, and R. Courtois. 2012. Ecologically based definition of seasons clarifies predator–prey interactions. Ecography 35:1–10.

Beale, C. M., and P. Monaghan. 2004. Behavioural responses to human disturbance: a matter of choice? Animal Behaviour 68:1065–1069.

Bjornn, T. C. 1971. Trout and salmon movements in two Idaho streams as related to temperature, food, stream flow, cover, and population density. Transactions of the American Fisheries Society 100:423–438.

Brooker, R. M., P. L. Munday, I. M. McLeod, and G. P. Jones. 2013. Habitat preferences of a corallivorous reef fish: predation risk versus food quality. Coral Reefs 32:1–10.

Bunnefeld, N., L. Börger, B. van Moorter, C. M. Rolandsen, H. Dettki, E. J. Solberg, and G. Ericsson. 2011. A model-driven approach to quantify migration patterns: individual, regional and yearly differences. Journal of Animal Ecology 80:466–476.

Burch, E. S., Jr. 1972. The caribou/wild reindeer as a human resource. American Antiquity 37:339–368.

Collins, W. B., and T. S. Smith. 1991. Effects of wind-hardened snow on foraging by reindeer (*Rangifer tarandus*). Arctic 44:217–222.

Connell, S. D., and M. J. Kingsford. 1998. Spatial, temporal and habitat-related variation in the abundance of large predatory fish at One Tree Reef, Australia. Coral Reefs 17:49–57.

Cornelius, C., N. Estrella, H. Franz, and A. Menzel. 2012. Linking altitudinal gradients and temperature responses of plant phenology in the Bavarian Alps. Plant Biology 15:57–69.

Darmon, G., C. Calenge, A. Loison, J.-M. Jullien, D. Maillard, and J.-F. Lopez. 2012. Spatial distribution and habitat selection in coexisting species of mountain ungulates. Ecography 35:44–53.

Dussault, C., J.-P. Ouellet, R. Courtois, J. Huot, L. Breton, H. Jolicoeur, and D. Kelt. 2005. Linking moose habitat selection to limiting factors. Ecography 28:619–628.

Fancy, S. G., and R. G. White. 1985. Energy expenditures by caribou while cratering in snow. Journal of Wildlife Management 49:987–993.

Fancy, S. G., and R. G. White. 1987. Energy expenditures for locomotion by barren-ground caribou. Canadian Journal of Zoology 65:122–128.

Fauchald, P., T. Tveraa, C. Henaug, and N. Yoccoz. 2004. Adaptive regulation of body reserves in reindeer, *Rangifer tarandus*: a feeding experiment. Oikos 107:583–591.

Fernandez, E. A., E. P. Souza Neto, P. Abry, R. Macchiavelli, M. Balzarini, B. Cuzin, C. Baude, J. Frutoso, and C. Gharib. 2010. Assessing erectile neurogenic dysfunction from heart rate variability through a generalized linear mixed model framework. Computer Methods and Programs in Biomedicine 99:49–56.

Gaillard, J.-M., M. Festa-Bianchet, N. G. Yoccoz, A. Loison, and C. Toïgo. 2000. Temporal variation in fitness components and population dynamics of large herbivores. Annual Review of Ecology and Systematics 31:367–391.

Gilliam, J. F., and D. F. Fraser. 1987. Habitat selection under predation hazard: test of a model with foraging minnows. Ecology 68:1856–1862.

Godin, J.-G., and S. Crossman. 1994. Hunger-dependent predator inspection and foraging behaviours in the threespine stickleback (*Gasterosteus aculeatus*) under predation risk. Behavioral Ecology and Sociobiology 34:359–366.

Graham, K., A. P. Beckerman, and S. Thirgood. 2005. Human–predator–prey conflicts: ecological correlates, prey losses and patterns of management. Biological Conservation 122:159–171.

Hagemoen, R. I. M., and E. Reimers. 2002. Reindeer summer activity pattern in relation to weather and insect harassment. Journal of Animal Ecology 71:883–892.

Hansen, B. B., R. Aanes, I. Herfindal, J. Kohler, and B.-E. Saether. 2011. Climate, icing, and wild arctic reindeer: past relationships and future prospects. Ecology 92:1917–1923.

Hansen, B. B., R. Aanes, and B.-E. Sæther. 2010. Feeding-crater selection by high-arctic reindeer facing ice-blocked pastures. Canadian Journal of Zoology 88:170–177.

Hebblewhite, M., D. H. Pletscher, and P. C. Paquet. 2002. Elk population dynamics in areas with and without predation by recolonizing wolves in Banff National Park, Alberta. Canadian Journal of Zoology 80:789–799.

