Research Article

Are females more scared than males? Sexual differences in the spatiotemporal responses of deer to wolves

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Abstract

Predators can indirectly stimulate the development of anti-predator strategies in prey species. Within populations, these behavioral responses may vary according to sex and age classes of individuals, although the existing literature presents conflicting results. Using camera trapping, spatiotemporal responses to the wolf *Canis lupus* were assessed in relation to sex and age classes in two prey species, the fallow deer *Dama dama* and the roe deer *Capreolus capreolus*, within a Mediterranean area recently recolonized by this canid. In fallow deer, results suggest stronger temporal avoidance in females than in adult males, increasing their diurnal activity as the wolf detection rate increased and reducing their temporal overlap with the predator. In roe deer, the avoidance responses were less marked, but females, particularly during the warm period, exhibited different activity patterns compared to males. Smaller body size (fallow deer) and presence of offspring are expected to make females more vulnerable to predation, which would emphasize the perceived predation risk in these individuals, in turn promoting a stronger response to predators compared to males. Females of both species may adopt different activity patterns from males to minimize temporal overlap with the wolf and reduce the risk of direct predator encounters. By providing support to sexual differences in antipredator responses, our results provide a novel contribution to increasing knowledge on the indirect effects of recolonizing predators in human-dominated landscapes of Europe.

Introduction

The composition of ecological communities is shaped by interspecific interactions (Birch, 1957; Rosenzweig, 1966). Predator-prey dynamics are among the most influential interactions, capable of significantly altering food webs and generating cascading effects across different trophic levels (Hebblewhite et al., 2005; Estes et al., 2011). Predators influence prey not only by increasing mortality rates but also by altering prey density, distribution, habitat selection, and behaviour. (Ripple and Beschta, 2012; Weterings et al., 2022). For example, the presence of a predator can stimulate the development of anti-predator behavioural strategies by the prey. These responses may include increased vigilance, larger group sizes, and behaviours that reduce spatial and/or temporal overlap with the predator (Ross et al., 2013; Lazzeri et al., 2024a). Specifically, to minimise the probability of encountering a predator, prey may avoid activity centres and areas with high predator density ("spatial avoidance"; Creel et al., 2005; Fortin et al., 2005; Kuijper et al., 2013) and/or modify their circadian activity patterns to reduce temporal overlap with the predator (Palmer et al., 2021). Such strategies are driven not only by natural predators but also by humans, who, as apex predators, can exert pressures similar to those of natural predat-

ors (Estes et al., 2011; Darimont et al., 2015). Anthropogenic activities, such as hunting, urbanisation, and recreational activities, can alter wildlife behaviour, changing their activity patterns and space use to reduce the risk of interaction with humans (Kuijper et al., 2016).

European contexts, heavily altered by human activities, are characterised by the recolonisation of large predators, such as the wolf *Canis lupus* (Chapron et al., 2014; Di Bernardi et al., 2025). In these areas, several studies have examined the spatiotemporal dynamics between predators and prey (Kuijper et al., 2013, 2015; Sand et al., 2021; Rossa et al., 2021). Information is scarce on how these responses to predators may differ based on sex and age. For example, females have been often shown to carry out vigilance activities more frequently and for longer time than males (e.g., red deer *Cervus elaphus*: Childress and Lung, 2003; Kuijper et al., 2014; roe deer *Capreolus capreolus*: San José et al., 1996; Apennine chamois *Rupicapra pyrenaica ornata*: Ferretti et al., 2014; fallow deer: Pecorella et al., 2019). In species showing sexual-size dimorphism, this difference has been linked to a higher vulnerability to predation in females than males, associated with smaller body size as well as the presence of offspring (Main et al., 1996; Ruckstuhl and Neuhaus, 2002; Bowyer, 2004). Furthermore, younger individuals are generally vulnerable to predation because of inexperience (Jorgenson et al., 1997; Gaillard et al., 2000). These differences in some aspects of antipredator behaviour may suggest the potential

for sexual differences in spatiotemporal responses to predators, but information is still scarce.

For females, vulnerability to predation risk may primarily arise from two factors. First, body size influences individual sensitivity to predation risk (Cohen et al., 1993; Sinclair et al., 2003). In polygynous species, where females are generally smaller than males, they may perceive a higher risk, as their lower body mass makes them more vulnerable to predatory attacks (Main et al., 1996; Ruckstuhl and Neuhaus, 2002; Bowyer, 2004). Secondly, the offspring represent one of the most vulnerable categories to predation (Linnell et al., 1995). During the periods when females are accompanied by their offspring, they are more exposed to the risk of predation due to the increased visibility and vulnerability associated with the presence of kids (Hunter and Skinner, 1998; Childress and Lung, 2003; White and Berger, 2001). Among males, young individuals may use ineffective anti-predatory behaviours because they may not have yet developed the skills to recognise danger signals or to adopt effective defensive behaviours (Jorgenson et al., 1997; Apollonio et al., 1998; Gaillard et al., 2000; Mech and Peterson, 2003). Considering these observations, differences in perceived predation risk would be expected among individuals of different sex and age (Main et al., 1996; Bowyer, 2004; Owen-Smith , 2008). The most vulnerable categories would adopt more pronounced anti-predator strategies, such as altering their spatiotemporal behaviour through the use of sites deemed safer and/or specific times of the day when the risk of predation is reduced (Caro et al., 2004; Ciuti et al., 2006; Ross et al., 2013; Grignolio et al., 2019).

This study evaluated sexual differences in spatial and temporal responses to the wolf, in relation to sex and age classes, in two prey species, the fallow deer *Dama dama* and the roe deer, within a Mediterranean area recently recolonised by the predator. Previous work showed a strong response of fallow deer based on temporal avoidance, with a progressive switch to diurnal rather-than-nocturnal activity throughout the years since wolf recolonisation, whereas results were not conclusive for the roe deer (Rossa et al., 2021; Esattore et al., 2023; Lazzeri et al., 2024a). The occurrence of sexual differences in temporal and spatial response to the wolf was not tested. We expected that females showed a lower temporal overlap with the wolf, a stronger temporal response (i.e., a greater diurnal activity), as well as spatial response to the wolf than males. Among males, we expected stronger responses in young individuals compared to adult ones (Ciuti et al., 2006; Ross et al., 2013). This outcome may be due to the smaller body size of females (only in fallow deer) and the need to protect offspring, whereas young males may be more vulnerable due to their inexperienced defensive behaviour (Gaillard et al., 2000; Sinclair et al., 2003; Lung and Childress, 2007).

