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Plasticity in Diel Activity Patterns of Red Deer (*Cervus elaphus*) at Northern Latitudes: Across Intense Changes in Daylight Levels

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Ecology

Abstract

Understanding when animals are active is essential to comprehend their ecology fully, since time represents a vital, yet often overlooked, axis of a species' ecological niche. Diel activity patterns are among the most direct manifestations of this temporal niche in wildlife. However, in northern ecosystems, where daylight swings from near-constant daylight to near-constant darkness, there is limited knowledge about how wildlife adjusts their diel activity under shifting photoperiods. This is even more true when these changes coincide with anthropogenic pressures and different biological seasons. Therefore, I investigated the diel activity of red deer (*Cervus elaphus*) over an entire year on an island off the coast of Norway using a camera trap setup. Overall, red deer exhibited a clear and synchronized bimodal activity pattern — peak early and later in the day — across all demographics. However, in winter, when darkness dominates, diel activity becomes more evenly distributed patterns over 24 hours and increasingly nocturnal, with this shift emerging at the hunting onset. Additionally, these patterns varied by sex, age, and behavior, revealing high plasticity in red deer diel activity, driven by both light regimes and anthropogenic disturbances. Therefore, integrating temporal dynamics into conservation and management has the potential to mitigate problematic interactions between red deer and humans in northern regions, especially during periods of extended darkness (i.e., winter). Management needs to consider more continuous deer activity over a 24-hour cycle under decreasing daylight by regulating human access or implementing traffic regulations (e.g., reduced maximum speed) to reduce conflict and disturbance risks.

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Introduction

Understanding a species' ecological niche is essential to determine which habitats and spatial niches a species occupies in the ecosystem. Equally important, yet often overlooked, is the temporal dimension of that ecological niche (Frey et al. 2017; Gaston 2019; Hut et al. 2012; Kronfeld-Schor et al. 2003). Ecologically speaking, this concept of "when" an animal is active (i.e., physically moving or physiologically active), and how it uses its environment in time, is referred to as the temporal niche (Frey et al. 2017; Smarr et al. 2013). This temporal niche, rather than a binary diurnal or nocturnal classification, spans on a spectrum, including crepuscular temporal uses and even not preferences at all (Refinetti 2008). Additionally, the temporal niche is neither fixed across nor within species, nor constant within the same population (Cox et al. 2021; Refinetti 2008). It can even vary throughout and individual's lifetime, allowing a species to adapt its temporal niche in response to its ecosystem (Cox et al. 2021). The temporal niche hence reflects adaptive responses to environmental conditions (Refinetti 2008; Cox et al. 2021; Sánchez-Hernández et al. 2025).

Studying these patterns informs us about the physiological, ecological, and behavioral processes that govern part of species' survival and fitness (Refinetti 2008; Cox et al. 2021; Sánchez-Hernández et al. 2025). For example, mammals have evolved physiological and metabolic traits (e.g., endothermy, sensory systems, and homeostasis regulation) to support activity under different temporal regimes (Crompton et al. 1978; Riede et al. 2017; Sánchez-Hernández et al. 2025). These temporal niches are further modulated by the environment, including intra- and interspecific interactions (e.g., competition and predation) (Sovie et al. 2019; Vazquez et al. 2019; Takashi et al. 2021; Vallejo-Vargas et al. 2022). Optimizing activity timing thus constitutes a key adaptive strategy to mitigate risk and maximize fitness (van der Vinne et al. 2019).

To avoid these risk, temporal niche differentiation, both between and within species, enables coexistence by partitioning time as a resource, thereby reducing direct interactions, regulating community structure (Kelly 2008), and promoting biodiversity (Tan et al. 2013). Moreover, as species adapt their temporal niche in response to change, shifts in activity timing can serve as an indicator of ecological changes, including landscape alterations (Frey et al. 2017), seasonal cycles, and resource fluctuations (Jia et al. 2023). Therefore, studying the temporal niche can reveal ecosystem-specific dynamics and underlines which factors are at play.

A temporal niche can be examined at various scales, such as yearly, monthly, daily or even according to lunar phases (Hut et al. 2012; Bischof et al. 2024). However, the daily light cycle is a critical factor in shaping a species' adaptation to its environment (Hut et al. 2012). Thus, studying the temporal niche via diel activity (the distribution of activity over a 24-hour period) is an effective way to identify which factors shape species temporal use.

An essential aspect dictating diel activity in wildlife is the light regime (Hut et al. 2012; Refinetti 2008; Vazquez et al. 2019). In natural settings, the circadian system controls diel activity by integrating photic cues at dawn, day, dusk, and night (Riede et al. 2017). This system interprets these cues to regulate physiology and behavior (Brown et al. 2007; Dibner et al. 2010; Riede et al. 2017), thereby establishing daily routines necessary for survival (Riede et al. 2017). While the circadian system has been primarily under laboratory conditions, diel activity dynamics under naturally variable light regimes remain a gap in scientific knowledge (Riede et al. 2017).

In northern latitudes, where daylight variation across a year fluctuates greatly (Vazquez et al. 2019), offer a natural region for assessing how shift in light regime shape diel activity. What happens when, in extreme cases, there is 24 hours of daylight or night (i.e., no more light cues are available to regulate the diel activity and the circadian system)? Some studies have tried to answer this question with various results. Arctic rodents' diel activity patterns under midnight sun (i.e., 24 hours of daylight) maintained their 24 hours cycles of activity and rest (Folk et al. 2006), whereas laboratory experiments in the same conditions have shown extended activities period with longer than 24 hours cycles (Aschoff 1960). Other species have also been shown to adapt their temporal niche in response to longer or shorter days

(Boulos et al. 2005), such as the Eurasian lynx (*Lynx lynx*). This species has shown a change of diel activity patterns on a latitudinal gradient ranging from central Europe to Scandinavia (Heurich et al. 2014). In the northern regions, their activity peaks were less intense, and their bimodal activity patterns were more narrowed compared to southern individual (Heurich et al. 2014). However, this change was not only due to the direct effect of different light regimes, but also changes in their prey (e.g., roe deer (*Capreolus capreolus*) in the south, and reindeer (*Rangifer tarandus*) in the north) activity patterns influenced by the different photoperiod regimes along the latitudinal gradient (Heurich et al. 2014).

Cervidae indeed adjust their diel activity to their environment (Takashi et al. 2021; Proudman et al. 2021; Bonnot et al. 2020). In extreme photoperiods, reindeer rewire their circadian rhythms and activity patterns to the polar night or midnight sun (Arnold et al. 2018). Even at southern latitude, cervids modulate their temporal niche under moderate daylight changes (Pagon et al. 2013). Therefore, Cervidae can potentially adjust their diel activity patterns in northern latitudes, demonstrating behavioral plasticity (Ensing et al. 2014).

Diel activity also reveals adaptation strategies beyond light regime, but to its environment as well (Kronfeld-Schor et al. 2013). Seasonal variation in activity in northern mammals can arise from increased predation risk or differences in thermal constraints during continuous daylight (Bennie et al. 2014; Bleicher et al. 2019; Ikeda et al. 2016). Diel activity patterns are closely adapted to local conditions and species-specific adaptations, such as their physiology or feeding guild (Cox et al. 2021; Frey et al. 2017; Vallejo-Vargas et al. 2022). Therefore, combining abiotic (e.g. light regime) and biotic (e.g., species interactions) effects on the diel activity is essential to correctly assess a species' temporal niche (Frey et al. 2017).

Beyond light, diel activity patterns reveal details about a species intra- and interspecific interactions, unveiling the trade-offs an individual faces (Vazquez et al. 2019; Suselbeek et al. 2014; Vallejo-Vargas et al. 2022). When a species forage is indeed not just when daylight and resource are available, but they need to consider also the potential moment when competition is most intense and predation is most likely (Vazquez et al. 2019; Suselbeek et al. 2014; Vallejo-Vargas et al. 2022). For example, predation pressure can promote nocturnality (Cox et al. 2021; Sovie et al. 2019; Vallejo-Vargas et al. 2022; van der Vinne et al. 2019). Alternatively, a predator can time its activity to peak during the day, when its prey is active, and avoid its own predators, who are active at night (Bischof et al. 2014). Understanding diel activity thus provides insight into how activity patterns overlap among species in an ecosystem and how they time their activity differently to avoid costly situation (e.g., more competition or predation risk) (Ridout et al. 2009; Vallejo-Vargas et al. 2022).

More intrinsic factors, such as sex, age, energy resources, physiological characteristics, and metabolism also influence diel activity (Cox et al. 2021; Crompton et al. 1978; Riede et al. 2017; Sovie et al. 2019; Vallejo-Vargas et al. 2022; van der Vinne et al. 2019). Yet recent surges in human-caused disturbances (e.g., roads, habitations, and farming activities) threaten to affect an organism’s precise temporal niche out of sync with its environment (Gaynor et al. 2018; Menichetti et al. 2019; Pfeiffer et al. 2020; Gallo et al. 2022). Humans frequently intrude into wildlife habitats, leading to conflicts and challenges (Manfredo 2008). Increasing outdoor recreational activities, such as hiking, further modulated a species diel activity (Larson et al. 2016; Marion et al. 2021). In addition, rising light pollution as well (Cox et al. 2021; Gaston et al. 2015) is another example of anthropogenic activities influencing the diel activity of wildlife, especially knowing how crucial light regimes are for temporal niches (Ensing et al. 2014).

Certain species are more at risk of anthropogenic activities’ influence, like Cervidae since they are often observed interacting with anthropogenic activities (Carpio et al. 2021; Menichetti et al. 2019). Additionally, they are game species, ranking even among Europe's most hunted species (Abrantes et al. 2023), and hunting further alters their temporal niche by potentially making them more nocturnal (Espinosa et al. 2017; Gaynor et al. 2018; Proudman et al. 2021). Given the many intrinsic and extrinsic drivers of cervid diel activity, especially light regimes, there is a need to quantify their relative effects to better understand Cervidae temporal niche plasticity.

Cervids are therefore ideal models for northern ecosystems diel studies, and red deer (*Cervus elaphus*) in particular are known to adjust their diel activity in response to photoperiod changes (Ensing et al. 2014). Yet red deer temporal niche remains not fully examined in high latitude regions. In addition, anthropogenic changes can also mold red deer diel activity (Fattebert et al. 2019; Richter et al. 2020). These pressures, such as agricultural conflicts, road accidents, and forestry disruptions (Carpio et al. 2021; Comte et al. 2022; Duarte et al. 2015), are rising alongside growing red deer population in Europe, even subject to overabundance (Carpio et al. 2021; Solberg et al. 2022). Altogether, these increasing trends threaten to lead to more negative red deer and human interactions. In this context, a better understanding of red deer diel activity can help inform effective management strategies to mitigate these potential conflicts (Carpio et al. 2021; Comte et al. 2022; Duarte et al. 2015). Therefore, studying red deer diel activity in northern latitude, where intense shifts in daylight coinciding with anthropogenic pressures, provides important insights into how these drivers shape red deer temporal niche plasticity. One problem remains: How can wildlife be studied continuously over a certain period without disturbances.

Continuous, low intrusion observations across space and time remain indeed challenging, leaving diel activity's knowledge limited as a consequence (Rowcliffe et al. 2014). Recently, new methods, such as GPS tracking and camera trapping, have emerged as valuable tools to capture these temporal patterns in relatively undisturbed natural settings (Rowcliffe et al. 2014; Vazquez et al. 2019; Frey et al. 2017), with camera traps offering truly constant 24-hour sampling and minimal disturbance on wildlife (Frey et al. 2017). Long-term, large-scale camera trap studies, — ranging from cryptic predators to cervids, even across continent — demonstrates its power for quantifying temporal niches (Bischof et al. 2014; Bischof et al. 2024; Farris et al. 2015; Vallejo-Vargas et al. 2022; Devarajan et al. 2025). Furthermore, camera trapping can collect observations of multiple species across time and space, yielding comprehensive insights into temporal patterns of specific species (e.g., red deer) across different latitudes (Devarajan et al. 2025). Camera trapping is especially suited to remote or low accessibility regions (Jia et al. 2023), as in northern latitudes where winter limits accessibility (Marchand 2014). Therefore, implementing an extensive and strategically deployed camera trap network holds immense potential for advancing the understanding of red deer temporal niche plasticity in northern ecosystems (Frey et al. 2017; Caravaggi et al. 2017).

Objectives

Here, this study aims to enhance our knowledge of *C. elaphus* diel activity at northern latitudes on an island off the west coast of Norway. To achieve this, a camera trap setup recorded red deer diel activity continuously over an entire year. The main objectives were to

1. Quantify how red deer diel activity varies with changes in lighting conditions across season, demographic category, and behavior,
2. Examine differences in diel activity in relation to the hunting season, and
3. Assess the overlap in diel activity patterns among demographic groups throughout the year.

Red deer activity diel patterns are predicted to change throughout the year, with lower activity levels during the day in winter, when harsh conditions and extended darkness limit daylight activity (Clutton-Brock et al. 1982; Ensing et al. 2014). Furthermore, because red deer activity is triggered by direct light cues, rather than by an internal circadian rhythm, a bimodal pattern (peaks around dawn and dusk) is expected whenever there is a clear light–dark transition (Ensing et al. 2014; Pagon et al. 2013). Conversely, under longer darkness period with no sharp transition (i.e., in winter), red-deer diel activity patterns are predicted to lose their bimodal activity pattern between individual, and should become more desynchronized, irregular and arrhythmic (Ensing et al. 2014).

I also predict that the hunting season increase nocturnality (Chassagneux et al. 2019; Sunde et al. 2009), and reduce foraging activity during daylight due to heightened vigilance (Benhaiem et al. 2008; Jayakody et al. 2008; Proudman et al. 2021). Red deer, males in particular, are expected to shift time invested in foraging to rutting behaviors, during daylight as hunting overlaps with the rut (Clutton-Brock et al. 1982).

Finally, activity overlap patterns are anticipated to be synchronize for most of the year between demographics (Pagon et al. 2013). Adults females and males diel activity is predicted to overlap during the rut since males keep harem of females (Clutton-Brock et al. 1982), while female and juveniles overlap is expected to be important during calving when juveniles are dependent of their mother. (Clutton-Brock et al. 1982).

Methods

Study area

The study was conducted in Vestland County, Norway, on an island named Svanøya (61.48730° N; 5.09369° E) in the Kinn municipality (Fig. 1). On the island, the light regime varies from 5.3 hours of daylight and 16.5 hours of darkness in winter, to 19.5 hours of daylight and 0 hours of darkness in summer. Svanøya is approximately ten square kilometers in size and situated about five kilometers from the mainland. The red deer population on the island consists of around 100 to 140 individuals (J. A. Stavang, personal communication, 1 May 2025). Therefore, this site is ideal for studying red deer, as it has a dense deer population and is a more closed system than the mainland. However, it is important to state that Svanøya is not a completely closed system, as *C. elaphus* are known to swim between islands and even occasionally to the mainland. The winter season on the island is typically mild, with little snowfall. In the winter of 2024, minimal snow was present on the island for approximately one month, from January 15 to February 15.

