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Behavioural responses to ecological stressors: sex-specific shifts in wild boar activity over the Mediterranean summer

Martina Calosi [a, *], Niccolò Fattorini [a, b], Chiara Gabbrielli [a], Lorenzo Lazzeri [a], Annalisa Mestieri [a], Irene Belardi [a], Noemi Pallari [a, b], Francesco Ferretti [a, b]

[a] Research Unit of Behavioural Ecology, Ethology and Wildlife Management, Department of Life Sciences, University of Siena, Siena, Italy
[b] National Biodiversity Future Center, Palermo, Italy

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Ecological perturbations associated with the Anthropocene are increasingly affecting animal populations. The interactions between rising temperatures, landscape features, human activities and predators can alter mammal behaviour, yet these factors are rarely examined simultaneously. Understanding how mammals respond to multiple stressors is key to improving knowledge of their behavioural flexibility and predicting shifts in interspecific and human–wildlife interactions. We investigated the effects of temperature, habitat features, human activity and predator activity on daily activity levels and nocturnality in a widespread ungulate, the wild boar, *Sus scrofa*. We conducted population level and sex-specific analyses of camera trap data collected in eight Mediterranean protected areas during the summers of 2021–2024 (19 306 camera-days; 208 sites). While an effect of temperature on daily activity level was not supported, wild boar increased nocturnality on warmer days, indicating a temporal redistribution of activity rather than an overall decline in activity in response to heat. Activity increased near persistent water sources and, for males, this relationship was stronger on hotter days. Activity also increased near agricultural land, which was used at night as open habitat. Wild boar activity decreased at sites with higher human visit rates. Individuals also showed predominantly nocturnal and crepuscular activity patterns, suggesting spatiotemporal avoidance of humans. However, fine-scale temporal adjustments emerged: males and females without offspring tended to show nocturnal and crepuscular activity patterns. Females with offspring showed greater diurnal activity, consistent with increased avoidance of nocturnal predators, the grey wolf, *Canis lupus*. These results suggest that wild boar cope with Mediterranean summers through flexible, sex-specific temporal adjustments shaped by thermal, ecological and risk-related drivers. Our study emphasizes the importance of considering multiple stressors when assessing behavioural responses to environmental variation.

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Ecological perturbations associated with the Anthropocene are placing increasing pressure on animal populations (Wilson et al., 2020). The interactions between temperature variation, human activities and landscape features may drive flexible behavioural responses and lead to long-term adaptive changes in phenotypic traits (Buchholz et al., 2019). Individual behavioural flexibility primarily depends on intrinsic characteristics, with sex and age playing important roles (Bergmüller & Taborsky, 2010; Griffin et al., 2015; Mazza & Eccard, 2018). Extrinsic factors may further influence behaviour, and activity patterns can serve as key indicators of these responses (Krebs & Davies, 2009). Among extrinsic factors, photoperiod, temperature variation, food availability, predator activity and human activities may exert important pressures on animal behaviour (Ashby, 1972; Ciuti et al., 2012; Keuling et al., 2008a; Keuling et al., 2013). Thermoregulation and predation risk can strongly affect animal activity through complex trade-offs, whose costs and benefits may themselves be influenced by landscape features (Bellón et al., 2022; Orazi et al., 2024). Understanding how these pressures influence animal activity patterns and how landscape features modulate these effects is crucial for assessing how species may cope with ongoing ecological perturbations.

During the last century, global surface temperatures increased by approximately 1–1.3 °C (Lee et al., 2023), reaching levels that,

* Corresponding author.
E-mail address: martina.calosi2@unisi.it (M. Calosi).

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especially in summer, can increase the energetic costs of thermoregulation in homeothermic species such as mammals (Terrien et al., 2011). As a consequence, individuals may shift their ranges or select habitats based on their potential to provide thermal refugia (e.g. poleward latitudes, higher elevations or cooler microhabitats: Mason et al., 2014; Parmesan, 2006; Scheffers et al., 2014). Adjusting temporal activity patterns is another key strategy for avoiding heat stress, for example, through increased crepuscular and nocturnal activity (Brivio et al., 2024; Levy et al., 2019; Thel et al., 2024). However, such behavioural shifts may entail fitness costs, particularly during summer (Greives et al., 2015; Lesmerises et al., 2018; Takahashi et al., 2008). At temperate latitudes, summer nights are substantially shorter than summer days, so increased nocturnal activity can reduce overall foraging opportunities for typically diurnal species. Moreover, high temperatures, often coupled with drought, can further constrain the availability of natural food resources. Together, these factors may limit individual mass gain and ultimately reduce fitness (Fernández-Llario et al., 1999; Massei et al., 1997; Terrien et al., 2011). Additionally, increased nocturnality in prey species may elevate the risk of encounters with nocturnal predators (Lesmerises et al., 2018). This risk may be further amplified by the recent recovery of apex predators across Europe (Chapron et al., 2014; Di Bernardi et al., 2025). This recovery has increased the probability of predator–prey overlap and affected prey behaviour and ecology (Lazzeri et al., 2024; Orazi et al., 2024).

Human activity is another factor that potentially shapes behaviour because humans are frequently perceived as predators (Johann et al., 2020; Marchand et al., 2014; Salvatori et al., 2024). Both lethal (e.g. hunting) and nonlethal recreational activities may be perceived as stressors by wild animals (Frid & Dill, 2002), potentially triggering avoidance responses in animal populations. These responses may manifest as changes in activity patterns (Johann et al., 2020; Marchand et al., 2014; Ohashi et al., 2013) or increased nocturnality (Johann et al., 2020; Marchand et al., 2014; Podgórski et al., 2013; Salvatori et al., 2023, 2024).

Landscape features may further modulate the effects of both thermoregulatory challenges and perceived risk from humans and predators. The presence and spatial configuration of key habitats (e.g. agricultural land, riparian areas or densely vegetated habitats) may provide thermal refugia, essential food resources and shelter from predators and humans (Bellón et al., 2022; O'Connell et al., 1993). By shaping patterns of habitat use and activity timing, these landscape characteristics may influence individual behaviour, foraging opportunities and ultimately fitness and population dynamics (Bellón et al., 2022; He et al., 2019; Norris et al., 2010).

Here, we investigated whether the complex interactions between summer temperatures, landscape features and human and predator activity influenced daily activity levels and nocturnality in wild boar, *Sus scrofa*, across Mediterranean landscapes, at the population and sex-specific levels. The wild boar is a widely distributed mammal known for its remarkable ecological and behavioural plasticity, which enables it to inhabit a wide range of environments and climates (Scandura et al., 2022). This plasticity includes a high degree of flexibility in activity patterns in response to external factors (e.g. Brivio et al., 2017; Massei et al., 1997; Ohashi et al., 2013; Podgórski et al., 2013). The wild boar is an excellent thermoregulator (Ruf et al., 2023) and may respond behaviourally to temperature increases to reduce the energetic cost of thermoregulation (Güldenpfennig et al., 2025). Examples include reducing locomotor activity levels under suboptimal weather conditions (Brivio et al., 2017; Güldenpfennig et al., 2025; Ohashi et al., 2013; Thurfjell et al., 2014), increasing nocturnal activity (Brivio et al., 2017; Podgórski et al., 2013), seeking shaded habitats for resting during the daytime (Spitz & Janeau, 1990) and wallowing in mud to dissipate body heat (Bracke, 2011; Olczak et al., 2015; Ruf et al., 2023). Wild mammals may also reduce locomotor activity in response to high predation risk (Borowski & Owadowska, 2010) and enhance nocturnality on darker (e.g. moonless) nights, when reduced visibility constrains predators' hunting ability (Gordigiani et al., 2022). Temporal patterns may also shift from diurnal to crepuscular or nocturnal in response to human activity (Ohashi et al., 2013; Podgórski et al., 2013).

The wild boar is a generalist omnivore (Scandura et al., 2022), able to exploit above- and below-ground food resources according to their availability (Herrero et al., 2006). Harsh climatic conditions, such as prolonged aridity, may limit its foraging ability, either directly by hindering digging activity or indirectly by reducing vegetation and soil productivity (Calosi et al., 2024). These constraints may increase individual home range size and, in turn, the locomotor activity required to locate food resources and meet daily energetic requirements (Podgórski et al., 2013). During periods when crops are available, agricultural land may serve as a cost-effective buffer against natural resource scarcity by supplying energy-rich food resources (Herrero et al., 2006). Under high temperatures and low availability of natural resources, wild boar may increase their activity in transitional habitats bordering open habitats (Keuling et al., 2009), where dense vegetation could provide shelter from heat and humans. In turn, they may exploit open habitats when temperatures are lower and human activity is reduced, such as at night (Johann et al., 2020; Keuling et al., 2009). Specific responses may vary across habitats, populations and individuals (Massei & Genov, 2004). Sex, age and physiological status are important determinants of individual behaviour (Brogi et al., 2022; Vetter et al., 2016). Reproductive females typically give birth in spring (Scandura et al., 2022) and are therefore likely to still be weaning their offspring during summer, resulting in higher food requirements than those of nonreproductive females or males (Ruf et al., 2021). Moreover, offspring face a higher risk of predation (Mattioli et al., 2011; Nores et al., 2008), potentially prompting sows to be more active in habitats and periods of the day that balance food availability and protection from predators (Spitz & Janeau, 1990; Vetter et al., 2016). Males may adopt compensatory behavioural strategies to mitigate seasonal challenges, such as reducing their mobility (Massei et al., 1997), increasing nocturnality and selecting habitats that offer thermal shelter and proximity to food resources (Ruf et al., 2023).

