

Same place, different time, head up: Multiple antipredator responses to a recolonizing apex predator

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Abstract

Prey adjust their antipredator behavioral tactics to minimize the risk of an encounter with predators. Spatiotemporal responses of prey to predators have been reported, but the nature of antipredator response is not ubiquitous and it is the object of increasing interest, especially considering the recent recovery of large carnivores in Europe, and the potential for behavioral antipredator responses to elicit consequences at the ecosystem level. We have tested multiple antipredator responses by fallow deer *Dama dama* to wolf *Canis lupus* in a Mediterranean protected area recently recolonized by this apex predator. Through intensive camera trapping, we tested for temporal and spatial association between predator and prey, and we have also studied deer vigilance in forest habitats where focal observations are usually impossible. Wolf detection rates were spatially associated with those of fallow deer. Accordingly, no evidence was found for fallow deer avoiding sites with higher predator detection rates. Temporal activity patterns were significantly different between the 2 species, with the wolf being mainly nocturnal whereas fallow deer was active especially during daylight. A comparison with a preliminary study strongly suggests an increase in the diurnal activity of fallow deer along with the stabilization of wolf presence in the area. Both the rate and the duration of vigilance of female fallow deer increased with the local frequency of wolf activity. We suggest an antipredator response based on temporal—rather than spatial—avoidance, as well as increased vigilance.

Key words: antipredator responses, deer, interspecific interactions, temporal patterns, vigilance.

Apex predators play a fundamental role in ecosystems (Wallach et al. 2015). Operating as a top-down force, they can affect the ecology of competitors and prey (Beschta and Ripple 2009), with the potential to shape the dynamics of communities (Paine 1969). Besides their potential direct effects on prey population size through increased mortality (Ripple et al. 2014), large predators may influence density (Ripple and Beschta 2012), distribution (Weterings et al. 2022), and habitat selection through effects on prey behavior, for example, by affecting their movement patterns, selection of foraging and resting sites, or grouping behavior (Lima and Dill 1990; Schmitz et al. 1997; Fortin et al. 2005).

Several behavioral tactics can be adopted by prey to mitigate the risk of predation (Endler 1986; Creel and Christianson 2008; Kuijper et al. 2013). For example, prey can show an increase in individual vigilance (Sirot and Touzalin 2009; Périquet et al. 2010) or group size (Lima and Dill 1990). Increased vigilance maximizes the chances to spot a predator (Pulliam 1973; Roberts 1996) but it may elicit negative consequences on individual foraging efficiency (Creel et al. 2014). The benefits of increased group size lie in dilution

(Delm 1990) and confusion effects (reviewed in Schradin et al. 2019), which reduce individual predation risk. Individual foraging efficiency may increase in larger groups (Lipetz and Bekoff 1982), with a decrease in individual vigilance time (Delm 1990). Non-lethal effects of predators on prey behavior include also modifications of prey space use (Lima 1998; Thaker et al. 2011) and shifts of prey activity to less risky parts of the day (Lima and Bednekoff 1999; Tambling et al. 2015). These behavioral patterns should reflect a trade-off between meeting physiological needs and escaping predation through spatiotemporal avoidance (Sirot et al. 2021). Prey species are expected to adjust their antipredator tactics to the level of risk (Hebblewhite et al. 2005), to the hunting strategy of the predator (i.e., cursorial or ambush predators, Makin et al. 2017), and to the structural complexity of the environment (Hebblewhite et al. 2005; Shrader et al. 2008). Furthermore, different species may adopt different strategies in response to the risks elicited by the same predator (Lingle 2001; Lingle and Pellis 2002; Lingle et al. 2005; Valeix et al. 2009).

Temperate ecosystems are facing a rapid increase in populations of apex predators and their prey, with a special reference

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to the wolf *Canis lupus* (Apollonio et al. 2010; Chapron et al. 2014), and there is a considerable debate on the potential for antipredator behavioral responses of ungulates to trigger cascading effects on other ecosystem components (e.g., Creel et al. 2005; Fortin et al. 2005; Mech 2012; Ripple et al. 2014; Ford et al. 2015; Kuijper et al. 2016; Martin et al. 2020). Mechanisms adopted by prey to mitigate predation risk are not consistent across studies. Antipredator responses based on spatial (e.g., Creel et al. 2005; Fortin et al. 2005; Mao et al. 2005) or temporal avoidance (e.g., Kohl et al. 2018; Palmer et al. 2021) of wolves by their main prey have been shown. However, spatiotemporal antipredator responses seem not to be ubiquitous (Cusack et al. 2020), and there is emerging evidence supporting several factors influencing predator–prey behavioral relationships, including the presence of livestock, human activity, as well as the presence of competitors (e.g., Prugh et al. 2009; Bensen et al. 2022; Ripari et al. 2022; Salvatori et al. 2022). For instance, in relatively anthropized ecosystems, the lack of vast undisturbed natural areas has been suggested to reduce the opportunities for prey to move from risky to predator-free areas (Kuijper et al. 2013, 2016). Thus, the potential for a spatial variation of perceived predation risk would be low, leading to weak effects of predators on prey spatial behavior (e.g., Samelius et al. 2013; Bubnicki et al. 2019; Sand et al. 2021). Furthermore, the effects of predators on prey behavior can be exceeded by those of human activities (Theuerkauf and Rouys 2008; Bubnicki et al. 2019; Sand et al. 2021). Moreover, only a few studies have investigated the risk perception and consequent antipredator behavior in closed environments (i.e., forests, bushes; Kuijper et al. 2014). The presence of dense vegetation reduces both the distance at which prey can detect the approach of predators (e.g., Chen et al. 2021) and the possibility of escaping (e.g., Wilson et al. 2015), increasing the opportunities for a successful ambush (e.g., Davidson et al. 2012).

In this study, we considered the wolf, i.e., the main large predator in temperate ecosystems, in a coastal Mediterranean area that has been recently recolonized by this predator, and its relationship with its main prey. Previous work has shown that, in our study area, wolves preyed especially upon the fallow deer *Dama dama* both in the colder semester and in the warmer one; this deer was selected over wild boar *Sus scrofa* and roe deer *Capreolus capreolus* (Ferretti et al. 2019). We concentrated on wolf–fallow deer relationships to assess potential antipredator responses of fallow deer based on (i) temporal avoidance, (ii) spatial avoidance, and (iii) vigilance behavior. We took advantage of detailed data on prey behavior collected through a camera-trapping study (e.g., Ferretti et al. 2021; Rossa et al. 2021) and through which we could assess the vigilance behavior also in wooded and concealed habitats (e.g., scrubwood). Previous work suggested a potential for temporal avoidance of the wolf by fallow deer, with the latter being mainly diurnal in sites highly used by wolves, and being active especially at dawn/dusk and night in the sites less attended by predators (Rossa et al. 2021). Considering that fallow deer were shown to be the local main prey of wolves, we would expect a limited possibility for the former to spatially avoid the latter. If so, antipredator responses should be based mainly on other behavioral mechanisms, for example, temporal shifts or increased vigilance. Thus, we expected (i) the wolf to be more active in the sites with a higher frequency of activity of fallow deer. We expected the fallow deer to react

to the predation risk by modifying its temporal—rather than spatial—behavior, thus showing (ii) greater temporal activity in times of the day when the wolf is less active, i.e., during the day, and (iii) spatial variation of detection rates not affected by wolf detection rates. Last, we expected (iv) fallow deer vigilance to be greater in sites and times with a higher frequency of wolf detections.

Material and Methods

Study area

Our study was conducted in the Maremma Regional Park, a protected coastal area in central Italy (about 90 km²; Figure 1; 42.626371°N, 11.099303°E). The local climate is Mediterranean, with hot-dry summers. The mean daily temperature ranges from 9 °C in January to 24 °C in August, and monthly rainfall ranges from 9.3 mm in July to 81.8 mm in November (Ferretti et al. 2021). According to Mencagli and Stefanini (2008), the vegetation is mainly composed of Mediterranean sclerophyllic scrubwood (58%) of 3 main wood types: oakwood, mainly holm oak *Quercus ilex* trees with an average height >7 m; scrubwood, principally holm oak and strawberry tree *Arbutus unedo*, with a height <7 m; garrigue, with bushes, mainly holm oak, rosemary *Rosmarinus officinalis*, juniper *Juniperus spp.*, rockrose *Cistus spp.*, with a height <2 m. Other habitats are represented by pinewood (10%, mainly domestic pine *Pinus pinea*), abandoned olive groves and pastures (15%), set-aside grassland (4%), and crops (12%, mainly cereals and sunflower). For details on vegetation and habitats of our study area, see Sforzi et al. (2013) and Melini et al. (2019). Wolves were reported as sporadic in coastal southern Tuscany at the beginning of the 20th century (Ghigi 1911), and they were absent from our study area in the mid-1970s when the Maremma Regional Park was established (Arrigoni 1976). A pack of wolves (with signs of admixture with dogs: Caniglia et al. 2013) reproduced in the Park between 2005 and 2008. After a few years without reproduction, no signs of presence were reported after 2013. A pack of wolves settled in the central part of the Park in 2015 followed by a second one in 2017 (Ferretti et al. 2019) and a third one in 2019–2020. Apart from the wolf, 3 species of ungulates (i.e., the fallow deer, the wild boar, and the roe deer), many medium-sized species, for example, the crested porcupine *Hystrix cristata*, the introduced coypu *Myocastor coypus*, the European brown hare *Lepus europaeus*, the red fox *Vulpes vulpes*, the Eurasian badger *Meles meles*, the wildcat *Felis silvestris*, the stone marten *Martes foina*, the pine marten *Martes martes*, and a few species of smaller mammals occur in the area. Ungulate density is high (wild boar: about 10–12 individuals/km²; fallow deer: about 8–9 individuals/km²; roe deer: about 3–4 individuals/km² throughout our study, Ferretti et al., unpublished data, estimated through feces counts as in Fattorini et al. 2011; Ferretti and Fattorini 2021). Livestock (about 20 heads/km²; Ferretti et al. 2019) includes free-ranging cattle and horses, which roam in sectors of pinewood and abandoned olive groves and pastures, and 2 sheep herds in localized sectors of the study area. Population control of wild boar and fallow deer is conducted under the responsibility of the Park Agency through culling (both species) and trapping (wild boar), to limit the negative impacts of these ungulates on habitats/species with conservation and agriculture relevance.