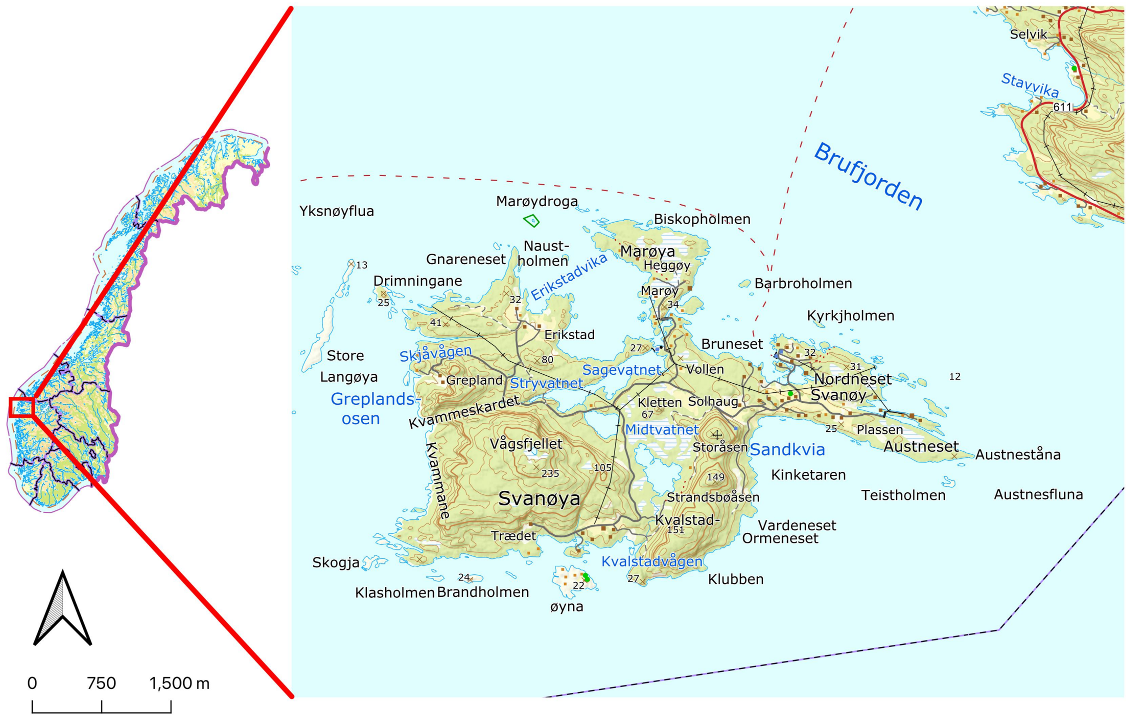

Figure 1: The small map on the left shows Norway, while map on the right indicates the location of the study site, the island of Svanøya, five kilometers away from the mainland and the nearest town being Florø. The base layer of the map is "Kartdata 3" from: http://wms.geonorge.no/skwms1/wms.kartdata3.

The island features, despite its relatively small size, diverse habitats, including several mires, coniferous and mixed woodland forests, coastline, open areas, lowlands, infield pastures and hills, with the highest point reaching 235 meters. Vegetation on the island consists mainly of Scots pine (*Pinus sylvestris*), with areas of Norway spruce (*Picea abies*) plantations. There are also some deciduous trees such as holly (*Ilex aquifolium*), hazel (*Corylus avellana*), and birch (*Betula* species). The understorey includes shrubs such as bilberry (*Vaccinium myrtillus*), heather (*Calluna vulgaris*), and juniper (*Juniperus communis*). There is also some non-native species like the Sitka spruce (*Picea sitchensis*). Additionally, three main bodies of water are located around the middle of the island (Fig. 1). Svanøya is home to approximately 50 human residents, with the main industries being cattle (*Bos taurus*) and sheep (*Ovis aries*) farming in the northwestern part of the island (Erikstad), free roaming goats (*Capra hircus*), and a salmon fish farm near the Marøya region (Fig. 1). There are also six red deer enclosures, for a total of 0.45 km^2 and approximatively 60 deer and around 30 calves by summer (J. A. Stavang, personal communication, 1 May 2025), located near the southern area of the island (Fig. 1). The island also has a no-hunting zone in the southwestern region, which acts as a refuge for the deer during the hunting season. Finally, there is no red deer predators, outside of humans, on the island.

Camera trap survey

To study the diel activity patterns of *C. elaphus*, a camera trap survey was initiated on Svanøya in January 2024. For this purpose, the island was divided into 250 by 250 meters grid cells. 66 camera traps were placed across the island according to these grid cells, with a maximum of one camera per grid cell (Fig. 2). The placement of cameras within each grid cell was determined accordingly to the traditional ecological knowledge (TEK) of the Norwegian red deer center staff to maximize the likelihood of capturing images of red deer. No lures were used to attract red deer, and data from January 2024 to February 2025 were analyzed, covering a complete year.

The cameras were positioned to accurately represent the diverse habitats on Svanøya and encompass various scenarios (e.g., edge to pastures, clearings in the forest, forest or water holes) (Fig. 3). Information on site location (i.e., longitude and latitude) was recorded for each camera trap site, but also information about the local habitat, terrain, camera orientation and height, impact on vegetation, and elevation.

The study employed four camera trap models: DarkOpsHDPro BTC-6HDPX, DarkOpsHDPro BTC-6HDP, DarkOpsHDPro BTC-PXD, and SpecOpsFullHD. The cameras were manufactured by the “Browning Trail Camera” company located in Morgan, Utah, in the United States of America. Each unit was an infrared-triggered camera (i.e., infrared flash), and was configured to the correct date, set to capture three rapid-fire photographs with a five-second delay between each burst of pictures. Every three to four months, SD cards from the camera were retrieved for analysis and replaced with empty cards. During these check-ups, batteries were also checked and replaced as needed.

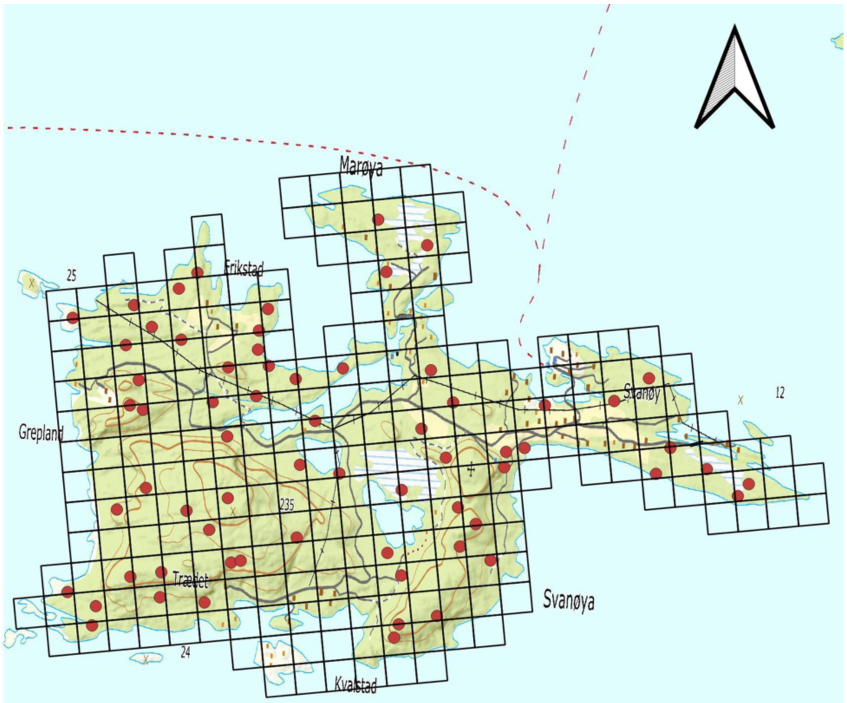

Figure 2: Map representing the study area, Svanøya island, showing the 250 by 250 meters grid cells. Red dots indicate the location of the 66 camera traps deployed. The base layer of the map is "Kartdata 3" from: http://wms.geonorge.no/skwms1/wms.kartdata3.

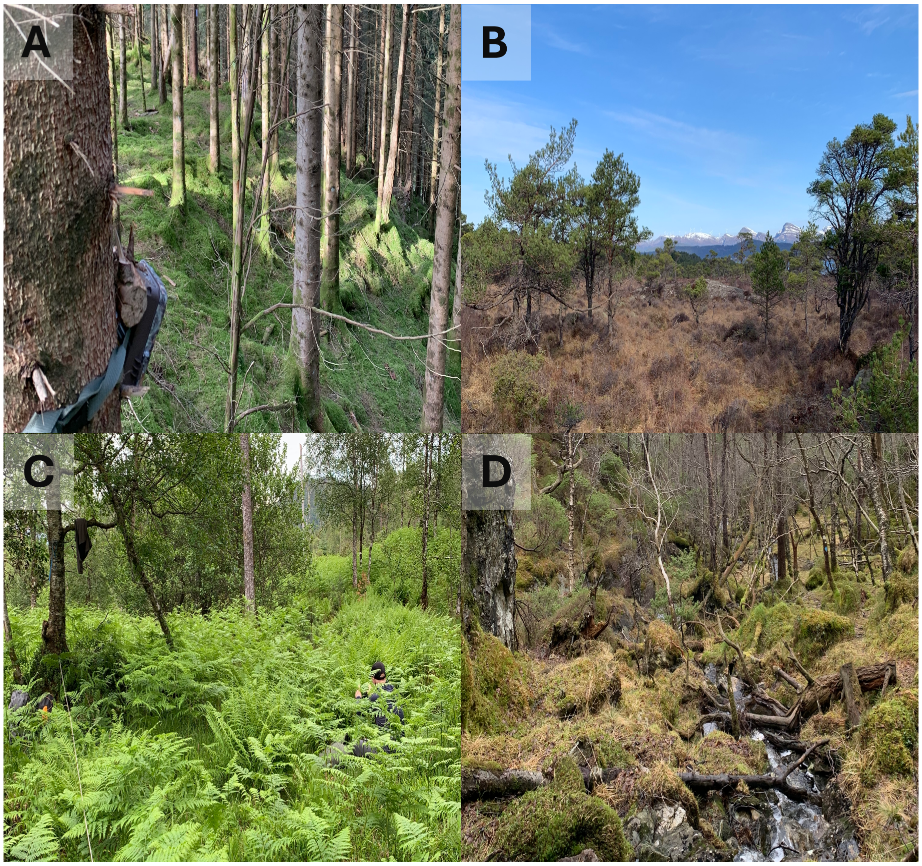

Figure 3: Series of pictures exemplifying different terrains and habitats for a camera trap location. The pictures represent **A** a Norway spruce plantation on a hillside, **B** a mire site on top of a hill, **C** an open

area covered in ferns in a flat lowland, and **D** a site near a small stream in a mixed forest. Photo credit: Thomas Leathead

Data collection and preparation

All pictures were uploaded to the Agouti website (https://www.agouti.eu) for filtering and species identification. The website utility was to synthesize pictures corresponding to one series of the same «moment» of the camera trap recording. Human observers then proceed to identify the species present and the number of individuals in each series of pictures.

During this review process, the sex and age of the red deer were noted. Subadults correspond to individuals between one year old and two year old, whereas juveniles were the ones under one year old. The fur and the deer size were the main techniques used to differentiate between both subadult and juvenile. Juveniles were the smallest with white dots on their fur (Fig. 4). Subadults had an uncompleted patchy fur without white dots and were smaller than adults (Fig. 4). The sex of juveniles and subadults were not identified since it was impossible to tell with only the picture if it was a male or a female. To differentiate adult females from adult males, the antlers were the key differences. Males had antlers (or visible pedicles if the antlers had fallen), and thicker necks, whereas female had no antlers and smaller necks (Fig. 4). Observations where the sex of adults was not identifiable were removed since that information was needed for analysis. Same applied for observations where the age of individual was not available.

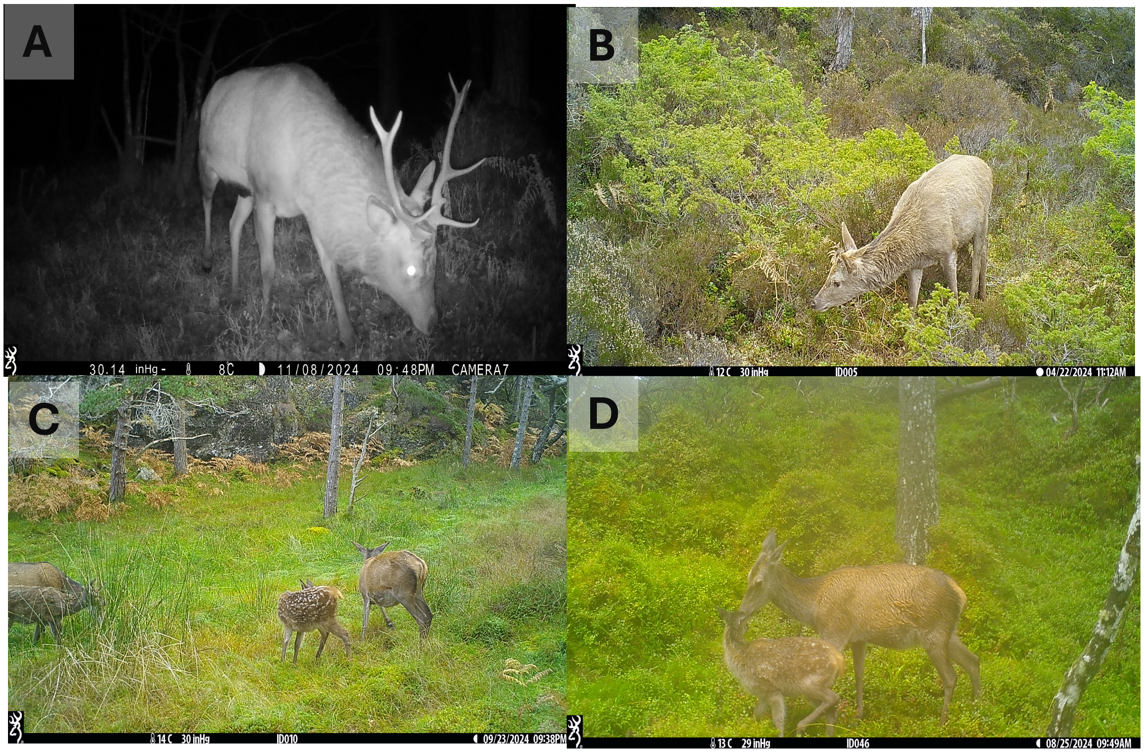

Figure 4: Series of picture representing the different categories of red deer sex and ages. Pictures represent **A** a male adult with antlers and a thick neck, **B** a subadult with incomplete fur, **C** a female adult and a subadult with incomplete fur on the left, and a female adult and a juvenile with white dots on its fur on the right, and **D** a female adult (no antlers), and a juvenile with white dots on its fur. Photo credit: Project DeerLab/NMBU

The behaviour of the deer, such as grazing, browsing, nursing or simply resting, was also recorded. Grazing corresponded to when a deer was foraging on grasses and herbs at ground level, whereas browsing corresponded to when a deer was feeding on trees, shrubs or heathers (Fig. 5). If it was not possible to identify if the deer was feeding on herbs or dwarf shrubs (e.g., bilberry), both grazing and browsing were selected as behavior (Fig. 5). The deer was considered to be resting when it was lying on the ground with little to no movement for multiple pictures (Fig. 5). In the end, a spreadsheet was generated and exported where each row corresponded to one sequence of pictures (i.e., one moment of activity), and its annotation (i.e., species, date, time, behaviours, etc.). Observations when the identified behavior was «resting» were removed from the analysis since the goal was to identify activity.

Figure 5: Series of picture representing the different categories of red deer behaviors. Pictures represent **A** a male adult resting, **B** a juvenile and a female adult grazing, **C** a female adult and a subadult identified as browsing and grazing since it was not possible to determine if they were feeding on herb or bilberry, and **D** a male adult browsing on a tree. Photo credit: Project DeerLab/NMBU

Seasons were determined based on biological and anthropogenic events: winter (December to February), growing season (March to May, i.e., spring), calving season (June to August, i.e., summer), and hunting season (September to November, i.e., rutting and fall) (Fig. 6). Even though there were some hunting events in December, since it was a very small amount and ended in the middle of the month, it was considered a winter month, in order to have three months of data in each category. (Fig. 6) Two additional ten-day periods were defined as: before the hunting season onset (August 22 to August 31), and after the hunting season onset (September 1 to September 10).

All behaviors were categorized into one variable with two levels: when there is foraging (i.e., grazing and browsing) or all the other behaviors (e.g., running, wallowing or nursing). Finally, the sex and age of each red deer identified were classified into a variable with four categories representing a priori identification: female adult, male adult, subadult, and juvenile.

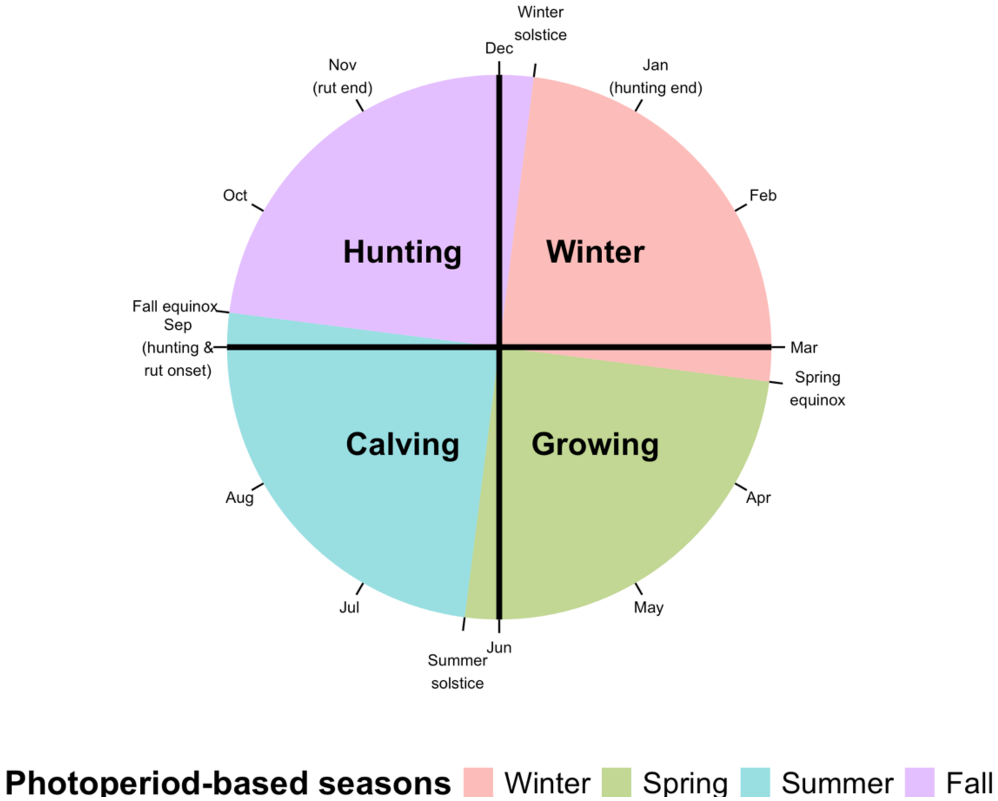

Figure 6: Diagram showing important event and various stage of a red deer life during a year. The main seasons used for analysis are represented in bold in their respective quarter: winter (from December to March), growing (from March to June), calving (from June to September), and hunting (from September to December). Around the circle each month are identified with their abbreviations, and more precise information about the hunting and rut period. Important solar events are also identified around the circle: the winter solstice (day with the less amount of daylight), the spring equinox (around 12 hours of daylight), the summer solstice (day with the most amount of daylight), and the fall equinox (around 12 hours of daylight). The different colors represent the actual photoperiod-based seasons (i.e., winter from the winter solstice to the spring equinox, spring from spring equinox to the summer solstice, summer from the summer solstice to the fall equinox, and fall from fall equinox to the winter solstice).

To represent the diel activity of *C. elaphus*, a «time of day» categorical variable with four levels was then produced. The four levels were dawn, day, dusk and night, representing the full light spectrum in a 24-hour period. The detection (i.e., a sequence of picture taken by a camera trap) was used as a proxy for activity. To accomplish so, the packages «suntools», «suncalc», and «lubridate» in R were used (Grolemund et al. 2011; Bivand et al. 2023; Thieurmel et al. 2019). The sun altitude was then extracted to associate each observation with a period of the day (i.e., dawn, day, dusk and night). The duration of each of these four periods was also extracted to then create an «exposure» variable in hours since the amount of day and night vary substantially throughout the year (ranging from 0 to 16.55 hours of night and from 5.35 to 19.50 hours of day). All the following statistical analysis was realized in R software version 4.3.2 (R Core Team 2023).

Statistical analysis

Red deer diel activity throughout the year

To observe which intrinsic and extrinsic factors were influencing the timing of the red deer activity a multinomial model was generated, using the VGAM package in R (Yee 2017; Yee 2010). The response variable was the period of the day where the activity occurred (i.e., dawn, day, dusk or night). An offset was also added to the model to correct for the varying amount of daylight throughout the year in northern latitudes. The offset corresponded to the logarithm of the exposure variable. Moreover, site-specific variation in camera placement may affect activity patterns and is usually accounted for through random effects in camera trap models (Comte et al. 2022; Ikeda et al. 2021; Vallejo-Vargas et al. 2022). However, random effects were omitted because standard multinomial models cannot accommodate both random effects and an offset, implementing this would require custom models (e.g. Bayesian), which are beyond this study's scope. The offset for varying daylight was prioritized because the main goal of this research is to observe the effect of light regimes.

Different candidate models were built with the most complex one containing the demographic category (i.e., female adult, male adult, subadult or juvenile), the behavior (i.e., foraging or other behaviors as described earlier), the season (i.e., winter, growing, calving or hunting), the interaction between the demographic category and the season, the interaction between the demographic category and the behavior, and the interaction between the foraging behavior and the season. There was a total of 18 different models created (Table S1). The best model was then selected using the Akaike Information Criterion (AIC) (Burnham et al. 1998). After comparison, all models within a $\Delta AIC < 2$ were considered as a possible option for analysis (Burnham et al. 1998). Finally, the 95 % confidence interval of the predicted probability of being active during a certain diel period was calculated by using bootstrap resampling with 500 iterations in the «boot» library (Canty et al. 2017). In other words, original observations were resampled 500 times with replacement, and the model was refitted on each bootstrap sample (i.e., resampling) to generate predicted values. These predictions were then used to compute the 95 % confidence intervals.

The effect of the hunting season on the red deer diel activity

To better understand the impact of the hunting season, two ten-day periods were used. As explained before, one was representing before, and one after the onset of the hunting season (1 September). Once again, multinomial models, with the diel period as the response variable and the «exposure» offset to correct for the varying availability of darkness, daylight, and twilight, were created using the VGAM package (Yee 2017; Yee 2010). Site-specific random effects were once more ignored for the reason explained before. Different candidate models were built with the most complex one containing the demographic category, the behavior (i.e., foraging or other behavior), the hunting period (i.e., before or after the onset of the hunting season), the interaction between the demographic category and the hunting period, the interaction between the demographic category and the foraging behavior, and the interaction between the foraging behavior and the hunting period. There was a total of 18 different models created (Table S5). Once again, to select the best model of the set, an AIC model selection method was used (Burnham et al. 1998). After the comparison, models within a $\Delta AIC < 2$ were considered as an option for analysis (Burnham et al. 1998). Lastly, with the help of a bootstrap sample with 500 iterations in the «boot» library, a 95 % confidence value of the predicted probability of being active during a certain period of the day was calculated (Canty et al. 2017).

Overlap between red deer diel activity

To capture not only shifts in red deer diel activity patterns across diel period but also to observe changes in activity profiles over a 24-hour cycle, a separate analysis of kernel density distributions of camera trap detections (i.e., activity) was estimated over 24 hours. These density estimates were computed by demographic category, season and foraging behavior. The advantages of the kernel density estimation over multinomial model are that it offers a smooth and continuous curve of activity levels. It provides more detailed information about the shape of the activity profile over a 24-hour period (Węglarczyk 2018), whereas a multinomial model uses discrete category (e.g., dawn, day dusk and night), lacking nuance and small precision by using general grouping. Although kernel density curves cannot be directly compared quantitively since there is no incertitude, they still remain a valuable tool for visualizing qualitatively temporal patterns.

To compare the difference in overlaps between the demographic categories across seasons and behaviors, the coefficient of overlap (ΔDhat4) and its 95 % confidence interval were calculated using the overlap package (Meredith et al. 2013; Ridout et al. 2009) (Table S5). The 95 % confidence interval was calculated using a bootstrap sample with 500 iterations (Canty et al. 2017). The same was also done (i.e., kernel density figure and ΔDhat4 estimations) to observe differences in overlap of activity patterns ten days before and ten days after the onset of the hunting season, but without including demographic category (Table S6).

Results

The data were collected over a full year on Svanøya island, Norway. A total of 66 camera traps were active, covering most of the island. On average, each camera recorded 155 (SD = 162) sequences of pictures, with a minimum of 9 and a maximum of 744 sequences.

In total, there was 10 217 observations (i.e., picture sequences) of red deer across all cameras, distributed by season, behavior, and demographic category (Table 1). Specifically, there were 882 observations from the juvenile demographic category, 871 from the subadult, 6731 from the female adult, and 1733 from the male adult demographic (Table 1). Of all sequences, there were 3336 capturing deer foraging, and 6881 capturing other behaviors (Table 1). By season, there was 1325 observations in winter, 2190 in the growing season, 4189 in the calving season, and 2513 in the hunting season (Table 1). Across diel periods, there were 794 sequences at dawn, 5931 during daylight, 2140 at dusk, and 1352 at night. Finally, the duration of diel periods varied seasonally: dawn and dusk ranged from 0.72 to 2.28 hours, daylight from 5.35 to 19.50 hours, and night from 0 to 16.54 hours.

Table 1. Contingency table representing camera trap picture sequences over one year, by demographic category (juvenile, subadult, female adult or male adult), season (winter, growing, calving or hunting), and behavior (foraging or other).

Demographic category	Winter		Growing		Calving		Hunting	
	Foraging	Other	Foraging	Other	Foraging	Other	Foraging	Other
Juvenile	15	33	4	13	39	620	16	142
Subadult	26	110	130	134	45	199	59	168
Female adult	368	609	858	726	854	1842	458	1016
Male Adult	42	122	131	194	176	414	115	539

Red deer diel activity throughout the year

Using year-round camera trap data from *C. elaphus* on Svanøya island, I studied their diel activity patterns and their determinants. After comparing the 18 candidate models, two models fell within a ΔAIC < 2: M1 (diel period ~ demographic category + behavior + season + demographic category*season + behavior*season) and M2 (diel period ~ demographic category + behavior + season + behavior*season) (Table 2, S1). The only additional term in M1 was the interaction between demographic category and season (Table 2). Although, when examining this term, only one of the 27 level of the interaction was statistically significant (Table S2). Thus, retaining that interaction added complexity without clearly improving the model fit. For simplicity and interpretability, I therefore selected M2 since the simple formulation captured all the effect with minimal parameters, facilitating ecological inference (Table 2).

Table 2. The top five multinomial models ranked by ΔAIC values explaining the variance in the diel period (dawn, day, dusk or night) probability of a red deer being active over an entire year. The three possible predictors were the demographic category (juvenile, subadult, female adult or male adult), the season (winter, growing, calving or hunting), and the behavior (foraging or other). All models included an offset variable representing the amount of hour available for the corresponding diel period. Data are from 66 camera traps on Svanøya island, Norway.

Model	Formula	AIC	ΔAIC
M1	Diel period ~ demographic category + behavior + season + demographic category*season + behavior*season	23668.04	0.00
M2	Diel period ~ demographic category + behavior + season + behavior*season	23668.05	0.01
M3	Diel period ~ demographic category + behavior + season	23670.47	2.43
M4	Diel period ~ demographic category + behavior + season + demographic category*season	23671.21	3.17
M5	Diel period ~ demographic category + behavior + season + demographic category*behavior + demographic category*season + behavior*season	23672.42	4.38

In that model selected (M2; Table 2), all comparisons are made relative to the reference level: juveniles red deer demographic not foraging during winter and active at night.

Overall, the probability of this baseline being active at dawn (estimate = - 2.52, $p < 0.001$), day (estimate = - 1.61, $p < 0.001$), or dusk (estimate = - 2.15, $p < 0.001$) was significantly lower than at night (Table S3). Compared to the juvenile demographic baseline, subadults, female adults, and male adults were less likely to be active during the day in winter, with the most pronounced effect in the male demographic (estimate = - 1.39, $p < 0.001$) (Table S3). Seasonal changes had positive significant effects on the probability of being active across all diel periods for the reference group: activity probability at dawn, day, and dusk during the growing, calving and hunting seasons was consistently higher than the probability of being active at night in winter (Table S3). Although the effect of foraging alone did not significantly alter activity patterns of the reference group, its interaction with season revealed notable effects (Table S3). Within the hunting season, foraging behavior reduced the odds of being active during day (estimate = - 0.66, $p < 0.01$) and dusk (estimate = - 0.64, p

<0.01) compared to non-foraging behavior at night across all demographics (Table S3).

To help visualized results, predictions and their 95 % confidence interval were extracted (Fig. 7 and Table S4). The offset value used for the predictions was the average value of «exposure» across the data analyzed, so 11.15 hours. Confidence intervals was greater for juveniles than for the other demographics, probably due to lower sample size (Fig. 7)

Overall, all four demographic categories tended to follow the same trend: more probable to be photographically captured (i.e., probability of being active) at day, following by dusk, then dawn, and minimal probability at night (Fig. 7). However, in winter, a different diel activity pattern emerged (Fig. 7). It still seemed probable for a deer to be active during the day, but that daily probability was the smallest of all seasons (Fig. 7). In winter, it was even similarly possible for a deer, when doing something else than foraging, to be active no matter the period of the day (i.e., the probability of being active at dawn, dusk and night increased, while the one for the day decreased) (Fig. 7). For example, male adult deer in the calving season when not foraging (i.e., other behaviors) had a 77 % (CI: 74 % - 79 %) chance of being active during the day whereas in winter it was only 32 % (CI: 27 % – 36 %) (Fig. 7). In the same conditions, the probability of nocturnal activity on the other hand increased by almost 35 % for males between the calving and the winter season when not foraging ($p_{calving}$ = 0.2 %, CI: 0 % - 0.4 %; p_{winter} = 36 %, CI: 29 % - 44 %) (Fig. 7). In addition, in winter, juveniles tended to be 50 % likely to be active during daylight, whereas other demographic that odd was around 35 % (Fig. 7)

During the hunting season, the probability of deer being active during the day did also decrease and the one for dawn and night increased as a consequence in all demographic categories compared to the growing and calving season (Fig. 7). For example, female adults when not foraging were 7 % less likely to be active during the night in the growing season (p = 1 %, CI: 0% - 2 %) than during the hunting season (p = 8 %, CI: 7 % – 10 %) (Fig. 7). Additionally, males tended to be more active at night then other demographics when foraging: 5 % more likely than female demographics, 8 % more than subadult and 12 % more than juveniles (Fig. 7).

While looking at differences between foraging and the other behaviors, they were not significant across all diel period, meaning no matter if feeding or doing something else, the deer were following the same diel activity patterns over a year (Fig. 7 and Table S4). However, in the hunting season, the difference between day and night activity probability was smaller when foraging than when red deer were having other behaviors. For example, the difference in probability between males foraging at night ($p_{hunting}$ = 18 %, CI: 13 % – 24 %) and at day ($p_{hunting}$ = 50 %, CI: 45 % – 54 %) was of 32 %, whereas when not foraging that difference was 40 % (Fig. 7).

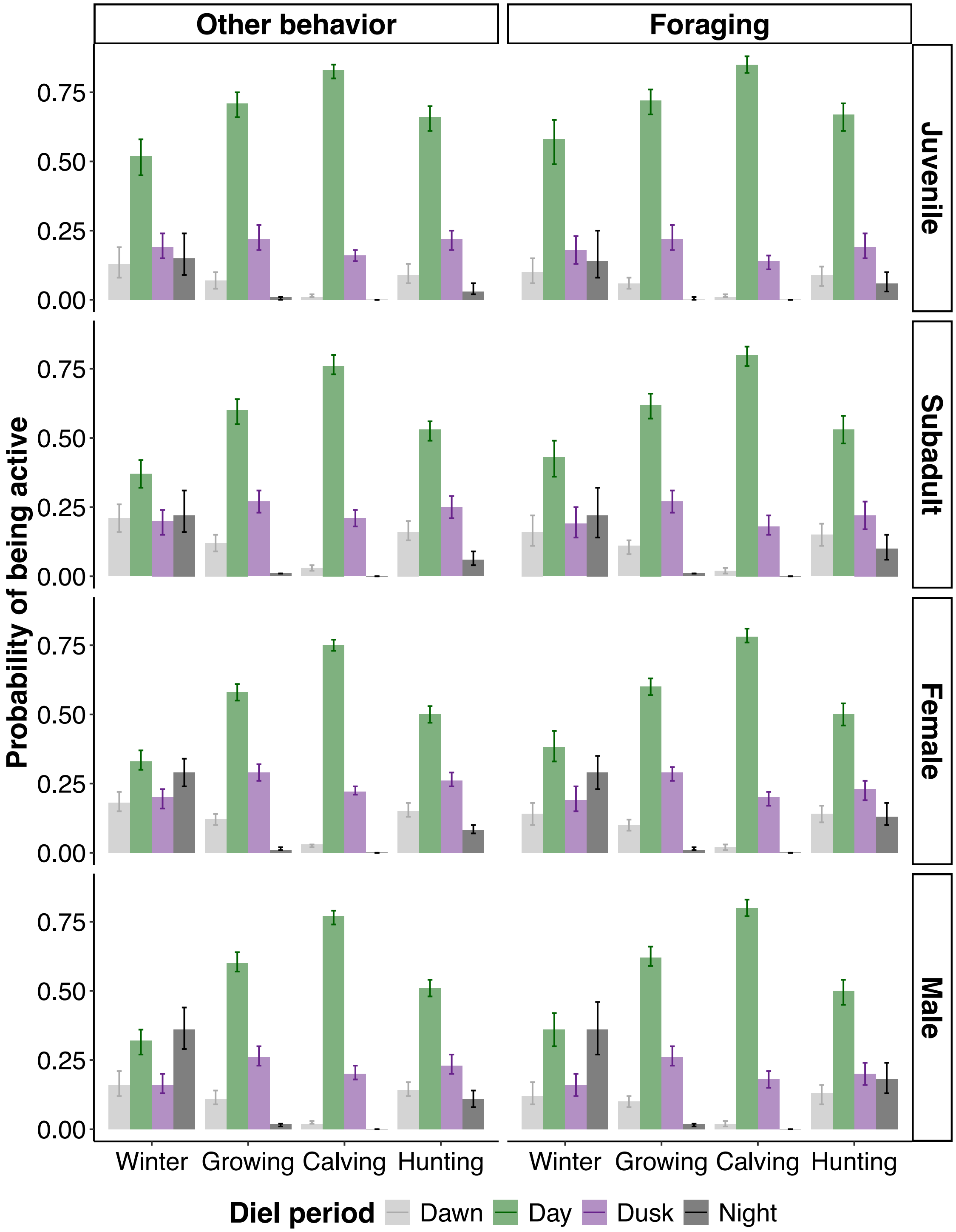

Figure 7 Differences in diel activity pattern of *C. elaphus* over a year on an island off the west coast of Norway, Svanøya, represented by their probability of being active in four different diel period (i.e., dawn, day, dusk and night). These patterns were represented by different demographic categories (juvenile, subadult, female adult or male adult), behavior (foraging or other) and seasons (winter: December - February, growing: March - May, calving: June – August, or hunting: September – November). The 95 % confidence interval of each probability is also included as error bars. An offset of 11.15 hours was used to correct for the varying amount of daylight during the study period (01/2024 to 02/2025). Data are from 66 camera traps.

The effect of the hunting season on the red deer diel activity

To assess the effect of the hunting season on red deer diel activity, the data were divided into two periods: before and after the onset of hunting season. Among the 18 candidate models, only one model (MH1) had a ΔAIC < 2 (Table 3, S5), indicating it was the best possible model. This model was therefore used for further analysis. It included only behavior and hunting period as predictors of diel period (diel period ~ behavior + hunting period) (Table 3).

Table 3: The top five multinomial models ranked by ΔAIC values explaining the variance in the diel period (dawn, day, dusk or night) a red deer is likely active around exclusively the hunting onset of 1 September (study period ranging from 21/08/2024 to 10/09/2024). The three possible predictors were the demographic category (juvenile, subadult, female adult or male adult), the hunting period (before or after), and the behavior (foraging or other). All models included an offset variable representing the amount of hour available for the corresponding diel period. Data are from 66 camera traps on Svanøya island, Norway.

Model	Formula	AIC	ΔAIC
MH1	Diel period ~ behavior + hunting period	1472.147	0.00
MH2	Diel period ~ demographic category + behavior + hunting period	1476.477	4.33
MH3	Diel period ~ behavior * hunting period	1477.528	5.38
MH4	Diel period ~ demographic category + behavior + hunting period + demographic category* hunting period	1480.808	8.66
MH5	Diel period ~ demographic category + behavior + hunting period + behavior*hunting period	1481.994	9.84

The reference baseline in the selected model (MH1; Table 3) was a deer not foraging after the onset of the hunting season (Table S6). Under these conditions, the probability of deer being active at dawn was significantly lower than at night (estimate = - 0.59, $p < 0.05$), whereas daytime activity probability was higher than nighttime probability (estimate = 0.60, $p < 0.01$) (Table S6). Foraging behavior alone did not significantly affect diel period, indicating whether deer are foraging or not, similar patterns are expected (Table S6). By contrast, during the period before hunting began, deer were significantly more likely to be active at day (estimate = 1.33, $p < 0.01$) and dusk (estimate = 0.81, $p < 0.05$) compared to the post-hunt night activity probability (Table S6).

To help visualized results, predictions and their 95 % confidence interval were extracted (Fig. 8 and Table S7). The offset value used for the predictions was the average value of «exposure» across the data analyzed, so 9.70 hours.

This time, each demographic category had the same diel activity pattern during 20-day period around the hunting offset, indicated by the model not having demographic category was a predictor (Table 3, S6).

On the other hand, when focusing on the hunting period (i.e., before or after the onset of hunting), a small decrease in day activity, in concordance with an increase in night activity, and dusk activity, is observed from before to after the onset of hunting (Fig. 8). For example, when deer were doing something else than foraging, before the hunting season, they had 66 % (CI: 60 % – 71 %) chance of being active during the day, and 52 % (CI: 46 % – 58 %) after the onset of hunting (Fig. 8). On the other hand, the probability of night activity increased by 2 % between before and after the onset of hunting (p_{before} = 1 %, CI: 0 % – 2 %; p_{fafter} = 3 %, CI: 2 % – 5 %), whereas the probability of being active at dusk increased by 7 % (p_{before} = 22 % CI: 17 % – 27 %; $p_{femaleafter}$ = 29 %, CI: 23 % – 35 %) (Fig. 8).

Furthermore, when foraging, deer tended to be more active during daylight than when they were doing something else (Fig. 8). The difference between day activity probability when deer was foraging or not was of 18 % before the onset and of 23 % after the onset, showing a higher probability of daylight use when foraging than when not (Fig. 8). A contrary diel activity pattern was observed with dusk and dawn, deer were more likely to use these two periods when not foraging than when they were (Fig. 8).

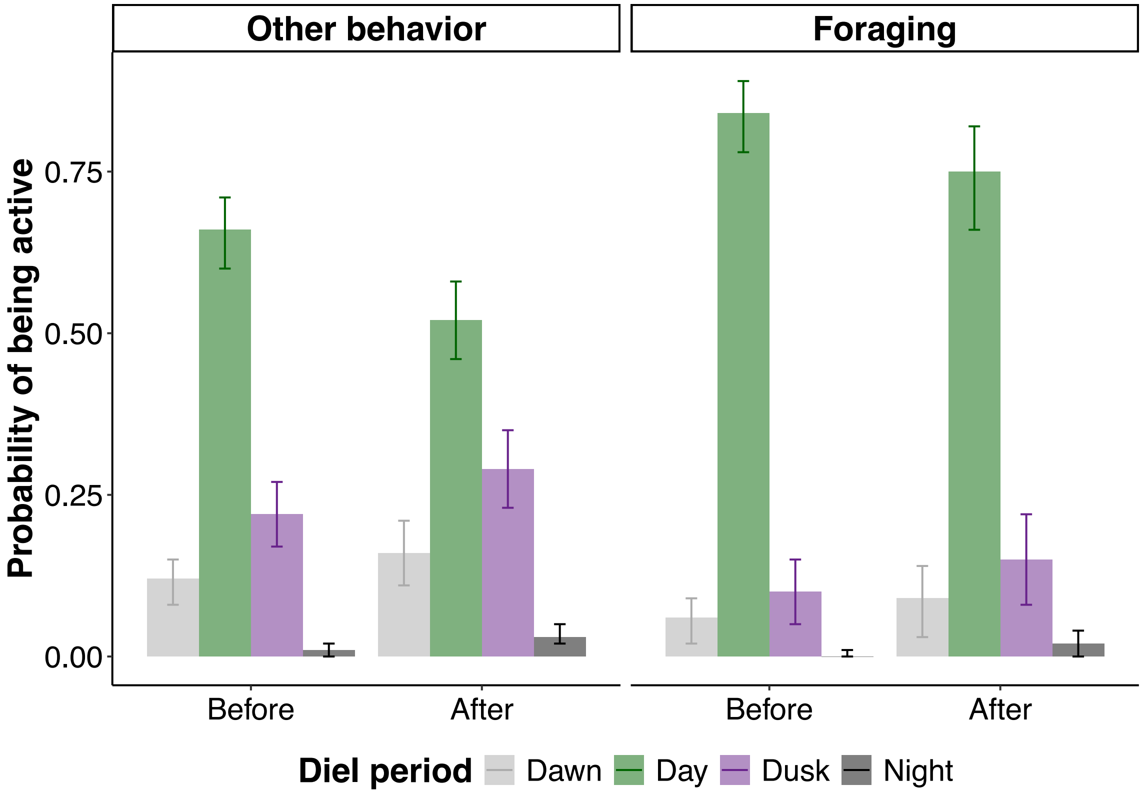

Figure 8: Changes of diel activity pattern in C. *elaphus* ten days before (22 August to 31 August) and after (1 September to 10 September) the onset of the hunting season on an island off the west coast of Norway, Svanøya, represented by behaviors (foraging or other), and hunting period (before or after the hunting onset). The probability of being active was calculated for four diel period (i.e., dawn, day, dusk and night). The 95 % confidence interval of each probability is also included as error bars. An offset of 9.70 hours was used to correct for the varying amount of daylight during the analyzed period (22/08/2024 to 10/09/2024).

Overlap between red deer diel activity

To add to the understanding of the change in the diel activity patterns of C. *elaphus*, overlap estimates and kernel density curves were extracted. When looking at the diel activity patterns throughout the year, overall, the activity of red deer no matter the sex and age was quite similar across three seasons: the calving, growing and hunting season where a bimodal activity pattern was observable (Fig. 9).

However, the only season where kernel density curves did not follow two distinct activity peaks was during winter (Fig. 9). All demographic categories across all behaviors had flattened density curves (Fig. 9). When not foraging, all coefficient overlap were over 80 % between demographics in winter (Table S8). In these conditions, subadults and juveniles (ΔDhat4 = 93 %, CI: 70 % – 92 %) continuously increased their activity levels from the beginning of the 24-hour cycle until the end of the day (Fig. 9 and Table S8). On the other hand, females and males (ΔDhat4 = 89 %, CI: 82 % – 93 %) had still two activity peaks, although visually less intense than compared to other seasons (Fig. 9 and Table S5). While foraging in winter, juveniles were the only demographics with overlap coefficients smaller than 80 % with the other demographics (Table S8). Males and females both seemed to have only one peak in density when foraging and it was later in the day (ΔDhat4 = 83 %, CI: 69 % - 90 %) (Fig. 9 and Table S8).

Juveniles had also lower overlap with other demographics during the hunting season when foraging: with males they 61 % overlap (CI: 41 % – 74 %), 68 % with subadults (CI: 45 % – 82 %), and 66 % with females (CI: 46 % – 78 %), whereas all other overlaps were over 80 % (Fig. 9 and Table S8). During the hunting seasons, juveniles only had one large peak of activity between, whereas all other demographic categories followed a bimodal diel activity pattern (Fig. 9). On the other hand, when closely looking at the overlap between juvenile and female demographics when they were not foraging, the highest overlap estimate occurred during the calving season (ΔDhat4 = 89 %, CI: 85 % - 91 %), the hunting season (ΔDhat4 = 93 %, CI: 85 % - 95 %), and in winter (ΔDhat4 = 90 %, CI: 70 % - 92 %) (Table S8).

Finally, during the growing season when foraging, the smallest overlap coefficients occurred — ranging from 27 % to 35 % overlap with the other demographics — over all seasons with juveniles having a different activity pattern by starting to be active later in the day (Fig. 9 and Table S8). Females, males and subadults were relatively in sync with two distinct peaks and overlap estimate ranging from 80 % to 92 %, similar to the other season, except winter (Fig. 9 and Tables S8).

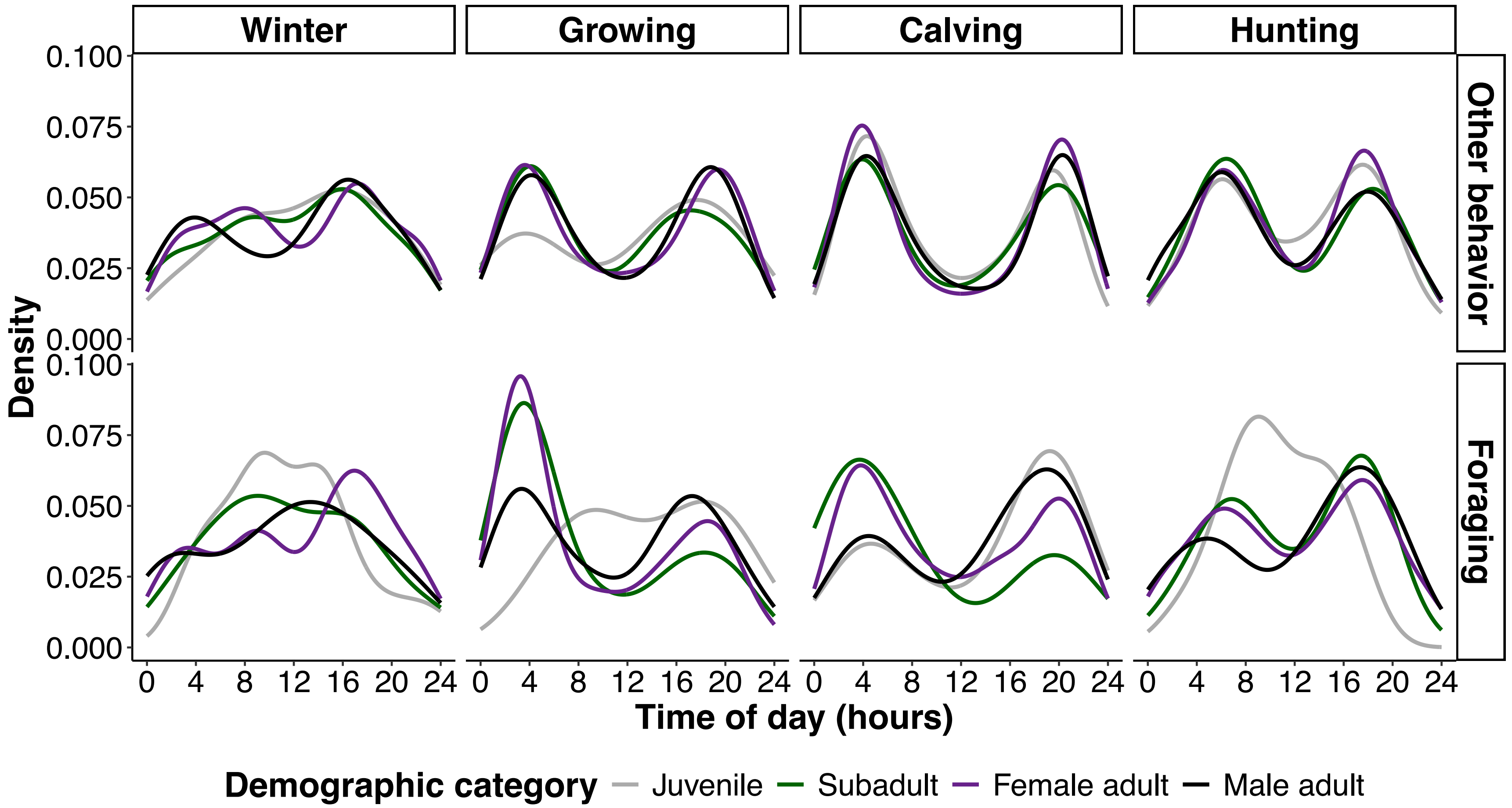

Figure 9: Kernel density variation represented on a 24-hour cycle (i.e., diel activity) in relation to a demographic category (juvenile, subadult, female adult and male adult), biological season (winter: December - February, growing: March - May, calving: June – August, or hunting: September – November), and behavior (foraging or other) of *C. elaphus* on an island off the west coast of Norway, Svanøya. Data was compiled over a complete year (from 01/2024 to 02/2025) using pictures for 66 camera traps.

When looking precisely at the effect of the hunting onset, the kernel density curves showed a bimodal diel activity pattern qualitatively, and were similar across behaviors, with overlap coefficients of 83 % (CI: 77 % - 90 %) before the onset and of 80 % (CI: 65 % - 87 after the onset (Fig. 10 and Table S9). Therefore, no difference was observable between density curves before and after the hunting onset and between foraging and other behavior. In addition, demographic category was not represented, since in the selected model, this variable was not part of the predictors (Table 3, S6).

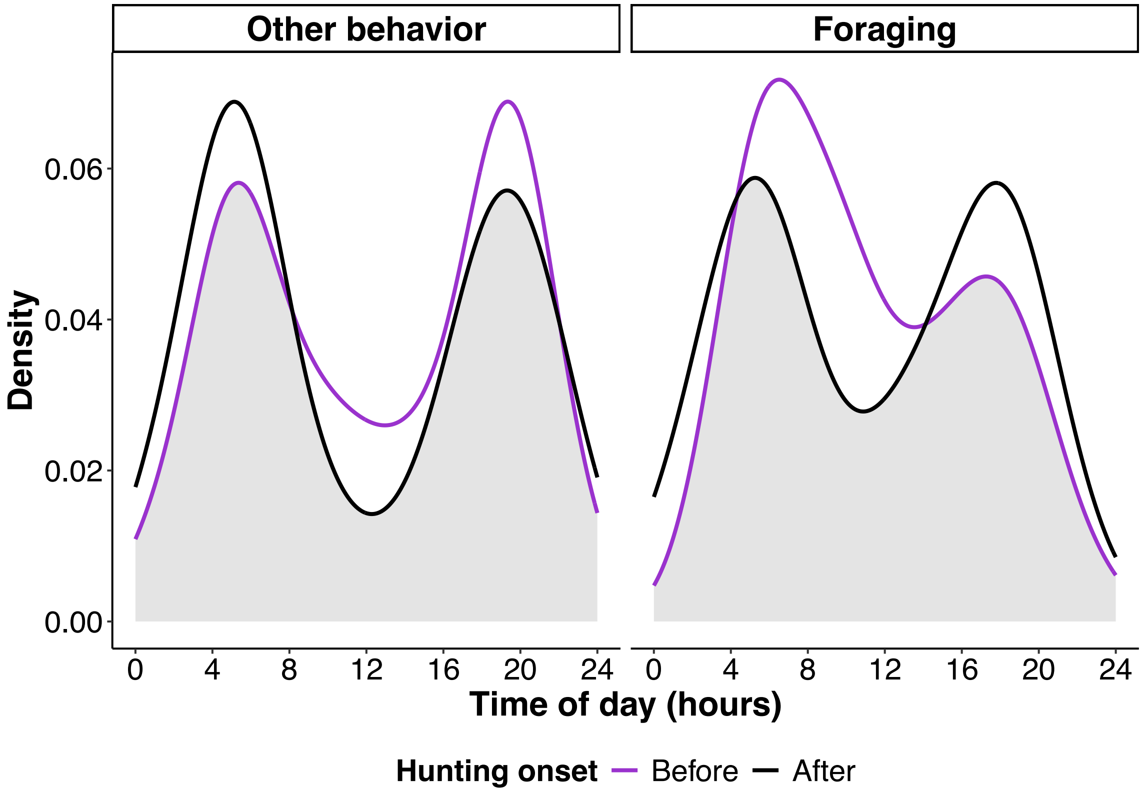

Figure 10: Kernel density variation represented on a 24-hour cycle (i.e., diel activity) in relation to the hunting onset of 1 September, and foraging behavior of *C. elaphus* on an island off the west coast of Norway, Svanøya. Data used was a 10-day period before the hunting onset (22/08/2024 to 31/08/2024) and a 10-days period after the hunting onset (01/09/2024 to 10/09/2024) using camera trap pictures. The grey shaded area under the kernel density curves represents the overlap between the two curves. The ΔDhat 4 overlap coefficient for the "other behavior" category was 83 % (CI: 77 % - 90%) and for the "foraging category" was 80 % (CI: 65 % - 87 %).

Discussion

Here, I investigated the intricate relationship between the diel activity of *C. elaphus* and its environment throughout a complete year with the help of camera trap network on the island of Svanøya, off the coast of Norway. My study revealed clear evidence of seasonal variations in diel activity patterns, modulated by light regimes. I also observed temporal shifts in response to the onset of hunting across behaviors. Finally, I found high overall overlap of activity profiles, although this overlap varied among demographic groups and behaviors throughout the year.

Therefore, most predictions were confirmed. Diel activity patterns did indeed follow a bimodal trend when daylight was available, with important overlap in activity across demographic. However, when darkness started to increase, nocturnality appeared until the bimodality is completely lost in winter and deer activity is more equally distributed over the different diel periods, with an important decrease in daylight activity. Hunting did also lead to a direct increase in nocturnality, and a decrease in foraging activity during daylight. Lastly, overlap in activity between juveniles and female adults was indeed important when juveniles were still dependent on their mother.

Overall activity pattern over an entire year

Seasonal variation in deer diel activity patterns is still a debated subject (Comte et al. 2022; Ikeda et al. 2021; Ikeda et al. 2016). In this study, diel activity patterns follow a consistent bimodal trend for most of the year, reflecting peak at early daylight and at the last moment of light as expected for red deer (Clutton-Brock et al. 1982; Pagon et al. 2013). This pattern is often observed across many deer species for thermoregulation (i.e., avoid midday heat) and predation avoidance reasons (Bonnot et al. 2016; Pagon et al. 2013; Wolff et al. 2020)

Yet, at the onset of the hunting season, nocturnality emerge in the deer diel activity profiles. In winter, when daylight is scarce, activity become even more nocturnal and arrhythmic. The synchronised bimodal pattern observed in other seasons disappeared, giving way to more evenly distributed activity over a 24-hour cycle. It is although important to note that this study covers one year only, so interannual variation in environmental conditions and population dynamics remains untested. Long-term monitoring would clarify whether these patterns persist across multiple years.

Moreover, additional seasonal factors influence diel activity. Environmental stressors, such as wind, snow, and rain can significantly alter activity patterns (Clutton-Brock et al. 1982; Kamler et al. 2007; Krop-Benesch et al. 2013), and Svanøya is frequently exposed to those. Although snow is usually rare on Svanøya, a prolonged snowfall in the winter likely affected red deer diel activity by limiting forage access (Clutton-Brock et al. 1982).

Overall, the observed flexibility in temporal niches underscores the behavioral plasticity of red deer. Such plasticity, documented in other mammals, enables individuals to balance foraging, risk avoidance, and competition across varying light regime to optimize their survival and fitness (Bonnot et al. 2020; Devarajan et al. 2025; Ensing et al. 2014).

How red deer respond to changes in daylight?

This plasticity in red deer diel activity profiles confirms the crucial role daylight has on these patterns. Daylight exerts a strong influence on red deer diel activity, with deer responding directly to photic cues rather than internal circadian rhythms (Ensing et al. 2014). The increasing daylight of the sunrise leads to a peak in activity early in the day, the same way the decreasing daylight at sunset leads to a second peak in activity (i.e., bimodal diel activity pattern) (Clutton-Brock et al. 1982; Pagon et al. 2013). This is also observable when days are starting to shorten, red deer nocturnality start to increase, following the “missing” light cues.

In winter at northern latitudes, daylight shrink to about six hours in this study, red deer hence need to adapt to this challenging aspect of their environment. Bimodality constricts around noon, or even completely vanishes, as deer maximize limited light for essential behaviors (Krop-Benesch et al. 2013). This arrhythmic diel pattern may indicate an opportunistic feeding strategy adopted, foraging when and where resources allow it in winter (Dumont et al. 2005; Luccarini et al. 2006). This confirms how environmental factors (e.g., light regime) influencing resource availability or energy use (e.g., less sunlight, leading to colder temperature, resulting in higher energy use to stay warm) has the potential to transform diel activity patterns in deer (Clutton-Brock et al. 1982). Cold conditions further complicate energy budgets. Lower temperatures drive metabolic adjustments in red deer such as a reduced heart rate, body temperature, and activity levels in order to decrease energy expenses (Arnold et al. 2004; Turbill et al. 2011), which likely dampen overall activity in winter.