We assessed support to the following predictions: (*i*) females and young males exhibit different activity patterns compared to adult males, with a lower temporal overlap with the apex predator; (*ii*) occurrence of diurnal *vs.* nocturnal activity of females and young males – but not that of adult males – increases in sites with higher wolf detection rates; (*iii*) the spatial variation of detection rates of females and young males – but not that of adult males – is negatively affected by that of wolves.

Materials and methods

Study area
Our study was conducted in the Maremma Regional Park, a protected area located in central Italy (MRP; ∼ 90km², Figure 1; 42.626 371° N, 11.099 303° E). The local climate is Mediterranean, with dry summers and wet winters (mean daily temperature: 9–24°C; monthly precipitation: from 9.3 mm in July to 81.8 mm in November; Ferretti et al., 2021a). The topography of the study area is predominantly hilly, with the highest point being the Uccellina Hills (417 m a.s.l.).

The vegetation is predominantly composed of Mediterranean scrub wood (40 %), dominated by holm oak *Quercus ilex* L. and including species such as strawberry tree *Arbutus unedo* L., rosemary *Salvia rosmarinus* L., juniper *Juniperus* spp., rockrose *Cistus* spp., and other trees/shrubs typical of Mediterranean habitats (e.g. *Pistacia lentiscus* L., *Juniperus* spp., *Phyllirea* spp., and *Myrtus communis* L.). Other
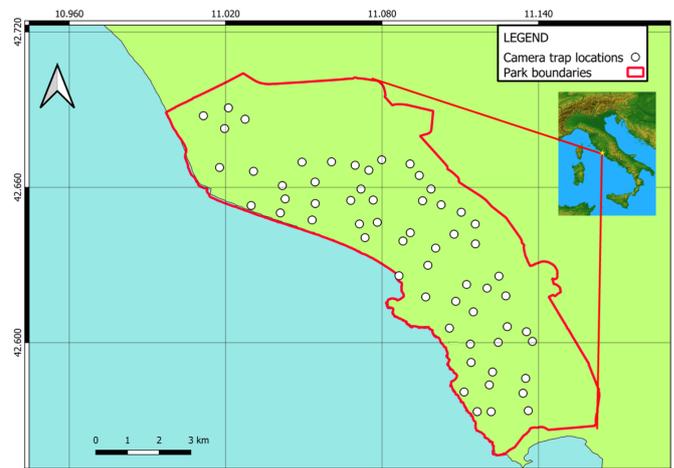
Figure 1 – Map of the study area with the location of the camera trapping sites (points) monitored from April 2022 to March 2023. The red line indicates the borders of Maremma Regional Park.

habitats present in the area are pine forests (9 %, mainly domestic pine, *Pinus pinea*), wetlands (5 %), crops (30 %; mainly wheat, cereals, and sunflowers in summer, locally irrigated) and habitats which we termed "ecotones" composed of open meadows, set-aside grasslands, and pastures, including olive groves partially abandoned and recolonised by scrubwood (13 %). The remaining area is covered by human settlements (2 %) and other habitats (mostly seaside, 1 %). Three wolf packs were present in the area during our study (Ferretti et al., 2023b). The diversity of habitats and prey present in the Park, along with the well-documented process of wolf recolonisation (Esattore et al., 2023; Lazzeri et al., 2024a,b), makes the area an ideal site to study the potential impact that an apex predator can have on mammal communities. In addition to wolves, large wild mammals in the area include fallow deer, wild boar *Sus scrofa*, and roe deer. Medium-sized mammals present in the region are the crested porcupine *Hystrix cristata*, the coypu *Myocastor coypus* (an alien species), the European brown hare *Lepus europaeus*, the red fox *Vulpes vulpes*, the European badger *Meles meles*, the European wildcat *Felis silvestris*, the stone marten *Martes foina*, and the pine marten *Martes martes*, with several species of smaller mammals. Livestock are also present locally (∼ 20 heads/km²), including free-ranging cattle and horses, in addition to two sheep flocks (Ferretti et al., 2019). The study area is characterised by a high density of wild ungulates (fallow deer: 6.8 individuals/km²; roe deer: 2.9 individuals/km²; wild boar: 10.4 individuals/km²), with estimates based on faeces counts conducted in the summer of 2022 (Ferretti et al., 2023a; Lazzeri et al., 2024b). Hunting is forbidden in the Park; the Park Agency carries out the numerical control of fallow deer and wild boar populations to minimise the negative impact of these species on priority habitats and agriculture. During our study, wild ungulates dominated the wolf diet, with wild boar and fallow deer being the major prey (60–46 % and 32–23 % occurrences/volumes in diet, respectively, 2016-2023, Ferretti et al., 2019; Lazzeri et al., 2024b)

Data collection
Data were collected using camera trapping from April 2022 to March 2023. The non-agricultural region of the study area (approximately 60 km²) was divided into cells by overlaying a sampling grid (cell size 1× 1 km; Lazzeri et al., 2024a) using a Geographic Information System (QGIS 3.16 Hannover). A single camera trap was deployed within each cell, followed by placement at suitable sites for detecting mammal activity. In this way, 60 camera trap locations were identified and installed. Camera traps have been deployed at an average height of *c*. 75 cm and placed on suitable trees, along animal paths,trails, forest roads, to optimise the detection of medium/large mammals. The camera traps were located at a minimum distance of about 700 meters between each camera. Various motion-sensitive camera models were