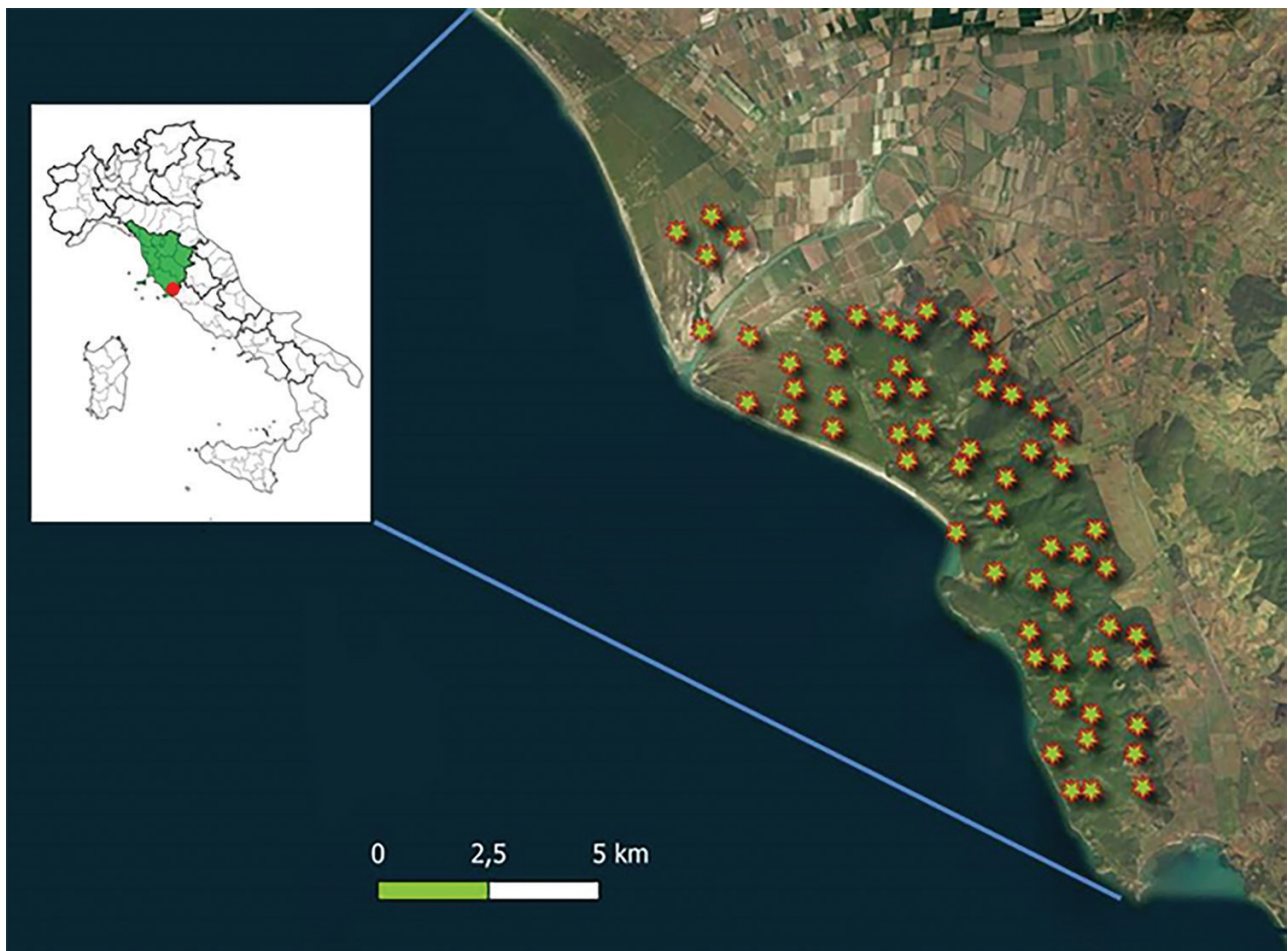


Figure 1 Map of the study area with the locations of camera traps.

Data collection—temporal and spatial patterns

Spatiotemporal activity patterns of wolf and fallow deer, as well as fallow deer behavior, were assessed through camera trapping (for our study area: [Ferretti et al. 2021](#); [Rossa et al. 2021](#)), from April 2019 to March 2020. We also recorded each detection of humans, to assess their effect on wolf/fallow deer patterns. Fifty-seven locations ([Figure 1](#)) were selected using a sampling grid (cells size: 1×1 km) superimposed on the study area through a Geographic Information System (G.I.S., 1 location per suitable cell). Locations were monitored according to a rotational scheme: overall, each location was monitored *circa* 30 days for each season (spring: April–June; summer: July–September; autumn: October–December; winter: January–March). The cameras (IR-Plus HD-2; ScoutGuard) were placed at a height of *circa* 30–100 cm on animal trails/forest roads ([Ferretti et al. 2021](#); [Rossa et al. 2021](#)) suitable to detect carnivores and ungulates ([Li et al. 2010, 2012](#); [Bu et al. 2016](#); [Torretta et al. 2017](#)) and were set to be active 24 h/day, recording 30-s videos, with no lag between consecutive ones; trigger time was ≤ 1 s. They were equipped with 16-GB SD memories and external 6-V batteries and were checked every *circa* 15 days to download data and replace cards/batteries. All videos were classified, recording the following data in Microsoft Excel sheets: date, time of day (solar time), location, species, sex, age class (for fallow deer), and the number of individuals. We defined the age classes according to general morphology, body development, and

antler size/shape of fallow deer. Thus, we considered: fawns (i.e., < 1 year old), subadult/adult females (1–2 years old), subadult males (2–4 years old), and adult males (>4 years old). Daylight-saving time was not considered, to allow the evaluation of the temporal patterns relative to the sun's position ([Foster et al. 2013](#)). Videos of the same species recorded within intervals of 30 min were considered as a single event, that is, only the first video was considered for analyses, and we defined it as “detection” ([Rowcliffe et al. 2008](#); [Tobler et al. 2008, 2017](#); [Lucherini et al. 2009](#); [Torretta et al. 2016](#)).

Data analyses—temporal patterns

Temporal activity patterns were assessed through kernel density estimation ([Ridout and Linkie 2009](#)), obtaining density functions related to time as a continuous and circular variable (i.e., in radians). Graphically, the area under the curve depicted by the function corresponds to the probability of observing individuals throughout the 24 h ([Foster et al. 2013](#); [Bu et al. 2016](#)). The Watson test was performed to evaluate the homogeneity of activity patterns ([Lund et al. 2017](#)). The temporal overlap between wolf and fallow deer was calculated using the overlap coefficient, Δ ([Weitzman 1970](#)): this index ranges from 0 (no overlap) to 1 (complete overlap). According to [Ridout and Linkie \(2009\)](#), we selected the Δ_4 index, as recommended for sample sizes >75. Consistent with [Monterroso et al. \(2014\)](#), we defined as “low” those overlap

estimates ≤ 0.50 , whereas overlap patterns with $0.50 < \Delta_4 \leq 0.75$ were defined as “moderate”, and $\Delta_4 > 0.75$ were defined as “high” overlap values.

Besides temporal activity patterns of wolves and fallow deer and their mutual interspecific overlap, we also compared the temporal activity of the fallow deer between sites with high versus low wolf activity (Oberosler et al. 2017; Mori et al. 2020; Rossa et al. 2021). For each location, the frequency of wolf activity (i.e., its detection rate) was calculated as N detections/ N days (N days = days of actual camera functioning). Thus, for the specific purpose of contrasting temporal patterns of fallow deer between sites with different wolf activity, we calculated the mean detection rate of wolves across all locations, to separate “high wolf sites” (i.e., with wolf detection rate higher than or equal to the mean) and “low wolf sites” (i.e., with a detection rate lower than the mean). Fallow deer activity patterns were compared between the 2 groups of sites by calculating the temporal overlap of deer between high and low wolf sites and evaluating the significance of this difference through the Watson nonparametric 2-sample test for homogeneity. The temporal overlap between the wolf and the fallow deer was also calculated for each class of site. For all the overlap coefficients, 0.95 confidence intervals (CIs) were obtained with a simple random sampling with replacement on 1,000 bootstraps (Lund et al. 2017; Meredith et al. 2017). All the analyses were conducted on seasonal (spring: April–June; summer: July–September; autumn: October–December, and winter: January–March), semestral (warm period: spring–summer; cold period: autumn–winter), and yearly scales. All the statistical analyses were performed through the R software, version 3.6.2, using the “circular” (Lund et al. 2017) and “overlap” (Meredith and Ridout 2017) packages.

Data analyses—spatial patterns

For each location, we estimated the detection rate of wolves and fallow deer as the ratio of the number of detections over the number of operational days of cameras. We also considered the rate of human activity, to evaluate its potential effect on spatial patterns of wolf and fallow deer. In the case of humans, we considered a 3-min threshold between consecutive detections, when we could be able to assess that they belonged to different groups. For these analyses, we did not consider the “A4” location, because human detections were not consistently recorded in summer. Thus, these analyses were based on 2,640 fallow deer detections and 620 wolf detections over 4,634 sampling days.

We evaluated whether spatial patterns of wolf and fallow deer activity were statistically associated with prey or predator frequency of activity, respectively. We used generalized linear mixed models with negative binomial errors (Zuur et al. 2009). We fitted full models where the number of detections of the focal species in each location and each season was the response variable. The log (number of camera operating days) was included as an offset variable to account for differences in sampling effort across locations. The camera-trapping location ID was fitted as a random effect. For models relevant to the wolf, the following variables were included as predictors: fallow deer detection rate; roe deer detection rate; wild boar detection rate; human detection rate (either on foot or by bike/car/on horses); habitat type (scrubwood; oakwood; pinewood; ecotone/meadows); camera type (Ir-plus; ScoutGuard); season. For the fallow deer models, we included the following predictors: wolf detection rate; wild

boar detection rate; human detection rate; habitat; season; and camera type. We initially evaluated whether spatial patterns of wolves and fallow deer were influenced by spatial patterns of prey/predator over different temporal scales, i.e., seasonal, 6-month, and yearly temporal scale. Thus, for each response variable, we initially built up 3 full models including, among predictors, detection rates of prey/predator/humans at 3 different temporal scales (i.e., season, semester, and year). Then, we compared the fit of global models by comparing their Akaike Information Criterion values corrected for small samples (AICc). For the wolf, the full model including prey seasonal detection rates showed the best fit (season: AICc = 834.5; semester: 834.9; year: 838.1). Conversely, for the fallow deer, the full model including predator yearly detection rates showed the best fit (season: AICc = 1,274.3; semester: AICc = 1,273.7; year: AICc = 1,272.6). Thus, in our subsequent analyses, we modeled wolf detection rates against prey seasonal detection rates, and fallow deer spatial patterns against predator yearly detection rates.

For each model set (i.e., wolf spatial patterns and fallow deer spatial patterns), we fitted a number of candidate models that represented different *a priori* hypotheses (Burnham and Anderson 2002), each of them including different combinations of predictors (wolf: $n = 11$ candidate models; fallow deer: $n = 10$ candidate models; Supplementary Tables 1 and 2). The model selection used AICc and models were selected if they had $AICc \leq 2$, and if their AICc value was lower than that of any simpler alternative (Burnham and Anderson 2002). Standardized model weight was calculated among selected models. Model selection was conducted through the R package ‘MuMIn’ (Barton 2012). We estimated the parameters (B coefficients and 95% CIs) of the best models using the R packages ‘glmmTMB’ (Magnusson et al. 2017) and ‘lme4’ (Bates et al. 2015). Best models were validated through visual inspection of residuals through the ‘DHARMA’ package (Hartig 2019).

