Wolf and wild boar in the Alps: Trophic, temporal and spatial interactions in an Alpine protected area

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A B S T R A C T

In predator-prey systems, interspecific interactions at the spatial and temporal scale may affect different components of the ecosystem. Despite a growing interest in the topic, little is known about these interactions in many regions, particularly in areas recently recolonized by apex predators, such as the Alps. Using a multidimensional approach, we assessed wolf-wild boar interactions in a recently recolonized protected area of the Western Alps (Gran Paradiso National Park, Italy) by combining camera trapping and wolf scat analyses. First, we quantified the importance of wild boar in the wolf diet by comparing two different periods (October 2018–September 2020 vs. October 2021–September 2022). Second, we evaluated prey selection in 2021–2022, when data on prey availability were collected. Then, we assessed spatiotemporal interactions between the wild boar and the wolf. Finally, we calculated combined spatiotemporal associations between the wolf and the wild boar in comparison to other ungulate prey. We found a remarkable increase in wild boar consumption between the two periods; roe deer and wild boar were consumed in proportion to their availability, while the chamois was positively selected and the red deer and the ibex were less consumed in relation to their availability. Although we found no negative association between wolf and wild boar detection rates, in winter the wild boar limited its temporal overlap with the predator by being less active in sites more frequently used by the wolf, suggesting some spatial modulation of a temporal antipredator response. Among ungulate species, the wild boar had the highest combined spatiotemporal association with the wolf, particularly in autumn-winter. Our results suggest complex interspecific interactions in alpine areas recently recolonized by the wolf.

1. Introduction

There is an increasing interest in understanding the dynamics of prey-predator interactions, because of their potential to directly or indirectly affect trophic levels, possibly triggering large-scale top-down effects (Callan et al., 2013; Fortin et al., 2005; Hebblewhite et al., 2005). For instance, the perception of the spatiotemporal variation of predation risk may influence prey behavior, by triggering avoidance of risky areas and/or reduction of activity in riskier times of day (Bonnot et al., 2013; Kohl et al., 2018; Ross et al., 2013). In

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turn, prey species can modulate their spatiotemporal behavior, which can vary among different features of the environment (such as habitat type, relative proximity to refuge sites or slope) and during the 24h- cycle, as a result of a heterogeneous "landscape of fear" that may have complex ecological consequences (Laundre et al., 2010). However, information is conflicting among studies. Although spatial avoidance has been locally reported (Kohl et al., 2018; Mao et al., 2005; Thaker et al., 2011), temporal avoidance has been suggested to play a major role (Bonnot et al., 2013; Tambling et al., 2015), especially in contexts where the availability of suitable habitat for prey is limited by anthropogenic factors (Murphy et al., 2021). This is often the case in the European continent, where large carnivore populations are rapidly recovering after decades or, in some cases, centuries of absence (Chapron et al., 2014).

The wolf (*Canis lupus*) is the most abundant large carnivore species in Europe and most of its populations have been increasing since the beginning of the 21st century (Chapron et al., 2014). The Alpine range experienced a rapid recolonization process which is still in progress: for example, on the Italian side, the number of wolf reproductive units increased from 1 to 124 in less than 25 years, most of them being located in the western portion (Marucco et al., 2022). Wild boar (*Sus scrofa)* is another large mammal that is expanding across European countries (Keuling et al., 2018). Many populations have been hunted to extinction by the end of the 19th century and are now rapidly increasing in abundance and distribution (Massei et al., 2015), often triggering economic and social conflicts (Scandura et al., 2022). At the beginning of the XXth century, the Italian wild boar population was eradicated from the Alpine regions and severely fragmented in the rest of the peninsula (Apollonio et al., 1988). The recolonization of the Alps seems to have started in 1919 in the western portion with individuals dispersing from France (De Beaux and Festa, 1927), while releases for hunting purposes have been conducted across the peninsula (Apollonio, 2004).

Both these large mammals play significant roles in ecosystems and are highly relevant from ecological and management points of view (Barrios-Garcia and Ballari, 2012; Ripple et al., 2014). As a top predator, the wolf has the potential to trigger cascading effects mediated by prey and competitors (Hebblewhite et al., 2005), influencing prey population dynamics (Christianson and Creel, 2014; Randon et al., 2020) and behavior (e.g. Esattore et al., 2023; Kuijper et al., 2014; van Beeck Calkoen et al., 2021), and even affecting abiotic factors such as the carbon cycle (Wilmers and Schmitz, 2016). However, wolf effects seem to be less pronounced or even absent in anthropogenic landscapes, where human activities may be much more important in shaping interspecific interactions (Ausilio et al., 2021; Kuijper et al., 2016; Mech, 2012; van Beeck Calkoen et al., 2023). The wild boar is also able to exert a significant impact on habitats and communities. Searching for invertebrates and below-ground vegetation portions, the wild boar has the potential to strongly impact soil and plant communities due to its rooting activity (Barrios-Garcia and Ballari, 2012; Sandom et al., 2013; Sims et al., 2014). Nonetheless, null or positive effects are also reported in some cases (Baltzinger et al., 2016; Barrios-Garcia and Ballari, 2012; Cabon et al., 2022; Labadessa and Ancillotto, 2023), suggesting complex and context-dependent responses in different ecosystems. Furthermore, the trophic plasticity of the wild boar allows it to exploit animal food sources (Schley and Roper, 2003) via scavenging, but also through predation (e.g., on ground-nesting birds and small mammals, Barasona et al., 2021; Carpio et al., 2014b, 2014a; Massei and Genov, 2004; Mori et al., 2021; Schley and Roper, 2003). Thus, spatio-temporal interactions between the wolf and the wild boar have the potential to trigger effects whose consequences may propagate across trophic levels.

Despite the Alps are experiencing a rapid recolonization by these two ecologically, socially and economically relevant mammals, interspecific interactions between the wolf and the wild boar have been still poorly studied in this geographical context. While often representing the staple prey of the wolf in many studies in Southern Europe (Newsome et al., 2016) and particularly in Italy (Mori et al., 2016), in some alpine areas roe deer (*Capreolus capreolus)*, Alpine chamois (*Rupicapra rupicapra rupicapra)* and red deer (*Cervus elaphus)* are the most used prey species, probably due to their higher availability (Gazzola et al., 2005; Palmegiani et al., 2013). Quantifying the importance of the wild boar in the wolf diet at present is crucial because the predator recolonization could potentially trigger an antipredator response, the magnitude of which may depend on the intensity of the predation pressure. If frequently consumed, the wild boar may adopt stronger spatial and/or temporal avoidance strategies in relation to the encounter probability with the predator. Conversely, the wolf could tend to maximize the encounter probability by synchronizing its diel activity with this suid. One of the few studies on this topic in the Italian Alps found that the wolf seemed to adjust its activity rhythms to increase its temporal overlap with the wild boar and the roe deer, which represented its main prey in that area (Torretta et al., 2017).

