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A Game of Risk: Human Activities Shape Roe Deer Spatial Behavior in Presence of Wolves in the Southwestern Alps

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Abstract: In human-dominated landscapes, human activities shape prey spatial behavior, creating complex landscapes of risks. We investigated habitat selection of roe deer using resource selection functions in a human-dominated mountain system located in the southwestern Alps, characterized by a high presence of wolves and human disturbance. Our study aimed to assess how the interplay of hunting, presence of infrastructures, and recreational activities in the presence of wolves influenced roe deer spatial responses inside and outside a protected area. We documented that during the hunting period, roe deer increased selection of high-wolf-density areas, with the strongest effect observed during wild boar drive hunts, supporting the risk enhancement hypothesis, where avoiding one predator increases exposure to another, and highlighting the temporary yet significant impact of hunting on predator–prey dynamics. During the period of the wild boar drive hunt, roe deer also showed stronger selection for proximity to buildings, supporting the human shield hypothesis. Protected areas had an increased effect on roe deer avoidance of trails, where hiking and recreational activities are more concentrated. Our findings revealed the complex trade-offs that roe deer face in navigating multiple risks within human-modified landscapes, important for the development of effective conservation and human sustainability strategies.

Keywords: human disturbance; landscape of fear; human shield; risk enhancement; human–wildlife interactions

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Academic Editor: Li Zhang

Received: 18 January 2025
Revised: 31 January 2025
Accepted: 1 February 2025
Published: 5 February 2025

Citation: Ruco, V.; Marucco, F. A Game of Risk: Human Activities Shape Roe Deer Spatial Behavior in Presence of Wolves in the Southwestern Alps. *Diversity* **2025**, *17*, 115. https://doi.org/10.3390/d17020115

1. Introduction

Anthropogenic use of the landscape has substantially restructured natural ecosystems, causing not only habitat loss and fragmentation [1], but also species declines as well as changes in the interactions among species [2,3]. Humans and their activities have assumed an important role in shaping ecological communities [4,5], introducing additional complexity to the relationships between predators and prey [6]. Wildlife increasingly faces the challenge of navigating human-altered environments [1], with animals adapting in various ways to the presence of human activities [7,8]. Beyond inducing direct wildlife mortality, human activities such as hunting, land modification, infrastructure development, and recreational use reshape landscapes of fear in ways that can affect habitat selection and activity patterns of prey and predators, as well as antipredator behaviors [9,10].

Ungulates have to navigate spatiotemporal risks from both humans and natural predators in heterogeneous habitats [11]. In the case of highly anthropized environments, the complexity of the interplay of human–prey–predator interactions is exacerbated. Prey avoiding one risk might increase their vulnerability to another, a phenomenon known as risk enhancement [12,13], or prey may select for proximity to human features as a shield to minimize risk [14]. Wildlife species respond to human activities in complex spatial ways, influenced by the type, intensity, and frequency of disturbance [15,16], as in the case of recreational activities or hunting.

Hunters employ specific strategies to optimize hunting efficiency, which interact with different habitat characteristics and anthropogenic features within the landscape and affect prey spatial behavior [17,18]. Hunters typically rely on different approaches depending on the target game species but are generally restricted to daylight hours and specific periods over the year. Human linear features, such as roads and trails, create additional risks to wildlife also by intensifying human access to remote areas, which may indirectly alter species interactions [19]. These features are also used for various types of recreation, ranging from activities such as hiking and biking to motorized activities [20]. Non-consumptive outdoor recreation can have significant behavioral effects on wildlife, including ungulates, through spatial avoidance [21], increased movement speeds [22], or shifts in diel activity patterns [23]. For example, in a study on red deer and sheep interaction, both species were more likely to be detected further from the path during the day, suggesting that hiking pressure influenced spatio-temporal interactions [24]. Outdoor activities like hiking and biking also induced avoidance responses in wapiti [25,26] and chamois, with higher intensity in popular recreational areas, such as natural protected areas [27]. In other cases, human infrastructures have been used by prey as shields to predation risks [14,28]. Hence, in human-dominated landscapes, there is a need to understand the complexity of the spatial interactions of prey, natural predators, and human activities to allow management decisions that optimize long-term sustainability.

Our study investigates the spatial interplay of the effects of human disturbance and predator presence on roe deer spatial behavior, inside and outside a natural protected area. Roe deer provides an excellent model species for studying these dynamics, given that it is widely spread and abundant in Europe [29–31] and in the area of study [32], where it is the main hunted species for both hunters and wolves [33], and demonstrates high tolerance and plasticity for anthropogenic disturbances [34]. By quantifying the spatial and temporal effects of combined human activities and wolf presence spatial risks, we aim to investigate how spatial variation in human disturbance, arising from both recreational activities and hunting, affects roe deer habitat selection in and outside a protected area, providing key insights for conservation and wildlife management in heavily human-impacted landscapes.

