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# Seasonal and Demographic Patterns of Red Deer Habitat Selection: Influence of Extrinsic and Intrinsic Factors

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Natural Resource Management

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Ås

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# Abstract

Understanding how animals select habitats is fundamental for effective wildlife management, especially in predator-free environments shaped by human activity. Habitat selection is influenced by both spatial and temporal factors, which can shift in response to ecological pressures and anthropogenic disturbance. In this study, I explored seasonal and sex-specific patterns of habitat selection in red deer (*Cervus elaphus*) using a year-long camera trap dataset from Svanøy, a 10 km² predator-free island off the coast of western Norway, inhabited by approximately 50 residents.

The results revealed that both males and females exhibited similar patterns of *habitat use* across seasons, with no distinct sex-based differences. Both sexes showed strong *use* of open areas, such as infield pastures and arable land, particularly during the fall. No sex-specific preference for forested habitats was observed, especially in the winter months. However, *spatial use* was higher in remote areas with greater forest cover, particularly near forest edges, transitional zones that provide both cover and access to open foraging areas. A marked decline in red deer *activity* was observed following the onset of the hunting season, likely indicating behavioral avoidance of high-risk, easily accessible areas. This pattern was further supported by a significant *spatial use* of areas with greater cover and greater distances from trails, roads, and forest edges *during* the 10-day period both *before* and *during* the start of the hunting season. This response was evident in both sexes, suggesting a general risk-avoidance strategy rather than distinct sex-specific differences in seasonal habitat selection.

Contrary to expectations, there is little evidence of strong seasonal habitat selection in red deer on Svanøy. Instead, they show flexible *spatial use* of forest features (cover and edges), proximity to roads and trails, and overall *use* open habitats. This pattern appears generalized and consistent across sexes, with limited variation in response to seasonal changes.

Although these patterns are shaped by the low-disturbance conditions of Svanøy, they offer valuable insights for managing red deer in more complex, heavily used landscapes. The findings underscore the need for adaptive management strategies that incorporate spatial refuges and seasonal behavioral changes. Strategies such as rotating hunting pressure, protecting critical forest habitats during sensitive periods, and adjusting monitoring protocols to capture temporal variation in detection could enhance sustainable red deer management. Future research should focus on diel activity patterns and movement using GPS and behavioral data to assess the costs associated with human-induced risk avoidance.

# Sammendrag

Å forstå hvordan dyr velger leveområder er avgjørende for effektiv forvaltning av viltbestander, særlig i predatorfrie miljøer som er formet av menneskelig aktivitet. Habitatvalg påvirkes både av romlige og tidsmessige faktorer, som igjen kan endre seg i møte med økologiske betingelser og menneskeskapt forstyrrelse. I denne studien undersøkte jeg sesongmessige og kjønnsavhengige mønstre i habitatvalg hos hjort (*Cervus elaphus*), basert på et årslangt datamateriale fra viltkameraer på Svanøy, en 10-km² stor rovdyrfri øy utenfor kysten av Vestlandet, med om lag 50 fastboende innbyggere.

Resultatene viste at både hannlige og hunnlige individer hadde lignende mønstre i *habitatbruk* gjennom året, uten tydelige kjønnsforskjeller. Begge kjønn viste høy bruk av åpne områder, som innmarksbeiter og dyrket mark, særlig om høsten. Det ble ikke observert noen kjønnsavhengig preferanse for skogsområder, heller ikke i vintermånedene. Derimot var den romlige bruken større i avsidesliggende områder med høyere skogdekning, spesielt nær skogkanter, overgangssoner som gir både skjul og tilgang til åpne beiteområder. Etter starten på jaktsesongen ble det registrert en tydelig nedgang i hjortens *aktivitet*, noe som trolig gjenspeiler en atferdsmessig unngåelse av risikoutsatte og lett tilgjengelige områder. Dette mønsteret ble ytterligere støttet av økt bruk av områder med tettere dekning og større avstand til stier, veier og skogkanter i de ti dagene både før og under jaktstart. Denne responsen var lik hos begge kjønn, noe som tyder på en generell strategi for risikounngåelse, snarere enn spesifikke kjønnsforskjeller i sesongbasert habitatvalg.

I motsetning til forventningene finnes det lite bevis for sterkt sesongbasert habitatvalg hos hjort på Svanøy. I stedet viser hjort en fleksibel *romlig bruk* av skoglignende områder (dekning og kanter), nærhet til veier og stier, samt generelt bruk av åpne habitater. Dette mønsteret fremstår som generalisert og konsistent på tvers av kjønn, med begrenset variasjon i respons til sesongmessige endringer.

Selv om disse mønstrene er formet av de lavt forstyrrede forholdene på Svanøy, gir de viktige innsikter for forvaltning av hjort i mer komplekse og sterkt brukte landskap. Funnene fremhever behovet for tilpasningsdyktige forvaltningsstrategier som inkluderer romlige refugier og sesongbaserte atferdsendringer. Strategier som rotering av jakttrykk, vern av viktige skogsområder i sensitive perioder, og justering av overvåkingsprotokoller for å fange opp tidsmessige variasjoner i deteksjon, kan bidra til en mer bærekraftig forvaltning av hjortebestander. Fremtidig forskning bør fokusere på døgnrytmer og bevegelsesmønstre ved hjelp av GPS og atferdsdata for å vurdere kostnadene forbundet med menneskeskapt risikounngåelse.

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# 1 Introduction

## 1.1 Background

Over the past decade, research on ungulate habitat use and behavioral ecology has increasingly emphasized the effects of human activities (Chitwood et al., 2022; Lamichhane et al., 2020; Newmark & Rickart, 2012) and the role of large herbivores as ecosystem engineers (Fløjgaard et al., 2017; Martin et al., 2018). Large herbivores are considered keystone species because they shape vegetation structure, influence plant community composition, and contribute to overall ecosystem functioning (Danell et al., 2006, p. 1). In Norway, this is particularly relevant due to the marked growth of the red deer (*Cervus elaphus*) population in recent decades (Mysterud et al., 2010). Now the country's most abundant wild ungulate, red deer have shown a steady increase in both population size (Apollonio et al., 2010, p. 17) and harvest numbers (Statistics Norway, 2024). This makes them an ecologically and economically significant species: red deer hunting provides income for landowners through meat sales and hunting leases (Skonhoft et al., 2013).

However, this population increase also brings ecological and management challenges. Red deer contribute to crop damage (Corgatelli et al., 2019; Månsson et al., 2021; Skonhoft et al., 2013), , browsing on commercially important tree species (Olaussen & Mysterud, 2012; Skonhoft et al., 2013; Øpstad et al., 2022), and elevate the risk of disease transmission to livestock and other wildlife (Böhm et al., 2007; Cowie et al., 2016). The ecological and economic consequences underscore the importance of understanding how red deer interact with their environment.

Understanding how animals use and select habitats is a key part of ecological research (Dale et al., 2000). *Habitat use* refers to how animals exploit available resources for survival, reproduction, and habitat occupancy (Krausman, 1999),while *habitat selection* refers to the process of choosing among available options, often based on preference (Mayor et al., 2009). Multiple factors, including food quality and availability, shelter, and the risk of predation influence habitat selection (Godvik et al., 2009; Lima & Dill, 1990). These trade-offs vary throughout the year as environmental conditions change (Bowyer, 2004; Gregory et al., 2009; Wong & Candolin, 2015). For example, open pastures offer better forage but little cover, while forests provide shelter from predators and weather (Massé & Côté, 2009; Mysterud & Østbye, 1999). Habitat selection also depends on population density. When preferred areas become crowded, animals may be forced to use suboptimal habitats (Pérez-Barbería et al., 2013; Webber et al., 2024). To capture this complexity, models often include landscape features and density dependence (Alves et al., 2014; Rosenzweig, 1991).

Habitat selection in red deer also varies by sex due to differences in reproductive roles, physiology, and energy demands (Clutton-Brock et al., 1982, p. 155). Males prioritize body growth and strength to compete for mates, while females focus on avoiding predation and meeting the energetic needs of their offspring (Main et al., 1996). These divergent strategies result in distinct habitat preferences: males often use more open habitats that support dominance behaviors and accommodate their digestive ability for lower-quality forage, whereas females select higher-quality forage and avoid areas with aggressive males, especially during sensitive periods such as calving and lactation. Females, on the other hand, seek higher-quality forage and avoid males during certain times due to aggression (Main et al., 1996). This sexual segregation typically occurs seasonally, with females occupying denser, safer habitats (Bowyer, 2004; Ruckstuhl & Neuhaus, 2002).

These sex-specific patterns are embedded within red deer life history. Males and females tend to remain spatially segregated for most of the year, coming together only during the autumn rut (Clutton-Brock et al., 1987). Social structure reinforces these patterns: females form matrilineal groups, while males associate in bachelor groups outside the breeding season (Bonenfant et al., 2004). Calving occurs in late May to early June, during which females isolate themselves and their calves to minimize predation risk (Loe et al., 2005).

These seasonal dynamics in behavior and habitat use are closely aligned with reproductive timing and environmental variation (Isle of Rum Red Deer Project, n.d.). During winter and spring, males and females occupy different areas. As the rut begins in mid-September and continues through mid-November, males seek out female groups and engage in mating competition (Jarnemo et al., 2017; Loe et al., 2005). After the rut, males withdraw to safer habitats to recover body reserves, while females focus on gestation and survival through winter.

Importantly, these natural patterns unfold in landscapes increasingly shaped by anthropogenic pressures, most notably hunting. Hunting is a powerful selective force that influences both red deer behavior and habitat selection (Chassagneux et al., 2020). Deer frequently show spatial and temporal avoidance of human activity during hunting seasons (Lone et al., 2015). Hunting is often highly predictable in both time and space (Potratz et al., 2024; Proudman et al., 2020), creating what is referred to as the "*phenology of fear*" (Cromsigt et al., 2013). In response, red deer may reduce group sizes, shift to safer habitats, or alter their daily activity patterns to avoid detection (Bojarska et al., 2024; Cromsigt et al., 2013; Lone et al., 2015; Proudman et al., 2020).

Although many studies have examined the behavior of red deer, less is known about how habitat selection changes throughout the year and varies by sex. GPS telemetry has significantly advanced our understanding of ungulate behavior by revealing individual movement patterns (Ensing et al., 2014), fine-scale spatial behavior (Killeen et al., 2014), migration routes (Sawyer et al., 2009), and temporal activity patterns (Eriksen et al., 2011). However, these studies often rely on small sample sizes, which can limit their generalizability (Hebblewhite & Haydon, 2010). In contrast, camera traps offer a complementary approach, enabling long-term, non-invasive monitoring over large areas. They are cost-effective, require minimal field labor, and can generate large datasets that reveal patterns in species presence, habitat use, and behavior (Caravaggi et al., 2017; McCallum, 2013). Camera traps have been particularly valuable for monitoring elusive species and analyzing activity and species interactions (Bischof, Hameed, Ali, Kabir, & Nawaz, 2014; Bischof, Hameed, Ali, Kabir, Nawaz, et al., 2014; Bischof et al., 2024)

In this study, I investigated a semi-isolated red deer population in western Norway**,** an area without predators but subject to regular seasonal hunting. Using a full year of camera trap data, I examined how red deer selected habitats in response to seasonal changes and human disturbance. Specifically, I explored differences in habitat selection between sexes across reproductive and seasonal periods and assessed how the onset of the hunting season influenced these patterns.