We studied wolf-wild boar interactions in the Gran Paradiso National Park, a protected area of the Western Alps recently recolonized by these two mammals, thus offering the opportunity to study predator-prey coexistence strategies in early recolonization stages. Preliminary information suggests a high local temporal overlap between these two species, in winter (Berardi et al., 2022). However, no recent data is available on the contribution of wild boar to the wolf diet, as well as on the spatiotemporal variation of the wild boar activity in relation to that of the wolf. To fill these gaps, we used a multidimensional approach to study wolf-wild boar interactions, by first quantifying the role of the wild boar in the predator diet throughout four years, and then focusing on both their temporal and spatial interactions, to evaluate the potential for temporal and/or spatial avoidance *vs.* association. We predicted an increase in wild boar consumption by the wolf due to its rapid expansion; as a response, we expected an antipredator strategy based on temporal rather than spatial avoidance, due to the limited suitable habitats for the wild boar in Alpine environments. Finally, as we expected wild boar to be an increasingly important prey for wolf, we predicted a high spatiotemporal association between the two species.

2. Materials and methods

2.1. Study area

This study was carried out in two adjacent valleys of the Western Italian Alps, in Gran Paradiso National Park (Orco and Soana valleys, Piedmont region) with a total surface of 336 km². Inside the park, hunting is forbidden; selective culling of wild boar is

performed by the park rangers at the bottom of the valley, as a measure to control the population. Wild boar culling is limited to the immediate surroundings of villages and is carried out selectively by a team that drives during the night on the main road to spot and shoot the animals; carcasses are not left on the field, but carried in a slaughterhouse to be analyzed. The alpine environment is quite heterogeneous, going from broadleaved forests (up to 1200–1300 m) to more extensive coniferous forests; alpine pastures, glaciers and steep, rocky areas are found at higher elevations (2000 – 4000 m). The climate is typical of the alpine regions: cold winters with generally abundant snow and short, cool summers. Human population density is low (100–300 inhabitants per village) and located only at the bottom of the valleys; urban and agricultural areas represent less than 2 % of the entire Park (http://greatinterreg.eu/downloads/4a_2.pdf).

The ungulate community is rich and composed of several species: apart from the wild boar, other large herbivores are the ibex (*Capra ibex*), the Alpine chamois, the roe deer and the red deer; this latter is still present at very low densities, mainly below the tree line of Soana valley. The wild boar started to recolonize the study area in the '80s (Gran Paradiso National Park, 2020); a first wolf pack established its territory within the Park in 2007, in Aosta Valley (Palmegiani et al., 2013) while, within our study area, the first pack reproduced starting from 2013 (Avanzinelli and Marucco, 2018).

2.2. Data collection and analysis

2.2.1. Wolf food habits

To quantify the occurrence and volume of wild boar in the wolf diet, we analyzed the food habits of this predator through the identification of prey remains in faecal samples (Ciucci et al., 1996; Lovari et al., 1994; Patalano and Lovari, 1993). Wolf scats were identified by distinctive features: size, shape, smell, place of deposition, content, and surrounding tracks when snow cover occurred (Ciucci et al., 1996; Meriggi et al., 1996). Scats were collected by the park rangers and by us both opportunistically and along systematic transects (total length: 94 km, walked monthly) from October 2018 to September 2020 and from October 2021 to September 2022. All the scats were geo-referenced, marked with an individual ID code and then stored in a freezer. All samples were put in an oven at 80°C for >3 h in order to inactivate parasites; after that, the scats were washed through a 1–3 mm sieve to separate undigested material such as hair and bones (Kruuk and Parish, 1981). Hair identification was carried out through macro- and microscopical evaluations, following atlases (De Marinis and Asprea, 2006; Teerink, 2004) and by comparing the sample with our reference collection of hair from the study area. Identification was only conducted by a trained operator (IB) who successfully completed a blind test, correctly assigning at least 95 % of the reference samples (n=75). Following the approach of Ferretti et al. (2019), three indices of diet composition were computed for each food item: absolute frequency of occurrence, relative frequency of occurrence and estimated volume in the diet (Ciucci et al., 1996; Reynolds and Aebischer, 1991). All domestic species (goat, sheep, cattle) were incorporated in one "livestock" category. The absolute frequency of occurrence of each i-th category was calculated as the percentage of scats including that category. The relative frequency of occurrence of each category was calculated as the ratio between the number of scats containing that category and the number of vertebrate food items, expressed as a percentage. The relative volume of each food category was visually estimated considering the median values of the following volumetric classes: 1–5, 6–25, 26–50, 51–75, 76–95 and >95 % (Kruuk and Parish, 1981) and expressed in percentage as V = (total estimated volume of each prey species/ total estimated volume of all prey species) × 100. In order to assess variations in wild boar consumption, we used these metrics to compare wolf food habits in the two reference periods (Ferretti et al., 2021b; Ferretti et al., 2021a). To assess statistical differences in main prey consumption between the two periods, we used a Generalized Linear Model with presence/absence of wild boar in each scat as a response variable (binomial, link function: logit) and the study period as a categorical predictor (reference level: first period 2018–20).

To quantify the relative selection by the wolf towards the wild boar with respect to the other ungulate species, we used the Jacobs selectivity index: $(r - p)/(r + p - 2rp)$, where r is the proportion of each prey in wolf's diet and p is its relative abundance (Bugir et al., 2021; Hayward, 2006; Jacobs, 1974; Upadhyaya et al., 2018). To estimate the relative availability of each ungulate species, we used camera trap data (see paragraph below) to calculate the species-specific, group size-adjusted detection rates (Relative Abundance Index, i.e., $RAI_{individuals}$, *sensu* Ferretti et al., 2023). These indices were computed as the ratio between the cumulative number of individuals detected across camera trapping sites, and the total number of days when camera traps were working. Recent studies suggest that this index can reflect relative abundance patterns between different ungulate species, strongly correlating with other independent estimates (Ferretti et al., 2023; Palmer et al., 2018; Tanwar et al., 2021). The Jacobs index, using RAI estimates for prey availability, was therefore calculated for the 2021–2022 period, i.e. when camera trapping data were available. Confidence Intervals (95 %, CIs) were calculated with a bootstrapping procedure using 1000 resamplings. Jacobs index values range from −1 (maximum avoidance) to +1 (maximum selection). We considered that a prey species was positively selected when the lower bound of the CIs was > '0', negatively selected when the upper bound of CIs was < '0', and used according to availability when CIs included '0'.

