

Decomposing risk: Landscape structure and wolf behavior generate different predation patterns in two sympatric ungulates

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Abstract. Recolonizing carnivores can have a large impact on the status of wild ungulates, which have often modified their behavior in the absence of predation. Therefore, understanding the dynamics of reestablished predator–prey systems is crucial to predict their potential ecosystem effects. We decomposed the spatial structure of predation by recolonizing wolves (*Canis lupus*) on two sympatric ungulates, moose (*Alces alces*) and roe deer (*Capreolus capreolus*), in Scandinavia during a 10-year study. We monitored 18 wolves with GPS collars, distributed over 12 territories, and collected records from predation events. By using conditional logistic regression, we assessed the contributions of three main factors, the utilization patterns of each wolf territory, the spatial distribution of both prey species, and fine-scale landscape structure, in determining the spatial structure of moose and roe deer predation risk. The reestablished predator–prey system showed a remarkable spatial variation in kill occurrence at the intra-territorial level, with kill probabilities varying by several orders of magnitude inside the same territory. Variation in predation risk was evident also when a spatially homogeneous probability for a wolf to encounter a prey was simulated. Even inside the same territory, with the same landscape structure, and when exposed to predation by the same wolves, the two prey species experienced an opposite spatial distribution of predation risk. In particular, increased predation risk for moose was associated with open areas, especially clearcuts and young forest stands, whereas risk was lowered for roe deer in the same habitat types. Thus, fine-scale landscape structure can generate contrasting predation risk patterns in sympatric ungulates, so that they can experience large differences in the spatial distribution of risk and refuge areas when exposed to predation by a recolonizing predator. Territories with an earlier recolonization were not associated with a lower hunting success for wolves. Such constant efficiency in wolf predation during the recolonization process is in line with previous findings about the naïve nature of Scandinavian moose to wolf predation. This, together with the human-dominated nature of the Scandinavian ecosystem, seems to limit the possibility for wolves to have large ecosystem effects and to establish a behaviorally mediated trophic cascade in Scandinavia.

Key words: *Alces alces*; *Canis lupus*; *Capreolus capreolus*; catchability; dilution effect; kill occurrence; moose; predation risk; predator recolonization; prey refugia; roe deer; Scandinavia.

INTRODUCTION

The recovery of large predators in most parts of Europe and North America is one of the most dramatic ecological changes to have occurred in these areas in recent decades (Ray et al. 2005, Terborgh and Estes 2010). Although this process is generally supported as an effective way to promote biodiversity and to restore the complexity of trophic interactions inside ecosystems (Treves and Karanth 2003), it also poses a series of potential threats to the status of the preexisting ungulate populations, which often have lived in the absence of

natural predation for several generations, and are therefore often claimed to have become more vulnerable (Berger et al. 2001, Sand et al. 2006). Moreover, global change and the impact of human activities on natural ecosystems are rapidly changing the characteristics of the environments in which such recolonization processes are occurring (Karl and Trenberth 2003). Thus, native ungulates are in most cases faced with the combined challenges of a new unknown mortality risk and of a rapid modification of their environment.

Both ecological theory and a large body of empirical studies suggest that landscape can play a key role in shaping predator–prey interactions (Gorini et al. 2012), and that landscape structure can buffer the demographic impact of predation on prey species by creating a mosaic of risk and refuge areas in which predators have

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different probabilities of killing (Kareiva and Wennegren 1995, Ellner et al. 2001, Kauffman et al. 2007). The possibility for native ungulates to benefit from such spatial variation in predation risk, after recolonization by a large predator, depends on their ability to shift their resource selection in favor of those habitat types in which predation risk is lower (Lima and Dill 1990). When such a shift occurs, the hunting success of a newly established predator (hereafter referred to as catchability) may decrease over time, with prey re-adapting to its presence, or as an effect of increased density and competition among predators (Kauffman et al. 2007). Progressive modifications in prey distribution and habitat use also can affect the movements of predators inside their home ranges, with the expectation that they will spend more time in patches where prey are more vulnerable or present at higher densities (Bergman et al. 2006). Landscape structure also can affect hunting success of predators on prey individuals of different age (Gorini et al. 2012), thus influencing the age composition of kills and the resulting demographic impact of predation (Gervasi et al. 2012).

Most of the interventions that humans make on forest ecosystems consist of either manipulating animal densities and distribution through harvest, or modifying landscape structure (through infrastructure development, logging, and so forth). Therefore, decomposing the spatial structure of predation into contributions from each of these three components (prey spatial distribution, predator space use, and landscape structure) is essential not only to understand the potential effects of recolonizing predators on native species, but also to assess the impact of human activities on both predator and prey populations. Nevertheless, although a few studies on single predator–prey systems have revealed some crucial aspects of the spatial interactions between recolonizing carnivores, native prey, and landscape structure (Kunkel and Pletscher 2000, Kauffman et al. 2007), most often predators do not rely exclusively on a single prey, but rather kill to a different extent a variety of prey species, each of them exhibiting a different relationship with the landscape. Moreover, although much is known about the role of landscape structure in mediating predation risk at a large geographical scale (Kauffman et al. 2007), very limited information is available about the same type of effect at a fine scale, the one playing a role inside each predator's home range.

The recolonizing Scandinavian wolf population offers a special opportunity to explore these questions. (1) Scandinavian wolves rely almost entirely on two native ungulates, moose (*Alces alces*) and roe deer (*Capreolus capreolus*), as their prey (Wikenros et al. 2009). This offers the opportunity to assess the spatial structure of their predation in a multi-prey context, where species-specific patterns of resource selection and predatory behavior can potentially generate contrasting predation risk patterns in sympatric ungulates. (2) South-central

Scandinavia, in which the wolf population is distributed, is dominated by extensive, but intensively managed, boreal forest, which is to a great extent homogeneous at a large scale, but exhibits a high level of spatial variation in the different habitat types at a fine scale, mainly as a consequence of forest management practices by humans. This allows one to test if fine-scale landscape structure has a relevant role in determining the spatial distribution of predation risk inside each wolf territory. (3) Scandinavian wolves have been intensively studied since the beginning of their recolonization process by tracking on snow (Wabakken et al. 2001), supplemented by the use of Very High Frequency (VHF) and Global Positioning System (GPS) collars from 1998 and onward (Sand et al. 2005, 2012). A large body of high-resolution data on individual movements, prey densities, and predation patterns is therefore available for a significant part of the recolonization process.