used (Owlzer Guard Z2; Comitel Guard Micro 2; Ir-Plus HD and Ir-Plus 110 °C; Comitel Guard), activated by a passive infrared (PIR) sensor with a trigger time of ≤ 1 second. The cameras were supplied with 32/64 GB SD cards and external batteries, set to operate around the clock and to record videos of 10 seconds each. The sampling effort at each location was determined by the number of days between the installation and checkout of the camera, excluding the days with malfunctioning or battery failure. The camera traps were checked monthly to ensure their proper functioning and to collect the videos stored on the SD cards. From each video, the following information was extracted: date, solar time, species, number of individuals, group size, and camera location. All these data were included in a dataset. Subsequently, an operator (I.B.) classified each individual of the study species (fallow deer and roe deer) based on sex and age class. The 'fawns' age class (i.e., < 1 year old individuals) was not considered, as it is known from the species' ecology that these individuals are always accompanied by the mother or other adults (Boitani et al., 2003). Therefore, the spatial and temporal behaviour of fawns is strongly influenced by that of the mother. The video recordings, of sufficient quality to identify sex and age class, when possible, allowed the recognition of species-specific distinctive features even at night. When identification was not possible, individuals were classified as 'undetermined' (22 % of the total classified individuals). For roe deer, a simple distinction was made between males and females. In the case of fallow deer, the classification was initially based on sex, with a further subdivision of male individuals into two age classes: 'adult' males (males older than 24 months, i.e., pooling together subadult and adult individuals) and young males (i.e., yearling males, aged between 12 and 24 months). Considering potential problems in identifying male age classes of fallow deer in spring-early summer, especially at night, during the period of antler development, for this species the analyses were conducted for the October-March period. To statistical control for the effects of some key environmental variables on species detection rates (Hofmeester et al., 2019), site-specific variables were collected at each location: (*a*) habitat where each camera was installed (open/ecotone area, oak, pinewood, shrub), (*b*) camera height above the ground, (*c*) camera model and (*d*) the percentage of shrub cover (i.e. grass, bushes, trunks, etc., up to 150 cm in height) within a 10 m radius around the camera trap (Table S1).

Temporal relationship

For the analyses, when the same camera recorded consecutive videos of the same species within 30 minutes (Monterroso et al., 2014; Torretta et al., 2016; Lazzeri et al., 2024a), these were counted as a single "detection", with the capture time corresponding to the timestamp of the first video. When consecutive videos of people from the same group were recorded within 3 minutes, they were counted as a single "detection" (Esattore et al., 2023; Ferretti et al., 2023b). In addition to people on foot, the following categories – runners, bikers, hikers, field workers, forest rangers, and vehicles, both motorised and non-motorised – were classified as "people".

To test the formulated predictions, temporal activity models of the focal species (roe deer, fallow deer, wolf, and people) were estimated on a semi-annual scale, dividing the analyses into two periods: warmer period (April 2022 – September 2022) and colder period (October 2022 – March 2023). Specifically, for the two species of wild ungulates, separate activity models were fitted for each sex (male and female) and, for fallow deer, also for different age classes (adult male and young male). Circadian activity rhythms were estimated using nonparametric Kernel Density Estimation (Bu et al., 2016; Rossa et al., 2021). To compare the activity distributions of each sex and age class of ungulates (fallow deer and roe deer) and to assess potential significant differences, the Two-Sample Watson's Test of Homogeneity was used to compare the two distributions (Lund et al., 2017). Subsequently, the overlap between the temporal activity models of the ungulates (distinct by sex and age class) and those of the wolf was calculated using the overlap coefficient (Δ; Weitzman, 1970), which can range from $\Delta = 0$ (no overlap) to $\Delta = 1$ (complete overlap) (Ridout and Linkie M., 2009). The Δ_4 coeffi-

cient was specifically used, as the smallest sample in each comparison always consisted of ≥ 75 events (Ridout and Linkie M., 2009). According to a classification scale suggested by Monterroso et al. (2014), the overlap coefficients were interpreted as "low" ($\Delta \leq 0.50$), "moderate" ($0.50 < \Delta \leq 0.75$), and "high" ($\Delta > 0.75$; Monterroso et al., 2014). A 95 % confidence interval (CIs) for each overlap coefficient was then calculated through a resampling bootstrap (1000 resampling). For the temporal relationship, the R software was used through the RStudio interface, employing the "overlap" and "activity" packages (Rowcliffe et al., 2014; Meredith and Ridout , 2022).

Diurnal activity

To assess the factors influencing the diurnal activity of the sexes and age classes of the study species, sunset and sunrise times were initially calculated for each date through the package 'suncalc' (Thieurmel and El Marhraoui, 2022; Lazzeri et al., 2024a). This allowed the distinction between 'diurnal' and 'nocturnal' detections, i.e., those recorded between sunset and sunrise. Subsequently, Generalised Linear Mixed Models (GLMMs; Zuur et al., 2009) were set up. A dichotomous response variable was created and was modelled using binomial errors (link: logit), labelling diurnal events as '1' and nocturnal events as '0'. Monthly detection rates for the wolf, people, and each ungulate species under study (fallow deer and roe deer, distinguished by sex and age class) were estimated as the ratio of the number of monthly detections over the actual number of working days for each camera trap in each month. In the first step, global models were built for each sex and age class of wild ungulates. These model types included all the predictors considered, such as: (*i*) "habitat" around the camera locations (oak; pinewood; shrub; open/ecotone; Esattore et al., 2023; Ferretti et al., 2023b); (*ii*) "season" ('autumn': October-December; 'winter': January-March; 'spring': April-June; 'summer': July-September); (*iii*) "monthly wolf detection rate"; (*iv*) "monthly people detection rate"; and (*v*) "shrub cover"; (*vi*) 'camera model'; and (*vii*) 'camera location'. In the models for roe deer, the 'monthly detection rate of the fallow deer' was also included as a predictor, as it represents a potential direct competitor capable of influencing the spatiotemporal dynamics of the roe deer (Ferretti et al., 2011; Ferretti and Fattorini, 2021b). The variable 'camera location' was included as a random effect in all models. In contrast, the variable 'camera model' was excluded from the models for adult male fallow deer and male roe deer, as it did not contribute significantly to the explained deviance in either case. In the second step, starting from each global model, all possible combinations of predictors were calculated, generating several models, each representing a different theoretical hypothesis to be tested. The models were then evaluated using a selection procedure based on the comparison of AICc scores (Akaike's Information Criterion). Model selection with the nesting rule was used to avoid retaining overly complex models (Richards et al., 2011; Harrison et al., 2018). The best model was identified as the one with the lowest AICc (Burnham and Anderson, 2002; Richards et al., 2011). In addition, all models with AICc ≤ 2 were selected for inference (Burnham and Anderson, 2002; Harrison et al., 2018), and among these, only those that were not more complex versions of any simpler nested model (Richards et al., 2011). For each selected model, the marginal and conditional R^2 values were calculated, along with the model weight, which was standardised within the subset of selected models (Nakagawa et al., 2017). The parameters of the best model were estimated, including 95 % confidence intervals, B coefficients, standard errors (SE), and p-values. The model was then validated through visual inspection of the residual distribution (Zuur et al., 2009).