## 1.1 Aim, hypotheses, and associated predictions

The aim of this study was to investigate how seasonality, demographic differences, and human disturbance influence habitat selection patterns in red deer, with the goal of informing evidence-based wildlife management. Based on this aim, I formulated the following hypotheses and associated predictions:

### H1 Seasonal habitat selection will differ by sex due to sexual dimorphism.

Seasonal habitat selection differs between demographic groups due to ecological constraints and sex-specific strategies, and these patterns are influenced by environmental factors such as proximity to roads, forest cover, and edges. I will test the following predictions:

*P1.1 Stronger relative selection for forested habitats by females than males*

Red deer generally prefer habitats that provide greater concealment, such as areas with higher forest density and proximity to forest edges, while avoiding features linked to human disturbance (e.g., roads and trails) (Jiang et al., 2008). Females are expected to show a stronger preference for such covered, less-disturbed habitats than males, likely due to heightened sensitivity to predation risk and the need to protect offspring (Meisingset et al., 2022; Meisingset et al., 2013; Sigrist et al., 2022).

*P1.2 Convergent relative habitat selection for forest during winter.*

Red deer activity typically decreases in winter as individuals respond to harsher environmental conditions. Both sexes are predicted to favor forested areas that offer thermal cover and shelter from snow and wind. Spatial variables such as high forest cover, and greater distance from open areas are expected to be more strongly associated with red deer presence in winter, particularly for females, who face greater energetic demands (Mysterud & Østbye, 1999).

*P1.3 Reduced sex differences in relative habitat selection during the rut.*

During the rut, increased male activity in search of mates is expected to reduce sex-based differences in habitat selection, as males enter areas more frequently used by females. This convergence may be further influenced by hunting pressure, which also intensifies during this period (Apollonio et al., 1998). Open habitats, such as infield pastures and arable land, which are typically more frequented by females during the growing season for foraging, may experience increased male presence due to rut-related shifts in movement and habitat selection.

**H2 Hunting pressure causes spatiotemporal shifts in habitat selection.**

Hunting increases predation risk, prompting red deer to alter their habitat selection. I will test the following predictions:

*P2.1 Overall reduced relative spatial use after the hunting onset.*

Following the start of the hunting season, red deer activity are expected to decrease, particularly in open habitats and areas near roads and trails. This response is anticipated in both sexes as a reaction to increased risk during the rut. Previous research has shown that red deer tend to avoid open and accessible areas under hunting pressure, shifting toward denser, more concealed habitats as a risk-avoidance strategy (Mysterud & Østbye, 1999).

*P2.2 Increased relative selection of remote forests by female after the hunting onset.*

During the hunting season, females are expected to shift toward areas with dense forest cover and greater distances from anthropogenic features such as roads, trails, and open edges. Spatial characteristics associated with concealment and remoteness are predicted to show a stronger positive correlation with female detections than male detections, reflecting females' heightened sensitivity to risk, especially among individuals with dependent young (Bonnot et al., 2013; Ciuti, Northrup, et al., 2012; Lone et al., 2015).

# 2 Material and methods

## 2.1 Study site

This study was carried out from January 2024 to February 2025 on Svanøy, a 10.3 km² island in Kinn Municipality, Vestland County, western Norway. Surrounded by the Førdefjord and several smaller islands, Svanøy has an oceanic climate, with a mean annual temperature of 8.8 °C. The island lies within the boreonemoral zone and is predominantly covered by old-growth Scots pine (*Pinus sylvestris*) forests, interspersed with rugged terrain and elevations exceeding 300 meters above sea level.

The understory is primarily composed of Ericaceae dwarf shrubs, including bilberry (*Vaccinium myrtillus*), lingonberry (*Vaccinium vitis-idaea*), and heather (*Calluna vulgaris*), alongside various thermophilic species such as holly (*Ilex aquifolium*), hazel (*Corylus avellana*) (Hegland et al., 2021). Birch (Betula spp.), a widespread and ecologically versatile genus, is also present throughout the forest matrix. In addition, parts of the island are planted with Norway spruce (*Picea abies*). Svanøy's forests are inhabited year-round by large herbivores, most notably red deer, as well as free-ranging domestic livestock including goats (*Capra hircus*), sheep (*Ovis aries*), and cattle (*Bos taurus*). Agricultural activity is concentrated in the lowland areas, where infield pastures and arable land are located.

Svanøy offers a unique opportunity to study red deer habitat selection in a relatively enclosed ecosystem. Its diverse topography and habitat types, combined with the absence of natural predators, limited immigration, and human hunting as the primary population control mechanism, make it a valuable “natural laboratory” for ecological research.

## 2.2 Study system

Red deer is the most common ungulate on the west coast of Norway and a forest-dwelling species that has reached historically high post-glacial population densities since approximately 1995 (Hegland et al., 2013; Hegland et al., 2021). Densities remain high in many areas, with increasing trends in population indices reported across the region (Solberg et al., 2022). The red deer population on Svanøy is considered representative of conditions typical for western Norway (Hegland et al., 2021). The known population of red deer is around 100 to 140 individuals (pers.comm, J. A. Stavang, 07. May 2025).

In addition to free-ranging red deer, there are six enclosures managed by the Norwegian Red Deer Centre, the largest being about 150,000 m$^2$. The total fenced area is 450,000 m$^2$, with approximately 60 deer (pers.comm, J.A. Stavang, 07. May 2025). The Norwegian Red Deer Centre is also responsible for the population management of wild red deer on Svanøy, with annual culling of approximately 25–35 individuals. Management practices prioritize the removal of calves, while allowing prime adult animals, including potential trophy stags, to reproduce (pers. comm. J.A. Stavang, 07. May 2025). Male red deer over 12 years of age are selectively culled, whereas individuals between four and twelve years are generally spared, contributing to a higher proportion of mature stags in the population. Hunting is conducted across the island using a variety of methods, including dog-assisted strategies. The hunting season extends from 1 September to 23 December, with most activity occurring shortly after the season's onset (**Fig A1**).

## 2.3 Study design

In this observational study, 66 camera traps were deployed, including four different models from Browning Trail Cameras (Morgan, Utah, USA): DarkOps HD Pro BTC-6HDPX, BTC-6HDP, BTC-PXD, and Spec Ops Full HD. Each unit was equipped with an infrared-triggered sensor and flash, programmed to record the correct date and to capture three rapid-fire photographs per trigger, with a five-second interval between bursts. All cameras were set to operate in trail mode for still photography.

Camera deployment followed a systematic grid-cell layout, with each cell measuring 250 × 250 meters (**Fig1**). The placement of cameras aimed to achieve comprehensive spatial coverage of the study area and representation of key habitat types. Placement decisions were informed by local knowledge of red deer movements and habitat use, as well as logistical collaboration with the Norwegian Red Deer Centre and the Western Norway University of Applied Sciences. Within each grid cell, camera traps were positioned strategically to maximize detection probability and capture habitat variability across the landscape.

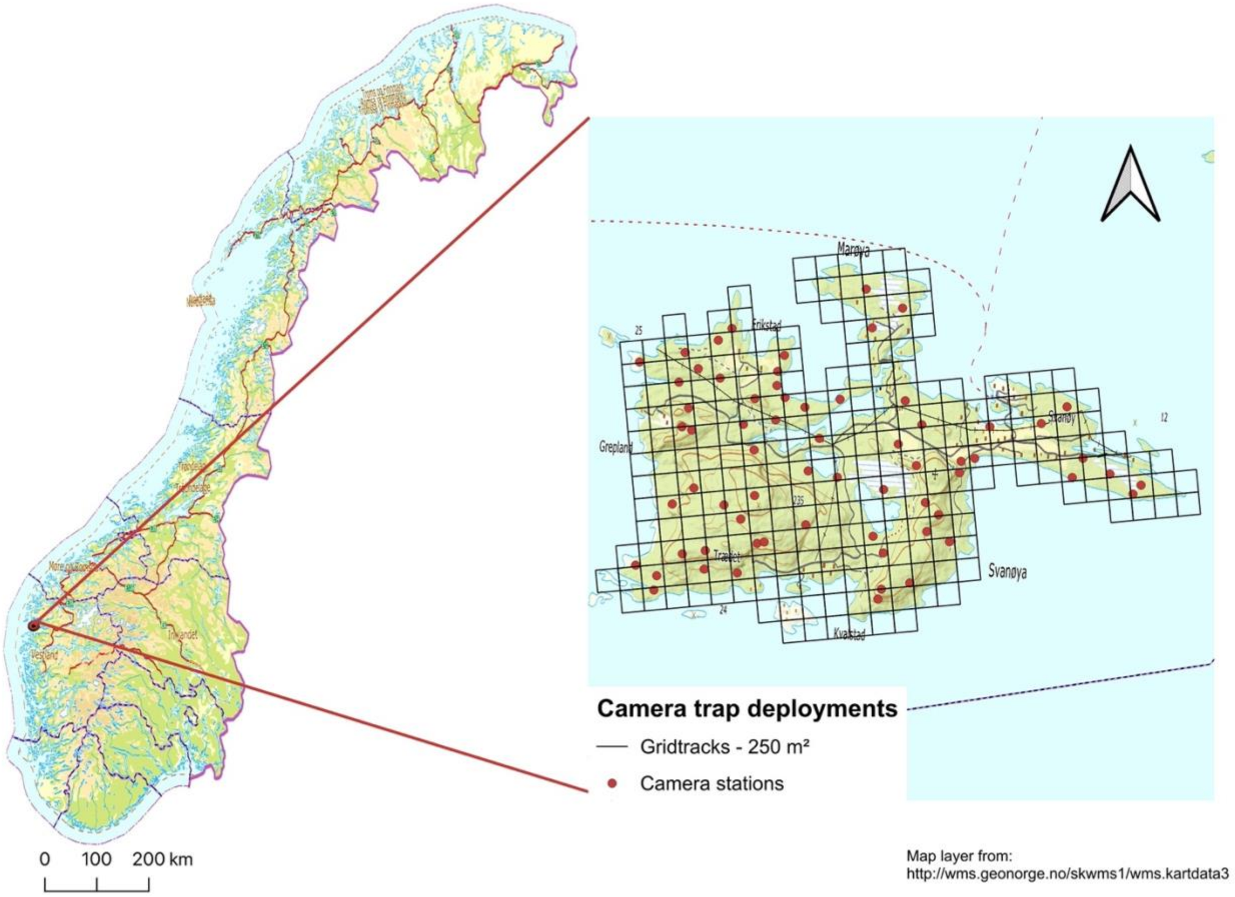

**Fig 1.** Camera trap deployments with a grid cell system (250 x 250 m) and stations on Svanøy, an island on Norway's west coast. The background map is Kartdata 3 from http://wms.geonorge.no/skwms1/wms.kartdata3.

## 2.4 Data collection

### *2.4.1 Camera trap deployment*

To comply with the Norwegian Data Protection Authority, camera traps were installed in locations where the likelihood of capturing people was minimal (Norwegian Data Protection Authority, n.d.). All units were clearly labeled to indicate the monitored area (**Fig 2b**).