Heggberget, T. M., E. Gaare, and J. P. Ball. 2002. Reindeer (*Rangifer tarandus*) and climate change: importance of winter forage. Rangifer 22:13–32.

Helle, T. 1984. Foraging behaviour of the semi-domestic reindeer (*Rangifer tarandus* L.) in relation to snow in Finnish Lapland. Report from Kevo Subarctic Research Station 19:35–47.

Helle, T., and L. Tarvainen. 1984. Determination of winter digging period of semi-domestic reindeer in relation to snow conditions and food resources. Report from Kevo Subarctic Research Station 19:49–56.

Hetherington, D. A., and M. L. Gorman. 2007. Using prey densities to estimate the potential size of reintroduced populations of Eurasian lynx. Biological Conservation 137:37–44.

Hillen, J., T. Kaster, J. Pahle, A. Kiefer, O. Elle, E. M. Griebeler, and M. Veith. 2011. Sex-specific habitat selection in an edge habitat specialist, the western barbastelle bat. Annales Zoologici Fennici 48:180–190.

Houston, A. I., J. M. McNamara, and J. M. C. Hutchinson. 1993. General results concerning the trade-off between gaining energy and avoiding predation. Philosophical Transactions of the Royal Society B 341:375–397.

Johnson, C. N., and P. G. Bayliss. 1981. Habitat selection by sex, age and reproductive class in the red kangaroo, *Macropus rufus*, in western New South Wales. Wildlife Research 8:465–474.

Kauffman, M. J., N. Varley, D. W. Smith, D. R. Stahler, D. R. MacNulty, and M. S. Boyce. 2007. Landscape heterogeneity shapes predation in a newly restored predator–prey system. Ecology Letters 10:690–700.

Klein, D. R. 1999. The roles of climate and insularity in establishment and persistence of *Rangifer tarandus* populations in the high arctic. Ecological Bulletins 47:96–114.

Kumpula, J. 2001. Winter grazing of reindeer in woodland lichen pasture: Effect of lichen availability on the condition of reindeer. Small Ruminant Research 39:121–130.

Kumpula, J., and A. Colpaert. 2007. Snow conditions and usability value of pastureland for semi-domesticated reindeer (*Rangifer tarandus tarandus*) in northern boreal forest area. Rangifer 27:25–39.

Kumpula, J., S. Lèfrere, and M. Nieminen. 2004. The use of woodland lichen pasture by reindeer in winter with easy snow conditions. Arctic 57:273–278.

Landa, A., M. Lindén, and I. Kojola. 1999. Action plan for the conservation of wolverines (*Gulo gulo*) in Europe. Convention for the Conservation of European Wildlife and Natural Habitats, Strasbourg, France.

Laundré, J. W., L. Hernández, and W. F. Ripple. 2010. The landscape of fear: ecological implications of being afraid. Open Ecology Journal 3:1–7.

Lima, S. L., T. J. Valone, and T. Caraco. 1985. Foraging-efficiency-predation-risk trade-off in the grey squirrel. Animal Behaviour 33:155–165.

Lucht, W., I. C. Prentice, R. B. Myneni, S. Sitch, P. Friedlingstein, W. Cramer, P. Bousquet, W. Buermann, and B. Smith. 2002. Climatic control of the high-latitude vegetation greening trend and Pinatubo effect. Science 296:1687–1689.

Mabille, G., S. Descamps, and D. Berteaux. 2010. Predation as a probable mechanism relating winter weather to population dynamics in a North American porcupine population. Population Ecology 52:537–546.

Mattisson, J., J. Odden, E. B. Nilsen, J. D. Linnell, J. Persson, and H. Andrén. 2011. Factors affecting Eurasian lynx kill rates on semi-domestic reindeer in northern Scandinavia: Can ecological research contribute to the development of a fair compensation system? Biological conservation 144(12):3009–3017.

Mattisson, J., J. Persson, H. Andrén, and P. Segerström. 2011. Temporal and spatial interactions between an obligate predator, the Eurasian lynx (*Lynx lynx*), and a facultative scavenger, the wolverine (*Gulo gulo*). Canadian Journal of Zoology 89:79–89.

May, R. 2007. Spatial ecology of wolverines in Scandinavia. Dissertation. Norwegian University of Science and Technology, Trondheim, Norway.

McKenzie, H. W. 2006. Linear features impact predator–prey encounters: analysis with first passage

time. Thesis. University of Alberta, Edmonton, Alberta, Canada.

Milakovic, B., K. L. Parker, D. D. Gustine, R. J. Lay, A. B. D. Walker, and M. P. Gillingham. 2012. Seasonal habitat use and selection by grizzly bears in Northern British Columbia. Journal of Wildlife Management 76:170–180.