Spatial relationship

To evaluate the factors that could influence the detection rates of each sex and age class of wild ungulate species, GLMMs with negative binomial error distributions were used (Zuur et al., 2009). In the models, the number of detections for each sex and age class was considered as the response variable, calculated for each location on a monthly scale. Firstly, global models were set up, including all the considered predict-
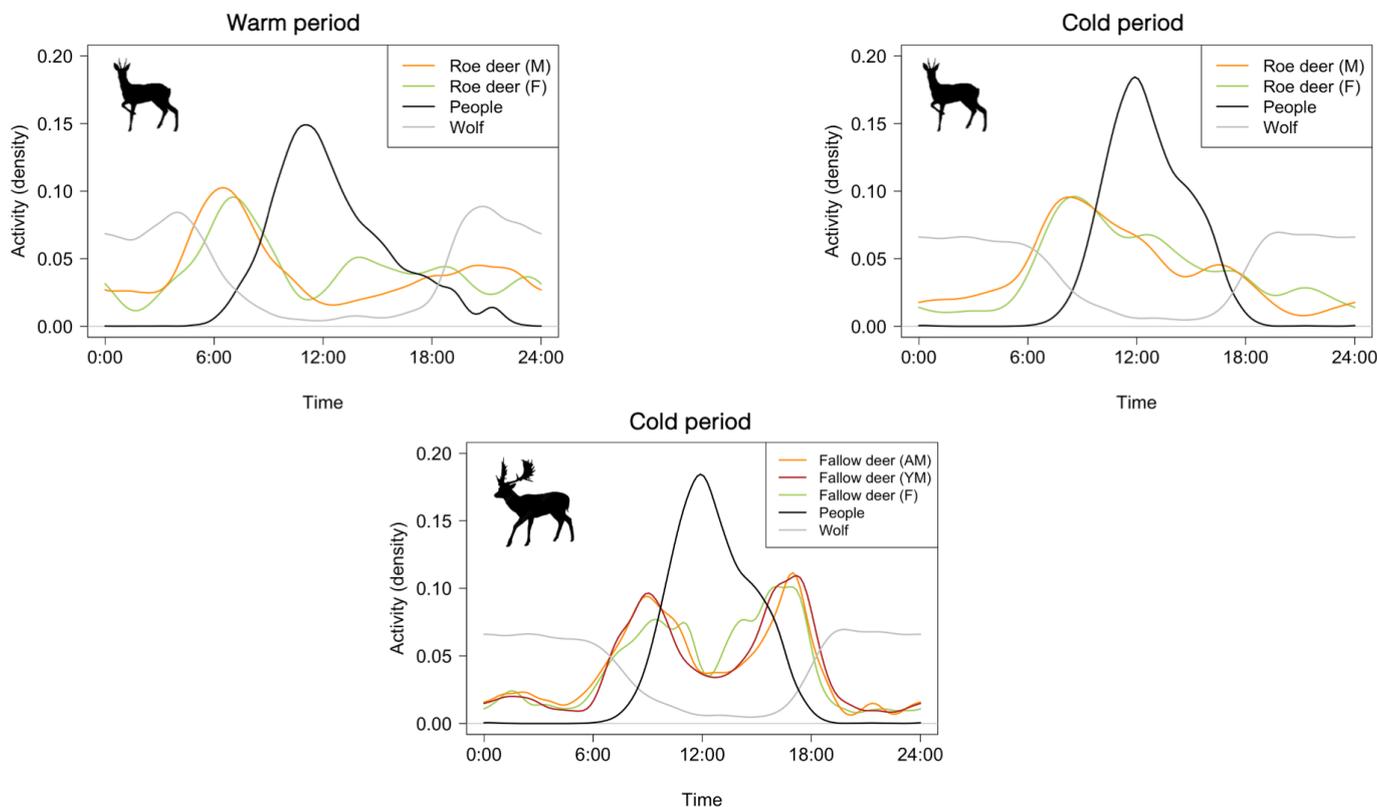
Figure 2 – Temporal activity patterns of each age class (AM: adult male; YM: young male) and sex (M: male; F: female) of target ungulate species, in comparison with wolf and human activity rhythms, in each study period (warmer period: April 2022 – September 2022; colder period: October 2022 – March 2023).

ors: (*i*) "habitat" around the camera positions (oak, pinewood, shrub, open/ecotone; Esattore et al., 2023; Ferretti et al., 2023b); (*ii*) "season" ('autumn': October–December; 'winter': January–March; 'spring': April–June; 'summer': July–September); (*iii*) "monthly wolf detection rate"; (*iv*) "monthly people detection rate"; (*v*) "shrub cover"; (*vi*) "camera location"; and (*vii*) camera height. The variable 'camera model' was excluded as a predictor, as it did not contribute significantly to the explained deviance in any of the models. The control variables (shrub cover and camera height) were integrated into the models to indirectly account for the species' detectability factor in the modelling process (Table S1). The variable 'camera location' was included as a random effect in all models. As with the models for the diurnal activity analysis, the models for roe deer also included the ' fallow deer monthly detection rate' as a predictor, since it represents a potential competitor to the roe deer (Ferretti et al., 2011; Ferretti and Fattorini, 2021b). The log of the monthly 'working days' for each location was included as an offset to standardise the response variables according to the actual sampling effort. Secondly, starting from each global model, all possible predictor combinations were calculated, thus generating different models, each of which represented a different theoretical hypothesis worth testing. The generated models were then evaluated using the same model selection procedure employed for the diurnal activity models (see Diurnal Activity section).

Results

The total sampling effort consisted of 17,413 actual camera trapping days (colder period: $n = 8,171$; warmer period: $n = 9,242$), during which 18,512 detections were obtained (Table 1).

Temporal activity patterns

During the colder period, adult males, young males, and females of fallow deer exhibited a predominantly diurnal activity pattern, avoiding the central hours of the day (Figure 2). Specifically, the bimodal activity patterns of adult and young males showed no significant differences (Watson Test: $U = 0.07$; $p > 0.05$; Table 2), characterised

Table 1 – The number of detections for each age class (AM: adult male; YM: young male) and sex (M: male; F: female) of the target ungulate species, recorded during each period (warm period: April 2022 – September 2022; cold period: October 2022 – March 2023). Data refers to camera trapping in the Maremma Regional Park from April 2022 to March 2023.

