*Integrative Zoology*

**ORIGINAL ARTICLE** OPEN ACCESS

# Temporal Responses to Warming: Do Wild Herbivores Trade Off Heat, Predators, and Humans?

Noemi Pallari[1,2] | Niccolò Fattorini[1,2] | Martina Calosi[1] | Lorenzo Lazzeri[1] | Giulia Tettamanti[1,3] | Sandro Lovari[1,4] | Francesco Ferretti[1,2]

[1]Department of Life Sciences, University of Siena, Siena, Italy | [2]NBFC, National Biodiversity Future Center, Palermo, Italy | [3]Department of Physics, Chemistry and Biology, Linköping University, Linköping, Sweden | [4]Maremma Natural History Museum, Grosseto, Italy

**Correspondence:** Niccolò Fattorini (niccolo.fattorini@unisi.it)

**Received:** 12 December 2024 | **Revised:** 8 August 2025 | **Accepted:** 27 October 2025

**Keywords:** activity | global warming | human disturbance | nocturnality | predator presence

## ABSTRACT

Ongoing environmental changes are affecting behavioral responses of animal populations. Both warming temperatures and increased human disturbance may trigger adjustments in mammal activity patterns, for example, favoring activity switch to nighttime despite a greater risk of encountering nocturnal predators. Disentangling the relative roles of these stressors is critical for predicting the population-level consequences of environmental changes, yet the joint effect of multiple stressors is poorly understood. Here we investigated how ambient summer temperature, predators, and human presence influenced temporal responses in two herbivorous mammals (the roe deer *Capreolus capreolus* and the fallow deer *Dama dama*) across Mediterranean protected areas. By conducting intensive camera trapping (~12,400 trapping days; 196 sites), we evaluated changes in daily activity level and nocturnality of deer species. Both herbivores reduced their daily activity with warmer temperatures, emphasizing the need to minimize thermoregulatory costs, yet only roe deer increased nocturnality following diel warming. Conversely, nocturnality of the more heat-tolerant fallow deer was only affected by wolf (*Canis lupus*) visitation rate, although weakly, suggesting that fallow deer traded off heat avoidance with predator avoidance. We found neither reductions in daily activity levels nor an increase in nocturnality in response to higher human visitation rate, possibly depending on our relatively undisturbed protected areas (i.e., areas with low human population density and sustainable levels of outdoor recreational activities) or the stronger effect of heat avoidance. Under the anticipated warming, species-specific consequences of these behavioral responses on population viability may be expected.

## 1 | Introduction

Among the ongoing environmental changes, the increase in temperature is expected to trigger the most significant effects on animal behavior and ecology (Parmesan 2006). On average, the global surface temperature was ~1–1.3°C higher in the last decade than over a century ago, and it is projected to increase further (Lee et al. 2023). Thus, increasingly stronger impacts on individual and population-level behavioral responses should be expected (e.g., Mason et al. 2014; Fattorini et al. 2023).

In endotherms, ambient temperature can influence the allocation of energy reserves to vital behaviors such as foraging, resting, and moving between habitat patches (Aublet et al. 2009; Riek et al. 2019). Individual fitness is maximized when body temperature is close to the physiological optimum (Maloney et al. 2019; Levesque and Marshall 2021). When environmental temperature deviates from the thermoneutral zone (i.e., a species-specific range of temperatures that minimize energy costs; Hill et al. 2016), mammals may respond through behavioral thermoregulation to maintain their body temperature within the optimal level, which

*Integrative Zoology*, 2026; 0:1–13
https://doi.org/10.1111/1749-4877.70061

is thought to be less energetically expensive than autonomic thermoregulation (Terrien et al. 2011). For example, mammals may employ heat-dissipating behavior patterns such as the increase of respiratory frequency via panting in dogs (*Canis lupus familiaris*; Goldberg et al. 1981), saliva spreading in kangaroos (*Osphranter rufus*; Needham et al. 1974), enhanced conductive cooling through changed body postures in koalas (*Phascolarctos cinereus*; Briscoe et al. 2014), and ear fanning in elephants (*Loxodonta africana*; Phillips and Heath 2001). Species may also shift their ranges to evade rising temperatures by moving to poleward latitudes (Parmesan 2006), to higher elevations (Mason et al. 2014), or by increasing the use of thermally buffered microhabitats (Scheffers et al. 2014). Growing evidence suggests that changing temporal activity patterns in response to ambient temperatures is also common in wild mammals (rodents: Rezende et al. 2003; giant anteaters: Giroux et al. 2023; mesocarnivores: Zub et al. 2009; ungulates: Brivio et al. 2024; and large carnivores: Rafiq et al. 2023) and could reduce the need to search for thermal shelters. Such behavioral flexibility can allow animals to mitigate some of the negative effects of rapidly changing temperatures (Beever et al. 2017). Therefore, investigating how temperature influences temporal activity patterns is crucial to better understand the adaptability of wild animal species and to predict their persistence under future climate scenarios. Moreover, it would improve our knowledge of the flexible behavioral responses to warming.

Activity rhythms are critical to control the energy balance of animals (Daan and Aschoff 1982). Vital activities entail energy expenditure and increase metabolic heat production, thus their reduction during the hottest hours may allow individuals to avoid hyperthermia. High temperatures may lead animals to reduce diurnal activity, in turn increasing the levels of nocturnal activity (Brivio et al. 2024; Bourgoin et al. 2011; Levy et al. 2019; Thel et al. 2024). At temperate latitudes, the night is significantly shorter than the day in summer; thus, the shift from diurnal to nocturnal activity may not allow individuals to compensate for the loss of foraging opportunities during daylight, with consequences on mass gain (Garel et al. 2004). Modifications of temporal activity patterns may further impact individual fitness negatively, for example, by increasing encounter risk with predators (Lesmerises et al. 2018), by leading to mismatches in interactions with conspecifics (Greives et al. 2015), or by increasing the risk of disease infections (Takahashi et al. 2008).

With the growth of human activities and the recolonization of temperate ecosystems by large carnivores, wild herbivores are expected to adopt behavioral responses to reduce their exposure to these risk factors, which may involve changes in activity patterns (e.g., Ciuti et al. 2012; Gaynor et al. 2018; Palmer et al. 2021; Rossa et al. 2021). Where hunting is forbidden, as in most protected areas, the development of outdoor activities has increased. Although recreational activities are non-lethal, humans may be perceived as a source of disturbance by animal populations (Frid and Dill 2002), leading to avoidance behavior and possibly changes in activity patterns (Ciuti et al. 2012; Marchand et al. 2014; Larson et al. 2016; Salvatori et al. 2022, 2024). The evaluation of the relative roles of environmental stressors in affecting the behavior and ecology of species is important to predict population consequences of environmental changes. Yet, disentangling the potential effects of temperature, predators, and human presence on the temporal activity of mammals has been poor, so far.

In this study, we have combined animal activity data obtained through intensive camera trapping with temperature data to evaluate the direct effect of summer temperature, and its interaction with environmental and anthropogenic stressors, on the temporal activity patterns of two herbivorous mammals. Across several Mediterranean protected areas, we investigated the roles of ambient temperature, predator, and human presence on the changes in activity level and nocturnality of these wild herbivores. In the Mediterranean biome, winter is relatively warm and summer is usually the limiting season. These regions are predicted to warm up at a ∼20% higher rate than the global annual mean surface temperature, and the overall duration of summer is projected to reach 6 months by 2100 (Lionello and Scarascia 2018; Pfleiderer et al. 2019). Warmer temperatures and drier conditions reduce plant production and availability of water sources (Lee et al. 2023; Hatfield and Prueger 2015). A decrease in nutritional intake, in turn body mass, could affect the fitness of herbivores during summer (Plard et al. 2014; Semenzato et al. 2021). We considered two widespread herbivores in Europe, the roe deer (*Capreolus capreolus*) and the fallow deer (*Dama dama*). The roe deer is well adapted to wood-field ecotones and relies on highly nutritious vegetation for survival and reproduction ("concentrate selector": Hofmann 1989). In this ungulate, offspring survival and reproductive success are strongly influenced by environmental conditions in spring–summer (Gaillard et al. 1997; Pettorelli et al. 2005). Conversely, the fallow deer, a herbivore native to Asia Minor and best adapted to semi-arid environments (Novak 1991), can exploit both nutritious and fibrous vegetation ("intermediate or mixed feeder": Hofmann 1989). The fallow deer is known to be a superior competitor over the roe deer, affecting its distribution and density, as well as showing behavioral intolerance to it (Focardi et al. 2006; Ferretti et al. 2011; Elofsson et al. 2017; Ferretti and Fattorini 2021; Gryz et al. 2024).