Given these theoretical premises and the availability of a suitable study case, we decomposed the spatial structure of wolf-killed moose and roe deer in Scandinavia during winter into contributions from three main factors, namely the utilization patterns of each wolf territory, the spatial distribution of both prey species, and the fine-scale landscape structure at the intra-territorial level. We compared the resulting spatial structure of predation risk for each of the prey species inside each wolf territory, and explored the following research questions:

- 1) Do moose and roe deer experience different patterns of risk when exposed to predation by the same wolves inside the same territory?
- 2) Does landscape structure play a role in modulating the spatial distribution of risk and refuge areas for the two prey species?
- 3) Is there a trade-off between habitat quality and predation risk for the two prey species?
- 4) Do environmental factors affect predation risk among prey age classes?
- 5) Did the efficiency of wolf predation on moose change during the course of the recolonization process?

MATERIALS AND METHODS

GPS monitoring and surveys of wolf kill sites

During winters 2002–2011, we monitored 18 wolves with GPS collars, distributed over 12 territories (average territory size 1017 km²; Mattisson et al. 2013), with some territories that were monitored for more than one year. Given the expanding nature of the Scandinavian wolf population, some of the territories were newly established when included in the study, whereas others had been first occupied as much as 21 years before the study was conducted. All data were collected through a schedule of one GPS location every 30 or 60 minutes. In particular, we used a 30-minute schedule for those territories hunting a large proportion of roe deer, to

prevent the risk that some predation events, especially on juveniles, could remain undetected. Between February and April, we identified all clusters of two or more locations less than 200 m apart as potential kill sites (Sand et al. 2005, 2008), and visited them to search for body parts, blood, or other remains that could confirm a predation event. When an ungulate carcass was found, we identified the species, and whenever possible its sex and age class (calf/fawn vs. older individual). This resulted in 333 confirmed wolf kills (239 moose and 94 roe deer). In the majority of the territories, moose was the dominant prey species (60–100%), with the exception of two territories (Hasselfors and Riala), in which roe deer constituted 70% and 95% of all ungulates killed. Procedures for capturing and handling wolves, and for cluster identification, are described in Sand et al. (2005, 2006, 2008) and Zimmermann et al. (2007). Details about the wolf territories included in the study are provided in Appendix A.

Wolf use of territories

The probability of a kill occurring at a given site inside a wolf territory was expected to be determined by the amount of time wolves spent in that area when searching for a prey. Therefore, to characterize the space use of wolves inside their territories, we constructed a utilization distribution (UD) at a resolution of 25 m, starting from all GPS locations available for each territory during each winter. We used a fixed kernel estimator (Seaman and Powell 1996) and applied a 20% reduction of the reference smoothing factor to account for the clumped distribution of wolf locations (Kie et al. 2002). This allowed us to assess the relative probability of a wolf visiting a specific portion of its home range during the study.

Because we were only interested in the wolves' UD when searching for a prey, and because locations related to post-kill handling time could potentially cause an overestimation of the UD around kills, we excluded all locations within 48 h and within 1000 m from each kill, and calculated the UD on the remaining locations. We also tested the sensitivity of the estimated UD to variation in temporal and spatial criteria for the identification of handling time, but no difference emerged in the best-supported models and parameter estimates. Details about handling time and UD estimation are provided in Appendix B.

Moose and roe deer density

A second component expected to influence the spatial distribution of wolf kills was the variation of prey density inside each territory. Supposedly, the higher the density of a given prey, the higher the probability that one prey individual will be killed at that site. Therefore, we developed a Resource Selection Function (RSF) for each of the two prey species to predict the spatial variation of the relative prey density inside each wolf territory. We used data derived from a set of pellet count

surveys, performed inside each wolf territory in the same year in which the wolf predation study was conducted. Previous studies on the same geographic area and species (Rönnegård et al. 2008, Månsson et al. 2011) have tested and confirmed the reliability of the method for describing both resource selection patterns and relative density variation.

In each territory, a grid of 1×1 -km plots was systematically distributed over the total territory area (~50–100 plots per territory). Each square plot contained 40 circular subplots along its perimeter, each of them covering 100 m^2 for moose and 10 m^2 for roe deer. All sample plots were surveyed in spring, between 4 April and 20 June. During data collection, we looked at the structure, consistency and color of the pellets, and their position in relation to the vegetation in order to include only new pellet groups, i.e., produced after leaf fall in the previous autumn.

Based on pellet group counts, we performed the RSF analysis at two levels: one using the cumulative number of pellet groups counted at each square plot as the sampling unit, the other based on the actual number of pellets groups observed in each circular subplot. By performing all subsequent analyses with both data sets, we revealed no additional contribution of the subplot data in improving model performance and the proportion of variance explained by the model. Therefore, we only present the results derived by the analysis conducted with square plots as sample units.

For each sampling unit (plot), we created a series of increasingly larger buffers, ranging from 25 m to 3 km, because different environmental factors could potentially influence prey density at different scales (Rhodes et al. 2009). Then, for each buffer distance we reported a set of Geographic Information System (GIS) environmental variables, potentially explaining the variation in the number of pellet groups sampled at each plot. We included altitude above sea level, slope, average snow accumulation, density of both forest gravel roads and asphalt roads, and the proportion of land occupied by the following land use categories: agricultural fields, urban areas, wetlands, clearcuts, young forest plantations, older forest (the Swedish Corine land cover map, Lantmateriet, Sweden, $25 \times 25 \text{ m}$). The choice of these predictors was based on previous knowledge about moose and roe deer resource selection patterns in the boreal forest ecosystem (Andersen et al. 1998, Månsson et al. 2011). A collinearity analysis revealed no excessive level of correlation in the final set of explanatory variables. For moose, we used a negative binomial distribution for the dependent variable to account for the observed over-dispersion in the data (Zuur et al. 2009), whereas a zero-altered negative binomial model was applied for the roe deer analysis to account for the excess of sampling units with zero observed pellet groups (Zuur et al. 2009). Then, for each of the two approaches, we started from a fully parameterized model and used the Akaike Information Criterion (AIC) of model fit

(Burnham and Anderson 2002) to select the most parsimonious one. Models with $\Delta\text{AIC} < 2$ were considered to be equally supported by the data. We also used AIC to assess the optimal buffering distance for each variable. After selecting the best-supported models, we applied a k -fold cross-validation (Boyce et al. 2002) to evaluate model performance in predicting moose and roe deer density inside each wolf territory. Based on the most parsimonious model, we extrapolated the RSF to the whole study area and used the predicted number of pellet groups in each cell as an index of the variation in the relative moose and roe deer density inside each wolf home range. Because the extrapolation of pellet counts to absolute density estimates relies on several assumptions, not formally tested across our study area, we only used a relative density index for all subsequent analyses.

