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Sciences**

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Wildlife Management Engineering

**Comparitive analysis of Camera Trap data to assess Red
Deer and Wild Boar movement parameters in Gemenc area of
Hungary**

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1. Introduction

Red deer (*Cervus elaphus*) and wild boar (*Sus scrofa*) are key ungulate species in Central European Forest ecosystems, playing vital roles in ecological processes such as herbivory and seed dispersal, and representing the primary species of Europe's hunting sector. Although their broad ecology and behaviour have been extensively studied, fine-scale temporal activity patterns, particularly seasonal shifts in response to environmental change, is still not fully clear within localised habitats; especially in a unique location like the Gemenc floodplain forest in the south of Hungary.

Previous research has documented general diel activity patterns in these species (Reinke et al. 2021), but few studies have captured multi-year temporal data that span critical autumn-to-winter transitions in floodplain forests (Pankova 2013), where fluctuating water levels and resource availability may significantly influence behaviour (Fuller et al., 2016).

To address this knowledge gap, I used motion-activated camera traps deployed over several years to non-invasively monitor animal activity. The study of animal activity patterns yields valuable data on species' daily and seasonal ecology. The practical applications of this research are significant, directly informing wildlife managers on ethical and effective hunting schedules for population control, while also guiding strategies to reduce crop damage and wildlife-vehicle collisions by predicting peak activity times. From a theoretical perspective, observing behavioural adjustments to diminishing daylight and lowering temperatures provides a crucial baseline for understanding phenotypic responses to environmental change, including climate change. This detailed understanding of winter activity patterns is particularly critical for the precise planning of management activities.

The aim of this study is to quantify and compare the diel activity patterns of sympatric Red deer (*Cervus elaphus*) and wild boar (*Sus scrofa*) in the Gemenc floodplain forest, with a specific focus on evaluating their seasonal, interannual, and photoperiod-driven behavioural plasticity. My objectives were the following:

- **To compare the diel activity patterns of Red deer and Wild boar to quantify their temporal niche partitioning.**
- **To investigate the seasonal plasticity in activity for both species by comparing activity patterns across the autumn-to-winter transition (October-December) and assess the interannual consistency of activity patterns by comparing data between 2022 and 2023 seasons.**

- **To determine the influence of seasonal changes in photoperiod on the timing of peak activity for both species.**

2. Literature review

2.1. Red deer

The Red deer is one of the largest and most widespread deer species globally, inhabiting a vast range that includes most of Europe, the Caucasus Mountains, parts of Western Asia, and an isolated population in the Atlas Mountains of North Africa, making it the only deer species native to the African continent (Geist 1998; Melletti and Focardi 2025). Due to its significant ecological role as a large herbivore and its economic importance as a primary game species, its biology and management have been the subject of extensive study across Europe (Skog et al. 2009; Melletti and Focardi 2025).

Red deer exhibit sexual dimorphism. Stags (males) are larger than hinds (females), typically measuring 175–250 cm in length and weighing between 160–240 kg. Hinds are shorter and more slender, generally weighing 120–170 kg (David W. Macdonald 2001). Females are slimmer with no antlers, and males grow antlers between spring to late summer coinciding with reproductive readiness and influencing social behaviours (Skog et al. 2009). This size variation is even more pronounced across the species' range, with some of the largest individuals found in the Carpathian Mountains, where stags can reach weights of up to 500 kg (Geist, 1998). In contrast, subspecies in less productive habitats, such as the Corsican red deer (*C. e. corsicanus*), are significantly smaller (Geist 1998; Melletti and Focardi 2025).

The most prominent feature of the stag is its large antlers (secondary sexual characteristic), which are grown and shed annually. Antler growth begins in the spring, induced by high testosterone levels and supported by a highly vascularised skin covering known as 'velvet'. The antlers can grow at a rate of up to 2.5 cm per day and are fully developed by late summer. As autumn approaches and testosterone levels build for the mating season (the rut), the velvet is shed and the bone calcifies, prompting the males to clean and scrape them on trees and rocks, thus transforming the antlers into weapons for intraspecific competition (Melletti and Focardi 2025).

Red deer are highly social animals that typically live in single-sex groups for most of the year. Hinds live in matriarchal herds with their calves and yearlings, while stags form looser bachelor groups (Melletti and Focardi 2025). This segregation breaks down during the autumn mating season, known as the rut. The rut is a period of intense competition where mature stags compete to gather and defend harems of hinds, engaging in ritualised displays and physical clashes to establish dominance. These displays include parallel walking and a distinctive

roaring vocalisation. The roar of the European Red deer is an adaptation to forested environments and serves to attract females and intimidate rivals (Reby and McComb 2003). Dominant stags may hold harems of up to 20 hinds and can lose up to 20% of their body weight, entering the winter in a severely depleted state. This energetic investment in autumn is compensated for by behavioural adjustments in the subsequent winter months, such as altered foraging activity and habitat selection to facilitate recovery (Reby and McComb 2003).

Red deer utilise a diverse range of habitats, typically found in deciduous woodlands but also in coniferous forests and open moorland, as observed in Scotland (Ahlén 1965; Skog et al. 2009). This adaptability is further reflected in their feeding strategy; they are classified as mixed or intermediate feeders, adapting their browsing and grazing habits to available vegetation (Hofmann 1989). They are known to influence vegetation structure and composition through their foraging behaviour, which can lead to both positive and negative impacts on biodiversity (Garcia et al. 2025).

The species' distribution has been heavily influenced by humans through reintroductions and introductions (e.g., to New Zealand and Argentina), but in its native Central European range it remains a cornerstone of forest ecosystems (Lovari et al. 2015).

Within the Central European region, male home ranges tend to be largest in autumn, while female home ranges are largest in winter (Kamler et al. 2008; Jerina 2012). Within the Carpathians, Red deer showed distinct seasonal migrations, with some individuals remaining resident while others migrated (Kropil et al. 2015). Red deer are also known to adjust their activity patterns based on seasonal changes- they have been reported to show higher group sizes and increased activity during winter compared to summer (Jędrzejewski et al. 2006).

2.2. Wild boar

The wild boar (*Sus scrofa*) is a significant species in European forests and hunting systems due to its adaptability, high reproductive rate, and impact on ecosystems. Wild boars (*Sus scrofa*) are highly adaptable omnivores with one of the broadest geographical distributions among all species (Ballari and Barrios-García 2014). It is widely distributed across Europe and has been expanding its range northwards, often facilitated by human activities such as supplementary feeding and habitat modifications (Markov et al. 2022).

Wild boar are characterised by a powerfully built body with a large head, short neck, and relatively short legs. The body is covered in a coat of coarse, dark bristles overlying a layer of finer underfur, which provides insulation in colder climates. Coat colour varies geographically and seasonally, from black to brown to grey, and piglets are born with a

distinctive coat of light longitudinal stripes that provides camouflage and fades after three to four months (Geptner 1988). The species exhibits notable sexual dimorphism; adult males are typically 5-10% larger and 20-30% heavier than females (sows). A key distinguishing feature of males is their continuously growing canine teeth, which develop into formidable tusks. The upper canines are sharpened against the lower ones, creating self-sharpening weapons used for defense and in intraspecific fights during the mating season. The species is divided into numerous subspecies across its vast range, which are generally grouped into four major regional clades based on morphology (Keuling et al. 2017).

The wild boar's ecological success is largely attributed to its adaptability as a habitat generalist. It thrives in a wide array of environments, from boreal taiga and deserts to alpine zones up to 4,000 metres in Central Asia. The key habitat requirements are cover for shelter (dense brush), water for drinking and bathing, and an absence of persistent, deep snow. In Europe, they favour deciduous and mixed forests, particularly those with oak and beech, which provide critical seed mast (Keuling et al. 2017; Geptner 1988).