Wild herbivores could show two non-mutually exclusive temporal behavioral responses to warmer temperatures via changes in activity patterns: they may reduce their general level of activity (Mason et al. 2014; Güldenpfennig et al. 2025), and/or they may shift their activity to nighttime (Brivio et al. 2024; Levy et al. 2019; Thel et al. 2024). We considered both responses and formulated predictions stemming from previous evidence for the potential effects of temperature, predator, and human presence (Table 1), and coupled them with predictions on possible interactive effects. We expect that the roe deer, as a heat-sensitive species, would reduce its general level of daily locomotor activity and increase nocturnality when the weather is hot, to avoid overheating (Levy et al. 2019). However, this prey species should be less active at night in sites highly used by wolves (*Canis lupus*). We expect that the fallow deer, due to greater adaptability to warmer environments, would show a milder response to hot temperatures than roe deer. Since fallow deer have been shown to be more diurnal as an antipredator response to wolves (Rossa et al. 2021; Esattore et al. 2023; Lazzeri et al. 2024), we expect increased diurnal activity in sites highly used by wolves. Thus, we predict increased nocturnality in response to rising temperatures only in sites with lower wolf visitation rates. Finally, a general reduction in daily activity level and/or increased nocturnal activity could also help both species avoid human presence (Bonnot et al. 2020),

**TABLE 1** | Predictions about the potential effects of focal predictors (temperature, predator, and human presence) on temporal responses of roe and fallow deer.

| Behavioral indicator | Variable | Prediction on the behavioral response | Supporting reference |
|---|---|---|---|
| Daily activity level | Temperature | Lower activity on warmer days | Mason et al. 2014 |
| | Wolf | Lower activity in sites with higher wolf visitation rates | Palmer et al. 2021 |
| | Humans | Lower activity in sites with higher human visitation rates | Marchand et al. 2014 |
| Nocturnal activity | Temperature | Greater nocturnality following diel warming | Levy et al. 2019 |
| | Wolf | Lower nocturnality in sites with higher wolf visitation rates | Rossa et al. 2021 |
| | Humans | Greater nocturnality in sites with higher human visitation rates | Gaynor et al. 2018 |

hence, we predicted reduced activity and increased nocturnality in sites with higher human visitation rates.

## 2 | Materials and Methods

### 2.1 | Study Areas

We conducted our study in eight protected areas located in central Italy, including seven Nature Reserves, NRs, and one Regional Park, RP (Figure 1a; Table S1). These areas are representative of the elevational and longitudinal gradients of climatic variation of this Mediterranean region, spanning elevations of 0–1453 m above sea level, and including from coastal to low-mountain sites. The plain or hilly study areas along the coastline and inland, characterized by relatively mild winters and hot-dry summers, are dominated by sclerophyllous vegetation, and gradually switch to slightly cooler and wetter areas located closer to the Apennine Mountain chain, at a higher elevation. The roe deer is present in all areas, whereas the fallow deer is relatively rare in two areas, which were therefore excluded from the relevant analysis. The wolf is the apex predator and occurs in all areas, with a predominantly nocturnal activity (Figure S1). All areas are inhabited by no or few people (range of mean human population density per area: 0.14–3.84 inhabitants/km$^2$; data from Schiavina et al. 2023), but in summer they are visited by tourists for recreational outdoor activities (e.g., hiking), mainly in daytime (Figure S1), with spatially heterogeneous human visitation rates within areas (cf. Results). For more details about the study areas, see Supporting Information.

### 2.2 | Camera Trapping

We estimated daily locomotor activity level and nocturnality of deer through camera trapping, during summer (June, July, and August), in 2021, 2022, and 2023. We sampled each study area for at least 2 years (Table S1). We deployed cameras using sampling grids to obtain a spatially balanced sampling and achieve a consistent sampling effort across areas (grid size: 1.5 × 1.5 km in NRs, and 1 × 1 km in the RP; 1 camera location per grid cell). We sampled 8-to-60 locations per area in each study year, depending on the study area size (Figure 1b; Table S1). We placed infrared cameras in sites suitable to detect mammal activity, on trees generally at a height of 20–150 cm from the ground (although we discarded for analyses the few sites where cameras were at a height >130 cm to increase homogeneity in camera detectability). We used several camera models with similar technical characteristics, accounting for them in our analyses (Salvatori et al. 2022, 2024). We set up cameras to record 10-s videos, with 1-s lag between consecutive recordings. We supplied devices with SD cards and 6 or 12 V rechargeable external batteries that allowed a functioning period of 24 h/day, for at least 30–45 days. We checked cameras every 30–40 days to change the SD cards and batteries, thereby maximizing the continuous functioning of the cameras (i.e., the number of working days) at each site. Checking cameras required generally <5 min of attendance by the operator at each site, which was considered in the calculation of human visitation rate (see below). When the same camera trap took more than 1 video of the same species in less than 30 min, we considered them as "non-independent" detections and used only the first detection for subsequent analyses (Tobler et al. 2008; Torretta et al. 2016; de Satgé et al. 2017). For human detections, a 3-min threshold was considered (Esattore et al. 2023). For analyses, we excluded sites where cameras worked for less than 20 days each per study year, thus retaining an overall number of 196 camera sites and 12 406 trapping days (~63 sampling days per site, on average).

### 2.3 | Temperature and Environmental Predictors

We retrieved temperature data from Servizio Idrologico Regionale (Regione Toscana—https://www.sir.toscana.it/termometria-pub) and Arpae Emilia-Romagna (https://simc.arpae.it/dext3r/). Data included air temperature (°C) recorded at 2 m from the ground every 15 min by professional weather stations close to each of our study areas (~4.5 km from the centroid of each study area, on average; Figure S2). We performed a linear interpolation to obtain 15-min temperature data in one of the study areas (Alpe della Luna NR), as the relevant weather station recorded data at a temporal resolution of 30 min.

We categorized the habitat type at each camera location by discriminating between covered and open habitats and took it as an index of thermal shelter (covered habitats: shrubland and woodland, i.e., densely vegetated and shaded habitats with substantial canopy cover; open habitats: ecotones and meadows, i.e., almost unshaded habitats with scarce/no canopy). We visually

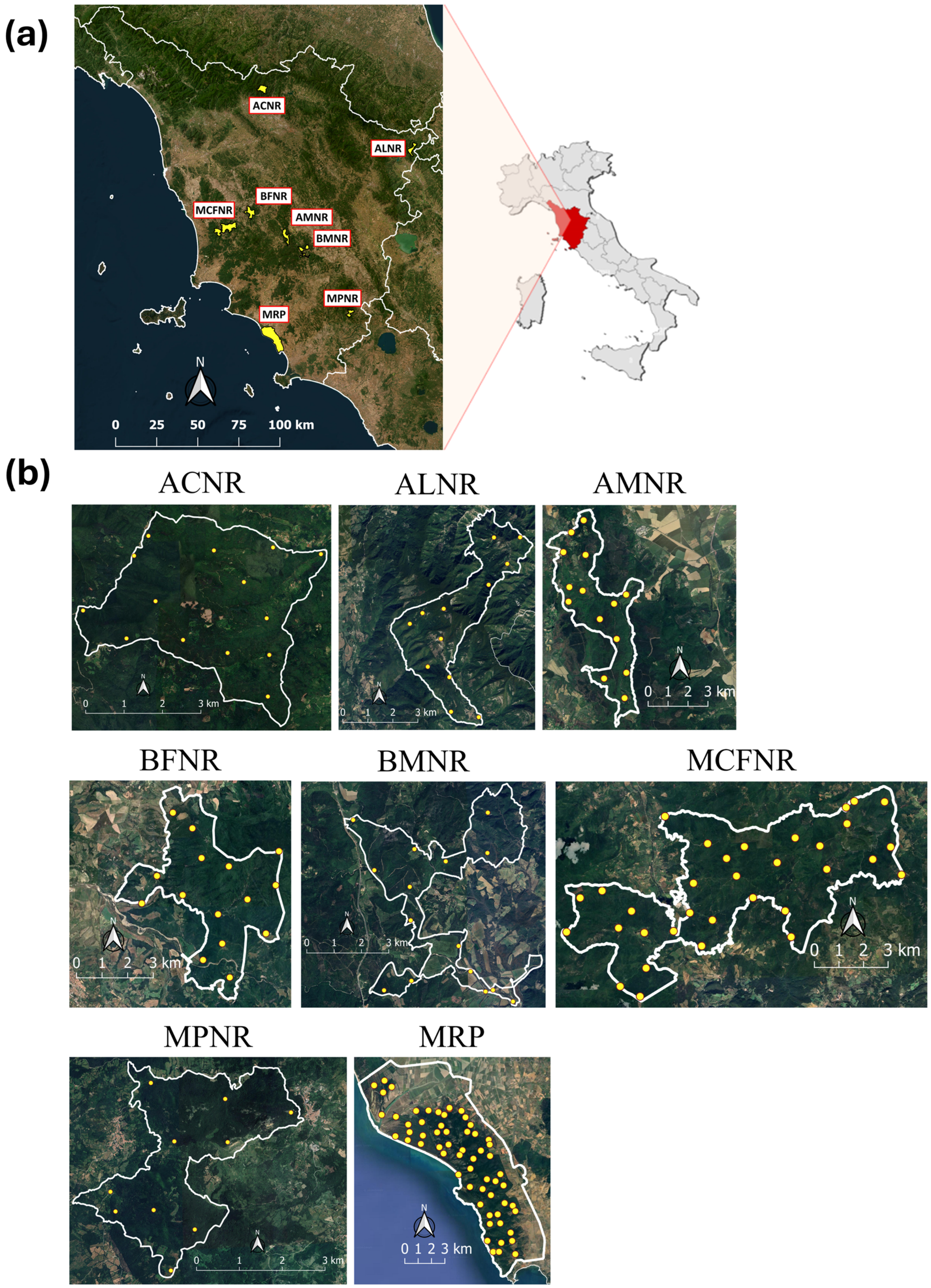

**FIGURE 1** | (a) Locations of the study areas in central Italy. In yellow, from top to bottom: Acquerino-Cantagallo Nature Reserve (ACNR), Alpe della Luna Nature Reserve (ALNR), Foresta di Berignone Nature Reserve (BFNR), Foresta di Monterufoli-Caselli Nature Reserve (MCFNR), Alto Merse Nature Reserve (AMNR), Basso Merse Nature Reserve (BMNR), Monte Penna Nature Reserve (MPNR); and Maremma Regional Park (MRP). (b) Camera trap locations (yellow dots) within each study area. Imagery provided by Google Satellite and ESRI Satellite.

estimated the percentage of shrub cover (height ≤1.5 m) within a 10 m-radius around each camera and used it as an index of vegetal impediment for the relevant camera at the recording height. The elevation (meters above sea level) of each camera location was obtained using the software QGIS 3.34.2 and the digital elevation model provided by SITA-Regione Toscana (http://dati.toscana.it/dataset/dem10mt; spatial resolution: 10 m).