Kill site models

To model the spatial variation in the probability of occurrence of wolf kills inside each territory, we used conditional logistic regression in R (R Development Core Team 2008), with the package *survival* version 2.37 (Therneau and Lumley 2009), comparing the characteristics of known kill sites with those derived from a set of random locations (Manly et al. 2002). To this aim, we built a case-control design for each of the two prey species, in which every known wolf kill was matched to 20 control points, randomly placed inside the wolf territory (Hosmer and Lemeshow 2000) at >500 m from a known kill site. Wikenros et al. (2009) reported average chasing distances of 76 m and 237 m for wolf-killed moose and roe deer in our study area; thus, our design aimed to have no random point generated inside any area where a known wolf kill had occurred.

Case-control design is particularly suited when “use” is rare so that, if the probability of a predation event occurring is close to zero, random sites can be treated as “non-use” sites (Keating and Cherry 2004). Under this assumption, case-control logistic regression provides the probability that a given location is actually a kill site, with respect to its control locations. Therefore, the relative probability of kill occurrence ψ for a given site (e.g., χ_1 is site 1) can be derived from the odds ratios (Keating and Cherry 2004), with reference (subscript R) to the mean values of each variable in the whole study area (χ_R):

$$\psi(\chi | \chi_R) = \exp[\beta_1(\chi_1 - \chi_R) + \beta_2(\chi_2 - \chi_R) + \dots + \beta_n(\chi_n - \chi_R)].$$

Thus, $\psi(\chi | \chi_R) = 3$ for a given site indicates that the probability of a wolf kill occurring at that site is three times higher than the average probability over the study area.

We started model selection by comparing four basic models: (1) an intercept-only model, in which the spatial occurrence of predation events was totally random; (2) a

“wolf” model, in which predation occurrence was described by the wolf UD of the winter territory; (3) a “prey” model, using the spatial variation of moose and roe deer density to explain the spatial distribution of kills; and (4) an “encounter rate” model, including both the wolf UD and prey density, thus generating the probability distribution that a wolf and a prey individual would be at the same site. For each explanatory variable in the encounter rate model, we tested if a linear, quadratic, or logarithmic relationship was most supported by the data. We used the Akaike Information Criterion (AIC) of model fit (Burnham and Anderson 2002) to select the most parsimonious model, with models showing a $\Delta\text{AIC} < 2$ being considered equally supported.

After identifying the best starting model, we tested if the addition of landscape structure would increase or decrease model fit. Landscape structure was described through slope, density of forest gravel roads, openness, average snow depth during winter, presence of water bodies within 500 m from the site, and by three successional stages of the forest management cycle (clearcut, young plantation, and older forest). Variables were included at a resolution of 50 m, and absence of excessive collinearity among them was checked prior to their use in the regression models.

After accounting for the wolf-prey encounter probability and for the effect of landscape structure, we tested if the effect of these factors was influenced by the number of years since wolf establishment in a given territory, under the hypothesis of a progressive behavioral adaptation by moose and roe deer to wolf presence. To this aim, we built a new set of models in which the wolf UD, prey density, and landscape structure interacted with the number of years since a given territory had been first occupied by wolves. The absence of longitudinal data for the same territory all along the recolonization process did not provide us with the optimal design to test for such an effect, but the inclusion of this variable in a GLM context assured that the covariation between the time since wolf establishment and other potentially confounding factors (habitat suitability for both prey species, landscape structure, and so forth) was taken into account when estimating regression slopes.

Finally, we investigated if the same factors included in the kill site model also had an influence on the age of killed moose. We performed a logistic regression analysis in which the response variable was the age class of each moose in the data set (1 = calf; 0 = yearling or older), thus estimating the relative probability that a wolf-killed moose would be a calf, conditional on the probability of occurrence of the kill, as estimated in the kill site model. We were not able to test what factors influenced the age of wolf-killed roe deer, as we were only able to determine age for a minor proportion of roe deer carcasses, due to the high degree of consumption.

TABLE 1. Parameter estimates for the best-supported moose RSF (resource selection function) model, used to estimate spatial variation in moose density at the intraterritorial level in south-central Scandinavia, 2002–2011.

Factor	β	SE	<i>P</i>
Intercept	2.781	0.280	<0.001
Forest	1.265	0.548	0.02
Forest ²	-1.392	0.500	0.005
Urban	-5.196	1.979	0.008
Agriculture	-1.577	0.763	0.039
Wetland	-1.416	0.291	<0.001
Altitude	-0.026	0.003	<0.001
Main roads	-4.637	1.540	0.002
No. subplots	0.051	0.005	<0.001

Individual risk and prey catchability

The kill site model for the two prey species provided a spatial description of the probability of occurrence of a wolf kill at each location inside a wolf territory. Starting from this, we generated three additional models for each prey species: one describing the individual predation risk by a single prey (prey risk model), one modeling the probability that a wolf would make a kill (wolf catchability model), and the last describing the effect of landscape structure taken alone (landscape model). We obtained the prey risk model by removing the effect of prey density from the kill site model, thus mimicking the risk experienced by a single moose in each portion of a wolf territory. The wolf catchability model resulted from removing the effect of the wolf UD inside each territory, whereas the landscape model contained neither the effect of prey density nor that of the wolf UD, thus simulating a spatially homogeneous probability for a wolf to encounter a prey. This allowed us to perform all subsequent analyses from both the predator and the prey perspectives, and to decompose predation risk into contributions from the predator-prey encounter rate and from landscape structure.

RESULTS

Moose and roe deer density models

The best-supported moose density model included a second-order polynomial effect on moose density of the percentage of forest inside each plot (Table 1). Conversely, a significant negative effect emerged for altitude, urban areas, agricultural fields, wetlands, and main roads. Each wolf territory also exhibited a specific intercept summarizing the differences in moose density among territories, which were not explained by the effect of the previously cited variables. The effects of altitude and of the proportion of forest land in each plot are shown in Fig. 1.