Simultaneously with less daylight, there is also harsher conditions in winter, which are known to reduce activity levels and affect diel activity patterns of red deer (Clutton-Brock et al. 1982; Kamler et al. 2007). Snowfall is known to affect the temporal niche used by red deer, reducing activity levels (Mysterud et al. 1995; Comte et al. 2022). Less daylight also means less vegetation growing and available for deer. Therefore, by combining the harsher conditions with the reduced resource and daylight availability in winter, competition can increase among the deer population (Ratkiewicz et al. 2024). As a consequence, intensifying competition is likely another reason why deer are forces into less synchronized diel activity, to a more disturbed activity patterns across a 24-hour cycle to spread competition across different temporal niche.

Furthermore, in lower latitudes, where daylight changes are less drastic, red deer and other cervids maintained their bimodality patterns, even in winter (Comte et al. 2022; Ensing et al. 2014; Ikeda et al. 2021), although it was still adjusted (Banjade et al. 2021; Ensing et al. 2014). Therefore, compared to lower latitudes, northern deer exhibit unique diel adjustments under light regime varying greatly.

In brief, one of the key results of this study is that red deer seemed to be more heavily influenced by the absence of daylight (e.g., in winter), than by the absence of darkness. The only moment where the bimodality is lost was when daylight was scarce, demonstrating are important this moment is for understanding red deer diel activity plasticity. On the other hand, bimodality only occur when daylight and resource are more available like during the growing or calving season (Debeffe et al. 2017).

How red deer are impacted by hunting?

Anthropogenic activities affect temporal activities of red deer (Debeffe et al. 2017; Richter et al. 2020). Hunting introduces a strong predation risk, creating a landscape of fear (Laundre et al. 2014; Lima et al. 1990), which in turn affects temporal behavior (Meisingset et al. 2022). At hunting onset, deer start to shift their activity from day to dawn, dusk and night, avoiding peak hunters' presence (Clutton-Brock et al. 1982; Fattebert et al. 2019). Hunting pressure can indeed lead to a shift in the moment of activity in favor to nocturnal activity to avoid hunting (Abrantes et al. 2023; Ikeda et al. 2019; Krop-Benesch et al. 2013), shift observable as early as ten days after the onset of hunting according to this study. Although, it is important to note that the overall bimodal pattern persisted during hunting while night and crepuscular activities increase.

Knowing the potential effect of hunting, a carryover effect of the hunt is potentially another factor influencing the increased nocturnality in winter. Residual effects of hunting, such as increased nocturnality, past the end of the hunting season has been observed in other ungulates, similarly to what is describe in this study (Ikeda et al. 2019). However, the main hunting effect remain precisely during the time hunting events occur.

Then, let's focus solely on the effect the hunting onset had on diel activity patterns of *C. elaphus*. While overall diel activity patterns were similar across groups, deer keep their usual bimodal activity pattern (Pagon et al. 2013). This similarity among demographics may represent one technique used by deer to avoid predation: aggregating (Jayakody et al. 2008). By being all active at the same time, they potentially reduce their overall individual predation risk explaining the similarity in temporal niche and activity overlap between demographic during the hunting season.

Furthermore, hunting increases vigilance in deer as a protective mechanism (Benhaiem et al. 2008; Jayakody et al. 2008; Proudman et al. 2021), and vigilance reduces foraging efficiency. Therefore, red deer need food to be relatively availability — which is still the case at beginning of the hunting season — so they can feed while remaining somewhat vigilant (Benhaiem et al. 2008). Therefore, on way to meet the best of both world is to forage at night where hunting risk is reduced greatly (Ikeda et al. 2019; Fattebert et al. 2019; Godvik et al. 2009).

However, it is important to note that there is a discrepancy where deer are and where the cameras are. Cameras were mostly in forested areas; areas were deer most likely move to during hunting as a cover to forage freely (Laguna et al. 2021; Lone et al. 2015). Therefore, the increase in night and crepuscular activities signify maybe only that deer just feed more in the forested areas (i.e., where most cameras are) during those diel period, instead of open areas and field edges, which are more at risk of hunting (Laguna et al. 2021). That habitat therefore offers a valuable trade-off between habitat and foraging quality and survival (i.e., forest has less valuable resource quality than open areas but offer better chance of survival because they are less easily detected in forest) (Godvik et al. 2009; Lone et al. 2015). Yet my study does not capture this fine-scale habitat tuning selection by red deer over time. Further studies integrating specific habitat selection by red deer modelling over time and key events like hunting, could distinguish between habitat shifts and pure temporal changes.

These activity patterns emerging from diel activity observations of red deer could provide valuable insights to management. Knowing when a deer is most likely to be active during the day can increase the hunt success and thus reduce the stress cause by unsuccessful and long hunting events on deer population (Bojarska et al. 2024; Meisingset et al. 2022). The logic can also be applied if management agencies decide to perform a culling of the population, knowing when red deer are active will lead to more successful culling in a shorter period of time (Ikeda et al. 2019; Ikeda et al. 2015). Therefore, understand diel activity patterns could make management control of deer species more efficient (Davies et al. 2020).

Hunting, however, is not the only anthropogenic activities affecting red deer. Other anthropogenic pressures not included in this research also affect *C. elaphus* diel activity, such as roads and hiking paths (Jayakody et al. 2008; Marion et al. 2021, 2022). These activities were ignored because Svanøya has a low human population density and only two roads, so such effects are likely minimal compared to the major influences season, age, sex, behavior, and hunting can have on the temporal niche of red deer.

How red deer diel activity is influenced by different demographics?

Beside the effects of light regime and hunting have on red deer diel activity, differences in demographics exerted modest effects on diel activity patterns. In winter, juveniles exhibit greater daylight activity possibly reflecting higher thermoregulatory need (Clutton-Brock et al. 1982). Winter is a critical season for younger deer, as juvenile mortality is important during this time (Clutton-Brock et al. 1982). Being more at risk, they may need to maximise their use of daylight to stay warm and forage to assure their survival throughout winter. Juveniles high overlap in activity with females confirms they may be still fragile and dependent on their mother to survive at that time (Clutton-Brock et al. 1982).

Moreover, winter is synonym of resource scarcity, competition intensifies (Ratkiewicz et al. 2024) and may force different demographic groups to temporally partition foraging activities as observed in cervids species (Rautiainen et al. 2021; Stone et al. 2018). By fostering competition, the winter season may force less dominant individual to occupy a less valuable temporal niche (Stone et al. 2018), which may be another explanation of the more important night activity probability in the male demographic.

Further differences between demographics were expected and has been studied for a long time (Clutton-Brock et al. 1982; Kamler et al. 2007; Prebanić et al. 2015). For example, since females have different energetic needs than males, differences in diel activity were expected (Clutton-Brock et al. 1982; Debeffe et al. 2017). They should have been potentially more active during the dawn and day, especially during the calving season (Clutton-Brock et al. 1982). Females often need higher quality resource to support their energetic demands (e.g., pregnancy and lactation), leading them to forage more frequently and thus be more active (Clutton-Brock et al. 1982; Pépin et al. 2009), whereas male aim for food quantity to support their more important body size (Wearmouth et al. 2012) and thus a more distributed temporal niche as observed in winter and slightly in the hunting period. Females were expected to be active earlier (e.g., at dawn) than males to have access have access to the resource of better quality (Bischof et al. 2012; Debeffe et al. 2017).

Another essential consideration during the hunting season is that it overlaps with the rut. The rut is likely at play in the sudden increase in dawn activity in the hunting season compared to the season before (calving). During the rut, deer in general are more active, especially males who become even aggressive (Clutton-Brock et al. 1982; Pépin et al. 2009; Volodin et al. 2016). Males need to be active more early to be able to actively protect their harem of females against younger deer (e.g., subadults) (Clutton-Brock et al. 1982), but also defend their rutting territory (Jarnemo et al. 2017). The same goes for subadults, who start being active later than dominant males (Jarnemo et al. 2017; Tennenhouse et al. 2012). Males also tend to have more riskier behavior and be more active while in rut (Alves et al. 2013). In this situation, females may avoid competitive males (Carranza et al. 1999) to reduce injury risk (Clutton-Brock et al. 1982). Surprisingly, red deer temporal niche, despite these known differences, was quite similar across demographics.

This could be explain that the observed period does not represents precisely the rut, which peaks only for about a month with the first two week being more intense (Clutton-Brock et al. 1982; Csányi et al. 2022). This study system therefore probably lacks a precise scope on the rut to identify clear temporal niche differentiation during the rut. Further study should consider focusing on the rut to correctly assess the temporal aspect of that period.

This is especially true since the temporal niche in the rut is sometimes unclear in deer (Stopher et al. 2011), due various factors are at play such as sexual dimorphism, foraging difference and social factors (Wearmouth et al. 2012). By looking accurately at the rut, difference in spatial use might be observed (Alves et al. 2013), while temporal use stays the same niche may stay the same according to this study. Therefore, females may spatially avoid males (Carranza et al. 1999) while being active at the same time as them. Considering the difference between the spatial and temporal scale while looking at the rut, it demonstrates how understanding the temporal niche of a species can add nuances and precisions to a spatial niche, leading to more complete assessment of the overall ecological niche.

In summary, the hunting season increases nocturnality in deer through fear (Laundre et al. 2014; Lima et al. 1990) and has similar impact on different classes of sex and ages in the *C. elaphus* Svanøya population. However, the hunting season occurred at the same time as the rut, leading to mixed effects where deer tend to temporally avoid hunter, while performing the rut and being more active at the same time. Therefore, this may lead to interaction between the risk of hunting and the need to reproduce, leading to overall synchronized diel activity patterns across demographic categories, but if looking at a more precise scale, difference in temporal niche between demographics are likely present (Clutton-Brock et al. 1982; Csányi et al. 2022; Jarnemo et al. 2017).

How does other factors may potentially affect the diel activity of red deer?

Also, there exist other important factors potentially influencing diel activity patterns of red deer across the year. For example, in winter, food is scarcer as briefly mentioned before. Red deer might adopt more opportunistic and random strategies, feeding whenever and on whatever they can find. Also, since food is rarer, red deer need to spend more time foraging in winter than in summer, which can lead to increased nocturnal activity (Clutton-Brock et al. 1982). On the same note, seasonal shift in plant phenology also aligns with dawn activity of red deer in the growing season as new forage opportunities emerge (Bischof et al. 2012). Deer indeed time their foraging activity with the increase of food quantity and quality to optimize this rapid increase of resource when daylight period are lengthening (Bischof et al. 2012). Therefore, the reduced amount of daylight with a decrease in food supply likely forces red deer to be active even at night to answer their nutritional needs and early on the day (i.e., at dawn) when food start to grow back, showing once more their diel activity plasticity to maximise their survival.

Importance for management

Understanding diel activity patterns of red deer is essential to ensure effective management strategies, especially since it is a species with increasing population across Europe (Carpio et al. 2021). With increasing numbers, being able to adequately estimates population and density number is key for management. Having a better understanding of the activity pattern improves density estimates since activity and density are linked together (Henrich et al. 2022; Palencia et al. 2023; Ramirez et al. 2021). Because, as it has been observed in this study, red deer changes when they are active (i.e., changes in diel activity patterns) throughout the year, failing to use these activities pattern to correctly estimates density will hence bias the estimates to what was observed at the specific moment of estimation (Henrich et al. 2022).

Moreover, seasonal knowledge of diel patterns can mitigate interactions between wildlife and humans. Knowing when a deer is active can help preventing conflicts, such as road accident or foraging on sampling from the forestry industry or crops (Carpio et al. 2021; Comte et al. 2022; Duarte et al. 2015). Better assessment of these activity patterns can also favor positive wildlife and human interactions. For example, by knowing when a deer is most likely to forage, management could redirect deer during that period to protect open habitats (e.g., grasslands and heathlands) and replace livestock grazing (Riesch et al. 2019).

In terms of other anthropogenic disturbances, understanding the daily activity pattern of deer could help reduce collision with vehicles, by installing mitigating measures according to these activity profiles, such as caution signs lighting up in peaks activity hours, reflectors and speed limit (Meisingset et al. 2013; Mastro et al. 2008; Riginos et al. 2018). For example, in northern latitudes, as red deer have a more distributed diel activity pattern in winter, having reduced speed limit over that season has the potential to reduce collision risk, especially since there is already a higher risk of collisions in winter (Meisingset et al. 2014). In addition, hiking activities can also disturb wildlife (Marion et al. 2021, 2022), thus closing trail or reducing the number of hikers during peak diel activity hours of red deer depending on the season could also help mitigate the consequences of anthropogenic activity have on deer population.

Uses and limitations of camera traps

Studying diel activity using camera traps has huge potential, since it offer cost-effective, non-invasive monitoring of wildlife (Frey et al. 2017). With each pictures having the time stamp directly on them makes camera traps a useful scientific tool for assessing both aspect of an ecological niche (i.e., spatial and temporal part) with huge potential.

Camera traps survey, once implanted, can gather large amount of data with relatively low cost and effort (Burton et al. 2015). It can replace more expensive and demanding methods, such as GPS tracking and telemetry, with similar results (Iannino et al. 2025; Donini et al. 2025). It can also cover different species across different continent (Vallejo-Vargas et al. 2022). By having direct pictures of deer in their habitat, it is also possible to identify precise behavior (Burton et al. 2015), which influence diel activity patterns. However, sometimes those same pictures are not so clear and do not allow for the identification of behavior, sex, age or even species (Burton et al. 2015), as it happened during this study, resulting in dropping some data. Additionally, using camera trapping make it more difficult to track individual, the same one individual may hence be represented multiple time across the same diel period limiting the interpretation of “reel” activity in camera trap survey (Nakashima et al. 2017; Rowcliffe et al. 2014)

Some problems also occurred during the analysis and interpretation, since camera traps setup cannot fully cover an area, some type of habitat may be overrepresented or underrepresented, influencing the results (Burton et al. 2015). Adding random variables to adjust for this site location effect adds complexity to the analysis. Moreover, since camera trapping does not focus on only one species or demographics, it could lead to low level of samples, as it was the case for juveniles in this study. These results can potentially lead to unstable and unreliable analysis (Burton et al. 2015).

In summary, camera traps are unparallel, non-intrusive ecological tools to study red deer, and other wildlife, diel activity patterns over a long period of time, gathering plenty of observations with little to no effort. However, it comes with a cost, data analysis and statistical models need to explicitly account for possible imperfect detection, site-specific effects, and low samples size for certain specific categories.

Conclusion

Northern latitudes therefore offer a unique opportunity to study animals in environments with intense photoperiod changes. My findings highlight how light regimes affect red deer by altering their bimodal diel activity patterns, especially in winter. Red deer lose their photoperiod cues in these conditions and starts being active equally at night than day. Demographics maintained similar patterns, indicating that the temporal niche used is similar no matter the life stage. The increase in nocturnality associated with a decrease of day activity in fall appears to be driven by hunting pressure, where deer reduce risk by avoiding periods of hunting activities. In conclusion, *C. elaphus* demonstrated plasticity in their temporal niche through complex and flexible relationship between diel activity, seasonality, foraging behavior, and demographic group. Their temporal niche seems to be more influenced by the absence daylight (i.e., winter), than by the absence of darkness, emphasising how key daylight is to regulate red deer diel activity. Future research should focus on collecting long-term data and developing hierarchical models capable of incorporating random effects, offsets, spatial variables, and multinomial modelling to better capture the intricacies of diel activity dynamics.