Each camera was mounted on a tree at a height of 150–300 cm to optimize viewshed coverage (**Fig 2a**). Vegetation within a 1–3-meter radius was cleared to reduce visual obstruction and glare from infrared flashes during nocturnal operation. At each station, GPS coordinates and compass bearings were recorded to document location and camera orientation. Warning signs were placed at natural access points 15–25 meters from the camera to inform passersby of the monitoring (**Fig 2b**). Contextual photographs were also taken from multiple angles to document the camera's placement and surrounding environment.

Cameras were revisited four times during the study (March 2024, June 2024, October 2024, and February 2025) to inspect functionality, perform maintenance, and retrieve stored images.

**Fig 2.** Contextual pictures of camera trap sites: **a)** the installation of camera traps, as well as **b)** one of the access points marked with a warning tag (© Richard Bischof and Trine Gullberg Skogli).

### *2.4.2 Hunting data*

Hunting data were obtained in collaboration with the Norwegian Red Deer Centre. These records included the date of each hunting event and the number of hunting events per day, enabling fine-scale temporal analyses of red deer responses to hunting pressure.

### *2.4.3 Habitat classification and spatial covariates*

#### **Habitat classification**

Habitat classification at each camera trap site was based on AR5, a high-resolution land cover dataset from the Norwegian Mapping Authority (NIBIO, n.d.). AR5 includes spatial data on vegetation, land use, and tree species composition. While it maps all major habitat types on the island (e.g., built-up areas, roads, arable land, forest, mire, freshwater; Fig 3), only four were used in this study: *arable land*, *infield pasture*, *forest*, and *mire* (Fig 4). These were selected because they were suitable for camera trap deployment and relevant to red deer habitat use, while habitats dominated by human infrastructure were excluded.

The dominant land cover within a 50-meter buffer around each camera was used to classify habitat at the station level. Based on this, a categorical habitat variable was created, with four classes: *forest*, *mire*, *infield pasture*, and *arable land*.

### Spatial covariates

To quantify fine-scale spatial features relevant to red deer habitat selection, additional covariates were derived. Using the Felles Kartdatabase (Geonorge, n.d,), the shortest distance (in meters) from each camera to the nearest road and house was calculated to represent potential anthropogenic disturbance (**Fig A1**).

In addition, two continuous forest-related variables were derived from the AR5 data:

1) *Forest cover (%)*, calculated as the proportion of forest within a 50-meter buffer around each station, representing local forest density; and
2) *Distance to forest edge (m)*, measured as the linear distance from each camera to the nearest forest to non-forest boundary, capturing the proximity to habitat edges.

It is important to distinguish between the categorical habitat variable (based on dominant cover type) and these continuous forest metrics. For example, a site classified as "*mire*" may still have high forest cover nearby or be close to a forest edge, features that can influence red deer behavior. This separation allows for a more detailed assessment of both broad habitat type and finer-scale landscape structure.

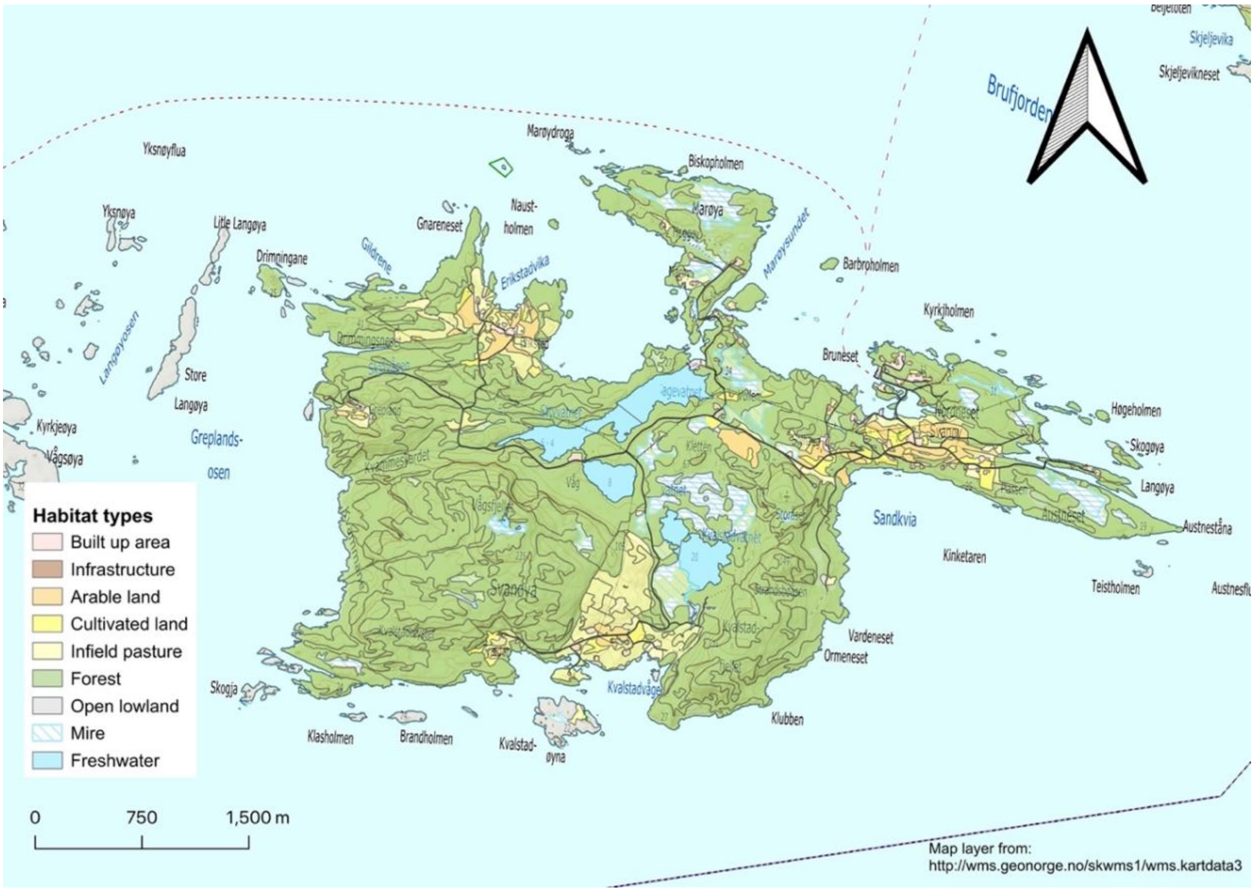

**Fig 3.** All habitat types on Svanøy from the AR5 map layer were downloaded from NIBIO. The background map is Kartdata 3 from: http://wms.geonorge.no/skwms1/wms.kartdata3.

**Fig 4.** Examples of detection from camera traps placed in different habitats on Svanøy in accordance with AR5: **a**) *infield pasture,* **b**) *mire*, **c**) *forest,* and **d**) *arable land* (© DeerLab/NMBU)

### *2.4.4 Biological seasons*

Biological seasons were defined based on key ecological and anthropogenic events. *Winter* (December–February) was considered a recovery phase; *spring* (March–May) corresponded to the growing season; *summer* (June–August) to the calving period; and *fall* (September–November) encompassed both the rutting and hunting periods (**Fig 5**). Although the official hunting season extends from September 1st to December 23rd, most hunting activity occurred in early September (**Table A1; Fig A2**). To assess potential short-term responses to the onset of hunting, two ten-day periods were defined: a pre-hunting period (August 22nd–31st) and a post-onset hunting period (September 1st–10th).

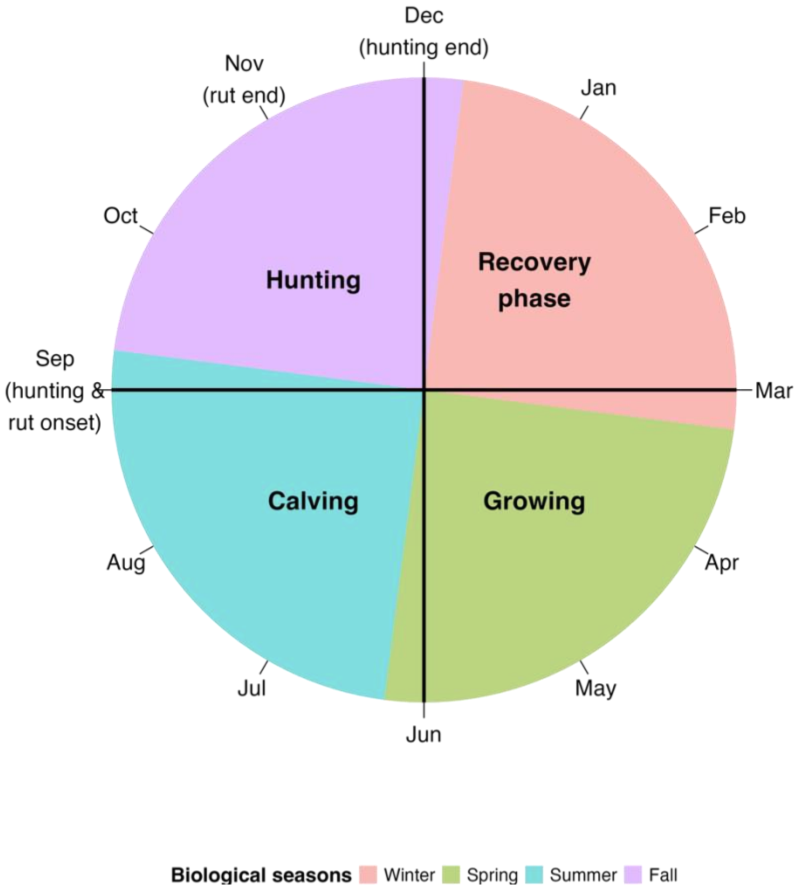

**Fig 5.** Circular representation of biological seasons across the year for red deer. The plot is divided into four distinct seasons: Winter, Spring, Summer, and Fall, each represented by a colored wedge. The seasonal phases: Recovery, Growing, Calving, and Hunting, are annotated within the plot, and months of the year are labeled along the circumference. The onset and end of the hunting season, as well as the rut period, are marked with specific month labels. This visualization highlights the temporal distribution of red deer life stages and behavioral phases throughout the annual cycle.

## 2.5 Data handling and image analysis

Camera traps were deployed continuously for one year, with the first image recorded on January 16th, 2024, and the final image captured on February 6th, 2025. Over this period, a total of 10,653 images of red deer were collected. After a preliminary quality check, all camera trap images were uploaded to Agouti, an artificial intelligence-assisted platform developed by Wageningen University and the Research Institute for Nature and Forest (INBO) (https://www.agouti.eu).

Image annotations were sequence-based and organized by station ID, with each independent detection defined as a new sequence if at least two minutes had elapsed since the previous image. All images were manually reviewed to verify species identification. For red deer detections, individuals were further classified by sex, age class, and behavior (**Fig A3**).

Sex and age class were recorded where possible. Three age categories were used: juveniles (less than one year old), sub-adults (one to two years old), and adults. Juveniles were identified by their small body size and characteristic, white-spotted coats. Sub-adults were larger, lacked spots, and typically exhibited an incomplete adult coat. Due to limited distinguishing features, sex was not assigned to juveniles and sub-adults.

Adult individuals were classified as males if they exhibited antlers, visible pedicles, or a thick neck, and as females if they lacked antlers and had a slender neck. Based on these criteria, red deer were categorized into the following classes:

- ◊ *Juveniles*: smallest individuals, white-spotted fur (**Fig 6 & Fig 8**)
- ◊ *Sub-adults*: intermediate size, incomplete adult coat, no spots (**Fig 8**)
- ◊ *Adult males*: antlers or pedicles, thick neck (**Fig 7**)
- ◊ *Adult females*: no antlers, slender neck (**Fig 6 & Fig 8**)

**Fig 6.** Mother and calf feeding is categorized as “browsing” and “grazing” on Agouti, as it is difficult to distinguish between grazing on grasses and forbs or browsing on bilberry and other woody vegetation (© DeerLab/NMBU).