As a versatile omnivore, the wild boar's diet is broad and shifts according to local and seasonal food availability. The bulk of its diet typically consists of plant matter, particularly high-energy food sources like acorns, chestnuts, and beechnuts (mast), which are crucial for building fat reserves before winter. They are also adept at foraging for underground food items (called rooting), using their powerful snouts and neck muscles to root for rhizomes, tubers, and bulbs. This rooting behaviour makes them significant ecosystem engineers, as their soil disturbance can alter soil properties, influence plant succession, and affect the invertebrate community (Tierney and Cushman 2006). In addition to plant matter, their diet is supplemented with animal protein, including earthworms, insects, carrion, and occasionally small vertebrates such as amphibians, reptiles, and the young of ground-nesting birds and deer (Katona and Heltai 2018).

Wild boars exhibit a matriarchal social structure. The primary social unit is the "sounder," consisting of related sows and their offspring, led by an old matriarch (Keuling et al. 2017). Subadult males leave their natal sounder at 8–15 months, while females may remain or establish new territories nearby. Adult males are typically solitary outside the breeding season, which is a trait reflected in the species' name in many Romance languages (e.g., French "sanglier" from *singularis porcus*, meaning 'solitary pig') (personal communications).

The breeding period (rut) in most areas lasts from November to January. Males travel long distances to locate sounders, engage in fierce fights with rivals, and can mate with 5–10 sows (ENETWILD-consortium et al. 2022). The gestation period varies with the age of the sow

(114–140 days), with farrowing typically occurring between March and May. Litter sizes average 4–6 piglets but can reach 10–12, demonstrating a high reproductive potential (Heptner et al., 1988). This high fecundity is a key component of the species' invasiveness and its ability to sustain high hunting pressure, as populations can exhibit compensatory responses such as earlier sexual maturity and increased birth rates (Massei et al. 2014).

The species' range has undergone dramatic fluctuations. Extirpated from large parts of its native range, including Great Britain by the 13th Century, it has staged a massive comeback since the mid-20th century. Populations have been increasing in the continent since the 1980s (Massei et al. 2014) and this growth is attributed to factors like mild winters, reforestation, intensive crop production, supplementary feeding, and the species' compensatory population responses to hunting pressure (Massei et al. 2014; Markov et al. 2022).

In its native range, the primary predator of the wild boar is the grey wolf (*Canis lupus*), which can be a significant source of mortality, particularly for piglets and subadults, and especially in winter when deep snow impedes the boar's movement (Geptner 1988). In parts of Asia, tigers and leopards also prey on wild boar. However, throughout much of Europe, the absence or low density of large natural predators means that human hunting is the principal source of mortality for adult boar. The species' interactions with humans are complex; it is both a highly valued game animal and widely considered a pest due to significant damage to agricultural crops and, increasingly, conflicts in suburban and urban environments (ENETWILD-consortium et al. 2022).

In terms of seasonal variation- Wild boars are primarily nocturnal, but their activity patterns can shift seasonally. During summer, they exhibit more diurnal activity, while in winter, they are predominantly nocturnal (Bollen et al. 2024).

3. Material and Methods

3.1 Study Area

My study was conducted in the Gemenc floodplain forest and game management unit (GMU code: 17 451210 409), located along the Danube River in southern Hungary between the cities of Szekszárd and Baja (Fig 1). The region is internationally recognised for its unique ecological character, designated as a Ramsar Wetland of International Importance and forming the core of the Duna-Drava National Park, which was established in 1996. Gemenc is widely considered to be Europe's largest remaining floodplain forest, representing a dynamic ecosystem shaped by the hydrological regime of the Danube (Gemenc | Ramsar Sites Information Service, n.d.).

Gemenc lies on the alluvial plain of the Danube, with an elevation ranging from 86–94 meters above sea level. The internal topography is a mosaic of slightly elevated mounds and low-lying flats, dissected by a network of old, dry riverbeds and numerous oxbow lakes (holtágak) that retain water year-round. The forest's hydrology is almost entirely dependent on the Danube's water levels, with annual floods inundating the area for an average of 50–60 days per year. This periodic flooding is the primary driver of the ecosystem's structure, nutrient cycling, and high biological productivity.

The study area is characterised a mosaic of floodplain habitats. The dominant vegetation consists of dense forest blocks, primarily composed of species adapted to periodic inundation. Close to the river and in lower-lying areas, forests are dominated by softwoods such as white willow (*Salix alba*) and black poplar (*Populus nigra*). On slightly higher ground are stands of hardwood oak-ash-elm forests, with pedunculate oak (*Quercus robur*) being a major species. The game management unit where the study was primarily conducted is mostly woodland, interspersed with meadows and wetlands, while the surrounding landscape is largely agricultural.

Gemenc is renowned for its population of Red deer, which is valued for its outstanding genetic stock. Alongside Red deer, the forest supports dense populations of Wild boar and Roe deer (*Capreolus capreolus*). While smaller carnivores such as the European wildcat (*Felis silvestris*), Golden jackal (*Canis aureus*), Red fox (*Vulpes vulpes*) and European otter (*Lutra lutra*) are present, large natural predators like the Grey wolf (*Canis lupus*) are not currently established in the Gemenc GMU itself. The absence of these apex predators means that population dynamics of large ungulates are primarily regulated by environmental factors and human management.

The area is managed by the Gemenc Forest and Game Co. Ltd., which oversees both forestry operations and hunting activities. Hunting is a major form of land use in Hungary but also a significant source of disturbance for wildlife. The red deer hunting season for stags runs from September to January, with the peak of the rut occurring in September and early October. Wild boar are hunted year-round, often through large-scale driven hunts during the autumn and winter months; both coinciding with our CT schedule. The high density of ungulates is considered by many local foresters as a potential threat to forest regeneration, making population control through hunting a key management objective. In addition to forestry and hunting, the area also supports regulated tourism and recreational activities (SÁNDOR, n.d.; Gemenc Forest and Game Co. Ltd. and Blaser 2025; Gemenc Zrt. 2025).

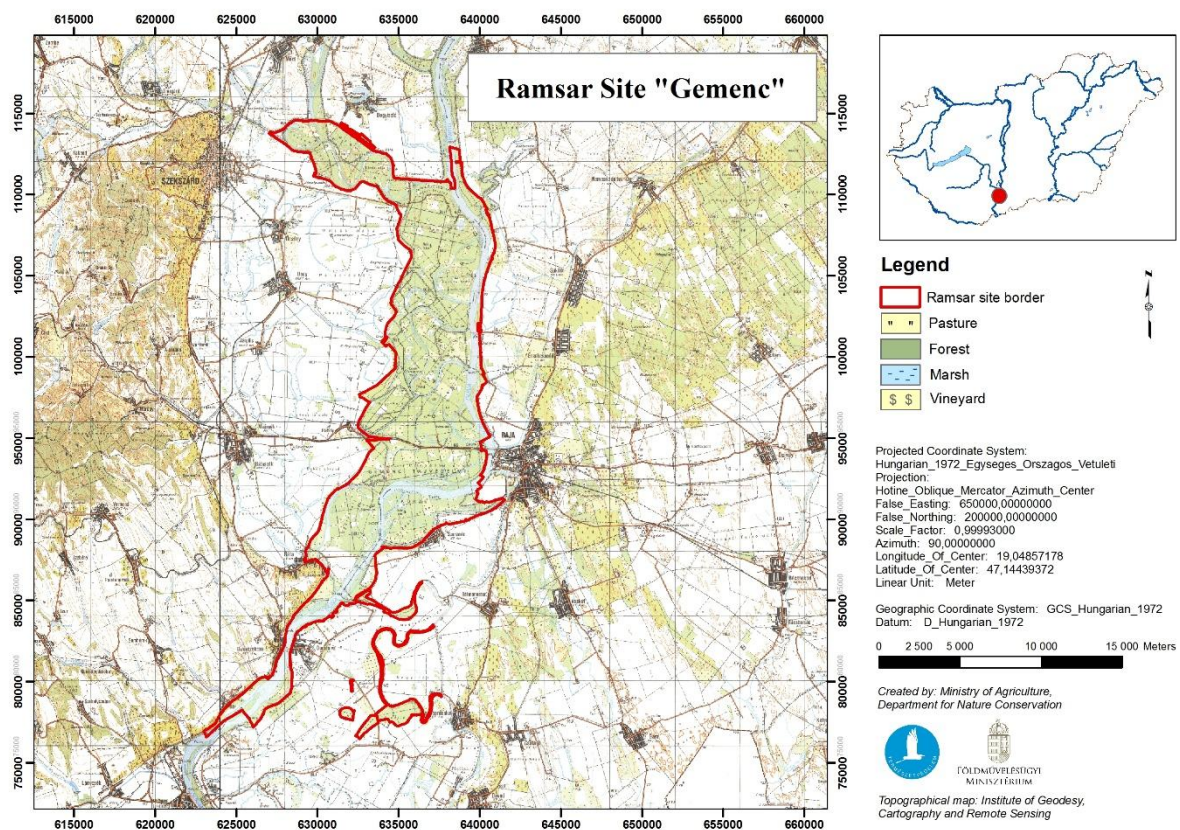


Fig 1. Ramsar Sitemap of Gemenc Floodplain Forest

3.2 Field Data Collection: Background and Camera Trapping Protocol

The camera trapping survey design was based on the standardised protocols developed for the ENETWILD consortium by the European Observatory of Wildlife (EOW). The monitoring of widespread, transboundary wildlife populations, such as wild boar and red deer presents significant logistical and methodological challenges to European range states and