We used camera trap data collected over 4 years at 208 sites across eight Mediterranean protected areas to evaluate changes in daily activity levels and nocturnality in wild boar in relation to temperature, landscape features, predator activity and human activity. We assessed support for a number of predictions derived from the literature (Table 1).

METHODS

Study Area

The study was conducted over 4 years (2021–2024), during summer (mid-June to August), in eight protected areas in central Italy. The mean (± SD) size of the study areas was 29.9 ± 24.8 km^2 (range ca. 10.5–90 km^2), and the mean elevation above sea level was 478.2 ± 109.3 m (range 0–1453 m; Fig. 1, Table S1). All study areas were located within the Mediterranean bioregion, encompassing longitudinal and elevational climatic gradients that gradually transitioned from sub-Mediterranean and temperate conditions to more continental conditions with increasing elevation and distance from the coastline as the areas approached the

Table 1
Predictions about the potential effects of focal predictors (temperature, predator activity, human activity and landscape features) and their interactions with other environmental factors on the temporal responses of wild boar, *Sus scrofa*

Variable	Hypothesis	Prediction of the behavioural response			
		Daily activity		Nocturnal activity	
Temperature	Temporal activity patterns would be affected by temperature to minimize heat stress (Brivio et al., 2017; Güldenpfennig et al., 2025)	1a	Lower activity levels on warmer days	1b	Greater nocturnality following warmer days
Elevation	Increased activity at higher elevations (i.e. thermal refugia) would help mitigate heat stress in summer (Singer et al., 1981)	2a	Higher activity levels at higher elevations	2b	Greater nocturnality at lower elevations
Habitat*temperature	The effect of temperature on activity patterns would depend on habitat type (Morelle et al., 2015)	3a	Higher activity levels in covered habitats on warmer days	3b	Greater nocturnality in open habitats following warmer days
Distance from persistent water sources*temperature	The effect of temperature on activity patterns would depend on water availability, which may help prevent hyperthermia (Güldenpfennig et al., 2025; Ruf et al., 2023)	4a	Higher activity levels near persistent water sources during warmer days	4b	Greater nocturnality near persistent water sources following warmer days
Distance from agricultural land	During periods of natural resource scarcity, activity patterns would be affected by the availability of agricultural land, which provides high-quality food (Bollen et al., 2024; Keuling et al., 2009)	5a	Higher activity levels near agricultural land	5b	Greater nocturnality near agricultural land
Human visit rate	Wild boar would perceive humans as a risk and thus minimize encounters by adjusting their temporal activity patterns (Johann et al., 2020; Ohashi et al., 2013)	6a	Lower activity levels at sites with higher human visit rates	6b	Greater nocturnality at sites with higher human visit rates
Wolf visit rate	Wild boar would perceive grey wolves, *Canis lupus*, as a risk and thus minimize encounters by adjusting their temporal activity patterns (Palmer et al., 2021)	7a	Lower activity levels at sites with higher wolf visit rates	7b	Lower nocturnality at sites with higher wolf visit rates
Presence of offspring	Offspring presence would affect temporal activity patterns of females to prioritize piglet survival (Andersson et al., 2011; Keuling et al., 2008b)		Untested	8	Lower nocturnality in females with offspring
Night sky brightness	Nocturnal illumination would affect activity patterns (Gordigiani et al., 2022)		Untested	9	Lower nocturnality during brighter nights

Apennine chain (Pesaresi et al., 2014). In the Mediterranean bioregion, summers are generally hot and dry, while winters are mild, with no or limited snow cover. Rainfall is mainly concentrated in spring and autumn. The study areas were predominantly covered by woodland (mean ± SD = 81.2 ± 17.7%), followed by agricultural land (10.0 ± 12.1%), shrubland (4.5 ± 4.2%) and grassland (2.5 ± 2.6%; Fig. 1). Artificial surfaces, bare and rocky soil and water bodies accounted for 3.1 ± 2.3% of the total area. The main geographical and environmental features of each study area are detailed in Table S1.

All study areas had low human population density, with a mean (± SD) of 1.1 ± 1.2 inhabitants/km^2 (range 0.1–3.8 inhabitants/km^2: Schiavina et al., 2023), although they were visited for recreational activities (e.g. hiking), particularly in summer. Recreational hunting was prohibited in all study areas under Italian legislation. Population control of wild boar was conducted by the local Park authority or by the regional authority. In the largest area, Maremma Regional Park (MRP), population control was conducted repeatedly throughout the study period using either shooting or trapping and removal. There were seven shooting operations in Alto Merse Nature Reserve in 2023 and two in Acquerino-Cantagallo Nature Reserve in 2024. Wild boar occurred in all study areas, with a mean (± SD) population density of 10.8 ± 4.9 individuals/km^2 during the study period (range 1.7–22.2 individuals/km^2: Calosi et al., 2025). Grey wolves, *Canis lupus*, and red foxes, *Vulpes vulpes*, represent the only natural predators of wild boar (Capitani et al., 2004; Ferretti et al., 2019; Lazzeri et al., 2024; Lovari & Sangiuliano, 2006; Mattioli et al., 2004; see Mori et al., 2017, for a review of wild boar predators in Italy) and were present in all study areas.

Camera Trapping

We investigated wild boar daily activity levels and nocturnality using camera traps. We sampled each study area for at least 2 years, with a mean (± SD) sampling period of 3.1 ± 0.6 years (range 2–4 years; Table S2). We superimposed a sampling grid on each study area to ensure spatially balanced sampling effort, with a cell size of 1.5 × 1.5 km in the nature reserves and 1 × 1 km in MRP. We placed one infrared camera in each grid cell at sites suitable for detecting medium- to large-sized mammals (e.g. animal pathways, trails or forest roads). The mean (± SD) distance between cameras was 927.4 ± 321.8 m, and camera height was standardized at 70.6 ± 19.2 cm above the ground (range 20–150 cm). We oriented cameras to maximize detection of animal movements and ensure consistent monitoring conditions across all sites (Cusack et al., 2015). Depending on the size of the study area, between 8 and 60 camera traps were active for 24 h each day (Table S2), recording 10 s videos with minimal lag between consecutive triggers. We checked cameras every 30–45 days to replace memory cards and

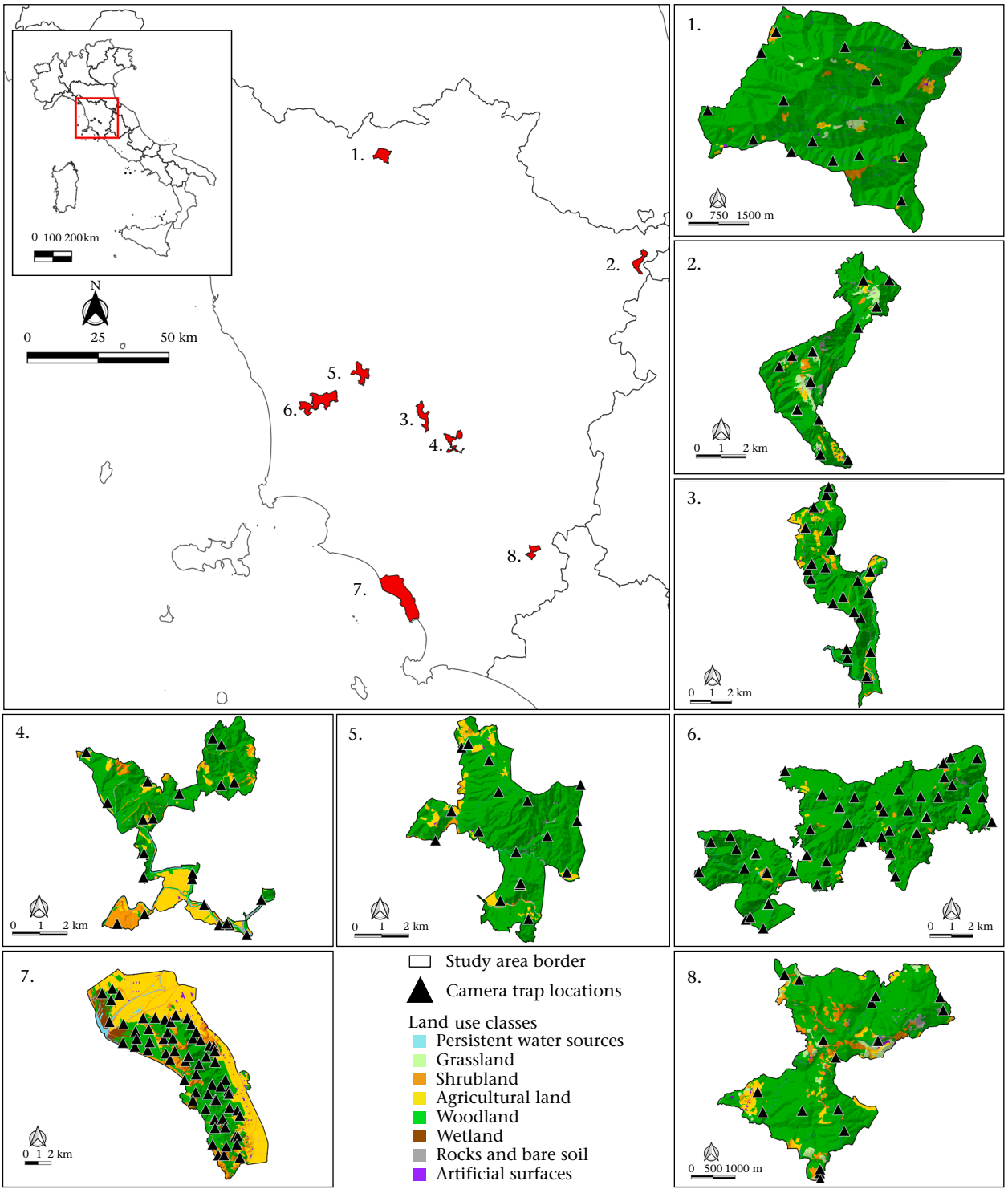


Figure 1. (a) Location of the study areas in Italy. Habitat composition (land use classes) and locations of camera traps in: (1) Acquerino-Cantagallo NR, (2) Alpe della Luna NR, (3) Alto Merse NR, (4) Basso Merse NR, (5) Foresta di Berignone NR, (6) Foresta di Monterufoli e Caselli NR, (7) Maremma RP and (8) Monte Penna NR. NR = Nature Reserve; RP = Regional Park.

batteries. We grouped camera models into seven classes based on similar technical characteristics (Table S3) and included these classes in the statistical analyses to account for potential variation in detectability (Salvatori et al., 2023, 2024). When the same camera trap recorded sequential videos of the same species (wild boar and grey wolf), we considered only the first detection within each 30 min period as an independent detection to reduce temporal autocorrelation (De Satgé et al., 2017; Tobler et al., 2008; Torretta et al., 2016). Conversely, because human passages were typically brief and isolated, we used a shorter 3 min interval to avoid underestimating independent human detections (Esattore et al., 2023).

For each wild boar detection, individuals were classified by age class and sex based on body development, the presence of sex-specific characteristics in adults and subadults and coat colour in newborns and juveniles. Two age classes were identified: (1) adults/subadults and (2) offspring, comprising newborns with striped coats and juveniles with red coats. When sex could be determined unambiguously, adult and subadult individuals were also sexed. Sex and age classification was conducted throughout the study period in all study areas, except in MRP, where these classifications were conducted only in 2022. For analyses, we discarded sites where cameras were operational for fewer than 20 days per study year or were placed above 130 cm, retaining 208 camera sites monitored for a total of 19 306 camera-days (mean ± SD = 43.1 ± 12.9 camera-days/year/site).

Wolf and Human Visit Rates, Temperatures and Environmental Predictors

The visit (i.e. detection) rates of wolves and humans at each camera location and in each study year were used as proxies for the intensity of site use by predators and humans, respectively (Pallari et al., 2026; Salvatori et al., 2023, 2024). These visit rates were calculated as the number of individuals detected across independent detections divided by the number of camera-days for wolves and as the number of independent detections divided by the number of camera-days for humans.

Air temperature (°C) data recorded at 15 min intervals at 2 m above ground level were obtained from Servizio Idrologico Regionale Toscana (https://www.sir.toscana.it/termometria-pub) and Arpae Emilia-Romagna (https://simc.arpae.it/dext3r/). We selected the professional weather stations closest to the centroid of each study area, with a mean (± SD) distance of 4.65 ± 1.95 km (range 1.47–6.81 km; Table S4). The closest station to Alpe della Luna Nature Reserve (ALNR) recorded data at 30 min intervals. We therefore used linear interpolation to obtain 15 min temperature values and ensure consistency across study areas.

The habitat type at each camera location was visually classified as covered or open. Covered habitats were defined as forested habitats (e.g. deciduous, sclerophyllous, coniferous or mixed forest) and other densely vegetated and shaded habitats, such as shrubland, whereas open habitats were defined as mainly unshaded habitats with no or scattered trees or bushes, such as grassland, meadow and agricultural land. Habitat type was therefore considered a proxy for vegetation-based shelter from heat (Pallari et al., 2026; van Beest et al., 2012). At each location, the percentage of shrub cover at heights $\leq$ 1.5 m was visually estimated within a 10 m radius circular buffer around each camera. Given the difficulty of precisely delineating the detection zone of a camera trap in the field, this approach allowed us to standardize an index of vegetation obstruction across camera models, which could affect camera detectability.

We extracted the elevation (m) above sea level of each camera trap location from the 10 × 10 m resolution digital elevation model provided by the Sistema Informativo Territoriale ed Ambientale (SITA) Regione Toscana (https://geoblog.regione.toscana.it/-/open-geodata). We calculated the distance (m) from each camera trap location to the nearest agricultural land as a proxy for proximity to high-quality food resources. We identified the locations of each study area covered by cereal crops, vineyards, arable land and set-asides using the regional land use and land cover data set provided by SITA-Regione Toscana. This data set refines the Coordination of Information on the Environment (CORINE) Land Cover (CLC) class 2 through a regional classification (https://dati.toscana.it/dataset/ucs). The data set had a reference year of 2019 and was based on CLC 2018 (Table S5). We calculated the distance between each camera site and the nearest persistent water source as a proxy for water availability, because proximity to water may facilitate cost-effective summer thermoregulation through mud bathing (Ruf et al., 2023). We generated a spatial layer of persistent water sources by integrating inland water bodies identified as CLC class 5.1 (Tables S5–S6) with the hydrographic network and water infrastructure data provided by SITA-Regione Toscana (https://www.regione.toscana.it/-/reticolo-idrografico-e-di-gestione). Although ephemeral water bodies (e.g. small ponds and ditches) were not georeferenced, potentially leading to an underestimation of water availability, we conducted the surveys in summer, during the dry season. Consequently, persistent water sources (e.g. ponds, rivers and lakes) probably represented the primary water sources available to wild boar during the study period.

We developed a sky brightness index (Mori, Cozzi, et al., 2020) to account for night-time darkness in the analysis of wild boar nocturnal activity. For each event at date and time i, sky brightness was calculated as: sky brightness index = night brightness$_i$ × (1 − cloud cover$_i$), where values closer to 0 indicate darker nights and those closer to 1 indicate brighter nights. Night brightness (lx) was obtained using the R package 'skylight' (Hufkens et al., 2023), which provides sky brightness values from 0 (completely dark, with no moonlight) to 0.5 (full moon), with values exceeding 0.5 in the presence of moonlight and high levels of light pollution. Cloud cover data, expressed as continuous values from 0 (no clouds) to 1 (fully cloud-covered sky), were retrieved from the European Centre for Medium-Range Weather Forecasts Reanalysis 5th Generation (ERA5) hourly data set provided by the Copernicus Climate Change Service (Climate Data Store; Hersbach, 2023) via the R package 'ecmwfr' (Hufkens et al., 2019).

Statistical Analyses: Temporal Activity Patterns and Spatiotemporal Overlap

We analysed temporal activity patterns of wild boar, both at the population and sex-specific levels, as well as those of wolves and humans, using independent camera trap detections with associated dates and solar times. These patterns were evaluated over the entire study period using kernel density estimation with the R package 'overlap' (Meredith et al., 2013). We estimated 95% confidence intervals using 1000 bootstrap replicates. Watson's two-sample tests of homogeneity were applied using the R package 'circular' to compare intrapopulation and interspecific activity patterns (Lund et al., 2017). We quantified the overlap in temporal activity patterns between the investigated categories (i.e. wild boar–humans, wild boar–wolves, males–females and females without offspring–females with offspring) using the nonparametric overlap coefficient, Δ (Ridout & Linkie, 2009; Weitzman, 1970), which ranges from 0 (no overlap) to 1 (complete overlap). The Δ_4 estimator was selected because it is recommended for sample sizes exceeding 50 observations (Ridout & Linkie, 2009). We calculated this estimator and its 95% confidence intervals using 10 000 bootstrap replicates for each pairwise comparison (Dias et al., 2019). Temporal overlap was considered 'high' when $\Delta_4 \geq 0.75$, 'moderate' when $0.50 \leq \Delta_4 < 0.75$ and 'low' when $\Delta_4 < 0.50$ (Monterroso et al., 2014).

Statistical Analyses: Daily Activity Level

The total number of wild boar detections on a given day was used as an index of species-level daily activity levels (Rowcliffe et al., 2014). We investigated the potential drivers of wild boar daily activity levels using generalized linear mixed models (GLMMs) in R version 4.4.0 (R Core Team, 2024) with the package

'glmmTMB' (Brooks et al., 2017). This approach allowed us to include both fixed and random effects to account for hierarchical or repeated observations and to analyse count data appropriately (Zuur et al., 2009). We fitted the models with a negative binomial distribution and a log link function, as recommended for overdispersed count data (Zuur et al., 2009). The total number of detections obtained during each 24 h sampling period at each site was modelled as the response variable and included both focal and control predictors. The focal predictors used to investigate the potential ecological drivers of wild boar activity were (1) mean daily temperature over the same 24 h sampling period (°C), (2) wolf visit rate (number of individuals/day) and (3) human visit rate (number of detections/day). These predictors were included to investigate whether wild boar reduced their daily activity on hotter days and to assess the relationships between local site use by predators or humans and wild boar daily activity levels. We also included (4) distance to the nearest agricultural land (m), (5) distance to the nearest persistent water source (m), (6) habitat type at the camera trap location (reference level: covered) and (7) ln transformed elevation (m above sea level) to assess the potential role of these environmental variables in shaping wild boar daily activity. Predictors 1–5 and 7 were continuous, whereas predictor 6 was categorical. We also included two interaction terms: (8) the interaction between mean daily temperature and habitat type, to investigate whether wild boar activity decreased on hotter days only in habitats providing little thermal shelter (i.e. open habitats: Morelle et al., 2015) and (9) the interaction between mean daily temperature and distance to the nearest persistent water source, to assess whether the role of persistent water sources as thermal buffers increased with temperature (Ruf et al., 2023). Additionally, we included two continuous control predictors to account for potential variations in the daily number of detections related to camera detectability: (10) shrub cover within a 10 m circular buffer around each camera trap (%) and (11) camera height above the ground (cm). Camera location nested within study area and camera model were included as random intercepts to account, respectively, for repeated measurements of daily activity at the same camera location within the same area and for repeated measurements recorded by the same camera model.

To assess sex differences in daily activity levels, we included the same set of predictors, interactions and random effects (a) at the population level, (b) for adult males and (c) for adult females. Because of convergence issues with the female model, we could not include additional parameters to account for the presence of offspring (e.g. the percentage of female detections involving offspring), nor could we fit a model for females without offspring. Because this parameter was considered important, given that females nursing and weaning offspring may adjust their daily activity levels to protect them from environmental stressors, we fitted an additional model using the total number of detections of (d) females with offspring within each 24 h sampling period as the response variable. Because sex classification in the largest study area (MRP) was performed only in 2022, we also re-ran the population scale model after excluding wild boar detections from MRP in 2021 and 2023 to assess whether removing these years affected the results.

Statistical Analysis: Nocturnal Activity

Each wild boar detection was categorized as either nocturnal or diurnal/crepuscular to investigate the drivers of nocturnal activity (Pallari et al., 2026; Torretta et al., 2026). We used the recording date and solar time to classify each detection as either nocturnal or diurnal/crepuscular, through the R package 'suncalc' (Thieurmel & Elmarhraoui, 2022). Night was defined as the period between the end of civil twilight in the evening and the start of civil twilight the following morning, using a reference solar angle of 6° below the horizon to define civil dawn and dusk (Brivio et al., 2024; Gupta et al., 2023). Each detection occurring during the night was coded as 1, whereas diurnal/crepuscular detections were coded as 0. This binary response variable was modelled using a GLMM with a binomial distribution and a logit link function, following recommendations for analysing binary data (Zuur et al., 2009). We included the same focal and control predictors (i.e. fixed effects 1–11) and random effects used in the daily activity model. Because this analysis was conducted at the level of independent detections, predictor (1) was refined. Specifically, mean temperature (°C) over the 24 h preceding each detection was included as a continuous variable to assess whether wild boar were more likely to be active at night following warmer temperatures. This approach ensured consistency with the temporal scale of the previous analysis and allowed us to examine the effect of temperature while accounting for its diel variation throughout the 24 h cycle (Pallari et al., 2026). In addition, (12) the sky brightness index was included as a continuous variable (an index ranging from 0, dark, to 1, bright) to investigate the effect of night-time visibility on the probability of nocturnal activity. Finally, the model included (13) night duration (h) as a continuous control variable to account for the increase in the proportion of the 24 h cycle occurring at night from June to August, during which night-time duration increases by approximately 30%–40% and consequently increases the probability of obtaining a nocturnal detection.

As in the daily activity level analyses, we tested the same set of predictors, interactions and random effects (a) at the population level, (b) for males and (c) for females. For the female model, we additionally included (14) offspring presence as a categorical focal predictor (reference level: no offspring) to investigate whether offspring affected the probability of nocturnal activity in females. As before, we also re-ran the population level model using the same set of predictors and random effects but excluding wild boar detections in MRP in 2021 and 2023. At all levels of the investigation, the population scale model refitted after removing these data provided qualitatively identical results to the model fitted to the full data set, although the statistical significance of some coefficients was reduced, probably as a consequence of the decreased sample size (Table S7). A summary of the global models at each level of investigation can be found in Table S8.

Statistical Analyses: Model Selection

Before model fitting, we explored the data by assessing collinearity and linearity assumptions, evaluating potential outliers and inspecting residual patterns using the 'DHARMa' package (Hartig, 2025). No collinearity was detected among explanatory variables in any global model, with all Pearson correlation coefficients having absolute values below 0.5 and all variance inflation factors (VIFs) being $\leq$ 1.7. We standardized covariates to improve coefficient interpretability, facilitate model convergence and allow comparison of effect sizes across predictors. For each response variable, we conducted all-subset model selection using the 'MuMIn' package (Bartoń, 2023) to evaluate all possible combinations of predictors, with each combination representing a candidate model underpinning a plausible hypothesis (Harrison et al., 2018). Detectability-related variables, namely shrub cover around the camera, camera height and, in the nocturnality analysis, night duration, were retained in all candidate models to account for variation in camera detectability between sites. Thus, model selection assessed whether more complex hypotheses received greater support than a null model explaining wild boar daily activity and nocturnality solely in terms of camera detectability. Therefore, all candidate models, including the null model

(i.e. the model containing only the random intercepts and detectability-related covariates), were ranked and weighted according to Akaike's information criterion corrected for small sample size (AICc). For each model, ΔAICc was calculated, and all models within 2 ΔAICc units of the top-ranked model were initially selected. Then, following the 'nesting rule' (Harrison et al., 2018), we excluded models that were more complex and had a higher AICc than any simpler nested alternative to avoid retaining overly complex models. This procedure resulted in one to three best models per analysis, depending on the analysis (Tables S9–S10). Model weights were standardized within these subsets. For each analysis, we focused on the model with the highest weight (i.e. the lowest AICc; hereafter, the top-ranked model) for inference. We checked the top-ranked model from each investigation for spatial patterns and temporal autocorrelation in the residuals to determine whether unexplained variation showed any spatial or temporal structure. Since spatial dependence between study areas was already accounted for in all GLMMs by including camera location nested within study area as a random effect (e.g. Lovell et al., 2022), we checked for potential spatial patterns within study areas in the DHARMa residuals using the Mantel test, which was performed separately for each study area (Legendre et al., 2015). Because camera trap data are inherently spatially structured, some degree of spatial autocorrelation could be expected, particularly for animals, such as wild boar, whose movements extend well beyond the 700–1200 m separating camera locations (Massei et al., 1997). Mantel tests indicated significant spatial autocorrelation in only a few study areas and not consistently across levels of investigation (Table S11). This suggests that the detected spatial autocorrelation was not intrinsic to the overall data structure but instead reflected localized patterns specific to individual study areas that did not persist across spatial scales. We assessed temporal autocorrelation by visually examining whether scaled DHARMa residuals averaged by day of the year showed any relationship or pattern with day of the year, because the smallest temporal units of our analysis were either the daily or diel cycle. Plots of residuals against day of the year showed no evident patterns (Fig. S1), indicating an absence of meaningful temporal autocorrelation in the residuals of any model. For each top-ranked model, we estimated predictor coefficients and their 95% confidence intervals and assessed the influence of each predictor by checking whether its 95% confidence interval included zero. Because the GLMMs were fitted using log or logit link functions and the predictors were standardized, we also quantified effect sizes by exponentiating each standardized coefficient, thereby expressing the magnitude of the effect on the response scale (Nakagawa & Cuthill, 2007).

Ethical Note

Data were collected using a noninvasive method (camera trapping, with no bait or lure) that did not involve direct contact with or manipulation of study animals; thus, the study did not require ethical approval. To minimize disturbance to animals, field operators spent the minimum necessary time at each camera site and preserved surrounding vegetation. The study complied with European (GDPR 2016/679) and Italian privacy regulations (D.Lgs. 196/2003 as modified by D.Lgs. 101/2018): informative signage was posted to notify passersby of the monitoring, cameras were secured with padlocks and any video footage capturing humans was permanently deleted soon after camera retrieval. As our study did not directly involve humans, we did not ask for ethical approval from our institutional human ethics committee. This research complied with the ASAB/ABS Guidelines for the ethical treatment of nonhuman animals in behavioural research and teaching (https://doi.org/10.1016/j.anbehav.2025.123421).

RESULTS

We recorded a total of 4223 wild boar detections. The breakdown of detections by age and sex classes, is provided in Table 2. Descriptive statistics for the focal and detectability-related predictors are reported in Table 3.

Temporal Activity Patterns and Spatiotemporal Overlap

Wild boar were predominantly nocturnal (Fig. 2, S2). At the population level, wild boar showed low temporal overlap with humans (sensu Monterroso et al., 2014: $\Delta_4 = 0.30$), with humans being diurnal, and high temporal overlap with wolves ($\Delta_4 = 0.83$; Fig. S2).

Males showed low temporal overlap with humans ($\Delta_4 = 0.22$) and high overlap with wolves ($\Delta_4 = 0.86$). Females exhibited higher diurnal activity than males (temporal overlap with males: $\Delta_4 = 0.75$; Fig. 2, S2). Their temporal overlap with humans was low ($\Delta_4 = 0.45$), whereas that with wolves was moderate ($\Delta_4 = 0.72$). Females without offspring showed low temporal overlap with humans ($\Delta_4 = 0.36$) and high overlap with wolves ($\Delta_4 = 0.80$). Females with offspring were more active during the day than those without offspring (temporal overlap: $\Delta_4 = 0.80$; Fig. S2) and showed moderate temporal overlap with both humans ($\Delta_4 = 0.53$) and wolves ($\Delta_4 = 0.64$).

Daily Activity Level

Two models explaining wild boar daily activity levels were selected for the population level investigations: two including years without wild boar sex classification and two excluding those years. A summary of the dropped and retained predictors for each

Table 2
Summary of wild boar, *Sus scrofa*, detections recorded, categorized by age class and sex

Category	Number of detections
Total	4223
Adult males	1174
Adult females	1199
Offspring	1101
Undetermined adults	576
Undetermined age class/sex	1527

Note that the sum of detections across age and sex classes exceeds the total number of unique detections because multiple classes could occur within a single detection event.

Table 3
Summary of the descriptive statistics for the focal and detectability-related predictors used in the analyses

Predictor	Mean	SD
Mean temperature (°C)	22.9	2.3
Temperature in the previous 24 h (°C)	24.0	2.7
Wolf visit rate (individuals/day)	0.1	0.2
Human visit rate (events/day)	0.3	1.7
Distance from agricultural land (m)	419.5	403.6
Distance from a persistent water source (m)	188.8	173.2
Elevation above sea level (m)	362.5	306.4
Camera height (cm)	69.6	18.2
Shrub cover (%)	19.8	20.7
Sky brightness index (lx)	0.004	0.01

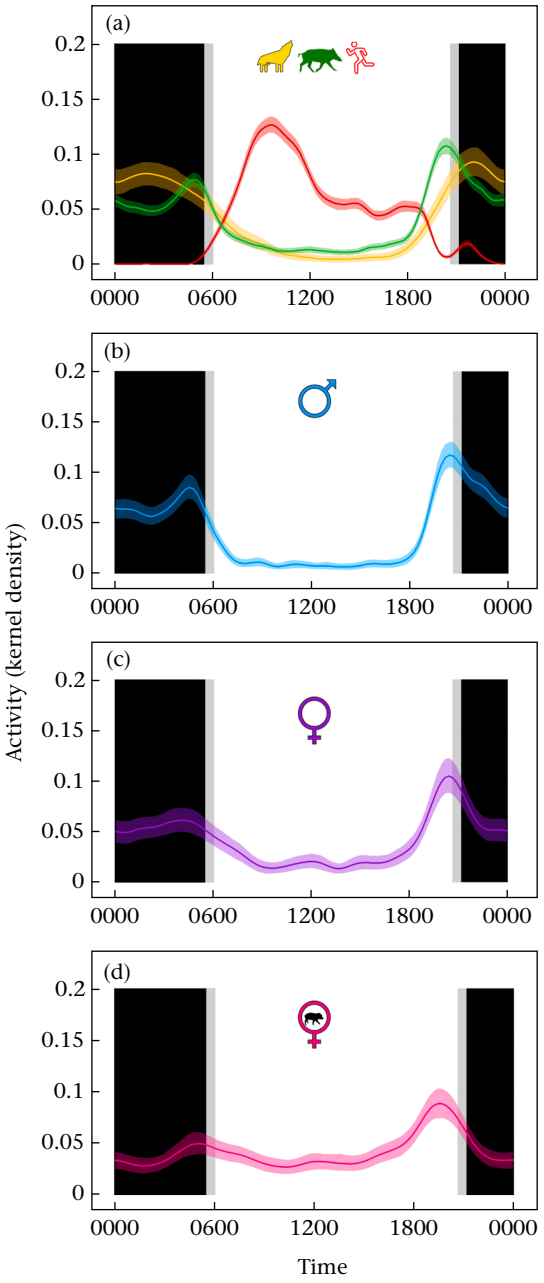


Figure 2. Activity patterns of (a) wild boar, *Sus scrofa*, at the population level (green line), humans (red line) and grey wolves, *Canis lupus* (yellow line), (b) wild boar males, (c) wild boar females without offspring and (d) wild boar females with offspring. These were obtained by combining independent detections across study areas and research years. Night hours, twilight periods and daytime are indicated by the black, grey and white areas, respectively. Solid lines represent kernel density estimates and bands represent 95% confidence intervals.

level of investigation is provided in Table S9. For each level of investigation, wild boar daily activity levels were strongly associated with wolf visit rate, distance from agricultural land and distance from persistent water sources (Fig. 3, Table 4). An increase of one SD in wolf visit rate was associated with an approximately 34–45% increase in daily activity levels. In contrast, an increase of one SD in distance from agricultural land was associated with a 29–43% decrease in daily activity, whereas an increase of one SD in distance from persistent water sources was associated with an 18–33% decrease (Table 4). Elevation was associated with an estimated 18% increase in daily activity for an increase of one SD, although its 95% confidence interval included zero, indicating substantial uncertainty around this estimate. The population level analyses excluding years without sex classification yielded a comparable hierarchy of associations (Table S7).

An increase of one SD in human visit rate was associated with an approximately 83% decrease in daily activity levels in males. The interaction between mean temperature and distance to persistent water sources indicated that the negative effect of distance from persistent water sources on daily activity levels intensified with increasing temperature (Fig. 3). Mean temperature was associated with changes in daily activity of less than 10%, with confidence intervals overlapping zero, indicating weak or negligible support for biologically relevant effects (Fig. 3, S3, Table 4).

In the models for females and females with offspring, in addition to the predictors described above (i.e. wolf visit rate, distance to persistent water sources and distance to agricultural land), an increase of one SD in human visit rate was associated with approximately 46% and 87% decreases in daily activity levels, respectively.

Nocturnal Activity

Two models that best explained wild boar nocturnal activity were selected for each of the population level, male and female analyses (see Table S10 for a summary of dropped and retained predictors). Across all levels of investigation, the probability of wild boar nocturnal activity showed the strongest associations with sky brightness index, distance from agricultural land, and mean temperature over the previous 24 h (Fig. 4, Table 4). Specifically, an increase of one SD in sky brightness index was associated with an 83–90% increase in the probability of nocturnal activity, an increase of one SD in distance from agricultural land was associated with a 15–17% decrease in the probability of nocturnal activity and an increase of one SD in mean temperature over the previous 24 h was associated with a 15–18% increase in the probability of nocturnal activity (Table 5).

At the population level, open habitats were associated with a 52% higher probability of nocturnal activity compared with covered habitats (Table 5). Wolf visit rate was associated with a modest increase in nocturnality (ca. 14%), but its confidence interval overlapped zero, indicating weak support for an effect. Analyses excluding years without sex classification showed a comparable hierarchy of associations, although wolf visit rate was not retained and confidence intervals for some predictors were wider (Table S7).

For males, no additional predictors were retained beyond those described above (i.e. sky brightness index, distance from agricultural land and mean temperature over the previous 24 h). For females, the presence of offspring was associated with an approximately 68% lower probability of nocturnal activity than the absence of offspring. Open habitats were also associated with an estimated 40% greater nocturnal activity than covered habitats but the confidence interval included zero, suggesting weak support for this effect.

DISCUSSION

By analysing the interactions between multiple stressors (i.e. temperature, human activity and predators), our study contributes to disentangling the relative influence of key environmental and anthropogenic factors on the temporal behaviour of a large mammal. The results showed that wild boar modified the total amount and temporal distribution of daily activity during summer,

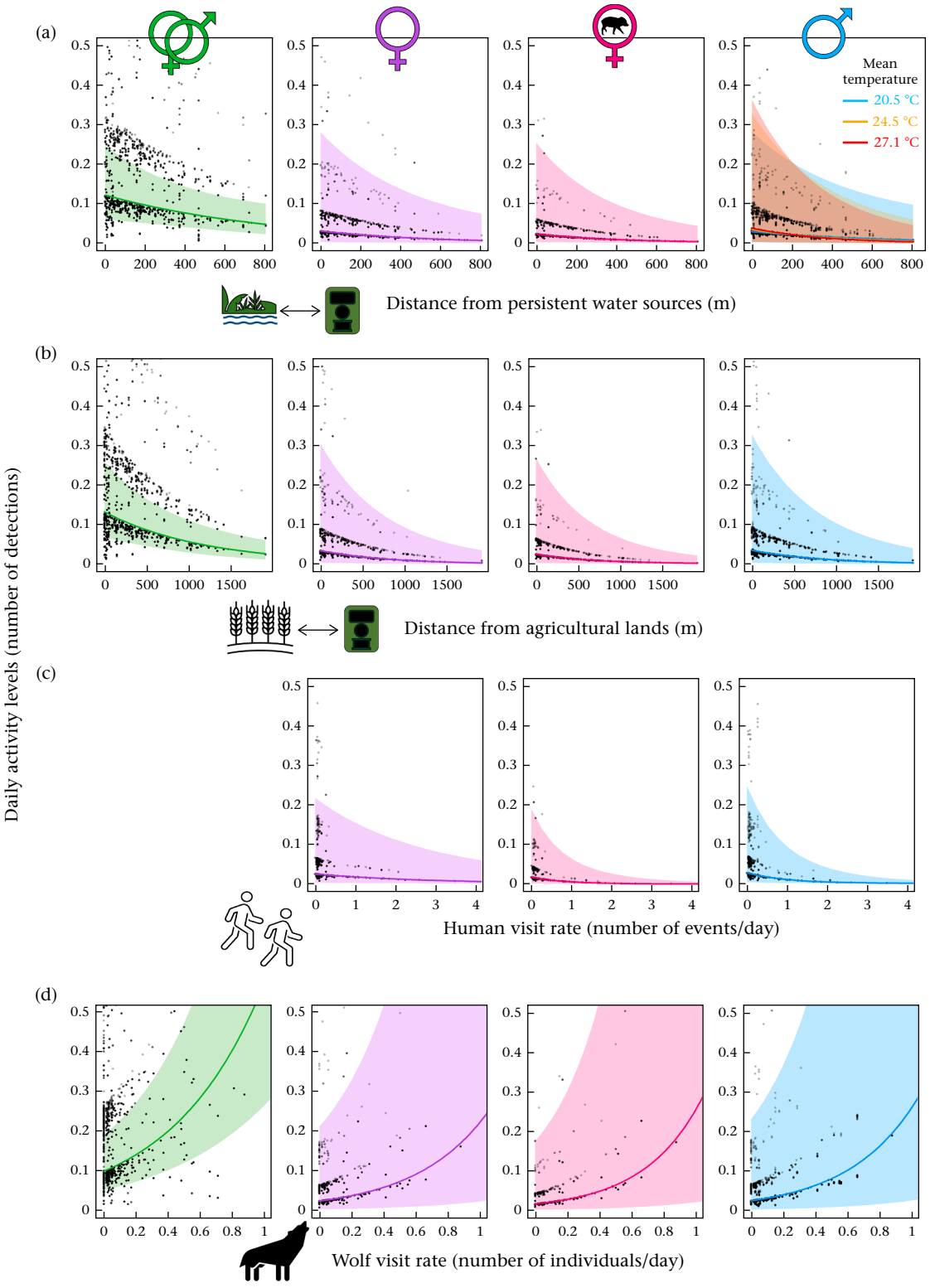


Figure 3. Plots showing the relationship between wild boar, *Sus scrofa*, daily activity levels and (a) distance from persistent water sources, (b) distance from agricultural land, (c) human visit rates and (d) grey wolf, *Canis lupus*, visit rates. These are shown at the population level (green plots), for females (violet plots), females with offspring (pink plots) and males (blue plots). Lines represent predicted values, bands indicate 95% confidence intervals and grey dots represent the distribution of partial residuals for each predictor. In panel (a), the plot for males shows the relationship between daily activity levels and the interaction between mean temperature and distance from persistent water sources. Mean temperature corresponds to the 25th (20.5 °C; light blue), 50th (24.5 °C; orange) and 75th (27.1 °C; red) percentiles. For a detailed visualization, see Fig. S3.

Table 4
Parameters estimated from the top-ranked generalized linear mixed models predicting wild boar, *Sus scrofa*, daily activity levels at the population level, for males, females and for females with offspring

Predictor	Population Log-mean β (95% CI); % change	Males Log-mean β (95% CI); % change	Females Log-mean β (95% CI); % change	Females with offspring Log-mean β (95% CI); % change
Intercept	-1.99 (**-2.32; -1.66**); 0.00	-3.63 (**-4.22; -3.03**); 0.00	-3.31 (**-3.95; -2.67**); 0.00	-4.59 (**-5.43; -3.75**); 0.00
Wolf visit rate	0.29 (**0.22; 0.36**); 33.67	0.37 (**0.24; 0.50**); 44.99	0.35 (**0.22; 0.48**); 42.47	0.44 (**0.29; 0.59**); 55.27
Human visit rate	–	-1.82 (**-2.78; -0.85**); -83.74	-0.62 (**-0.99; -0.26**); -46.35	-2.05 (**-3.32; -0.78**); -87.08
Distance from agricultural land	-0.34 (**-0.50; -0.19**); -28.94	-0.46 (**-0.68; -0.24**); -36.86	-0.47 (**-0.69; -0.26**); -37.78	-0.57 (**-0.84; -0.30**); -43.29
Distance from persistent water	-0.20 (**-0.36; -0.05**); -18.48	-0.37 (**-0.59; -0.14**); -30.61	-0.30 (**-0.51; -0.09**); -25.70	-0.40 (**-0.66; -0.14**); -32.92
Ln elevation	-0.20 (-0.41; 0.02); -17.93	–	–	–
Habitat: open	–	–	–	–
Mean temperature	–	0.01 (-0.59; 0.08); 1.27	–	–
Mean temperature*habitat: open	–	–	–	–
Mean temperature*distance from persistent water source	–	-0.09 (**-0.17; -0.00**); -7.40	–	–
Camera height	-0.09 (-0.22; 0.04); -8.87	-0.20 (**-0.39; -0.02**); -18.33	-0.28 (**-0.46; -0.10**); -24.55	-0.27 (**-0.48; -0.05**); -23.31
Shrub cover	-0.05 (-0.16; 0.06); -4.79	-0.00 (-0.15; 0.14); -0.16	-0.14 (-0.30; 0.02); -13.02	-0.16 (-0.36; 0.04); -14.63
σ^2location:area	0.94	1.11	1.08	1.19
σ^2area	0.36	0.61	0.48	0.39
σ^2camera type	0.14	0.37	0.57	0.87
R^2m	0.12	0.48	0.18	0.47
R^2c	0.46	0. 69	0.51	0.70
Data points	18 179	16 145	16 145	16 145

For each model parameter, the coefficient estimate (β), its 95% confidence interval (95% CI) and the percentage change associated with an increase of one SD in the predictor, calculated as $(e^{\beta \times SD} - 1) \times 100$, are shown. Coefficients whose 95% CIs do not include 0 are highlighted in bold. The variance of the random intercepts (σ^2), the marginal (R^2m) and conditional (R^2c) R^2 values and the number of data points are provided for each model. Dashes indicate that the parameter was not included in the top-ranked model following the model selection procedure. Details of the structure of the other top-ranked models are provided in Table S9.

a critical period in their biological cycle, particularly in Mediterranean areas. Our findings suggest that these stressors were perceived differently according to sex and offspring presence, emphasizing the importance of integrating individual-level factors when assessing behavioural responses.

The Role of Temperature and Natural Landscape Features

Wild boar daily activity levels were not associated with temperature variation, thus not supporting the prediction of reduced overall activity on warmer days (prediction 1a). In contrast, the probability of nocturnal activity increased with increasing temperatures over the preceding 24 h, supporting the expected shift towards greater nocturnality (prediction 1b). Similar shifts in activity patterns have been reported in other ungulates, such as chamois, *Rupicapra rupicapra* (Thel et al., 2024), ibex, *Capra ibex* (Brivio et al., 2024) and roe deer, *Capreolus capreolus* (Pallari et al., 2026), suggesting that temporal redistribution of activity may represent a widespread strategy among homeothermic species for coping with heat stress. Güldenpfennig et al. (2025) reported that wild boar in continental ecozones reduced total daily activity under high daily temperatures, unless rainfall occurred, despite exhibiting predominantly nocturnal behaviour. Their study did not explicitly examine changes in nocturnality and therefore described a reduction in overall activity rather than a shift in activity timing. In contrast, our results indicate a different response in the Mediterranean bioregion, characterized by warm and dry summers, where individuals appeared to cope with high temperatures primarily through a temporal reallocation of activity rather than by suppressing activity following hotter days. This pattern may also reflect the use of alternative thermoregulatory behaviours, such as wallowing and the use of shaded habitats (Bracke, 2011; Ruf et al., 2023).

Elevational shifts may mitigate heat stress in mountain-dwelling species (e.g. ibex: Brivio et al., 2019; Semenzato et al., 2021). Across our study areas, which were located at low-to-moderate elevations (i.e. < 1500 m above sea level), this topographic feature did not appear to influence wild boar nocturnality, thus providing no support for the predictions of higher activity at higher elevations (prediction 2a) or greater nocturnality at lower elevations (prediction 2b) to cope with heat. This result suggests that elevation alone may not provide sufficient thermal relief in Mediterranean environments compared with more direct behavioural adjustments. Instead, wild boar may prioritize tracking key resources, such as water and food (Keuling et al., 2009; Scandura et al., 2022; Yang et al., 2024), thereby mitigating thermal stress through fine-scale behavioural flexibility rather than avoiding warmer environments through broad elevational shifts.

There was support for differences in wild boar nocturnality and, to a lesser extent, total activity across habitats. Nocturnal activity was consistently higher in open than covered habitats, but activity levels and nocturnality in open habitats were not associated with temperature variation. These results neither confirmed the prediction of higher activity in covered habitats on warmer days (prediction 3a) nor that of greater nocturnal activity in open habitats following higher temperatures (prediction 3b). In anthropized ecosystems, wild boar have been shown to concentrate foraging during the first half of the night (Erdtmann & Keuling, 2020), with foraging activity increasing with night length (Reinke et al., 2021). The use of open habitats at night would allow access to resource-rich grasslands and transitional habitats when the risk of human encounters is reduced, while allowing wild boar to seek shaded habitats for resting during the day (Spitz & Janeau, 1990). Accordingly, nocturnality in open habitats may be shaped mainly by avoidance of humans while accessing food-rich habitats rather than by thermal constraints.

Activity levels were higher near persistent water sources. For males, this association strengthened with increasing temperatures, whereas for females, it was not mediated by temperature, partially supporting the prediction of higher activity near water sources during the hottest days (prediction 4a). Nocturnality was not related to proximity to persistent water sources, providing no support for the expected shift towards nocturnal activity near water following warmer days (prediction 4b). During summer, thermally buffered habitats, such as riparian shorelines, may become increasingly important. These areas provide dense

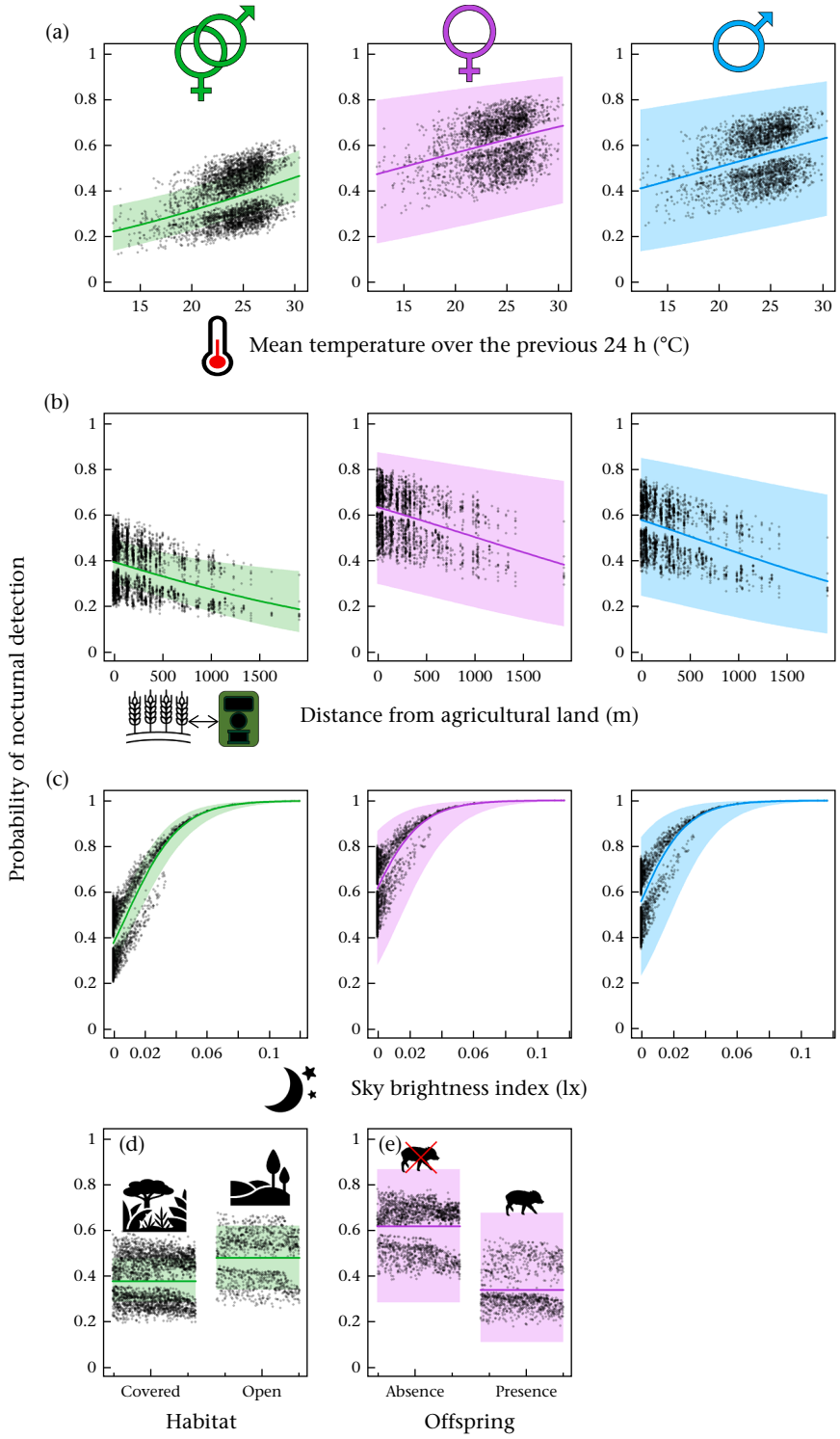


Figure 4. Plots showing the relationship between the probability of wild boar, *Sus scrofa*, nocturnality and (a) mean temperatures in the previous 24 h, (b) distance from agricultural land, (c) sky brightness index, (d) habitat type and (e) offspring presence. These are shown at the population level (green plots), for females (violet plots) and males (blue plots). Lines represent predicted values, bands indicate 95% confidence intervals and grey dots represent the distribution of the partial residuals for each predictor.

vegetation for resting (Allwin et al., 2016), opportunities for wallowing (Bracke, 2011; Mayer, 2009; Ruf et al., 2023) and resource-rich soils that promote rooting and high-quality forage (Brivio et al., 2017; Giralt-Rueda & Santamaría, 2023; Ramírez-Hernández et al., 2021). During this period, females typically form large family groups with dependent offspring (Scandura et al., 2022), requiring high energetic intake, access to water and dense cover to enhance offspring survival (Ruf et al., 2021). Accordingly, the lack of a temperature-mediated effect of distance to water in females may reflect a consistently high reliance on water sources, irrespective of temperature variation. Conversely, solitary males may reduce mobility and increase

Table 5
Parameters estimated from top-ranked generalized linear mixed models predicting probability of nocturnal activity in wild boar, *Sus scrofa*, at the population level, for males and for females

Predictor	Population Log-odds β (95% CI); % change	Males Log-odds β (95% CI); % change	Females Log-odds β (95% CI); % change
Intercept	0.24 (-0.14; 0.62); 0.00	0.21 (-0.13; 0.55); 0.00	0.57 (**0.19; 0.94**); 0.00
Wolf visit rate	0.13 (-0.05; 0.31); 14.25	–	–
Human visit rate	–	–	–
Distance from agricultural land	-0.17 (**-0.29; -0.04**); -15.30	-0.18 (**-0.33; -0.04**); -16.68	-0.17 (**-0.32; -0.02**); -15.55
Distance from persistent water	–	–	–
Ln elevation	–	–	–
Habitat: open	0.42 (**0.08; 0.75**); 20.60		0.34 (-0.02; 0.70); 14.41
Previous 24 h mean temperature	0.16 (**0.08; 0.24**); 17.53	0.14 (**0.04; 0.24**); 15.34	0.14 (**0.04; 0.24**); 14.94
Previous 24 h mean temperature*habitat: open	–	–	–
Previous 24 h mean temperature*distance from persistent water source	–	–	–
Sky brightness index	0.66 (**0.55; 0.77**); 93.98	0.64 (**0.52; 0.77**); 89.91	0.61 (**0.48; 0.73**); 83.44
Camera height	0.16 (**0.02; 0.30**); 17.34	0.16 (**0.00; 0.33**); 17.75	0.17 (**0.00; 0.34**); 18.62
Shrub cover	0.07 (-0.06; 0.21); 7.77	0.12 (-0.03; 0.26); 12.31	0.10 (-0.04; 0.24); 10.38
Night duration	0.29 (**0.21; 0.37**); 33.85	0.33 (**0.23; 0.43**); 39.07	0.33 (**0.24; 0.43**); 39.76
Offspring presence	NA	NA	-1.14 (**-1.32; -0.96**); -42.22
σ^2location:area	0.67	0.70	0.69
σ^2area	0.39	0.37	0.35
σ^2camera type	0.13	0.03	0.10
AUC	0.76	0.76	0.77
Data points	4223	3034	3034

For each model parameter, the coefficient estimate (β), its 95% confidence interval (95% CI) and the percentage change associated with an increase of one SD in the predictor, calculated as $(e^{\beta \times SD} - 1) \times 100$, are shown. Coefficients whose 95% CIs do not include 0 are highlighted in bold. The variance of the random intercepts (σ^2), the area under the curve (AUC) values and the number of data points are provided for each model. 'NA' indicates that the parameter was not included in the global model. Dashes indicate that the parameter was not included in the top-ranked model following the model selection procedure. Details of the structure of the other top-ranked models are provided in Table S10.

nocturnality in summer compared with other seasons (Cavazza et al., 2024; Podgórski et al., 2013; Ruf et al., 2023), relying more heavily on targeted visits to water sources under acute thermal stress. If so, the increased reliance on persistent water sources under rising temperatures among males but not females would reflect sex-specific differences in behavioural responses to ecological constraints. Adult and subadult wild boar showed no substantial summer mass loss in our largest study area, except for adult females during the driest years (Calosi et al., 2026), indicating a general ability to cope with thermal stress. Nevertheless, the roles of fine-scale thermal heterogeneity and temporary water source availability in driving activity patterns could not be assessed. To this end, fine-scale soil moisture data, local temperature measurements and GPS tracking of wild boar movements would improve our understanding of the factors driving activity patterns.

The Role of Humans and Predators

During periods of reduced availability and quality of natural food resources (i.e. summer in the Mediterranean and winter in northern Europe), easily accessible, high-energy foods such as crops can attract wild ungulates (wild boar in continental climates: Geisser & Reyer, 2004; Schley et al., 2008; wild boar in Mediterranean climates: Herrero et al., 2006; other species: Putman & Staines, 2004; Widén et al., 2023). We found increased activity levels and a higher probability of nocturnal activity near agricultural land, supporting the predictions of greater use of foraging areas (prediction 5a) and increased nocturnality in proximity to crops (prediction 5b; Bollen et al., 2024; Keuling et al., 2009). In our study areas, agricultural land covered an average of 10.9% of the surface and included mainly wheat, other cereals and sunflowers, which are generally in the ripening stage in summer, thus providing food resources for wild boar (Ferretti et al., 2021).

The activity levels of male and female wild boar were negatively associated with human visit rates, although this relationship did not emerge at the population level, partially supporting the prediction of reduced activity in areas frequently used by humans (prediction 6a). No effect of human visit rate on wild boar nocturnality was detected, providing no support for the expected increase in nocturnal activity at more disturbed sites (prediction 6b). Humans are generally perceived as predators by wild boar, probably as a consequence of decades of hunting (Keuling et al., 2013; Keuling & Massei, 2021), resulting in a 'landscape of human risk' (Apollonio et al., 2010; Salvatori et al., 2024; Stillfried et al., 2017). Wild boar have been shown to reduce their temporal or spatial overlap with humans by increasing nocturnality or avoiding sites with higher human activity (Brivio et al., 2017; Brogi et al., 2022; Podgórski et al., 2013; Salvatori et al., 2024). A recent study conducted in ecologically comparable areas showed that wild boar could adopt two broad risk-taking strategies: individuals exhibiting strong site fidelity and avoidance of humans and individuals showing risk-prone behaviours, such as low selection for some types of covered habitats, depending on forest structure and composition (Weterings et al., 2022), and high mobility (Brogi et al., 2022). Intrapopulation behavioural diversity suggests that population level approaches may oversimplify behavioural patterns that differ among individuals (Brogi et al., 2022; Keuling et al., 2009), potentially masking some responses that emerge at finer scales of investigation. Accordingly, our sex-specific analyses revealed responses to human activity that were probably masked when data were aggregated at the population level. In sparsely populated areas such as our study areas, human activity in summer is generally associated with recreation and agriculture, with

the exception of population control conducted in Maremma Regional Park near crops and, rarely, in other areas (2–4 individuals shot in just two areas in 2023: Ferretti et al., 2024). However, the relatively small size of our study areas (ca. 11–89 km^2), compared with the potential annual movement range of wild boar (up to ca. 20 km^2: Massei et al., 1997), implies that their behaviour may also be influenced by pressures outside study area boundaries, including hunting. Accordingly, human-related antipredator responses may persist even in relatively undisturbed sites and during hunting-free periods.

Although the results were consistent with wild boar of both sexes avoiding sites and times of day with higher human activity, heterogeneity in temporal responses between sexes emerged. While the results supported combined spatial and temporal avoidance of humans by males and females without offspring, females with offspring were relatively more diurnal and showed a greater temporal overlap with humans, supporting the prediction of a shift towards diurnal activity in sows (prediction 8). Males may be the primary focus of hunters (our study areas: Regione Toscana, 2019; Poland: Kamieniarz et al., 2020), whereas offspring represent the most vulnerable age class to predation by wolves (Mattioli et al., 2011; Nores et al., 2008). As a result, males may prioritize spatial and temporal avoidance of humans, whereas minimizing contact with natural predators may be comparatively more important for females with offspring (see also Keuling et al., 2008b).

The results indicated a general spatial association between wolf visit rates and wild boar activity levels. Wild boar nocturnality tended to increase weakly with wolf visit rates at the population level only (the confidence intervals overlapped zero), while it increased markedly during brighter nights. Overall, these results did not support the prediction of lower activity in wolf-frequented areas (prediction 7a), the expected reduction in nocturnality (prediction 7b) or lower nocturnal activity during brighter nights (prediction 9). At our latitudes, wild boar represent the primary prey of wolves (Lazzeri et al., 2024; Mattioli et al., 2011; Mori et al., 2017). The two species generally co-occur, and wolves generally track wild boar movements, resulting in spatiotemporal synchronization (Lazzeri et al., 2024; Mori, Bagnato, et al., 2020). Although some degree of predator–prey temporal overlap is unavoidable (Lazzeri et al., 2024; Mori, Bagnato, et al., 2020) and increased prey movement could theoretically increase predation risk (Borowski & Owadowska, 2010), wild boar did not reduce their daily activity in response to wolf presence. Instead, they appear to rely on finer-scale temporal adjustments. Specifically, wild boar activity peaks occurred slightly before (at dusk) and after (at dawn) those of wolves, suggesting partial temporal mismatches around key diel transitions. Such slight mismatches between activity peaks may substantially influence predator–prey dynamics (Orazi et al., 2024), as prey and predators continuously adjust their activity rhythms to balance survival and foraging success, respectively. Furthermore, nocturnality increased during brighter nights, indicating that wild boar in this system may not perceive moonlight as an additional source of risk. Previous studies have reported contrasting responses to nocturnal light conditions (Brivio et al., 2017; Gordigiani et al., 2022), which have often been interpreted as alternative antipredator strategies. In our context, increased wild boar nocturnality under brighter conditions may reflect the use of improved visibility to enhance predator detection or facilitate movement while still maintaining subtle temporal mismatches with peak predator activity. Future studies combining GPS tracking of both species are needed to further clarify the magnitude of human- and wolf-related effects on wild boar temporal responses.

Conclusions

Thermoregulation and predation risk can have complex and interacting effects on animal activity, which may be mediated by landscape features. Accounting for interactions between these factors is essential for interpreting activity patterns in heterogeneous environments. Our results indicated that temperature, landscape features and the activity of both humans and predators influenced wild boar activity patterns. High temperatures mainly affected the timing of activity, which shifted towards night. Natural and human-modified landscape features affected wild boar activity spatially and temporally: wild boar showed greater activity near persistent water sources, higher nocturnality in open habitats and greater use of sites near agricultural land, particularly at night. Moreover, our results suggested that wild boar avoided sites and times of day with higher human activity, although diurnality was more pronounced in females with offspring, consistent with some degree of temporal avoidance of wolves. Overall, our results indicated that multiple determinants influenced wild boar activity, resulting in temporal plasticity, habitat-mediated buffering and sex-specific strategies in response to the most relevant perceived risks. This behavioural flexibility probably contributes to the ecological success of wild boar in changing environments.

Author Contributions

Martina Calosi: Writing – original draft, Investigation, Formal analysis, Data curation, Conceptualization. **Niccolò Fattorini:** Writing – review & editing, Supervision, Formal analysis, Conceptualization. **Chiara Gabbrielli:** Investigation. **Lorenzo Lazzeri:** Investigation, Data curation. **Annalisa Mestieri:** Investigation. **Irene Belardi:** Investigation. **Noemi Pallari:** Investigation. **Francesco Ferretti:** Writing – review & editing, Supervision, Investigation, Formal analysis, Data curation, Conceptualization.

Data Availability

All data used in this study are available in the Zenodo Data repository: https://doi.org/10.5281/zenodo.22058726.

Declaration of Interest

None.

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Supplementary Material

Supplementary material associated with this article is available at https://doi.org/10.1016/j.anbehav.2026.123748.

The Supplementary Material has not been copy-edited and the content, formatting and file functionality are the sole responsibility of the author(s).

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