## 2.4 | Site Use by Predator, Competitors, and Humans

For each study year and camera location, we used the group size-adjusted detection rates of wolf and fallow deer as proxies for site use by the predator and by the possible roe deer competitor, respectively. Site use by fallow deer—the superior competitor over roe deer—could be expected to influence roe deer activity. However, roe deer is unlikely to influence fallow deer activity patterns; in turn, there was no need to account for roe deer detection rate when analyzing the daily activity level and nocturnality of fallow deer. For both wolf and fallow deer, separately for each study year and camera location, we calculated detection rates as the sum of individuals counted across all independent detections of the species divided by the number of days in which the camera was active. Because one detection may include more than one individual, this adjustment considers differences in group size between detections, better reflecting the intensity of site use by gregarious species (Ferretti et al. 2023). Similarly, we used the detection rate of humans as a proxy for site use by humans (Salvatori et al. 2022, 2024). The latter was calculated as the number of independent human detections divided by the number of days in which the camera was active. In this calculation, we also included the operator detections to account for possible human disturbance associated with camera checks.

## 2.5 | Statistical Analysis: Daily Activity Level

The use of motion-sensitive cameras implies recording animals when they move, either for foraging or other activities. Hence, we defined “activity” as any occurrence of animal locomotor activity. Assuming that the activity level is the determinant of the daily rate at which cameras detect animals, the trap rate on a given day can be used as an approximation of the overall level of activity in the population on that day (Rowcliffe et al. 2014). Therefore, to investigate the potential effects of temperature, predator, and human presence on daily locomotor activity levels of deer species, we employed species-specific generalized linear mixed models (GLMMs) with negative binomial errors (*log* link function) to model the total number of detections obtained in each sampling date at each location. We considered the following predictors: (1) mean daily temperature calculated over the 24 h of each sampling date (continuous, in °C), to investigate whether deer reduced their daily activity level on hotter days; (2) wolf detection rate (continuous, as number of individuals/day), and (3) human detection rate (continuous, as number of detections/day), to evaluate the potential roles of predator and human presence on deer activity level, respectively. We also considered potential confounding variables that may influence daily activity level: (4) fallow deer detection rate (only for model relevant to roe deer; continuous, as number of individuals/day), to account for the potential effects of interspecific encounters on the daily activity level of roe deer; (5) habitat type (categorical; reference level: covered), to consider the habitat-dependent thermal buffering effect; (6) the ln-transformed elevation (continuous, meters a.s.l.), to consider the elevation-dependent thermal buffering effect, with observed temperature exhibiting a logarithmic decrease over the elevation range of our study area (a constant term was added before ln-transformation for the analysis of roe deer nocturnality, due to model convergence issues). In addition, we included other control predictors to account for the potential variation in the daily number of detections due to camera detectability, namely (7) shrub cover around the camera (continuous, as %), and (8) camera height from the ground (continuous, in cm). In this model, the interaction between the mean daily temperature and the habitat type was also included to verify whether deer activity decreased on hotter days only in habitats providing low shelter (i.e., open habitats). Finally, we included the camera location nested within the study area and the camera model as random intercepts, to account for repeated measurements of activity recorded on the same camera location within the same area, and to control for repeated measurements of activity recorded by the same camera model.

## 2.6 | Statistical Analysis: Nocturnal Activity

We used GLMMs to assess whether deer species increased their nocturnal activity to cope with warmer temperatures. First, each detection was categorized into either nocturnal or diurnal/crepuscular by considering the recording date and solar time, through the R package *suncalc* (Thieurmel and Elmarhraoui 2022). We defined as night the period after civil twilight ends, in the evening, and before civil twilight begins the next morning (reference angle of the sun below the horizon = 6°, i.e., civil dawn/dusk) (Brivio et al. 2024; Gupta et al. 2023). Nocturnal detections were coded as “1” (presence of nocturnal activity), whereas diurnal/crepuscular ones were coded as “0” (absence of nocturnal activity). For each species, every detection was thus modeled as a binary response variable using a GLMM with binomial errors (*logit* link function). We analyzed the influence of environmental and anthropogenic factors on the probability of deer being nocturnal by including the same fixed and random effects included in the model of daily activity. Since this analysis is conducted on camera detections, we considered differently the predictor (1); specifically, we included the mean temperature in the 24 h before the detection (continuous, in °C), to investigate whether the presence of nocturnal activity increased when deer experienced warmer temperature in the previous 24 h before being active. This allowed us to match the temporal scale of the previous analysis and evaluate the effect of temperature while considering its variability over an entire 24 h cycle. In addition, we included another potential confounding variable: (9) night duration (continuous, in decimal hours), to account for changing night availability throughout June–August, during which it varies from ~30% to 40% of the 24 h cycle, on the probability of obtaining a nocturnal detection. This model also differed from that of daily activity level in the interactive effects considered. Here, the interactive effects of temperature with focal predictors 2–5 were included to investigate whether the effect of temperature experienced 24 h before the detection may depend on them. For example, if deer species increase or decrease their nocturnal activity in response to greater activity of predators or humans, respectively, this behavioral response may be increased on warmer days. Moreover, nocturnal activity in open habitats may increase on warmer days.

### 2.7 | Statistical Analysis: Model Selection

Before fitting the models, we checked collinearity between covariates (all Pearson correlation coefficients were <|0.5|) and we scaled them to improve model convergence and interpretability of interactive effects, as well as allowing estimation of standardized coefficients. We performed scaling by mean-centering covariates and dividing them by their standard deviations (Schielzeth 2010).

For each species and response variable, we built a global model including all the predictors. All candidate models, each one having a different combination of predictors, that is, reflecting a different plausible hypothesis, were then ranked and compared using the Akaike's Information Criterion corrected for small samples (AICc, Harrison et al. 2018). However, each candidate model always retained predictors potentially affecting detectability, that is, shrub cover around the camera and camera height, as well as night duration in the analysis on nocturnality. Therefore, the null model in our cases was a model explaining the data variability only in terms of variation in animal detectability. Following the conservative "nesting rule," we selected models only if they had $\Delta$AICc $\leq 2$ (where $\Delta$AICc is the difference in AICc between each model and the best model, i.e., that with the lowest AICc) and if their AICc value was lower than that of any simpler nested alternative to avoid retaining overly complex models (Harrison et al. 2018). From $\Delta$AICc, we also obtained the Akaike model weight for each model, namely the probability that any model is the best one amongst all possible candidates (Guo et al. 2022). We standardized the model weight within the subset of selected models. In the four model selections, we obtained either one or two selected models (Tables S2 and S3), depending on the analysis. In the only case in which we obtained two selected models, the second selected model only differed to the best one by the exclusion of one predictor. Thus, we always used the best model to identify informative predictors by assessing whether 95% confidence intervals of coefficients overlapped "0." We conducted GLMMs and model selections, respectively, through the R packages *glmmTMB* (Brooks et al. 2017) and *MuMIn* (Bartoń 2023). We checked the best models for the absence of multicollinearity (all VIFs were <2.1), and validated them through visual inspection of residuals.

## 3 | Results

Throughout our study areas and summer research periods, the mean daily temperature on sampling dates oscillated between 12.5°C and 31.1°C (mean ± SD: 23.9°C ± 2.9°C). We observed a mean year-specific human visitation rate of ~0.33 people detections/day at each camera site (SD: 1.70; range: 0–25.86; median: 0.06; 1st quartile: 0.03; 3rd quartile: 0.009), almost exclusively during daytime (Figure S1). Sites also experienced a mean year-specific wolf visitation rate of ~0.06 individuals/day (SD: 0.15; range: 0–1.43; median: 0; 1st quartile: 0; 3rd quartile: 0.05), almost exclusively at nighttime (Figure S1). Variability in both human and wolf year-specific visitation rates across sites in the same area was high (% coefficient of variation; humans, range: 9.7–350, median: 53.5, 1st quartile: 29.6, 3rd quartile: 179.6; wolf, range: 115–241.7, median: 184, 1st quartile: 156.2, 3rd quartile: 205), implying spatial heterogeneity of human and predator attendance across camera sites within each area. We obtained 3251 deer detections (fallow deer: $n = 1693$ detections; roe deer: $n = 1558$ detections). Generally, both deer species were recorded slightly more often in daytime or crepuscular periods than at night, showing 23.0% (fallow deer) and 38.8% (roe deer) of nocturnal detections (Figure S3).