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Appendix

Table S1. The 18 multinomial models created ranked by ΔAIC values explaining the variance in the diel period (dawn, day, dusk or night) a red deer is active over an entire year. The three possible predictors were the demographic category (juvenile, subadult, female adult or male adult), the season (winter, growing, calving or hunting), and the behavior (foraging or other). All models included an offset variable representing the amount of hour available for the corresponding diel period. Data are from 66 camera traps on Svanøya island, Norway.

Model	Formula	AIC	ΔAIC
M1	Diel period ~ demographic category + behavior + season + demographic category*season + behavior*season	23668.04	0.00
M2	Diel period ~ demographic category + behavior + season + behavior*season	23668.05	0.01
M3	Diel period ~ demographic category + behavior + season	23670.47	2.43
M4	Diel period ~ demographic category + behavior + season + demographic category*season	23671.21	3.17
M5	Diel period ~ demographic category + behavior + season + demographic category*behavior + demographic category*season + behavior*season	23672.42	4.38
M6	Diel period ~ demographic category + behavior + season + demographic category*behavior behavior*season	23674.16	6.12
M7	Diel period ~ demographic category + behavior + season + demographic category*behavior + demographic category*season	23677.62	9.58
M8	Diel period ~ demographic category + behavior + season + demographic category*behavior	23679.40	11.36
M9	Diel period ~ demographic category + season	23680.50	12.46
M10	Diel period ~ demographic category * season	23680.74	12.70
M11	Diel period ~ behavior * season	23728.82	60.78
M12	Diel period ~ behavior + season	23730.53	62.49
M13	Diel period ~ season	23737.06	69.02
M14	Diel period ~ demographic category	26329.64	2661.60
M15	Diel period ~ demographic category * behavior	26330.61	2662.57
M16	Diel period ~ demographic category + behavior	26332.71	2664.67
M17	Diel period ~ 1	26470.35	2802.31
M18	Diel period ~ behavior	26475.91	2807.87

Table S2. Candidate multinomial model summary showing coefficient estimates, the standard errors, *z* values and *p* values for all terms in the following model: diel period ~ demographic category + behavior + season + demographic category*season + behavior*season. The model included an offset variable representing the amount of hour available for the corresponding diel period. The reference level of the response variable is “night”. Data are from 66 camera traps on Svanøya island, Norway.

Predictor	Period	Estimate	Standard error	*z* value	*p* value

Intercepts					
(Intercept)	Dawn	−2.88	0.54	−5.35	< 0.001*
(Intercept)	Day	−1.62	0.37	−4.33	< 0.001*
(Intercept)	Dusk	−2.77	0.51	−5.46	< 0.001*
Model terms					
Demographic category (reference = juvenile)					
Subadult	Dawn	0.51	0.61	0.83	0.406
Subadult	Day	- 0.03	0.44	- 0.06	0.953
Subadult	Dusk	0.63	0.57	1.11	0.267
Female adult	Dawn	- 0.05	0.55	- 0.09	0.931
Female adult	Day	- 0.68	0.38	- 1.79	0.074
Female adult	Dusk	- 0.08	0.51	- 0.16	0.870
Male adult	Dawn	- 0.03	0.59	- 0.05	0.962
Male adult	Day	- 0.83	0.43	- 1.94	0.052
Male adult	Dusk	- 0.33	0.57	- 0.58	0.563
Behavior (reference = other)					
Foraging	Dawn	- 0.22	0.20	−1.10	0.271
Foraging	Day	0.16	0.16	1.06	0.292
Foraging	Dusk	0.01	0.19	0.05	0.962
Season (reference = winter)					
Growing	Dawn	1.68	1.57	1.07	0.284
Growing	Day	2.86	1.17	2.44	0.015*
Growing	Dusk	2.64	1.32	2.00	0.046*
Calving	Dawn	2.15	1.28	1.69	0.092
Calving	Day	6.08	1.07	5.68	< 0.001*
Calving	Dusk	5.57	1.13	4.94	< 0.001*
Hunting	Dawn	2.13	0.64	3.31	< 0.001*
Hunting	Day	2.43	0.47	5.16	< 0.001*
Hunting	Dusk	2.51	0.60	4.18	< 0.001*
Interactions: demographic*season					
Subadult * Growing	Dawn	- 0.06	1.62	- 0.04	0.970
Subadult * Growing	Day	- 0.11	1.22	- 0.09	0.927
Subadult * Growing	Dusk	- 0.32	1.37	- 0.24	0.814
Female adult * Growing	Dawn	1.09	1.57	0.69	0.489
Female adult * Growing	Day	0.80	1.18	0.68	0.500
Female adult * Growing	Dusk	0.97	1.33	0.73	0.466
Male adult * Growing	Dawn	1.17	1.62	0.72	0.471
Male adult * Growing	Day	1.30	1.23	1.06	0.290
Male adult * Growing	Dusk	1.10	1.38	0.80	0.425
Subadult * Calving	Dawn	0.36	1.52	0.23	0.815
Subadult * Calving	Day	- 1.48	1.31	- 1.13	0.260

Subadult * Calving	Dusk	- 1.69	1.37	- 1.24	0.217
Female adult * Calving	Dawn	1.24	1.34	0.93	0.355
Female adult * Calving	Day	0.12	1.14	0.10	0.918
Female adult * Calving	Dusk	- 0.02	1.20	- 0.02	0.986
Male adult * Calving	Dawn	1.46	1.50	0.97	0.330
Male adult * Calving	Day	0.05	1.30	0.04	0.972
Male adult * Calving	Dusk	- 0.19	1.36	- 0.14	0.888
Subadult * Hunting	Dawn	- 0.93	0.75	- 1.25	0.213
Subadult * Hunting	Day	- 0.90	0.56	- 1.59	0.111
Subadult * Hunting	Dusk	- 1.26	0.69	- 1.82	0.069
Female adult * Hunting	Dawn	- 0.92	0.66	- 1.40	0.161
Female adult * Hunting	Day	- 0.63	0.48	- 1.31	0.190
Female adult * Hunting	Dusk	- 0.92	0.61	- 1.50	0.133
Male adult * Hunting	Dawn	- 1.63	0.71	- 2.31	0.021*
Male adult * Hunting	Day	- 1.02	0.53	- 1.95	0.052
Male adult * Hunting	Dusk	- 1.03	0.66	- 1.55	0.121
Interactions: behavior*season					
Foraging * Growing	Dawn	0.22	0.31	0.73	0.467
Foraging * Growing	Day	0.01	0.25	0.03	0.978
Foraging * Growing	Dusk	0.10	0.28	0.37	0.715
Foraging * Calving	Dawn	1.09	1.10	1.00	0.319
Foraging * Calving	Day	1.09	1.06	1.03	0.302
Foraging * Calving	Dusk	1.08	1.07	1.01	0.313
Foraging * Hunting	Dawn	- 0.41	0.27	- 1.54	0.125
Foraging * Hunting	Day	- 0.71	0.20	- 3.49	< 0.001*
Foraging * Hunting	Dusk	- 0.66	0.24	- 2.71	0.007*

Table S3. Summary of the selected multinomial model showing coefficient estimates, the standard errors, *z* values and *p* values for each explanatory variable in the following model: diel period ~ demographic category + behavior + season + behavior*season. The models included an offset variable representing the amount of hour available for the corresponding diel period. The reference level of the response variable is “night”. Data are from 66 camera traps on Svanøya island, Norway.

Predictor	Period	Estimate	Standard error	z value	p value
Intercepts					
(Intercept)	Dawn	- 2.52	0.29	- 8.63	< 0.001*
(Intercept)	Day	- 1.16	0.23	- 5.14	< 0.001*
(Intercept)	Dusk	- 2.15	0.24	- 8.83	< 0.001*
Model terms					
Demographic category (reference = juvenile)					
Subadult	Dawn	0.02	0.32	0.08	0.938
Subadult	Day	- 0.74	0.25	- 3.00	0.003*
Subadult	Dusk	- 0.38	0.26	- 1.46	0.143
Female adult	Dawn	- 0.34	0.28	- 1.22	0.224
Female adult	Day	- 1.10	0.22	- 5.10	< 0.001*
Female adult	Dusk	- 0.64	0.23	- 2.80	0.005*
Male adult	Dawn	- 0.70	0.29	- 2.39	0.017*
Male adult	Day	- 1.39	0.23	- 6.12	< 0.001*
Male adult	Dusk	- 1.06	0.24	- 4.40	< 0.001*
Behavior (reference = other)					
Foraging	Dawn	- 0.25	0.20	- 1.23	0.217
Foraging	Day	0.14	0.16	0.91	0.363
Foraging	Dusk	- 0.03	0.19	- 0.16	0.873
Season (reference = winter)					
Growing	Dawn	2.65	0.20	13.60	< 0.001*
Growing	Day	3.65	0.17	22.05	< 0.001*
Growing	Dusk	3.49	0.18	19.33	< 0.001*
Calving	Dawn	3.25	0.34	9.43	< 0.001*
Calving	Day	6.00	0.32	18.88	< 0.001*
Calving	Dusk	5.32	0.32	16.39	< 0.001*
Hunting	Dawn	1.10	0.14	7.65	< 0.001*
Hunting	Day	1.69	0.12	14.48	< 0.001*
Hunting	Dusk	1.57	0.14	11.58	< 0.001*
Interactions: behavior*season					
Foraging * Growing	Dawn	0.23	0.31	0.76	0.448
Foraging * Growing	Day	- 0.00	0.25	- 0.02	0.987
Foraging * Growing	Dusk	0.13	0.28	0.48	0.634
Foraging * Calving	Dawn	1.24	1.09	1.14	0.256

Foraging * Calving	Day	1.20	1.06	1.13	0.257
Foraging * Calving	Dusk	1.19	1.06	1.12	0.262
Foraging * Hunting	Dawn	- 0.37	0.27	- 1.40	0.161
Foraging * Hunting	Day	- 0.66	0.20	- 3.28	0.001*
Foraging * Hunting	Dusk	- 0.64	0.24	- 2.66	0.008*

Table S4. Predictions made for each possible combination of the predictors with the four different levels of the response variable (diel period) with the best model with an offset (11.15 hours) describing the diel activity pattern of red deer throughout the year, selected by AIC. The model was the following: diel period ~ demographic category + behavior + season + behavior*season. The 95 % percent confidence interval (CI) was calculated using a bootstrap of the best model with 500 iterations. Data are from 66 camera traps on Svanøya island, Norway.

Demographic category	Foraging behavior	Season	Diel period	Predicted probability of being active	CI lower value (95 %)	CI upper value (95 %)
Male adult	Other	Winter	Dawn	0.16	0.12	0.21
Female adult	Other	Winter	Dawn	0.18	0.15	0.22
Subadult	Other	Winter	Dawn	0.21	0.16	0.26
Juvenile	Other	Winter	Dawn	0.13	0.08	0.19
Male adult	Foraging	Winter	Dawn	0.12	0.09	0.17
Female adult	Foraging	Winter	Dawn	0.14	0.10	0.18
Subadult	Foraging	Winter	Dawn	0.16	0.11	0.22
Juvenile	Foraging	Winter	Dawn	0.10	0.06	0.15
Male adult	Other	Winter	Day	0.32	0.27	0.36
Female adult	Other	Winter	Day	0.33	0.30	0.37
Subadult	Other	Winter	Day	0.37	0.32	0.42
Juvenile	Other	Winter	Day	0.52	0.45	0.58
Male adult	Foraging	Winter	Day	0.36	0.30	0.42
Female adult	Foraging	Winter	Day	0.38	0.33	0.44
Subadult	Foraging	Winter	Day	0.43	0.36	0.49
Juvenile	Foraging	Winter	Day	0.58	0.49	0.65
Male adult	Other	Winter	Dusk	0.16	0.13	0.20
Female adult	Other	Winter	Dusk	0.20	0.16	0.23
Subadult	Other	Winter	Dusk	0.20	0.15	0.24
Juvenile	Other	Winter	Dusk	0.19	0.15	0.24
Male adult	Foraging	Winter	Dusk	0.16	0.12	0.20
Female adult	Foraging	Winter	Dusk	0.19	0.15	0.24
Subadult	Foraging	Winter	Dusk	0.19	0.14	0.25
Juvenile	Foraging	Winter	Dusk	0.18	0.13	0.23
Male adult	Other	Winter	Night	0.36	0.29	0.44
Female adult	Other	Winter	Night	0.29	0.24	0.34
Subadult	Other	Winter	Night	0.22	0.16	0.31

Juvenile	Other	Winter	Night	0.15	0.09	0.24
Male adult	Foraging	Winter	Night	0.36	0.27	0.46
Female adult	Foraging	Winter	Night	0.29	0.23	0.35
Subadult	Foraging	Winter	Night	0.22	0.14	0.32
Juvenile	Foraging	Winter	Night	0.14	0.08	0.25
Male adult	Other	Growing	Dawn	0.11	0.09	0.14
Female adult	Other	Growing	Dawn	0.12	0.10	0.14
Subadult	Other	Growing	Dawn	0.12	0.09	0.15
Juvenile	Other	Growing	Dawn	0.07	0.04	0.10
Male adult	Foraging	Growing	Dawn	0.10	0.08	0.12
Female adult	Foraging	Growing	Dawn	0.10	0.08	0.12
Subadult	Foraging	Growing	Dawn	0.11	0.08	0.13
Juvenile	Foraging	Growing	Dawn	0.06	0.04	0.08
Male adult	Other	Growing	Day	0.60	0.57	0.64
Female adult	Other	Growing	Day	0.58	0.55	0.61
Subadult	Other	Growing	Day	0.60	0.55	0.64
Juvenile	Other	Growing	Day	0.71	0.66	0.75
Male adult	Foraging	Growing	Day	0.62	0.59	0.66
Female adult	Foraging	Growing	Day	0.60	0.57	0.63
Subadult	Foraging	Growing	Day	0.62	0.57	0.66
Juvenile	Foraging	Growing	Day	0.72	0.67	0.76
Male adult	Other	Growing	Dusk	0.26	0.23	0.30
Female adult	Other	Growing	Dusk	0.29	0.26	0.32
Subadult	Other	Growing	Dusk	0.27	0.23	0.31
Juvenile	Other	Growing	Dusk	0.22	0.18	0.27
Male adult	Foraging	Growing	Dusk	0.26	0.23	0.30
Female adult	Foraging	Growing	Dusk	0.29	0.26	0.31
Subadult	Foraging	Growing	Dusk	0.27	0.23	0.31
Juvenile	Foraging	Growing	Dusk	0.22	0.18	0.27
Male adult	Other	Growing	Night	0.02	0.01	0.02
Female adult	Other	Growing	Night	0.01	0.01	0.02
Subadult	Other	Growing	Night	0.01	0.01	0.01
Juvenile	Other	Growing	Night	0.01	0.00	0.01
Male adult	Foraging	Growing	Night	0.02	0.01	0.02
Female adult	Foraging	Growing	Night	0.01	0.01	0.02
Subadult	Foraging	Growing	Night	0.01	0.01	0.01
Juvenile	Foraging	Growing	Night	< 0.01	0.00	0.01
Male adult	Other	Calving	Dawn	0.02	0.02	0.03
Female adult	Other	Calving	Dawn	0.03	0.02	0.03
Subadult	Other	Calving	Dawn	0.03	0.02	0.04

Juvenile	Other	Calving	Dawn	0.01	0.01	0.02
Male adult	Foraging	Calving	Dawn	0.02	0.01	0.03
Female adult	Foraging	Calving	Dawn	0.02	0.01	0.03
Subadult	Foraging	Calving	Dawn	0.02	0.01	0.03
Juvenile	Foraging	Calving	Dawn	0.01	0.01	0.02
Male adult	Other	Calving	Day	0.77	0.74	0.79
Female adult	Other	Calving	Day	0.75	0.73	0.77
Subadult	Other	Calving	Day	0.76	0.73	0.80
Juvenile	Other	Calving	Day	0.83	0.80	0.85
Male adult	Foraging	Calving	Day	0.80	0.77	0.83
Female adult	Foraging	Calving	Day	0.78	0.76	0.81
Subadult	Foraging	Calving	Day	0.80	0.76	0.83
Juvenile	Foraging	Calving	Day	0.85	0.82	0.88
Male adult	Other	Calving	Dusk	0.20	0.18	0.23
Female adult	Other	Calving	Dusk	0.22	0.21	0.24
Subadult	Other	Calving	Dusk	0.21	0.18	0.24
Juvenile	Other	Calving	Dusk	0.16	0.14	0.18
Male adult	Foraging	Calving	Dusk	0.18	0.15	0.21
Female adult	Foraging	Calving	Dusk	0.20	0.17	0.22
Subadult	Foraging	Calving	Dusk	0.18	0.15	0.22
Juvenile	Foraging	Calving	Dusk	0.14	0.11	0.16
Male adult	Other	Calving	Night	< 0.01	0.00	< 0.01
Female adult	Other	Calving	Night	< 0.01	0.00	< 0.01
Subadult	Other	Calving	Night	< 0.01	0.00	< 0.01
Juvenile	Other	Calving	Night	< 0.01	0.00	< 0.01
Male adult	Foraging	Calving	Night	< 0.01	0.00	< 0.01
Female adult	Foraging	Calving	Night	< 0.01	0.00	< 0.01
Subadult	Foraging	Calving	Night	< 0.01	0.00	< 0.01
Juvenile	Foraging	Calving	Night	< 0.01	0.00	< 0.01
Male adult	Other	Hunting	Dawn	0.14	0.12	0.17
Female adult	Other	Hunting	Dawn	0.15	0.13	0.18
Subadult	Other	Hunting	Dawn	0.16	0.13	0.20
Juvenile	Other	Hunting	Dawn	0.09	0.06	0.13
Male adult	Foraging	Hunting	Dawn	0.13	0.09	0.16
Female adult	Foraging	Hunting	Dawn	0.14	0.11	0.17
Subadult	Foraging	Hunting	Dawn	0.15	0.11	0.19
Juvenile	Foraging	Hunting	Dawn	0.09	0.05	0.12
Male adult	Other	Hunting	Day	0.51	0.48	0.54
Female adult	Other	Hunting	Day	0.50	0.47	0.53
Subadult	Other	Hunting	Day	0.53	0.49	0.56

Juvenile	Other	Hunting	Day	0.66	0.61	0.70
Male adult	Foraging	Hunting	Day	0.50	0.45	0.54
Female adult	Foraging	Hunting	Day	0.50	0.46	0.54
Subadult	Foraging	Hunting	Day	0.53	0.48	0.58
Juvenile	Foraging	Hunting	Day	0.67	0.61	0.71
Male adult	Other	Hunting	Dusk	0.23	0.20	0.27
Female adult	Other	Hunting	Dusk	0.26	0.24	0.29
Subadult	Other	Hunting	Dusk	0.25	0.21	0.29
Juvenile	Other	Hunting	Dusk	0.22	0.18	0.25
Male adult	Foraging	Hunting	Dusk	0.20	0.16	0.24
Female adult	Foraging	Hunting	Dusk	0.23	0.19	0.26
Subadult	Foraging	Hunting	Dusk	0.22	0.17	0.27
Juvenile	Foraging	Hunting	Dusk	0.19	0.15	0.24
Male adult	Other	Hunting	Night	0.11	0.08	0.14
Female adult	Other	Hunting	Night	0.08	0.07	0.10
Subadult	Other	Hunting	Night	0.06	0.04	0.09
Juvenile	Other	Hunting	Night	0.03	0.02	0.06
Male adult	Foraging	Hunting	Night	0.18	0.13	0.24
Female adult	Foraging	Hunting	Night	0.13	0.10	0.18
Subadult	Foraging	Hunting	Night	0.10	0.06	0.15

Table S5. The 18 multinomial models created ranked by ΔAIC values explaining the variance in the diel period (dawn, day, dusk or night) a red deer is active around exclusively the hunting onset of 1 September (study period ranging from 21/08/2024 to 10/09/2024). The three possible predictors were the demographic category (juvenile, subadult, female adult or male adult), the hunting period (before or after), and the behavior (foraging or other). All models included an offset variable representing the amount of hour available for the corresponding diel period. Data are from 66 camera traps on Svanøya island, Norway.

Model	Formula	AIC	ΔAIC
MH1	Diel period ~ behavior + hunting period	1472.147	0.00
MH2	Diel period ~ demographic category + behavior + hunting period	1476.477	4.33
MH3	Diel period ~ behavior * hunting period	1477.528	5.38
MH4	Diel period ~ demographic category + behavior + hunting period + demographic category* hunting period	1480.808	8.66
MH5	Diel period ~ demographic category + behavior + hunting period + behavior*hunting period	1481.994	9.84
MH6	Diel period ~ demographic category + behavior + hunting period + demographic category*behavior	1485.545	13.40
MH7	Diel period ~ behavior	1485.996	13.85
MH8	Diel period ~ demographic category + behavior + hunting period + demographic category* behavior + behavior*hunting period	1486.122	13.97
MH9	Diel period ~ demographic category + behavior	1489.067	16.92
MH10	Diel period ~ hunting period	1489.218	17.07

MH11	Diel period ~ demographic category + behavior + hunting period + demographic category*behavior + demographic category*hunting period	1489.860	17.71
MH12	Diel period ~ demographic category + behavior + hunting period + behavior*hunting period + demographic category*hunting period	1490.988	18.84
MH13	Diel period ~ demographic category + behavior + hunting period + demographic category*behavior + demographic category*hunting period + behavior*hunting period	1494.788	22.64
MH14	Diel period ~ demographic category + behavior + hunting period + demographic category*hunting period	1495.737	23.59
MH15	Diel period ~ demographic category * behavior	1498.405	26.26
MH16	Diel period ~ demographic category * hunting period	1499.082	26.93
MH17	Diel period ~ 1	1503.381	31.23
MH18	Diel period ~ demographic category	1508.565	36.42

Table S6. Summary of the selected multinomial model showing coefficient estimates, the standard errors, *z* values and *p* values for each explanatory variable in the following model: diel period ~ behavior + hunting period. The reference level of the response variable is “night”. The model included an offset variable representing the amount of hour available for the corresponding diel period. Data are from 66 camera traps on Svanøya island, Norway.

Predictor	Period	Estimate	Standard error	z value	p value
Intercepts					
(Intercept)	Dawn	- 0.59	0.27	- 2.21	0.027*
(Intercept)	Day	0.60	0.22	2.68	0.008*
(Intercept)	Dusk	0.03	0.24	0.12	0.906
Model terms					
Behavior (reference = other)					
Foraging	Dawn	- 0.01	0.65	- 0.01	0.994
Foraging	Day	0.98	0.57	1.73	0.084
Foraging	Dusk	- 0.05	0.61	- 0.08	0.939
Hunting period (reference = After)					
Before	Dawn	0.78	0.42	1.84	0.065
Before	Day	1.33	0.37	3.58	< 0.001*
Before	Dusk	0.81	0.39	2.06	0.039*

Table S7: Predictions made for each possible combination of the predictors with the four different levels of the response variable (diel period) with the best model with an offset (9.70 hours) describing the diel activity pattern of red deer exclusively around the hunting season, selected by AIC. The model was the following: diel period ~ behavior + hunting period. The 95 % percent confidence interval (CI) was calculated using a bootstrap of the best model with 500 iterations. Data are from 66 camera traps on Svanøya island, Norway.

Foraging behavior	Hunting period	Diel period	Predicted probability of being active	CI lower value (95 %)	CI upper value (95 %)
Foraging	Before	Dawn	0.06	0.02	0.09
Other	Before	Dawn	0.12	0.08	0.15

Foraging	Before	Day	0.84	0.78	0.89
Other	Before	Day	0.66	0.6	0.71
Foraging	Before	Dusk	0.10	0.05	0.15
Other	Before	Dusk	0.22	0.17	0.27
Foraging	Before	Night	<0.01	0.00	0.01
Other	Before	Night	0.01	0.00	0.02
Foraging	After	Dawn	0.09	0.03	0.14
Other	After	Dawn	0.16	0.11	0.21
Foraging	After	Day	0.75	0.66	0.82
Other	After	Day	0.52	0.46	0.58
Foraging	After	Dusk	0.15	0.08	0.22
Other	After	Dusk	0.29	0.23	0.35
Foraging	After	Night	0.02	0.00	0.04
Other	After	Night	0.03	0.02	0.05

Table S8: Overlap estimates named ΔDhat4 and its 95 % confidence interval (CI) between different demographic categories of *C. elaphus*. Each possible combination of seasons, foraging behaviors and demographic categories were used to estimate every single ΔDhat4 and its 95 % confidence interval. Data are from 66 camera traps on Svanøya island, Norway.

Season	Behavior	Demographic category 1	Demographic category 2	ΔDhat4	CI lower value (95 %)	CI upper value (95 %)
Winter	Other	Subadult	Female adult	0.92	0.82	0.93
Winter	Other	Subadult	Male adult	0.90	0.76	0.92
Winter	Other	Subadult	Juvenile	0.93	0.70	0.92
Winter	Other	Female adult	Male adult	0.89	0.82	0.93
Winter	Other	Female adult	Juvenile	0.90	0.70	0.92
Winter	Other	Male adult	Juvenile	0.86	0.66	0.90
Winter	Foraging	Female adult	Subadult	0.84	0.63	0.88
Winter	Foraging	Female adult	Male adult	0.83	0.69	0.90
Winter	Foraging	Female adult	Juvenile	0.72	0.48	0.85
Winter	Foraging	Subadult	Male adult	0.80	0.58	0.87
Winter	Foraging	Subadult	Juvenile	0.79	0.50	0.86
Winter	Foraging	Male adult	Juvenile	0.74	0.48	0.84
Growing	Other	Male adult	Female adult	0.90	0.83	0.93
Growing	Other	Male adult	Subadult	0.84	0.76	0.90
Growing	Other	Male adult	Juvenile	0.74	0.50	0.83
Growing	Other	Female adult	Subadult	0.87	0.80	0.91
Growing	Other	Female adult	Juvenile	0.74	0.52	0.85
Growing	Other	Subadult	Juvenile	0.74	0.50	0.86
Growing	Foraging	Male adult	Subadult	0.79	0.66	0.86
Growing	Foraging	Male adult	Female adult	0.84	0.75	0.88
Growing	Foraging	Male adult	Juvenile	0.35	0.11	0.54
Growing	Foraging	Subadult	Female adult	0.92	0.82	0.92
Growing	Foraging	Subadult	Juvenile	0.27	0.07	0.49
Growing	Foraging	Female adult	Juvenile	0.31	0.09	0.48
Calving	Other	Male adult	Female adult	0.92	0.87	0.94
Calving	Other	Male adult	Subadult	0.89	0.81	0.92
Calving	Other	Male adult	Juvenile	0.88	0.81	0.91

Calving	Other	Female adult	Subadult	0.94	0.86	0.94
Calving	Other	Female adult	Juvenile	0.89	0.85	0.91
Calving	Other	Subadult	Juvenile	0.88	0.81	0.92
Calving	Foraging	Male adult	Female adult	0.84	0.78	0.90
Calving	Foraging	Male adult	Juvenile	0.76	0.61	0.86
Calving	Foraging	Male adult	Subadult	0.69	0.55	0.79
Calving	Foraging	Female adult	Juvenile	0.75	0.59	0.85
Calving	Foraging	Female adult	Subadult	0.82	0.67	0.88
Calving	Foraging	Juvenile	Subadult	0.65	0.45	0.78
Hunting	Other	Female adult	Male adult	0.93	0.87	0.95
Hunting	Other	Female adult	Subadult	0.91	0.84	0.95
Hunting	Other	Female adult	Juvenile	0.93	0.85	0.95
Hunting	Other	Male adult	Subadult	0.91	0.84	0.95
Hunting	Other	Male adult	Juvenile	0.89	0.81	0.93
Hunting	Other	Subadult	Juvenile	0.88	0.78	0.92
Hunting	Foraging	Female adult	Juvenile	0.66	0.46	0.78
Hunting	Foraging	Female adult	Male adult	0.91	0.81	0.94
Hunting	Foraging	Female adult	Subadult	0.86	0.74	0.92
Hunting	Foraging	Juvenile	Male adult	0.61	0.41	0.74
Hunting	Foraging	Juvenile	Subadult	0.68	0.45	0.82
Hunting	Foraging	Male adult	Subadult	0.82	0.69	0.89

Table S9: Overlap estimates named ΔDhat4 and its 95 % confidence interval (CI) between different demographic categories of *C. elaphus*. Each possible combination of hunting periods, foraging behaviors and demographic categories were used to estimate every single ΔDhat4 and its 95 % confidence interval. Data are from 66 camera traps on Svanøya island, Norway.

Behavior	Hunting period 1	Hunting period 2	ΔDhat4	CI lower value (95 %)	CI upper value (95 %)
Other	Before	After	0.83	0.77	0.90
Foraging	Before	After	0.8	00.65	0.87

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