The best-supported roe deer RSF model, in its binomial part, described an increasing probability of roe deer presence with an increasing proportion of agricultural land within the plot. It also included a positive effect of forest road density on roe deer presence, and a negative effect of increasing altitude

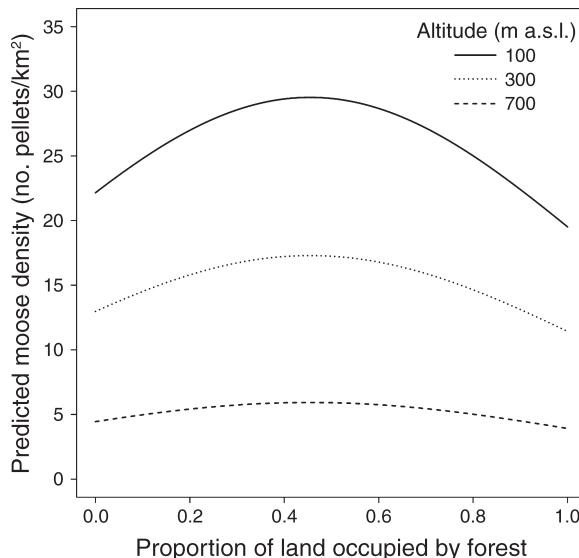


FIG. 1. Relationship between altitude, forest cover, and moose (*Alces alces*) density in south-central Scandinavia, as estimated by the best-supported resource selection function (RSF) model.

and slope (Table 2). The negative binomial part of the model also included a positive relationship between agricultural land, forest road density, and roe deer density, whereas a reduced roe deer density was observed at higher altitude, in and around wetlands, and with increasing slope (Table 2).

Moose kill site model

As expected, the spatial distribution of wolf-killed moose was highly influenced both by the wolf UD and by the distribution of moose density inside each territory. Among the four starting models, the “encounter rate” model outperformed all the others, showing that wolves killed moose at a higher rate in areas of

TABLE 2. Parameter estimates for the best-supported roe deer RSF model (zero-altered negative binomial model), used to estimate spatial variation in roe deer density at the intraterritorial level in south-central Scandinavia, 2002–2011.

Factor	β	SE	<i>P</i>
Binomial part (zero values)			
Intercept	1.654	0.536	0.002
Agriculture	6.431	2.160	0.002
Altitude	-0.012	0.001	<0.001
Slope	-0.289	0.103	0.005
Forest roads	438.391	161.121	0.004
Negative binomial part (nonzero values)			
Intercept	1.268	0.425	0.002
Agriculture	1.034	0.490	0.035
Wetland	-3.034	1.260	0.016
Altitude	-0.004	0.001	<0.001
Slope	-0.348	0.074	<0.001
Forest roads	172.456	78.651	0.028
No. subplots	0.014	0.008	0.009

TABLE 3. Model selection results for the analysis of moose predation risk in south-central Scandinavia, 2002–2011.

No.	Model	AIC	ΔAIC	Weight
1	log(wolf) + moose + clearcuts + plantations	773.05	0	0.650
2	log(wolf) + moose + roads + clearcuts + plantations	775.85	2.80	0.160
3	log(wolf) + moose + slope + roads + clearcuts + plantations	776.63	3.57	0.109
4	log(wolf) + moose + slope + roads + clearcuts + plantations + bogs	778.18	5.12	0.050
5	log(wolf) + moose + slope + roads + clearcuts + plantations + bogs + openness	779.86	6.80	0.022
6	log(wolf) + moose + slope + roads + clearcuts + plantations + bogs + water + snow	781.74	8.69	0.005
7	log(wolf) + moose + clearcuts + plantations + time since establishment	792.61	19.56	0.003
8	log(wolf) + moose	801.02	27.96	0.000
9	log(wolf)	805.31	32.25	0.000
10	wolf ²	809.13	36.07	0.000
11	wolf	826.15	53.09	0.000
12	moose	991.30	218.24	0.000
13	moose ²	996.61	223.55	0.000
14	log(moose)	997.4	224.34	0.000
15	random model	998.60	225.54	0.000

higher moose density and in those parts of their territory in which they spent more time when searching for prey (Table 3). The effect of the wolf UD on the spatial arrangement of kill sites was best described by a logarithmic function, whereas moose density exhibited a linear relationship with the probability of kill occurrence (Fig. 2a, b).

The inclusion of landscape structure into the kill site model substantially improved the performance of the model. The best “landscape + encounter” model exhibited ΔAIC = 27.96 with respect to the “encounter rate” model, showing that fine-scale landscape structure strongly determined where wolves were more likely to kill moose inside their territory (Table 3). In particular, the best-supported model (Model 1 in Table 3) showed a 10–20 times higher kill probability in and around forest clearcuts and young forest plantations, which emerged as particularly risky areas for moose. The resulting predation risk function for moose was as follows:

$$\begin{aligned} \psi(\chi_1 | \chi_R) = & \exp[1.09\{0.10\} \times (\log(\text{wolf})_1 - \log(\text{wolf})_R)] \\ & + 0.43\{0.01\} \times (\text{moose}_1 - \text{moose}_R) \\ & + 2.37\{0.63\} \times (\text{clearcuts}_1 - \text{clearcuts}_R) \\ & + 3.26\{0.70\} \times (\text{plantations}_1 - \text{plantations}_R)]. \end{aligned}$$

All models including a “time since wolf establishment” effect were less supported by the data than those excluding such an effect (Table 3). Thus, the data did not suggest any change with time in the spatial distribution of predation risk.

To evaluate the predictions of the kill site model, we used a *k*-fold cross-validation approach (Boyce et al. 2002). We divided the data set into five equal bins, fitted the model using 80% of the data, and used the remaining 20% to evaluate its performance. The validation provided an average Spearman’s correlation of $\rho = 0.85$ across the five iterations, corresponding to a good fit of the model to the data (Boyce et al. 2002).