**Fig 7.** Stag calling during the rutting season, and this was categorized as “calling” on Agouti (© DeerLab/NMBU).

**Fig 8.** Numerous red deer in all three demographic categories (juvenile, sub-adult and adult) are taking a mud bath. This was categorized as “wallowing” on Agouti (© DeerLab/NMBU).

## 2.6 Statistical analyses

All statistical analyses were conducted using R version 4.3.2 in RStudio (RStudio Team, 2023). Figures were primarily produced using the "*ggplot2*"-package , along with additional R packages for data wrangling, spatial processing, and statistical modeling, including "*dplyr*" and "*tidyr*" .

To investigate *relative habitat selection* and *seasonal space shifts* across habitats, I aggregated the data at a daily resolution, creating 24-hour intervals for each camera station. A binary variable was assigned to each interval to indicate whether at least one red deer photographic event occurred. By adjusting for differences in sampling effort across time and space, I ensured that observed differences in habitat selection reflected actual preferences rather than biases due to unequal sampling effort. For days with multiple detections within a 24-hour interval, I treated them as a single occurrence (presence/absence) to avoid overinflating detection rates, assuming that each day represented a distinct opportunity for red deer to be detected. Days with no detections were recorded as true "absence." This simplification was suitable for investigating broad trends in relative habitat selection.

To assess *relative habitat selection* and seasonal *shifts in space use*, I modeled photographic detection rates adjusted for sampling effort, using spatial and environmental covariates as predictors. These included distance to roads, trails, and habitat edges, as well as the proportion of forest cover. By applying generalized linear models (GLMs) with a binomial outcome (presence/absence), I accounted for variation in detection probabilities. This approach helped ensure that the inferences about habitat selection and shifts in space use were not confounded by environmental factors influencing detectability.

In this study, photographic detections served as a proxy for *relative space use*, based on the assumption that more frequent detections indicated more intensive use of a habitat. This approach aligns with established wildlife monitoring methods (e.g., Rowcliffe et al., 2008). However, I recognize the potential for biases, particularly in areas like roads and trails where higher detection rates may result from greater visibility rather than increased use by red deer. Thus, I interpreted higher detection rates as *relative indicators of habitat selection*, acknowledging that they do not necessarily reflect absolute space use.

To control for variation in sampling intensity across different habitats, I adjusted for differences in camera density and deployment duration (Table A2). For example, arable land and infield pastures had fewer cameras deployed but for longer periods, yielding higher detection rates per unit of effort compared to forested habitats, which had more cameras but shorter deployment periods. I calculated a normalized effort index to standardize detection rates across habitats, ensuring that comparisons reflected true differences in habitat selection rather than sampling effort. This methodology allowed me to explore how *relative habitat selection* changes seasonally and how red deer shift their space use in response to environmental and temporal factors, particularly during the onset of the hunting season.

To analyze photographic detection probability, a series of generalized linear models (GLMs) were fitted using the “lme4”-package (Bates et al., 2015). The binary response variable (presence/absence per 24-hour interval) was modeled assuming a binomial distribution with a logit link function. Candidate models included spatial and seasonal covariates, as well as biologically relevant interactions, to evaluate how habitat characteristics and seasonal changes influenced the probability of red deer detection.

Due to model limitations, a random effects model could not be implemented; therefore, fixed-effects models were used instead. However, the lack of random effects means that site-specific variation is not explicitly accounted for and should be considered when interpreting the results.

To support interpretation and highlight biologically meaningful patterns, the results were grouped into six key ecological dimensions based on the predictors and their interactions:

- ◊ *Activity* – effects of demographic categories alone, as well as hunting
- ◊ *Habitat use* – main effects of habitat types (arable land, infield pasture, forest) alone
- ◊ *Seasonal habitats use* – effects of season (fall, spring, summer, winter) alone
- ◊ *Seasonal activity* – effects of season and demographic category
- ◊ *Relative habitat selection* – interaction effects between demographics and habitat types (arable land, infield pasture, forest)
- ◊ *Spatial use* – effects of continuous spatial variables (distance to road/trail/edge, and cover) and their interactions with season.

This framework provides an ecologically grounded structure for presenting and interpreting the results.

Model selection was based on Akaike Information Criterion (AIC), with models within $\Delta$AIC < 2 considered equally supported. The most parsimonious model was selected for inference.

### *2.6.1 Correlation between spatial covariates*

To assess potential multicollinearity among spatial covariates, a Pearson correlation matrix was calculated (Wei & Simko, 2024). Pearson's correlation analysis results between spatial covariates (Fig A3) show a strong positive correlation between distance to the road and distance to buildings (r = 0.89). Therefore, I excluded distance to buildings from the models, as buildings are often closely linked to road networks. Additionally, the correlation between the proportion of forest and distance to nearest forest edge was fairly high (r = 0.56), but not high enough to justify excluding one of them from the model.

### *2.6.2 Seasonal shift in relative habitat selection*

To investigate seasonal shifts in relative habitat selection, I fitted a series of binomial generalized linear models (GLMs) with a logit link function, using red deer detection (presence/absence) as the response variable. Guided by Hypothesis 1 (**H1**), I included demographic group (*juveniles, subadults, adult females, adult males*), season (*spring, summer, fall, winter*), and areal type (*arable land, infield pasture, forest, mire*) as predictors, along with relevant interaction terms.

To account for spatial structure and key landscape features, I also included continuous predictors such as log-transformed distances to roads, trails, and feeding sites, as well as the proportion of forest cover within a 50 m buffer. I added a constant (+1) to distance variables to avoid issues with log-transformation of zero values.

I compared nine candidate models of increasing complexity using Akaike's Information Criterion (AIC) and selected the most parsimonious model with ΔAIC < 2 as the best-supported model (Table 1). I then used this final model to generate predicted probabilities of red deer detection across combinations of season and demographic group, which allowed me to visualize seasonal patterns in habitat selection (Table A3).

### *2.6.3 Immediate effect of hunting on habitat selection*

To investigate short-term effect of the onset of the hunting period in relation to relative habitat selection season (September 1), I tested several time windows (10, 15, and 20 days before and after the start of hunting) to identify the most sensitive interval (Table 2, A3, A4). The 10-day window showed the clearest signal and was retained for the final analysis, comparing red deer detections immediately before (August 22–31) and after (September 1–10) hunting began.

Based on Hypothesis 2 (**H2**), I fitted a series of binomial GLMs with red deer detection (presence/absence) as the response variable. Candidate models included demographic group, habitat type, hunting pressure, and continuous spatial predictors such as log-transformed distances to roads and houses, and the proportion of forest cover. Interaction terms between demographic group and hunting pressure were included to test for sex- and age-specific responses to hunting.

I compared nine candidate models using Akaike's Information Criterion (AIC**) and** selected the most parsimonious model with ΔAIC < 2 for inference (**Table 2**). This model was then used to generate predicted probabilities of red deer detection, allowing me to visualize how habitat use shifted in response to the onset of hunting**.**

# 3 Results

This study used camera trap detections to assess red deer *relative habitat use*, with detection probability as a proxy for *relative habitat selection*. While habitat use reflects the frequency of detections, habitat selection compares use to habitat availability. Adjustments were made for sampling effort differences across habitats (see 2.6 and **Table A2**). Random effects were not included due to convergence issues, focusing instead on fixed effects to simplify the analysis.

The results are structured into the six predefined ecological dimensions described in the **2.6**: (1) activity, (2) habitat use, (3) seasonal habitat use, (4) seasonal activity, (5) relative habitat selection, and (6) spatial use. This structure reflects the grouping of predictor types and their interactions in the modeling framework.

## 3.1 Relative habitat selection: seasonal shifts and sex-specific differences

The best-supported model for **H1** included demographic category (demCat), season, habitat type (arealtype), spatial covariates (log-transformed distances to road, trail, and forest edge, and proportion of forest cover), and their two-way interactions: demographic × season, demographic × arealtype, season × arealtype, as well as interactions between season and the spatial covariates (season × dist.road, season × dist.trail, season × prop.forest, season × dist.edge) (**Table 1**).

**Table 1.** AIC-based model comparison assessing red deer seasonal habitat selection using photographic detection probability as the response variable. Candidate models included combinations of demographic category (demCat), season, habitat type (arealtype), and spatial covariates (log-transformed distances to road, trail, and forest edge, and proportion of forest cover). The number of variables, degrees of freedom (df), AIC value, AIC difference (ΔAIC), and model weight are presented for each model. Lower AIC values and higher weights indicate more substantial support.

| **Models: seasonal and sex-specific habitat selection** | **df** | **AIC** | **ΔAIC** | **AICWeight (%)** |
|---|---|---|---|---|
| detected~ demCat*season + demCat*arealtype + season*arealtype + season*dist.road+ season*dist.trail+ season*prop.forest+ season*dist.edge | 53 | 36684.93 | 0.00 | 0.82 |
| detected~ demCat*season + demCat*arealtype + season*arealtype + season*demCat*arealtype + season*demCat*dist.road+ season*demCat*dist.trail+ season*demCat*prop.forest+ season*dem*cat*dist.edge | 101 | 36687.97 | 3.038 | 0.18 |
| detected~ demCat*season + demCat*arealtype + season*arealtype + demCat*dist.road+ demCat* dist.trail+ demCat*prop.forest+ demCat*dist.edge | 53 | 36702.68 | 17.754 | 0 |
| detected~ demCat*season + demCat*arealtype + season*arealtype + dist.road + dist.trail+ prop.forest+ dist.edge | 41 | 36719.19 | 34.263 | 0 |
| detected ~ demCat * season * arealtype | 64 | 37319.2 | 634.274 | 0 |
| detected~ demCat*season + demCat*arealtype + season * arealtype | 37 | 37336.22 | 651.296 | 0 |
| detected ~ demCat * season + arealtype | 19 | 37428.44 | 743.511 | 0 |
| detected ~ demCat + season * arealtype | 19 | 37876.68 | 1191.751 | 0 |
| detected ~ demCat + season + arealtype | 10 | 37899.34 | 1214.411 | 0 |

### *P1.1 Stronger relative selection for forest by females than males.*

Red deer *spatial use* showed positive effect of forest cover ($\beta = 1.48$, SE = 0.25, $z = 5.82$ $p < 0.001$; **Fig 10c & Table A5**), while distance to forest edge had a negative effect ($\beta = –0.25$, SE = 0.02, $z = -10.59$, $p < 0.001$; **Fig 10d & Table A5**), indicating higher *spatial use* of cover. However, no sex interactions were found, suggesting no sex-specific differences in *relative selection*.

### *P1.2 Convergent relative habitat selection for forest cover during winter.*

Red deer showed increased *spatial use* for areas closer to roads in *winter* (winter × distance to road: β = 0.15, SE = 0.06, z = 2.52, p = 0.012; **Fig 10a & Table A5**). No other spatial covariates showed seasonal effects, and no three-way interactions with sex were detected, indicating similar responses by both sexes.