2.2.2. Spatiotemporal relationships: data collection

To collect data on spatio-temporal interactions between the wolf and the wild boar, we used a standardized camera-trapping approach (Bu et al., 2016; Esattore et al., 2023). A 2×2 km grid was superimposed on the study area map using GIS software (QGIS 3.10). For safety reasons, all the cells including non-accessible areas (glaciers, cliffs) were excluded. A random point was generated within each suitable cell, resulting in 74 putative camera trap locations. Then, cameras were placed on the closest suitable site on animal trails within a buffer of 200 m from the random point. The high number of cameras allowed us to sample a wide elevational range (about 900–2900 m). Data were collected from December 2021 to November 2022. About 40 % of locations ($n = 29$) occurred in sites at low-to-middle elevations (i.e., lower than 1800 m a.s.l.) and were accessible during the winter despite the snow cover, allowing us to keep them active throughout the year. Locations at higher elevations were sampled from June to October ($n = $

45).

For each location, we collected data on deployment and environmental variables: elevation, height from the ground, bearing of cameras with respect to the north, and habitat type (Open, Wood or Ecotone). Habitat was defined as "Open" in the absence of trees, "Wood" in tree stands, and "Ecotone" in predominantly open areas with few sparse trees and non-continuous forest cover. The mean percentage of canopy cover was measured by an open-source Android app (CanopyCapture, developed by Nikhil Patel) on two different scales: inside the camera field of view (at 0, 5, 10 and 15 m in front of it) and within a circular buffer around it with a ten meters radius (at 0, 5 and 10 m in four perpendicular directions starting from the camera). Mean shrub cover (the percentage of ground covered by plants with height between 30 and 70 cm) was visually estimated at the same two scales of the canopy cover. Both canopy and shrub cover measures were then aggregated in discrete 10 %-classes ranging from 0 to 10, where class 0 represented 0 % and class 1 represented values between 1 % and 10 %. To quantify the visibility within the camera frame, we counted the number of visible quadrats on a standard panel (with 16 quadrats in total) from the camera perspective at 5 m, 10 m and 15 m at the centre of the field of view, at 45° left and 45° right with the standard panel at ground level and we repeated the measures in the same spots keeping it at 100 cm of height from the ground. Eventually, slope, aspect and Terrain Roughness Index (TRI) were obtained by a Digital Terrain Model with a resolution of 20 m, elaborated in QGIS 3.10. Cameras (Guard Micro 2, Comitel) were placed at 50 – 120 cm from the ground and set to record 20 s – 30 s videos with 1 s lag between consecutive ones; trigger time was <0.6 s. Cameras were visited monthly to check batteries, replace SD cards and download data. Videos were then carefully scrutinized; for each video, we recorded the date, time (solar), species, age class, sex and number of individuals. In order to avoid bias related to the same individuals staying within the camera field and generating several videos, consecutive videos of the same species within 30 min were considered the same "event" (hereafter "detection").

2.2.3. Temporal relationships: data analyses

All analyses were performed in RStudio 4.1.3. Temporal relations were assessed by quantifying the temporal overlap in activity rhythms of the two species (Monterroso et al., 2013; Ridout and Linkie, 2009) in the four seasons: winter (December-February), spring (March-May), summer (June-August), autumn (September-November). We used a kernel density estimation approach through the package "overlap" (Ridout and Linkie, 2009) and "activity" (Rowcliffe, 2022). Confidence intervals and final estimates of the overlap coefficient were calculated using a bootstrap with 1000 resamplings. Overlap coefficients were interpreted as "high" if $\geq$ 0.75, "moderate" if ranging from 0.5 to 0.75, and "low" if $\leq$ 0.5 (Monterroso et al., 2014).

To test whether the wild boar modulated its temporal behavior in relation to wolf activity, we compared temporal overlap coefficients between sites with 'higher' and 'lower' wolf use, within each season. We first computed the wolf detection rate for each location, as the ratio between the number of wolf detections and the number of working days; second, we calculated the mean wolf detection rate: every location with a detection rate $\geq$ the mean was considered to be a 'higher' wolf use site (HWS, Rossa et al., 2021). Then, we calculated coefficients of interspecific temporal overlap for both HWS and LWS, in each season. To evaluate the differences between coefficients in HWS and LWS, we considered the level of overlap of their confidence intervals using a threshold based on differences greater than 0.5 of the average margin of error (Cumming and Finch, 2005). We used a Wald test implemented in the "activity" package to assess the statistical difference in activity levels (i.e., proportion of time during the 24h-cycle spent active) between HWS and LWS ('lower' wolf sites) in each season. Finally, we used a randomization test (Rowcliffe, 2022) for both species to evaluate if the circular distribution of activity was significantly different between HWS and LWS in each season.

2.2.4. Spatial association of detection rates: data analyses

In RStudio, we used Generalized Linear Mixed Models (package "glmmTMB", Brooks et al., 2017) to evaluate the potential for a spatial association of detection rates of wolf and wild boar. The number of monthly detections of each of the two species in each camera trapping location was used as a response variable. As a preliminary assessment, we elaborated a correlation matrix with Spearman's test to evaluate correlation among potential predictors. The TRI was correlated ($|r| > 0.75$, Dormann et al., 2013) with the slope, while canopy and shrub cover measured in the ten metres buffer were correlated with those inside the field of view: these latter variables, together with the TRI, were therefore not included in the models, as considered to be less representative of the location features. For each species, we initially fitted a model including, as predictors, the following environmental variables: elevation, height from the ground, slope, aspect, habitat type (categorical, reference level: "edge") canopy cover, shrub cover, and visibility (see Methods section). The log (number of effective trapping days) for each camera was used as an offset to account for the sampling effort; the location ID of each camera trapping site was set as a random factor. Variables that showed coefficients resulting in a p-value < 0.05 were retained for the following analyses. During the second step, significant covariates were included in a global model with the same response variable (wolf or wild boar detections); other predictors were the detection rate of the other target species, people detection rate and season; for the model of wolf detections, we also included the detection rates of the other wild ungulates as predictors (i.e., those of chamois, roe deer, red deer, and ibex). We used the package "MuMIn" (Barton, 2020) to fit models including all potential combinations of predictors because each of them would represent a different *a priori* hypothesis; then, we compared AICc values (i.e., AIC values corrected for sample sizes) of models to define the best model, i.e., the one with the lowest AICc value, and to select all models with ΔAIC < 2 compared to the best model, and that did not represent more complex versions of simpler, selected alternatives (Richards et al., 2011). Finally, we validated models through visual inspection of residuals and evaluated model performance using the package "DHARMa" (Hartig, 2022).