### 3.1 | Daily Activity Level

The effect of temperature on daily activity level was supported by the best model, for both species, although the mediating effect of risk and temperature was not supported. The selected model best explaining the daily activity level for roe deer included the effects of the mean daily temperature, wolf detection rate, and elevation; the one for fallow deer included the mean daily temperature, habitat type, their interaction, and elevation (Table S2).

Roe deer reduced their daily activity level on hotter days, on average decreasing their daily activity by ~50% as the mean daily temperatures rose by ~15°C (Table 2a, Figure 2a). In addition, we found a positive association between daily activity level and wolf detection rates (Table 2a). Roe deer activity also increased with increasing elevation (Table 2a).

Fallow deer showed decreased daily activity levels on hotter days, with such a decrease being stronger in covered habitats than open ones (Table 2a, Figure 2b). In addition, fallow deer activity decreased with increasing elevation (Table 2a). Finally, we found a negative association between the shrub cover and the activity level of fallow deer (Table 2a).

### 3.2 | Nocturnal Activity

The effect of temperature on nocturnality was supported by the best model only for roe deer. The best model for the roe deer supported the effects of temperature and human detection rate; the one for the fallow deer supported the effects of habitat type and wolf detection rate (Table S3).

For roe deer, the occurrence of nocturnal activity increased with increasing mean temperature over the previous 24 h; on average, a ~15°C increase in mean temperature over the previous 24 h increased the probability of nocturnal activity by ~140% (Table 2b, Figure 3a). Roe deer nocturnality also decreased with increasing human detection rate (Table 2b). Moreover, we found that roe deer nocturnality decreased with increasing shrub cover (Table 2b).

For fallow deer, the occurrence of nocturnal activity increased in open habitats (Table 2b, Figure 3b). Moreover, the nocturnal activity of fallow deer tended to increase in sites with the lowest wolf detection rate, although this effect was weak, that is, with confidence intervals overlapping "0" (Table 2b).

**TABLE 2** | Results of best models for roe deer and fallow deer in which (a) the daily activity level and (b) the occurrence of nocturnal activity are the response variables. For each model predictor, the coefficient estimate and its 95% confidence interval are shown. Variance ($\sigma^2$) of random intercepts is also reported. Asterisks mark the 95% confidence intervals which do not include 0.

| | Species | Predictor | Coefficient | 95% Confidence interval |
|---|---|---|---|---|
| **a** | **Roe deer** | Intercept | −2.980 | −3.481; −2.478* |
| | $\sigma^2_{\text{Location:Area}} = 1.482$ | Mean daily temperature | −0.139 | −0.195; −0.083* |
| | $\sigma^2_{\text{Area}} = 0.99$ | Elevation | 0.450 | 0.143; 0.757* |
| | $\sigma^2_{\text{Camera type}} = 0.114$ | Wolf detection rate | 0.184 | 0.045; 0.322* |
| | | Camera height | −0.195 | −0.343; −0.046* |
| | | Shrub cover | −0.082 | −0.307; 0.143 |
| | **Fallow deer** | Intercept | −2.868 | −3.800; −1.937* |
| | $\sigma^2_{\text{Location:Area}} = 2.587$ | Mean daily temperature | −0.195 | −0.264; −0.125* |
| | $\sigma^2_{\text{Area}} = 0.670$ | Habitat type (open habitats) | 0.772 | 0.054; 1.490* |
| | $\sigma^2_{\text{Camera type}} = 0.202$ | Elevation | −0.630 | −1.018; −0.241* |
| | | Camera height | 0.190 | −0.004; 0.384 |
| | | Shrub cover | −0.433 | −0.766; −0.101* |
| | | Mean daily temperature × Habitat type (open habitats) | 0.151 | 0.041; 0.262* |
| **b** | **Roe deer** | Intercept | −0.590 | −0.824; −0.355* |
| | $\sigma^2_{\text{Location:Area}} = 0.453$ | Mean temperature in previous 24 h | 0.240 | 0.109; 0.371* |
| | $\sigma^2_{\text{Area}} = 0.043$ | Human detection rate | −0.241 | −0.470; −0.011* |
| | $\sigma^2_{\text{Camera type}} < 0.001$ | Night duration | 0.475 | 0.346; 0.604* |
| | | Camera height | 0.069 | −0.107; 0.244 |
| | | Shrub cover | −0.232 | −0.413; −0.050* |
| | **Fallow deer** | Intercept | −1.558 | −1.935; −0.180* |
| | $\sigma^2_{\text{Location:Area}} = 0.293$ | Habitat type (open habitats) | 0.411 | 0.021; 0.800* |
| | $\sigma^2_{\text{Area}} < 0.001$ | Wolf detection rate | −0.183 | −0.388; 0.021 |
| | $\sigma^2_{\text{Camera type}} = 0.039$ | Night duration | 0.236 | 0.112; 0.361* |
| | | Camera height | −0.013 | −0.187; 0.162 |
| | | Shrub cover | −0.009 | −0.191; 0.173 |

## 4 | Discussion

The distribution of activity round the clock is a key feature of animal responses to their environment (Rowcliffe et al. 2014). At a coarse timescale, activity patterns are often seasonally structured and mainly driven by photoperiod, environmental conditions, and species-specific constraints related to their biological lifecycle (Bourgoin et al. 2008). At a finer timescale, such as that for daily activity patterns, they strongly depend on internal drivers (Saper et al. 2005), as well as on external environmental determinants such as the weather (Levy et al. 2019), or activity patterns of other species (Hagemoen and Reimers 2002). At both the coarse and fine time scales, ambient temperature is among the most important regulators of activity patterns. Here, we disentangled the effects of ambient temperature, predators, and human activity on the daily activity levels and shifts toward nocturnality in two herbivore species. Our findings supported behavioral changes in roe and fallow deer due to increasing temperature during summer. Both herbivores reduced their daily activity levels, but only roe deer increased their nocturnality following diel warming. In contrast, for fallow deer, only predation risk influenced temporal activity changes.

### 4.1 | Factors Affecting Daily Activity Level

Both roe and fallow deer reduced their daily activity levels on hotter days. This behavioral response should minimize heat-related stress and energy expenditure (Levy et al. 2019; Semenzato et al. 2021). However, reduced activity due to heat may lead to a lower daily food intake on hot days compared to less thermally stressful days (Levy et al. 2019). This forage loss must be compensated, indeed the shift to nocturnal activity observed in roe deer may be a strategy to allow for limited daytime foraging opportunities in hot weather. Given the need to balance foraging demands with predator avoidance, we also expected a reduction

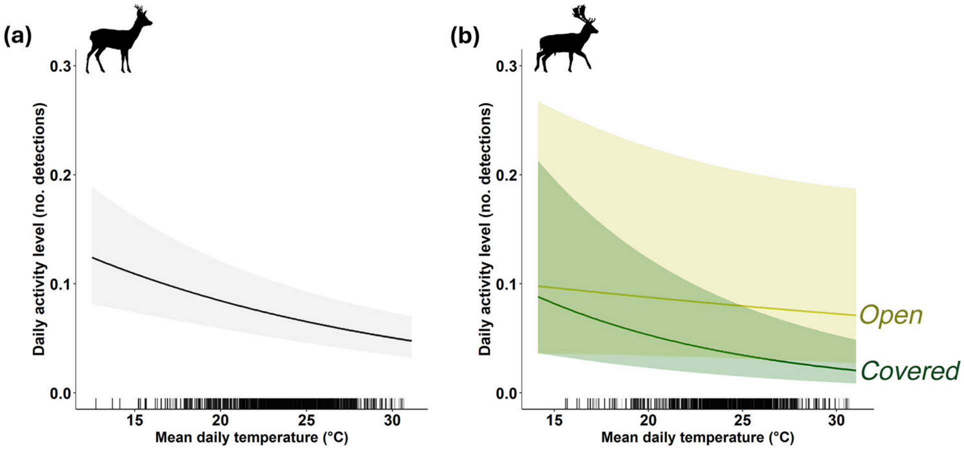

**FIGURE 2** | Plots showing (a) the relationship between roe deer daily activity level and mean daily temperature; (b) the negative relationship between fallow deer daily activity level and mean daily temperature in covered and open habitats. The lines show predicted values, while the bands indicate the 95% confidence intervals. Marks along *x*-axis show the distribution of observed values.