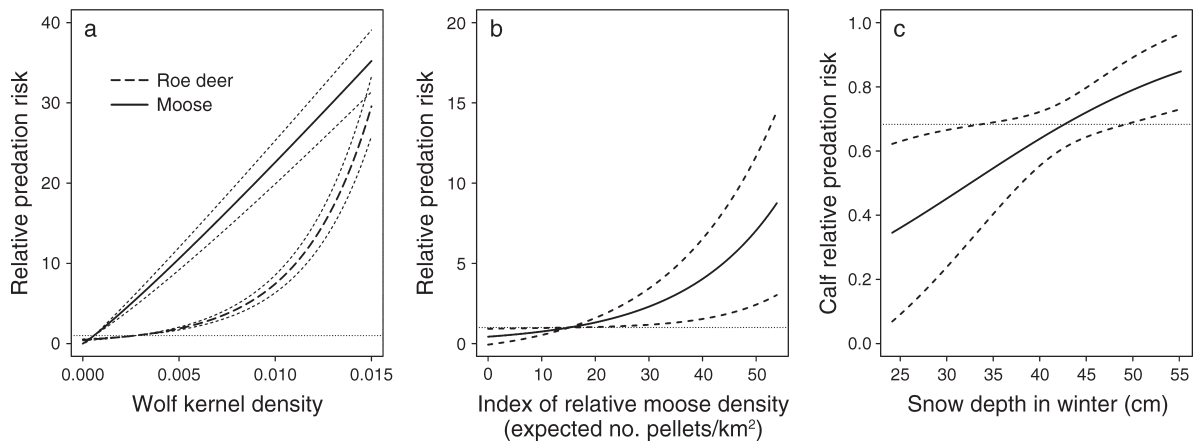


FIG. 2. (a) Relationship between the wolf kernel density (the average value of the Utilization Distribution, calculated in a circle of 500 m around each wolf kill) inside each territory and the resulting relative predation risk for moose and roe deer (*Capreolus capreolus*). (b) Relationship between moose density (as predicted by the resource selection function (RSF) model) at the intra-territory level and relative predation risk. (c) Relationship between snow depth and the relative probability that a wolf-killed moose is a calf. Dotted boundaries in panel (a) and dashed boundaries in panels (b) and (c) indicate the 95% confidence interval around the mean. The thin dotted horizontal lines refer to the baseline average risk in the study area.

TABLE 4. Model selection results for analysis of roe deer predation risk in south-central Scandinavia, 2002–2011

No.	Model	AIC	Δ AIC	Weight
1	wolf + openness + plantations	400.39	0	0.716
2	wolf + water + openness + plantations	403.64	3.25	0.137
3	wolf + slope + water + plantations + openness	405.9	5.51	0.042
4	wolf + slope + roads + plantations + bogs + openness	406.01	5.62	0.039
5	wolf + slope + roads + clearcuts + plantations + bogs + water + openness	406.31	5.92	0.030
6	wolf + openness + plantations + time since establishment	407.38	6.99	0.021
7	wolf + slope + roads + clearcuts + plantations + bogs + water + snow + openness	408.25	7.86	0.014
8	wolf	420.4	20.01	0.000
9	log(wolf)	421.21	20.82	0.000
10	wolf + roe deer	423.01	22.62	0.000
11	wolf + log(roe deer)	423.32	22.93	0.000
12	wolf ²	454.03	53.64	0.000
13	roe deer	536.1	135.71	0.000
14	log(roe deer)	553.94	153.55	0.000
15	null model	560.19	159.8	0.000

The logistic regression analysis of the age of wolf-killed moose showed that snow depth influenced the probability that a killed moose was a calf vs. an adult. The best-supported model showed an increased predation risk for calves in areas of deep snow (Fig. 2c). For average snow conditions (~35 cm of snow depth), wolves killed an average of 65% calves, but the percentage increased to almost 90% in areas where mean snow depth was 60 cm (Fig. 2c).

Roe deer kill site model

In contrast to what we observed for moose, the spatial distribution of wolf-killed roe deer was not best explained by the “encounter rate” model, among the four possible initial models. The “wolf model” exhibited the lowest AIC, showing that wolves were more likely to kill roe deer in areas in which they spent more time when searching for a prey, but not in proportion to the spatial distribution of roe deer density (Table 4). Also, the effect of the wolf UD on kill probability was best described by a linear function on the logit scale (Fig. 2a). To confirm the robustness of this result, we repeated the analysis including data only from the two territories where wolves selected roe deer as their primary prey. The results were not different, confirming that roe deer density did not determine where wolves were more likely to kill a roe deer inside their territory.

Similarly to what we found for moose kills, landscape structure emerged as a strong predictor of the spatial distribution of roe deer kills at the intra-territory level, but in a different direction than observed for moose. The best-supported “landscape + encounter” model (Model 1 in Table 4), which exhibited Δ AIC = 20.0 with respect to the “wolf” model, showed a reduced kill probability in and around open areas and young forest plantations. Therefore, these landscape features emerged as refuge areas for roe deer, in contrast to what was observed for moose. The resulting predation risk function for roe deer (standard error estimates in brackets) was as follows:

$$\begin{aligned} \Psi(\chi_1 | \chi_R) &= \exp[275.2\{2.83\} \times (\text{wolf}_1 - \text{wolf}_R) \\ &\quad - 1.70\{0.23\} \times (\text{openness}_1 - \text{openness}_R) \\ &\quad - 4.79\{1.70\} \times (\text{plantations}_1 - \text{plantations}_R)]. \end{aligned}$$

Also for the roe deer analysis, models including a “time since wolf establishment” effect were not supported by the data. No change emerged with time since colonization in the spatial distribution of roe deer predation risk inside wolf territories. The *k*-fold cross-validation procedure for the roe deer kill model provided an average Spearman correlation of $\rho = 0.89$, showing a good fit between real data and predictions. The different spatial structure in the probability of occurrence of moose and roe deer kills is illustrated in Fig. 3.

Individual risk and catchability

After generating the “prey risk,” “catchability,” and “landscape” models, we compared them to assess which factors were most relevant in determining predation risk and the relative probability that a wolf would make a kill (catchability), and to test if the relative contribution of these factors was different for moose and roe deer. For each territory and prey species, we reported the range in predation risk, as predicted by the “prey risk” and “landscape” models. Also, we computed a Spearman’s correlation index between moose and roe deer predation risk inside each wolf territory, to estimate the degree of overlap in the spatial distribution of the two risk patterns. The results from the “prey risk” model indicated a much higher variation in predation risk for moose than for roe deer. Moose predation risk ranged from about 0 to more than 100, implying a relative predation risk 100 times higher than the average in certain portions of the territory, whereas the highest risk for roe deer was only 8.2 times higher than the average (Table 5), corresponding to a much more uniform spatial distribution of risk. Only between 8% and 38% of