2.2.5. Spatiotemporal associations

We combined the information on temporal overlap with that on spatial association, to estimate the potential for spatiotemporal

association between the wolf and the wild boar and to compare it with those observed between the wolf and the other ungulate species (Allen et al., 2021; Ngoprasert et al., 2012; Sehgal et al., 2022). Thus, we elaborated a time-space overlap graph comparing the cold (autumn and winter) and warm (spring and summer) seasons. For each species and each period, we calculated the same temporal overlap coefficient described above and reported it on the y-axis of the plot. Using a presence-absence matrix derived from the same camera traps, the Jaccard index (Jaccard, 1908; Real and Vargas, 1996) was elaborated, as $J = Ov / Tot$, where Ov was the number of locations where both species were detected, and Tot was the number of locations where at least one of the two species was detected. This index was used to quantify the spatial overlap, and its results were shown on the x-axis of the plot. Both the temporal and the spatial overlap were assessed at the 6-month scale ("cold" period: autumn-winter; "warm" period: spring-summer). This analysis lies on the assumption that higher combined temporal and spatial overlap leads to higher potential encounter probability and, therefore, a higher spatiotemporal association.
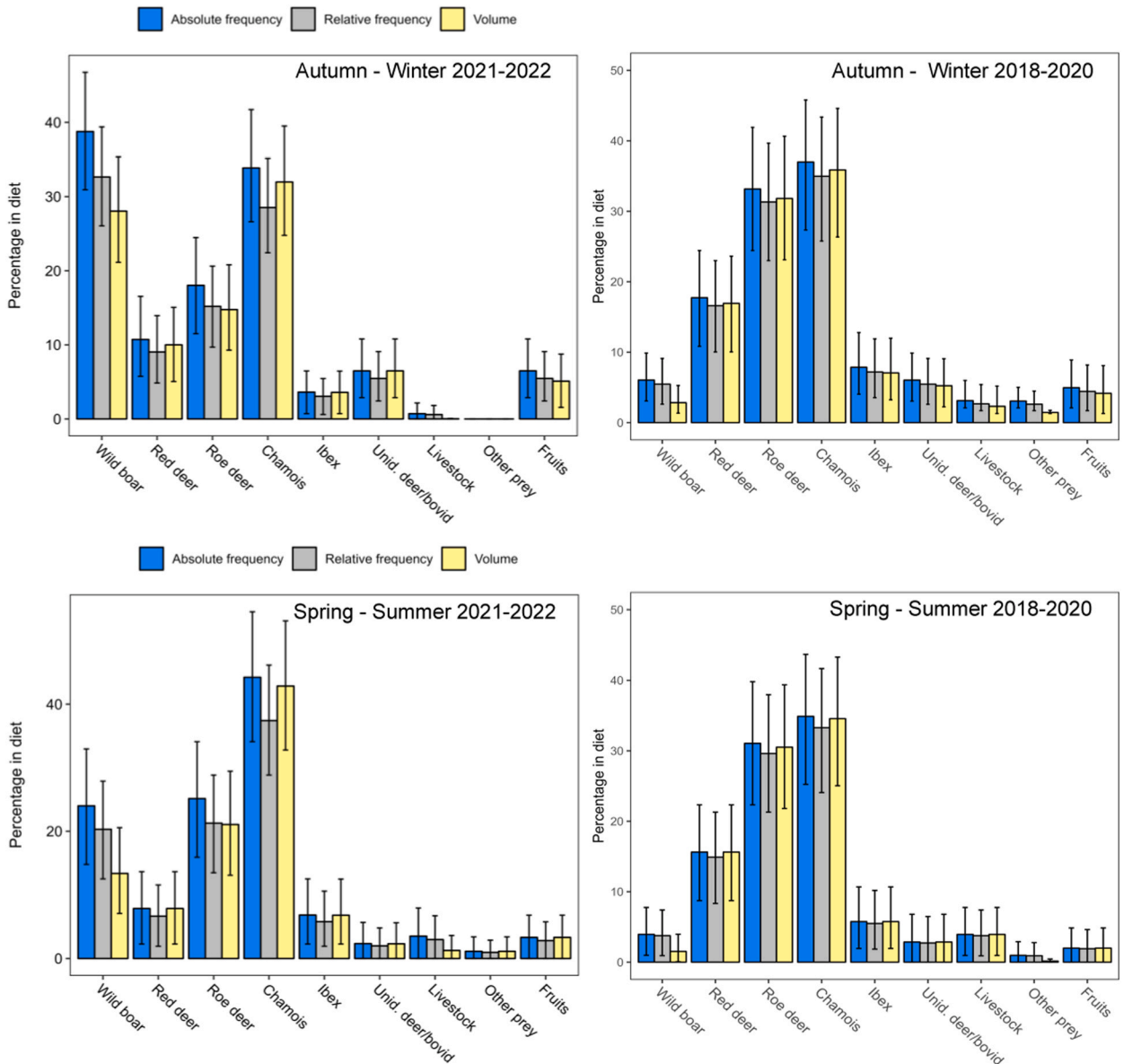

Fig. 1. Wolf diet composition in October 2018-September 2020 (N = 103 scats, Spring-Summer = 68, Autumn-Winter = 35) and October 2021-September 2022 (N = 228 scats, Spring-Summer = 90, Autumn-Winter = 138); absolute frequency, relative frequency and volume were estimated for each food item, together with bootstrapped 95 % confidence intervals (1000 resamplings). Samples that were assigned to wild ruminants but were not possible to classify at the species levels were included in the "Unidentified deer/bovid" category.

3. Results

3.1. Wolf food habits and prey selection

A total of 331 scats were collected and analyzed (2018–2020: $n = 103$; 2021–2022: $n = 228$). The chamois was the most used prey in both periods, accounting for 30–36 % of the diet, depending on the index (Fig. 1). A statistically significant increase in wild boar use was found, passing from 3 % to 4 % in 2018–2020–23–33 % in 2021–2022 (Fig. 1; B: 2.39, S.E.: 0.32, p-value < 0.001). The opposite pattern was found for roe deer, which decreased from 23 % to 31 % to 18–21 % (B:1.02, S.E.: 0.31, p-value < 0.05). The ibex accounted for less than 5–6 % of the diet in both periods, as well as domestic species and other small prey (marmot, small rodents and cat).