Data analyses—vigilance

We collected data on all individuals whose head was visible in the video and that could be assigned to a sex/age class. Then, for these analyses, we considered all the videos for which the head of at least 1 individual fallow deer could be observed for at least 20 s. We defined a “head lift” as a vigilance posture where the animal lifted its head above the body axis, intently looking at/around and orienting the ears towards the source of disturbance, if any (San José et al. 1996; Ferretti et al. 2008; Sönnichsen et al. 2013). Thus, for each observed individual, we recorded the duration (in seconds) of the interval where its head was visible and recorded both the number and the duration of head lifts.

For the analyses, we concentrated on female fallow deer, considering the small sample size of males (females: 897 individual observations, see below; adult males: $n = 85$; subadult males: $n = 60$; yearling males: $n = 185$). We considered 2 indices: (i) “vigilance rate”, i.e., the number of head lifts in the observation bout; (ii) “vigilance duration”, i.e., the time spent in vigilance in the observation bout. Consistently with analyses of spatial patterns, we selected the best temporal scale to analyze the variation of vigilance in relation to spatial changes in wolf or human activity, to evaluate whether variation in fallow deer behavior was better explained by predator/human activity at shorter *vs.* longer temporal scales. Thus, for this purpose, we tested whether vigilance indices were

influenced by wolf detection rates at the seasonal, semester, or yearly temporal scale. We used generalized linear mixed models with Poisson (number of head lifts) and quasi-Poisson (vigilance duration) errors, and we modeled the indices as 2 response variables: (i) the number of individual head lifts in the video, and (ii) the total duration of individual vigilance in the video. The log of total time when the head of the focal individual was visible was included as an offset variable to standardize the indices for the actual observation time. To limit the effects of pseudoreplication resulting from potential repeated observations of the same individuals in different videos during the same day, as well as to control for the potential effects of specific conditions of the observation day (e.g., a passage of predators or humans), the date of each video was set as a random effect.

Preliminary analyses also included the random effects of the video ID and the locations ID, and provided comparable results: we show the simplest models in the main text (see also [Supplementary Tables 3 and 4](#)), and the preliminary ones in [Supplementary Tables 5 and 6](#). For each variable, we inserted the following predictors in global models: habitat type, season, group size, time of day (as a quadratic term), wolf detection rate (at the seasonal, semestral, or yearly temporal scale), and human detection rate (at the seasonal, semestral or yearly temporal scale). The assessment of the size of large groups through camera trapping may be constrained by the field of view of camera traps and by vegetation cover. To limit potential biases across camera traps in assessments of large group sizes, we set an upper limit of 25 individuals, that we assigned

to the focal observations of individuals in larger groups ($n = 1$ out of 897 focal observations). For each index, global models were built including all the predictors, and were compared across temporal scales considering their AICc scores. In both cases, models including wolf and humans yearly detection rate showed the lowest AICc values (vigilance rate, season: AICc = 1,896.7, semester: AICc = 1,882.68, year: 1,868.4; vigilance duration, season: AICc = 3,693.7, semester: AICc = 3,681.0, year: AICc = 3,666.4). Thus, we used models at the yearly scale for model selection, which was performed as described above. Then, we built 9 candidate models for each response variable and performed a model selection through the criteria described above ([Supplementary Tables 3 and 4](#); [Supplementary Figure 1](#)).

Results

Temporal patterns

In 4,747 effective trapping days, we obtained 2,689 fallow deer detections and 728 wolf detections useful for analyses according to our filtering criteria. Both species showed non-uniform temporal activity patterns, the wolf being typically active at night ([Figure 2](#); $U = 11.36-18.31$, $P < 0.01$), and the fallow deer being mainly diurnal, especially in autumn–winter, with peaks at dawn and dusk more evident in spring–summer ([Figure 3](#); $U = 34.19-73.43$, $P < 0.01$). Interspecific temporal overlap was the greatest in spring ($\Delta_4 = 0.71$) and the lowest in autumn ($\Delta_4 = 0.49$; [Figure 4](#)).

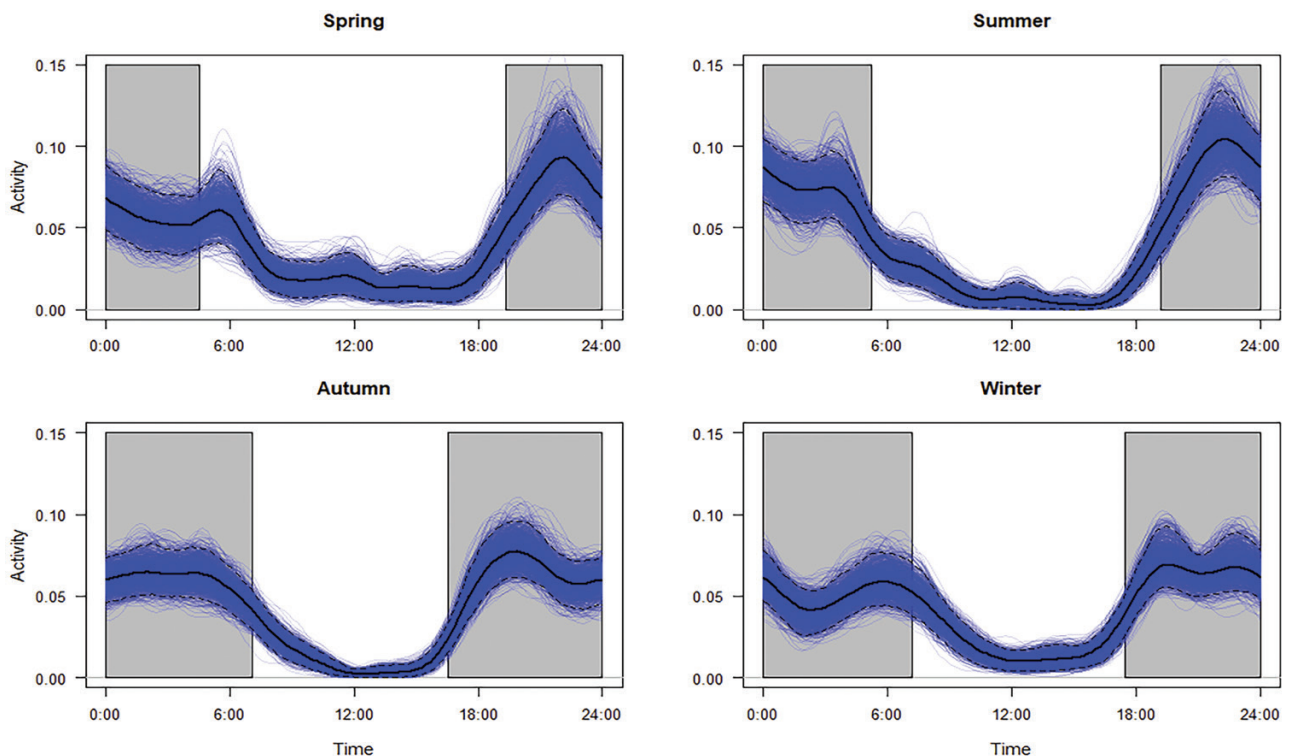


Figure 2 Temporal activity patterns of the wolf in the Maremma Regional Park assessed through camera trapping and estimated through kernel density estimation, obtaining density functions related to time as a continuous and circular variable (Spring: April–June 2019, $n = 150$ detections; Summer: July–September 2019, $n = 154$; Autumn: October–December 2019, $n = 242$; Winter: January–March 2020, $n = 182$). Graphically, the area under the curve depicted by the function corresponds to the probability of observing individuals throughout the 24 h. Colored lines represent bootstrapped estimates of activity patterns; dashed black lines represent 0.95 CIs. Gray rectangles indicate times of day preceding the dawn and following the dusk, considering the median day of each season (see online for color figures).

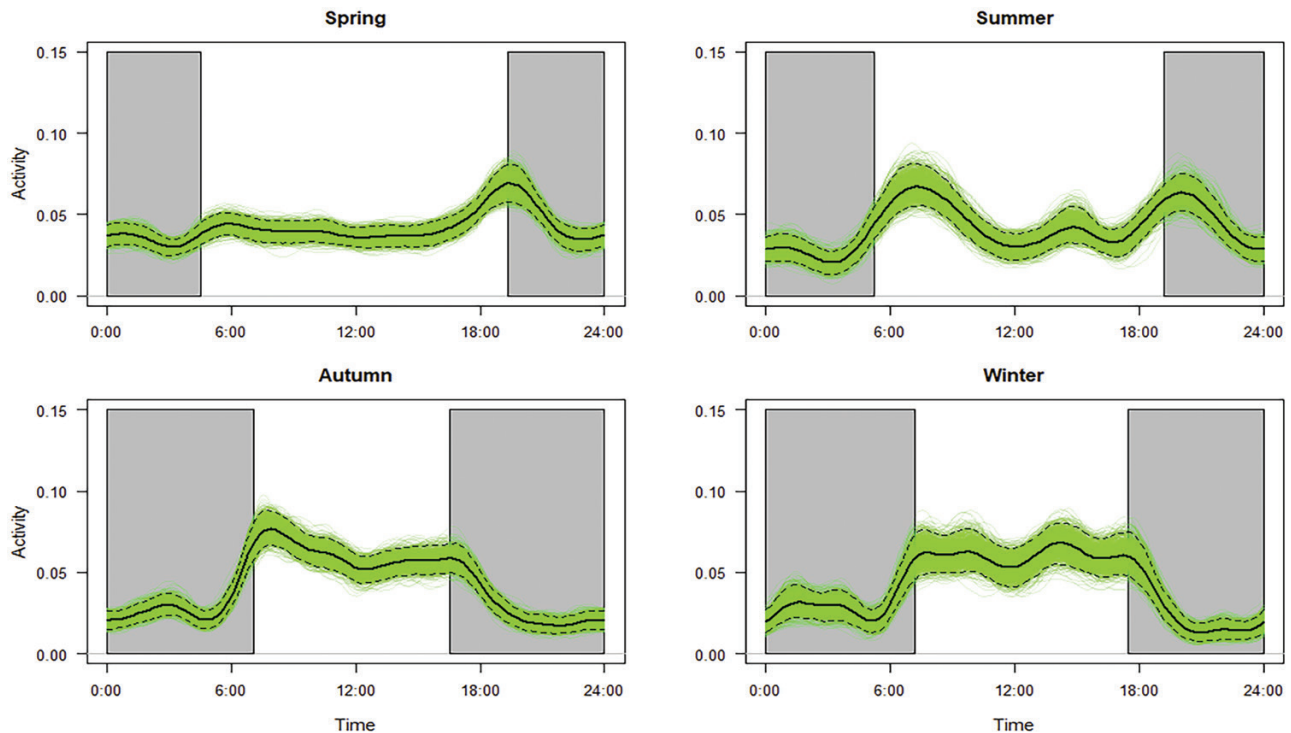


Figure 3 Temporal activity patterns of the fallow deer in the Maremma Regional Park assessed through camera trapping and estimated through kernel density estimation, obtaining density functions related to time as a continuous and circular variable (Spring: April–June 2019, $n = 867$ detections; Summer: July–September 2019, $n = 444$; Autumn: October–December 2019, $n = 942$; Winter: January–March 2020, $n = 436$). Colored lines represent bootstrapped estimates of activity patterns; dashed black lines represent 0.95 CIs. Gray rectangles indicate times of day preceding the dawn and following the dusk, considering the median day of each season (see online for color figures).