### *P1.3 Reduced sex differences in relative habitat selection during the rut.*

During the rut (*fall)*, both *adult females* (β = 0.71, SE = 0.11, z = 6.25, p < 0.001; **Fig 9 & Table A5**) and *males* (β = 1.36, SE = 0.12, z = 10.85, p < 0.001; **Fig 9 & Table A5**) showed increased *seasonal activity* compared to juveniles (reference). Red deer showed *relative habitat selection* for open areas: *arable land* (β = 0.65, SE = 0.28, z = 2. 36, p = 0.018; **Fig 9 & Table A5**), and *infield pasture* (β = 0.62, SE = 0.23, z = 2.42, p = 0.008; **Fig 9 & Table A5**). Red deer also increased their *spatial use* near roads (β = 0.14, SE = 0.05, z = 2.83, p = 0.005; **Fig 10a & Table A5**), with no other significant spatial or sex-based interactions.

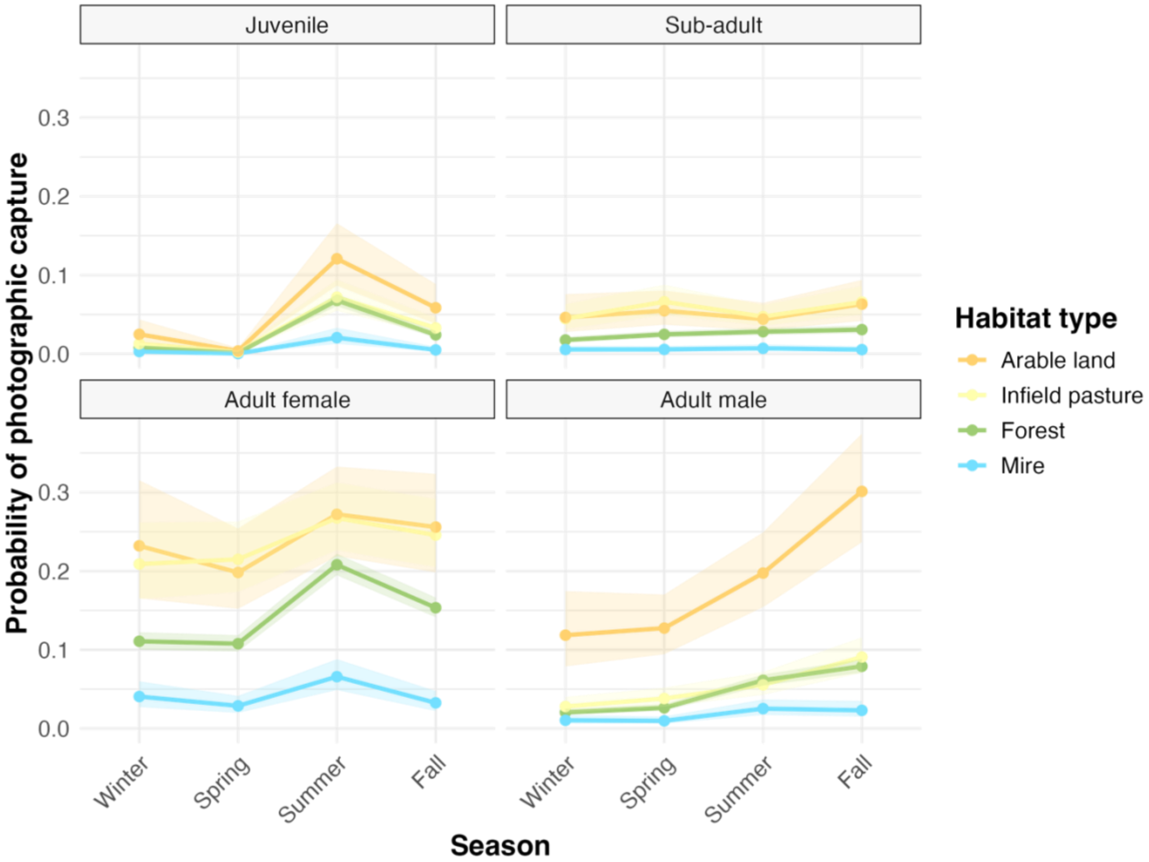

**Fig 9.** Estimated probability of photographic detection of red deer across four different habitats (*Infield pasture, arable land, forest, and mire*) and seasons (*winter, spring, summer, fall*). Predictions are derived from a generalized linear model (GLM) with a binomial error structure, including demographic categories (*juvenile, subadult, adult female, adult male*) and their interactions with the season and habitat type. The lines represent the predicted detection probabilities for each habitat type. Semi-transparent bands indicate the 95% confidence intervals around estimated probabilities.

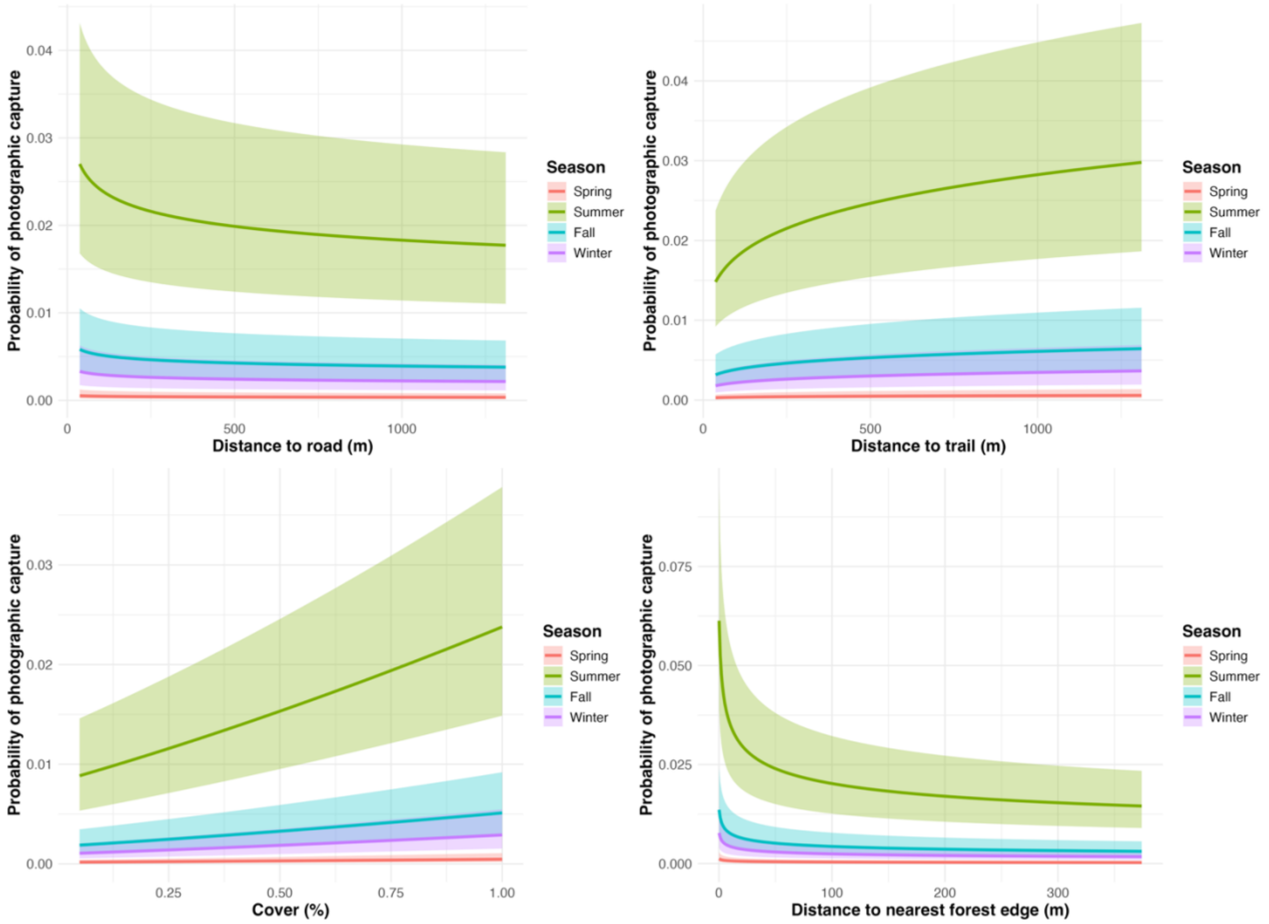

**Fig 10.** Predicted probability of photographic detection of red deer as a function of **a)** distance to the nearest road, **b)** distance to the nearest trail, **c)** proportion of forest cover, and **d)** distance to the nearest forest edge. Each panel shows predicted values from the top-ranked generalized linear model (GLM) including 95% confidence intervals (semi-transparent bands).

## 3.2 Immediate impact of hunting on red deer relative habitat selection

The best-supported model ($\Delta AIC < 2$) revealed that hunting, habitat type, demographic category, and interactions between spatial covariates (such as distances to roads, trails, and forest edges, and forest cover) all play significant roles in explaining red deer photographic detection during the hunting season (**Table 2**). The model with the strongest support ($\Delta AIC = 0.00$) included interactions among these factors, specifically between log-transformed distances (to roads, trails, and forest edges) and the proportion of forest cover.

Daily hunting pressure during the 10-day window was investigated (**Table A6**), showing only two hunting days during the period, with nine hunting events in total, equaling 0.9 hunting events per day.

**Table 2.** AIC-based model comparison assessing the immediate effect of hunting period on habitat selection on red deer, using photographic detection probability as the response variable. Candidate models included combinations of demographic category (demCat), hunting (TRUE/FALSE), habitat type (arealtype), and spatial covariates (log-transformed distances to road, trail, and forest edge, and proportion of forest cover). The number of variables, degrees of freedom (df), AIC value, AIC difference (ΔAIC), and model weight are presented for each model.

| **Models:** **immediate effect of hunting period** | **df** | **AIC** | **ΔAIC** | **AICWeight (%)** |
|---|---|---|---|---|
| detected ~ Hunting + arealtype + demCat + dist.road* dist.trail* cover * dist.edge | 23 | 2523.94 | 0.00 | 1.00 |
| detected ~ Hunting * arealtype + demCat + dist.road + dist.trail + cover + dist.edge | 15 | 2630.80 | 106.86 | 0.00 |
| detected ~ Hunting + demCat * arealtype + Hunting * dist.road + Hunting * dist.trail + Hunting * cover + Hunting * dist.edge | 25 | 2633.46 | 109.52 | 0.00 |
| detected ~ Hunting + demCat * arealtype + demCat * dist.road + demCat * dist.trail + demCat * cover + demCat * dist.edge | 33 | 2640.36 | 116.42 | 0.00 |
| detected ~ Hunting + arealtype + demCat | 8 | 2655.58 | 131.64 | 0.00 |
| detected ~ Hunting + arealtype * demCat | 17 | 2655.83 | 131.89 | 0.00 |
| detected ~ Hunting * arealtype + demCat | 11 | 2659.36 | 135.42 | 0.00 |
| detected ~ Hunting * arealtype + Hunting * demCat | 14 | 2664.81 | 140.87 | 0.00 |
| detected ~ Hunting * demCat * dist.road + dist.trail + cover + dist.edge | 40 | 2687.010 | 163.0697 | 0.00 |

### *P2.1 Avoidance of open and accessible areas following hunting onset.*

The onset of the hunting season led to a significant decline in red deer *activity* (β = -0.28, SE = 0.11, z= -2.63, p = 0.009; **Fig 11 & Table A6**). During the 10 day-window before as well as after the onset of hunting, there was a *relative selection* for open habitats: *arable land* (β = 3.67, SE = 0.65, z = 5.68, p < 0.0001; **Fig 11 & Table A6**) and *infield pastures* (β = 2.68, SE= 0.63, z = 4.23, p < 0.0001; **Fig 11 & Table A6**).