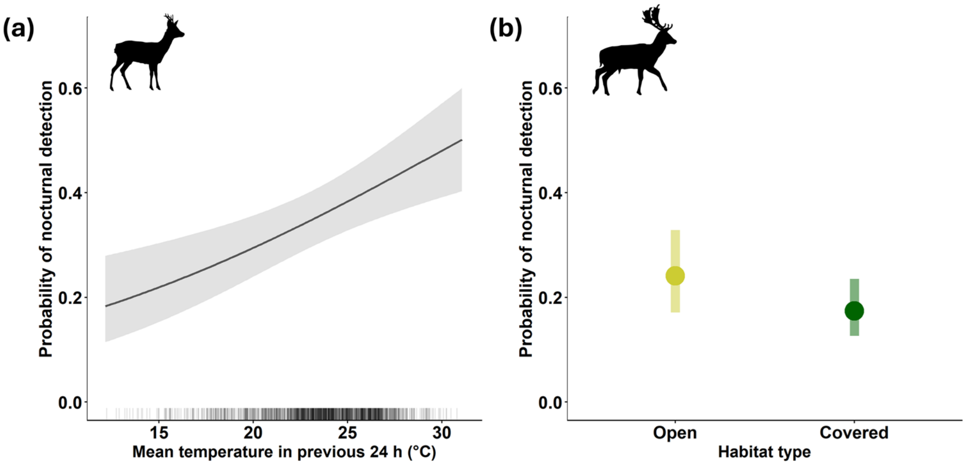

**FIGURE 3** | Plots showing the relationship between the probability of a nocturnal detection and (a) mean temperature experienced during 24 h prior to the detection, for roe deer; (b) habitat type, for fallow deer. The line (a) or filled circle (b) shows the predicted values, and the band (a) or the error bar (b) represents the 95% confidence intervals. Marks along *x*-axis (a) show the distribution of observed values.

in prey activity in sites with greater wolf occurrence (Palmer et al. 2021). In contrast, we found a positive relationship between the daily activity level of roe deer and wolf detection rates. This result may suggest that the wolf tended to use the sites where roe deer were more active, which would be consistent with data on wolf food habits showing roe deer among the primary prey of this canid across our study region (Capitani et al. 2004; Mattioli et al. 2004; Lovari and Sangiuliano 2006; Ferretti et al. 2019; see also Mori et al. 2017, for a review on wolf diet in Italy). Predation rates of wolves over roe deer have been shown to decrease with increased vegetation cover (Mattioli et al. 2004). The elusive behavior of this deer is emphasized by selection of sites providing adequate shelter, by reducing activity in the brightest nights, or by living solitarily or in small, family groups in summer, which would be expected to reduce detectability by wolves (Mattioli et al. 2004; Bongi et al. 2008; Ferretti et al. 2019; Lazzeri et al. 2025). In turn, spatial avoidance may not be a strong antipredator response in this deer (Lazzeri et al. 2024).

Compared to the roe deer, the effect of temperature was weaker for the fallow deer. This reduction of activity appeared to be stronger in covered habitats compared to open ones, although the support for an interactive effect of temperature and habitat on activity was weak, and confidence intervals of estimated relationships were large. These findings would not support the behavioral thermoregulatory tactic of avoiding direct sunlight by moving into forests (Scheffers et al. 2014). Nevertheless, this result comes from the overall daily activity analysis, and the reduction of activity in closed habitats by fallow deer might depend on that occurring during nocturnal hours, as revealed by the higher nocturnality we found in open habitats. Densely covered habitats and shrub cover are expected to limit visibility, thus reducing the potential to detect predators and increasing the perceived predation risk by fallow deer (Esattore et al. 2023; Lazzeri et al. 2024), which fits our results showing a reduced daily activity level in covered habitats and sites with higher shrub cover.

In contrast with our predictions, the analyses did not provide support for the effect of human detection rate on the daily activity level of either deer species. For fallow deer, this finding agrees with a recent study conducted in our largest study area, where no spatial association between their presence and the detection rate of humans at camera sites was found (Esattore et al. 2023). Possibly, the relatively low average human pressure from outdoor recreationists visiting our camera locations may not have been sufficient to trigger reductions in herbivore daily activity. Additionally, the absence of a detectable effect could have been due to the marked spatial variability in human visitation rates within areas, with a few high values concentrated in some sites but much lower people attendance values in most of the others, potentially masking consistent shifts in herbivore daily activity.

## 4.2 | Factors Affecting Nocturnality

In warm seasons, cooler nocturnal temperatures reduce thermoregulation costs, allowing herbivorous mammals to forage for longer periods and to compensate for limited daytime foraging opportunities in hot weather (Brivio et al. 2024; Levy et al. 2019; Semenzato et al. 2021). Consistent with our prediction, roe deer showed increased nocturnality following warmer temperatures on a 24 h scale. The behavioral thermoregulation hypothesis would predict that animals move to densely covered patches as cooler microhabitats (Scheffers et al. 2014). Our results agree with this expectation only partially. The interactive effects of temperature and habitat type on daily activity and nocturnality were not supported, suggesting that roe deer did not increase the use of forest/shrub during hotter days. However, a greater roe deer diurnal activity was observed in sites with a higher shrub cover. A selection for sites providing adequate shelter has been repeatedly acknowledged as an important determinant of habitat choice for this deer species (Tufto et al. 1996; Mancinelli et al. 2015; Padié et al. 2015). Although bushy vegetation may also provide a thermal refuge during the day, greater diurnal activity in sites with denser shrub cover may be associated with a lower perception of risk, which may drive the spatial modulation of activity. Overall, these results suggest that roe deer may mitigate the effects of rising summer temperatures by shifting their activity to nocturnal hours (Hetem et al. 2012; Davimes et al. 2017).

We predicted that the same strategy should be used to avoid human recreational activities during daylight hours, which may elicit antipredatory responses in prey species even in the absence of a lethal threat (Bonnot et al. 2020). In contrast, roe deer were less active at night in areas with higher human detection rates, that is, they tended to be more diurnal in sites more used by humans, although the relationship was rather weak and confidence intervals were close to include "0." Roe deer have been shown to trade human risk avoidance for foraging (Benoit et al. 2023), possibly explaining this finding. This result may also be explained by the study being conducted within our protected study areas, where human activity is generally limited (~0.33 people detection/day at each camera site, on average) and primarily diurnal (Figure S1), with hikers usually concentrated on main trails during spring and summer (our observations) and showing unbalanced spatial distribution across sites within areas (cf. Results). This finding is also consistent with data reported for other herbivorous mammals, which avoided hot temperatures more than hikers (Thel et al. 2024). Nevertheless, a recent study on a meta-community of mammals found a shift toward nocturnality in response to human outdoor activity within protected areas throughout early summer–late autumn, where the wolf was also present, but much higher rates of human visitation occurred (mean: ~2.3 people detections/day at each site, st.dev: 3.4, range: 0—26; Salvatori et al. 2024). The discrepancy with our results may be due to the availability of alternative suitable sites for feeding and resting in our relatively undisturbed study areas, suggesting that other factors, such as individual spatial preferences (Spiegel et al. 2017), may have also influenced the outcomes of our analysis. Moreover, the study by Salvatori et al. (2024) also included cooler months, where activity rhythms of mammals should be less constrained by heat avoidance, and species could be more prone to respond to human presence, which may partly contribute to explaining differences in results between studies.

Usually, the presence of nocturnal carnivores favors prey shifts to daylight activity rather than the other way round (Tambling et al. 2015; Veldhuis et al. 2020). Surprisingly, we found no influence of site use by wolves on roe deer nocturnality. Brivio et al. (2024) also showed that the increase in nocturnality of a heat-sensitive mountain herbivore was independent of wolf presence. Our study suggests that, for roe deer, the need to reduce thermoregulatory costs likely outweighs the importance of avoiding nocturnal predators.

Differently from roe deer, results did not support a major role of heat stress in influencing changes in the temporal activity patterns of fallow deer. According to our predictions, the nocturnal activity of fallow deer was relatively greater in sites characterized by lower predator use, although the effect of this predictor was weak as confidence intervals overlapped "0." This result suggests that fallow deer may trade off heat avoidance with predator avoidance. This is consistent with fallow deer being adapted to the warm Mediterranean climate and relatively heat tolerant (De Marinis et al. 2022). Moreover, this result confirms previous findings from our largest study area, indicating predator avoidance as a major determinant of temporal activity patterns of this deer, with an increase of diurnal activity being a tactic to reduce temporal overlap with the wolf (Rossa et al. 2021; Esattore et al. 2023; Lazzeri et al. 2024).

Analyses provided no support for a habitat-mediated effect of temperature on fallow deer nocturnality, and showed an increase in nocturnal versus diurnal detections in open habitats, such as ecotones and meadows interspersed with bushes. Ecotones are optimal habitats for deer species (e.g., McLoughlin et al. 2007; Miyashita et al. 2008) as they provide them with both food and close distance to cover, unlike Mediterranean scrub wood, where food availability is relatively low (Minder 2006). In our largest study area, fallow deer are attracted to edge and open habitats, where they reach great local densities (Ferretti et al. 2011; Ferretti and Fattorini 2021; Esattore et al. 2023) and form large groups of up to several tens of individuals to improve antipredatory vigilance (Pecorella et al. 2019). In open habitats, the effect of warmer temperatures during the day may be greater due to the absence of cover providing shade and thermal shelter. Temperatures drop at night, creating a more favorable environment for foraging in open habitats. Fallow deer may have increased their nocturnality in open habitats to compensate for the forage loss they endured during the day in covered habitats, which also supports our findings on their daily activity level.

### 4.3 | Conclusion

This study provides the first insights into the complex interplay between temperature, predator–prey dynamics, and anthropogenic influence in shaping changes in activity patterns of wild herbivores in the Mediterranean area. Our study suggests that Mediterranean roe deer primarily allocated their energy to avoid heat stress rather than predation. This result provides support to the "heat dissipation limit theory," which emphasizes the critical importance of the endotherm capacity to dissipate heat over other environmental requirements (Speakman and Król 2010). Additional information from sites more impacted by human activities, such as non-protected areas, is needed to confirm the present findings. For fallow deer, our results have provided some support for a slight reduction of daily activity with higher temperatures, whereas their nocturnal activity was more affected by wolf attendance. Future studies should consider areas where wolves are absent to better understand the spatiotemporal behavioral responses of this ungulate to increasing temperatures.