beyond. To address this, the ENETWILD consortium was established with funding and support from the European Food Safety Authority (EFSA). The project's overarching goal is to harmonise wildlife population monitoring across Europe, thus improving the data available for risk assessments related to animal diseases, particularly African Swine Fever (ASF), and also to serve as a foundation for transboundary wildlife research. The consortium aims to connect researchers, wildlife managers, and governmental agencies from across the continent (and even beyond in some cases) to promote a collaborative network for data collection and analysis. A key initiative of ENETWILD is the European Observatory of Wildlife (EOW), which aims to develop, extend and implement international standards for data collection and provide guidance on robust methods for estimating wildlife abundance and density (ENETWILD-consortium et al. 2023).

My study was conducted originally as Hungary and MATE's contribution to this framework, adhering to its standardised protocols to ensure that the data collected in the Gemenc floodplain forest is comparable to data from all other sites across Europe. Data was collected over three autumn-winter field seasons: 2022, 2023, and a shortened 2024 season. The methodology employed in this thesis therefore not only addresses my local research questions but also contributes to a broader scale understanding of ungulate population dynamics.

Across the study area, a regular 0.3×0.3 grid with 36 points for motion-activated camera trap placement was deployed (Fig 2). All map plots presented are in a Web Mercator projection (EPSG:3857) due to the use of *leaflet* package function dependency by the ENETWILD R package *camtrapDensity*; the scale bar provides an approximation of distance at this latitude. The number of active cameras was 12 in 2022 and 2024, and 11 in 2023. Cameras were mounted on trees at a height of approximately 70 cm and angled slightly downwards. The detection zone was set to approximately 10 meters, and vegetation in the immediate foreground was minimally cleared to prevent false triggers.

Cameras were configured to operate 24 hours per day. They were set to capture a burst of consecutive images per trigger with a 3-second quiet period between triggers. The sensitivity of the passive infrared (PIR) sensor was set to medium. Cameras were deployed in three rounds every year, each lasting about 20 days, resulting in 33–36 unique deployments per year.

Total survey effort was quantified in trap-days, where one trap-day represents a single camera operating for 24 hours. The precise operational duration was calculated for each of the deployments based on the start and end timestamps recorded in the deployment metadata.

The survey periods were as follows:

- 2022: 14 September to 1 December (36 deployments), accumulating an estimated 948 trap-days.
- 2023: 20 September to 16 December (33 deployments), accumulating an estimated 1598 trap-days.
- 2024: 12 October to 6 November (36 deployments). This season was curtailed due to significant flooding of the Danube, which necessitated the relocation of some cameras and resulted in a shorter overall study period.



Fig 2. Location grid of the CT placement sites in Gemenc where each of the 12 cameras were placed. Each CT was general placed in the same location, with relocation done in case of logistical issues or exceptional conditions of the site (eg. 2024 period had nearly all cameras to be relocated to other grid points because of flooding)

3.3 Data Management and Pre-Processing

Image data were managed and annotated using the Agouti online platform (agouti.eu) co-developed by the Zoological Society of London (ZSL and Wageningen University and utilised the Random Encounter Model (REM) following the EOW workflow. To expand on REM; it is an analytical framework designed for populations where mark-recapture models are not possible to be used, or individuals cannot reliably be identified through photographs. First outlined in full by (Rowcliffe et al. 2008), it is derived from the principles of gas kinetics and collision theory, treating animals and camera traps as particles moving randomly within an area. The general formula for REM is-

$$D = (y / t) * (\pi / (v * r * (2 + \theta)))$$

Where:

- y/t (Encounter Rate): The number of independent animal detections (y) divided by the total camera trapping effort (t , in trap-days). This is the core data collected by the cameras.
- v (Animal Speed): The average distance an animal travels per day (also referred to as day range). This is estimated from camera trap images by measuring the distance an animal moves across the camera's field of view over a known time.
- r (Detection Radius): The effective radius of the camera's detection zone.
- θ (Detection Angle): The angle of the camera's detection zone, in radians.

Due to the scale of data-collection sites, variables in setup rigour and technical expertise of site personnel, REM was picked as the model of choice for population analysis by the ENETWILD team (Palencia et al. 2022; Jourdain et al. 2020). The detection zone parameters (r and θ) are measured at each camera deployment using calibration methods like photogrammetry, as outlined in the EOW protocol (ENETWILD-consortium 2022). The Agouti platform provides specialised tools to digitise animal movements and deployment calibrations, streamlining the process of extracting the necessary parameters (v , r , and θ) from the image data.

Species were identified, and individuals were counted for each image sequence. All sequences showing non-natural behaviour, such as direct animal interaction with the camera, were identified and excluded from the subsequent temporal analysis.

Within Agouti, images were grouped into sequences based on a 120-second sequence separation interval. This setting, while useful for data organisation in ENETWILD, was deemed insufficient for my study to ensure statistical independence for activity pattern analysis of large mammals. The fully annotated dataset, including metadata on deployments and observations, was exported from Agouti in the CamtrapDP standard format for further processing in R (ENETWILD-consortium et al. 2023).

3.4 Statistical Analysis

All subsequent data preparation and statistical analyses were conducted in the R programming environment (v4.3.3; R Core Team, 2023) using the packages *tidyverse* for data manipulation, *lubridate* for date-time handling, *camtrapDensity* for data import, *suncalc* for photoperiod calculations, and *circular* and *overlap* for temporal activity analysis. I developed a custom R script (*01_master_dataset.R*) to process the raw Camtrap DP export. The primary purpose of this script was to convert the raw sequence data into a final dataset of statistically independent detection events suitable for activity pattern analysis.

First, erroneous observations with timestamps from 2020 and 2021, identified as data entry errors, were programmatically filtered out. This involved applying a post-hoc 30-minute independence filter. An event was defined as the first detection of a given species at a specific camera location that was separated by at least 30 minutes from the preceding detection of that same species at that location. This ensures that a single, continuous visit by an animal or group is treated as a single data point. For each independent event, a series of analytical columns were calculated. Clock times were converted to solar time (in radians, ranging $0-2\pi$) using the *activity::solartime* function, which accounts for the specific date and geographic coordinates (latitude, longitude) of each detection. Events were also categorised into one of four photoperiods (Night, Dawn, Day, Dusk) based on local sunrise and sunset times, calculated using the *suncalc::getSunlightTimes* function. A 30-minute buffer was used to define the crepuscular periods (Dawn and Dusk). A second R script (*02_analysis_code.R*) was used to perform all statistical tests and generate figures, based on the finalized independent event dataset. The significance level for all tests was set at $\alpha = 0.05$.

3.5. Definitions

- **No. of Events:** The number of times a species was captured by a camera at any point in its operating period within the interval window applied for the study
- **Effort days:** The total number of trap days (one camera operating for 24 hrs) accumulated across all the stations during a specified time period.
- **Trap Rate:** The percentage of the ratio between the No. of events by the Effort days. Can be represented as $(n_events/effort_days) * 100$

4. Results

4.1. General results

To assess changes in the overall amount of animal activity during the autumn-winter transition, monthly trap rates were calculated for each species. As shown in Table 1, both Red deer and Wild boar exhibited an increasing trend in activity from October to December. The trap rate for red deer increased from 42.6 to 59.8 events per 100 days, while for wild boar it increased from 47.2 to 58.9 over the same period, indicating a higher level of overall activity as winter progressed.

Table 1. Seasonal trap rates by species, aggregated and arranged per month. We see an increasing trend for trap rates as winter sets in

Species	Red deer			Wild boar		
	Oct	Nov	Dec	Oct	Nov	Dec
No. Events	382	450	271	423	524	267
Effort Days	897	1026	453	897	1026	453
Trap Rate	42.6	43.9	59.8	47.2	51.1	58.9

In addition to the significant differences found in the diel activity patterns between years, the overall amount of activity was also compared. Table 2 summarises the annual trap rates for both species, calculated from the 2022 and 2023 datasets. The results show a consistent, albeit slight, increase in the overall trap rate from 2022 to 2023 for both Red deer (from 47.2 to 49.3 events/100 days) and Wild boar (from 54.6 to 57.6 events/100 days).

Table 2. Trap rates of both species between 2022 and 2023. 2024 not included due to exceptional flooding of the Danube causing disruption to animal movements and CT deployments

Species	Year	No. of Events	Effort Days	Trap Rate
Red deer	2022	418	885	47.2
	2023	485	983	49.3
Wild boar	2022	483	885	54.6
	2023	566	983	57.6

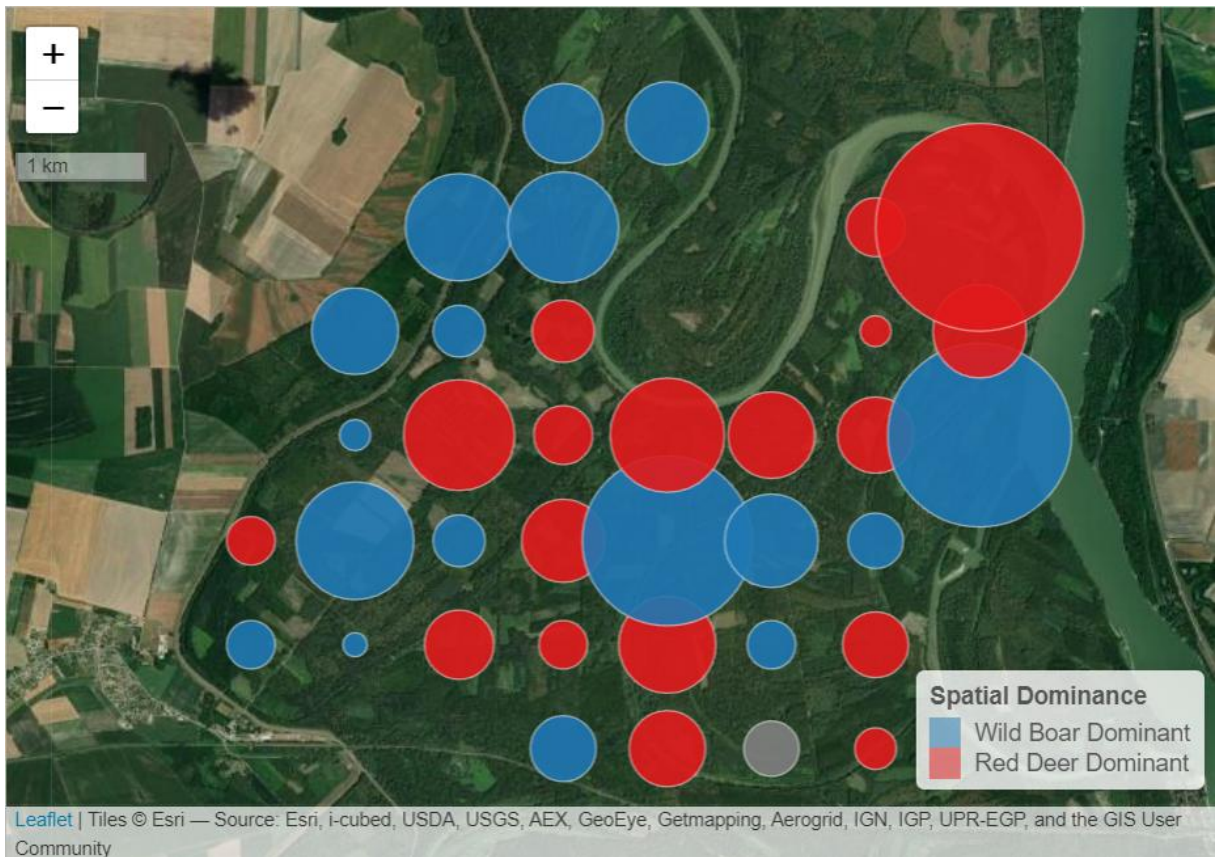


Figure 3. Spatial Dominance between the two species (quantified as trap rate specific comparison for each location)



Figure 4. Hotspots for Species activity; Comparison of *Cervus elaphus* between October and December (Autumn to Winter)

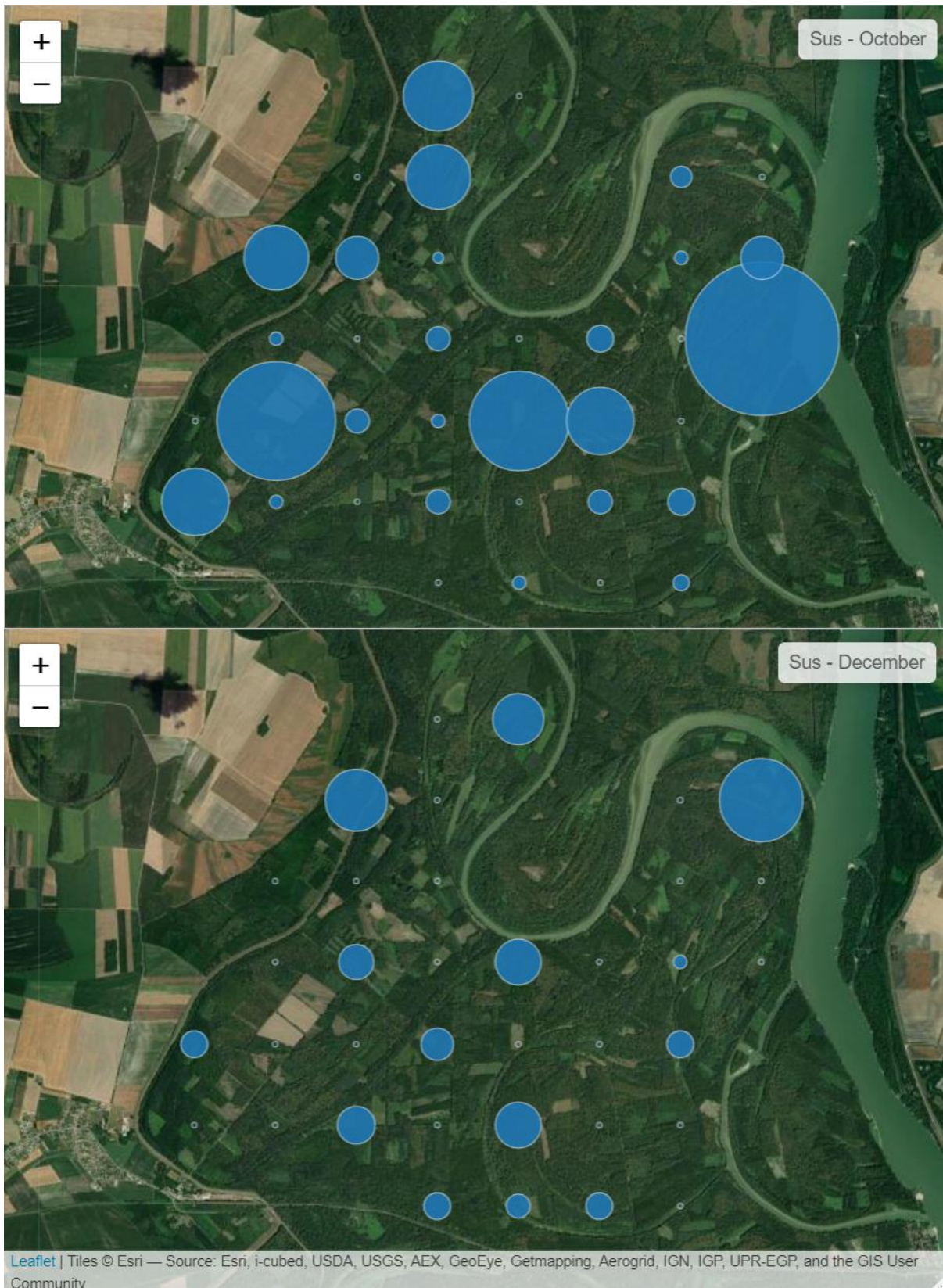


Figure 5. Hotspots for Species activity; Comparison of *Sus scrofa* between October and December (Autumn to Winter)

4.2. Diel Niche Partitioning

There was a highly significant difference in the overall diel activity patterns between Red deer and Wild boar (Watson-Wheeler test: $W = 70.42$, $p < 0.001$). This temporal partitioning was also evident in the species' differential use of photoperiods (Pearson's Chi-squared test: $\chi^2(3) = 102.47$, $p < 0.001$). The strength of this association was small to moderate (Cramér's $V = 0.19$), reflecting a distinct but not absolute separation in temporal resource use. As illustrated in Fig 6., Red deer exhibited a classic crepuscular pattern with clear activity peaks centered around dawn and dusk, while wild boar were predominantly nocturnal. Despite these differences in peak activity timing, the overall temporal overlap between the two species was high (Overlap coefficient $\Delta_4 = 0.82$, 95% CI: 0.79–0.86), indicating substantial co-occurrence in time, likely during transitional crepuscular hours.

Diel Activity Pattern Overlap of Red Deer and Wild Boar

Data from Gemenc Floodplain Forest (2022-2023)

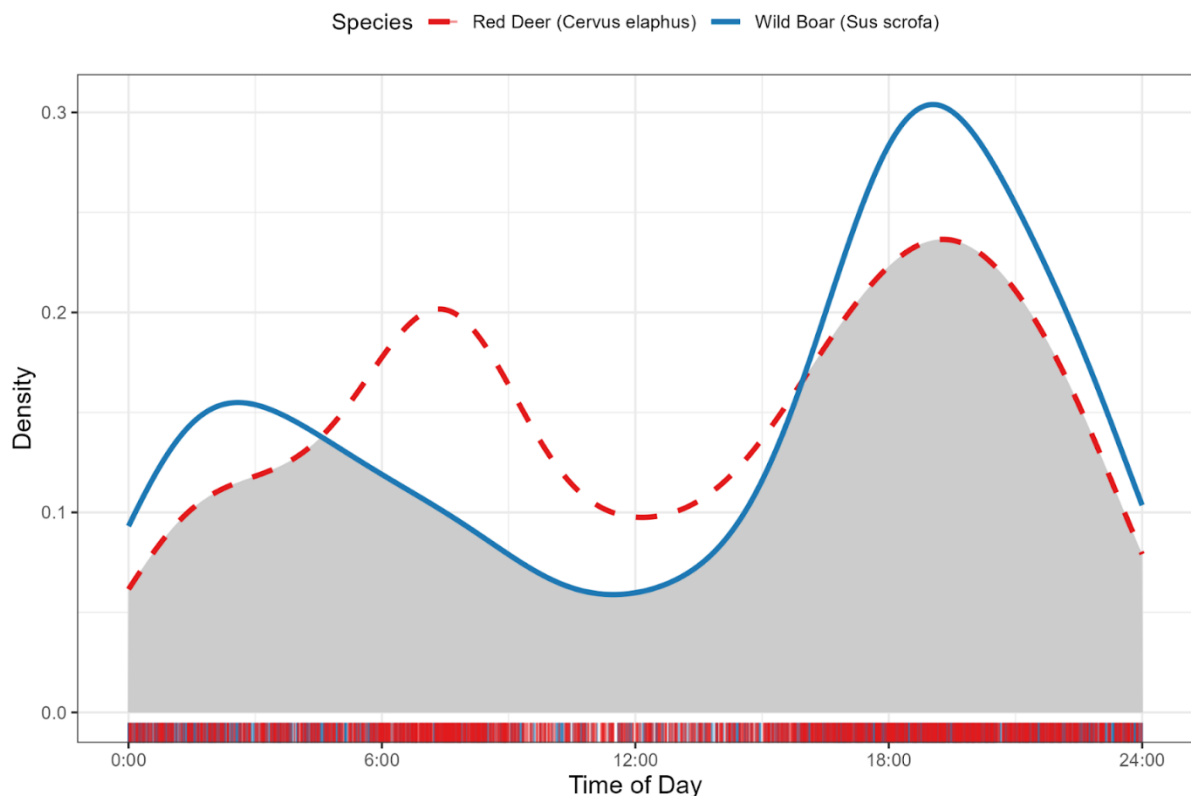


Figure 6. Diel activity patterns of Red deer and Wild boar in the study site. The y-axis represents the kernel density of an observation, and the x-axis represents the time of day of observation over a 24-hour cycle. The gray shaded area indicates the degree of temporal overlap between the two species' activity patterns. The rugs along the x-axis show the timing of each independent detection event for Red deer (red) and Wild boar (blue).

4.3. Seasonal and Interannual Plasticity in Activity Patterns

Both species demonstrated significant behavioural plasticity, altering their temporal activity patterns in response to both seasonal changes within a year and broader differences between years.

Seasonal Shifts: From October to December, both species significantly altered their activity patterns. The overall distribution of Red deer activity changed profoundly as winter approached (Watson-Wheeler test: $W = 56.88$, $p < 0.001$). This was characterised by a broadening of the activity window into the diurnal hours, rather than a simple shift of the crepuscular peaks, as there was no significant change in the median activity time (Kruskal-Wallis test: $p = 0.122$). Wild boar also showed a significant seasonal change in their activity distribution (Watson-Wheeler test: $W = 13.29$, $p = 0.01$). This manifested as a trend towards more concentrated nocturnal activity later in the night, though a significant shift in the median time of activity was not detected (Kruskal-Wallis test: $p = 0.068$).

Interannual Variation: Activity patterns were not fixed between years. Both Red deer (Watson-Wheeler test: $W = 19.40$, $p < 0.001$) and Wild boar ($W = 19.56$, $p < 0.001$) exhibited significantly different diel activity distributions between 2022 and 2023.

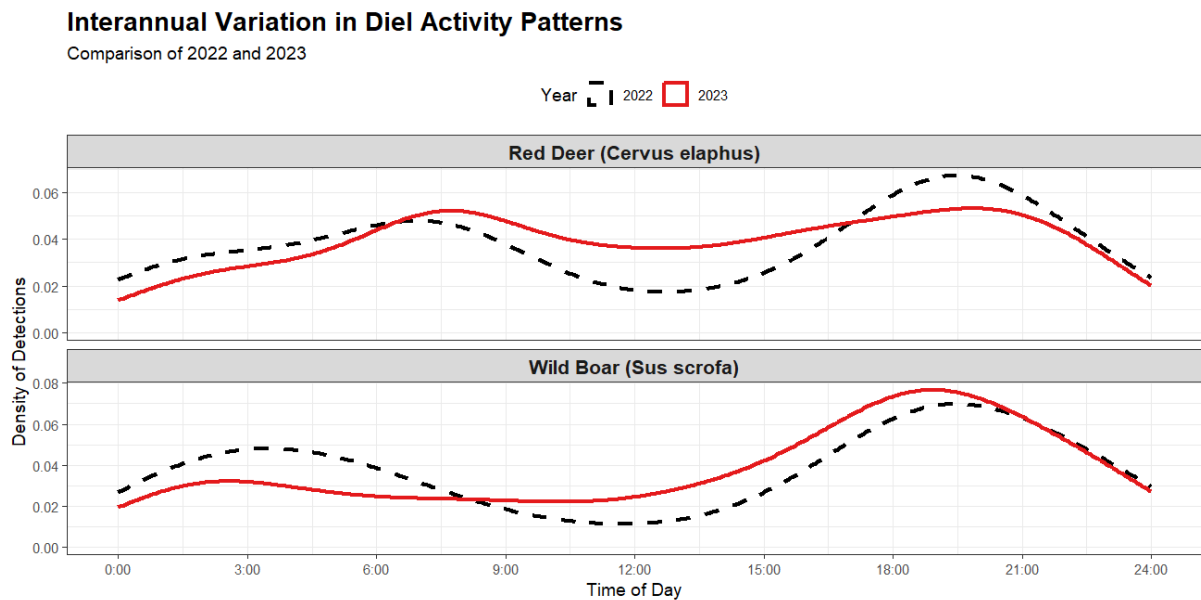


Figure 7. Interannual variation in the diel activity patterns for (top panel) red deer and (bottom panel) wild boar. Lines represent the kernel density estimate of activity for 2022 (black, dashed line) and 2023 (red, solid line).

Seasonal Shift in Diel Activity Patterns

Comparison of October, November, and December

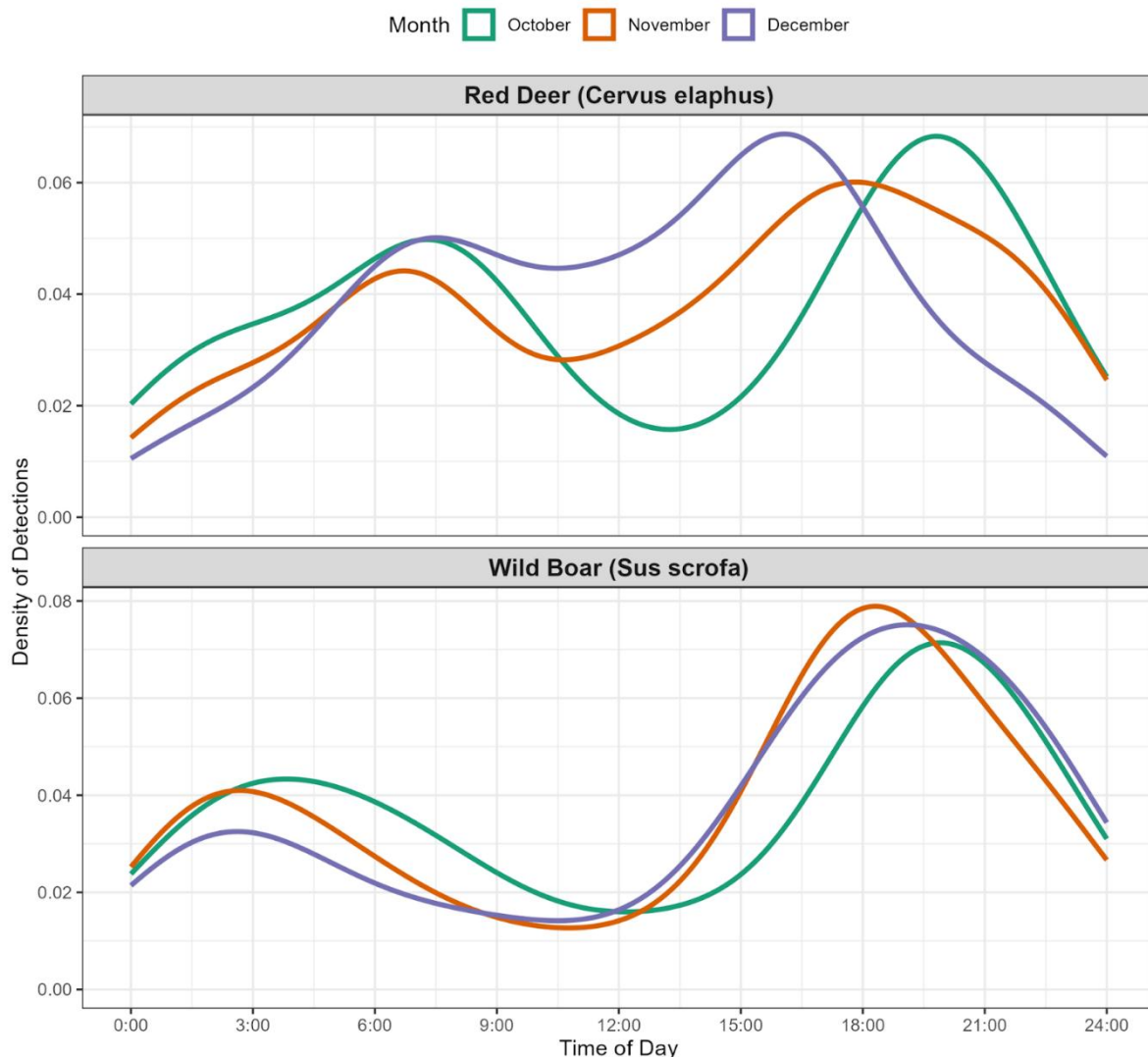


Figure 8. Seasonal shifts in the diel activity patterns for (top panel) Red deer and (bottom panel) Wild boar during the October to December transition. Lines represent the kernel density estimate of activity detection for October (green), November (orange), and December (purple).

4.4. Correlation with Photoperiod

The timing of activity for both species was strongly coupled with seasonal changes in the photoperiod, as visually demonstrated by the tracking of sunrise and sunset times throughout the year (Fig. 9).

Statistical analysis confirmed this relationship. The timing of the red deer's evening activity peak was significantly and positively correlated with sunset times ($R^2 = 0.15$, $p < 0.001$), shifting later in the day as sunset occurred later in the year. Similarly, the onset of evening activity in wild boar was significantly tied to sunset ($R^2 = 0.05$, $p < 0.001$).

The relationship with sunrise was more varied. The cessation of the boar's morning activity was weakly but significantly correlated with sunrise ($R^2 = 0.03$, $p = 0.01$), suggesting

their activity window is constrained by daylight. In contrast, the timing of the red deer's morning peak showed no significant linear relationship with sunrise ($p = 0.22$), indicating that other factors may be more influential in driving the start of their morning activity.

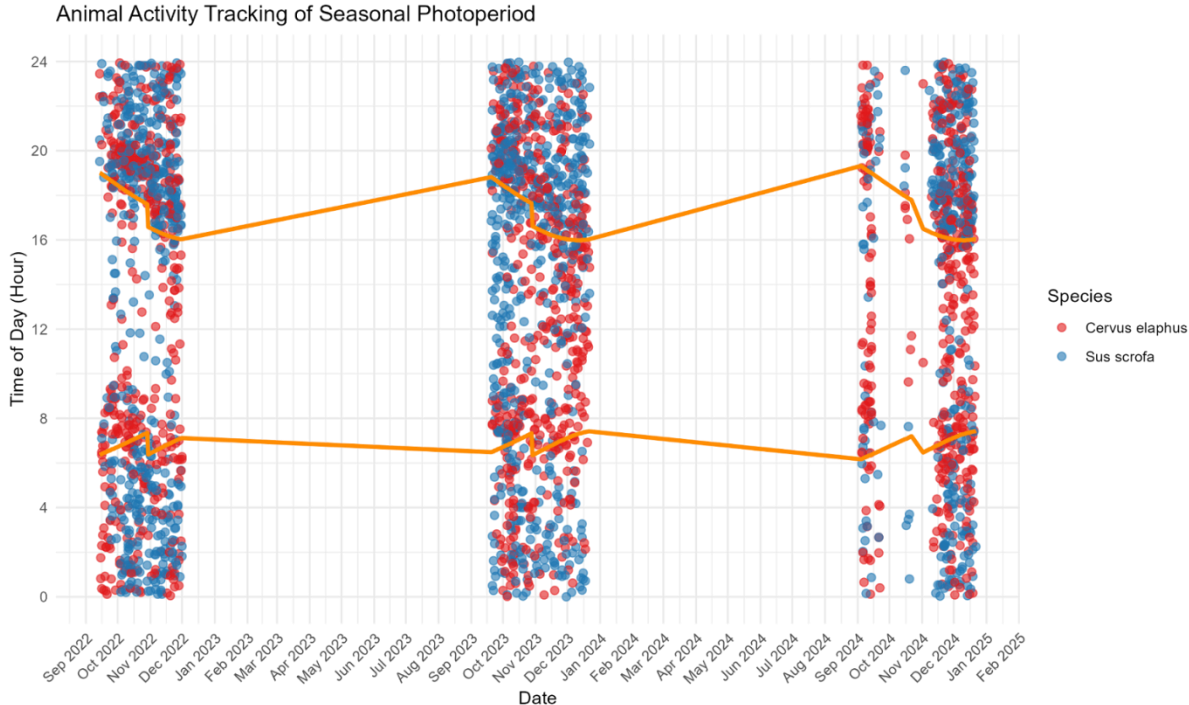


Figure 9. Correlation of animal activity with seasonal photoperiod, where each point represents the time of an independent detection event for red deer (red) or wild boar (blue). The solid orange lines plot the daily time of local sunrise (bottom line) and sunset (top line) over the study period. The figure visually demonstrates that the activity timings of both species track the seasonal changes in day length, particularly the onset of nocturnal activity in wild boar and the evening activity peak in red deer, which closely follow the sunset curve.