### *P2.2 Increased relative selection of remote forests by female after the hunting onset.*

In the 10-day period surrounding the start of the hunting season, females showed increased *activity* (β = 1.44, SE = 0.15, z = 9.60, p < 0.0001; **Fig 11 & Table A6**). Red deer showed higher degree of *spatial use* of remote, forested areas, specifically those with greater distances from roads (β = 25.05, SE = 5.81, z= 4.31, p < 0.0001; **Fig 12a & Table A6** ), trails (β = 22.99, SE = 5.88, z = 3.91, p < 0.0001; **Fig 12b & Table A6**), and forest edges (β = 66.34, SE = 13.03, z = 5.09, p < 0.0001; **Fig 12d & Table A6**). There were strong negative interactions between road and edge (β = -15.57, SE = 2.75, z = -5.66, p < 0.0001; **Fig 11a+d & Table A6**), trail and edge (β = -15.55, SE = 2.66, z = -5.86, p < 0.0001; **Fig 12b+e & Table A6**), cover and edge β = -71.76, SE = 19.71, z = -3.64, p < 0.0001; **Fig 12c+d & Table A6**).

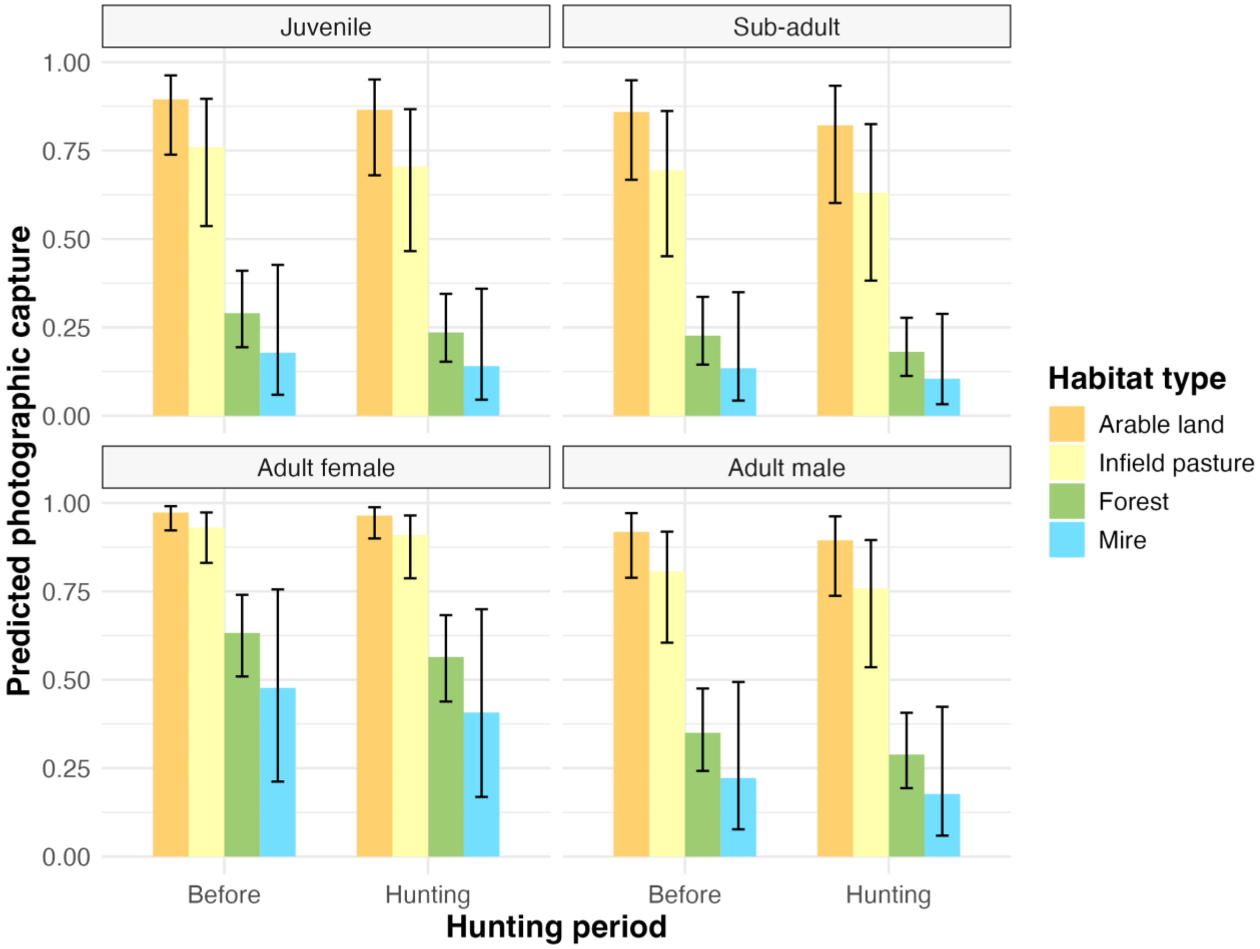

**Fig 11.** Predicted photographic probability of detecting red deer *before* (from 22nd August to 31st August) and the *hunting* season (from 1st September to 10th September) across four habitat types (infield pasture, arable land, forest, and mire), grouped by demographic category. Estimates are based on a binomial generalized linear model that includes interactions between demographic category and habitat type. Bars represent model-predicted detection probabilities, while error bars indicate 95% confidence intervals around those predictions.

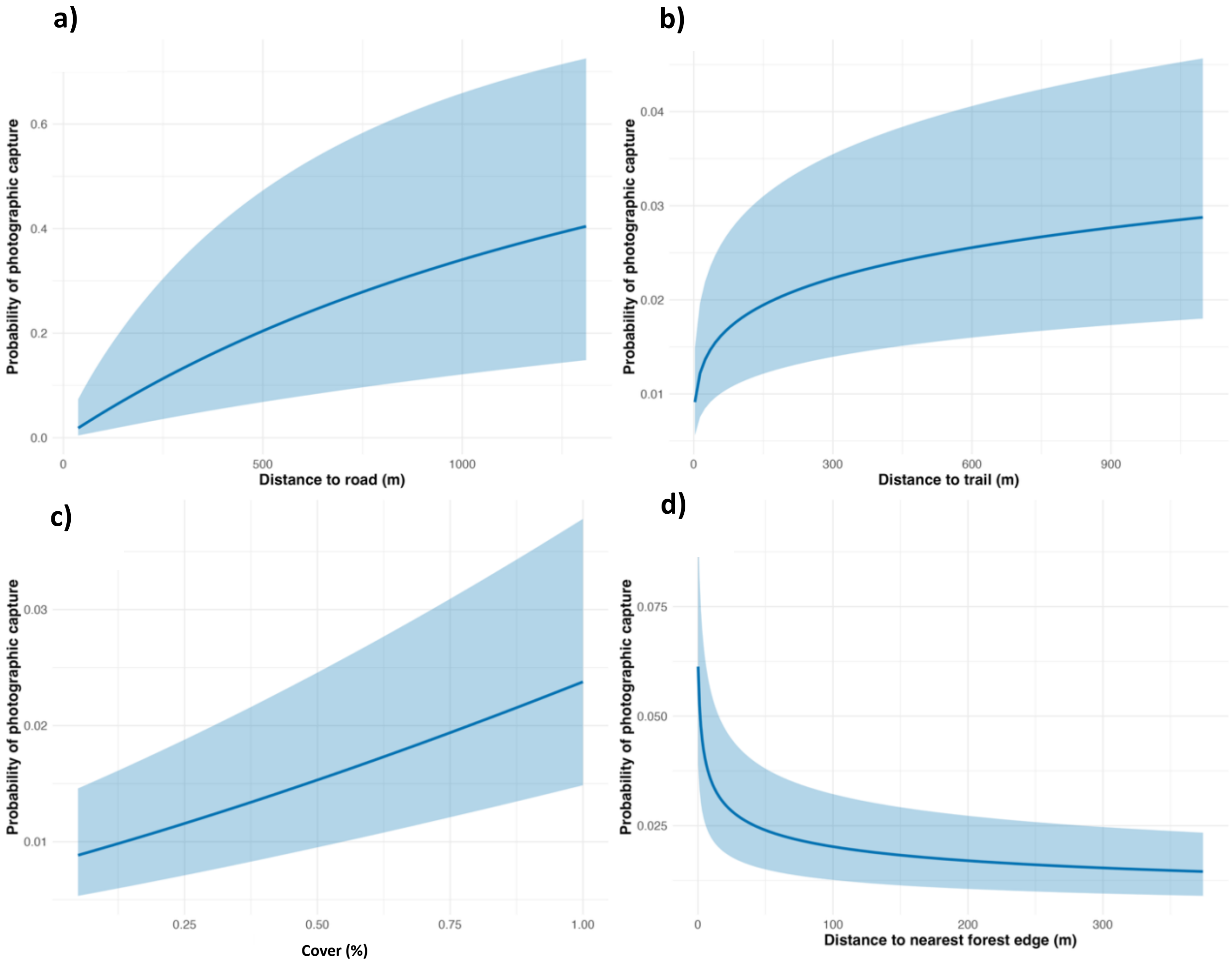

**Fig 12.** Predicted probability of photographic capture of red deer, both *before* the 10-day window of hunting and *during* the hunting period in relation to **a)** distance to road, **b)** distance to trail, **c)** forest cover, and **d)** distance to forest edge. Predictions are based on a generalized linear model, with all other covariates at their mean values. Semi-transparent bands represent 95% confidence intervals.

# 4 Discussion

Although sex-specific habitat selection driven by reproductive strategies and ecological constraints is commonly expected in ungulates, my findings provided limited support for such patterns. Instead, red deer seemed to be more shaped by *space use* (landscape features,) such as forest cover and proximity to roads, than by sex or seasonal reproductive behavior. The onset of the hunting season coincided with potential changes in red deer behavior, including increased overall *activity*. However, these activity changes did not correspond to sex-specific shifts in spatial habitat use. Across individuals, red deer increased their use of remote and less accessible areas during the hunting period.

## 4.1 Relative habitat selection: seasonal shifts and sex-specific differences

Overall, I found partial support for Hypothesis 1 (**H1**). Although all demographic groups showed higher *use* of open habitats (arable land and infield pasture), these differences were not statistically significant. However, females exhibited the highest overall *spatial use* across habitats and seasons. Pronounced seasonal shifts were observed, particularly in the increased *seasonal activity* in open areas during autumn and the rutting period by both sexes. Summer had the overall highest *activity,* though not significant. This was also evident in the landscape features, with increased *spatial use* of areas close to roads during the fall and winter, and less use of areas closer to trails during spring. Furthermore, areas with greater cover were used relatively more during winter.

### *P1.1 Stronger relative selection for forested habitats by females than males*

Prediction P1.1, which anticipated stronger selection for forested habitats by females than males, was not supported. There were no significant differences in *relative habitat selection* between sexes across seasons or habitat types. The expectation that females would preferentially select more forested habitats, for predator avoidance or maternal behavior was not met. However, red deer generally exhibited greater *spatial use* of areas with higher forest cover and closer proximity to forest edges. It is important to note that this pattern reflects an increased use of spatial features typically associated with forested environments, rather than a direct selection for "forested habitats" per se. Additionally, this pattern was more strongly influenced by seasonal variation than by demographic factors (sex).