For the time being, global warming does not seem to halt and, in the future, Mediterranean species may face much greater temperatures accompanied by reduced rainfall, thus lower water and quality-food accessibility, as well as greater risk of heat stress (Lionello and Scarascia 2018; Pfleiderer et al. 2019). Our findings suggest that these herbivores may respond to warming by reducing their daily activity or shifting some of this activity toward nighttime to minimize thermoregulatory costs. However, whether these responses would be adaptive or not is yet to be understood, as species-specific consequences on population viability might also be expected, for example, due to reduced daily food intake or higher predation risk at night. Future management strategies should acknowledge the impact of increasing temperatures as a significantly stressful factor. Monitoring these effects is crucial to determine whether they overshadow other environmental stressors, such as predation risk or human disturbance. Rising temperatures may become a major element affecting herbivorous species, influencing their vital rates and shaping their interactions with other ecosystem components.

### Author Contributions

Supervision: Francesco Ferretti and Niccolò Fattorini. Conceptualization: Francesco Ferretti, Niccolò Fattorini, and Noemi Pallari. Investigation: Lorenzo Lazzeri, Francesco Ferretti, Noemi Pallari, Martina Calosi, and Giulia Tettamanti. Data curation: Niccolò Fattorini, Noemi Pallari, Martina Calosi, and Giulia Tettamanti. Formal analysis: Niccolò Fattorini, Giulia Tettamanti, and Noemi Pallari. Writing – original draft: Noemi Pallari. Writing – review and editing: Niccolò Fattorini, Giulia Tettamanti, Sandro Lovari, Francesco Ferretti.

### Acknowledgments

We thank Maremma Regional Park (MRP) and Regione Toscana—Settore Tutela della Natura e del Mare (RTSTNM) for financial support. Francesco Ferretti, Niccolò Fattorini, and Noemi Pallari acknowledge the financial contribution of the National Biodiversity Future Center—NBFC, project funded under the National Recovery and Resilience Plan (NRRP), Mission 4 Component 2 Investment 1.4 – Call for tender No. 3138 of December 16, 2021, rectified by Decree n.3175 of December 18, 2021 of Italian Ministry of University and Research funded by the European Union—NextGenerationEU; Award Number: Project code CN_00000033, Concession Decree No. 1034 of June 17, 2022 adopted by the Italian Ministry of University and Research, CUP B63C22000650007, Project title National Biodiversity Future Center—NBFC. We are grateful to G. Ruberti, S. Rusci, E. Giunta, and all the staff of RTSTNM and MRP for their logistic and technical support and for providing us with research permits to work in relevant protected areas. We thank Servizio Idrologico Regionale—Regione Toscana and Arpae—Emilia-Romagna for providing us with temperature data. Special thanks go to Ente Terre Regionali Toscane, and the many landowners who allowed us to conduct fieldwork. We thank all the students and collaborators who helped in data collection/entry, especially C. Riggio, G. Fini, C. Gabbrielli, O. Petrillo, G. Cesaretti, A. Mestieri, A. Rocchigiani, M. Galdangelo, and T. Gosani.

Open access publishing facilitated by Universita degli Studi di Siena, as part of the Wiley - CRUI-CARE agreement.

### Ethics Statement

This work did not require ethical approval from a human subject or animal welfare committee. We received the required research permits to work in protected areas from the responsible institutions, namely Maremma Regional Park (MRP) and Regione Toscana—Settore Tutela della Natura e del Mare (RTSTNM).

### Conflicts of Interest

The authors declare no conflicts of interest.

### Funding

Funding was provided by National Biodiversity Future Center—NBFC, project funded under the National Recovery and Resilience Plan (NRRP), Mission 4 Component 2 Investment 1.4 – Call for tender No. 3138 of December 16, 2021, rectified by Decree n.3175 of 18 December 2021 of Italian Ministry of University and Research funded by the European Union—NextGenerationEU; Award Number: Project code CN_00000033, Concession Decree No. 1034 of June 17, 2022 adopted by the Italian Ministry of University and Research, CUP B63C22000650007, Project title National Biodiversity Future Center—NBFC, by the Maremma Regional Park (MRP) Authority and by Regione Toscana—Settore Tutela della Natura e del Mare (RTSTNM).

### References

Aublet, J. F., M. Festa-Bianchet, D. Bergero, and B. Bassano. 2009. "Temperature Constraints on Foraging Behavior of Male Alpine Ibex (*Capra ibex*) in Summer." *Oecologia* 159: 237–247.

Bartoń, K. 2023. MuMIn: Multi-Model Inference. R Package Version 1.47.5. https://CRAN.R-project.org/package=MuMIn.

Beever, E. A., L. E. Hall, J. Varner, et al. 2017. "Behavioral Flexibility as a Mechanism for Coping with Climate Change." *Frontiers in Ecology and the Environment* 15: 299–308.

Benoit, L., N. Morellet, N. C. Bonnot, et al. 2023. "Reproductive Tactics, Birth Timing and the Risk-Resource Trade-Off in an Income Breeder." *Proceedings of the Royal Society B: Biological Sciences* 290: 20230948.

Bongi, P., S. Ciuti, S. Grignolio, et al. 2008. "Anti-Predator Behavior, Space Use and Habitat Selection in Female Roe Deer During the Fawning Season in a Wolf Area." *Journal of Zoology* 276: 242–251.

Bonnot, N. C., O. Couriot, A. Berger, et al. 2020. "Fear of the Dark? Contrasting Impacts of Humans Versus Lynx on Diel Activity of Roe Deer Across Europe." *Journal of Animal Ecology* 89: 132–145.

Bourgoin, G., M. Garel, P. Blanchard, D. Dubray, D. Maillard, and J. M. Gaillard. 2011. "Daily Responses of Mouflon (*Ovis gmelini musimon* × *Ovis* sp.) Activity to Summer Climatic Conditions." *Canadian Journal of Zoology* 89: 765–773.

Bourgoin, G., M. Garel, B. Van Moorter, et al. 2008. "Determinants of Seasonal Variation in Activity Patterns of Mouflon." *Canadian Journal of Zoology* 86: 1410–1418.

Briscoe, N. J., K. A. Handasyde, S. R. Griffiths, W. P. Porter, A. Krockenberger, and M. R. Kearney. 2014. "Tree-Hugging Koalas Demonstrate a Novel Thermoregulatory Mechanism for Arboreal Mammals." *Biology Letters* 10: 20140235.

Brivio, F., M. Apollonio, P. Anderwald, et al. 2024. "Seeking Temporal Refugia to Heat Stress: Increasing Nocturnal Activity Despite Predation Risk." *Proceedings of the Royal Society B: Biological Sciences* 291: 20231587.

Brooks, M. E., K. Kristensen, K. J. Van Benthem, et al. 2017. "ETH Library glmmTMB Balances Speed and Flexibility Among Packages for Zero-Inflated Generalized Linear Mixed Modelling." *The R Journal* 9: 378–400.

Capitani, C., I. Bertelli, P. Varuzza, M. Scandura, and M. Apollonio. 2004. "A Comparative Analysis of Wolf (*Canis lupus*) Diet in Three Different Italian Ecosystems." *Mammalian Biology* 69: 1–10.

Ciuti, S., J. M. Northrup, T. B. Muhly, et al. 2012. "Effects of Humans on Behavior of Wildlife Exceed Those of Natural Predators in a Landscape of Fear." *PLoS ONE* 7: e50611.

Daan, S., and J. Aschoff. 1982. "Circadian Contributions to Survival." In *Vertebrate Circadian Systems: Structure and Physiology*, 305–321. Springer.

Davimes, J. G., A. N. Alagaili, M. F. Bertelsen, et al. 2017. "Temporal Niche Switching in Arabian Oryx (*Oryx leucoryx*): Seasonal Plasticity of 24 h Activity Patterns in a Large Desert Mammal." *Physiology and Behavior* 177: 148–154.

De Marinis, A. M., R. Chirichella, and M. Apollonio. 2022. "Common Fallow Deer *Dama dama* (Linnaeus, 1758)." In *Terrestrial Cetartiodactyla*, 115–154. Springer International Publishing.

de Satgé, J., K. Teichman, and B. Cristescu. 2017. "Competition and Coexistence in a Small Carnivore Guild." *Oecologia* 184: 873–884.

Elofsson, K., J. T. Mensah, and P. Kjellander. 2017. "Optimal Management of Two Ecologically Interacting Deer Species—Reality Matters, Beliefs Don't." *Natural Resource Modeling* 30: e12137.

Esattore, B., A. C. Rossi, F. Bazzoni, et al. 2023. "Same Place, Different Time, Head Up: Multiple Antipredator Responses to a Recolonizing Apex Predator." *Current Zoology* 69: 703–717.

Fattorini, N., S. Lovari, S. Franceschi, et al. 2023. "Animal Conflicts Escalate in a Warmer World." *Science of the Total Environment* 871: 161789.

Ferretti, F., and N. Fattorini. 2021. "Competitor Densities, Habitat, and Weather: Effects on Interspecific Interactions Between Wild Deer Species." *Integrative Zoology* 16: 670–684.

Ferretti, F., S. Lovari, V. Mancino, L. Burrini, and M. Rossa. 2019. "Food Habits of Wolves and Selection of Wild Ungulates in a Prey-Rich Mediterranean Coastal Area." *Mammalian Biology* 99: 119–127.

Ferretti, F., R. Oliveira, M. Rossa, et al. 2023. "Interactions Between Carnivore Species: Limited Spatiotemporal Partitioning Between Apex Predator and Smaller Carnivores in a Mediterranean Protected Area." *Frontiers in Zoology* 20: 20.

Ferretti, F., A. Sforzi, and S. Lovari. 2011. "Behavioral Interference Between Ungulate Species: Roe Are Not on Velvet with Fallow Deer." *Behavioral Ecology and Sociobiology* 65: 875–887.

Focardi, S., P. Aragno, P. Montanaro, and F. Riga. 2006. "Inter-specific Competition from Fallow Deer *Dama dama* Reduces Habitat Quality for the Italian Roe Deer *Capreolus capreolus italicus*." *Ecography* 29: 407–417.

Frid, A., and L. Dill. 2002. "Human-Caused Disturbance Stimuli as a Form of Predation Risk." *Conservation Ecology* 6: 11.

Gaillard, J. M., J. M. Boutin, D. Delorme, G. Van Laere, P. Duncan, and J. D. Lebreton. 1997. "Early Survival in Roe Deer: Causes and Consequences of Cohort Variation in Two Contrasted Populations." *Oecologia* 112: 502–513.

Garel, M., A. Loison, J. M. Gaillard, J. M. Cugnasse, and D. Maillard. 2004. "The Effects of a Severe Drought on Mouflon Lamb Survival." *Proceedings of the Royal Society B: Biological Sciences* 271: S471–S473.

Gaynor, K. M., C. E. Hojnowski, N. H. Carter, and J. S. Brashares. 2018. "The Influence of Human Disturbance on Wildlife Nocturnality." *Science* 360: 1232–1235.

Giroux, A., Z. Ortega, N. Attias, et al. 2023. "Activity Modulation and Selection for Forests Help Giant Anteaters to Cope with Temperature Changes." *Animal Behavior* 201: 191–209.

Goldberg, M. B., V. A. Langman, and C. R. Taylor. 1981. "Panting in Dogs: Paths of Air Flow in Response to Heat and Exercise." *Respiration Physiology* 43: 327–338.

Greives, T. J., S. A. Kingma, B. Kranstauber, et al. 2015. "Costs of Sleeping in: Circadian Rhythms Influence Cuckoldry Risk in a Songbird." *Functional Ecology* 29: 1300–1307.

Gryz, J., D. Krauze-Gryz, and K. D. Jasińska. 2024. "Alien *vs*. Native — Influence of Fallow Deer (*Dama dama*) Introduction on the Native Roe Deer (*Capreolus capreolus*) Population." *Forests* 15: 1014.

Güldenpfennig, J., N. Fattorini, M. Ježek, K. Morelle, and T. Podgórski. 2025. "Effects of Summer Weather and Heatwaves on Wild Boar Activity." *Royal Society Open Science* 12: 242208.

Guo, Q., X. Liu, Y. He, and Y Chen. 2022. "Detecting and Comparing Extinction Debts of Amphibians in Different Habitats of Southwestern China." *Ecological Indicators* 140: 109007.

Gupta, P., A. Sinha, S. Malik, and S. Rani. 2023. "Dawn and Dusk Chorus as a Potential Zeitgeber." *Biological Rhythm Research* 54: 41–51.

Hagemoen, R. I. M., and E. Reimers. 2002. "Reindeer Summer Activity Pattern in Relation to Weather and Insect Harassment." *Journal of Animal Ecology* 71: 883–892.

Harrison, X. A., L. Donaldson, M. E. Correa-Cano, et al. 2018. "A Brief Introduction to Mixed Effects Modelling and Multi-Model Inference in Ecology." *PeerJ* 6: e4794.

Hatfield, J. L., and J. H. Prueger. 2015. "Temperature Extremes: Effect on Plant Growth and Development." *Weather and Climate Extremes* 10: 4–10.

Hetem, R. S., W. M. Strauss, L. G. Fick, et al. 2012. "Does Size Matter? Comparison of Body Temperature and Activity of Free-Living Arabian Oryx (*Oryx leucoryx*) and the Smaller Arabian Sand Gazelle (*Gazella subgutturosa marica*) in the Saudi Desert." *Journal of Comparative Physiology B* 182: 437–449.

Hill, T. M., H. G. Bateman II, F. X. Suarez-Mena, T. S. Dennis, and R. L. Schlotterbeck. 2016. "Changes in Body Temperature of Calves up to 2 Months of Age as Affected by Time of Day, Age, and Ambient Temperature." *Journal of Dairy Science* 99: 8867–8870.

Hofmann, R. R. 1989. "Evolutionary Steps of Ecophysiological Adaptation and Diversification of Ruminants: A Comparative View of Their Digestive System." *Oecologia* 78: 443–457.

Larson, C. L., S. E. Reed, A. M. Merenlender, and K. R. Crooks. 2016. "Effects of Recreation on Animals Revealed as Widespread Through a Global Systematic Review." *PLoS ONE* 11: e0167259.

Lazzeri, L., G. Fini, M. Maiorana, A. Rocchigiani, and F. Ferretti. 2025. "Night-Time Symphony: Lunar Effects on the Activity Patterns of the Wolf and Its Prey in a Mediterranean Protected Area." *Journal of Zoology* 326: 364–380.

Lazzeri, L., G. Pacini, I. Belardi, G. Fini, C. De Lillo, and F. Ferretti. 2024. "Switch or Perish? Prey–Predator Interactions in a Mediterranean Area." *Animal Conservation* 27: 830–850.

Lee, H., K. Calvin, D. Dasgupta, et al. 2023. "IPCC, 2023: Climate Change 2023: Synthesis Report." In *Contribution of Working Groups I, II and III to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change*, edited by H. Lee and J. Romero, 1–34. IPCC.

Lesmerises, F., C. J. Johnson, and M. H. St-Laurent. 2018. "Landscape Knowledge Is an Important Driver of the Fission Dynamics of an Alpine Ungulate." *Animal Behavior* 140: 39–47.

Levesque, D. L., and K. E. Marshall. 2021. "Do Endotherms Have Thermal Performance Curves?" *Journal of Experimental Biology* 224: jeb141309.

Levy, O., T. Dayan, W. P. Porter, and N. Kronfeld-Schor. 2019. "Time and Ecological Resilience: Can Diurnal Animals Compensate for Climate Change by Shifting to Nocturnal Activity?" *Ecological Monographs* 89: e01334.

Lionello, P., and L. Scarascia. 2018. "The Relation Between Climate Change in the Mediterranean Region and Global Warming." *Regional Environmental Change* 18: 1481–1493.

Lovari, S., and A. Sangiuliano. 2006. "Il Lupo Sul Monte Amiata. Progetto Sui Grandi Canidi (Lupo, Cane) Nel Territorio Dell'Amiata grossetana e senese." In Comunità Montana Amiata Grossetano e Ministero Dell' Ambiente, Arcidosso e Roma. Technical Report. https://doi.org/10.13140/RG.2.1.3653.2648.

Maloney, S. K., G. Goh, A. Fuller, K. Vesterdorf, and D. Blache. 2019. "Amplitude of the Circadian Rhythm of Temperature in Homeotherms." *CABI Reviews* 2019: 1–30. https://doi.org/10.1079/PAVSNNR201914019.

Mancinelli, S., W. Peters, L. Boitani, M. Hebblewhite, and F. Cagnacci. 2015. "Roe Deer Summer Habitat Selection at Multiple Spatio-Temporal Scales in an Alpine Environment." *Hystrix, the Italian Journal of Mammalogy* 26: 11223.

Marchand, P., M. Garel, G. Bourgoin, D. Dubray, D. Maillard, and A. Loison. 2014. "Impacts of Tourism and Hunting on a Large Herbivore's Spatio-Temporal Behavior in and Around a French Protected Area." *Biological Conservation* 177: 1–11.

Mason, T. H. E., P. A. Stephens, M. Apollonio, and S. G. Willis. 2014. "Predicting Potential Responses to Future Climate in an Alpine Ungulate: Interspecific Interactions Exceed Climate Effects." *Global Change Biology* 20: 3872–3882.

Mattioli, L., C. Capitani, E. Avanzinelli, I. Bertelli, A. Gazzola, and M. Apollonio. 2004. "Predation by Wolves (*Canis lupus*) on Roe Deer (*Capreolus capreolus*) in North-eastern Apennine, Italy." *Journal of Zoology* 264: 249–258.

McLoughlin, P. D., J. M. Gaillard, M. S. Boyce, et al. 2007. "Lifetime Reproductive Success and Composition of the Home Range in a Large Herbivore." *Ecology* 88: 3192–3201.

Minder, I. 2006. "Adaptive Parameters of the Diet of Roe Deer in a Coastal Mediterranean Area." PhD thesis. Department of Life Sciences, University of Siena.

Miyashita, T., M. Suzuki, D. Ando, G. Fujita, K. Ochiai, and M. Asada. 2008. "Forest Edge Creates Small-Scale Variation in Reproductive Rate of Sika Deer." *Population Ecology* 50: 111–120.

Mori, E., L. Benatti, S. Lovari, and F. Ferretti. 2017. "What Does the Wild Boar Mean to the Wolf?" *European Journal of Wildlife Research* 63: 9.

Needham, A. D., T. J. Dawson, and J. R. S. Hales. 1974. "Forelimb Blood Flow and Saliva Spreading in the Thermoregulation of the Red Kangaroo, *Megaleia rufa*." *Comparative Biochemistry and Physiology—Part A: Physiology* 49: 555–565.

Nowak, R. M. 1991. *Walker's Mammals of the World, II*, 5th edn. Johns Hopkins University.

Padié, S., N. Morellet, A. M. Hewison, et al. 2015. "Roe Deer at Risk: Teasing Apart Habitat Selection and Landscape Constraints in Risk Exposure at Multiple Scales." *Oikos* 124: 1536–1546.

Palmer, M. S., C. Portales-Reyes, C. Potter, L. D. Mech, and F. Isbell. 2021. "Behaviorally-Mediated Trophic Cascade Attenuated by Prey Use of Risky Places at Safe Times." *Oecologia* 195: 235–248.

Parmesan, C. 2006. "Ecological and Evolutionary Responses to Recent Climate Change." *Annual Review of Ecology, Evolution, and Systematics* 37: 637–669.

Pecorella, I., N. Fattorini, E. Macchi, and F. Ferretti. 2019. "Sex/Age Differences in Foraging, Vigilance and Alertness in a Social Herbivore." *Acta Ethologica* 22: 1–8.

Pettorelli, N., J. M. Gaillard, N. G. Yoccoz, et al. 2005. "The Response of Fawn Survival to Changes in Habitat Quality Varies According to Cohort Quality and Spatial Scale." *Journal of Animal Ecology* 74: 972–981.

Pfleiderer, P., C. F. Schleussner, K. Kornhuber, and D. Coumou. 2019. "Summer Weather Becomes More Persistent in a 2°C World." *Nature Climate Change* 9: 666–671.

Phillips, P. K., and J. E. Heath. 2001. "Heat Loss in Dumbo: A Theoretical Approach." *Journal of Thermal Biology* 26: 117–120.

Plard, F., J. M. Gaillard, T. Coulson, et al. 2014. "Mismatch Between Birth Date and Vegetation Phenology Slows the Demography of Roe Deer." *PLoS Biology* 12: e1001828.

Rafiq, K., N. R. Jordan, K. Golabek, J. W. McNutt, A. Wilson, and B. Abrahms. 2023. "Increasing Ambient Temperatures Trigger Shifts in Activity Patterns and Temporal Partitioning in a Large Carnivore Guild." *Proceedings of the Royal Society B: Biological Sciences* 290: 20231938.

Rezende, E. L., A. Cortés, L. D. Bacigalupe, R. F. Nespolo, and F. Bozinovic. 2003. "Ambient Temperature Limits Above-Ground Activity of the Subterranean Rodent *Spalacopus cyanus*." *Journal of Arid Environments* 55: 63–74.

Riek, A., A. Stölzl, B. R. Marquina, et al. 2019. "Energy Expenditure and Body Temperature Variations in Lamas Living in the High Andes of Peru." *Scientific Reports* 9: 4037.

Rossa, M., S. Lovari, and F. Ferretti. 2021. "Spatiotemporal Patterns of Wolf, Mesocarnivores and Prey in a Mediterranean Area." *Behavioral Ecology and Sociobiology* 75: 32.

Rowcliffe, J. M., R. Kays, B. Kranstauber, C. Carbone, and P. A. Jansen. 2014. "Quantifying Levels of Animal Activity Using Camera Trap Data." *Methods in Ecology and Evolution* 5: 1170–1179.

Salvatori, M., I. Greco, L. Petroni, et al. 2024. "Body Mass Mediates Spatio-Temporal Responses of Mammals to Human Frequentation Across Italian Protected Areas." *Proceedings of the Royal Society B: Biological Sciences* 291: 20232874.

Salvatori, M., V. Oberosler, M. Rinaldi, et al. 2022. "Crowded Mountains: Long-Term Effects of Human Outdoor Recreation on a Community of Wild Mammals Monitored with Systematic Camera Trapping." *Ambio* 52: 1085–1097.

Saper, C. B., J. Lu, T. C. Cholu, and J. Gooley. 2005. "The Hypothalamic Integrator for Circadian Rhythms." *Trends in Neurosciences* 28: 152–157.

Scheffers, B. R., D. P. Edwards, A. Diesmos, S. E. Williams, and T. A. Evans. 2014. "Microhabitats Reduce Animal's Exposure to Climate Extremes." *Global Change Biology* 20: 495–503.

Schiavina, M., M. Melchiorri, M. Pesaresi, et al. 2023. GHSL Data Package 2023, Publications Office of the European Union, Luxembourg, 2023. https://doi.org/10.2760/098587,JRC133256.

Schielzeth, H. 2010. "Simple Means to Improve the Interpretability of Regression Coefficients." *Methods in Ecology and Evolution* 1: 103–113.

Semenzato, P., F. Cagnacci, F. Ossi, et al. 2021. "Behavioral Heat-Stress Compensation in a Cold-Adapted Ungulate: Forage-Mediated Responses to Warming Alpine Summers." *Ecology Letters* 24: 1556–1568.

Speakman, J. R., and E. Król. 2010. "Maximal Heat Dissipation Capacity and Hyperthermia Risk: Neglected Key Factors in the Ecology of Endotherms." *Journal of Animal Ecology* 79: 726–746.

Spiegel, O., S. T. Leu, C. M. Bull, and A. Sih. 2017. "What's Your Move? Movement as a Link Between Personality and Spatial Dynamics in Animal Populations." *Ecology Letters* 20: 3–18.

Takahashi, J. S., H. K. Hong, C. H. Ko, and E. L. McDearmon. 2008. "The Genetics of Mammalian Circadian Order and Disorder: Implications for Physiology and Disease." *Nature Reviews Genetics* 9: 764–775.

Tambling, C. J., L. Minnie, J. Meyer, et al. 2015. "Temporal Shifts in Activity of Prey Following Large Predator Reintroductions." *Behavioral Ecology and Sociobiology* 69: 1153–1161.

Terrien, J., M. Perret, and F. Aujard. 2011. "Behavioral Thermoregulation in Mammals: A Review." *Frontiers in Bioscience* 16: 1428–1444.

Thel, L., M. Garel, P. Marchand, G. Bourgoin, and A. Loison. 2024. "Too Hot or Too Disturbed? Temperatures More Than Hikers Affect Circadian Activity of Females in Northern Chamois." *Animal Behavior* 210: 347–367.

Thieurmel, B., and A. Elmarhraoui. 2022. suncalc: Compute Sun Position, Sunlight Phases, Moon Position and Lunar Phase. R Package Version 0.5.1, https://CRAN.R-project.org/package=suncalc.

Tobler, M. W., S. E. Carrillo-Percastegui, R. Leite Pitman, R. Mares, and G. Powell. 2008. "Further Notes on the Analysis of Mammal Inventory Data Collected with Camera Traps." *Animal Conservation* 11: 187–189.

Torretta, E., M. Serafini, F. Puopolo, and L. Schenone. 2016. "Spatial and Temporal Adjustments Allowing the Coexistence Among Carnivores in Liguria (N-W Italy)." *Acta Ethologica* 19: 123–132.

Tufto, J., R. Andersen, and J. Linnell. 1996. "Habitat Use and Ecological Correlates of Home Range Size in a Small Cervid: The Roe Deer." *Journal of Animal Ecology* 65: 715–724.

Veldhuis, M. P., T. R. Hofmeester, G. Balme, D. J. Druce, R. T. Pitman, and J. Cromsigt. 2020. "Predation Risk Constrains Herbivores' Adaptive Capacity to Warming." *Nature Ecology and Evolution* 4: 1069–1074.

Zub, K., P. A. Szafrańska, M. Konarzewski, P. Redman, and J. R. Speakman. 2009. "Trade-Offs Between Activity and Thermoregulation in a Small Carnivore, the Least Weasel *Mustela nivalis*." *Proceedings of the Royal Society B: Biological Sciences* 276: 1921–1927.

## Supporting Information

Additional supporting information can be found online in the Supporting Information section.

**Table S1** Summary of geographic features of the eight study areas, with sampling periods and number of camera locations considered for analysis, for each study year **Figure S1** Activity patterns (kernel density) of roe deer, fallow deer, wolf, and humans obtained by combining independent detections across study areas and years. **Figure S2** (a) Locations of the professional weather stations used to obtain temperature data for each study area. (b) Variations in mean daily temperatures throughout the summer period, in each study area. **Figure S3** Bar charts showing (a) the number of diurnal/crepuscular and nocturnal independent detections of deer species in each study year; (b) the number of independent detections recorded during the entire study period for roe deer and fallow deer in the eight study areas, divided by diurnal/crepuscular and nocturnal detections. **Table S2** Output of model selections conducted to assess the daily activity level of (a) roe deer and (b) fallow deer **Table S3** Output of model selections conducted to assess the probability of nocturnal activity for (a) roe deer and (b) fallow deer