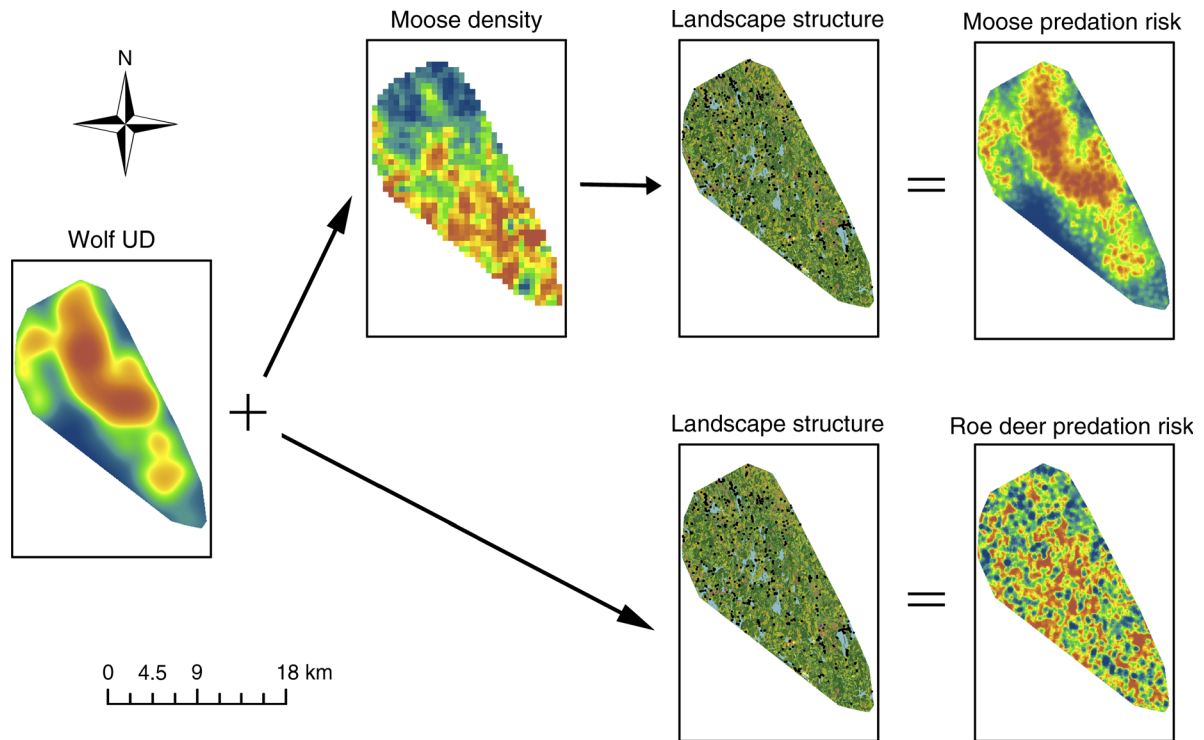


FIG. 3. Decomposition of wolf-induced predation risk for moose and roe deer in Scandinavia into its basic determinants, namely, the wolf Utilization Distribution (UD), the spatial variation of prey density, and landscape structure. The resulting spatial distribution of predation risk for moose and roe deer kills are shown for one of the territories (Ulriksberg). The gradient from cold to warm colors represents increasing probabilities for each map; that is, the warmest colors show increased wolf use, prey density, and predation risk. Models used to generate the risk maps are the best-supported ones in Tables 3 and 4. Roe deer density is not shown in the scheme because it has no effect on roe deer predation risk. As a result, roe deer predation risk strongly mimics landscape structure, whereas moose risk does not.

moose predation risk was explained by the effect of landscape structure, whereas in roe deer the percentage was 67–95%. The distributions of moose and roe deer predation risk showed a strong negative correlation (Table 5), with Spearman’s indices ranging from $\rho = -0.38$ to -0.81 .

To illustrate the different patterns of predation risk for moose and roe deer inside each wolf territory, we also explored the link between probability of occurrence of a kill, prey density, and predation risk for each prey individual in the population. Two processes interact to determine the probability that a single prey individual

TABLE 5. Structure of moose and roe deer predation risk in south-central Scandinavia.

Territory	Moose risk			Roe deer risk			Risk correlation index
	Prey	Land.	Land. (%)	Prey	Land.	Land. (%)	
Djurskog	14.4	5.4	38	3.0	2.6	88	-0.60
Hasselfors	67.4	5.6	8	2.5	1.8	72	-0.60
Fulufjellet	61.7	8.5	14	8.2	7.6	93	-0.81
Bogringen	67.0	6.9	10	5.9	5.6	95	-0.55
Kloten	27.9	7.6	27	3.1	2.5	80	-0.81
Tensskog	99.0	11.9	12	3.9	3.4	87	-0.78
Jangen	27.5	6.4	23	4.0	2.7	67	-0.80
Riala	29.0	3.8	13	4.7	2.2	46	-0.38
Nyskoga	89.0	9.0	10	4.3	3.8	89	-0.77
Tyngsjö	29.1	10.4	36	3.7	3.3	91	-0.70
Ulriksberg	34.1	6.2	18	2.7	2.3	86	-0.67
Gräsmark	101.9	11.3	11	3.4	2.9	85	-0.78

Note: For each species, “prey risk” is the range in predation risk inside a given territory; “landscape risk” refers to the range in predation risk due to landscape structure only; the percentage of total risk explained by landscape and the Spearman’s correlation between moose and roe deer risk are also reported.

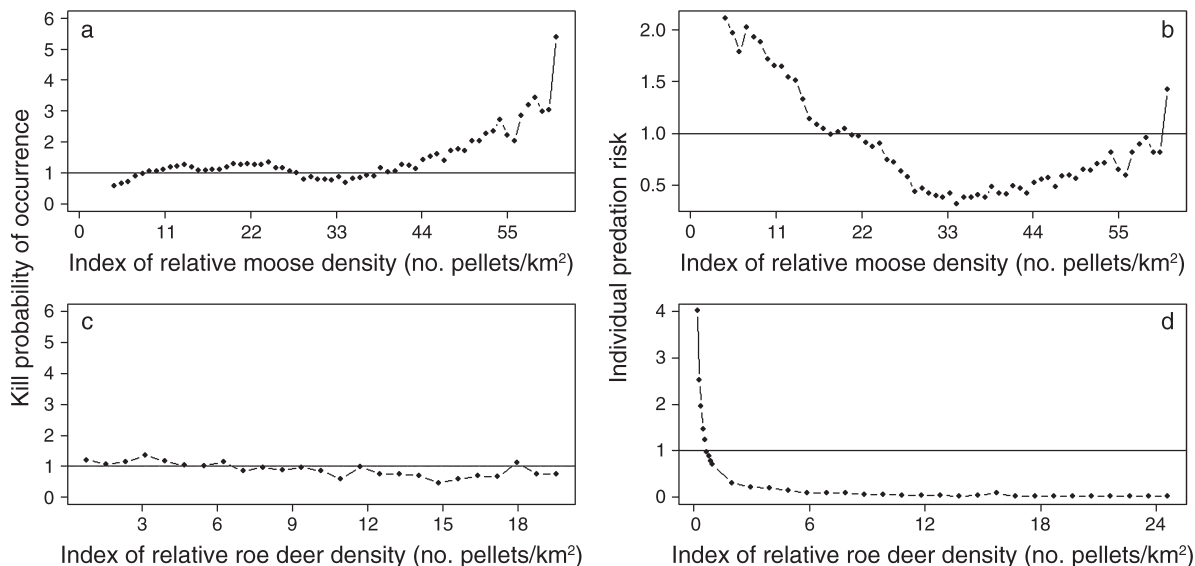


FIG. 4. (a) Relationship between moose density and the probability of occurrence of a wolf kill on moose, based on model 1 in Table 3. (b) Relationship between moose density and the relative individual predation risk for moose, based on model 1 in Table 4. (c) Relationship between roe deer density and the probability of occurrence of a wolf kill on roe deer. (d) Relationship between roe deer density and the relative individual predation risk for roe deer. Horizontal lines indicate the average risk in the study area. Note that kill probability of occurrence and individual predation risk are unitless indices, because they are a ratio between two probabilities, namely, the kill probability (or individual predation risk) at a given site and the average kill probability in the study area.

