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Environmental and anthropogenic features mediate risk from human hunters and wolves for moose

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Abstract

Landscape characteristics, seasonal changes in the environment, and daylight conditions influence space use and detection of prey and predators, resulting in spatiotemporal patterns of predation risk for the prey. When predators have different hunting modes, the combined effects of multiple predators are mediated by the physical landscape and can result in overlapping or contrasting patterns of predation risk. Humans have become super-predators in many anthropogenic landscapes by harvesting game species and competing with large carnivores for prey. Here, we used the locations of wolf (*Canis lupus*)-killed and hunter-killed moose (*Alces alces*) in south-central Scandinavia to investigate whether environmental and anthropogenic features influenced where wolves and hunters killed moose. We predicted that the combined effects of wolves and hunters would result in contrasting spatial risk patterns due to differences in hunting modes. We expected these contrasting spatial risk patterns also to differ temporally. During the hunting season, the probability of a wolf kill increased with distance to bogs, whereas it decreased with increasing building density and distance to clearcuts and young forests. After the hunting season, the probability of a wolf kill increased with increasing terrain ruggedness and decreased with increasing building density, distance to main roads, and distance to clearcuts and young forests. The probability of a hunter kill was highest closer to bogs, main and secondary roads, in less rugged terrain and in areas with lower building density. Hunters killed all moose during the day, whereas wolves killed most moose at night during and after the hunting season. Our findings suggest that environmental and anthropogenic features mediate hunting and wolf predation risk. Additionally, we found that hunter- and wolf-killed moose exhibited contrasting spatial associations to landscape features, most likely due to the different hunting modes displayed by hunters and wolves. However, wolf predation and hunting risks also contrasted over time since wolves killed mostly at night and hunters were restricted to hunting during daytime and during the

hunting season. This temporal segregation in risk might therefore suggest that moose could minimize risk exposure by taking advantage of spatiotemporally vacant hunting domains.

KEYWORDS
Alces alces, *Canis lupus*, habitat, harvest, kill site, landscape, predation

INTRODUCTION

Predation is an important source of mortality (Dahle et al., 2013; Jędrzejewski et al., 1992; Melis et al., 2013), fundamentally shaping species interactions and ecological communities (Estes et al., 2011; Lima, 1998; Werner & Peacor, 2003). Predators can have direct effects on prey species by killing them (lethal, consumptive effect; Preisser et al., 2005; Werner & Peacor, 2003) but also by inducing behavioral, physiological, or morphological changes in prey seeking to avoid predation (nonlethal, risk effect; Creel & Christianson, 2008; Fortin et al., 2005; Lima, 1998; Werner & Peacor, 2003). In many human-dominated landscapes, humans have become super-predators for many animal species, and game harvesting has become the leading cause of mortality among many prey species (Allendorf et al., 2008; Darimont et al., 2015). Hunting can be regarded as a predation process (Frid & Dill, 2002) because, similarly to "natural" predation, it can lead to reduced survival but also to the development of antipredator strategies aimed at reducing the risk of being killed (Caro, 2005; Creel & Christianson, 2008; Lima, 1998; Lima & Dill, 1990). For instance, several studies have associated forest cover with relatively "safe" habitats for some prey (Hernández & Laundré, 2005; Ordiz et al., 2011). Additionally, hunting and predation risk also vary temporally, at both finer (e.g., diel) and coarser (e.g., seasonal) timescales, following shifts in the foraging needs of both predator and prey (Druce et al., 2009; Hopcraft et al., 2014), the density of predators, but also the enforcement of limited hunting times and seasons (Proffitt et al., 2009). Hunters and predators use specific hunting modes to optimize predation efficiency (Preisser et al., 2007; Schmitz, 2005), which interact with different habitat domains and anthropogenic features within the landscape (Atwood et al., 2007; Miller et al., 2014; Preisser et al., 2007). For instance, ambush predators often sit-and-wait where there is a higher chance of encountering and killing prey, relying on cover and darkness for surprise attacks. On the other hand, hunters can deploy a variety of hunting methods, but are often restricted to hunting in daytime and in specific periods, while requiring open spaces and proximity to roads for safe shooting and accessibility. Therefore, the physical landscape also interacts with the hunting modes of hunters and predators to shape spatiotemporal patterns of predation risk.

The combined effects of hunters and predators can generate spatiotemporal risk patterns that are often overlapping or contrasting (Gaynor et al., 2021; Lone et al., 2014; Norum et al., 2015). Overlapping risks have similar spatiotemporal patterns and may therefore allow prey to adopt a universal antipredator strategy to reduce predation risk from hunters and predators. Such overlap would likely also increase the frequency of refuge areas within the landscape. More common is when hunters and predators hunt in different habitats and during different times of the day. In this case, the accumulated effects of hunters and predators often result in contrasting predation risks (Atwood et al., 2009; Cresswell & Quinn, 2013; Gaynor et al., 2021; Lone et al., 2014; Norum et al., 2015). According to earlier studies, the different hunting modes of hunters and ambush predators (e.g., felids) often generate spatiotemporal risk patterns associated with contrasting habitat characteristics (Gaynor et al., 2021; Lone et al., 2014). On the other hand, cursorial predators, like wolves (*Canis lupus*), travel over large areas searching for prey, which they actively and rapidly pursue (Schmidt & Kuijper, 2015). Cursorial predators often do not require cover to surprise attack prey, and because they roam large areas, their distribution and associated predation risk cues within the landscape are often unpredictable (Schmidt & Kuijper, 2015). For these reasons, cursorial predators often elicit weaker habitat-mediated fear effects (Kauffman et al., 2010; Thaker et al., 2011). Compared with ambush predators, there is little knowledge about how predation risk from hunters and cursorial predators is linked to habitat characteristics.

Within our study area in south-central Scandinavia, moose are exposed to two major sources of predation risk: they are the primary prey of wolves (Sand et al., 2005, 2008) and the most important game species for hunters (Wikenros et al., 2020). Moose hunting is an important leisure activity with historical and cultural traditions and has great economic and recreational value (Boman et al., 2011; Storaas et al., 2001). Hunters and wolves differ in their hunting modes and are also active

at different times of the day. Wolves are cursorial predators that can chase moose for long distances (Mech et al., 2015). In Scandinavia, however, successful moose attacks were associated with short chase distances (Wikenros et al., 2009). While wolves kill moose mostly at nighttime (Sand et al., 2005), hunters are limited to daytime. Hunters can employ a wide range of hunting strategies like calling and stalking, but the most common in Scandinavia is the use of unleashed dogs to find and push moose toward sit-and-wait hunters situated at predetermined spots in the landscape. Additionally, the risk of wolf predation is present all year round, whereas hunters are restricted to a fixed hunting season. As a result of these differences in hunting modes, the chance of a successful hunt for both wolves and humans depends on habitat characteristics (Ciuti et al., 2012; Farmer et al., 2006; Kauffman et al., 2007). How landscape features affect the risk of being killed by hunters and predators, both spatially and temporally, has become an important topic in recent years, especially in areas with extensive human harvesting of game species (Brodie et al., 2013; Ciuti et al., 2012; Cromsigt et al., 2013; Laundré et al., 2001). To our knowledge, no study has focused on how landscape features influence the distribution of risk from wolves and humans and to what extent this pattern is overlapping or contrasting. We set out to address the following questions:

1. What does the temporal distribution of hunter-killed and wolf-killed moose during the hunting season look like?
2. How do spatial attributes influence the spatial patterns of wolf predation (a) during and (b) after the moose hunting season?
3. How do spatial attributes influence the spatial patterns of hunting risk for moose during the moose hunting season?
4. During the hunting season, do wolf predation and human hunting interact with the habitat to generate overlapping or contrasting spatial risk patterns?