The Jacobs index (Fig. 2) revealed that the wild boar was consumed according to its availability, together with the roe deer. The chamois was positively selected, while a negative selection was found for red deer and ibex.

3.2. Temporal relationships

We obtained around 900 wolf and 1550 wild boar detections, over 9797 trapping days. Both species showed a consistent nocturnal activity pattern in all seasons (Fig. 3). Considering all sites, the temporal overlap was generally 'high' (*sensu* Monterroso et al., 2014) in each season ($\Delta_4 > 0.80$, Fig. 4). Comparing higher (HWS) and lower (LWS) wolf sites, we found a lower temporal overlap in HWS compared to LWS during the winter season (no overlapping confidence intervals), while no evident difference was found in other seasons as confidence intervals were widely overlapped (Cumming and Finch, 2005, Fig. 4).

The Wald test revealed that the wild boar was significantly less active in HWS than in LWS during summer and winter, and significantly more active in the latter sites than in the former ones in spring (Table 1). Results provided no support to differences in seasonal estimates of wolf activity levels between HWS and LWS (Table 1).

The randomization test provided support to different patterns of activity between HWS and LWS in spring and winter for the wild boar (Table 2. 3), while no differences was found for wolf activity in any season.

3.3. Spatial association of wolf and wild boar detection rates

After model selection, we selected one model for the wolf and two models for the wild boar. Best models showed that detection rates of both species were affected by some environmental variables, while no explicit support was found for interspecific spatial association or avoidance between our focal species (Table 2). Wolf detection rates were positively related to wood habitats and to people detection rate, and negatively related to the slope (Fig. 5). Conversely, wild boar detection rates were positively related to open and ecotonal habitats and to canopy cover, while they were negatively related to elevation and wood habitat (Table 2). People detection rate had a small, barely significant positive effect but it was not supported by the second best model (Table 2; Fig. 5).
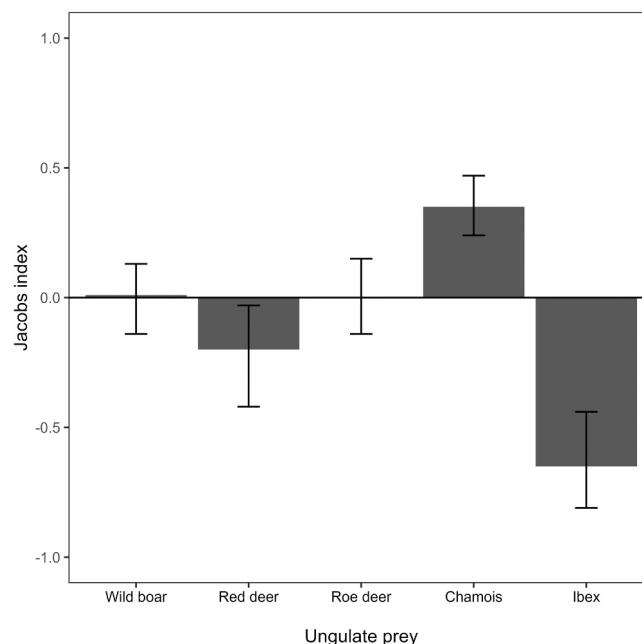

Fig. 2. Jacobs index of wolf prey selection in October 2021 – September 2022 and its relative bootstrapped 95 % confidence intervals (1000 resamplings).
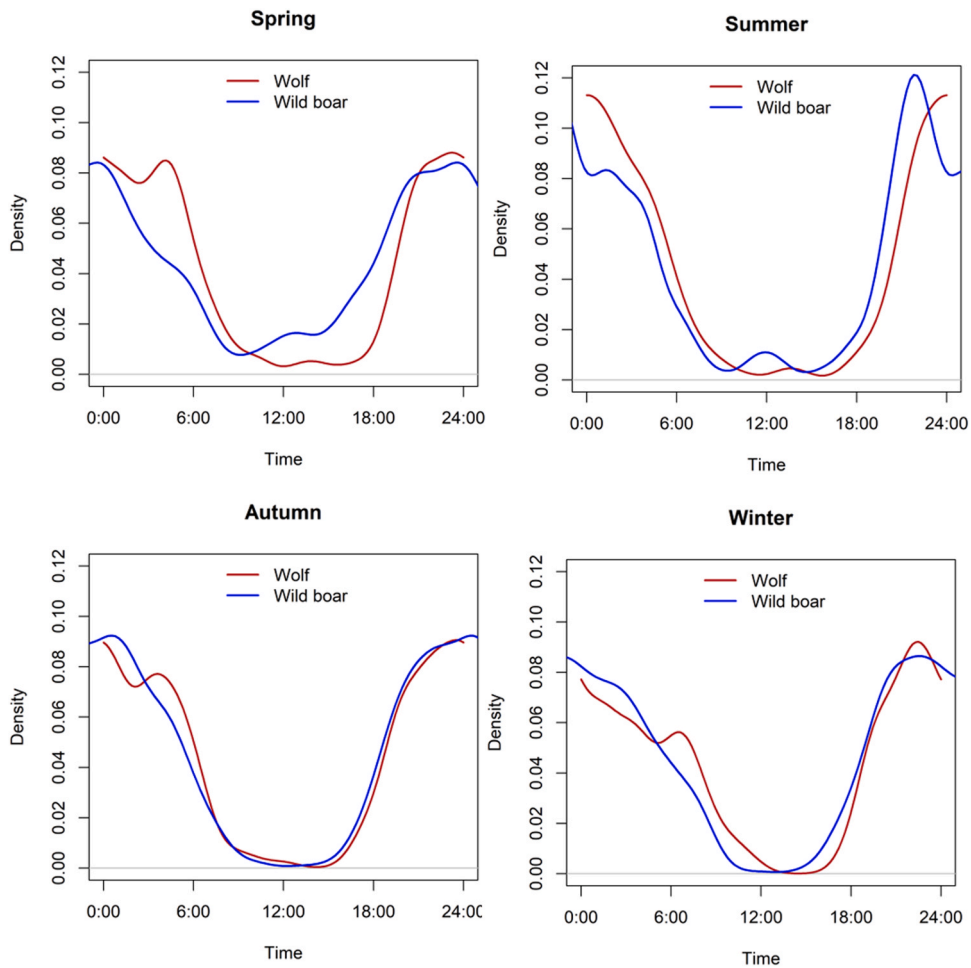
Fig. 3. Estimated density of activity of wolf and wild boar during the 24 h-cycle in spring (March–May), summer (June–August), autumn (September–November) and winter (December–February).