Murray, D. L., S. Boutin, M. O'Donoghue, and V. O. Nams. 1995. Hunting behaviour of a sympatric felid and canid in relation to vegetative cover. Animal Behaviour 50:1203–1210.

Mysterud, A., P. K. Larsen, R. A. Ims, and E. Østbye. 1999. Habitat selection by roe deer and sheep: does habitat ranking reflect resource availability? Canadian Journal of Zoology 77:776–783.

Mysterud, A., L. E. Loe, B. Zimmermann, R. Bischof, V. Veiberg, and E. Meisingset. 2011. Partial migration in expanding red deer populations at northern latitudes: a role for density dependence? Oikos 120:1817–1825.

Nakagawa, S., and H. Schielzeth. 2013. A general and simple method for obtaining R2 from generalized linear mixed-effects models. Methods in Ecology and Evolution 4:133–142.

Nemani, R. R., C. D. Keeling, H. Hashimoto, W. M. Jolly, S. C. Piper, C. J. Tucker, R. B. Myneni, and S. W. Running. 2003. Climate-driven increases in global terrestrial net primary production from 1982 to 1999. Science 300:1560–1563.

Nieminen, M., H. Norberg, and V. Maijala. 2011. Mortality and survival of semi-domesticated reindeer (Rangifer tarandus tarandus L.) calves in northern Finland. Rangifer 31:71–84.

Norberg, H., I. Kojola, P. Aikio, and M. Nylund. 2006. Predation by golden eagle aquila chrysaetos on semidomesticated reindeer Rangifer tarandus calves in northeastern Finnish Lapland. Wildlife Biology 12:393–402.

Nybakk, K., O. Kjelvik, and T. Kvam. 1999. Golden eagle predation on semi-domestic reindeer. Wildlife Society Bulletin 27:1038–1042.

Nybakk, K., O. Kjelvik, T. Kvam, K. Overskaug, and P. Sunde. 2002. Mortality of semidomestic reindeer Rangifer tarandus in central Norway. Wildlife Biology 8:63–68.

Pagel, J. E., D. M. Whittington, and G. T. Allen. 2010. Interim golden eagle inventory and monitoring protocols; and other recommendations. Division of Migratory Bird Management, US Fish and Wildlife Service, Arlington, Virginia, USA.

Parker, K. L., and C. T. Robbins. 1985. Thermoregulation in ungulates. Pages 161–182 in R. J. Hudson and R. G. White, editors. Bioenergetics of wild herbivores. CRC, Boca Raton, Florida, USA.

Pedersen, V., J. D. C. Linnell, R. Andersen, H. Andren, M. Linden, and P. Segerström. 1999. Winter lynx Lynx lynx predation on semidomestic reindeer

Rangifer tarandus in northern Sweden. Wildlife Biology 5:203–211.

Pellerin, M., C. Calenge, S. Said, J. M. Gaillard, H. Fritz, P. Duncan, and G. Van Laere. 2010. Habitat use by female western roe deer (Capreolus capreolus): influence of resource availability on habitat selection in two contrasting years. Canadian Journal of Zoology 88:1052–1062.

Persson, J. 2005. Female wolverine (Gulo gulo) reproduction: reproductive costs and winter food availability. Canadian Journal of Zoology 83:1453–1459.

Robinson, B., M. Hebblewhite, and E. Merrill. 2010. Are migrant and resident elk (Cervus elaphus) exposed to similar forage and predation risk on their sympatric winter range? Oecologia 164:265–275.

Rowhani, P., M. Linderman, and E. F. Lambin. 2011. Global interannual variability in terrestrial ecosystems: sources and spatial distribution using MODIS-derived vegetation indices, social and biophysical factors. International Journal of Remote Sensing 32:5393–5411.

Searle, K. R., N. T. Hobbs, and L. A. Shipley. 2005. Should I stay or should I go? Patch departure decisions by herbivores at multiple scales. Oikos 111:417–424.

Skarin, A. 2006. Reindeer use of alpine summer habitats. Dissertation. Swedish University of Agricultural Sciences, Uppsala, Sweden.

Skarin, A., Ö. Danell, R. Bergström, and J. Moen. 2008. Summer habitat preferences of GPS-collared reindeer Rangifer tarandus tarandus. Wildlife Biology 14:1–15.

Skogland, T. 1978. Characteristics of the snow cover and its relationship to wild mountain reindeer (Rangifer tarandus tarandus L.) feeding strategies. Arctic and Alpine Research 10:569–579.

Solberg, E. J., J. P. Jordhøy, O. Strand, R. Aanes, A. Loison, B.-E. Sæther, and J. D. Linnell. 2001. Effects of density-dependence and climate on the dynamics of a Svalbard reindeer population. Ecography 24:441–451.

Stahlschmidt, Z. R., J. Brashears, and D. F. DeNardo. 2011. The role of temperature and humidity in python nest site selection. Animal Behaviour 81:1077–1081.

Stenseth, N. C., A. Shabbar, K.-S. Chan, S. Boutin, E. K. Rueness, D. Ehrich, J. W. Hurrell, O. C. Lingjærde, and K. S. Jakobsen. 2004. Snow conditions may create an invisible barrier for lynx. Proceedings of the National Academy of Sciences USA 101:10632–10634.

Stien, A., L. Loe, A. Mysterud, T. Severinsen, J. Kohler, and R. Langvatn. 2010. Icing events trigger range displacement in a high-arctic ungulate. Ecology 91:915–920.

Sunde, P., T. Kvam, J. P. Bolstad, and M. Bronndal.

2000*a*. Foraging of lynxes in a managed boreal-alpine environment. Ecography 23:291–298.

Sunde, P., T. Kvam, P. Moa, A. Negård, and K. Overskaug. 2000*b*. Space use by Eurasian lynxes *Lynx lynx* in central Norway. Acta Theriologica 45:507–524.

Tappeiner, U., G. Tappeiner, J. Aschenwald, E. Tasser, and B. Ostendorf. 2001. GIS-based modelling of spatial pattern of snow cover duration in an alpine area. Ecological Modelling 138:265–275.

Teo, S. L. H., L. W. Botsford, and A. Hastings. 2009. Spatio-temporal covariability in coho salmon (*Oncorhynchus kisutch*) survival, from California to southeast Alaska. Deep Sea Research Part II: Topical Studies in Oceanography 56:2570–2578.

Tjernberg, M. 1981. Diet of the golden eagle *Aquila chrysaetos* during the breeding season in Sweden. Ecography 4:12–19.

Tjernberg, M. 1983. Prey abundance and reproductive success of the golden eagle *Aquila chrysaetos* in Sweden. Holarctic Ecology 6:17–23.

Tveito, O. E., E. J. Førland, B. Dahlström, E. Elomaa, I. Hanssen-Bauer, T. Jónsson, H. Madsen, J. Perälä, P. Rissanen, and H. Vedin. 1997. Nordic precipitation maps. Klima Report number 22/97. Norwegian Meteorological Institute, Oslo, Norway.

Tveito, O. E., et al. 2000. Nordic temperature maps. Klima Report number 09/00. Norwegian Meteorological Institute, Oslo, Norway.

Tveraa, T., P. Fauchald, C. Henaug, and N. Yoccoz. 2003. An examination of a compensatory relationship between food limitation and predation in semi-domestic reindeer. Oecologia 137:370–376.

Tveraa, T., P. Fauchald, N. G. Yoccoz, R. A. Ims, R. Aanes, and K. A. Høgda. 2007. What regulate and limit reindeer populations in Norway? Oikos 116:706–715.

Valeix, M., H. Fritz, A. Loveridge, Z. Davidson, J. Hunt, F. Murindagomo, and D. Macdonald. 2009. Does the risk of encountering lions influence African herbivore behaviour at waterholes? Behavioral Ecology and Sociobiology 63:1483–1494.

Vistnes, I., C. Nellemann, P. Jordhøy, and O.-G. Støen. 2008. Summer distribution of wild reindeer in relation to human activity and insect stress. Polar Biology 31:1307–1317.

von Arx, M., C. Breitenmoser-Würsten, F. Zimmermann, and U. Breitenmoser. 2004. Status and conservation of the Eurasian lynx (*Lynx lynx*) in Europe in 2001. KORA Bericht 19:1–330.

Watson, J. 1997. The Golden Eagle. T&AD Poyser, London, UK.

Wikenros, C., H. Sand, P. Wabakken, O. Liberg, and H. Pedersen. 2009. Wolf predation on moose and roe deer: chase distances and outcome of encounters. Acta Theriologica 54:207–218.

Wiktander, U., O. Olsson, and S. G. Nilsson. 2001. Seasonal variation in home-range size, and habitat area requirement of the lesser spotted woodpecker (*Dendrocopos minor*) in southern Sweden. Biological Conservation 100:387–395.

Wilmshurst, J. F., J. M. Fryxell, B. P. Farm, A. R. E. Sinclair, and C. P. Henschel. 1999. Spatial distribution of Serengeti wildebeest in relation to resources. Canadian Journal of Zoology 77:1223–1232.