Temporal activity patterns were significantly different between the 2 species (all sites: $U = 1.33$ – 5.65 , $P < 0.001$; sites with high wolf activity: $U = 1.02$ – 4.08 , $P < 0.001$; sites with low wolf activity: $U = 0.28$ – 1.29 , $P < 0.01$). Wolf–fallow deer temporal overlap was comparable between “high wolf” and “low wolf” sites in all seasons except for winter, when it was 1.3 times greater in “low wolf” than in “high wolf” sites (Table 1). There was no significant variation in the temporal activity patterns of fallow deer between sites with high and low wolf activities ($U = 0.07$ – 0.14 , $P > 0.05$), except for spring ($U = 0.26$, $P < 0.05$). Intraspecific temporal overlap between sites with high wolf and low wolf activities was ≥ 0.88 in all seasons (Table 1).

Spatial patterns

Only 1 model was selected for spatial patterns of wolf activity, including the effects of fallow deer detection rate, habitat, season, and camera type. Wolf detection rates were influenced by habitat type, being greater in ecotone/meadows than in other habitats and increased with fallow deer detection rate (Tables 2 and 3; Figure 5). Effects of season and camera type were not supported (Tables 2 and 3).

For the fallow deer, 2 models were selected (Table 2). A slight, positive relationship was supported between spatial patterns of fallow deer detection rates and those of wild boar and wolf (Table 3). Fallow deer detection rates were the lowest in winter and were lower in shrub and pinewood than in ecotone/open areas and oakwood (Tables 2 and 3). No effect of camera type was supported (Table 3).

Vigilance

We collected 897 focal observations of female fallow deer over a total of 523 detections (i.e., 7.1 observation hours). Mean group size was 1.7 individuals per detection in spring ($SE = \pm 0.7$, $n = 287$ detections), 1.5 individuals in summer ($SE = \pm 0.06$, $n = 150$), 4.1 individuals in autumn ($SE = \pm 0.8$, $n = 57$), and 3.8 individuals in winter ($SE = \pm 0.3$, $n = 29$).

For vigilance rate, 2 models were selected, whereas for vigilance time 1 model was selected. Overall, these models included the effects of wolf detection rate, habitat, season, group size, humans and time of day (Tables 2–4). The vigilance increased with the wolf detection rate (Table 4; Figure 6). Furthermore, vigilance was the lowest in ecotone/open habitats, being greater in shrub than in the other habitats, and was greater in autumn–winter than in spring–summer (Table 4; Figure 6). Vigilance rate also decreased with the increasing group size (Tables 2–4; Figure 6). The effect of human detection rate was not supported, whereas a slight effect of the time of the day was supported only by the second model for vigilance rate (Tables 2–4).

Discussion

Studies on behavioral relationships between recolonizing wolves and their main prey are rare for European areas (e.g., Kuijper et al. 2015; Sand et al. 2021), especially with regard to studies of multiple behavioral tactics of prey (e.g., Bubnicki et al. 2019). We assessed spatial and temporal patterns of activity of the wolf and its main prey, and prey vigilance behavior

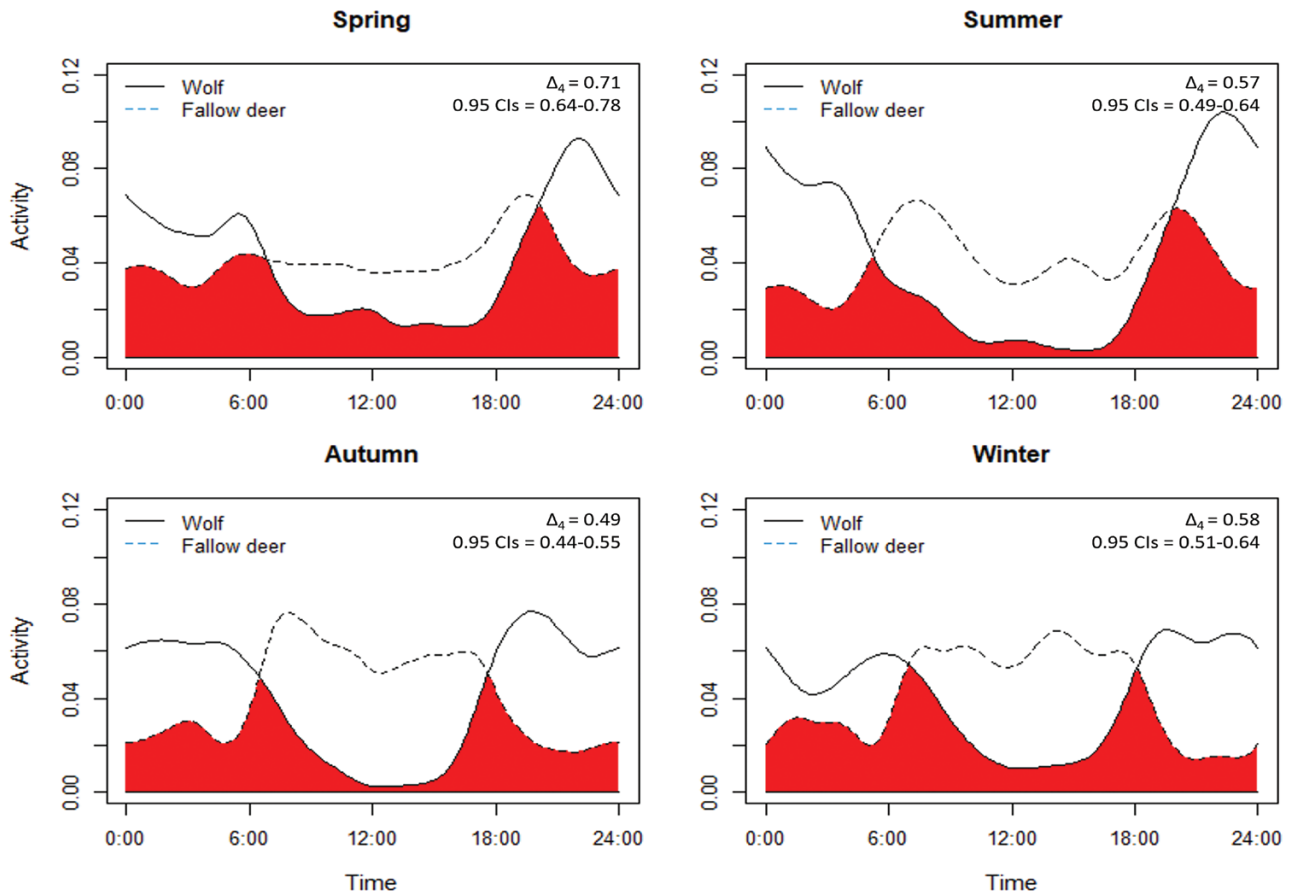


Figure 4 Temporal overlap between wolf and fallow deer assessed through camera trapping on a seasonal scale. Solid and dashed lines indicate temporal activity patterns of wolf and fallow deer, respectively. The red shaded area indicates the temporal overlap area between the 2 species. Temporal overlap was calculated using the overlap coefficient, Δ_4 ; 95% CIs were calculated through simple random sampling with replacement on 1,000 bootstraps. Overlap coefficients and CIs are shown in each panel (see online for color figures).

Table 1 Interspecific temporal overlap (Δ_4 overlap coefficient) between wolves and fallow deer in sites with high versus low wolf activity, as well as intraspecific temporal overlap (fallow deer) between high wolf and low wolf sites at the seasonal scale, and relevant 95% CIs (lower CI and upper CI)

Overlap	Season	Wolf activity	Temporal overlap (Δ_4)	Lower CI	Upper CI
Fallow deer–wolf	Spring	High	0.71	0.63	0.79
		Low	0.75	0.62	0.87
	Summer	High	0.58	0.49	0.67
		Low	0.56	0.44	0.69
	Autumn	High	0.49	0.43	0.56
		Low	0.48	0.39	0.58
	Winter	High	0.54	0.46	0.62
		Low	0.72	0.58	0.84
Fallow deer–fallow deer	Spring	High vs. Low	0.88	0.83	0.93
	Summer	High vs. Low	0.92	0.86	0.97
	Autumn	High vs. Low	0.92	0.88	0.96
	Winter	High vs. Low	0.88	0.81	0.95

in different habitats, including forested ones, where behavioral studies are usually constrained by poor visibility (e.g., Kuijper et al. 2014; Henrich et al. 2020) through an intensive study based on camera trapping over a full year. As expected, we observed (i) a spatial association between wolf activity and that of its main, selected prey, i.e., the fallow deer (Ferretti et al. 2019); (ii) no support to a spatial avoidance of sites with

high wolf activity by fallow deer. Moreover, we detected (iii) a moderate-to-low temporal overlap (*sensu* Monterroso et al. 2014) between the prey and its predator, with an increase in diurnal activity of fallow deer with respect to times when the wolf did not occur in the area (Niglio 1995; see Zanni et al. 2021 for another Mediterranean area where wolves are absent), and in respect to an initial stage of wolf recovery