While hunters are obliged to hunt during daylight hours, we expected wolves to kill mainly at night. During the hunting season, we predicted wolf predation risk to be higher closer to secondary roads since wolves are known to use roads to travel, especially during night hours (Zimmermann et al., 2014). We expected wolf predation risk to decrease with proximity to human settlements (Carricondo-Sanchez et al., 2020; Kaartinen et al., 2005) due to the higher human activity in those areas. After the hunting season, we expected wolf predation risk to increase closer to clearcuts and young forests, where moose are known to aggregate and forage during winter, and further away from bogs that do not provide food or cover. Lastly, we predicted wolf predation risk to decrease with proximity to secondary roads due to more snow accumulation on secondary roads than in the forest, which hinders movements when chasing moose. We predicted human hunting risk to be higher closer to bogs and roads and in flatter areas (low ruggedness) since hunters often rely on clear sightlines when shooting rifles. Lastly, we also expected hunting risk to be higher in the proximity to clearcuts and young forests. As a result of our predictions, we expected that the overall spatiotemporal risk patterns from wolves and hunters would contrast with one another.

MATERIALS AND METHODS

Study area

The study was performed across the Swedish–Norwegian border (60°33′–61°15′ N, 11°4′–12°55′ E), covering an area of 1699 km^2 in southeastern Norway and 969 km^2 in southwestern Sweden (Figure 1). The study area included two wolf territories and 106 hunting grounds (22 and 84 in Sweden and Norway, respectively). The moose population in our study area is partially migratory, moving from high-altitude ranges in summer to low-altitude ranges with less snow in winter. Pellet count surveys estimated the average winter density of moose within the study area to be 1.25 and 1.27 moose/km^2 in 2018/2019 and 2019/2020, respectively. Each year, moose hunting is managed by management units composed of several hunting teams within the same area (see Wikenros et al., 2020 for detailed information on how the Norwegian and Swedish hunting management system works). In our study area, the official hunting season started each year on the 25th of September and ended on the 23rd of December in Norway, whereas in Sweden, it began the first week of September and ended on the last day of February.

Wolves were declared functionally extinct in Scandinavia by the mid-1960s. In the 1980s, two individuals from the Finnish–Russian population reproduced in the study area and founded the current Scandinavian wolf population (Wabakken et al., 2001). In the winters of 2018/2019 and 2019/2020, the Scandinavian wolf population was estimated to 380 (95% CI = 300–494) and 450 (95% CI = 356–585) individuals, respectively (Svensson et al., 2019; Wabakken et al., 2020). Moose is the primary prey species of Scandinavian wolves and makes up more than 95% of their diet (Sand et al., 2005, 2008). During winter, approximately 70% of moose killed by wolves are calves (Sand et al., 2005). Within our study

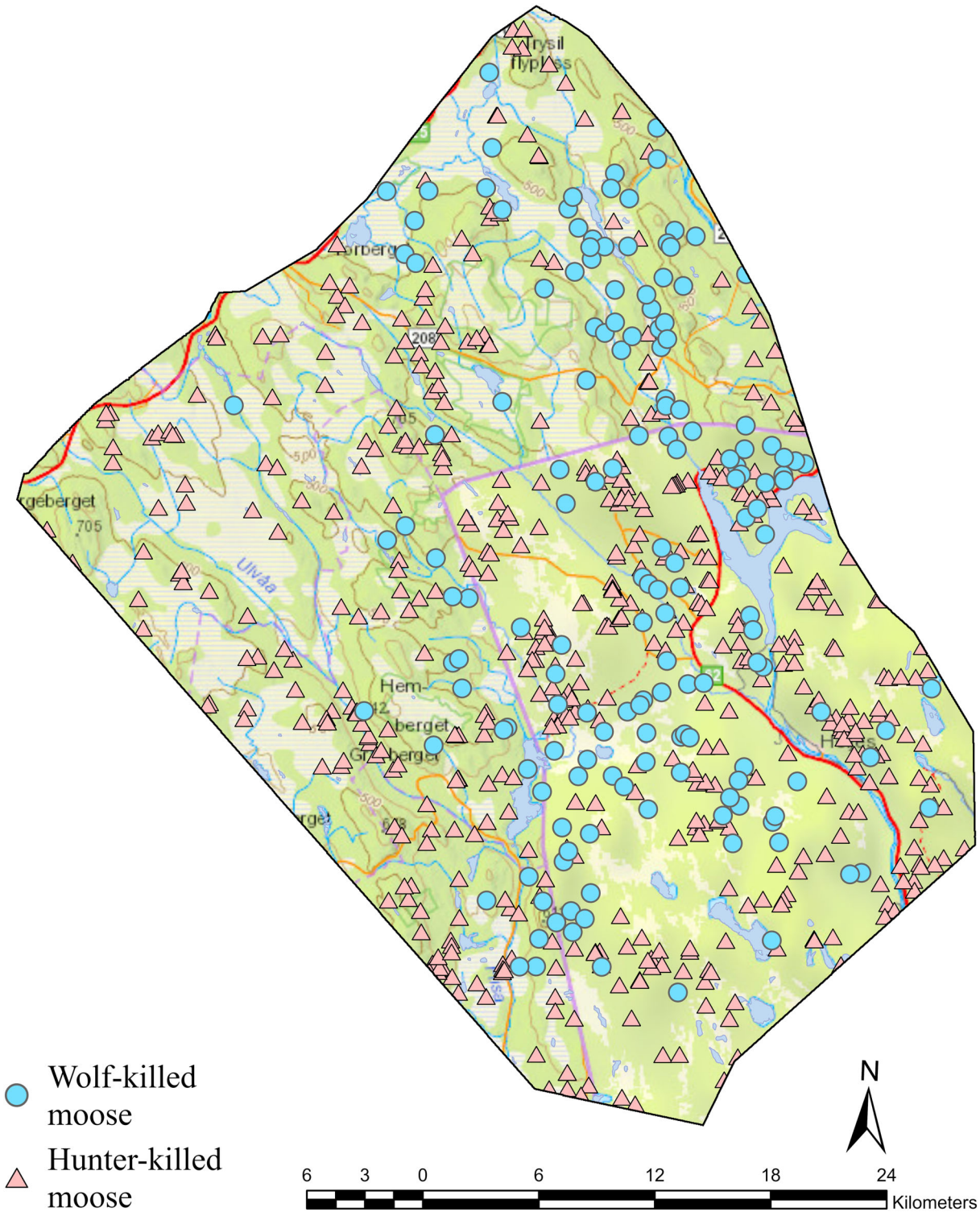

FIGURE 1 Locations of hunter-killed and wolf-killed moose within two wolf territories during two consecutive winters (2018/2019 and 2019/2020). Sites where hunters and wolves killed moose are represented by pink triangles and blue circles, respectively. The pink line denotes the border between Sweden and Norway.

area, four wolves (belonging to two packs) were equipped with GPS collars between 2017 and 2020. During winter 2018/2019, one pack consisted only of the alpha pair, whereas the other included the alpha pair and a puppy of the year (Svensson et al., 2019). During winter 2019/2020, the first pack included the alpha pair and possibly between three and five puppies, and the second pack only included the alpha pair (Wabakken et al., 2020).

Within our study area, the landscape is predominantly boreal forest, composed of Scots pine (*Pinus sylvestris*), Norway spruce (*Picea abies*), and a few deciduous species such as birch (*Betula* spp.) (Antonson, 2011; Christiansen, 2014; Statistisk Sentralbyrå, 2021). In general, snow covers the ground mainly between December and March. Intensive forestry has led to an extensive network of gravel roads, which, together with national and regional roads, resulted in a mean road density of 0.84 km/km^2 within the study area.