2. Materials and Methods

2.1. Study Areas and Data Collection

The study area was located in a mountainous region in the southwestern Alps, Italy (44°21′ N, 7°66′ W in EPSG:4326, WGS84) (Figure 1), ranging in elevation from 270 to 2160 m. The landscape is predominantly forested (59%, mainly deciduous), with open habitats (12%) and urbanized areas (29%). Part of the study area lies within the Marguareis Natural Park (PNM, 80.4 km^2), where ecotourism is highly developed and actively promoted. Hunting is prohibited within the protected area, while outside it is regulated by national law within a Hunting District following the guidance documents of the Regional Administration of Piedmont (Figure 1a). Between September and January, two main game species are hunted: wild boar, primarily through collective drive hunts, and roe deer, with single hunters using a sit-and-wait strategy. Roe deer, reintroduced into the study area in the late 1980s for both hunting and conservation purposes, are now widely distributed throughout the region. Wild boar began recolonizing the area in the 1990s. Roe deer were documented to be the most frequently recorded ungulate species on a simultaneous camera trap study conducted in the same area [32], with an estimated occupancy of 0.91 (SE = 0.03) over 56 sites [35], which indicates their wide distribution.

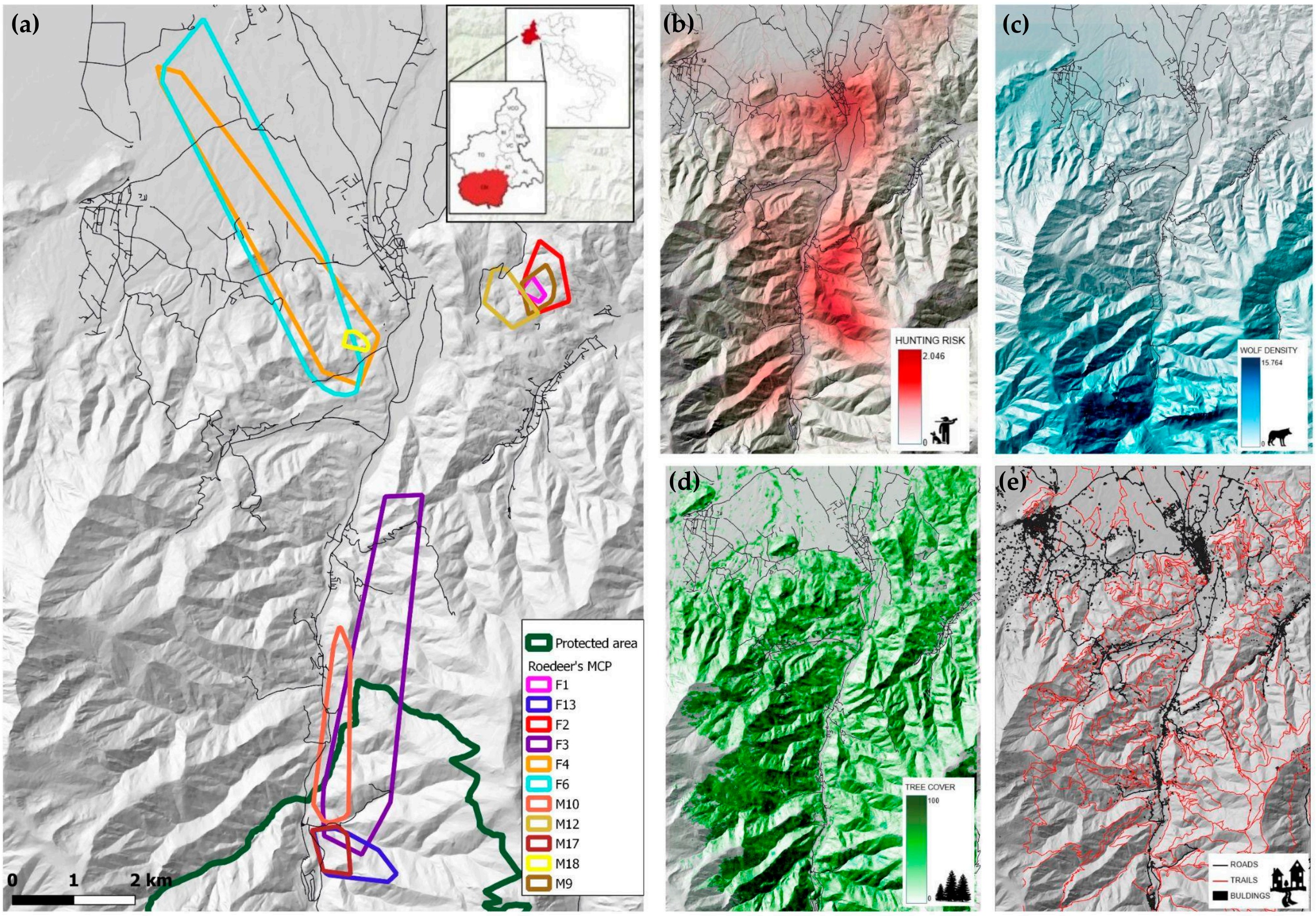

Figure 1. Description of the study area: site location and spatial distribution of roe deer home ranges (Minimum Convex Polygons, MCPs) within the study area (**a**). On the right, inset maps showing (**b**) hunting risk density (range: 0–2.046), (**c**) wolf density (range: 0–15.764); [36], (**d**) tree cover density (range: 0–100), and (**e**) the distribution of roads, trails, and buildings within the study area.

The study area is characterized by a medium-to-high level of rural urbanization typical of lower-altitude landscapes, with small villages, roads, and a dense network of trails. The region also hosts the higher density of wolves documented in the Italian Alps [36], which have been present since 1996 [37] through natural dispersals [38].

We used data from Global Positioning System (GPS)-collared roe deer to investigate habitat selection. Roe deer were captured throughout the study area during winters 2022–2024 using individual box traps with trap alarm systems, specifically built for this study based on roe deer local sizes and logistical needs to guarantee the safest capture method, commonly used for roe deer in other areas with severe winters [39] and efficient in terms of timing in responsiveness of the team intervention (20–30 min) [32]. Box traps were distributed in the study area to capture roe deer both in and outside hunting areas, and in areas with different gradients of anthropization disturbances, variables which are particularly important to represent in the study. No chemical immobilization was needed [32]. Roe deer were fitted with GPS collars (model Lotek Litetrack Iridium 360, Lotek Wireless, Newmarket, ON, Canada). Collars were programmed to attempt a fix at least every 7 h. GPS locations were screened for GPS errors or malfunctions, and only fixes with a level of accuracy of PDOP < 5 were considered. A systematic GPS collar test of the Lotek collar's performance was conducted in the different parts of study area to guarantee the homogeneity of the accuracy of the Positional Dilution Of Precision (PDOP): information acquired in the different areas [32]. We investigated roe deer habitat selection over a 7-month period to test for the effect of hunting, encompassing 3 typical distinct periods: (a) before the hunting season (1 August–15 September), (b) during the hunting season (hunting season started on 16 September and ended 31 December), and (c) after the hunting season (1 January–28 February). The hunting season was further characterized by two distinct periods: (1) "Roe deer hunt" in September–October, where hunting primarily targeted roe deer through a sit-and-wait hunting strategy, and (2) "Wild boar hunt" in November–December, when hunting activity was predominantly focused on wild boar through drive hunts.

In total, our dataset consisted of GPS telemetry data from 11 individuals, containing 7433 locations.

2.2. Anthropogenic and Environmental Covariates

We studied the influence of distinct environmental and anthropogenic covariates on roe deer habitat use, hypothesizing that these variables are correlated with spatial patterns of perceived risk or disturbance from humans and wolves (details of every covariate in Table S1 (Supplementary Table S1)). Environmental covariates included tree cover density (*tree cover*), representing the percentage of vegetation cover at each GPS point, derived from the Tree Cover Density layer using QGIS 3.34.6. The covariate has a high resolution of 10 m and was sourced from the Copernicus Land Monitoring Service (EAA Copernicus, https://land.copernicus.eu/en) (accessed on 1 march 2023). We evaluated this variable to test the hypothesis that forest might provide roe deer with refuge or increased opportunities to escape from predators, hunters and any human disturbance such as hikers or bikers.

Anthropogenic features included roads (all paved roads), trails (all unpaved paths), and buildings (all types of human dwellings) and were obtained by BBBIKE (https://extract.bbbike.org/) (accessed on 15 march 2023) from OpenStreetMap (OSM). For each of these covariates, we calculated the minimum Euclidean distance from each GPS point to the corresponding feature, resulting in the variables *dist.road*, *dist.trail*, and *dist.build*. We evaluated these variables to test for the hypothesis of human disturbance, considering in particular that roads are regularly used by people with motorized vehicles, whereas trails are used by hikers and bikers, and in general by recreational tourism in the study area [40,41].

To test for hunters encountering risk, we considered the georeferenced harvest data provided by hunter districts from 2016 to 2024 (n = 1281), and applied a 95% kernel density estimation to quantify the spatial density of hunted animals, using the R version 4.3.1, package *amt* [42] to generate a hunting risk map with a spatial resolution of 10 m, which was then scaled from 0 to 1 (huntrisk). We account for local wolf density of presence (*wolfden*), using the wolf density map estimated by Marucco et al. 2023 [36] for the whole Italian Alps based on a spatial capture–recapture model fitted to the noninvasive genetic data collected in winter 2020–2021.

To test how human activities affect resource selection of roe deer in relation to hunting periods we created two categorical temporal variables named "*Hseason1*" and "*Hseason2*". In *Hseason1*, we classified the study into the 3 periods previously described: *Before* (no hunting activity), *During_hunt* (period with active hunting), and *After* (post hunting period). In *Hseason2*, we further distinguished the hunting period into two distinct phases based on the type of hunting activity, named "*DuringROE_Hunt*" and "*During WB_Hunt*", as previously described. This variable categorization is meaningful to test the hypothesis of spatial responses to different hunting methods: roe deer hunting relies on a sit-and-wait mode, involving a single hunter either actively searching for animals or waiting passively in a specific location, while wild boar hunting relies on a drive hunt mode with a team of hunters working together with dogs to locate and stalk animals. The driving hunt mode is generally considered more disruptive due to the involvement of multiple hunters and dogs, which increase noise and movement across the landscape [43,44]. To test how spatial responses changed with hunting periods, we included interactions between *Hseason1 and Hseason2* and the most significant predictors (Table 1). Hence, the 2 variables *Hseason1 and Hseason2* allowed us to investigate the general effects of hunting risk and the specific impacts of different hunting strategies, respectively.

Table 1. Tested hypotheses, corresponding variables, and predictions of roe deer spatial response in anthropogenic landscape (interaction terms are expressed using "×" between the variables).

Hypothesis	Variables	Predicted Effect	Predictions
H1: Forest cover is an important refuge habitat in an anthropogenic landscape	*tree cover*	(+)	Roe deer is a woodland species with preference for ecotonal zone [45] P1: In an anthropogenic landscape, we predict that tree cover density may be important as a refuge area
H2: Spatial effect of recreational activity	*Dist.trail*	(+)	P2a: Roe deer may avoid trails used by hikers and bikers as recreational activities to minimize perceived risk from human disturbance
	Dist.trail × InsidePA	—	P2b: We predict roe deer avoidance of trails should be greater within the Protected Area where tourism is more concentrated
H3: Effects of pre–during–post hunting periods, and human shield strategy	*Huntrisk*		P3a: Roe deer habitat selection may be affected by the spatial presence of hunting activity
	Dist.build × Hseason1		P3b: stronger use of a human shield strategy during the hunting period than before (or after)
H4: Effects of different hunting modes	*Hseason2 vs. Hseason1 as temporal interaction terms*		Roe deer may exhibit varying responses depending on the distinct hunting practices. P4: Specifically, we predicted that wild boar hunting may have a greater impact due to the higher levels of disturbance associated with this activity. During the wild boar hunting period, we anticipate a stronger use of the human shield strategy
H5: Risk enhancement	*huntrisk × wolfden*	(+)	P5a: Roe deer may select areas where both risks are high simultaneously (cumulative exposure)
	huntrisk × wolfden	(−)	P5b: Roe deer, avoiding one predator, may select areas where the other predator is more common

The spatial categorical variable, named *InsidePA*, allowed us to test the hypothesis of a higher effect of recreational activities within the protected area, where tourism is more developed, specifically along trails. To test this hypothesis, we tested the interaction effect between *trail* and *InsidePA* (Table 1).

2.3. Resource Selection Function and Analytical Framework

We evaluated roe deer habitat selection building third-order resource selection functions (RSFs). RSFs evaluate the habitat features selected by animals by comparing used locations to available locations within the domain of availability, defined here as each individual roe deer's home range (third-order habitat selection, Johnson 1980). Individual home ranges were defined as the area encompassing 95% of the kernel density estimates estimated by the 'amt' package in R version 4.3.1 [42] and were calculated using roe deer GPS data collected between 1 August and 29 February 2022–2024. To characterize habitat availability within the home range, we considered 30 random locations for each GPS fix [46]. RSF parameters have been estimated using a Generalized Linear Mixed Model (GLMM) using glmmTMB package in [47], based on a mixed-effect logistic regression model for binary data for used locations (1) and random locations (0), and setting a random intercept for each individual to account for the non-independence of observations of a given roe deer and the unbalanced sampling design [48,49]. The general form of the model is as follows:

$$\text{logit}\ (p) = \beta 1X1 + \beta 2X2 + \ldots .\ \beta iXi$$

where p is the probability of selection, the x_is are the explanatory covariates or interactions, and β_i is their respective coefficient. Temporal covariates for *Hseason1 and Hseason2* entered the models only via their interactions with spatial covariates.

We built our RSF candidate models based on our specific hypothesis (Table 1). Before initiating the stepwise modeling process based on the delineated hypothesis, we screened for redundancy among predictors by calculating Pearson's correlation coefficients (r) using the cor() function in R. Variables with $r > 0.7$ were not included in the same model to prevent collinearity issues. To analyze the effect of independent covariates, we began by testing the effect of habitat and anthropogenic features first, then added risk variables, such as wolf density (*wolfden*) and hunting risk (*huntrisk*), without any interaction terms. Then, we sequentially added variables and interactions to test for specific hypotheses as indicated in Table 1, and identified the most significant predictors driving roe deer habitat selection across environmental, anthropogenic, and risk gradients, ensuring a robust and interpretable modeling framework.

The candidate models were ranked using the Akaike Information Criterion (AIC; [50]) and all the models were additionally checked for any multicollinearity using the Variance Inflation Factor (VIF) function of the package car, with a correlation threshold of 5 being applied or at least less than 10 only in case of the interaction term [51].

3. Results

The best models include interactions with the temporal covariate that considers the hunting periods and modes (*Hseason2*) and with the spatial covariate *InsidePA* (inside/outside the protected area), confirming that roe deer habitat selection is primarily explained by the complex interplay of multiple anthropogenic factors. In particular, the most parsimonious RSF model (M1, lowest Δ AIC, Table 2) explains the majority of the variance of the data (weight of 0.92) and included key predictors both in the form of a single covariate effect and their interactions (Table 2 and Figure 2).

Table 2. Summary of best candidate RSF models investigating the habitat selection of 11 roe deer before, during, and after the hunting season in the Pesio Valley, Maritime Alps.

Mod	Formula	Δ AIC	*W*
M1	~treecover + dist.trail + dist.build + wolfden + huntrisk + wolfden:Hseason2 + dist.build:Hseason2 + huntrisk:wolfden + dist.trail:InsidePA	0	0.92
M2	~treecover + dist.trail + dist.build + wolfden + huntrisk + wolfden:Hseason1 + dist.build:Hseason1 + huntrisk:wolfden + dist.trail:InsidePA	4.9	0.08
M3	~treecover + dist.trail + dist.build + wolfden + huntrisk + wolfden:Hseason2 + dist.build:Hseason2 + huntrisk:wolfden	46.8	0.00
M4	~treecover + dist.build + wolfden + huntrisk + wolfden:Hseason2 + dist.build:Hseason2 + huntrisk:wolfden	73.2	0.00
M5	~treecover + dist.trail + dist.build + wolfden:Hseason2 + dist.build:Hseason2 + dist.trail:InsidePA	166.6	0.00
M6	~treecover + dist.trail + huntrisk + wolfden + huntrisk:wolfden + dist.trail:InsidePA + dist.road	305.7	0.00
M7	~treecover + dist.trail + wolfden + huntrisk + wolfden:Hseason2 + dist.trail:InsidePA + huntrisk:wolfden	311.8	0.00
M8	~treecover + dist.trail + huntrisk + dist.trail:InsidePA + huntrisk:wolfden	348.9	0.00
M9	~dist.trail + dist.build + wolfden + huntrisk + wolfden:Hseason2 + dist.trail:InsidePA + huntrisk:wolfden + dist.build:Hseason2	472.1	0.00
M10	~treecover + dist.trail + dist.build + wolfden + huntrisk	90,176.2	0.00
M11	~treecover + dist.trail + dist.build + wolfden	90,206.6	0.00
M12	~treecover + dist.trail + dist.build	90,287.9	0.00
M13	~dist.trail + dist.build	90,357.8	0.00

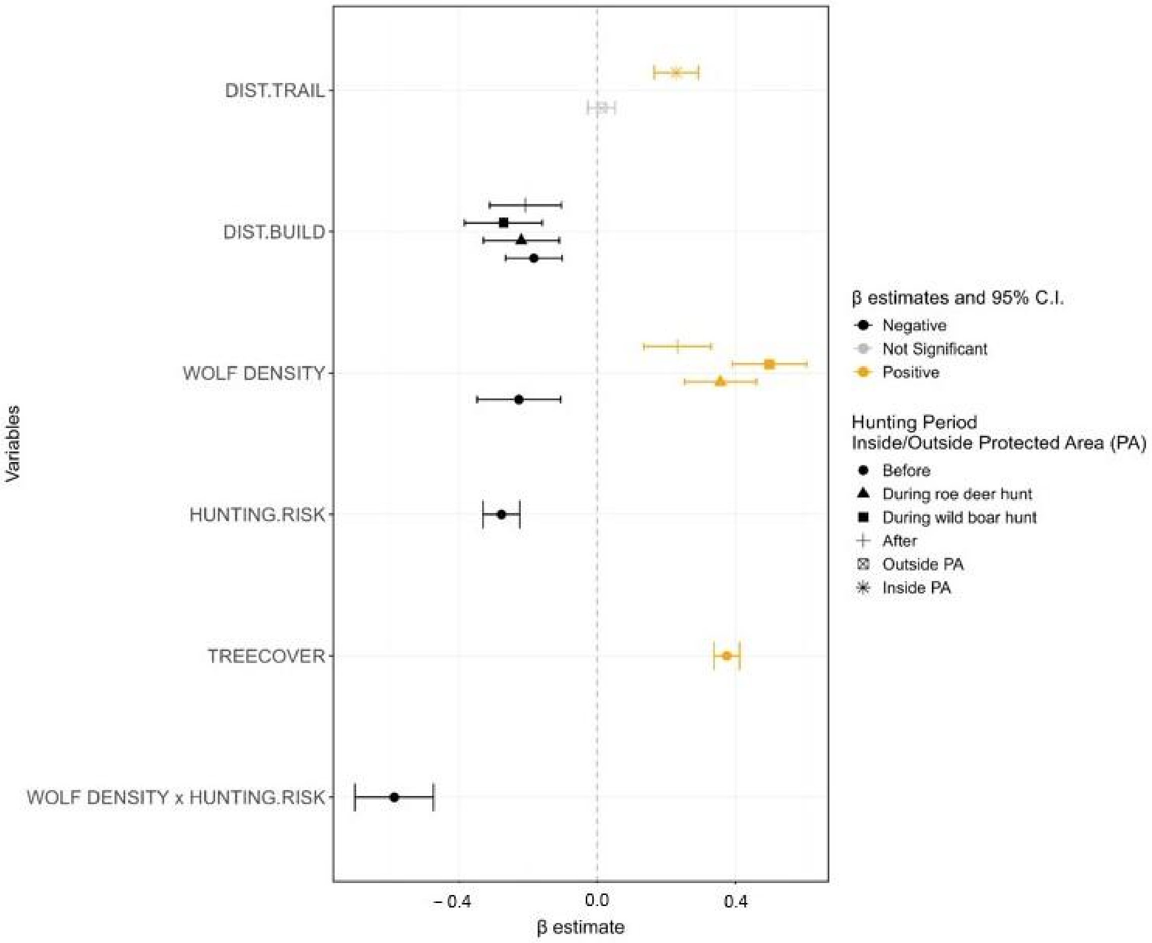

Figure 2. β coefficient plot of fixed terms (expressed as log-odds ratios) included in the most parsimonious model. The dashed line represents a level of use proportional to availability, and error bars represent 95% confidence intervals. The timing effect for each variable is indicated by different symbols: dots (before), triangles (during roe deer hunt), squares (during wild boar hunt), and crosses (after hunting period). The spatial effect of *dist.trail* is shown with striped squares and asterisks, representing coefficients for locations outside and inside the park, respectively. β coefficients are displayed in black if negative, orange if positive, and gray if not significant.

Tree cover density emerged as one of the most significant predictors: removing this variable from the model caused a notable decline in model performance, with the best model shifting from first (M1) to ninth (M9) (Table 2). Roe deer selected for high cover density, as indicated by the positive effect of tree cover covariate (β = 0.37, SE = 0.019, $p < 0.001$), testing for H1. Trails had no significant effect on roe deer habitat selection (β = 0.01, SE = 0.02023, $p = 0.541$). However, roe deer significantly avoided trails within the protected area, as indicated by the positive coefficient of the interaction term *dist.trail:InsidePA* when *InsidePA* = 1 (Figure 3 green line, β = 0.23, SE = 0.03252, $p < 0.001$), testing for H2.

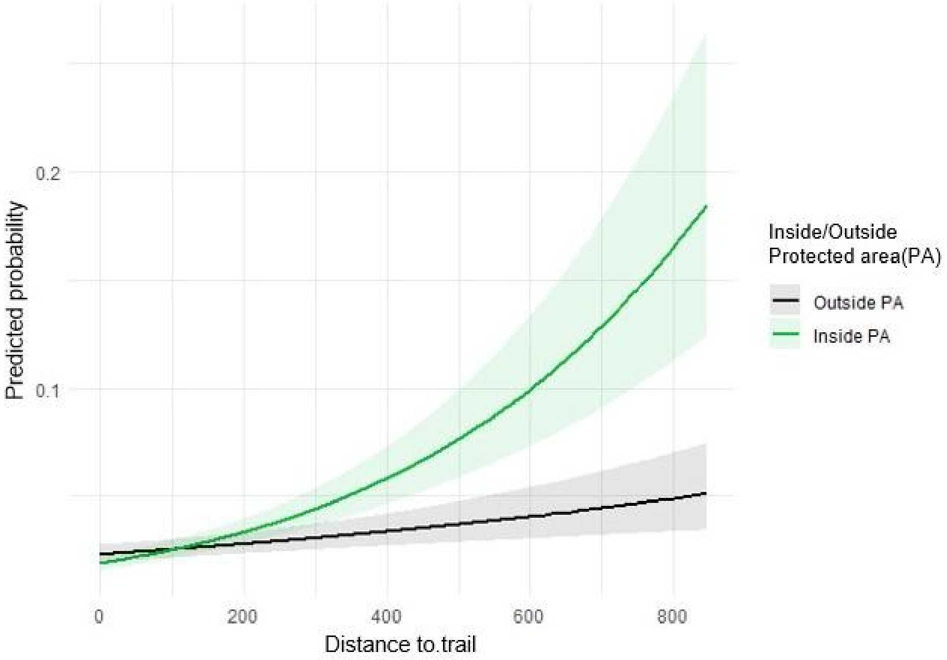

Figure 3. Predicted probability of trail use by roe deer inside (green line) and outside (black line) the protected area.

We observed a general avoidance of high-risk areas associated with hunting, as indicated by the negative main effect of *huntrisk* (β = −0.28, SE = 0.02725, $p < 0.001$), and a clear temporal effect of hunting on roe deer spatial responses, testing for H3 and H4. This temporal effect is better explained by considering the different hunting periods and modes (*Hseason2* in best model M1) rather than just the presence or absence of hunting (*Hseason1* in M2, Δ AIC = 4.9), testing H4. During the hunting season, roe deer responses to wolf density and proximity to buildings were influenced by the different temporal periods of hunting activities (Figure 4). Roe deer selection for proximity to buildings (dist.build) was consistently negative (β = −0.18, SE = 0.04162, $p < 0.001$), but increased over the hunting periods with the interaction term (*dist.build:Hseason2*), particularly during wild boar hunting, where the coefficient was higher compared to other periods (β = −0.27, SE = 0.05742, $p < 0.001$). This effect persisted after the hunting season ended (β = −0.21, SE = 0.05288, $p < 0.001$), although it was less pronounced, testing for H3b (Figure 4b).

The negative main effect of wolf density (wolfden), which reflects the effect in the absence of hunting, indicates that roe deer tend to avoid areas with high wolf presence (β = −0.23, SE = 0.06147, $p < 0.001$); moreover, there is a significant negative effect of the interaction term *wolfden:hutrisk* (β = −0.59, SE = 0.05798, $p < 0.001$), which indicates that roe deer, avoiding areas with risk from one predator, selected areas with high risk for the other (Figure 4a). In particular, roe deer responses to wolf presence changed within the different hunting periods: roe deer shifted their response from avoidance of wolf areas of presence before the hunting period to a selection of those areas during hunting, testing

H5 (Figure 4a). The selection was particularly strong during wild boar hunting (β = 0.50, SE = 0.05485, $p < 0.001$) and less pronounced during roe deer hunting (β = 0.36, SE = 0.05315, $p < 0.001$). After the hunting season, the effect diminished but remained positive (β = 0.23, SE = 0.04958, $p < 0.001$) (Figure 4a).

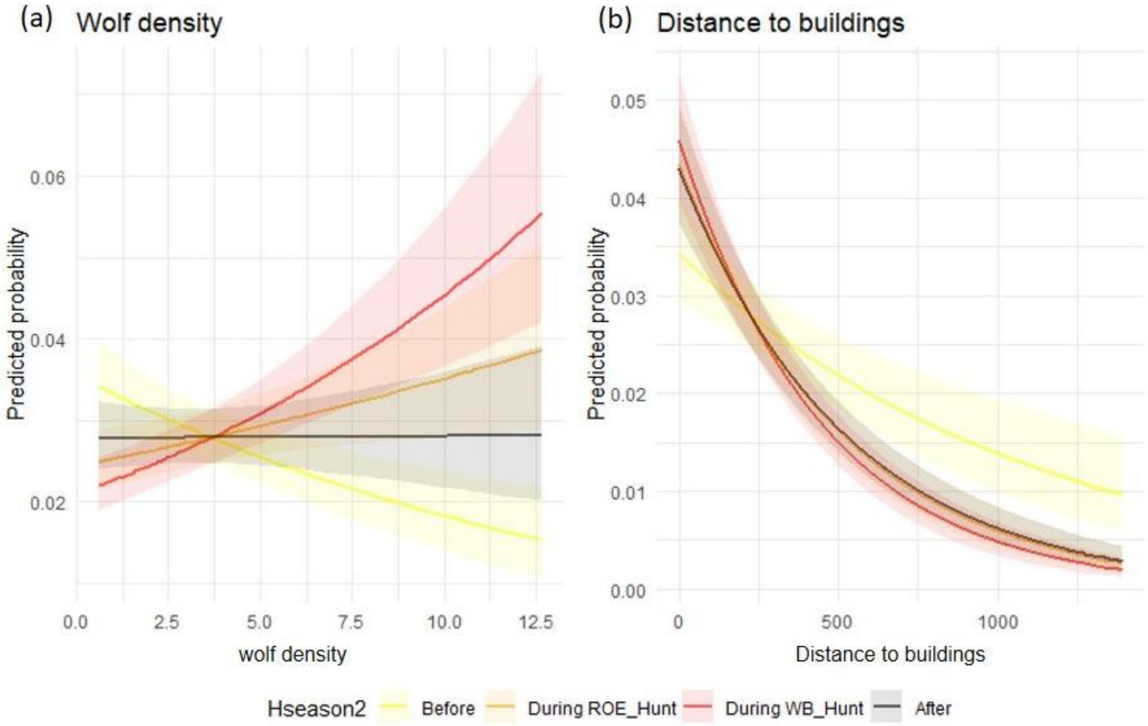

Figure 4. Predicted probability of habitat use by roe deer based on wolf density (**a**) and distance to buildings (**b**) across different temporal periods: Before, prior to the hunting season; During_ROE_Hunt, the first hunting period characterized by roe deer hunting; During_WB_Hunt, the second hunting period characterized by wild boar hunting; and After, following the closure of the hunting season.

4. Discussion

Human activity has significantly transformed natural ecosystems, shaping the composition and structure of ecological communities, and leading to alterations in species interactions [1,2]. This influence introduces additional layers of complexity into predator–prey relationships, often challenging the natural dynamics of these interactions. Hence, behavioral adaptations in the Anthropocene, such as changes in habitat selection or temporal activity, are important for the resilience of some species [7,52–54]. However, not all species can adapt successfully, leading to uneven impacts of disturbance across ecological systems. Few studies have explored ungulate responses to cumulative landscape disturbances involving multiple risks [55]. In this paper, we have investigated how human activities influenced roe deer habitat selection in relation to hunting, human infrastructures, and recreational activities in the presence of its most important natural predator, the wolf. We included random intercepts for individual ID in all our models, as recommended by Gillies et al. (2006) and Merrill and Hebblewhite (2009) [48,49], to account for differences in sample size per individual and controls for individual-specific effects in habitat selection. Our findings highlighted that human activities play a crucial role in shaping roe deer habitat selection strategies, in particular the timing and type of hunting and the distribution of trails and buildings, providing important insights into these complex spatial and temporal dynamics. Human-induced alterations and disturbances transform what ecologists refer to as “landscapes of fear” [56]. These landscapes influence how animals perceive and respond to threats in their environment driving critical behaviors [15]. Human activities might reshape the landscapes of fear, influencing habitat selection, activity patterns, and the effectiveness of anti-predator strategies [10,52] such as introducing "human shield strategies" [14]. In our study, we had the unique opportunity to investigate in detail how roe deer navigate a highly heterogeneous "landscape of fear" induced both by human disturbances and the presence of a natural predator, where risks varied both temporally and spatially. In particular, during the hunting season, roe deer were demonstrated to face intensified trade-offs, as human hunting activity overlapped in space and time with predator presence and all the other human pressures. At the same time, part of our study area is in a protected area, which experiences high levels of tourist activity throughout the year, especially along trails. Our results revealed that the combined pressure of anthropogenic infrastructures and variegated human activities, along with the presence of wolves, prompted roe deer to adopt differentiated strategies to balance their exposure to threats. This adaptive response is supported by the fact that roe deer behavior aligns with multiple hypotheses we predicted (from H1 to H5) rather than being explained by a single one. This suggests a complex interplay of various factors and strategies employed by this prey species in a highly anthropogenic context.

We documented strong support for our first hypothesis that tree cover density was one of the most significant drivers of habitat selection (H1). As a woodland and ecotonal species, roe deer rely on forested areas to ensure immediate escape routes [51,57]. Benhaiem et al. (2008) [58] showed that vigilance levels in roe deer decreased commensurately with the extent of woodland, further highlighting the role of forest cover in reducing perceived risk. This indicates a general adaptation of roe deer to the highly anthropogenic landscapes of our study area, where human pressures, combined with the presence of natural predators, create a complex landscape of risk, requiring prey to optimize their spatial strategies by using refuge areas more extensively. This finding also emphasizes the need to reconsider methodologies for ungulate population estimates in anthropized contexts that rely only on direct observations [59,60], which may be strongly affected by low and unpredictable detection rates [61]. Based on our findings, anthropogenic pressures might drive roe deer to increasingly select forested refuge areas, where detection rates are likely too low for direct observations to serve as methods for reliable population estimations.

Among human linear features, trails had the strongest effect on roe deer habitat selection. We hypothesized that deer would perceive these features as risky, due to their frequent use by hikers, bikers, and humans in general, especially where tourism is more concentrated (H2). In fact, we found support for our hypothesis (P2b) where roe deer displayed stronger avoidance of trails inside protected areas compared to outside them. This heightened avoidance within the protected area is likely influenced by the higher frequency of tourists and recreational activities inside the park. The rapid spread and diversification of outdoor recreation can impact wildlife in various ways, often leading to the avoidance of disturbed habitats [62,63]. Also, Mathisen et al. (2018) [64] showed that hiking and cycling activities on trails reduced deer space-use and browsing on tree saplings in their direct vicinity (<100 m).

Our results aligned with hypotheses H3 and H4, demonstrating that hunting periods modify roe deer habitat selection strategies. Roe deer change spatial behavior during the hunting season compared to a previous period characterized by the absence of hunting through an increased selection for proximity to buildings, particularly during the wild boar drive hunting period. Also, other studies have shown that drive hunting is particularly disruptive to wildlife [43]. This supports the hypothesis that roe deer use human buildings as refuges from hunting activities, indicating a well-developed human shield strategy [28]. Particularly interesting is also the effect of hunting activities on the relative use of areas with higher wolf densities. The β coefficients of wolfden shifted from negative before the hunting season to increasingly positive during the hunting season, peaking during the wild boar hunting period, and then returning to neutral immediately afterward. This clear temporal pattern (Figure 4a) highlights how hunting activity can play an important role in prey–predator interactions, likely driving both species to converge in the same remote areas, indicating that roe deer might not actively select high-wolf-density areas per se, but rather select locations characterized by refuge areas, which are also typically selected by wolves [65,66].

Additionally, as predicted in our risk enhancement hypothesis (H5), we found a negative interaction between hunting risk areas and high-wolf-density areas, suggesting that roe deer actively avoided areas where risks from both hunters and wolves overlapped. Several studies have investigated the risk effects in a multi-predator context, revealing that multiple predators may create areas of contrasting risk or double-risk zones within the same landscape [13,67]. For example, Lone et al. (2017) [13] found that roe deer exposed to hunters and lynx faced overlapping yet contrasting landscapes of fear, showing that the presence of one predator can influence prey exposure to another. This aligns with our findings that hunting risk interacts with areas of high wolf density, leading roe deer to dynamically adjust their habitat selection. Wild boar drive hunting induces high-intensity human disturbance, with many hunters and dogs, which likely amplifies risk perception and causes roe deer to alter their habitat selection more strongly during this time. These findings align with Norum et al. (2015) [67], who demonstrated that roe deer responses to human hunting strategies varied significantly, with notable differences between drive hunting and sit-and-wait hunting. When the hunting season ends, roe deer no longer select areas with high wolf density, which strongly underlines that this effect is driven by human activity, indicating how hunting can profoundly shape predator–prey relationships, as demonstrated in other studies [68].

To conclude, our findings emphasize the importance of considering both human-induced and natural predation risks in shaping prey spatial behavior, especially in multi-use landscapes where protected areas are interspersed with zones of active human hunting. These results underscore the importance of considering anthropogenic influences when analyzing predator–prey spatial dynamics, in order to find solutions to improve human–wildlife coexistence while engaging all different stakeholders in the process [69]. Given the temporal and spatial heterogeneity in roe deer responses, a one-size-fits-all approach to hunting regulations and tourism management may not be effective. Spatially explicit management strategies, such as zoning hunting activities to separate human disturbance areas from key wildlife habitats, could help balance human use and conservation goals [70]. While protected areas play a critical role in reducing direct human impacts, stronger efforts are needed to manage human activities within these areas, particularly in mitigating the perceived risks associated with recreational activities. Ensuring sufficient habitat connectivity of refuge options can help ungulates navigate complex landscapes of fear. In the Anthropocene era, human disturbance can even exceed the spatial effects of risk induced by apex predators [68,71]. In habitats becoming progressively more human-dominated, understanding the impact of human activities on wildlife behavior will become increasingly important for effective conservation and management strategies to develop human–wildlife coexistence.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/d17020115/s1, Table S1: List of covariates included in the fitted models as explanatory variables. https://data.mendeley.com/drafts/dfbpd4h9bj (accessed on 31 January 2025) [72].

Author Contributions: F.M. conceived the ideas and provided acquisition of the financial support for the study. F.M. and V.R. supervised field work and analysis. V.R collected the data. V.R. wrote the original draft. F.M. reviewed and edited the original draft. All authors contributed critically to the drafts and gave final approval for publication. All authors have read and agreed to the published version of the manuscript.

Funding: Funding for this study was provided by LIFE WolfAlps EU project (LIFE18 NAT/IT/000972—Action C3), and by INTERREG VI-A France-Italia ALCOTRA 2021–2027 n. 20140 "BIODIV-TOURALPS" project.

Institutional Review Board Statement: All appropriate permits and authorizations were obtained prior to capture and handling of the animals by the Cuneo Province, after the opinion of the Istituto Superiore per la Protezione e la Ricerca Ambientale (ISPRA), following national regulations. [Protocol codes, dates: 2022/12832, 28 February 2022].

Data Availability Statement: The data presented in this study are available on request from the corresponding author upon reasonable request.

Acknowledgments: We thank the staff of Ente di Gestione Aree Protette Alpi Marittime (APAM) and University of Turin (UNITO); in particular D. Sigaudo for field coordination, L. Martinelli for support on managing GPS collars, MV. Boiani for GIS support, and all Master's students and technicians who took part in the field work: A. Bolfo, V. Carlotti, M. Gatti, A. Cappati, M. Bertolino.

Conflicts of Interest: The authors declare no conflicts of interest.

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