3.4. Spatiotemporal association

Combining spatial and temporal overlap, most species showed an increased spatiotemporal association with the wolf during the cold semester (autumn-winter) compared to the warm semester (spring-summer) (Fig. 6). The red deer and the roe deer experienced a slightly lower temporal overlap with the wolf during the cold semester, while their spatial overlap with the predator increased in that period. We observed the strongest inter-period variation in wild boar, followed by chamois and roe deer. Moreover, wild boar showed the highest spatio-temporal overlap in both periods, while for chamois and roe deer we recorded a high spatial and a moderate-low temporal overlap. The opposite pattern was found for red deer, with a high temporal and a low spatial overlap; ibex was the species with the lowest combined spatiotemporal association with the wolf.

4. Discussion

Wild boar has been frequently reported as a major prey of the wolf (for Italy: Mori et al., 2016). However, the information available is contradictory across studies in the Alps, where this suid often played a marginal role in the wolf diet (Capitani et al., 2004; Gazzola et al., 2005). Conversely, chamois and roe deer have been identified as the main prey species in different areas of the Western Alps (Marucco et al., 2008; Palmegiani et al., 2013; Poulle et al., 1997). Most of these studies were conducted in periods when the abundance of wild boar was probably much lower than that of roe deer or chamois. Our results provided partial support to these findings, as we detected a positive selection of wolf towards chamois, that was generally the most used prey by this canid together with the roe deer.

Although in other mountainous areas chamois were reported as minor prey (e.g. Apennine chamois *Rupicapra pyrenaic ornata*: Ciucci et al., 2020; Alpine chamois: Gazzola et al., 2007), a study conducted in the northern sector of the Gran Paradiso National Park (Aosta Valley) indicated them as main prey (Palmegiani et al., 2013). The local abundance of Alpine chamois may partly explain this
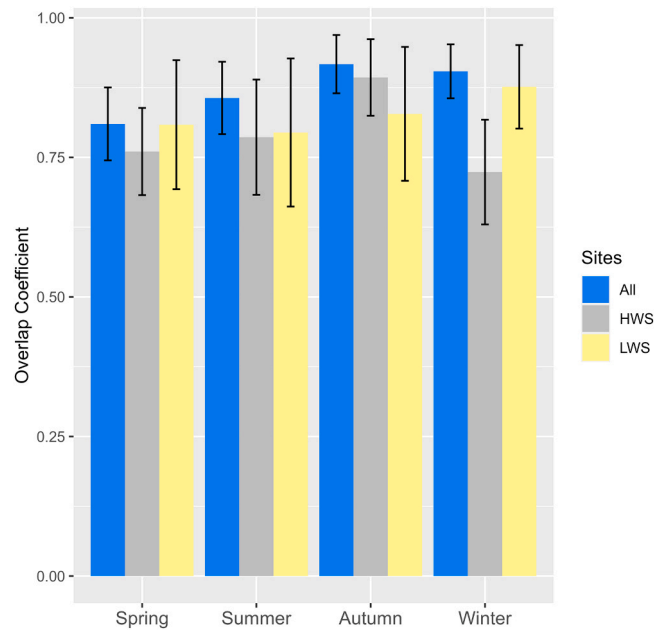
Fig. 4. Estimated temporal overlap coefficient (Δ_4) and relative bootstrapped confidence intervals between the wolf and the wild boar in spring (March-May), summer (June-August), autumn (September-November) and winter (December-February), considering: all sites combined, higher wolf use sites, i.e., sites where the detection rate of the wolf was $\geq$ the average value across all the locations (HWS) and lower wolf use sites (LWS).

Table 1
Wald test results for activity level differences between sites with higher wolf activity (HWS) and sites with lower wolf activity (LWS) for each season and species. Spring = March-May; Summer = June-August; Autumn = September-November; Winter = December-February. Difference values, standard errors (SE), test statistic (W) and relative p-values are shown, with significant results (< 0.05) in bold.

Species	Season	Difference HWS vs. LWS	SE	W	p-value
Wild boar	Spring	0.197	0.067	8.550	**0.003**
	Summer	−0.128	0.054	5.690	**0.017**
	Autumn	−0.042	0.043	0.952	0.328
	Winter	−0.136	0.047	8.141	**0.004**
Wolf	Spring	0.043	0.059	0.531	0.466
	Summer	−0.065	0.062	1.115	0.292
	Autumn	0.107	0.075	2.060	0.151
	Winter	−0.125	0.070	3.186	0.074

Table 2
Results of the randomization test for differences in the circular distribution of activity between sites with high wolf activity (HWS) and low wolf activity (LWS) in each season (Spring = March-May; Summer = June-August; Autumn = September-November; Winter = December-February). obs: observed overlap between the two distributions; null: expected randomised overlap between the two distributions under the null assumption (no differences); SE-null: standard error of the expected randomised overlap. P-values in bold indicate significant differences.

Species	Season	obs	null	SE-null	p-value
Wild boar	Spring	0.786	0.921	0.026	**0.001**
	Summer	0.850	0.886	0.029	0.118
	Autumn	0.938	0.933	0.023	0.533
	Winter	0.710	0.902	0.033	**0.001**
Wolf	Spring	0.909	0.847	0.043	0.946
	Summer	0.888	0.851	0.045	0.772
	Autumn	0.837	0.848	0.047	0.377
	Winter	0.851	0.892	0.031	0.104

result: census performed by the park rangers revealed that this species is likely the most abundant ungulate in our study area (Palmegiani et al., 2013). Extreme winter conditions in the Alps, combined with the harsh environment, seem to be a main limiting factor of chamois population in Gran Paradiso (Rughetti et al., 2011). The wolf killing rate is often positively affected by snow cover

Table 3

Factors influencing the spatial variation of monthly detection rates of the wolf and the wild boar, estimated through generalized linear mixed models with negative binomial errors: results of model selection based on AICc criteria. All models within ΔAICc < 2 are shown; selected models are shown in bold. Number of parameters (K), log-likelihood (logLik) and relative model weight are also reported.

| Species	Model	Predictors	K	logLik	AICc	ΔAICc	Weight
Wolf	**Best**	**Land cover + Slope + People D.R.**	7	−727.12	1468.38	0.00	0.50
	Second	Land cover + Slope + People D.R. + Wild boar D.R.	8	−726.70	1469.58	1.20	0.28
	Third	Land cover + Slope + People D.R. + Canopy cover	8	−726.91	1470.01	1.63	0.22
Wild boar	**Best**	**Land cover + Canopy cover + Elevation + People D.R.**	9	−776.56	1571.35	0.00	0.49
	Second	Land cover + Canopy cover + Elevation + Wolf D.R. + People D.R.	10	−775.92	1572.12	0.77	0.33
	Third	**Land cover + Canopy cover + Elevation**	8	−778.56	1573.31	1.97	0.18
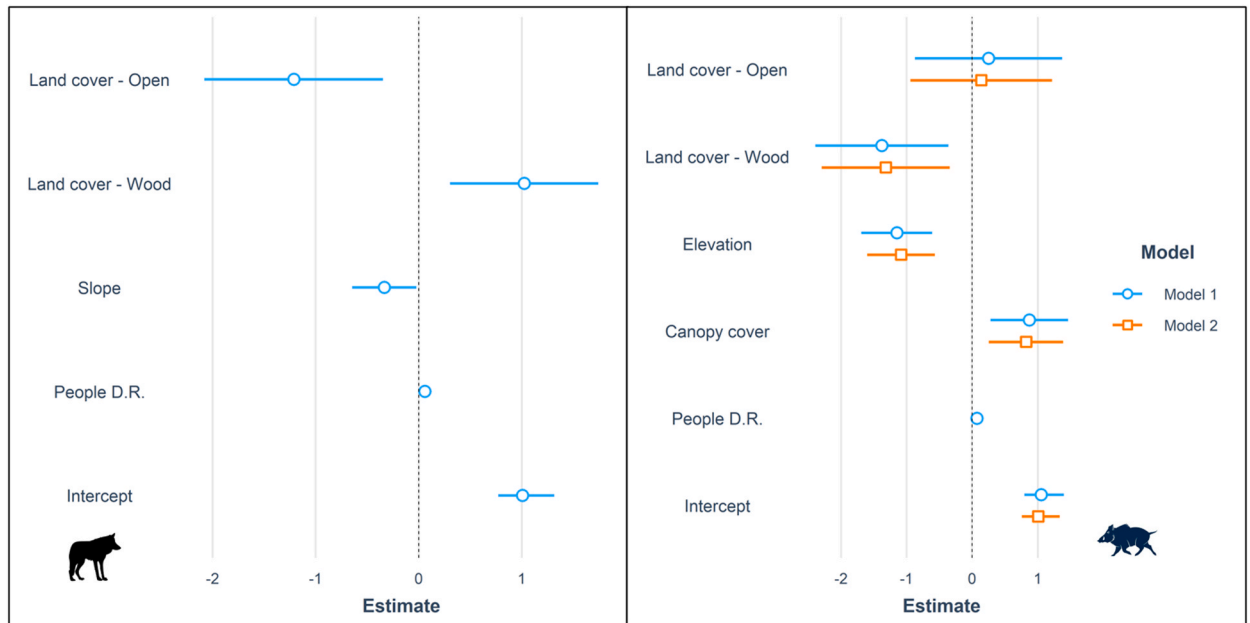
Fig. 5. Beta coefficients and their relative 95 % confidence intervals for significant predictors (p-value < 0.05) affecting spatial variation of monthly detection rates of the wolf (left) and wild boar (right), as estimated by the best-selected mixed model (based on AIC criteria) for the wolf and by the best and second-selected models for the wild boar.

(Nelson and Mech, 1986), which may increase the overall wolf predation on this species compared to less snowy areas.

Although the chamois and the roe deer were generally the main prey of the wolf during our study, the wild boar emerged as a substantial prey to this canid, being the most frequently used prey during the last autumn-winter period. The recent expansion of wild boar across Europe, including also the Alps (Massei et al., 2015), has contributed to increase the availability of a remunerative prey to wolves (Mori et al., 2016). Wolf is a plastic carnivore able to adapt its diet to the numerical fluctuations of prey populations and to the availability of new food items (Roffler et al., 2023; Sovie et al., 2023). The observed rapid increase in wild boar use in only a few years has also been reported in other studies (Lazzeri et al., 2024; Marucco et al., 2008). Long-term data on wolf diet is needed to discriminate whether the observed pattern of wild boar consumption is a stable trend or a temporary response to pulses in wild boar availability.

Wolf has been reported to select wild boar over other ungulates in Southern European countries, including Italy (Mori et al., 2016; Newsome et al., 2016; Zlatanova et al., 2014). Our results supported that the wolf used the wild boar according to its availability, thus no evidence of positive selection was provided. A major caveat to our interpretation of the Jacobs index is that, in the absence of data for all prey species, our estimates of prey availability could only be based on indices derived from camera trapping. Although we could not compare them with independent estimates of absolute densities used as reference values, indices based on the counts of individuals in each detection have been shown to strongly correlate with independent estimates in different study areas, ranking consistently ungulate species according to their estimated densities (Ferretti et al., 2023; Palmer et al., 2018; Tanwar et al., 2021). If confirmed for longer periods and at larger geographical scales, as well as by using estimates of prey densities obtained through independent methods, these results would indicate that wolf used wild boar according to their relative availability. If so, predation on this species would be expected to increase along with the spread of wild boar. Since the recolonization of the Alps by both species is a recent and ongoing process, future studies should assess patterns of wild boar use and selection by the wolf in the near future.

The temporal overlap between wolf and wild boar in all seasons indicated a substantial synchronization of the apex predator on this
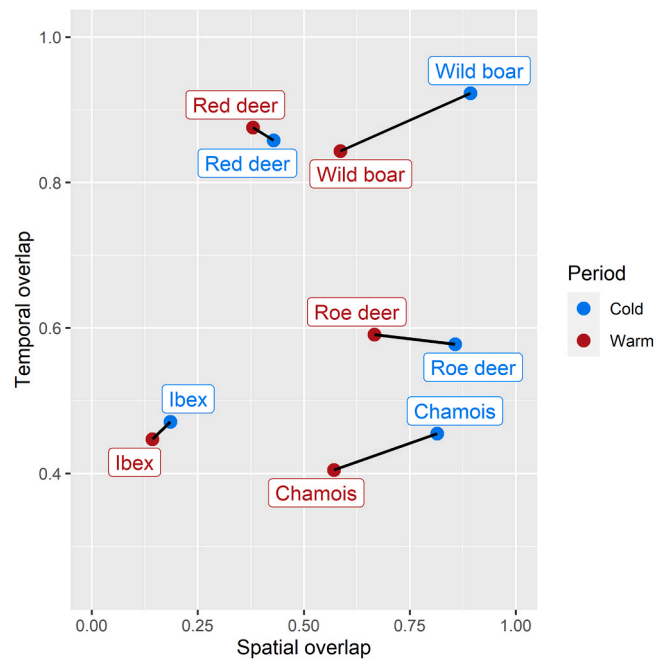
Fig. 6. Spatiotemporal associations between the five ungulate species occurring in the study area and the wolf, comparing autumn (September-November) and winter (December-February) with spring (March-May) and summer (June-August). Temporal overlap was estimated using the overlap coefficient (Ridout and Linkie, 2009), while spatial overlap was calculated using the Jaccard index.

suid (Mori et al., 2020; Rossa et al., 2021; Torretta et al., 2017). However, the reduction of temporal overlap and the lower activity of wild boar in sites with higher wolf activity in winter would suggest a potential spatio-temporal avoidance during that season. The randomization test confirms that the observed reduction of temporal overlap in winter was due to a change in wild boar pattern of activity. Being a thermophilic species, cold temperatures and snow are key limiting factors for wild boar (Scandura et al., 2022): winter is therefore likely to be a delicate season for this species, which may be more sensitive to wolf predation during this period. In summer, wild boar was less frequently detected in sites with higher wolf activity than in sites with lower wolf activity, but it did not modulate its temporal overlap with the predator, providing weaker support for temporal avoidance in this season. By simultaneously being less active (winter and summer) and by limiting its temporal overlap in sites more used by its predator (winter), wild boar confirmed its adaptability and plastic behavior even in a recently recolonized area. The higher activity of wild boar in HWS during spring suggests that wolf preferentially used sites where this suid was more active during this season. Combined with the high temporal overlap, this result indicates that wolf was able to increase predation on wild boar by synchronizing with the seasonal spatio-temporal patterns of this prey (Lazzeri et al., 2024; Torretta et al., 2017).

Our results suggest that the frequency of use of different sites by wolf was not driven by the wild boar one. We found the same pattern for the wild boar: as predicted, this ungulate may not rely on spatial avoidance as an antipredator strategy. In areas where suitable habitats are limited by ecological and/or anthropogenic factors, spatial avoidance seems to be very limited or absent (Ausilio et al., 2021; Murphy et al., 2021). In Alpine areas, steep slopes, rocky ground, as well as human encroachment on natural habitats, are therefore expected to lead wild boar to concentrate on the remaining patches of suitable habitats. In turn, the potential for antipredator behavior to develop into spatial avoidance would be limited. However, some differences in habitat associations emerged between our two study species. A decreased use of risky habitats, i.e. habitats where the predation risk is higher, is regarded as an antipredator response (Lima and Dill, 1990). Where predators use closed habitats more frequently, avoidance of these habitats in favour of open areas has been widely reported (Gehr et al., 2018; Gervasi et al., 2013; Mao et al., 2005; Thaker et al., 2011). However, ecotone and open habitats are also important foraging areas for wild boar (Ferretti et al., 2021b; Ferretti et al., 2021a). These habitats can provide both food resources and shelter and are usually selected because of nutritional and antipredator reasons. The availability of significant resources such as plants and invertebrates makes these habitats attractive to the wild boar, and rooting activity is often favored by soil features, humidity, as well as proximity to woodland (Calosi et al., 2024; Ferretti et al., 2021b; Ferretti et al., 2021a). Thus, further research is needed to clarify the relationship between habitat selection and predation risk in this species.

Combined spatiotemporal association was the highest for the wild boar, compared to the other ungulate species, particularly during the cold seasons. During this period, ungulates are usually forced by snow and cold temperatures to use lower elevations (Herfindal et al., 2019; Zweifel-Schielly et al., 2009). In V-shaped valleys such as the ones in our study area, this usually results in a smaller available area, which would explain the high spatial overlap with the wolf. Autumn and winter are therefore the seasons when the encounter probability with the predator would be expected to be higher. Results suggest that this may be particularly true for the wild boar, for which a substantial positive association with the wolf was recorded. These results underline the high potential vulnerability of

wild boar to wolf predation, especially during this delicate period, as supported by the analysis of wolf food habits: the suid was the most frequently used prey during the last autumn-winter of our study. During severe winters, weather conditions seem to play a major role in wild boar mortality, outweighing wolf predation (Jędrzejewski et al., 1992; Melis et al., 2006). However, as climate change is increasing mean winter temperatures, wild boar growth rate may be expected to increase (Melis et al., 2006; Vetter et al., 2015). The role of wolf predation in influencing wild boar populations under a climate change scenario should be assessed.

5. Conclusions

Our study contributes to shed light on wolf-wild boar interactions in recently recolonized areas of the Alps, a geographical region where complete information on these dynamics is still lacking. By simultaneously assessing interspecific interactions at three different scales, we were able to gain a wide overview of the role of wild boar in an alpine predator-multiprey system. Wild boar quickly passed from being an accessory prey to building up a major proportion of the wolf diet, becoming the prey with which this predator showed the highest combined spatiotemporal association within the whole ungulate community. Although our results provide some support for temporal avoidance in harsh seasons, alternative antipredatory strategies should be tested, such as variations in group size (Hebblewhite and Pletscher, 2002) or increased vigilance behavior (Chen et al., 2021; Esattore et al., 2023). In the context of predator-prey interactions, this suid is expected to gain more importance in the wolf diet even within the Alpine region (Mori et al., 2016), as the recolonization process goes on and temperature rise potentially favors growth rate and survival.

Considering the important ecological role of the wolf and the wild boar, their recent and ongoing spread in the Alps, as well as their relevance from the conservation and management points of view, assessing the temporal and spatial dynamics of their interactions will be crucial from both fundamental and applied perspectives. Increasing wild boar populations may be expected to further sustain and promote the spread of the wolf. In turn, the potential for wolf-wild boar dynamics to contribute to relaxed predation on other ungulates (e.g., the roe deer, Marucco et al., 2008, and the chamois, Palmegiani et al., 2013) or to other complex interspecific relationships (e.g., prey switching processes, Garrott et al., 2007, or apparent competition, Holt, 1977) should be assessed.

Ethics Statement

Not applicable: This manuscript does not include human or animal research.
If this manuscript involves research on animals or humans, it is imperative to disclose all approval details.

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Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Data availability

Data will be made available on request.

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