Contrary to expectations, a greater overall use of open habitats, such as infield pastures and arable land, was observed across all demographic groups, even after adjusting for effort. This finding suggests that red deer in this system may exhibit a stronger preference for open areas than previously anticipated, potentially due to increased foraging opportunities or reduced perceived predation risk in the absence of large predators. Similar trends have been documented in other studies, where red deer preferentially utilized open or human-modified landscapes in environments with low or absent predation pressures (e.g., Godvik et al., 2009).

Nevertheless, the differences in habitat use between sexes were not statistically significant. While females exhibited the highest overall spatial use across seasons, this was not attributable to a disproportionate use of either open or covered habitats. Instead, their elevated detection rates may be more accurately explained by behavioral or ecological factors, such as increased movement rates, larger group sizes, or distinct activity patterns (Bowyer, 2004). This further supports the idea that, in low-risk or relatively homogeneous landscapes, habitat use patterns are more influenced by local availability and resource distribution than by strong sex-specific preferences (van Beest et al., 2012).

Importantly, distance to the forest edge was negatively correlated with spatial use, indicating a preference for edge habitats over deeper forest interiors or completely open areas. These ecotones - transitional zones between dense vegetation and open habitats - likely provide optimal conditions by combining visual concealment, thermal shelter, and access to high-quality forage (Kuijper et al., 2009). This is consistent with previous research suggesting that red deer and other large herbivores frequently select ecotones where the benefits of both habitat types, cover and forage, can be exploited (Beier & McCullough, 1990; Ciuti, Muhly, et al., 2012). However, to robustly attribute this pattern to active selection for ecological benefits, further investigation into behavioral responses in these edge habitats, such as feeding, resting, and vigilance, is needed to understand the trade-offs between resource acquisition and risk avoidance (as shown in Ciuti, Northrup, et al., 2012).

Crucially, no interactions were observed between sex and habitat, nor was there any seasonal variation in this relationship. These results suggest that sex-based differences in *relative habitat* selection are minimal in this system and may only emerge in more heterogeneous or risk-prone environments (Alves et al., 2013; Sih et al., 2010). The lack of evidence for stronger use of forest habitats by females across seasons, habitat types, or spatial gradients further supports the notion that such differences are context-dependent. As suggested by Alves et al. (2013), this pattern may be a consequence of the absence of large predators and low disturbance levels on Svanøy, which reduces the ecological pressures that typically drive sex-specific spatial segregation.

In summary, these findings do not support the hypothesis that females exhibit stronger selection for covered habitats than males. Instead, patterns of spatial use appear to reflect habitat availability and structural features such as forest cover and edge proximity, rather than intrinsic demographic preferences. This supports the growing consensus that red deer habitat use is highly flexible and shaped primarily by landscape structure and context .

### *P1.2 Convergent relative habitat selection for forest during winter.*

The hypothesis that red deer, particularly females, would select forested habitats in winter for thermal benefits was not supported by the data. However, *spatial use* declined sharply in winter across all demographic groups, in line with expectations for ungulates during energetically constrained periods (Arnold et al., 2004; Zweifel-Schielly et al., 2009). Red deer are known to reduce their metabolic rate during winter (Arnold et al., 2004), which diminishes their need for active foraging.

Interestingly, although detection probabilities were lowest in winter across all demographic groups, interaction terms revealed a positive effect on detection probability for both sexes during this season. This may indicate that, despite an overall reduction in activity during winter, red deer maintained certain movement patterns or behaviors, such as increased movement in search of forage or shelter, that increased their detectability relative to baseline winter activity levels. These findings suggest that the observed convergence in habitat selection during winter may be primarily driven by shared physiological constraints, such as reduced energy availability and the need to conserve resources, rather than by reproductive or social behaviors (Marchand et al., 2015; Meisingset et al., 2013; Mysterud & Østbye, 1999). To determine whether these patterns also apply to Svanøy, future studies should investigate how physiological limitations interact with other environmental variables, such as snow depth and food availability, to refine our understanding of red deer's winter habitat use and activity.

This interpretation is further supported by the relatively mild winter conditions on Svanøy, which is characterized by a strongly oceanic climate, unlike regions with harsh, snow-dominated winters, where red deer typically reduce their movement and seek sheltered habitats for thermal protection (Mysterud et al., 2001). Svanøy experiences minimal snow accumulation and more moderate temperatures (Klimaservicesenter, n.d.). These milder conditions likely reduce the energetic stress associated with winter, thereby decreasing the necessity for significant shifts in habitat selection to seek thermal cover. As Beier and McCullough (1990) emphasized, both low temperatures and deep snow significantly restrict deer movement. The absence of such constraints on Svanøy may help explain the more flexible and less distinct seasonal habitat selection observed in this study.

Moreover, the lack of strong seasonal interactions with anthropogenic features, such as distance to roads or trails, suggests that the stability in habitat use across seasons may be linked to the low-disturbance environment of Svanøy. This island experiences minimal human activity and no significant predator pressure (Jayakody et al., 2008). Although winter detection probability slightly increased with distance from roads, there was no clear evidence that red deer actively avoid roads or alter their habitat use in response to human-made features. This may partly reflect the limited spatial contrast on a relatively small island like Svanøy, where the difference between areas "near" and "far" from anthropogenic features is minimal. As a result, red deer likely maintain consistent spatial patterns across seasons, driven more by physiological constraints, such as reduced activity in winter, than by behavioral responses to external pressures.

Red deer demonstrated a weak, non-significant trend toward greater *spatial use* of areas farther from roads and with higher levels of forest cover during winter, reflecting patterns observed in previous studies. As noted in Prediction P1.1, this tendency is consistent with findings by Beier and McCullough (1990), , who reported that large herbivores often prefer habitats offering greater cover, especially in regions with low human disturbance. Although the effect of distance to roads was not statistically significant, the observed pattern may still reflect an ecologically meaningful response, particularly during winter when energetic constraints are more pronounced and access to sheltered habitats likely becomes more critical for minimizing energy expenditure.

The apparent convergence in habitat use during winter, where both sexes exhibit similar spatial patterns, is likely shaped more by shared physiological constraints than by social or ecological drivers. In the absence of harsh climatic conditions and major anthropogenic disturbance, red deer on Svanøy display considerable habitat flexibility. This supports the idea that in relatively undisturbed environments with mild winters, winter habitat use may be governed primarily by energetic needs and local resource availability, rather than by behavioral responses to external pressures or social dynamics (Jayakody et al., 2008; Mysterud et al., 2001).

*P1.3 Reduced sex differences in relative habitat selection during the rut.*

The increased *activity* of females and males is consistent with previous studies on ungulate species (Bonenfant et al., 2004; Loe et al., 2006). Although males increased their activity during the rut, there was no evidence that this heightened movement occurred in the same areas as females. This indicates that, despite both sexes becoming more active during this period, they did not converge spatially in their habitat use. Instead, males appeared to maintain a preference for specific habitats, likely more open areas that enhance visibility for displaying to rivals and attracting mates, while females, especially those with calves, continued to use denser, more sheltered habitats that offer cover and foraging opportunities. As a result, increased activity during the rut did not translate into shared space use, and spatial segregation between the sexes persisted, shaped by their distinct reproductive strategies and habitat requirements.

The absence of a reduced sex differences may reflect the ecological trade-offs. Even during the rut, males tend to prioritize more open habitats for visibility and access to mates (Ciuti, Muhly, et al., 2012), while females, particularly those with calves, are more likely to select denser, more sheltered habitats for safety and foraging (Bonenfant et al., 2004). This preference for open versus sheltered habitats could result in differential use of habitat types, limiting spatial overlap despite increased activity by both sexes during the rut. This is in line with the idea that sexual segregation in habitat use is context-dependent and influenced by ecological constraints like resource availability and predation risk (Loe et al., 2006).

Moreover, my results suggest that the low disturbance levels on Svanøy may not be sufficient to override the fundamental reproductive strategies that drive habitat use. While low hunting pressure might encourage more frequent use of a wider range of habitats, the rutting behaviors of males, characterized by more conspicuous displays and increased movement, may still influence their selection of open habitats. Meanwhile, females, particularly those with calves, may continue to prioritize habitats offering cover and protection from potential threats. This is consistent with studies that show female red deer in areas with moderate disturbance may maintain spatial segregation with males, as they select more sheltered habitats (Alves et al., 2013).

The relatively low spatial overlap between sexes observed in this study is somewhat unexpected given the homogeneity of the landscape on Svanøy. In theory, a uniform environment with limited habitat variation and stable resource distribution should reduce the opportunity — or need — for pronounced sexual segregation, potentially resulting in more similar spatial use between males and females. However, the observed pattern may instead reflect subtle differences in how each sex utilizes available habitat types within a shared landscape, particularly in response to seasonal reproductive demands. On more heterogeneous or disturbed landscapes, stronger sexual segregation is often observed, with males more frequently using open areas and females favoring denser, protective cover (Ciuti, Northrup, et al., 2012). In contrast, on Svanøy, both sexes may be responding to a narrower range of habitat cues, leading to differential fine-scale use rather than large-scale spatial separation.

Sexual segregation is dynamic and context-dependent, as seen in the variable patterns of relative space use during the rut. Although my study did not observe a full reduction in sexual segregation during the rut, the increased photographic detections of both sexes in the fall signal that the rut does trigger a shift in space use patterns. These shifts may not represent full spatial overlap, but they highlight that males and females adjust their movements and habitat preferences in response to the seasonal reproductive drive, as well as habitat structure and disturbance levels.

Overall, the findings from this study contribute to our understanding of seasonal shifts in habitat selection and space use among male and female red deer. The limited spatial overlap observed on Svanøy supports the idea that reproductive behavior and ecological constraints continue to shape habitat preferences, even during periods of increased activity. This further emphasizes the importance of habitat selection models that incorporate spatial, environmental, and behavioral factors to better understand how ungulates adapt to varying ecological conditions (Ciuti, Muhly, et al., 2012; Rowcliffe et al., 2008).

Taken together, results from *P1.1–P1.3* indicate weak and context-dependent sexual segregation in relative habitat selection. Both sexes used forested and open areas and showed no clear winter shift to forest. They differed slightly during the rut, likely due to reproductive roles.

## 4.2 Immediate impact of hunting on red deer relative habitat selection

The onset of the hunting season led to a noticeable decrease in red deer *activity*, supporting **H2**. While this response is consistent with the idea that deer perceive hunters as a significant threat, the effect appears to be generalized across the landscape, rather than showing specific changes in habitat preference. Specifically, red deer increased their *spatial use* of more remote and densely forested habitats during the hunting season, suggesting a preference for areas that provide concealment and reduced human disturbance. These shifts were most pronounced with increasing distance from roads, trails, and forest edges.

*P2.1 Avoidance of open and accessible areas following hunting onset.*

Red deer activity declined markedly following the onset of the hunting season, supporting prediction *P2.1*. This broad reduction in activity aligns with antipredator strategies aimed at minimizing exposure under elevated perceived risk (Lima & Dill, 1990). According to this model, prey may perceive hunting risk as spatially diffuse or omnipresent, particularly in intensively hunted systems, leading to widespread behavioral suppression rather than localized habitat shifts.