Data collection

We collected data on wolf predation and human harvest during fall (1 September–21 December) and winter (22 December–30 April) for two consecutive years (2018/2019 and 2019/2020). Data on moose density were collected for the winter period (October–May) of the same years.

Wolf predation

Wolves were located on snow and immobilized by darts from helicopters (see Arnemo & Evans, 2017; Sand et al., 2006, for details). Handling protocols fulfilled the ethical requirements for research on wild animals in Sweden (decision ID C281/6 and C315/6) and Norway (The Norwegian Food Safety Authority, decision ID 15370). The baseline programming of the collars was to acquire one position every four hours. We used data on wolf movement during predation studies carried out in the fall and winter of 2019 to create two models to identify potential fall and winter wolf kill sites from GPS positions using machine learning methods (Figure 1; see Appendix S1 for a full detailed description of the methods used and results obtained). Our machine learning models had an overall accuracy of 94% and 98% for fall and winter, respectively (see Appendix S1 for more details). Each identified kill site was also time-stamped using the time of the first recorded GPS position at the kill site. Using kill sites as a metric of predation risk is a widespread and well-established method (Gervasi et al., 2013; Hopcraft et al., 2005; Lone et al., 2014; Thaker et al., 2011).

Hunter harvest

We contacted and surveyed 106 hunting teams within our study area for the coordinates of all the moose harvested during the hunting seasons of 2018/2019 and 2019/2020 (Figure 1). Obtaining the exact time of the day when moose were shot proved to be very difficult, so we asked hunters to provide us with a time interval within which moose were shot. Since all moose were shot between 8.30 and 18, we used this interval for all shot moose.

Wolf utilization distribution

To estimate the seasonal spatial distribution of wolves, we developed population-level utilization distributions (UDs) during (1 September–15 January) and after (16 January–30 April) the hunting season for each wolf territory within our study area. Wolf GPS relocations were subsampled at 4-h intervals to eliminate possible bias resulting from unequal relocation intervals. When a wolf pack had the adult pair collared during the same period, we used the GPS fixes from the individual whose collar was functional for the maximum portion of the study period (primary individual), only adding data from the other adult individual during periods when the primary individual's collar was not operational. We used the amt package (Signer et al., 2019) to develop probabilistic UDs (250 × 250 m cell size) using kernel density estimates for each wolf pack during and after the hunting season. We then multiplied each pack UD by the number of observed wolves in the pack to account for variation in wolf pack size (range: 2–6 wolves).

Moose density

Pellet count survey is an indirect method to estimate spatial variation in ungulate density (Marques et al., 2001; Neff, 1968; Rönnegård et al., 2008; Smart et al., 2004). We used winter moose pellet count surveys conducted within our study area to calculate moose density and interpolated it over the whole study area (see Appendix S2 for a detailed description of the methods).

Environmental and anthropogenic variables

Explanatory landscape variables included terrain ruggedness, distance to forest and main roads, distance to clearcuts and young forests, building density, and distance to bogs. Terrain ruggedness (range: 0–68 m) was derived from a digital elevation map (DEM) with a pixel size of 25 m (Copernicus Land Monitoring Service, 2018). Terrain ruggedness expresses the amount of elevation difference between adjacent cells of a digital elevation map (Riley et al., 1999). Distance to forest (range: 0–2386 m) and main roads (range: 0–8319 m) was calculated as the shortest Euclidean distance to the nearest

secondary (roads coded with P in Norway and gravel roads in Sweden) and main road (roads coded with K, F, and R in Norway and paved roads in Sweden). Distance to young forests (range: 0–5231 m) was calculated as the shortest distance to the nearest young forest or clearcut as classified by the Corine Land Cover (CLC) inventory (Copernicus Land Monitoring Service, 2018). Building density was calculated as the number of buildings (houses, cabins, farms, and other buildings) per square kilometer and was obtained from Matrikkeldata (Norwegian Mapping Authority, 2004) and Lantmäteriet (2022; Sweden; www.lantmateriet.se). Distance to bogs (range: 0–1520 m) was calculated by merging Swedish (Sverige Terrängkartan) and Norwegian (N50) vector data on bogs and generating a Euclidean distance raster.

Statistical analyses

Assess the spatial predictors of wolf-kills

Using machine learning methods (see Appendix S1), we identified 162 kill sites from two wolf territories during two consecutive winters. We then divided wolf kill sites into two datasets based on two time intervals: during the moose hunting season (1 September–15 January; 100 kill sites) and after the moose hunting season (16 January–30 April; 62 kill sites). We used logistic regression within the framework of weighted distribution theory (WDT) to analyze the probability of being a kill site relative to a random location (Fithian & Hastie, 2013). This framework requires that a sufficient number of available points (hereafter, random points) is included in the analysis to ensure that parameter estimates converge to stable values (Warton & Shepherd, 2010). Additionally, Fithian and Hastie (2013) showed that giving "infinite weight" to random points also ensures convergence to stability. Fieberg et al. (2021) suggest assigning a weight of 1000 or more to each random location and a weight of 1 to the observed locations (hereafter, kill sites). To evaluate parameter stability, we fitted logistic regression models to datasets with an increasing number of random locations (from 1 to 100 per kill sites). The intercept decreased as the number of random points increased, but, on average, the slope estimates did not change much once we included at least 50 random locations per kill site. Hence, we concluded that using 50 available points per kill site was sufficient to interpret the slope coefficients. The kill sites were combined with points (1:50 ratio) sampled randomly from within the two wolf territories (generated using minimum convex polygons using the wolf GPS positions). Both kill sites and random locations were then annotated with the environmental and anthropogenic variables, which were then centered (mean = 0) and scaled (SD = 1) (Gelman & Hill, 2006). We also created an indicator variable, labeled "case," taking the value of 1 for the actual kill sites and 0 for the random points. We assigned a weight of 5000 to the random locations and a weight of 1 to all kill sites (Fieberg et al., 2021; Fithian & Hastie, 2013). We first built two univariate models, where moose density and wolf UD were used as sole predictors of the spatial distribution of kills. We then built a model with moose density and wolf UD together as predictors. Subsequently, to assess the influence of landscape features on the spatial distribution of kills, we added all of our landscape variables and used the function dredge from the MuMIn package (Barton & Barton, 2015) to test all possible combinations while retaining the effects of wolf and moose distributions. We then evaluated candidate models using Akaike information criterion (AIC) and retained the candidate model with the lowest ΔAIC (Table 1). Multicollinearity was tested using the performance package (Lüdecke et al., 2021) in R (R Core Team, 2013, version 1.4.1717) and variables where $r \geq 0.5$ were never present in the same model.

We quantified relative predation risk during and after the hunting season at a given location in relation to the reference probability of a kill event based on the mean values for our landscape variables within the domain of availability (referred to as a reference vector; see Kauffman et al., 2007 for more details on the procedure). We obtained the odds ratio for a given location (25 × 25 m cell) within our study area using the following equation (Keating & Cherry, 2004):

$$\psi(x|x_R) = \exp\left[\beta_1(x_1 - x_{1R}) + \cdots + \beta_n(x_n - x_{nR})\right],$$

where β_1 corresponds to the coefficient of the first covariate in the top model and so on for all the covariates, x_1 is the first covariate's value at a given location (25 × 25 m cell), and x_{1R} is the mean value for that covariate across our study area. If the top model did not include moose density or wolf space use, we added them to the model used to create the odds ratio, as we wanted to account for differences in moose and wolf distribution in the landscape. The resulting odds ratio can be interpreted as relative predation risk, where $\psi(x|x_R) = 1$ indicates no difference in the probability of a kill event between a given location i and the mean kill probability on the landscape (reference), whereas $\psi(x|x_R) = 5$ denotes a kill probability five times greater than the average probability in the landscape. We then plotted the odds ratios for wolf predation risk over the entire study area (Figure 2a,b).

TABLE 1 Generalized linear models used to investigate the effect of environmental (distance to clearcut, distance to bogs, and terrain ruggedness), anthropogenic (distance to main and secondary roads, and building density) on the probability of a hunter-killed moose, wolf-killed moose (during and after the hunting season), and to compare hunter-killed versus wolf-killed moose.

Dataset	Model	df	ΔAIC	w_i
Hunter-killed moose	Build + distfor + distmain + moose + rug + distbog + distcl	7	0.00	0.666
	Moose	2	49.96	<0.001
	Intercept-only	1	71.63	<0.001
Wolf-killed moose				
Hunting season	Wolf + distcl + distbog + build	5	0.00	0.158
	Wolf + distcl + distbog + build + rug	6	0.28	0.138
	Wolf + distcl + distbog + build + moose	6	1.33	0.081
	Wolf + distcl + distbog + build + distmain	6	1.93	0.060
	Wolf + distcl + distbog + build + moose + rug	7	1.99	0.059
	Wolf	2	19.11	<0.001
	Moose	2	53.06	0.000
	Wolf + moose	3	20.98	<0.001
	Intercept-only	1	51.12	<0.001
After hunting season	Wolf + distcl + build + moose + distmain + rug	7	0.00	0.139
	Wolf + distcl + build + moose + distmain + rug + distbog	8	0.35	0.123
	Wolf + distcl + build + moose + distmain + rug + distfor	8	0.45	0.074
	Wolf + distcl + build + moose + distmain + rug + distbog + distfor	9	0.90	0.059
	Wolf + distcl + moose + distmain + rug + distbog + distfor	7	1.51	0.058
	Wolf + distcl + moose + distmain + rug	6	1.75	0.055
	Wolf + distcl + build + distmain + rug	6	1.93	0.053
	Wolf	2	23.38	<0.000
	Moose	2	97.99	<0.00
	Wolf + moose	3	24.24	<0.001
	Intercept-only	1	108.47	<0.001
Comparison hunter–wolf	Build + distbog + distcl + distmain + rug	7	0.00	0.164
	Build + distbog + distcl + distfor + distmain + rug	8	0.80	0.109
	Build + distbog + rug	5	0.88	0.106
	Build + distbog + distcl + rug	6	0.91	0.104
	Build + distbog + distmain + rug	6	1.12	0.093
	Build + distbog + distcl + distfor + rug	7	1.69	0.070
	Intercept-only	1	38.33	<0.001

Note: The first three analyses were conducted using actual kill sites (coded as 1) in comparison to random locations (coded as 0) in Scandinavia during two consecutive winters (2018/2019 and 2019/2020). The fourth analysis was carried out using wolf-killed moose (coded as 0) and hunter-killed moose (coded as 1). For each model, degrees of freedom (df), difference in Akaike information criterion (AIC)/AIC relative to the highest-ranked model (ΔAIC/AIC), and AIC weights (w_i) are displayed. Models with ΔAIC/AIC ≤ 2, univariate models for moose density and wolf space use, and intercept-only models are shown. See Table 2 for the estimates and standard errors of the top-ranked models in each analysis.

Assessing the spatial predictors of hunter-kills

The same WDT and logistic regression analysis were carried out with the hunter-killed moose dataset. We also found that using 50 random points per hunter-kills ensured parameter stability. We first developed a univariate model for moose density and then used the function dredge from the MuMIn

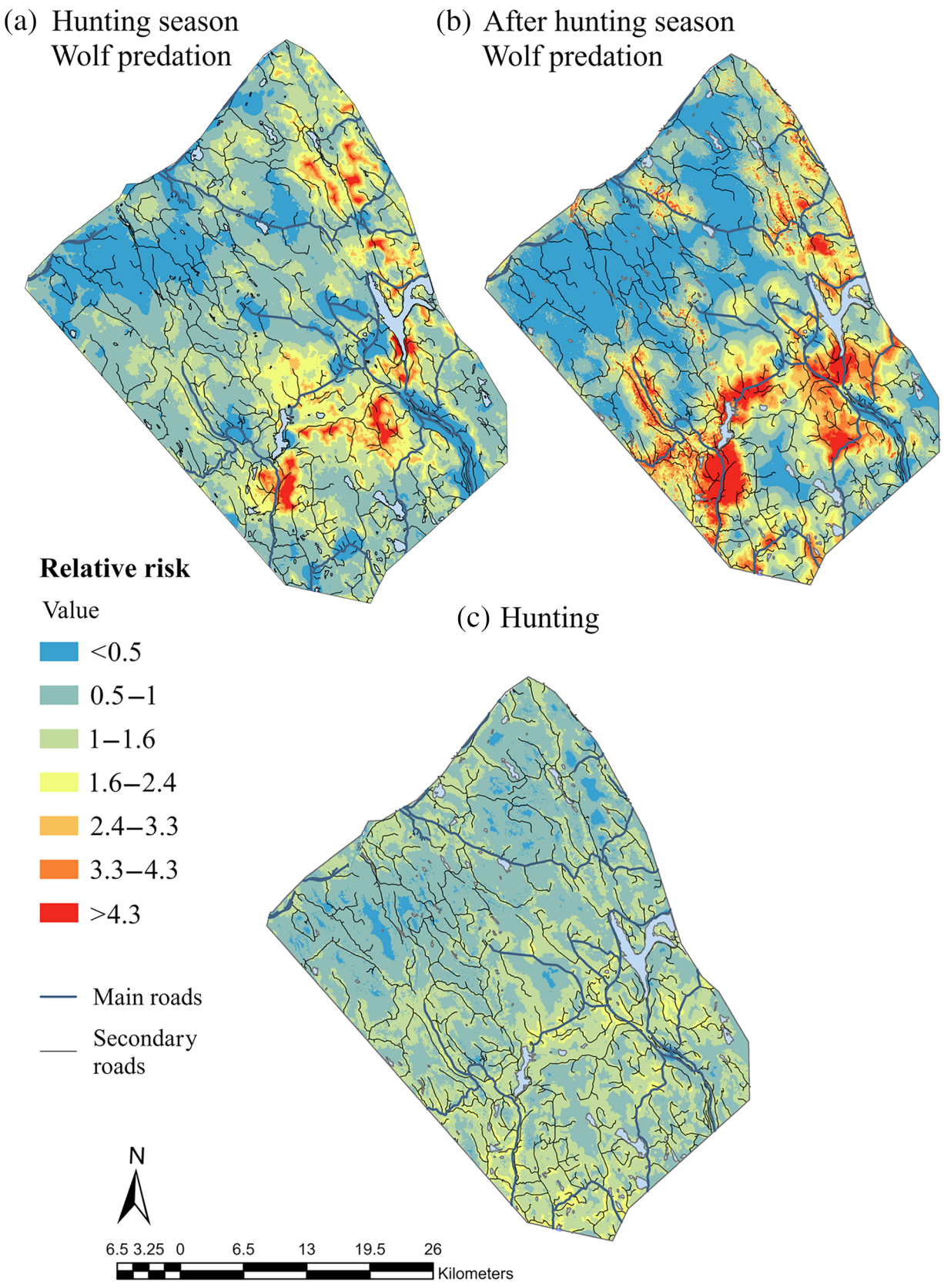

FIGURE 2 Cross-border predicted risk maps for relative wolf predation (a) during and (b) after the hunting season and for relative hunting risk (c). A value of 5 indicates that there is a five times higher predation risk than average in that location, whereas a value of 0.5 denotes 50% of the average risk. The coefficients of the top-ranked models for each analysis (hunter-killed moose and wolf-killed moose during and after the hunting season) were used to create the predicted risk maps.

package (Barton & Barton, 2015) to test all possible combinations of our landscape variables (while retaining moose distribution). We then evaluated candidate models using AIC and retained the candidate model with the lowest ΔAIC (Table 1). We then quantified and plotted the odds ratio of being shot by a hunter using the same method described for the wolf-killed moose (Figure 2c).

Wolf-kills versus hunter-kills

We selected wolf ($n = 100$) and hunting ($n = 608$) kill sites from overlapping time periods and excluded all hunting sites outside the wolf territories. We coded wolf kill sites as 0 and hunting kill sites as 1 and modeled the relative probability of a site being a hunting kill site compared with a wolf kill site using generalized linear models. Values below 0.5 and approaching 0 indicate a higher probability of a wolf-killed moose, whereas values above 0.5 and approaching 1 would mean a higher probability of a hunter-killed moose. We included the same landscape variables as above as explanatory variables.

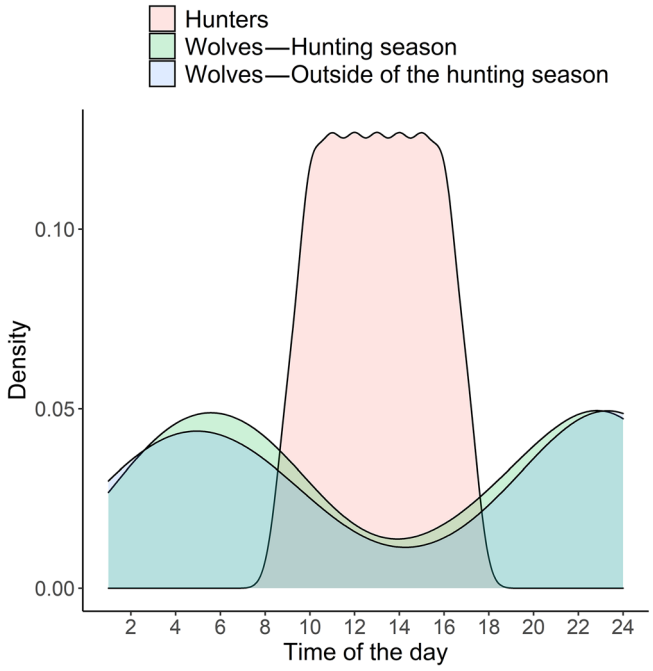

FIGURE 3 Diel distribution of hunter-killed and wolf-killed moose during and after the moose hunting season in south-central Scandinavia during two consecutive winters (2018/2019 and 2019/2020).

RESULTS

Temporal distribution of hunter-killed and wolf-killed moose

According to our survey, hunters shot moose between 8.30 in the morning and 18 in the evening (Figure 3). Wolves killed 84% and 80% of moose at nighttime during and after the hunting season, respectively (Figure 3).

Predictors of relative wolf predation risk

During the hunting season, the top model predicted relative wolf predation risk to decrease with increasing building density and distance to clearcuts and young forests but increase with increasing wolf utilization and distance to bogs (Figure 4, Tables 1 and 2). After the hunting season, the top model showed that relative wolf predation risk increased with increasing moose density, wolf utilization, and terrain ruggedness but decreased with increasing building density, distance to main roads, and distance to clearcuts and young forests (Figure 5, Tables 1 and 2). The top models including our landscape covariates outperformed the moose and wolf space use models.

Predictor of relative hunting risk

The top model predicted relative hunting risk to increase with increasing moose density, but to decrease with increasing building density, distance to clearcuts and young forests, terrain ruggedness, distance to bogs, and distance to main and secondary roads (Figure 6, Tables 1 and 2). The top model including landscape covariates outperformed the moose model.

Contrasting or overlapping risks of wolf predation and human hunting

The top model predicted that the probability of a hunter-killed moose in relation to a wolf-killed moose to increase with increasing building density but decrease with increasing distance to bog, terrain ruggedness, and distance to main roads (Figure 7, Tables 1 and 2).

DISCUSSION

Predictor of relative wolf predation risk

We found that both during and after the hunting season, landscape variables influenced the occurrence of wolf

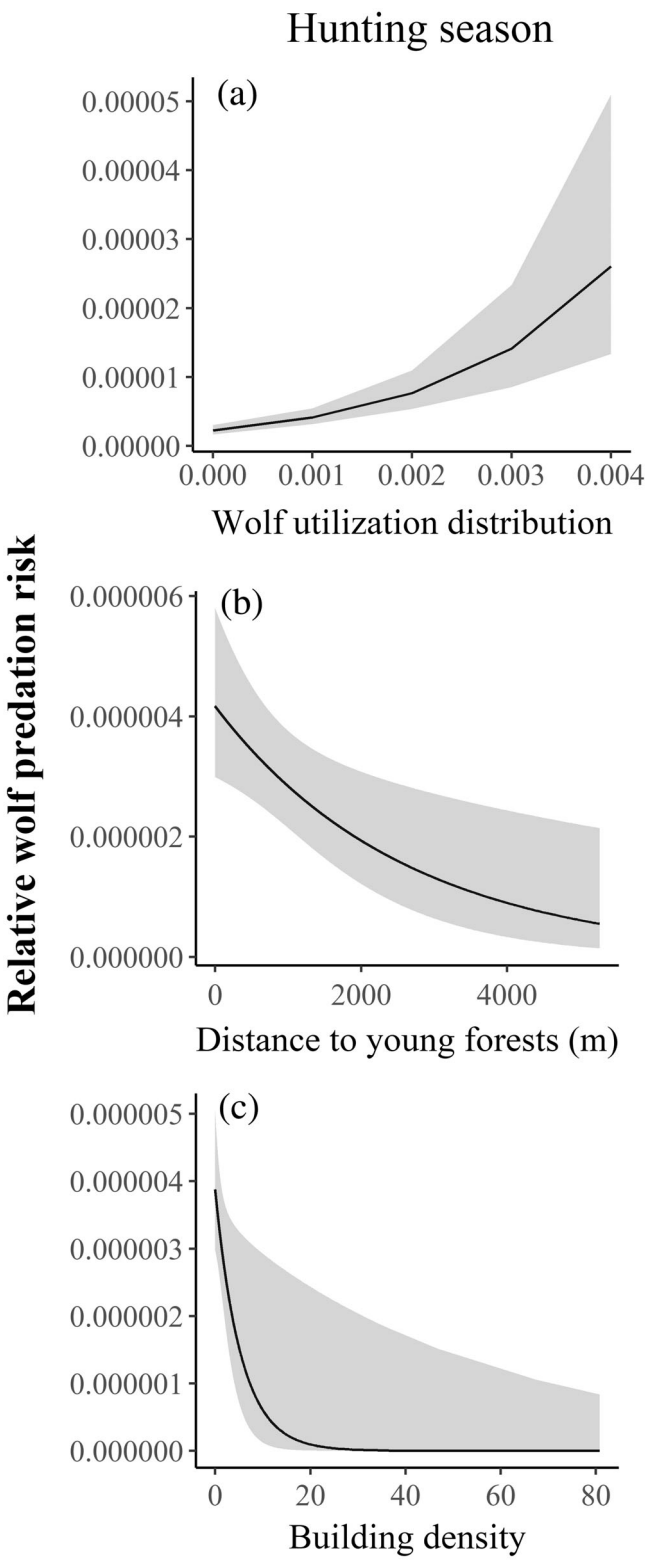

FIGURE 4 Relative wolf predation risk of moose in relation to (a) wolf space use; (b) distance to clearcuts and young forests (abbreviated to "distance to young forest"); and (c) building density during the moose hunting season. The relative wolf predation risk was calculated using actual wolf-killed sites in relation to random locations in the study area. The data were collected from 1 September to 15 January in 2018/2019 and 2019/2020 in south-central Scandinavia.

kill sites, even after accounting for the distribution of predator and prey. This suggests that environmental and anthropogenic features mediate predation by shaping wolf–moose encounter occurrence and outcome (Kauffman et al., 2007). First, during the hunting season, predation risk increased with the time spent by wolves in a given area of their territory but was not affected by moose density. Second, we found that relative wolf predation risk was higher farther away from human settlements and bogs but closer to clearcuts and young forests. Previous findings from Scandinavia showed that wolves select areas further away from buildings (Carricondo-Sanchez et al., 2020; Ordiz et al., 2020). This may indirectly suggest that wolves also avoid killing in the proximity of human attributes (Kunkel & Pletscher, 2000; Torretta et al., 2018). Our finding that bogs represent less risky places for moose is similar to those of Gervasi et al. (2013). We hypothesize that this pattern may arise from a combination of moose avoiding bogs (Nikula et al., 2004) but also the fact that during the hunting season, bogs are generally wet and may therefore be more energetically costly to move through, making it more difficult for wolves to chase and attack a moose successfully. Lastly, we found that clearcuts and young forests were riskier places for moose (Gervasi et al., 2013). Clearcuts and early successional pine plantations are usually open spaces that moose select (Gundersen, 2003; Månsson, 2009) and wolves might actively search for moose in these areas. We accounted for this by including moose density and wolf space use as covariates, but despite this, we still found that clearcuts and young forests were riskier habitats, probably because open spaces increase visibility and favor the cursorial hunting mode of wolves.

After the hunting season, the top model showed that relative wolf predation risk increased with increasing moose density, wolf utilization, and terrain ruggedness but decreased with increasing building density, distance to main roads, and distance to clearcuts and young forests (Figure 5, Tables 1 and 2). The top models including our landscape covariates outperformed the moose and wolf distribution models.

Similarly to during the hunting season, we found that wolf predation risk after the hunting season was positively correlated with wolf space use and negatively with building density and distance to clearcuts and young forests. We also found that wolf predation risk was higher in areas of higher moose density, more rugged terrain, and closer to main roads. These patterns may be explained by changes in landscape productivity and snow conditions, which influence moose distribution and wolf movements. In winter, moose in our study area migrate to areas of lower elevation, where food availability increases and snow depth decreases (Allen et al., 2016; Singh et al., 2012), aggregating even more in young pine forests

TABLE 2 Scaled estimates and standard errors of the top-ranked models in the wolf-killed, hunter-killed, and hunt versus wolf analyses.

	Wolf-killed							
	Hunt		After		Hunter-killed		Comparison hunt–wolf	
Explanatory variables	β	SE	β	SE	β	SE	β	SE
Terrain ruggedness	...	...	0.30	0.09	−0.14	0.05	−0.31	0.09
Distance to secondary roads	...	...	...	...	−0.17	0.04	...	...
Distance to main roads	...	...	−0.57	0.20	−0.11	0.04	−0.27	0.11
Distance to young forest	−0.36	0.14	−0.78	0.25	−0.12	0.05	...	...
Building density	−0.75	0.34	−0.36	0.23	−0.09	0.04	0.92	0.36
Distance to bogs	0.22	0.07	...	...	−0.19	0.05	−0.41	0.10
Moose density	−0.09	0.11	0.33	0.17	0.56	0.18	Excl	Excl
Wolf space use	0.37	0.06	0.45	0.04	Excl	Excl	Excl	Excl

Note: Variables excluded from the analyses are referred to as "Excl," whereas those not included in the top model are denoted with an ellipsis. The data were collected in two consecutive winters (2018 and 2019) in south-central Scandinavia.

(Gundersen, 2003) compared with early and late fall. This leads to a less homogeneous moose distribution in the landscape during winter, and wolves might select areas with higher moose density to increase the encounter rate, leading to an overall higher wolf predation risk. Moreover, more rugged terrain may facilitate traveling and sneaking upon a moose to initiate a surprise attack since rougher terrain holds less snow than smoother terrain (Lehning et al., 2011). Lastly, relative wolf predation risk was higher closer to main roads, most likely due to their placement along valley bottoms with reduced snow accumulation and higher moose density.

Because we accounted for the distribution of predator and prey, these findings suggest that landscape and anthropogenic features are important factors shaping interactions between wolves and moose, hence mediating predation in the landscape (Hebblewhite et al., 2005; Kauffman et al., 2007). The spatial variability in wolf predation risk may indicate the existence of habitat patches within the physical landscape that favor either the hunting or killing of moose by wolves.

Predictor of hunting risk

We found that habitat characteristics and topography influenced where hunters killed moose in the landscape. Accounting for moose density, relative hunting risk increased with moose density but decreased with increasing distance to bogs, distance to clearcuts and young forests, terrain ruggedness, building density, and distance to main and secondary roads. Some of these results are in accordance with previous studies and indicate that hunters predominantly kill moose in open terrains (e.g., bogs, clearcuts) (Ciuti et al., 2012; Lone et al., 2014) or in proximity to roads (Perry et al., 2020; Proffitt et al., 2013) and in areas characterized by low terrain ruggedness (Perry et al., 2020). The negative correlation between the occurrence of hunter-killed moose and building density is probably due to the highly skewed distribution of human settlements within our study area. Building density is relatively low across the study area and increases rapidly only in more populated towns, where hunting is not practiced. In other words, we found that open habitats favor hunting, most likely due to increased visibility and safety reasons associated with rifles and long-distance shooting. Hunting in the proximity of roads may also be beneficial because it facilitates the logistics of placing hunting towers in strategic places where moose might travel and transporting hunter-killed moose with motorized vehicles.

Even when accounting for moose density, the significant effect of habitat and topography may suggest that favorable hunting grounds, where the existing topography and habitat facilitate moose hunting, exist in our study area. However, extensive human forest management modifies habitats that are likely to increase hunting success (e.g., thinning and clearing practices), which may result in a more homogenous distribution of the risk of being shot compared with the risk of being killed by wolves. Hunters can also choose among various hunting methods (e.g., stalking, dogs, beats), which can increase encounter rate and hunting success (Andersen et al., 2007). Depending on the hunting method used, landscape features may have more or less pronounced or different effects on the probability of a moose being shot (Norum et al., 2015). These differences indicate that the spatial

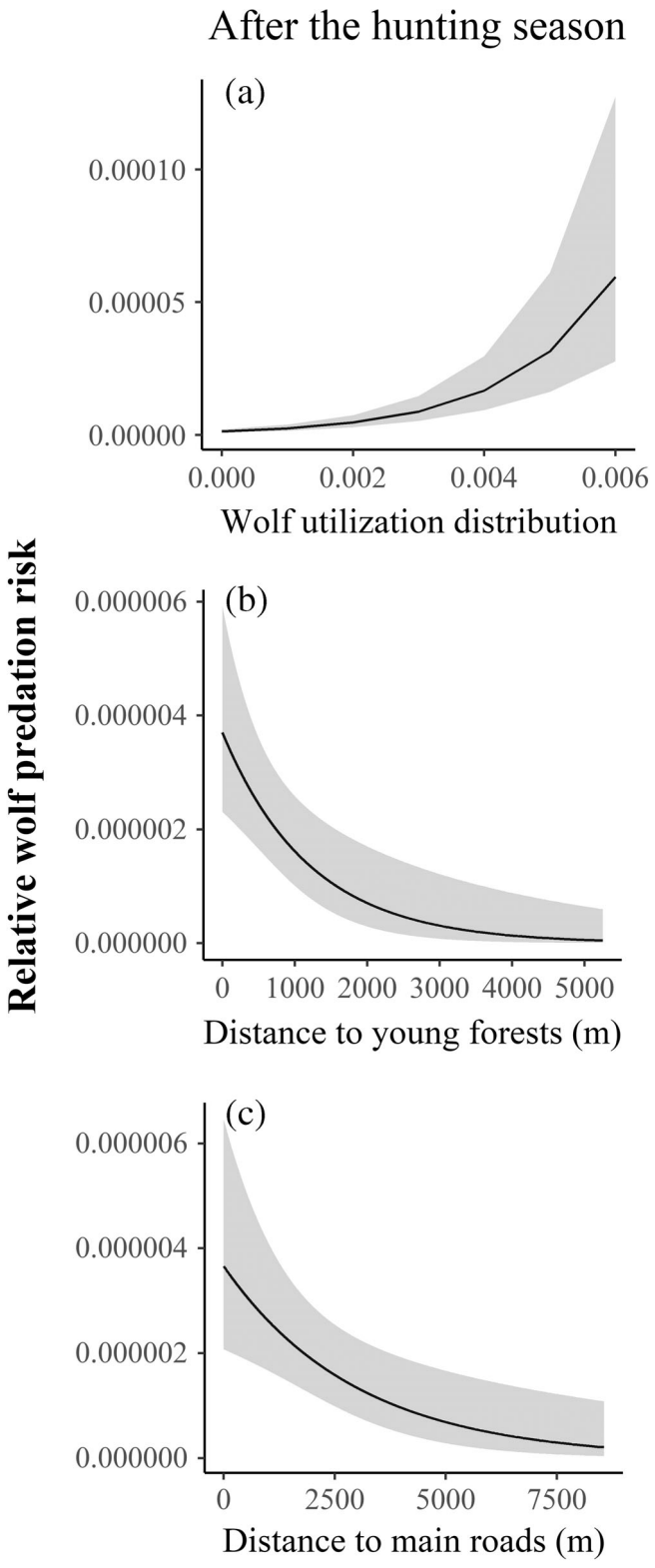

FIGURE 5 Relative wolf predation risk of moose in relation to (a) wolf space use; (b) distance to clearcuts and young forests (abbreviated to "distance to young forest"); and (c) distance to main roads after the hunting season. The relative wolf predation risk was calculated using actual wolf-killed sites in relation to random locations in the study area. The data were collected from 1 September to 15 January in 2018/2019 and 2019/2020 in south-central Scandinavia.

patterns of hunting risk may vary depending on the hunting method used to hunt moose (see Norum et al., 2015).

Contrasting risk of wolf predation and human hunting

Spatial risk patterns from humans and large carnivores often depend on how their hunting modes differ and interact with the physical environment (Atwood et al., 2007; Gaynor et al., 2021; Miller et al., 2014; Preisser et al., 2007). As a result, the spatial patterns of accumulated risks from hunters and large carnivores can overlap or contrast. In the Scandinavian system, we found that the spatial patterns of predation risk for moose from hunters and wolves contrasted with one another in relation to the physical landscape. This is most likely a consequence of the different hunting methods employed by hunters and wolves. Wolves are cursorial predators that can chase moose for long distances (Mech et al., 2015), whereas hunters can employ a wide range of strategies like calling and stalking. Still, the most common in Scandinavia is the use of unleashed dogs to find and push moose toward sit-and-wait hunters situated at predetermined spots in the landscape. As a result of these differences in hunting modes, the chance of a successful hunt for wolves and humans depends on habitat and anthropogenic features (Ciuti et al., 2012; Farmer et al., 2006; Kauffman et al., 2007). Hunters are often limited by visibility and safety constraints, requiring open areas to shoot safely, like bogs. Terrain ruggedness may help wolves sneak on moose while restricting hunters' access either by foot or motorized vehicles to transport shot moose. Hunters rely on main roads and proximity to human settlements for ease of transport and handling of shot moose, whereas wolves might avoid killing in the proximity of main roads and human buildings due to high anthropogenic activity during the hunting season. These results are partially consistent with our findings on the probability of being killed by wolves and hunters relative to random locations, supporting the contrasting spatial patterns of risk imposed by the different hunting modes of hunters and wolves.

In such a system with contrasting spatial risk, prey might find it difficult to spatially avoid all predators (Atwood et al., 2009; Cresswell & Quinn, 2013; Theuerkauf & Rouys, 2008). Prey species often respond to risk from predators that provide more reliable cues (Makin et al., 2017), and hunters are generally more conspicuous in the landscape than wolves. Additionally, avoiding certain habitats to decrease predation from one predator may lead to increased exposure to other predators, a phenomenon known as risk enhancement

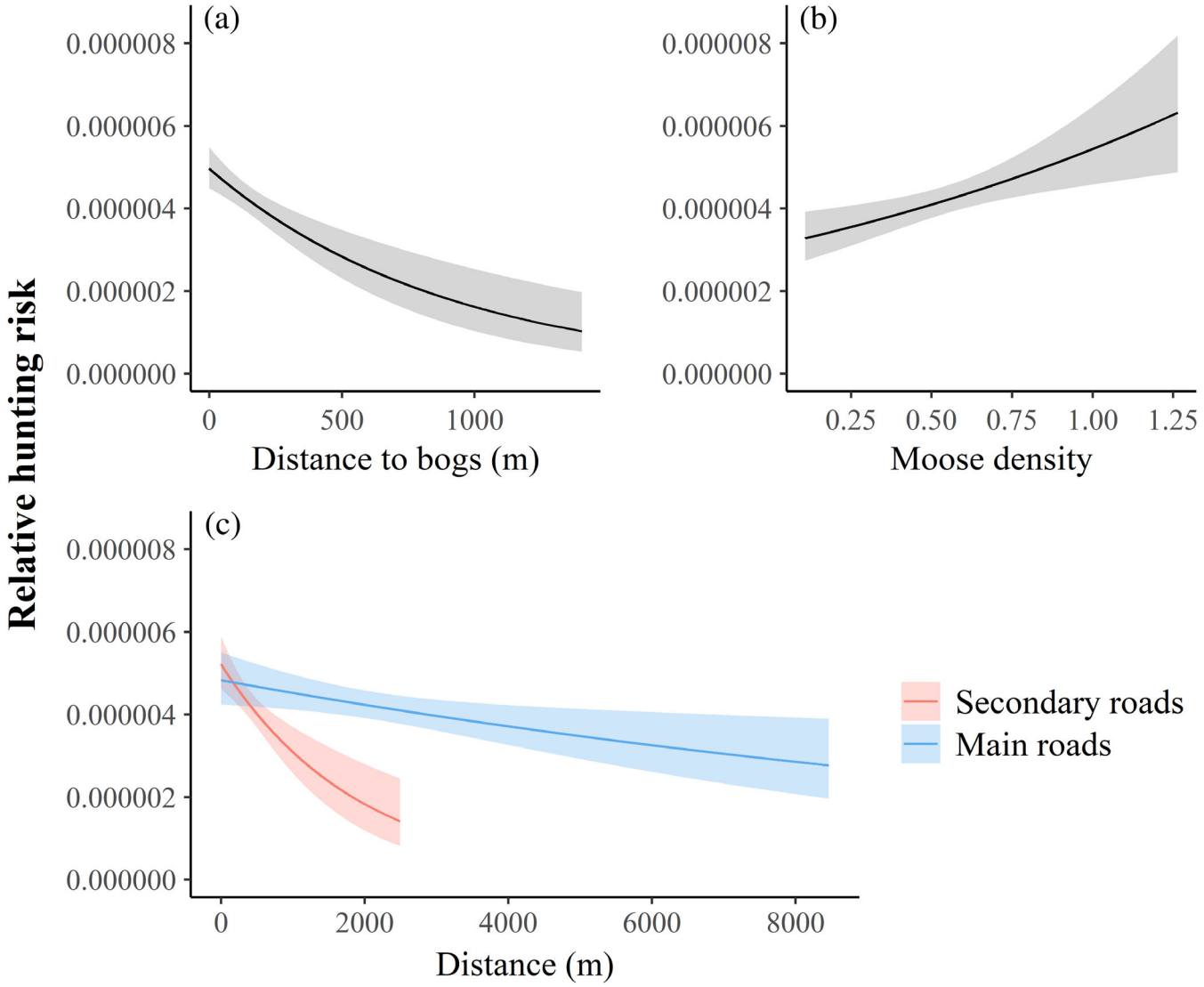

FIGURE 6 Relative hunting risk of moose in relation to (a) distance to bogs, (b) moose density, and (c) distance to secondary (red) and main (blue) roads. The relative hunting risk was calculated using actual hunter-killed sites in relation to random locations in the study area. The data were collected from 1 September to 15 January in 2018/2019 and 2019/2020 in south-central Scandinavia.

(Sih et al., 1998). For instance, elk moving into denser cover to avoid wolf predation exposed themselves more to cougar (*Puma concolor*) predation (Atwood et al., 2007). Moreover, Gehr et al. (2018) found that avoiding areas associated with higher hunting risk resulted in increased exposure to lynx predation for roe deer (*Capreolus capreolus*). Therefore, when risk patterns from multiple predators are spatially contrasting, focusing solely on spatial avoidance may prove inefficient. If, however, we consider that different predators are active at different times of the day, or that one predator may avoid diurnal human activity (Atwood et al., 2009; Cresswell & Quinn, 2013; Morosinotto et al., 2010) prey may instead focus on temporal avoidance, without necessarily increasing the risk of predation from the other predator (Kohl et al., 2019). In our study, wolves killed moose predominantly at night both during and after the hunting season, whereas hunters were restricted to hunting during the day and only during the hunting season. Therefore, the wolf predation risk maps (Figure 2a,b) most likely represent the distribution of risk during night both during and after the hunting season, whereas the hunting risk represents the distribution of risk during the day but only during the hunting season (Figure 2). When risks from predators are contrasting in time as well, prey species can take advantage of temporally vacant hunting domains (Gaynor et al., 2021; Kohl et al., 2019). This temporal segregation might therefore provide prey with the opportunity to adjust their antipredator behaviors only during risky times

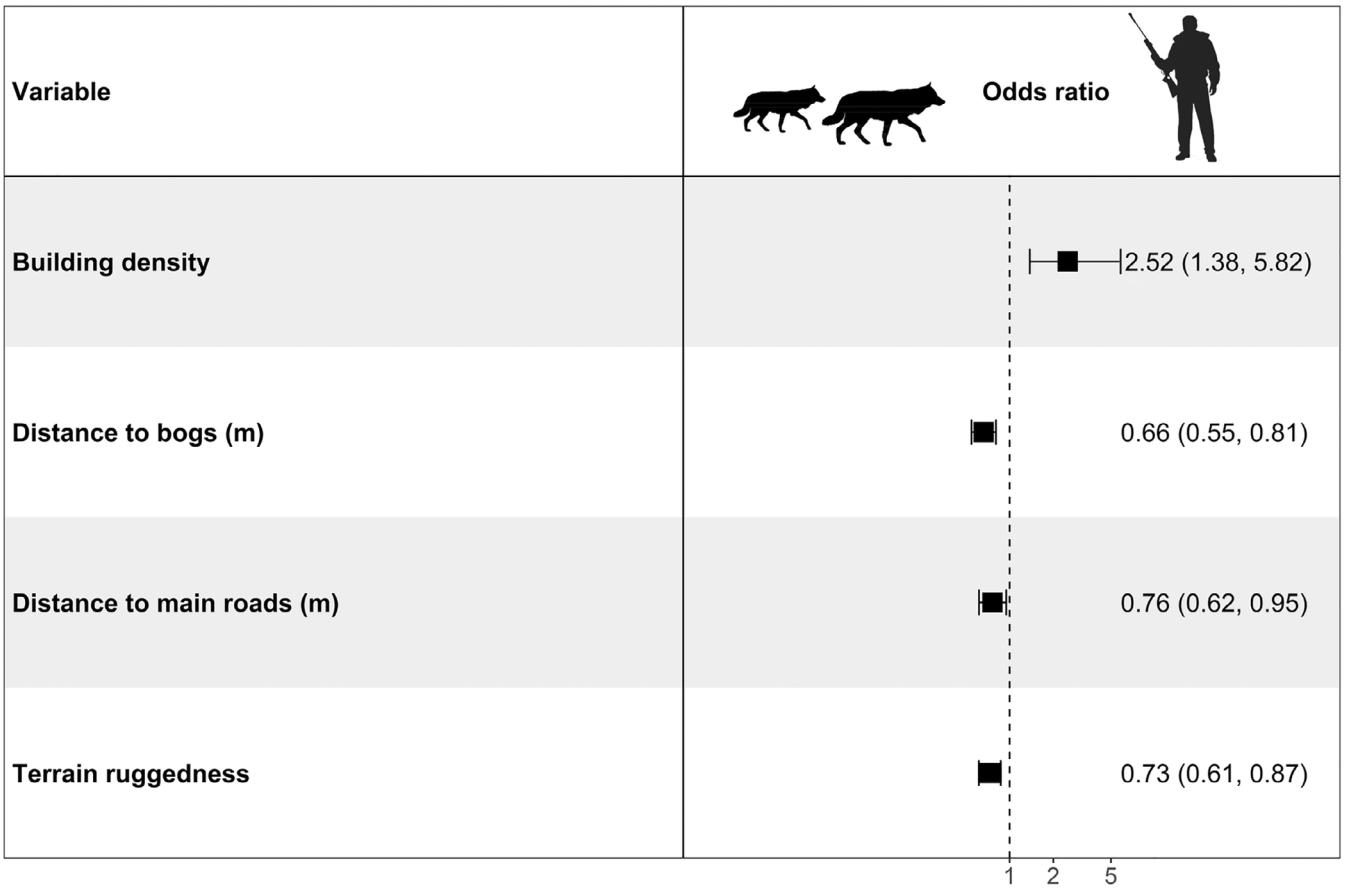

FIGURE 7 Odds ratios showing how the relative probability of a hunter-killed moose versus wolf-killed moose relates to different landscape variables. Estimates falling on the right side of 1 indicate a positive relationship (more likely to be a hunter-killed moose), whereas the left side shows a negative relationship (more likely to be a wolf-killed moose). The relative probability of a hunter-killed moose versus wolf-killed moose was measured using wolf- and hunter-killed moose locations within two wolf territories during two consecutive hunting seasons (September–January) in 2018 and 2019 in south-central Scandinavia. Silhouette credits: Colourbox.com/Illustrators: 81789 and 1594.

(Kuijper et al., 2016; Lone et al., 2015; Sönnichsen et al., 2013). For instance, the risk effects imposed by human hunters can be expected to be the main determinant of prey responses during the day during hunting season, while decreasing in importance in areas and at times when hunting is not permitted (Kuijper et al., 2016). On the other hand, the risk of wolf predation persists over the year and may become, in the absence of hunter harvest, the most dominant source of mortality for moose in late winter (January–April).

In this study, we focused on investigating how landscape and anthropogenic features influenced the spatial patterns of hunting risk and wolf predation risk during and after the hunting season and whether the accumulated risk from hunters and wolves resulted in contrasting or overlapping risks as a consequence of different hunting methods and requirements. Future studies should investigate whether moose respond to fluctuating hunting and wolf predation risk by taking advantage of temporal vacant hunting domains. This would allow disentangling possible behavioral changes in prey associated with temporal shifts in predator distribution and lethality.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data and R code (Ausilio et al., 2022) are available from Dryad: https://doi.org/10.5061/dryad.v41ns1rzf.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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