5. Discussion

5.1. General Results

Contrary to the expectation that animals might reduce activity to conserve energy in winter, we see that both species exhibited a significant increase in overall trap rates from October to December (Table 1). This may suggest that energetic budgets are a primary driver of winter activity levels. For red deer, this increased trap rate, combined with their slight expansion into diurnal hours, strongly indicates that they must forage for longer periods to compensate for lower-quality browse. For wild boar, the increase may be related to more time spent rooting for scarce resources or increased movement between foraging patches.

The species also exhibited some degree of spatial segregation (Fig. 3). Wild boar were the dominant species detected in the north west, while red deer showed higher relative activity near the center of the study area. This spatial pattern may reflect foraging preferences; red deer are intermediate feeders utilising edge habitats, while wild boar may prefer the forest interior for cover and rooting opportunities. So with high temporal overlap, fine-scale habitat partitioning may be an additional mechanism facilitating their coexistence.

The seasonal hotspot maps further show a significant spatial redistribution of activity over the onset of winter. While we already know that the overall trap rate for both species increased in December, this was by the intense use of a few key areas, while other sites saw a decrease in activity (Fig. 4 and Fig. 5). Notably, one station in the extreme northeast of the study area, which recorded no captures in October, became a major activity hotspot in December. This site strongly suggests the presence of supplementary feeding station provided by wildlife management for winter support, also insinuating that winter spatial behaviour for both species may be heavily influenced by the availability of artificial food resources.

5.2. Diel Niche Partitioning

The finding of a predominantly crepuscular pattern for red deer and a nocturnal pattern for wild boar is broadly consistent with most studies on these species in forest ecosystems (Qiu et al. 2022; Ahmed et al. 2024; Keuling et al. 2017). However, the high degree of temporal overlap ($\Delta_4 = 0.82$) is notable, and can be a consequence of the lack of apex predators for both species in the habitat, thus dampening the ‘landscape of fear’ activity patterns. In this predator-poor system, it may reflect daily commuting behaviour; the camera trap locations, located mostly within forested areas and edges, may be capturing the deer as they leave their diurnal

shelters to move towards more open foraging grounds (e.g., adjacent meadows or agricultural fields) in the evening, and as they return in the morning. The greater dissimilarity between the species' activity in the morning (Fig. 6) is particularly interesting. The earlier decline in wild boar activity may reflect a stronger imperative to return to dense, secure resting sites before full daylight, possibly driven by a greater sensitivity to human disturbance.

5.3. Seasonal and Interannual Plasticity in Activity Patterns:

The observed seasonal shifts may be interpreted in the context of both environmental conditions and the species' reproductive biology. The broadening of red deer activity into slight diurnal hours from October to December coincides with the post-rut recovery period for stags and increasing energetic demands for all individuals entering winter. Stags, having lost significant body condition during the autumn rut, must increase foraging time to survive the winter (Melletti and Focardi 2025). Conversely, the consolidation of wild boar activity into the nocturnal hours occurs as they enter their primary breeding season. This increased nocturnality may be driven by a combination of avoiding human disturbance from hunting and the energetic demands of mate-searching behaviour, which is often concentrated at night.

Although we compared just two consecutive years (as the 2024 CT season was highly irregular and thus was left out for more representative sampling), the still statistically significant interannual differences in activity may indicate that the temporal behaviours of these species are highly plastic and may respond to annual variations in environmental conditions or other unmeasured factors. It is also known that wild boar are more active during mast years, which 2023 has been verbally reported as earlier (Touzot et al. 2020; Shimada et al. 2024; Bisi et al. 2018). More detailed site-specific research is recommended for the future.

5.4. Correlation with Photoperiod

The strong correlation between evening activity and sunset for both species may suggest that sunset acts as a primary, reliable environmental indicator for initiating evening activity. The weaker and, in the case of red deer, statistically non-significant relationship with sunrise may suggest that the start of morning activity is governed by other factors. For wild boar, the weak but significant correlation suggests that sunrise acts as a constraint rather than a driver, forcing them to conclude their nocturnal activity and seek dense cover. For red deer, the start of morning foraging may be more influenced by overnight thermal conditions or the need to balance foraging with ruminating, rather than being strictly tied by sunrise itself.

A possible explanation of the sunrise variability is of hunting activity- as mentioned earlier, both species are hunted in the winter months beginning from Nov-Dec, and the hunting hours begin from sunrise and may go till dusk in these months, coinciding with the activity cessation periods for both species.

5.5. Study Limitations and Future Directions

While my study provides robust insights into the temporal ecology of red deer and wild boar, it is important to address the limitations, which also points to avenues for future research.

First, the study design involved a rotating panel of 11–12 cameras moved among a grid of 36 locations in discrete rounds. This means that not all sites were monitored simultaneously, and sampling effort was not uniform across all months. While our use of trap-rates standardises for effort, a study with continuous monitoring at all locations would provide more direct and representative evidence for the spatial redistribution of activity.

Second, my analysis of interannual variation was limited to two years (2022 and 2023), as the 2024 field season was severely disrupted by the exceptional flooding event. While the detected differences are statistically significant, a longer-term dataset would be needed to clearly distinguish trends from natural year-to-year variability.

Third, while the results demonstrate significant temporal patterns, we did not directly measure environmental variables that likely drive these behaviours. Future studies on this ecosystem and species could build upon this work by integrating fine-scale data on temperature, snow depth, and annual mast crop productivity to connect the influence of these factors from photoperiod.

Finally, some of the interpretations rely on the assumption that human disturbance (particularly hunting) is a major driver of movement behaviour. However, we lacked quantitative data on the daily timing and spatial intensity of hunting activities in the study site over our study period, as in the case of other studies like (Ahmed et al. 2024; van Doormaal et al. 2015; Drimaj et al., n.d.; Ohashi et al. 2013). Incorporating such human activity data into future models would allow a direct test of this hypothesis and provide a better understanding of the human-wildlife activity interface in this managed landscape.

Nevertheless, my thesis provides a detailed and valuable baseline of ungulate temporal plasticity in a unique European floodplain ecosystem.

6. Summary

Red deer (*Cervus elaphus*) and wild boar (*Sus scrofa*) are sympatric ungulate species in Central European forests, where understanding their temporal niche dynamics is important for both ecological research and effective wildlife management. While their general diel patterns are known, fine-scale behavioural plasticity, particularly in response to seasonal and annual environmental changes within dynamic floodplain ecosystems, remains poorly documented. This study aimed to quantify and compare the diel activity patterns of red deer and wild boar in Hungary's Gemenc floodplain forest, with a specific focus on evaluating their seasonal, interannual, and photoperiod-driven behavioural plasticity.

Data were collected over three autumn-winter seasons (2022–2024) using a systematic grid of motion-activated camera traps, following the standardised ENETWILD protocol. A post-hoc 30-minute independence filter was applied to the raw sequence data in R to generate a robust dataset for temporal analysis. Activity patterns were analysed using kernel density estimation, overlap coefficients (Δ_4), circular statistics (Watson-Wheeler test), and linear regression to address the study's four main objectives.

The results revealed a highly significant difference in the diel activity patterns between the two species ($p < 0.001$). Red deer exhibited a predominantly crepuscular pattern, while wild boar were strongly nocturnal. Despite these distinct peak activity times, the overall temporal overlap was high ($\Delta_4 = 0.82$, 95% CI: 0.79 - 0.86), indicating co-occurrence during transitional crepuscular hours. Both species demonstrated significant behavioural plasticity. Seasonally, the activity patterns of both species changed significantly from October to December ($p < 0.01$). This was seen by a broadening of the activity window into diurnal hours for red deer, while wild boar showed a trend towards more consolidated nocturnal activity. Contrary to expectations of reduced winter movement, overall trap rates for both species increased significantly in December. Furthermore, activity patterns for both red deer and wild boar differed significantly between 2022 and 2023 ($p < 0.001$), showing their capacity to respond to annual variations in environmental conditions. Finally, activity was strongly coupled with photoperiod; evening activity for both species was significantly correlated with sunset times ($p < 0.001$), whereas the relationship with sunrise was more varied.

In conclusion, this study reveals that red deer and wild boar in the Gemenc floodplain coexist through a combination of temporal niche partitioning and discernable behavioural plasticity. This flexibility in response to seasonal, annual, and photoperiodic cues suggests that their temporal behaviour is not fixed but is continuously shaped by energetic needs,

reproductive strategies, and (likely) avoidance of human disturbance. These findings have direct implications for evidence-based wildlife management, particularly for scheduling hunting activities and developing strategies to mitigate human-wildlife conflict.

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Comparative analysis of Camera Trap data to assess Red Deer and Wild Boar movement parameters in Gemenc area of Hungary

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Red deer (*Cervus elaphus*) and wild boar (*Sus scrofa*) are sympatric ungulate species in Central European forests, where understanding their temporal niche dynamics is important for both ecological research and wildlife management. While their general diel patterns are known, fine-scale behavioural plasticity, particularly in response to seasonal and annual environmental changes within the dynamic floodplain ecosystems, remains poorly documented. This study aimed to quantify and compare the diel activity patterns of red deer and wild boar in Hungary's Gemenc floodplain forest, with a specific focus on evaluating their seasonal, interannual, and photoperiod-driven behavioural plasticity.

Data were collected over three autumn-winter seasons (2022-2024) using a systematic grid of motion-activated camera traps, following the standardised ENETWILD protocol. A post-hoc 30-minute independence filter was applied to the raw sequence data in R to generate an appropriate dataset for temporal analysis. Activity patterns were analysed using kernel density estimation, overlap coefficients (Δ_4), circular statistics and linear regression to address the study's four main objectives.

The results revealed a highly significant difference in the diel activity patterns between the two species ($p < 0.001$). Red deer exhibited a predominantly crepuscular pattern, while wild boar were strongly nocturnal. Despite these distinct peak activity times, the overall temporal overlap was high ($\Delta_4 = 0.82$, 95% CI: 0.79-0.86), indicating co-occurrence during transitional crepuscular hours. Both species demonstrated significant behavioural plasticity. Seasonally, the activity patterns of both species changed significantly from October to December ($p < 0.01$). This was seen by a broadening of the activity window into diurnal hours for red deer, while wild boar showed a trend towards more consolidated nocturnal activity. Contrary to

expectations of reduced winter movement, overall trap rates for both species increased significantly in December. Furthermore, activity patterns for both red deer and wild boar differed significantly between 2022 and 2023 ($p < 0.001$), highlighting their capacity to respond to annual variations in environmental conditions. Finally, activity was strongly coupled with photoperiod; evening activity for both species was significantly correlated with sunset times ($p < 0.001$), whereas the relationship with sunrise was more varied.

In conclusion, this study reveals that red deer and wild boar in the Gemenc floodplain coexist through a combination of temporal niche partitioning and discernible behavioural plasticity. This flexibility in response to seasonal, annual, and photoperiodic cues suggests that their temporal behaviour is not fixed but is continuously shaped by energetic needs, reproductive strategies, and (likely) avoidance of human disturbance. These findings have direct implications for evidence-based wildlife management, particularly for scheduling hunting activities and developing strategies to mitigate human-wildlife conflict.

DECLARATION

Bhraaz Kashyap (student Neptun code: BN746G) as a consultant, I declare that I have reviewed the final thesis and that I have informed the student of the requirements, legal and ethical rules for the correct handling of literary sources.

I recommend / do not recommend¹ the final thesis / dissertation / portfolio to be defended in the final examination.

The thesis contains a state or official secret: yes no

Date: Gödöllő, 2025.11.10.



insider consultant

¹ The appropriate one should be underlined.

Declaration of Students and Doctoral Candidates on the Use of Artificial Intelligence (AI)”

1. general information:

Name of the student:	BHRAAZ KASHYAP
Neptun ID:	BN746G
Level of program (mark with X):	X BSc/BA <input type="checkbox"/> MSc/MA <input type="checkbox"/> Doctoral School (PhD) <input type="checkbox"/> Other:
Name and code of the subject*:	
Title of the work:	Comparative analysis of Camera Trap data to assess Red Deer and Wild Boar movement parameters in Gemenc area of Hungary

* Not required to be completed in the case of a doctoral dissertation.

2. Declaration on the Use of AI

I, the undersigned, fully aware of my ethical responsibility, make the following declaration:

(Please choose one of the options below!)

A) I have not used any artificial intelligence system or service.

(If you selected this option, completing the subsequent tables is not required.)

B) I have used an artificial intelligence system or service.

(Please fill in the relevant tables!)

3. Details of Artificial Intelligence Usage

TABLE I: Assistant or Minor Usage (e.g., translation, language proofreading, brainstorming, etc.)

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TABLE II: Significant Content Contribution (e.g., generating an entire figure or a longer text section)

(In these cases, documenting the key prompts used and the raw responses provided by the AI, and attaching them as an appendix to the work, is required.)

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For example: prohibition of AI use for certain types of tasks; only specific tools are permitted; different citation requirements; documentation format, etc.

Rules Prescribed by the Lecturer or Supervisor

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4. Declaration Applicable to All Students:

I declare that I have critically reviewed, edited, and incorporated any content potentially generated by AI in all cases. I take full responsibility for every element of the submitted work, including its originality and scientific validity. I acknowledge that the Hungarian University of Agriculture and Life Sciences may check the submitted work with an artificial intelligence detector and may initiate proceedings if my declaration is found to be false or incomplete.

Place and Date: Gödöllő, 2025. 11. 3.

.....

Signature of the Student

.....

Signature of the Advisor/Supervisor

MATE Organizational and Operational Regulations

III. Requirements for Students

III.1. Study and Examination Regulations

Appendix 6.13: The MATE Uniform Thesis /thesis / final thesis / portfolio guidelines

Annex 4.2: Declaration of public access and authenticity of the thesis/thesis/dissertation/portfolio

DECLARATION

the public access and authenticity of the thesis/dissertation/portfolio¹

Student's name: BHRAAZ KASHYAP _____
Student's Neptun code: BN746G _____
Title of thesis: **Comparative analysis of Camera Trap data to assess Red Deer and Wild Boar movement parameters in Gemenc area of Hungary**
Year of publication: 2025
Name of the consultant's institute: Institute of Wildlife Management and Nature Conservation
Name of consultant's department: Department of Wildlife Biology and Management

I declare that the final thesis submitted by me is an individual, original work of my own intellectual creation. I have clearly indicated the parts of my thesis or dissertation which I have taken from other authors' work and have included them in the bibliography. Furthermore, I declare that the artificial intelligence tools (e.g. text generation, linguistic correction, translation, data analysis) used during the preparation of the thesis did not substitute my own research and creative work; their use was indicated either in the list of sources or in the methodology section, and I acted in accordance with professional and ethical expectations.

If the above statement is untrue, I understand that I will be disqualified from the final examination by the final examination board and that I will have to take the final examination after writing a new thesis.

I do not allow editing of the submitted thesis, but I allow the viewing and printing, which is a PDF document.

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Student's signature

¹ While keeping the appropriate thesis type, all other types are to be removed.