Contrary to expectations, my results do not support the idea that red deer avoid open or high-risk habitats, such as arable land and infield pastures. Instead, red deer were observed using these open habitats during the 10-day period before and after the onset of hunting. This suggests that red deer do not specifically avoid these habitats but instead exhibit a more generalized use of them. This pattern implies that their spatial behavior may not be driven solely by the avoidance of risky habitats, but rather by a broader risk-avoidance strategy, consistent with the "landscape of fear" framework (Laundré et al., 2014).

This interpretation is supported by studies suggesting that deer can perceive even forested habitats, which are typically considered refuges, as unsafe when hunting pressure is high (Bonnot et al., 2013). On Svanøy, during the 10-day period following the onset of hunting, only two days included actual hunting events. This results in a relatively low daily hunting pressure, calculated to be 0.9 hunting events per hunting day (**Table A7**). Given this low hunting pressure, it is important to consider whether the uniformity in activity reduction observed could be a result of insufficient hunting pressure to trigger habitat-specific responses. The relatively mild hunting disturbance on Svanøy may not have been sufficient to evoke a clear avoidance of high-risk habitats or drive pronounced changes in habitat selection, suggesting that deer on Svanøy may not perceive the same level of threat from hunting pressure as deer in areas with more intensive hunting activity.

Additionally, the low number of hunting events raises concerns about whether hunting pressure was truly high enough to influence spatial behavior or if other factors, such as general environmental conditions or ecological constraints, played a larger role. This may also explain the lack of observed avoidance patterns. Furthermore, sampling bias, particularly the lower number of cameras deployed in open habitats, may have limited the ability to detect habitat-specific responses (**Table A2**). More subtle shifts in habitat use might have occurred but remained undetected due to reduced statistical power in underrepresented habitat types. Therefore, future studies should explore how different levels of hunting pressure influence habitat use and spatial behavior, particularly in areas with minimal hunting disturbance, to better understand how red deer adapt to varying levels of risk.

Taken together, the results suggest that red deer on Svanøy respond to hunting pressure with a broad suppression of activity rather than selective habitat shifts. This generalist strategy has been observed in other large herbivores (Suraci et al., 2019; Thurfjell et al., 2017) and may reflect an adaptive response in landscapes where risk is unpredictable or spatially diffuse. However, the effect of hunting pressure on Svanøy should be interpreted cautiously due to the relatively low intensity of hunting activity during the study period. With only two days of hunting events occurring during the 10-day post-hunting onset window, it is possible that the level of disturbance was insufficient to elicit habitat-specific avoidance behaviors.

### *P2.2 Increased relative selection of remote forests by female after the hunting onset.*

Prediction P2.2 anticipated a distinct shift in spatial use during the hunting season, particularly among females, toward remote, forested areas—consistent with evidence that maternal females often display heightened sensitivity to predation risk (Ciuti, Northrup, et al., 2012; Lone et al., 2015). While a seasonal decline in overall red deer activity was evident, this reduction appeared to be additive rather than interactive with habitat type, as discussed in *P2.1*. In other words, activity levels declined broadly across all habitats, without strong statistical support for a targeted shift toward more secluded environments.

Although no significant season-by-habitat interaction was detected, red deer consistently showed the highest spatial use in remote, forested areas far from anthropogenic features. A strong four-way interaction between forest cover and distances to roads, trails, and forest edges highlighted that these structurally complex, low-risk areas were used more frequently throughout the year. This pattern likely reflects a baseline spatial preference rather than a hunting-driven shift, aligning with studies showing persistent reliance on spatial refugia under chronic disturbance (red deer: Bojarska et al., 2024; roe deer: Bonnot et al., 2013).

This interpretation must also be considered in light of the relatively low hunting pressure on Svanøy (Table A7). Compared to mainland areas, hunting activity on the island is limited in both intensity and spatial extent, with fewer hunters and more restricted temporal coverage. Such subdued levels of disturbance may reduce the incentive for dramatic behavioral changes, allowing red deer to rely on stable, conservative space-use strategies. In this context, their consistent use of structurally secure areas throughout the year may not reflect an acute response to hunting but rather a general risk-averse approach. These findings support research suggesting that perceived or chronic risk, rather than immediate threat levels, can drive avoidance behaviors in large herbivores

Contrary to expectations, females did not exhibit stronger spatial shifts than males during the hunting season. This absence of sex-specific divergence runs counter to earlier studies emphasizing sex-based differences in risk mitigation strategies (Ciuti et al., 2006; Jayakody et al., 2008), but may reflect the overriding effect of a perceived omnipresent risk. One plausible explanation is that both sexes perceived a uniformly elevated level of threat, consistent with the “super predator” hypothesis (Suraci et al., 2019), whereby prey adjust behavior broadly and conservatively under human hunting pressure.

In terms of spatial use, red deer increased their use of areas located farther from roads, trails, and forest edges, landscape features typically associated with human access (Coppes et al., 2017), while simultaneously decreasing use in areas with low vegetation cover or situated far from any structural edge. These opposing trends showcase the complexity of spatial behavior under threat: while red deer clearly favored structurally secure, secluded environments overall, they also made opportunistic forays into riskier, open habitats during specific time windows (Lone et al., 2014). Such patterns point to a context-dependent strategy in which animals weigh trade-offs between forage availability and safety on a fine spatial and temporal scale.

Taken together, these results suggest that red deer responded to hunting pressure through subtle shifts in spatial use rather than through wholesale changes in habitat selection. Even in the absence of strong season-by-habitat interactions, the combination of increased use of remote areas and reduced presence in more accessible sites supports the broader interpretation that red deer adopt flexible, risk-averse strategies under human disturbance. These findings are consistent with research showing that large herbivores adjust space use in response to anthropogenic threats, often at an energetic cost (Gaillard et al., 2010).

In summary, the results from *P2.1* and *P2.2* indicate that red deer responded to hunting pressure with a general reduction in relative spatial use across all habitats, rather than a distinct shift in habitat selection. Both sexes exhibited similar patterns, increasing their spatial use of remote, forested areas. There was no clear seasonal habitat preference or significant sex-based differences, suggesting that red deer adopt a broad, risk-avoidance strategy in response to hunting pressure

## 4.3 Use of camera traps of studying habitat selection

Camera traps offer several advantages in ecological research, particularly for monitoring elusive or wide-ranging species such as red deer. As a non-invasive and scalable method, they allow for long-term, continuous monitoring across broad spatial extents and difficult terrain. In this study, camera traps proved effective in capturing red deer presence and behavior across seasons, including responses to hunting pressure. Their capacity for fine-scale temporal and spatial resolution made them particularly valuable in detecting seasonal shifts in habitat use, aligning with findings from previous studies (Gregory et al., 2014).

Despite these strengths, camera traps are subject to detection biases influenced by environmental conditions. Dense vegetation, heavy canopy cover, weather, and camera positioning can significantly affect detection rates (Ancrenaz et al., 2012, p.4; Madsen et al., 2020). In this study, detection rates were notably lower in dense forested areas, likely leading to an underestimation of red deer use in those habitats. This limitation has been observed in other studies as well (Laughlin et al., 2023). Although detection probability was not corrected in this study using occupancy models (e.g., Royle et al., 2005), future work should consider incorporating such methods to address habitat-related variation in detectability.

Another important limitation is spatial autocorrelation. The deployment of cameras in a grid increases the likelihood of repeated detections of the same individuals at nearby stations, violating assumptions of independence and potentially biasing estimates of habitat use (Niedballa et al., 2015). While this issue was not explicitly modeled in the current analysis, hierarchical frameworks that incorporate spatial and temporal structure (e.g., Royle & Nichols, 2003) offer promising solutions. Future studies could also reduce spatial redundancy through more strategic camera placement.

Camera traps capture presence data but do not necessarily reflect true habitat preference, particularly when movement is driven by risk avoidance rather than selection (Kays et al., 2021). In this study, observed shifts into denser habitats during the hunting season may reflect avoidance of open areas rather than active preference for forested cover. Additionally, camera traps do not permit individual identification, limiting the ability to track movement or behavior at the individual level (Rowcliffe et al., 2008). Consequently, while broad patterns in habitat use were inferred, individual decisions and variability could not be directly assessed.

To enhance the analytical power of camera trap data, integration with other methods is strongly recommended. Combining camera traps with individual-based data such as GPS collars (Hofmeester et al., 2021) would allow researchers to verify presence data, track individual movements, and distinguish between habitat preference and risk-driven movement. Moreover, incorporating detection-correcting models such as occupancy models or resource selection functions (RSFs) could improve the robustness of habitat selection inferences (Bischof, Hameed, Ali, Kabir, Nawaz, et al., 2014; Ferrer-Ferrando et al., 2023; Semper-Pascual et al., 2022)

Overall, camera traps offer a powerful tool for studying red deer habitat selection and behavioral responses to environmental changes. This study highlights both their utility and their limitations. While they enabled the detection of seasonal habitat shifts, such as increased male use of open areas and female use of denser habitats during the hunting season, interpretation must be cautious due to detection bias, spatial autocorrelation, and the lack of individual identification. Future research should build on this approach by incorporating detection-correcting models and individual-level tracking to provide a more nuanced and accurate understanding of red deer habitat use and behavioral ecology.

## 4.4 Management implications

The consistent relative spatial use of forested areas across both sexes and seasons highlights the importance of prioritizing these areas in spatial planning and conservation efforts on Svanøy. To ensure red deer populations are effectively supported, it is crucial to maintain continuous forest cover and prevent fragmentation of dense stands, especially during sensitive biological periods such as calving (May–June) and rutting (September–October). Although no clear seasonal convergence in habitat selection between sexes was observed, the preference for edge areas, where forested habitats meet open spaces, suggests that management should focus on maintaining these transitional zones. These areas seems important for red deer, providing access to both dense cover and open foraging areas. .

The immediate decline in red deer activity following the onset of the hunting season indicates a behavioral response to human disturbance. To reduce the risk of biased data in long-term monitoring, it is recommended that post-hunting months (September–December) be excluded or analyzed separately, unless the focus is on studying hunting effects (Ciuti, Muhly, et al., 2012). Increasing camera deployments before the hunting season, when detection probabilities are higher, would improve the accuracy of estimates related to undisturbed habitat use.

From a harvest management perspective, focusing efforts along the periphery of dense forest patches, particularly in edge zones were deer transition between foraging and refuge areas, would be an effective strategy. This approach aligns with known spatial avoidance behaviors after disturbance, helping to reduce pressure on critical core refugia while still targeting areas with high deer activity(Jayakody et al., 2008; Jayakody et al., 2011; Lone et al., 2015). Restricting hunting in the high-use forest cores would help preserve undisturbed zones necessary for year-round occupancy.
In broader land-use planning, the strong preference for both forested areas and open zones near habitat edges, coupled with the lack of marked avoidance of roads, highlights the need for careful evaluation of infrastructure development. New forest roads or clearings should be planned with consideration of maintaining connectivity between these habitats to avoid fragmenting crucial edge areas. Even in predator-free environments like Svanøy, human-induced fragmentation can alter deer movement, potentially affecting reproduction and population structure (Ciach & Pęksa, 2019).

The behavioral sensitivity of red deer to hunting disturbance emphasizes the need for adaptive, spatially informed management tools. