



Research Article

Ungulates and mesocarnivores temporal responses to wolf exposure: a case study on the ecology of fear in Gran Paradiso National Park

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Abstract

For both prey species and mesocarnivores, fear of predators can result in behavioural strategies that reduce predation risk and interspecific competition. Two common strategies are spatial avoidance of high-risk areas and modifying activity patterns. This study investigated, by the use of camera traps, the role of wolf (*Canis lupus*) predation risk in shaping the temporal patterns of four species of ungulates and two species of mesocarnivores in a protected area of the Italian Western Alps. Additionally, we looked into potential differences in the anti-predator behaviour of two species (the roe deer (*Capreolus capreolus*) and the wild boar (*Sus scrofa*)) related to the age class or the sex of the individuals. The activity of the wild boar resulted quite similar to that of wolf, but young and subadults were recorded more in low-risk sites. As regarding the main prey of the wolf, namely the roe deer, its activity became more diurnal in high-risk areas, with different peaks between male and female. The red fox (*Vulpes vulpes*) turned out to be strongly associated with the wolf, in terms of daily cycle, suggesting a positive interaction probably due to the trophic facilitation phenomenon. These findings further our understanding of the diversity of interspecific relationships and community responses to the gray wolf, a species whose range in Europe has undergone recent expansion.

Introduction

The concept of the ecology of fear has been adopted over the past two decades, to describe the whole impact of predators on prey populations and communities (Okarma, 1995; Brown, 1999; Kie, 1999; Creel et al., 2005; Winnie and Creel, 2007; Kittle et al., 2008; Zanette and Clinchy, 2019). Research on the “ecology of fear” starts from the assumption that the ecological role of predators does not end with direct killing, but rather prey efforts to avoid predation can cause a reduction in survival, with cascade effects across ecological scales (Gaynor et al., 2020; Daversa et al., 2021). For example, where predators are abundant, prey eat less and spend more time vigilant, and it has been demonstrated that this reduces prey growth and reproduction (Creel et al., 2014). In the ecological literature, fear is defined as an animal conscious or unconscious perception of predation risk and is manifested in specific behavioural outcomes. The combination of the spatial variation in predation risk, risk perception and prey response, create the so-called “landscape of fear” (Gaynor et al., 2019). The most common strategies to avoid death consist of adjustments in the spatiotemporal patterns or modulations of vigilance levels, foraging, movement, grouping and social behaviour (Ripple and Beschta, 2004; Theuerkauf and Rouys, 2008; Wirsing et al., 2010; Kuijper et al., 2013; Peers et al., 2018). These answers vary depending on individual factors such as sex, age, reproductive status, and body condition (Bontardelli et al., 2003; Winnie and Creel, 2007; Pipia et al., 2008). The ecology of fear is of major importance in large carnivores conservation. In fact, apex predators can also influence trophic networks where other carnivores insist (especially small and medium-sized species), by competition, in-

terspecific killing or trophic facilitation through carrion provisioning. Consequently, many carnivores mutate their space use and activity to minimize competition and predation (Forsyth et al., 2019). The complexity of these dynamics is affected by resource availability, habitat type and structure community (Sivy et al., 2018). The fear that top predators induce in mesocarnivores and large herbivores can affect the entire ecosystem structure and function, so the evolution of the “landscape of fear”, due to the loss of large carnivore in some areas and their expansion in other, represents a steady conservation issue (Clinchy et al., 2016).

In North America it has been observed that wolf affects habitat and resource selection in elk, moose, and white-tailed deer (Okarma, 1995; Creel et al., 2005; Winnie and Creel, 2007; Kittle et al., 2008). In Europe, the exposure to this predator increases the vigilance levels and shapes the escape tactics of the chamois and influences the spatial and temporal patterns of several species of ungulates and mesocarnivores (Baruzzi et al., 2017; Torretta et al., 2016; Grignolio et al., 2019; Rossa et al., 2021). The temporal patterns analysis is a good way to visualize the landscape of fear, since it provides information about the avoidance levels of the predator and the behavioural interactions between the species. Usually, in wolf-ungulates systems, temporal patterns show a partial overlap, and result from a compromise between food requirements and the anti-predator strategies. In mesocarnivores, these patterns are also the outcome of the niche partitioning, hence a certain degree of avoidance is expected, depending on the species. Few studies in Italy about the wolf have focused on the structure of the landscape of fear (Torretta et al., 2016; Mori et al., 2020; Rossa et al., 2021). Given the above, results significant to expand the knowledge on the ecological role of the wolf in the Alps, which is considered a priority area for conservation and one of the richest biodiversity hot spots in Europe

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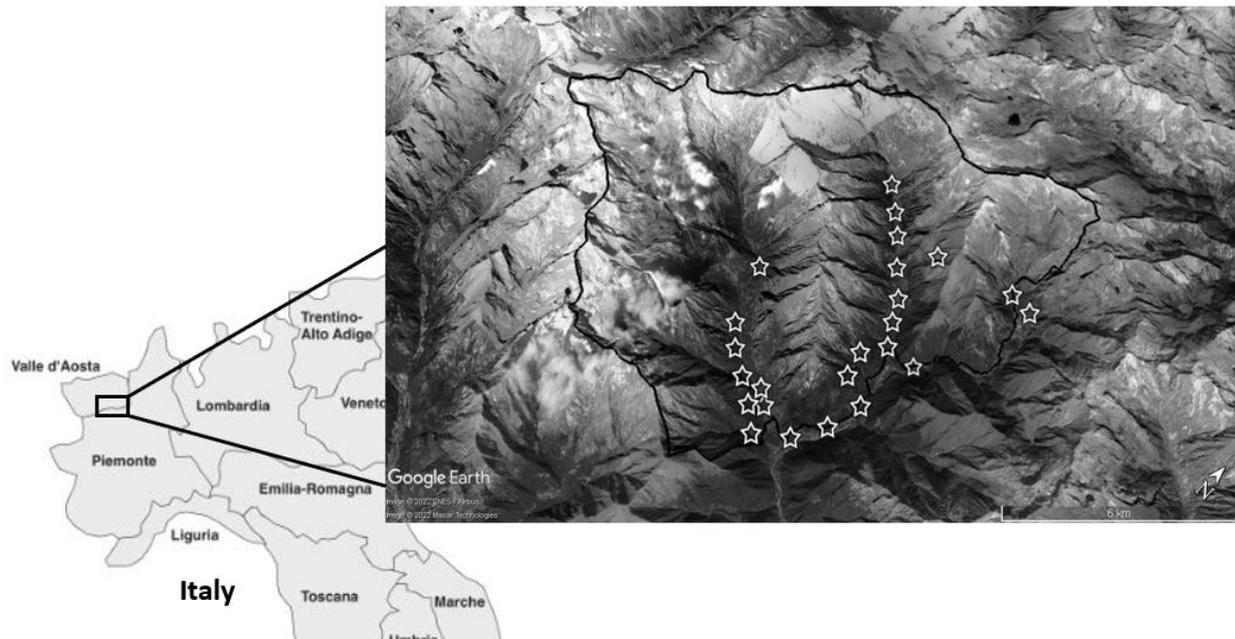


Figure 1 – Map of the study area showing camera traps locations. The black line marks the borders of the Soana Valley.

(Gazzola et al., 2005). In this paper, we aimed at investigating in a protected area of the north-western Italian Alps, using camera traps, the effect of wolf predation risk on the temporal patterns of four species of ungulates [the alpine chamois (*Rupicapra rupicapra*), the wild boar, the red deer (*Cervus elaphus*), and the roe deer] and two species of mesocarnivores [the badger (*Meles meles*) and the red fox]. In particular, we want to verify if: (i) the wolf presence can alter the temporal patterns of the other large mammal species evaluating the magnitude of any variation on the main prey (roe deer and chamois; see Larentis, 2016); (ii) the target species activity differ between sites more or less used by the top predator; (iii) there are sex-specific differences in the temporal distribution of the roe deer, related to an anti-predator proactive behaviour; and finally (iv) if the proportion of adults, subadults and young wild boar changes between sites more or less used by the wolf.

Material and Methods

Study area

The study took place in the Soana Valley (45°30'8.94" N 7°32'48.52" E), an alpine area of the Gran Paradiso National Park (c. 710 km², North-West Italy; Fig. 1), which extends for 152.6 km² from 345 to 3408 m a.s.l. The climate is continental, with prolonged snow cover in winter and short and fresh summers (Bisio, 2003). The vegetation cover consists of 10% deciduous forest dominated by beech (*Fagus sylvatica*), 15% coniferous forest dominated by larch (*Larix decidua*) and european spruce (*Picea abies*), 10% alpine shrublands, 30% alpine grasslands and 35% siliceous screes, cliffs and glaciers (Giuliano et al., 2019 for general information). Five wild ungulates reside in our study area: the wild boar, the red deer, the roe deer, the alpine ibex (*Capra ibex*), and the alpine chamois. Carnivores include the red fox, the badger, the least weasel (*Mustela nivalis*), the stoat (*Mustela erminea*), the stone marten (*Martes foina*), the pine marten (*Martes martes*) and a stable pack of seven Italian wolves (B. Bassano and E. Avanzinelli, unpubl. data). Other lagomorph and rodent species also occur in the Soana valley. The area is protected from hunting since 1922 and has a very low human population density.

Data collection: camera trapping

Data on temporal patterns were collected using camera traps for two straight winters, from November 2016 to March 2017 and from November 2017 to March 2018. Over both periods the cameras worked continuously. A total of 24 motion-sensitive cameras (IR-Plus UV565HD)

were placed on as many sites across the study area, at a height of 50 cm from the ground and ca. 500 m distant (Rehman et al., 2021). We used the same 24 sites in both years.

Our study design was opportunistic due to limited resources. Suitable points to install cameras were chosen based on wolves signs of presence, to maximize detections. We also used presence of prey species to identify camera locations. All the cameras were set to record videos of 60 seconds, reporting the time and day of capture, with no trigger delay and a minimum time lag of 5 seconds. We checked cameras every 10 days to replace batteries and download the files (Oberosler et al., 2017).

Data collection: video processing

By analysing the videos, we identified the target species, recording date, time, number of individuals and camera trap location. Plus, we noted the sex of the roe deer and the age class of the wild boar. Videos in which it was not possible to recognize the species and their features were discarded. To reduce pseudo-replication, multiple records of a same species in less than 30 minutes were considered as a single event, taking as reference the date and time of the first video.

Temporal patterns

All statistical analyses were conducted through the R software, version 4.0.3 (R Core Team, 2020), using the “activity”, “circular” and “overlap” packages (Lund et al., 2017; Meredith and Ridout, 2017; Rowcliffe, 2021).

According to Ridout and Linkie (2009), we investigated the temporal activity patterns in two ways: (a) We divided the records of each species in 4 classes: day (between 1 hour after sunrise and 1 hour before sunset), night (between 1 hour after sunset and 1 hour before sunrise), dawn (from 1 hour before sunrise and 1 hour after sunrise) and dusk (from 1 hour before sunset to 1 hour after sunset). Then, we determined the utilization of each class using Ivlev’s index of electivity, that varies from -1 (avoidance) to +1 (preference), with zero indicating random selection (Sanchez-Hernandez et al., 2014). The Ivlev index of electivity (E) derives from trophic ecology. It measures the utilization of food types (r) in relation to their abundance or availability in the environment (p), with the formula $E_i = (r_i - p_i)/(r_i + p_i)$, where r_i is the proportion of food in the diet and p_i is the proportion of food in the environment (Lechowicz, 1982). We employed this formula to compare the relative availability of different times of the day respecting

Table 1 – List of camera-trap records of each species. The naïve occupancy (ψ) is computed as the number of sites the species was trapped divided by all sites sampled ($n=24$). The capture rate (or RAI: relative abundance index) was calculated as the number of captures divided by all camera days and multiplied by 100 (i.e. records per 100 days of camera trappings).

Species	Guild	Records	RAI	Native ψ
Red fox	Omnivores	864	23.24	0.76
Roe deer	Herbivores	283	7.61	0.56
Wolf	Carnivores	280	7.53	0.92
Wild boar	Omnivores	141	3.79	0.72
Red deer	Herbivores	123	3.31	0.48
Badger	Omnivores	99	2.66	0.52
Alpine chamois	Herbivores	40	1.08	0.32

the total length of the day (p_i) and their relative utilization from each species (r_i). Since some times days are more available than others, we obtained the sunrise and sunset hours during each camera operational period using the software Moonphase (version 3.3) (Rossa et al., 2021); (b) We calculated the temporal patterns on a scale of 4 months (December–March) by applying Kernel’s density estimation method. This method returns specific density function wherein the area under the curve represents the probability to observe an animal at each time of the day.

Overlap coefficients

Temporal overlap assessment between the wolf and the other species was performed through the non-parametric calculation of the overlap coefficient (Δ) (Montoya et al., 2019). The overlap estimate can assume values ranging from 0 (no temporal overlap) to 1 (complete overlap). For each species we chose $\Delta 1$ coefficient when we had less than 75 time records, and coefficient $\Delta 4$ when the number of time records was greater than 75. Finally, we derived 95% confidence intervals for the overlap coefficients by 999 bootstrap resampling.

Temporal patterns in sites with low wolf and high wolf activity

To analyse daily activity patterns of prey and carnivores between sites more or less intensely used by wolves, we determined wolf average passage rate among all locations (number of observations/number of camera trap operational days) (Oberosler et al., 2017; Rossa et al., 2021). Using the mean as a threshold value (0.15 observation/day) we got 6 “high wolf activity sites” (HWS), in which wolf occurrence is equal or greater than 0.15, and 19 “low wolf activity sites” (LWS), in which wolf occurrence is lower than 0.15. Then we compared the overlap coefficients Δ between the wolf and each species in the two site types.

Roe deer sex-specific responses and wild boar age structure

Considering that ungulates’ antipredator strategies could be affected by individual features as age class and sex, we decided to 1) compare how female and male roe deer activity overlap with wolves and 2) determine the age structure of the wild boar and the capture frequencies of each age group between HWS and LWS. For the first purpose, we estimated the Δ overlap coefficient between the wolf and each sex. For the second purpose, the wild boar population has been divided in three age classes: young: < 1 year old; subadults: 1–3 years; adults: > 3 years. About age class distinction, our approach was to rely mainly on the coat colour, brown with dark longitudinal stripes in young individuals, uniformly red in the subadults and dark brown in adults. Subadults have been distinguished from adults also on the basis of the homogeneous distribution of the body mass, unlike the adults where it is more developed in the forequarters (Mattioli and De Marinis, 2009). Then we calculated the relative frequencies of each age class at two spatial levels: the study area and the LWS/HWS. The comparison of the age structure within HWS and LWS has been realized through Pearson’s chi-squared test for contingency tables (Bontardelli et al., 2003).

Results

Summary statistics & temporal patterns

In 3717 camera days, we collected 1830 videos. Descriptive statistics and records of each species are reported in Tab. 1.

The results of Ivlev’s index (Supplementary material: Figure SF1) show that the wolf, the wild boar, the badger, and the red fox are active mainly at night. Kernel’s density estimations for each species, with 95% confidence intervals, are reported in Fig. 2.

Interspecific overlap

The overlap coefficient between the wolf and red fox is high ($\Delta=0.82$), as well as between the wolf and the wild boar ($\Delta=0.81$). Slightly lower delta values appear for the badger and the red deer ($\Delta=0.69$).

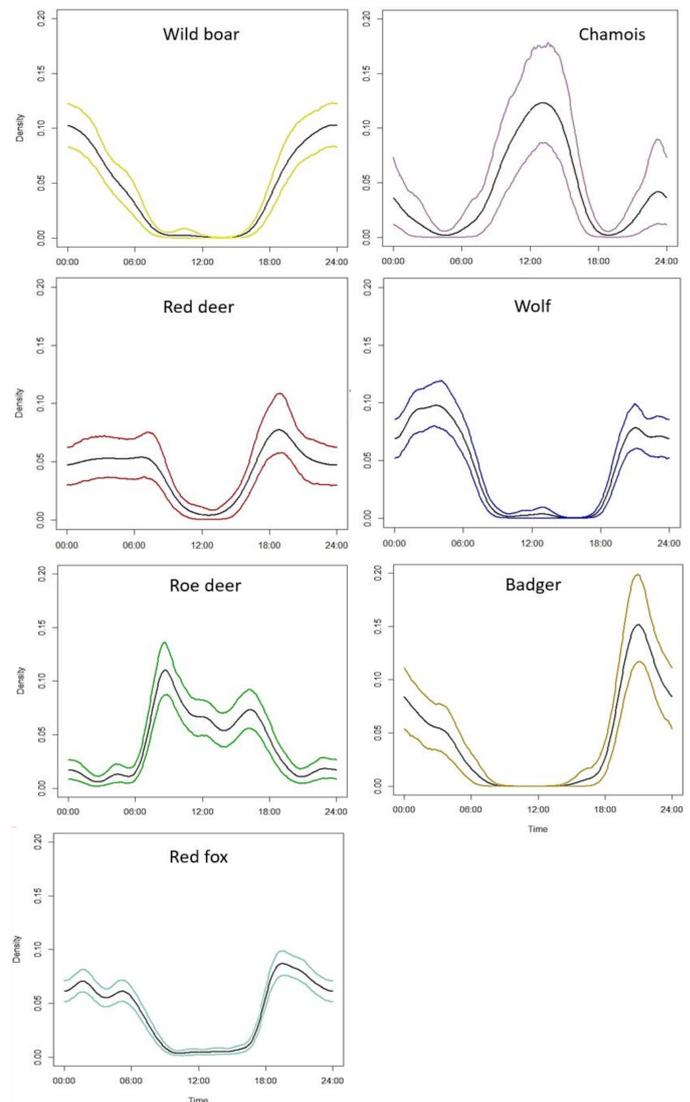


Figure 2 – Temporal activity patterns of the study species. Coloured lines represent 95% confidence intervals.

Table 2 – N. of videos for each species in high wolf and low wolf sites. In HWS the top predator passage rate is equal or greater than the average one. In LWS the passage rate is lower than the average one.

Species	HWS	LWS
Wild boar	100	43
Roe deer	98	188
Red fox	415	449
Badger	59	40

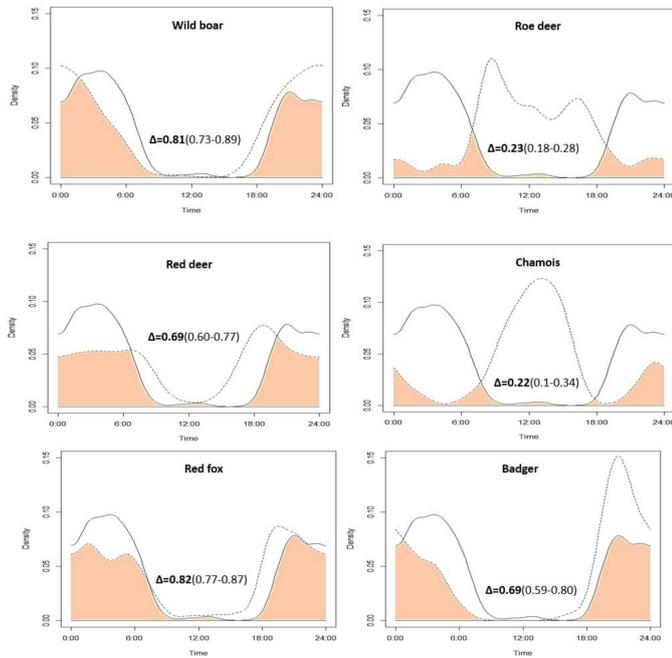


Figure 3 – Temporal overlap between the wolf and the study species. The solid line indicates wolf activity.

Conversely, the overlap between the wolf, the roe deer and the alpine chamois is very low ($\Delta=0.23$) (Fig. 3 and 4).

Comparison between LWS and HWS

These analyses concern only the wild boar, the roe deer, the badger and the red fox, because a minimum of 40 records is needed to build 95% confidence intervals. Table 2 shows the total number of records for each species in HWS and LWS.

The temporal overlap between the badger and the wolf, tends to increase in HWS, as shown by the difference in the confidence intervals for the two scenarios. The amount of wild boar, roe deer and red fox activity overlap with wolves is not affected by whether wolf use is high or low. Nevertheless, the roe deer has a different activity peak to wolves when wolf use is high (Fig. 5).

Roe deer sex-specific responses

The sample size was consistent for this analysis: we collected 108 records of male roe deer and 141 records of female roe deer. For both genders, the temporal overlap with the wolf is very low. Moreover, roe deer male and female do not have significantly different temporal pattern, as shown by their confidence intervals value. Instead, they have different activity peaks to wolves: female activity focuses on daytime hours, while male daily cycle looks bimodal with a peak after sunrise and another before sunset (Fig. 6).

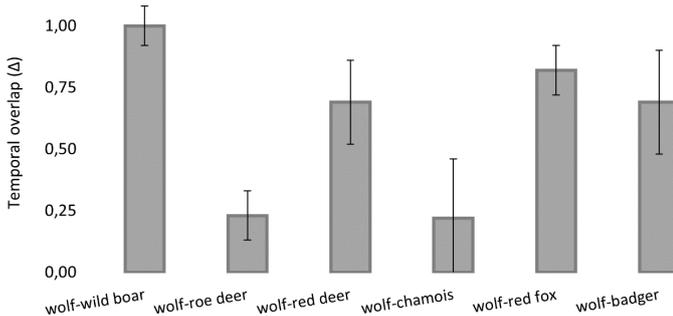


Figure 4 – Overlap coefficients (Δ) of temporal activity patterns between the wolf and six species of mammals with their 95% confidence intervals.

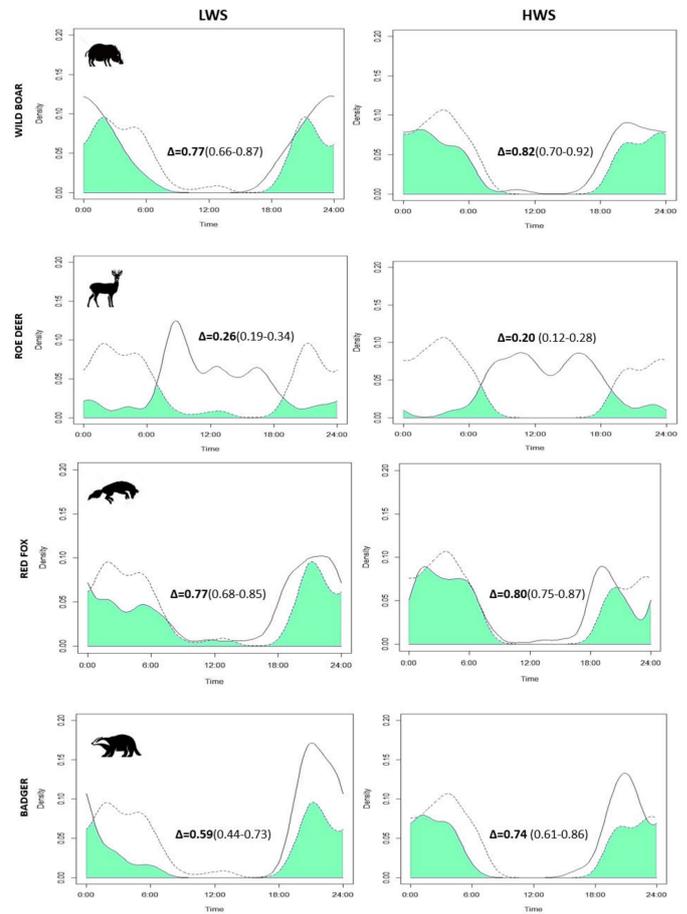


Figure 5 – Daily activity patterns (kernel densities) of the wild boar, the red fox, the badger and the roe deer in HWS and LWS. The light green area represents the overlap with the wolf. The dotted line indicates wolf activity, the solid line relates to the activity of the other species. Overlap coefficients (Δ) are shown with their confidence intervals.

Wild boar age structure

During our study period, 70% of the boars caught by the cameras were adult. The proportion of subadults was 28%, that of young was 2% (Figure SF2). There is a significant relation (Chi-squared test: $\chi^2=19$, $p<0.05$) between HWS/LWS and wild boar age classes: HWS are characterized by a greater number of adult individuals and a minor number of groups of adults, subadults and young (Fig. 7).

Discussion

Effects of wolf presence on ungulates

The structure of the landscape of fear depends by the frequency of wolf occurrence across the area, and on how it takes advantage of its hunting territory (Kittle et al., 2008). The interaction between these factors creates spatial and temporal refuges for the preys. Therefore, the temporal variable, referred to the daily cycle of a species, is a niche dimension in which prey may differ from predators, increasing their chances for survival (Smith et al., 2019). From this research we expected a validation of the typical dynamic relationship of predator-prey systems: wolf was supposed to synchronise its hunting pattern to the period of the day in which prey are most vulnerable, conversely ungulates, in particular the main prey, were supposed to reduce the temporal overlap with the wolf by harnessing its downtimes periods, or by dropping the activity during high-risk times (Monterroso et al., 2013). The results obtained show that the wolf is strictly nocturnal, during winter in the Soana Valley. This is consistent with both other findings (Pagon et al., 2013; Rossa et al., 2021) and its hunting strategy. In fact, wolf is a nocturnal and crepuscular predator which uses low light conditions to closely approach ungulates without detection (Ripple and Beschta, 2004). The overlap between the wolf and its main prey, the roe deer, turned out to be low. The interpretation of this result must consider the fact that

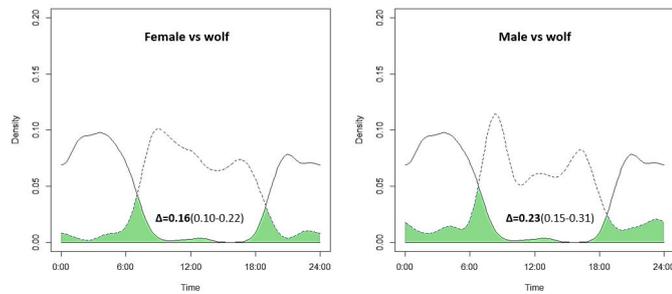


Figure 6 – Daily activity patterns (Kernel's densities) between wolf, male and female roe deer. The green area represents the overlap with the wolf. The solid line indicates wolf activity, the dotted line relates to roe deer activity. Overlap coefficients (Δ) are shown with their confidence intervals.

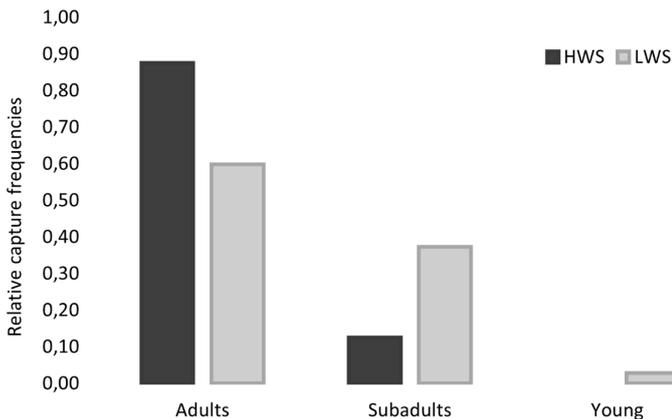


Figure 7 – Proportion of adults, subadults and young wild boar within HWS and LWS.

the activity levels of the roe deer reach a minimum peak during winter nights in temperate regions, consequently to the nocturnal hypometabolism of this species, a physiological adaptation to save energy (Pagon et al., 2013). In HWS, the daily cycle of the roe deer shows a diurnal bimodal pattern. While it is true that the roe deer is most diurnal during winter (Benesch et al., 2013; Stache et al., 2013; Niedballa et al., 2019), it has also been proven that ruminant bimodal patterns are in line with anti-predator strategies. A recent study conducted in nine geographical regions across Europe, shows a marked plasticity in roe deer diel activity patterns in response to spatio-temporal variation in predation risk. In particular, in the presence of their main natural predator, roe deer are relatively more diurnal (Bonnot et al., 2020). Hence, the two observed peaks of the roe deer observed in Soana Valley may reflect an intensification of the grazing efforts when the risk of predation is low (Monterroso et al., 2013). Endogenous factors, such as the sex of the individuals, drive roe deer's activity, but fluctuations arise only during spring and summer, when the male territoriality phase occurs (Pagon et al., 2013). Hence, it is conceivable that the different activity peaks observed between males and females are caused by sex-differences in vulnerability to predation, related to the social organization of the species. Indeed, during winter, males are solitary while females live in small groups, and the aggregation increases the detection of predators (Lingle, 2001). An anti-predator strategies based upon a temporal avoidance of the predator is functional for a species whose escaping possibilities given an encounter are low. In fact, the roe deer is not properly adapted to snowy environments (Ripple and Beschta, 2004; Canalis, 2016). Red deer activity in Soana Valley reflects the normal bimodal trend of the species during winter (Kamler et al., 2007). There is an interesting shift compared to wolf activity, perhaps because the red deer is the second prey in terms of biomass (Larentis, 2016). However, a larger sample is needed to investigate predation risk effects on this ruminant. The temporal pattern of the wild boar is quite similar to the wolf. We can explain this finding by making two considerations: first, the wild boar is not the mainstay of wolf's diet in Soana Valley (Lar-

entis, 2016); second, during the study period wild boar population was mainly composed of adults, for whom predation risk is very low, given that the wolf in Italy feeds on subadults and piglets (Mori et al., 2016). However, groups of young wild boars with adult females and groups of adult and subadult males have been spotted majorly in low risk areas. A low overlap value between the chamois and the wolf is in line with the expected, considering that this ungulate is a very diurnal species. Prey with a high probability of escaping from an encounter with the predator do not alter their temporal or spatial behaviour as an anti-predator response. The escape strategy of the chamois typically relies on the ability to reach quickly inaccessible rocky walls (Wirsing et al., 2010).

Effects of wolf presence on carnivores

Coexistence among different species of carnivores is promoted by reducing the breadth of utilization of one or more niche dimensions, and this might occur through a spatial and/or a temporal segregation (Monterroso et al., 2014). In Soana Valley, the temporal patterns of the red fox and the wolf are almost equal, as expected for the winter season. In alpine habitats, the snow cover affects red fox's diet, that becomes strictly dependent on ungulate carcasses to balance the lack of small mammals, fruits, and insects. The alpine chamois is the most eaten ungulate carcass by the red fox in the Gran Paradiso National Park during winter (Giuliano et al., 2019) and, concurrently, is the second prey of the wolf (Larentis, 2016). Wolf predations on roe deer and chamois shall leave a significant number of carcasses over the territory, and arguably the red fox benefits in following wolf movements and activity, according to studies which have proven that under high stress conditions, like those of the cold season, large predators indirectly facilitate mesocarnivores (Prugh and Sivy, 2020). As regarding the badger, based on previous works, we expected a low activity overlap with the wolf (Torretta et al., 2016). Our results show the contrary: the overlap is high, and badger's activity increases in high-risk areas. Even if it is well known that the badger is strictly nocturnal in all seasons (San et al., 2007), this partially explain our findings. At present, data on the relation between the wolf and the European badger are scarce, so this issue deserves a deeper investigation. This study is effectively on the impact of one pack of seven wolves. The behavioural tendencies, personalities, and culture of this pack as well as the specific local conditions and the personality of the other species, may greatly affect the transferability of these findings to other localities. We also recognize that an opportunistic sampling design has its limits, especially because it can incorrectly estimate detection, since species have different detection probabilities, or the detectability changes across different sites, but in some cases if resources are constrained and if the data are not used to estimate species occupancy or species-habitat relationships it may be appropriate (Stein et al., 2008; Ash et al., 2021). Interspecific relationships are extremely complex and regulated by subtle mechanism, and have the potential to affect individual behaviour, phenotypical traits and populations dynamics. Therefore, to deeply understand how wolf predation risk can structure alpine ecosystems and, consequential, the future role of this expanding species in Europe, we encourage a long-term research based on a rigorous sampling design, extended over all season and taking into account the specificities of different wolf packs together with the emergent properties of the communities. ☞

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Supplemental information

Additional Supplemental Information may be found in the online version of this article:

Figure S1 Day period selection from each species.

Figure S2 Proportion of adults, subadults and young wild boar detected in the study area.