Table 2 Summary of model selection

Response variable	Model	Variables	K	logLik	AICc	Δ AICc	Weight
Wolf detection rate	Best	Fallow deer + Habitat + Season + Camera type	11	-403.525	830.5	0.00	0.514
	2 nd	Fallow deer + Wild boar + Humans + Season + Habitat + Camera type *	13	-402.153	832.2	1.75	0.214
	3 rd	Fallow deer + Humans + Season + Habitat + Camera type	12	-403.510	832.7	2.24	0.168
	4 th	Habitat + Camera type	7	-409.724	834.0	3.57	0.087
	9 th	Null model	3	-415.580	837.3	6.82	0.017
Fallow deer detection rate	Best	Wild boar + Season + Habitat + Camera type	11	-623.966	1,271.3	0.00	0.338
	2 nd	Wolf + Season + Habitat + Camera type	11	-624.016	1,271.4	0.10	0.323
	3 rd	Wolf + Wild boar + Humans + Season + Habitat + Camera type *	13	-622.301	1,272.6	1.22	0.184
	4 th	Wolf + Humans + Season + Habitat + Camera type *	12	-623.617	1,272.9	1.57	0.154
	9 th	Null model	3	-640.778	1,287.7	16.33	0.000
Fallow deer vigilance rate	Best	Wolf + Humans + Group size + Season + Time of day ² + Habitat	12	-922.016	1,868.4	0.00	0.599
	2 nd	Wolf + Group size + Season + Time of day ² + Habitat	11	-923.444	1,869.2	0.80	0.401
	3 rd	Humans + Group size + Season + Time of day ² + Habitat	11	-838.747	1,899.8	31.41	0.000
	4 th	Group size + Season + Time of day ² + Habitat	10	-942.329	1,904.9	36.52	0.000
	9 th	Null model	2	-971.905	1,947.8	79.44	0.000
Fallow deer vigilance time	Best	Wolf + Group size + Season + Time of day ² + Habitat	12	-1,820.294	3,664.9	0.00	0.669
	2 nd	Wolf + Humans + Group size + Season + Time of day ² + Habitat *	13	-1,819.970	3,666.4	1.41	0.331
	3 rd	Humans + Group size + Season + Time of day ² + Habitat	12	-1,835.902	3,696.2	31.22	0.000
	4 th	Group size + Season + Time of day ² + Habitat	11	-1,837.448	3,697.2	32.25	0.000
	9 th	Null model	3	-1,869.075	3,744.2	79.24	0.000

Variables influencing spatial patterns of locomotory activity of wolves and fallow deer, as well as indices of vigilance of female fallow deer, estimated through generalized linear mixed models. Vigilance rate: number of individual head lifts in the video; Time in vigilance: duration of individual vigilance in the video. Selected models are shown in bold; models up to the fourth ranked one, and the null model (and its ranking), are shown for comparison purposes.

*These models were not selected for inference because they were more complex versions of previously selected models.

Table 3 Variables influencing detection rate of wolves and fallow deer estimated through generalized linear mixed models with negative binomial errors.

Species	Model	Variable	B	SE	0.95 CIs		P-value
					-	+	
Wolf	Best	Intercept	-2.69	0.26	-3.20	-2.19	<0.001
		Fallow deer	0.24	0.09	0.07	0.42	0.006
		Habitat [Ecotone/Open]	0.86	0.33	0.22	1.51	0.009
		Habitat [Pinewood]	0.02	0.40	-0.78	0.81	0.966
		Habitat [Shrub]	-0.24	0.33	-0.90	0.41	0.465
		Season [Summer]	0.18	0.19	-0.20	0.56	0.346
		Season [Autumn]	0.33	0.18	-0.03	0.69	0.073
		Season [Winter]	0.29	0.19	-0.08	0.66	0.125
		Camera type [Scout]	-0.20	0.26	-0.71	0.30	0.429
Fallow deer	Best	Intercept	-0.64	0.30	-1.22	-0.06	0.030
		Wild boar	0.35	0.17	0.02	0.67	0.036
		Habitat [Ecotone/Open]	-0.52	0.43	-1.36	0.33	0.230
		Habitat [Pinewood]	-0.88	0.50	-1.86	0.10	0.080
		Habitat [Shrub]	-0.86	0.41	-1.67	-0.06	0.035
		Season [Summer]	-0.30	0.17	-0.64	0.03	0.072
		Season [Autumn]	0.15	0.17	-0.17	0.47	0.368
		Season [Winter]	-0.63	0.17	-0.97	-0.30	<0.001
		Camera type [Scout]	0.23	0.28	-0.33	0.78	0.422
	Second	Intercept	-0.56	0.29	-1.14	0.01	0.055
		Wolf	0.36	0.17	-0.02	0.70	0.038
		Habitat [Ecotone/Open]	-0.73	0.45	-1.61	0.14	0.102
		Habitat [Pinewood]	-1.02	0.49	-1.97	-0.06	0.038
		Habitat [Shrub]	-0.89	0.41	-1.69	-0.09	0.030
		Season [Summer]	-0.31	0.17	-0.64	0.02	0.065
		Season [Autumn]	0.15	0.17	-0.17	0.47	0.362
		Season [Winter]	-0.63	0.17	-0.97	-0.30	<0.001
		Camera type [Scout]	0.23	0.28	-0.32	0.78	0.411

Variables included in the best models are shown.

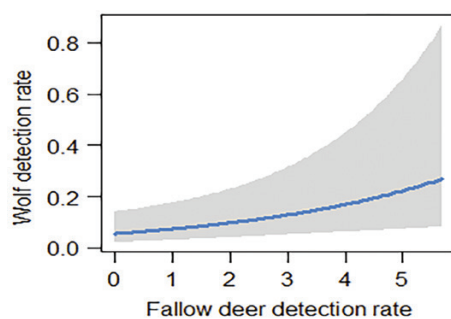


Figure 5 Frequency of wolf activity in relation to fallow deer detection rate (i.e., number of detections/number of days with operating cameras) estimated through generalized linear mixed models. Fitted relationship and relevant 0.95 CIs are shown.

in the area (Rossa et al. 2021), (iv) a greater frequency and duration of vigilance of female fallow deer in sites with higher wolf activity. These results suggest antipredator tactics based on temporal avoidance and increased vigilance.

The analysis of spatial patterns of wolf locomotory activity supported a positive effect of the local detection rate of

fallow deer and habitat. Although fallow deer availability in our study area was lower than that of wild boar (Ferretti et al. 2019), they have been reported to reach great local densities (i.e., up to more than 40–50 individuals/km², in ecotones and meadows, where they can form groups up to many tens of individuals: Pecorella et al. 2019; Ferretti and Fattorini 2021; Ferretti et al. 2021). Large body size (i.e., circa 40 kg, on average, but up to 100 kg for adult males: Ferretti et al. 2019), gregariousness, and attendance of habitats with open visibility make the fallow deer a substantial and remunerative prey to wolves. Accordingly, wolves showed the highest detection rates in sites and habitats with higher detection rates and density (Ferretti and Fattorini 2021) of fallow deer, probably to maximize the chances of spotting their favorite prey (MacNulty et al. 2007).

As to spatiotemporal antipredator tactics of fallow deer, our results suggest no avoidance of sites with a greater detection rate of wolves. Camera traps allow detection of animals during locomotory activity, which would underestimate the use of resting sites by wolves (e.g., homesites and rendezvous sites). Moreover, the spatial scale of wolf movements, which may be larger than our circa 60 km² study area, may not allow fallow deer to have suitable patches where they can avoid predators,

Table 4 Variables influencing indices of vigilance of female fallow deer estimated through generalized linear mixed models with Poisson errors

Index	Model	Variable	B	SE	0.95 CIs		P-value
					-	+	
Vigilance rate	Best	Intercept	-3.25	0.11	-3.46	-3.04	<0.001
		Wolf	0.28	0.05	0.19	0.37	<0.001
		Humans	0.07	0.04	-0.01	0.14	0.086
		Habitat [Ecotone/Open]	-0.92	0.12	-1.16	-0.68	<0.001
		Habitat [Pinewood]	-0.11	0.24	-0.57	0.36	0.655
		Habitat [Shrub]	0.39	0.18	0.05	0.74	0.027
		Season [Summer]	-0.32	0.12	-0.56	-0.07	0.011
		Season [Autumn]	0.38	0.16	0.06	0.69	0.018
		Season [Winter]	0.77	0.32	0.15	1.40	0.015
		Group size	-0.35	0.09	-0.52	-0.17	<0.001
	Time of day ²	-0.32	0.17	-0.65	0.02	0.065	
	Second	Intercept	-3.25	0.11	-3.46	-3.04	<0.001
		Wolf	0.29	0.04	0.21	0.38	<0.001
		Habitat [Ecotone/Open]	-0.91	0.12	-1.15	-0.67	<0.001
		Habitat [Pinewood]	-0.12	0.23	-0.59	0.34	0.595
		Habitat [Shrub]	0.39	0.18	0.04	0.73	0.029
		Season [Summer]	-0.31	0.12	-0.55	-0.06	0.013
		Season [Autumn]	0.42	0.16	0.11	0.73	0.007
		Season [Winter]	0.87	0.31	0.26	1.48	0.005
		Group size	-0.36	0.09	-0.53	-0.18	<0.001
Time of day ²		-0.34	0.17	-0.67	0.00	0.048	
Time in vigilance	Best	Intercept	-1.53	0.21	-1.94	-1.12	<0.001
		Wolf	0.32	0.11	0.09	0.54	<0.001
		Habitat [Ecotone/Open]	-0.99	0.31	-1.59	-0.38	<0.001
		Habitat [Pinewood]	-0.32	0.41	-1.13	0.49	0.144
		Habitat [Shrub]	0.37	0.35	-0.30	1.05	0.085
		Season [Summer]	-0.41	0.16	-0.73	-0.10	0.015
		Season [Autumn]	0.54	0.21	0.12	0.96	0.081
		Season [Winter]	1.01	0.43	0.16	1.85	<0.001
		Group size	-0.17	0.10	-0.37	0.03	<0.001
		Time of day ²	-0.26	0.21	-0.68	0.16	0.380

Variables included in the best models are shown. Vigilance rate: number of individual head lifts in the video; Time in vigilance: duration of individual vigilance in the video.

at a coarse spatial scale. However, finer-scale mechanisms of spatial avoidance may not be ruled out and, if any, satellite telemetry data would be needed to test for them (Cusack et al. 2020). Nevertheless, our results indicate that fallow deer did not avoid sites with a high frequency of wolf detections. Conversely, fallow deer showed diurnal activity patterns, especially in winter. In our study area, fallow deer showed peaks of activity at night, dawn, and dusk, in the absence of wolves (Niglio 1995; Zanni et al. 2021). An earlier study conducted just after the local wolf recovery showed peaks of fallow deer diurnal activity only in sites with high wolf activity (Rossa et al. 2021). A couple of years later, with a stable and continuous presence of wolves, our work revealed the diurnal activity of fallow deer across the whole study area, that is, both in “high wolf” and “low wolf” sites. Since the 1990s, fallow deer have been culled by park wardens all year round by stalking at night and dawn/dusk, and from fixed locations, in limited sectors of the study area, with no major changes in culling

procedures throughout our study period. Moreover, culling intensity has decreased from *circa* 223 individuals per year in 2011–2015 to *circa* 104 individuals per year in 2016–2020 (Maremma Regional Park data). Thus, the increase of diurnal behavior should not depend on avoidance of culling. Fallow deer might have increased diurnal activity to favor overlap with human activity, thus benefiting from “human shields” to avoid wolves (Shannon et al. 2014; Geffroy et al. 2015). The presence of tourists in the Park is usually concentrated in spring–summer along the beach and main touristic trails; however, our data indicate that (i) diurnal behavior occurred more in autumn–winter than in spring–summer, and (ii) no spatial association occurred between fallow deer and human detection rates at camera-trapping sites. Thus, the increase of diurnal activity by fallow deer may not depend on anthropogenic factors (e.g., the “human shield hypothesis”, Geffroy et al. 2015). Our results support the development of temporal avoidance of wolves by the deer. If so, these deer would show

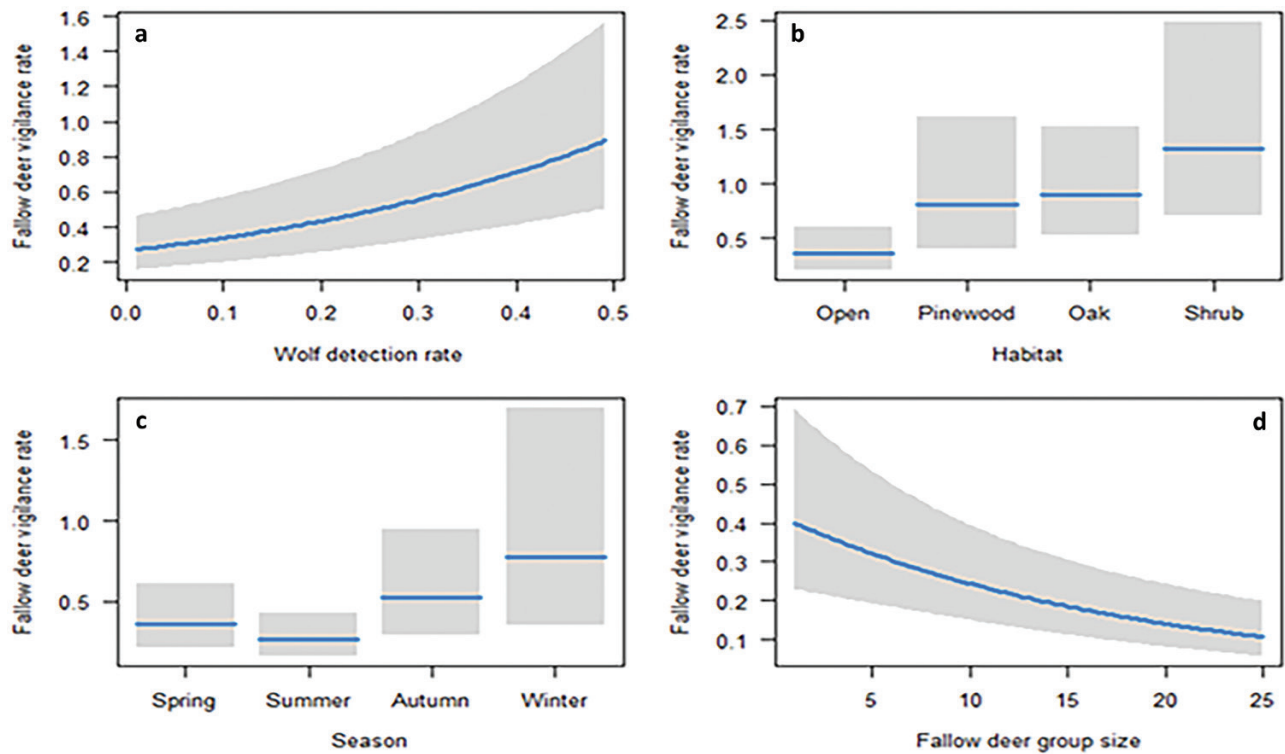


Figure 6. Vigilance rate (number of head lifts per video) of female fallow deer in relation to wolf activity (number of detections per day; A), habitat (B), season (C), and fallow deer group size (number of individuals in the video; D). Relationships estimated through generalized linear mixed models and relevant 0.95 CIs are shown.

a short-term antipredator response based on temporal avoidance (Kohl et al. 2018; Palmer et al. 2021).

Temporal overlap between fallow deer and wolves was generally low-to-moderate (*sensu* Monterroso et al. 2014), being lower in the cold semester (i.e., autumn and winter) than in the warm one. Moreover, wolf–fallow temporal overlap was comparable between “high wolf” and “low wolf” sites in all seasons except for winter, when it was 1.3 times greater in the latter sites than in the former ones. Preliminary information on wolf food habits suggested no increase in wolf predation on fallow deer from spring–summer to autumn–winter (Ferretti et al. 2019). Wolves showed nocturnal activity and daylight is shorter in the colder months than in warmer ones. Moreover, in autumn–winter, wolf pups are grown and join the rest of the pack in movements and hunting, which leads to a seasonal increase in the number of wolves moving across the area (Jedrzejewski et al. 2001; Mech and Boitani 2003), and consequently of the risk for the prey to be spotted and chased. The diurnal activity of fallow deer occurred especially in autumn–winter, suggesting that they tended to reduce their nocturnal activity in parts of the year when the risk of an encounter with a wolf pack was relatively higher.

Female fallow deer increased vigilance in sites with high wolf activity. Our findings suggest that female fallow deer could adjust their vigilance according to perceived spatial variation of risk of encounters with predators (Mooring et al. 2004; Périquet et al. 2010; Sönnichsen et al. 2013; Kuijper et al. 2014, 2015). Although observations of individually recognizable focal animals would be required to support our results, findings also suggest that female fallow deer tuned their vigilance according to environmental cues,

with alertness being greater in sites with shrubs and in the wood, as well as in winter. Vigilance has been reported to decrease with increasing group size in gregarious foragers (Delm 1990; Fryxell 1991; Schradin et al. 2019), including also fallow deer (Pecorella et al. 2019). Obstructive cover elicits vigilance (Frid 1997): in open habitat, good visibility allows animals to easily verify the presence of a predator (Chen et al. 2021), whereas the opposite should be expected in the presence of thick and bushy vegetation (Davies et al. 2016). Furthermore, the dense vegetation of shrubwood may favor ambush predation (Torretta et al. 2018). Female ungulates would be expected to increase their vigilance in spring–summer, owing to the presence of newborn offspring that are usually the most vulnerable individuals to predation (e.g., Toïgo 1999 and references therein; Lashley et al. 2014). In our study case, both group size and vigilance increased in the cold seasons. In autumn–winter, fallow deer mean group size was *circa* 2.2–2.6 times greater than in spring–summer: thus, the seasonal increase of vigilance was not related to decreasing group size. Our results are in line with a seasonal increase of diurnal activity and reduction of temporal overlap with the wolf, indicating a reinforcement of antipredator behavior during the cold period. Future work should assess the potential effects of such antipredator tactics on wolf spatiotemporal patterns, as well as food habits.

Thick and dense vegetation usually provides an excellent cover for stalking predators, such as lions (*Panthera leo*, Davies et al. 2016) and pumas (*Puma concolor*, Smith et al. 2020). Generally, canids prefer hunting in open habitats (Murray et al. 1995). However, wolves are flexible and opportunistic predators (Peterson and Ciucci 2003) who can resort to different hunting tactics (Muro et al. 2011; Mech et al.

2021), ranging from cursorial pursuit (Escobedo et al. 2014) to ambush (Nichols 2015; Gable et al. 2016, 2018; Mech et al. 2021). They can use vegetation also to conceal cues of their presence (Gable et al. 2021). Sectors with dense vegetation are abundant in our study area, which would influence perceived predation risk by fallow deer. Our results support that prey adjusted their antipredator behavior to local habitat features (Muro et al. 2011).

In conclusion, our study contributes to the debate on the nature of antipredator behavioral responses (e.g., Mech 2012; Ripple et al. 2014; Ford et al. 2015; Kuijper et al. 2016; Ausilio et al. 2021). The potential for predators to elicit antipredator responses based on spatiotemporal avoidance has stimulated a growing interest in researchers (e.g., Creel et al. 2005; Fortin et al. 2005; Kohl et al. 2018; Palmer et al. 2021). Large and relatively undisturbed landscapes are expected to provide herbivores with adequate opportunities to select alternative suitable sites for feeding and resting, thus avoiding risky areas (e.g., Creel et al. 2005; Fortin et al. 2005). Conversely, opportunities for modifying spatial movements may be limited in smaller areas where resources are clumped, which may occur in anthropized systems. Thus, antipredator strategies based on temporal avoidance (Kohl et al. 2018; Palmer et al. 2021; Sand et al. 2021) and increased vigilance may be expected. Our results emphasize that the nature of the antipredator response is not ubiquitous and that not all conclusions can be generalized across anthropized and relatively undisturbed ecosystems (see Cusack et al. 2020). The potential for such responses to elicit behaviorally induced trophic cascades should be assessed.

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Author Contributions

Conceptualization: FF; data collection: BE, ACR, FB, RO, CR, FF; data analyses: BE, ACR, FF; writing the first draft: BE, ACR, FF; writing and approval of the final manuscript: all authors; supervision: FF.

Conflict of Interest Statement

The authors have no competing interests to declare.

Supplementary Material

Supplementary material can be found at <https://academic.oup.com/cz>.

References

- Apollonio M, Andersen R, Putman R, 2010. *European Ungulates and Their Management in the 21st Century*. Cambridge: Cambridge University Press.
- Arrigoni PV, Gellini R, Innamorati M, Lenzi M, Grillini C et al., 1976. Relazione al consorzio per l'istituzione del "parco della maremma". *Inf Bot Ital* 8:283–324.
- Ausilio G, Sand H, Månsson J, Mathisen KM, Wikenros C, 2021. Ecological effects of wolves in anthropogenic landscapes: The potential for trophic cascades is context-dependent. *Front Ecol Evol* 8:481.
- Barton K, 2012. Mumin: Multi-model Inference. R Package Version 1.7.2. <https://CRAN.R-project.org/package=MuMIn>
- Bates D, Mächler M, Bolker B, Walker S, 2015. lme4: Linear Mixed-Effects Models Using Eigen and s4. R Package Version 1.1–7. 2014. <http://CRAN.R-project.org/package=lme4>.
- Beschta RL, Ripple WJ, 2009. Large predators and trophic cascades in terrestrial ecosystems of the Western United States. *Biol Conserv* 142(11):2401–2414.
- Bonsen GT, Wallach AD, Ben-Ami D, Keynan O, Khalilieh A et al., 2022. Tolerance of wolves shapes desert canid communities in the Middle East. *Glob Ecol Conserv* 36:e02139.
- Bu H, Wang F, McShea WJ, Lu Z, Wang D et al., 2016. Spatial co-occurrence and activity patterns of mesocarnivores in the temperate forests of Southwest China. *PLoS ONE* 11(10):e0164271.
- Bubnicki JW, Churski M, Schmidt K, Diserens TA, Kuijper DP, 2019. Linking spatial patterns of terrestrial herbivore community structure to trophic interactions. *ELife* 8:e44937.
- Burnham KP, Anderson DR. 2002 *A Practical Information-Theoretic Approach. Model Selection and Multimodel Inference*. Vol. 2, 2nd edn. New York: Springer.
- Caniglia R, Fabbri E, Greco C, Galaverni M, Manghi L et al., 2013. Black coats in an admixed wolf × dog pack is melanism an indicator of hybridization in wolves? *Eur J Wildlife Res* 59(4):543–555.
- Chapron G, Kaczensky P, Linnell JD, Von Arx M, Huber D et al., 2014. Recovery of large carnivores in Europe's modern human-dominated landscapes. *Science* 346(6216):1517–1519.
- Chen A, Reperant L, Fischhoff IR, Rubenstein DI, 2021. Increased vigilance of plains zebras *Equus quagga* in response to more bush coverage in a Kenyan Savanna. *Clim Change Ecol* 1:100001.
- Creel S, Christianson D, 2008. Relationships between direct predation and risk effects. *Trends Ecol Evol* 23(4):194–201.
- Creel S, Schuette P, Christianson D, 2014. Effects of predation risk on group size, vigilance, and foraging behavior in an African ungulate community. *Behav Ecol* 25(4):773–784.
- Creel S, Winnie J Jr, Maxwell B, Hamlin K, Creel M, 2005. Elk alter habitat selection as an antipredator response to wolves. *Ecology* 86(12):3387–3397.
- Cusack JJ, Kohl MT, Metz MC, Coulson T, Stahler DR et al., 2020. Weak spatiotemporal response of prey to predation risk in a freely interacting system. *J Anim Ecol* 89(1):120–131.

- Davidson Z, Valeix M, Loveridge AJ, Hunt JE, Johnson PJ et al., 2012. Environmental determinants of habitat and kill site selection in a large carnivore: Scale matters. *J Mammal* 93(3):677–685.
- Davies AB, Tambling CJ, Kerley GI, Asner GP, 2016. Effects of vegetation structure on the location of lion kill sites in African thicket. *PLoS ONE* 11(2):e0149098.
- Delm MM, 1990. Vigilance for predators: Detection and dilution effects. *Behav Ecol Sociobiol* 26(5):337–342.
- Endler J, 1986. Defence against predators. In: Feder M, Lauder G, editors. *Predator-Prey Relationships: Perspectives and Approaches from the Study of Lower Vertebrates*. Chicago (IL): University of Chicago Press, 109–134.
- Escobedo R, Muro C, Spector L, Coppinger R, 2014. Group size, individual role differentiation and effectiveness of cooperation in a homogeneous group of hunters. *J R Soc Interface* 11(95):20140204.
- Fattorini L, Ferretti F, Pisani C, Sforzi A, 2011. Two-stage estimation of ungulate abundance in Mediterranean areas using pellet group count. *Environ Ecol Stat* 18(2):291–314.
- Ferretti F, Fattorini N, 2021. Competitor densities, habitat, and weather: Effects on interspecific interactions between wild deer species. *Integr Zool* 16(5):670–684.
- Ferretti F, Lovari S, Mancino V, Burrini L, Rossa M, 2019. Food habits of wolves and selection of wild ungulates in a prey-rich Mediterranean coastal area. *Mamm Biol* 99:119–127.
- Ferretti F, Pacini G, Belardi I, ten Cate B, Sensi M et al., 2021. Recolonizing wolves and opportunistic foxes: Interference or facilitation? *Biol J Linn Soc* 132(1):196–210.
- Ferretti F, Sforzi A, Lovari S, 2008. Intolerance amongst deer species at feeding: Roe deer are uneasy banqueters. *Behav Proc* 78(3):487–491.
- Ford AT, Goheen JR, Augustine DJ, Kinnaird MF, O'Brien TG et al., 2015. Recovery of African wild dogs suppresses prey but does not trigger a trophic cascade. *Ecology* 96(10):2705–2714.
- Fortin D, Beyer HL, Boyce MS, Smith DW, Duchesne T et al., 2005. Wolves influence elk movements: Behavior shapes a trophic cascade in Yellowstone National Park. *Ecology* 86(5):1320–1330.
- Foster VC, Sarmiento P, Sollmann R, Törres N, Jácomo AT et al., 2013. Jaguar and puma activity patterns and predator-prey interactions in four Brazilian biomes. *Biotropica* 45(3):373–379.
- Frid A, 1997. Vigilance by female dall's sheep: Interactions between predation risk factors. *Anim Behav* 53(4):799–808.
- Fryxell JM, 1991. Forage quality and aggregation by large herbivores. *Am Naturalist* 138(2):478–498.
- Gable TD, Homkes AT, Johnson-Bice SM, Windels SK, Bump JK, 2021. Wolves choose ambushing locations to counter and capitalize on the sensory abilities of their prey. *Behav Ecol* 32(2):339–348.
- Gable TD, Stanger T, Windels SK, Bump JK, 2018. Do wolves ambush beavers? Video evidence for higher-order hunting strategies. *Ecosphere* 9(3):e02159.
- Gable TD, Windels SK, Bruggink JG, Homkes AT, 2016. Where and how wolves *Canis lupus* kill beavers *Castor canadensis*. *PLoS ONE* 11(12):e0165537.
- Geffroy B, Samia DS, Bessa E, Blumstein DT, 2015. How nature-based tourism might increase prey vulnerability to predators. *Trends Ecol Evol* 30(12):755–765.
- Ghigi A, 1911. Ricerche faunistiche e sistematiche sui mammiferi d'Italia che formano oggetto di caccia. *Natura* 2(10–11):289–337.
- Hartig F, 2019. Dharma: Residual Diagnostics for Hierarchical (Multi-level/mixed) Regression Models. R Package Version 0.1.0. <http://florianhartig.github.io/DHARMA>
- Hebblewhite M, Merrill E, McDonald T, 2005. Spatial decomposition of predation risk using resource selection functions: An example in a wolf - elk predator - prey system. *Oikos* 111(1):101–111.
- Henrich M, Niederlechner S, Kröschel M, Thoma S, Dormann CF et al., 2020. The influence of camera trap flash type on the behavioural reactions and trapping rates of red deer and roe deer. *Remote Sens Ecol Conserv* 6(3):399–410.
- Jedrzejewski W, Schmidt K, Theuerkauf J, Jedrzejewska B, Okarma H, 2001. Daily movements and territory use by radio-collared wolves *Canis lupus* in Białowieża Primeval Forest in Poland. *Can J Zool* 79(11):1993–2004.
- Kohl MT, Stahler DR, Metz MC, Forester JD, Kauffman MJ et al., 2018. Diel predator activity drives a dynamic landscape of fear. *Ecol Monogr* 88(4):638–652.
- Kuijper D, De Kleine C, Churski M, Van Hooft P, Bubnicki J et al., 2013. Landscape of fear in Europe: Wolves affect spatial patterns of ungulate browsing in Białowieża Primeval Forest, Poland. *Ecography* 36(12):1263–1275.
- Kuijper D, Sahlén E, Elmhagen B, Chamailé-Jammes S, Sand H et al., 2016. Paws without claws? Ecological effects of large carnivores in anthropogenic landscapes. *Proc R Soc B* 283(1841):20161625.
- Kuijper DP, Bubnicki JW, Churski M, Mols B, Van Hooft P, 2015. Context dependence of risk effects: Wolves and tree logs create patches of fear in an old-growth forest. *Behav Ecol* 26(6):1558–1568.
- Kuijper DP, Verwijmeren M, Churski M, Zbyryt A, Schmidt K et al., 2014. What cues do ungulates use to assess predation risk in dense temperate forests? *PLoS ONE* 9(1):e84607.
- Lashley MA, Chitwood MC, Biggerstaff MT, Morina DL, Moorman CE et al., 2014. White-tailed deer vigilance: The influence of social and environmental factors. *PLoS ONE* 9(3):e90652.
- Li S, McShea WJ, Wang D, Lu Z, Gu X, 2012. Gauging the impact of management expertise on the distribution of large mammals across protected areas. *Divers Distrib* 18(12):1166–1176.
- Li S, McShea WJ, Wang D, Shao L, Shi X, 2010. The use of infrared-triggered cameras for surveying phasianids in Sichuan Province, China. *Ibis* 152(2):299–309.
- Lima SL, 1998. Stress and decision-making under the risk of predation: Recent developments from behavioral, reproductive, and ecological perspectives. *Adv Study Behav* 27(8):215–290.
- Lima SL, Bednekoff PA, 1999. Temporal variation in danger drives antipredator behavior: The predation risk allocation hypothesis. *Am Naturalist* 153(6):649–659.
- Lima SL, Dill LM, 1990. Behavioral decisions made under the risk of predation: A review and prospectus. *Can J Zool* 68(4):619–640.
- Lingle S, 2001. Anti-predator strategies and grouping patterns in white-tailed deer and mule deer. *Ethology* 107(4):295–314.
- Lingle S, Pellis S, 2002. Fight or flight? Antipredator behavior and the escalation of coyote encounters with deer. *Oecologia* 131(1):154–164.
- Lingle S, Pellis SM, Wilson WF, 2005. Interspecific variation in anti-predator behaviour leads to differential vulnerability of mule deer and white-tailed deer fawns early in life. *J Anim Ecol* 74(6):1140–1149.
- Lipetz VE, Bekoff M, 1982. Group size and vigilance in pronghorns. *Z Tierpsychol* 58(3):203–216.
- Lucherini M, Reppucci JI, Walker RS, Villalba ML, Wursten A et al., 2009. Activity pattern segregation of carnivores in the High Andes. *J Mamm* 90(6):1404–1409.
- Lund U, Agostinelli C, Arai H, Gagliardi A, Portugues E et al., 2017. *Circular statistics*. R package version, 4–93.
- MacNulty DR, Mech LD, Smith DW, 2007. A proposed ethogram of large-carnivore predatory behavior, exemplified by the wolf. *J Mamm* 88(3):595–605.
- Magnusson A, Skaug H, Nielsen A, Berg C, Kristensen K et al., 2017. Package 'glmmTMB'. <https://github.com/glmmTMB>.
- Makin DF, Chamailé-Jammes S, Shrader AM, 2017. Herbivores employ a suite of antipredator behaviours to minimize risk from ambush and cursorial predators. *Anim Behav* 127:225–231.
- Mao JS, Boyce MS, Smith DW, Singer FJ, Vales DJ et al., 2005. Habitat selection by elk before and after wolf reintroduction in Yellowstone National Park. *J Wildlife Manag* 69(4):1691–1707.
- Martin JL, Chamailé-Jammes S, Waller DM, 2020. Deer, wolves, and people: Costs, benefits and challenges of living together. *Biol Rev* 95(3):782–801.
- Mech L, Boitani L, 2003. *Wolf Social Ecology: Wolves Behavior, Ecology and Conservation*. Chicago (IL): University of Chicago Press. 1–34.

- Mech LD, 2012. Is science in danger of sanctifying the wolf? *Biol Conserv* 150(1):143–149.
- Mech LD, Smith DW, MacNulty DR, 2021. Introduction: The wolf as a killing machine. In: Mech LD, Smith DW, MacNulty DR, editors. *Wolves on the Hunt: The Behavior of Wolves Hunting Wild Prey*. Chicago (IL): University of Chicago Press, 1–9.
- Melini D, Agrillo E, Ferretti F, Tonelli L, 2019. *Piano di gestione della zsc/zps it51a0016 monti dell'uccellina*. Alberese: Ente Parco Regionale della Maremma.
- Mencagli M, Stefanini P, 2008. *Carta della vegetazione per il piano del parco*. Alberese: Ente Parco Regionale della Maremma.
- Meredith M, Ridout M, 2017. Overlap: Estimates of Coefficient of Overlapping for Animal Activity Patterns. R Package Version 0.30. <https://cran.r-project.org/package=overlap>. Accessed May 2017.
- Meredith M, Ridout M, Meredith M, 2017. Estimates of coefficient of overlapping for animal activity patterns. R CRAN Repository.
- Monterroso P, Alves PC, Ferreras P, 2014. Plasticity in circadian activity patterns of mesocarnivores in Southwestern Europe: Implications for species coexistence. *Behav Ecol Sociobiol* 68(9):1403–1417.
- Mooring MS, Fitzpatrick TA, Nishihira TT, Reisig DD, 2004. Vigilance, predation risk, and the allele effect in desert bighorn sheep. *J Wildlife Manag* 68(3):519–532.
- Mori E, Bagnato S, Serroni P, Sangiuliano A, Rotondaro F et al., 2020. Spatiotemporal mechanisms of coexistence in an European mammal community in a protected area of Southern Italy. *J Zool* 310(3):232–245.
- Muro C, Escobedo R, Spector L, Coppinger R, 2011. Wolf-pack *Canis lupus* hunting strategies emerge from simple rules in computational simulations. *Behav Proc* 88(3):192–197.
- Murray DL, Boutin S, O'Donoghue M, Nams VO, 1995. Hunting behaviour of a sympatric felid and canid in relation to vegetative cover. *Anim Behav* 50(5):1203–1210.
- Nichols TC, 2015. Cooperative hunting of Canada geese *Branta canadensis* by gray wolves *Canis lupus* in Northern Quebec. *Can Field-Naturalist* 129(3):290–292.
- Niglio M, 1995. *Home ranges, ritmi di attività e scelta dell'habitat di femmine di daino nel parco regionale della maremma* [M. Sc. Thesis]. Bologna: University of Bologna.
- Obersoler V, Groff C, Iemma A, Pedrini P, Rovero F, 2017. The influence of human disturbance on occupancy and activity patterns of mammals in the Italian Alps from systematic camera trapping. *Mamm Biol* 87(1):50–61.
- Paine RT, 1969. A note on trophic complexity and community stability. *Am Naturalist* 103(929):91–93.
- Palmer MS, Portales-Reyes C, Potter C, Mech LD, Isbell F, 2021. Behaviorally-mediated trophic cascade attenuated by prey use of risky places at safe times. *Oecologia* 195(1):235–248.
- Pecorella I, Fattorini N, Macchi E, Ferretti F, 2019. Sex/age differences in foraging, vigilance and alertness in a social herbivore. *Acta Ethol* 22(1):1–8.
- Périquet S, Valeix M, Loveridge AJ, Madzikanda H, Macdonald DW et al., 2010. Individual vigilance of African herbivores while drinking: The role of immediate predation risk and context. *Anim Behav* 79(3):665–671.
- Peterson R, Ciucci P, 2003. The wolf as a carnivore. In: Mech LD, Boitani L, editors. *Wolves: Behavior, Ecology, and Conservation*. Chicago (IL): Chicago Press, 104–130.
- Prugh LR, Stoner CJ, Epps CW, Bean WT, Ripple WJ et al., 2009. The rise of the mesopredator. *BioScience* 59(9):779–791.
- Pulliam HR, 1973. On the advantages of flocking. *J Theor Biol* (38):419–422.
- Ridout MS, Linkie M, 2009. Estimating overlap of daily activity patterns from camera trap data. *J Agric Biol Environ Stat* 14(3):322–337.
- Ripari L, Premier J, Belotti E, Bluhm H, Breitenmoser-Würsten C et al., 2022. Human disturbance is the most limiting factor driving habitat selection of a large carnivore throughout Continental Europe. *Biol Conserv* 266:109446–109446.
- Ripple WJ, Beschta RL, 2012. Large predators limit herbivore densities in northern forest ecosystems. *Eur J Wildlife Res* 58(4):733–742.
- Ripple WJ, Estes JA, Beschta RL, Wilmers CC, Ritchie EG et al., 2014. Status and ecological effects of the world's largest carnivores. *Science* 343(6167):1241484.
- Roberts G, 1996. Why individual vigilance declines as group size increases. *Anim Behav* 51(5):1077–1086.
- Rossa M, Lovari S, Ferretti F, 2021. Spatiotemporal patterns of wolf, mesocarnivores and prey in a Mediterranean area. *Behav Ecol Sociobiol* 75(2):1–13.
- Rowcliffe JM, Field J, Turvey ST, Carbone C, 2008. Estimating animal density using camera traps without the need for individual recognition. *J Appl Ecol* 45(4):1228–1236.
- Salvatori M, Obersoler V, Augugliaro C, Krofel M, Rovero F, 2022. Effects of free-ranging livestock on occurrence and inter-specific interactions of a mammalian community. *Ecol Appl* 32:e2644.
- Samelius G, Andrén H, Kjellander P, Liberg O, 2013. Habitat selection and risk of predation: Re-colonization by lynx had limited impact on habitat selection by roe deer. *PLoS ONE* 8(9):e75469.
- San José C, Lovari S, Ferrari N, 1996. Temporal evolution of vigilance in roe deer. *Behav Proc* 38(2):155–159.
- Sand H, Jamieson M, Andrén H, Wikenros C, Crowsigt J et al., 2021. Behavioral effects of wolf presence on moose habitat selection: Testing the landscape of fear hypothesis in an anthropogenic landscape. *Oecologia* 197(1):101–116.
- Schmitz OJ, Beckerman AP, O'Brien KM, 1997. Behaviorally mediated trophic cascades: Effects of predation risk on food web interactions. *Ecology* 78(5):1388–1399.
- Schradin C, Vonk J, Shackelford T, 2019. Confusion effect. In: Vonk J, Shackelford TK, editors. *Encyclopedia of Animal Cognition and Behaviour*. Cham, Switzerland: Springer, 375–376.
- Sforzi A, Tonelli L, Cortés-Selva F, Mastacchi R, Lanzi L et al., 2013. *Piano di gestione dei sic/sir it51a0039 [sie 113 e a113 (zps)] palude della trappola e bocca d'ombrore, it51a0014 [sir 114] pineta granducale dell'uccellina e it51a0015 [sir 115] dune costiere del parco dell'uccellina*. Ente Parco Regionale della Maremma.
- Shannon G, Cordes LS, Hardy AR, Angeloni LM, Crooks KR, 2014. Behavioral responses associated with a human-mediated predator shelter. *PLoS ONE* 9(4):e94630.
- Shrader AM, Brown JS, Kerley GI, Kotler BP, 2008. Do free-ranging domestic goats show 'landscapes of fear'? Patch use in response to habitat features and predator cues. *J Arid Environ* 72(10):1811–1819.
- Sirot E, Blanchard P, Loison A, Pays O, 2021. How vigilance shapes the functional response of herbivores. *Funct Ecol* 35:1491–1500.
- Sirot E, Touzalin F, 2009. Coordination and synchronization of vigilance in groups of prey: The role of collective detection and predators' preference for stragglers. *Am Naturalist* 173(1):47–59.
- Smith JA, Donadio E, Bidder OR, Pauli JN, Sheriff MJ et al., 2020. Where and when to hunt? Decomposing predation success of an ambush carnivore. *Ecology* 101(12):e03172.
- Sönningh L, Bokje M, Marchal J, Hofer H, Jędrzejewska B et al., 2013. Behavioural responses of European roe deer to temporal variation in predation risk. *Ethology* 119(3):233–243.
- Tambling CJ, Minnie L, Meyer J, Freeman EW, Santymire RM et al., 2015. Temporal shifts in activity of prey following large predator reintroductions. *Behav Ecol Sociobiol* 69(7):1153–1161.
- Thaker M, Vanak AT, Owen CR, Ogden MB, Niemann SM et al., 2011. Minimizing predation risk in a landscape of multiple predators: Effects on the spatial distribution of African ungulates. *Ecology* 92(2):398–407.
- Theuerkauf J, Rouys S, 2008. Habitat selection by ungulates in relation to predation risk by wolves and humans in the Białowieża Forest, Poland. *Forest Ecol Manag* 256(6):1325–1332.
- Tobler MW, Carrillo-Percastegui SE, Leite Pitman R, Mares R, Powell G, 2008. An evaluation of camera traps for inventorying large- and medium-sized terrestrial rainforest mammals. *Anim Conserv* 11(3):169–178.
- Toïgo C, 1999. Vigilance behavior in lactating female alpine ibex. *Can J Zool* 77(7):1060–1063.

- Torretta E, Caviglia L, Serafini M, Meriggi A, 2018. Wolf predation on wild ungulates: How slope and habitat cover influence the localization of kill sites. *Curr Zool* 64(3):271–275.
- Torretta E, Mosini A, Piana M, Tirozzi P, Serafini M et al., 2017. Time partitioning in mesocarnivore communities from different habitats of NW Italy: Insights into Martens' competitive abilities. *Behaviour* 154(2):241–266.
- Torretta E, Serafini M, Puopolo F, Schenone L, 2016. Spatial and temporal adjustments allowing the coexistence among carnivores in Liguria (NW Italy). *Acta Ethol* 19(2):123–132.
- Valeix M, Fritz H, Loveridge AJ, Davidson Z, Hunt JE et al., 2009. Does the risk of encountering lions influence African herbivore behaviour at waterholes? *Behav Ecol Sociobiol* 63(10):1483–1494.
- Wallach AD, Izhaki I, Toms JD, Ripple WJ, Shanas U, 2015. What is an apex predator? *Oikos* 124(11):1453–1461.
- Weitzman MS, 1970. *Measures of Overlap of Income Distributions of White And Negro Families in the United States*. Washington (DC): US Bureau of the Census.
- Weterings MJ, Meister N, Fey K, Jansen PA, van Langevelde F et al., 2022. Context-dependent responses of naïve ungulates to wolf-sound playback in a human-dominated landscape. *Anim Behav* 185:9–20.
- Wilson RP, Griffiths IW, Mills MG, Carbone C, Wilson JW et al., 2015. Mass enhances speed but diminishes turn capacity in terrestrial pursuit predators. *Elife* 4:e06487.
- Zanni M, Brivio F, Grignolio S, Apollonio M, 2021. Estimation of spatial and temporal overlap in three ungulate species in a Mediterranean environment. *Mamm Res* 66(1):149–162.
- Zuur A, Ieno EN, Walker N, Saveliev AA, Smith GM, 2009. *Mixed Effects Models and Extensions in Ecology with R*. Springer Science & Business Media.