will be killed by a wolf: (1) the probability that a wolf kill occurs at a given site, as described by the kill site model; (2) the dilution effect, i.e., the probability that each individual prey is the one actually killed, among all the conspecifics occupying the same area. To explore this issue, we first plotted the predicted probability of occurrence of a moose or roe deer kill as a function of prey density (Fig. 4a, c). Then, we divided such probability by our index of prey density, thus generating a relationship between prey density and individual predation risk (Fig. 4b, d). The lowest individual predation risk for moose was observed at intermediate density, with higher risk values at both lower and higher moose densities (Fig. 4b). In contrast, the highest risk for roe deer was observed at low roe deer density, because the dilution effect generated a rapid decrease in individual predation risk as soon as roe deer density increased (Fig. 4d).

Finally, to further investigate if wolf predation efficiency had changed during the recolonization process, we tested if the average probability of making a kill inside each territory, as described by the “catchability” model, exhibited a negative or positive relationship with the time since a given territory had been first occupied by wolves. A linear regression model between these two variables showed that the slope of the relationship was not significantly different from zero. As shown in Fig. 5, the average wolf catchability remained constant during the recolonization process, despite a large inter-territorial variation in the average catchability, with some

packs having an efficiency of predation double that of others.

DISCUSSION

The reestablished predator–prey system of south-central Scandinavia (wolf–moose–roe deer) exhibited a

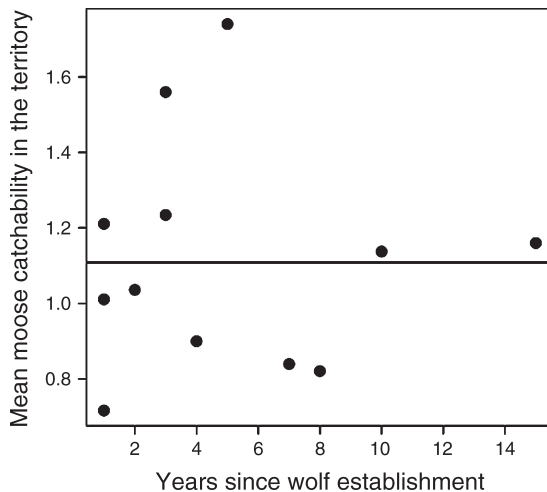


FIG. 5. Average moose catchability inside each wolf pack in south-central Scandinavia (2002–2011), as a function of the number of years since wolf establishment. The horizontal line represents the estimated regression curve between the two variables. Catchability is a unitless ratio between two probabilities, namely, the probability of a wolf a kill at a given site, and the average probability of a wolf kill kill in the study area.

remarkable level of spatial variation in kill occurrence at the intra-territorial level, with relative kill probabilities varying by several orders of magnitude inside the same territory. This shows that well-defined risk and refuge areas exist at a fine spatial scale inside wolf territories in Scandinavia, with the potential to affect both wolf space use and the patterns of resource selection by their native ungulate prey. Because variation in predation risk was also evident when mimicking a spatially homogeneous probability for a wolf to encounter a prey, we can infer that fine-scale landscape structure in the Scandinavian boreal forest can induce a large variation in predation risk, independently from the effect of local densities of predator and prey.

Additionally, we found that even inside the same territory, with the same landscape structure, and when exposed to predation by the same wolves, the two prey species experienced a significantly different spatial distribution of predation risk (Fig. 3). First, moose were more at risk in areas of higher moose density (Fig. 2b), whereas the probability for a wolf to kill a roe deer was not at all affected by the local roe deer density. Secondly, moose predation risk increased steadily with the time spent by wolves in a given part of their territory, whereas roe deer risk was to a much lower extent correlated with the intensity of wolf presence in a given area (Fig. 2a). Finally, the relationship between landscape structure and predation risk was opposite in the two prey species. Spending time in open areas increased predation risk for moose, especially in clearcuts and young forest stands, but decreased it for roe deer, which often feed in agricultural fields and closer to human settlements (Torres et al. 2011). Although the mechanism behind the effect of landscape structure on roe deer risk is probably related to their increased ability to detect predators and to promptly escape (Andersen et al. 1998), the link between open areas and moose predation risk is less straightforward. Improved detection by wolves may be one explanation, as suggested by the increased alert behavior by moose when feeding farther from cover (Molvar and Bowyer 1994), but others are more related to the possibility that moose defend themselves from attacking wolves. Thus, there may be a deliberate choice made by wolves to wait to attack until they reach a more open area. Wikenros et al. (2009) have found that Scandinavian moose have the highest chance to avoid wolf predation when they are able to run away before the actual chase starts; thus, it seems reasonable that the effect of landscape structure on predation risk operates mainly by modulating the predator–prey detection process.

Moose were the most common prey in the majority of wolf territories, so the interpretation of the observed differences in predation risk between the two prey species should be seen in light of wolf predatory behavior in southern Scandinavia being mainly oriented toward moose rather than roe deer. Consistent with such a pattern, moose predation risk exhibited a well-defined

spatial structure and was mainly driven by the effect of predator–prey encounter rates (Table 5), implying that wolves actively tried to maximize their chances to kill a moose by searching in areas of higher moose density, by intensively patrolling the areas where predation events were more likely to occur, and by taking advantage of those landscape features (open areas) in which an attack was more likely to be successful. In contrast, predation on roe deer only differed to a minor extent from a random process, and was to a large degree driven by the effect of landscape structure. This indicates that wolves did not kill roe deer where they were present at higher density, but rather they killed roe deer opportunistically, whenever a favorable situation occurred (mainly in forested areas and far away from agricultural fields).