Specie	Category	Cold period	Warm period	TOT
Roe deer	M	92	249	341
	F	82	140	222
Fallow deer	F	2240	–	2240
	AM	647	–	647
	YM	302	–	302
Wolf	–	1136	797	1933
People	–	3997	8830	12827
TOT	–	8496	10016	18512

by two well-defined and homogeneous peaks of diurnal activity (Figure 2). In contrast, there was support to females displaying a different activity pattern compared to males (Watson Test: $U = 0.61$; $p < 0.05$; Table 2), with a less pronounced peak in the morning and an anticipated increased activity in the second part of the day (Figure 2).

Table 2 – Results of the Watson Two-Sample Test (U and relative p-value): comparison of activity rhythms of each age class (AM: adult male; YM: young male) and sex (M: male; F: female) of the target ungulate species, in each study period (warm period: April 2022 – September 2022; cold period: October 2022 – March 2023). In bold, statistically supported differences..

Specie	Category	Cold period		Warm period	
		P-value	*U*	*P*-value	*U*
Roe deer	M - F	> 0.05	0.05	**<0.05**	**0.21**
Fallow deer	F - AM	**< 0.05**	**0.61**	–	–
	F – YM	**< 0.05**	**0.28**	–	–
	AM - YM	> 0.05	0.07	–	–

Regarding roe deer, during the colder period, both males and females avoided nocturnal hours, exhibiting a similar crepuscular/diurnal activity pattern (Watson Test: $U = 0.05$; $p > 0.05$; Table 2), characterised by a peak of activity during the early morning hours and a progressive decline until dusk (Figure 2). During the warmer period, both sexes displayed an unimodal crepuscular activity pattern, with a peak of activity at dawn and avoidance of the central hours of the day (Figure 2). There was support to females exhibiting a slightly different pattern compared to males (Watson Test: $U = 0.21$; $p < 0.05$; Table 2), characterised by a weak increase in activity during the afternoon hours (Figure 2).

The wolf exhibited a nocturnal activity pattern in both periods, with an increase in activity during the crepuscular hours in the warmer period (Figure 2). In both periods, humans displayed an unimodal activity pattern, characterised by a marked peak during the central hours of the day (Figure 2).

Temporal overlap with the wolf

During the colder period, adult males, young males, and females of both fallow deer and roe deer exhibited a 'low' temporal overlap ($\Delta \leq 0.50$) with wolves (Figure 3). In the warmer period, the temporal overlap of male and female roe deer with wolves was 'moderate' ($0.50 < \Delta \leq 0.75$; Figure 3). For both species and in both periods, females showed lower overlap coefficients with the wolf than males (Figure 3).

Diurnal activity

Two models were selected for each age class and sex of fallow deer, except for adult male fallow deer, for which only one model was selected (Table S2). There was no support for an effect of the spatial variation of wolf detection rates on the spatial occurrence of diurnal *vs.* nocturnal activity in adult male fallow deer. For these individuals, only the variable 'season' was retained in the best model, although its effect on diurnal activity did not receive statistical support (Table 3). In contrast, young males showed lower diurnal activity in winter compared to autumn (Table 3). Wolf detection rates were retained in the best model
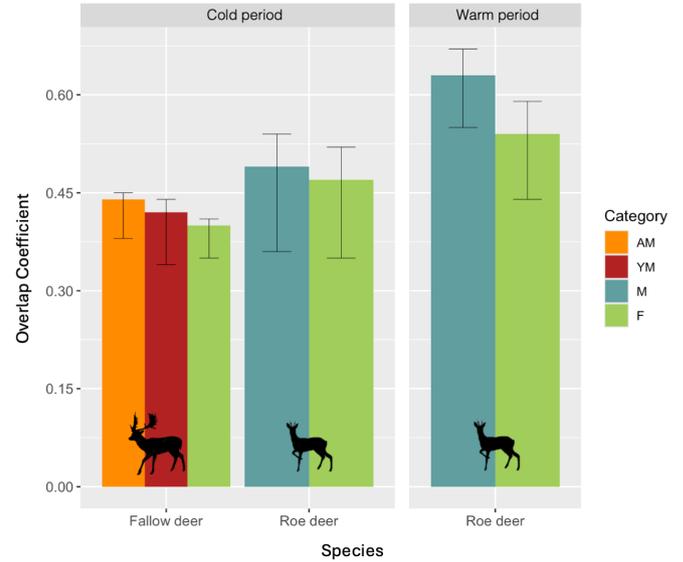
Figure 3 – Coefficients of temporal overlap between the wolf and the age classes (AM: adult male; YM: young male) and sexes (M: male; F: female) of the target ungulate species, for each study period (warmer period: April 2022 – September 2022; colder period: October 2022 – March 2023). The error bars represent the 95% confidence interval, calculated by resampling (bootstrapping) the dataset (n=1000 replicates). For sample size see Table 1.

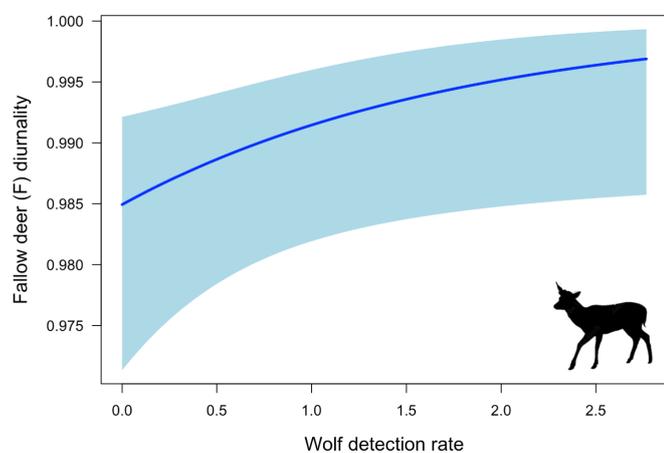for young male diurnal activity, but the effect was not statistically supported (Table 3).

There was statistical support to an effect of the spatial variation of wolf detection on the probability of diurnal activity of female fallow deer, with the probability of female diurnal activity increasing with the wolf detection rate (Table 3; Figure 4). People detection rate was also included in the best model for fallow deer females, although it did not have any significant effect on the response variable (Table 3).

Table 3 – Factors influencing occurrence of diurnal vs. nocturnal detections of each age class and sex of the target wild ungulate species, estimated through generalized linear mixed models with binomial errors. Estimates of model coefficients (B), their standard errors (SE), 95% confidence intervals (CI-low, CI-high) and probability value (P-value; significance level < 0,05) are shown. In bold, predictors for which an effect was statistically supported. Random effects of camera-traps position and month were included in all models; sampling effort was included as an offset variable as 'log (number of sampling days)'. Only the best models are reported in this table.

Specie	Response variable	Variables	β	SE	CI_low	CI_high	P - value
Roe deer (M)	**Period**	**Intercept**	**2.099**	**0.386**	**1.341**	**2.856**	**< 0.001**
		Fallow deer	0.350	0.259	-0.157	0.857	0.176
		Season [Summer]	**-2.316**	**0.399**	**-3.098**	**-1.534**	**< 0.001**
		Season [Autumn]	**-2.236**	**0.634**	**-3.478**	**-0.995**	**< 0.001**
		Season [Winter]	0.120	0.501	-0.861	1.101	0.811
Roe deer (F)	**Period**	**Intercept**	**1.753**	**0.351**	**1.064**	**2.442**	**< 0.001**
		Season [Summer]	**-1.263**	**0.439**	**-2.123**	**-0.403**	**0.004**
		Season [Autumn]	-0.722	0.507	-1.716	0.272	0.154
		Season [Winter]	0.126	0.553	-0.958	1.210	0.820
Fallow deer (F)	**Period**	**Intercept**	**1.593**	**0.267**	**1.068**	**2.117**	**< 0.001**
		People	0.167	0.112	-0.052	0.386	0.135
		Wolf	**0.206**	**0.102**	**0.006**	**0.406**	**0.043**
Fallow deer (AM)	**Period**	**Intercept**	**1.066**	**0.262**	**0.552**	**1.581**	**< 0.001**
		Season [Winter]	-0.207	0.268	-0.732	0.317	0.439
Fallow deer (YM)	**Period**	**Intercept**	**1.696**	**0.525**	**0.666**	**2.725**	**<0.001**
		Wolf	-0.439	0.234	-0.897	0.019	0.060
		Season [Winter]	**-1.033**	**0.408**	**-1.833**	**-0.233**	**0.011**

Table 4 – Factors influencing monthly detection rates variation of each age class and sex of the target wild ungulate species, estimated through generalized linear mixed models with negative binomial errors. Estimates of model coefficients (B), their standard errors (SE), 95% confidence intervals (CI-low, CI-high) and probability value (P-value; significance level < 0,05) are shown. In bold, predictors for which an effect was statistically supported. Random effects of camera-traps position and month were included in all models; sampling effort was included as an offset variable as 'log (number of sampling days)'. Only the best models are reported in this table.

Specie	Variables	β	SE	CI_low	CI_high	P - value
Roe deer (M)	**Intercept**	**-3.791**	**0.471**	**-4.714**	**-2.869**	**< 0.001**
	Habitat [Open]	**-1.606**	**0.539**	**-2.663**	**-0.550**	**0.003**
	Habitat [Pinewood]	**-1.501**	**0.567**	**-2.613**	**-0.390**	**0.008**
	Habitat [Shrub]	-0.374	0.442	-1.240	0.492	0.397
	Fallow deer	-0.476	0.272	-1.010	0.058	0.080
	Height	0.286	0.170	-0.048	0.620	0.093
	Shrub cover	-0.362	0.202	-0.759	0.034	0.073
	Season [Summer]	-0.305	0.241	-0.778	0.168	0.206
	Season [Autumn]	**-1.964**	**0.313**	**-2.577**	**-1.351**	**< 0.001**
	Season [Winter]	**-0.665**	**0.250**	**-1.156**	**-0.175**	**0.008**
Roe deer (F)	**Intercept**	**-4.358**	**0.335**	**-5.015**	**-3.701**	**< 0.001**
	Habitat [Open]	**-1.527**	**0.626**	**-2.754**	**-0.300**	**0.015**
	Habitat [Pinewood]	-1.047	0.638	-2.297	0.204	0.101
	Habitat [Shrub]	0.019	0.484	-0.929	0.968	0.969
	Fallow deer	-0.637	0.383	-1.388	0.115	0.097
	Height	0.367	0.200	-0.026	0.759	0.067
	Shrub cover	**-0.451**	**0.223**	**-0.888**	**-0.015**	**0.043**
	Season [Summer]	-0.188	0.268	-0.714	0.338	0.484
	Season [Autumn]	**-0.909**	**0.292**	**-1.481**	**-0.337**	**0.002**
	Season [Winter]	**-0.738**	**0.286**	**-1.299**	**-0.177**	**0.010**
Fallow deer (F)	**Intercept**	**-3.064**	**0.278**	**-3.608**	**-2.519**	**< 0.001**
	People	-0.267	0.190	-0.640	0.106	0.160
	Season [Winter]	**-0.327**	**0.133**	**-0.587**	**-0.066**	**0.014**
Fallow deer (AM)	**Intercept**	**-3.824**	**0.498**	**-4.800**	**-2.848**	**< 0.001**
	Season [Winter]	**-0.968**	**0.237**	**-1.434**	**-0.503**	**< 0.001**
Fallow deer (YM)	**Intercept**	**-6.323**	**0.602**	**-7.502**	**-5.143**	**< 0.001**
	People	-1.260	0.740	-2.710	0.190	0.089
	Shrub cover	-0.822	0.434	-1.673	0.028	0.058

Figure 4 – Influence of wolf detection rate on the probability of diurnal activity of female fallow deer, estimated through generalised linear mixed models with binomial errors. Coloured lines: predicted values. Coloured bands: 95% confidence intervals of the estimated relationship.

Spatial relationship

For the female and young male fallow deer, two models were selected, while for the adult males only one model was selected (Table S3). In no case, was there statistical support to an effect of the spatial variation of wolf detection rates on those of fallow deer (Table 4). For young male fallow deer, no predictor showed significant effects on the response variable (Table 4). In contrast, both female and adult male fallow deer showed lower detection rates during the winter season (Table 4).

Three models were selected for both sexes of the roe deer (Table S3). In no case, there was statistical support to an effect of the spatial variation of wolf detection rates on those of roe deer (Table 4). The same predictors were included in the best models of roe deer males and females (Table 4). For both sexes, detection rates decreased in winter and autumn (Table 4). The roe deer detection rate and the height of the camera trap did not show significant effects on the response variables (Table 4). For males, the detection rate was lower in ecotone/open habitats and pinewood than in oakwood and shrubwood, while for females it was the lowest in ecotone/open habitats (Table 4; Figure 6). Shrub cover had a significant negative effect on female detection rates (Table 4).

Discussion

In this paper, we assessed whether spatiotemporal responses of fallow deer and roe deer to the wolf could differ based on sex and age classes. No differences were supported in roe deer, whereas in fallow deer an increased probability of diurnal activity in sites with higher wolf detection rates was found in females but not in males.

Regarding fallow deer, both sexes and all age classes exhibited a bimodal diurnal activity pattern, consistent with previous findings in our study area (Rossa et al., 2021; Esattore et al., 2023; Lazzeri et al., 2024a). This behaviour differs from another Mediterranean area without predators, where fallow deer tend to exhibit a predominantly

Regarding roe deer, two models were selected for the males and only one for the females (Table S2). The fallow deer detection rate was included in the male roe deer model, although its effect was not statistically supported (Table 3). The roe deer male reduced his diurnal activity in summer and autumn compared to the other seasons, while the female reduced it only during the summer (Table 3; Figure 5).

nocturnal activity pattern (Zanni et al., 2021). Coefficients of temporal overlap with the wolf were 'low' (i.e., < 0.50 on a 0-1 scale) in both periods. Furthermore, no negative relationship was supported between the spatial variation of fallow deer detection rates and those of the wolf. Previous studies in our study area recorded a shift in the activity rhythms of fallow deer, from nocturnal/crepuscular to diurnal, following the progressive recolonisation of the area by the wolf (Lazzeri et al., 2024a). These findings indicate an antipredator strategy based on temporal avoidance of the wolf, whose activity pattern is predominantly nocturnal (Rossa et al., 2021; Esattore et al., 2023; Lazzeri et al., 2024a). Although diurnal activity was consistent across sexes and age classes, a slight difference was supported between sexes, and a spatial modulation of diurnal *vs.* nocturnal activity according to wolf detection rates (cf. Rossa et al., 2021) was detected only in females. These results supported a more pronounced temporal avoidance in females than males.

In sexually-size dimorphic species, larger body size may make males less vulnerable to predation than females (Oehlers et al., 2011). In fallow deer, males are larger and possess antlers, while females are approximately 40 % smaller than adult males (local data on mean full body mass of adult individuals culled in population control operations in 2000-2023, males: 78 kg, SD: 11.8 kg, maximal weight: 107 kg, n = 39 individuals; females: 43.8 kg, SD; 5.9 kg, maximal weight: 57 kg, n = 78 individuals). Although both sexes are vulnerable to predation, as neither exhibits body masses that would exclude predation by wolves, females may still be more sensitive due to their smaller size, which could heighten their perception of predation risk compared to males. Secondly, offspring represent one of the most vulnerable categories to predation due to their small size and limited ability to detect and escape potential predators (Linnell et al., 1995; Gaillard et al., 2000; Grovenburg et al., 2011). Although the offspring had already been weaned during the cold period (October–March), fallow deer females were usually still accompanied by their offspring, who continued to stay close to their mothers for protection and social cohesion, typical of this developmental stage (Lent, 1974; Apollonio et al., 1998). We expect these factors to increase the perceived risk of predation by females, leading them to adopt more pronounced antipredator strategies (Molinari-Jobin et al., 2004; Higdon et al., 2019). Our results support these predictions, as females showed an increase in diurnality in response to the wolf detection rate, as well as a lower temporal overlap with the wolf compared to males.

It has been hypothesised that younger individuals may adopt more pronounced anti-predatory strategies due to their greater vulnerability to predation, mainly related to inexperience and a reduced ability to recognise potentially dangerous situations (Apollonio et al., 1998; Gaillard et al., 2000; Mech and Peterson, 2003). The results do not support these predictions, as no significant differences were found in avoidance strategies between young and adult males. In fact, the activity patterns and temporal overlap coefficients with wolves observed in young males were similar to those of older individuals. However, the methods used in the study were limited to assessing and testing potential differences in the spatiotemporal avoidance responses between the two age classes of fallow deer. Therefore, the possibility cannot be excluded that any differences between the age classes may lie in other anti-predatory strategies, such as increased vigilance (Lung and Childress, 2007; Pecorella et al., 2019).

Regarding roe deer, during the cold period, both sexes exhibited similar crepuscular/diurnal activity rhythms (Pagon et al., 2013; Lazzeri et al., 2024a) and 'moderate' temporal overlap coefficients (*sensu* Monterroso et al., 2014) with the wolf. These results suggest the absence of significant differences in temporal responses to the wolf between male and female roe deer during the cold period. This uniformity in behaviour may be attributed to a similar vulnerability to predation for both sexes during this period (Molinari-Jobin et al., 2004). Specifically, the reduced sexual dimorphism, characterised by a small difference in body size and the presence of relatively small antlers even in adult male individuals (Andersen et al., 1998), could lead the wolf not to select one category of individuals over the other in predation. As a result, males
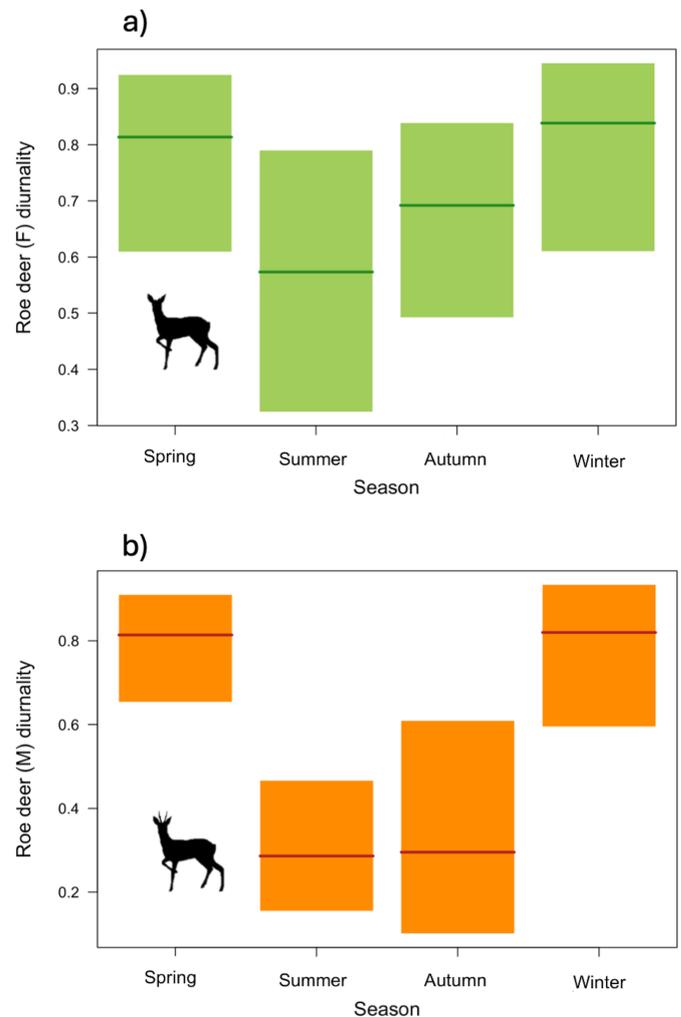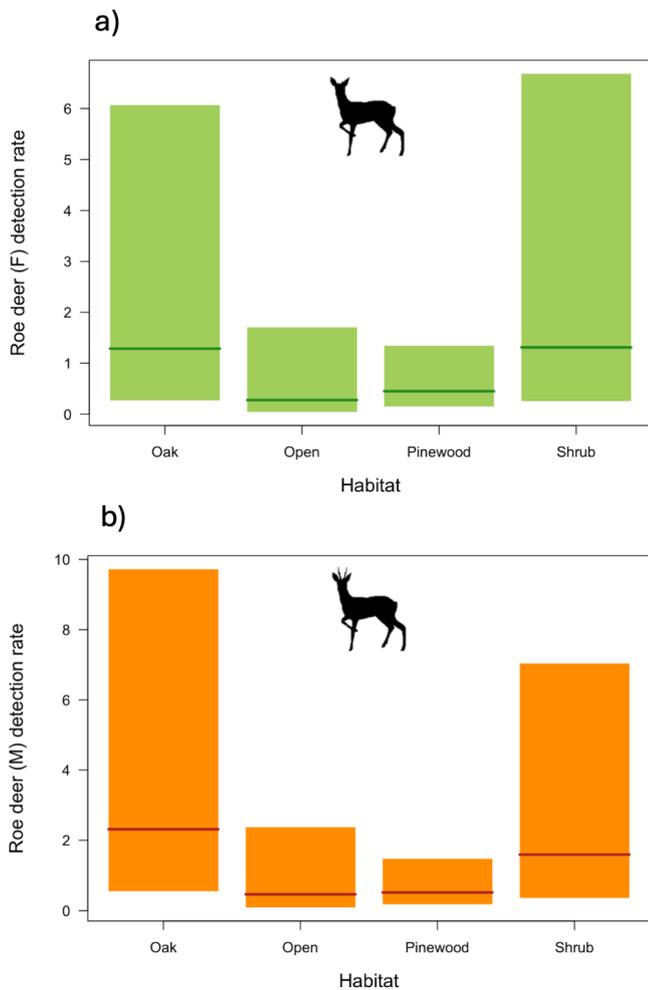
Figure 5 – Influence of season on the probability of diurnal activity of female (green, a) and male (orange, b) roe deer, estimated through generalised linear mixed models with binomial errors. Coloured lines: predicted values. Coloured bands: 95% confidence intervals of the estimated relationships.

and females might not be induced to exhibit different spatiotemporal responses to the wolf during the cold period. Conversely, during the warm period, the presence of offspring may influence female behaviour (Gaillard et al., 1997; Grovenburg et al., 2011). In our study area, it was observed that during the birthing period female roe deer accompanied by fawns exhibited the highest levels of vigilance (Fattorini and Ferretti, 2019). Accordingly, we expect females to adopt more pronounced antipredator strategies compared to males (Alonso-Alvarez and Velando, 2012; Higdon et al., 2019). Our results are consistent with these expectations, as females exhibited significantly different activity patterns from males during the warm period, as well as less temporal overlap with the wolf compared to males.

As suggested, both wolves and people activity have the potential to influence the spatiotemporal behaviour of ungulates (Kuijper et al., 2016). The study area is characterised by a peak of touristic presence in spring-summer, with activity peaking during the central hours of the day. The results show that both ungulate species avoid these hours, regardless of sex and age class. However, no significant effect of people activity was found on the monthly detection rate or diurnality of roe deer and fallow deer. Avoidance strategies acting at finer temporal or spatial scales may not be ruled out and should be further tested (Lazzeri et al., 2024a).

An important limitation of the study is that camera traps mainly detect locomotor activity, lacking information on other more detailed behaviours. To gain a more comprehensive understanding of animal behaviour, combining camera trap data with methods like satellite telemetry,

Figure 6 – Detection rate of female (green, a) and male (orange, b) roe deer in relation to habitat, estimated through generalised linear mixed models with negative binomial errors. Coloured lines: predicted values. Coloured bands: 95% confidence intervals of the estimated relationships.

which offers precise temporal tracking and insights into non-motor activities, could enhance data interpretation and ecological validity. In conclusion, this study provides support that spatiotemporal responses of prey to predators may differ based on the sex and age classes of individuals. Risk perception, combined with specific ecological and morphological characteristics, could be one of the key factors underlying these observed differences in anti-predatory behaviour (Caro et al., 2004; Pecorella et al., 2019; Grignolio et al., 2019). These results highlight the importance of considering behavioural variability due to age and sex when designing wildlife management strategies, as understanding these differences can optimise interventions and prey control programs. Future research on marked individuals (e.g., through satellite telemetry) could provide further insights into the variability of avoidance strategies in prey populations (e.g., according to finer spatiotemporal scales and on the presence/absence of offspring), which are essential for a deeper understanding of predator-prey dynamics.

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Supplemental information

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

Table S1 List and sampling method of environmental variables and variables associated with the placement of each camera trap.

Table S2 Results of model selection for factors influencing the probability of diurnal activity ('diurnality') of each age class and sex of the target wild ungulate species.

Table S3 Results of model selection for factors influencing monthly detection rates variation of each age class and sex of the target wild ungulate species.