Although predator density traditionally has been used as the main predictor for predation risk (Creel and Winnie 2005), several studies have questioned the general value of this statement, suggesting that the numeric component of predation (how many predators occupy a given area) in most cases might be less relevant than its spatial component (in what type of landscape a given predator encounters a potential prey). Kauffman et al. (2007) found that landscape structure, more than local predator density, was the main driver of elk (*Cervus elaphus*) predation risk in Yellowstone's Northern Range. Similarly, Hebblewhite et al. (2005) found a fourfold variation in elk predation risk from wolves, simply due to the effect of landscape attributes, in Banff National Park, Canada. By expanding these previous studies to a multi-prey context and by including spatial variation in prey density, we here show that even in the same landscape structure, prey selection patterns and a differential predatory behavior by the same carnivore toward two sympatric prey species can generate remarkably different distributions of predation risk.

Trade-offs between foraging opportunities and predation risk are thought to fundamentally drive the spatial distribution of large herbivores in areas in which they are subject to predation (Hebblewhite and Merrill 2009). The need to maximize energy intake while minimizing predation risk has the potential to drive herbivore group size formation (Fortin et al. 2009), resource selection patterns (Kittle et al. 2008), and the spatial variation of their density (Creel and Winnie 2005), but the relative extent to which predation avoidance can play a role in shaping ungulate spatial behavior, and thus induce ecosystem effects, is still debated. Elk in the Yellowstone ecosystem have been shown to have modified their movement patterns (Fortin et al. 2005) and habitat use (Mao et al. 2005) in response to wolf predation, but how such a shift also could have induced cascading effects is far from being clarified (Mech 2012, Winnie 2012). The accumulation of studies on this subject is progressively revealing that behaviorally induced trophic cascades are not a ubiquitous trait of ecosystems, but rather the result of complex system-specific interactions of multiple factors (Kauff-

man et al. 2010). The simple trade-off between predation risk and resource acquisition can lead to both positive and negative indirect effects of predators on plant resources and hence cannot predict the sign and strength of their possible ecosystem effects (Schmitz et al. 2004). Making predictions would require at least knowledge of habitat and resource use by prey with regard to predator's presence, and habitat use and hunting mode by other competing predators (Schmitz et al. 2004, Schmitz 2008). Therefore, when exploring the potential for Scandinavian wolves to also affect prey behavior and spatial distribution, and to generate ecosystem effects, we need to account for the characteristics of this specific predator-prey system. The most obvious characteristic is the human-dominated nature of all trophic levels within the Scandinavian ecosystem. At first glance, if we only look at the spatial distribution of wolf-induced predation risk, which generates well-defined risk and refuge areas, a potential for a predator-mediated trophic cascade would exist in Scandinavia, if wolf predation were able to induce a shift in prey behavior and resource selection. In this sense, moose and roe deer clearly exhibit a different potential for the previously described trade-offs. As shown in Fig. 4b, a potential trade-off between habitat suitability and predation risk exists for moose, whose best balance is expected to be found at intermediate moose densities. Such trade-off results in an apparent selective pressure for an individual moose to avoid both areas with very low and very high habitat suitability, in the presence of wolf predation. In contrast to moose, no strong trade-off between resource selection and predation risk appeared for roe deer. As roe deer risk decreased dramatically with increasing roe deer density (Fig. 4d), a selective pressure toward living in areas with high habitat suitability emerged, thus showing no evident conflict between the need to maximize resource availability and that of minimizing predation risk by wolves. However, when evaluating the overall "foraging vs. survival" trade-off, we need to account for all of the existing mortality risks, and for the human-modified nature of the Scandinavian ecosystem, which strongly limits a numerical response of predator to prey density, and greatly reduces their potential to affect the demography and behavioral ecology of their prey and to initiate trophic cascades. Human harvest in Scandinavia accounts for >90% of moose mortality overall (Sand et al. 2012), and still for >50% of mortality inside wolf territories (Wikenros et al. 2010), whereas 70% of roe deer mortality is due to causes other than wolf predation, among which is a consistent predation from the Eurasian lynx (*Lynx lynx*; Gervasi et al. 2012). This clearly suggests that, even in the presence of wolf predation, minimizing human-related mortality risks is likely the best behavioral choice for Scandinavian ungulates, even at the cost of increased wolf-related predation risk. Supporting this, moose did not show any significant shift in resource selection after wolf recolonization in central Sweden (Milleret 2012),

nor did they modify their mobility (Balogh 2012) or activity patterns (Eriksen et al. 2011). Therefore, even if the spatial arrangement of predation risk predicts the potential for the wolves to establish a "landscape of fear" (Laundré et al. 2001) in Scandinavia, the overall evaluation of all mortality factors suggests that it will mainly be a "landscape of fear of humans." Consistent with such expectation, we found no evidence that territories with an earlier wolf recolonization history provided a lower catchability of moose for wolves.

Although our study does not allow us to fully reveal the underlying mechanism generating such a constant trend in predation efficiency, it still supports previous findings (Sand et al. 2006) about the naïve nature of Scandinavian moose and about the lack of a behavioral adjustment by moose in response to wolf predation, and the more general finding that large-bodied ungulates have a reduced behavioral response when exposed to predation from cursorial predators (Thacker et al. 2011). Other potential explanations are available, but less likely to be the main drivers of the whole process. Prey animals under nutritional limitation, especially when living in herds, have been shown to strongly reduce their response to predators (Mao et al. 2005, Winnie and Creel 2007, Vijayan et al. 2012), but moose in our study area are not likely to experience significant nutritional constraints (Sand et al. 2012) or density dependence (Sand et al. 2006, Grøtan et al. 2009).

Therefore, while a large body of work has been produced in exploring the ecosystem function of carnivores in protected areas (Fortin et al. 2005, Hebblewhite et al. 2005, Kauffmann et al. 2007), many relevant open questions still need to be answered about their role in human-dominated ecosystems. When interacting with humans, the potential for carnivores to affect prey behavior and to initiate trophic cascades competes with the effect of a human "super predator" that is able to simultaneously shape predator numbers, prey distributions, and the structure of the landscape in which the predation process occurs. To this aim, it will be crucial to assess to what extent the spatial aspects of predation, which we explored in this work, can influence the more numerical components of the process, such as kill and predation rates. They are the direct link between predators and prey demography, and they ultimately determine the potential population and ecosystem consequences of predation.

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SUPPLEMENTAL MATERIAL

Appendix A

Wolf territories included in the study of moose and roe deer predation risk, south-central Scandinavia, 2002–2011 (*Ecological Archives* A023-087-A1).

Appendix B

Effect of different definitions of handling time on the Utilization Distribution (UD) of wolf winter territories (*Ecological Archives* A023-087-A2).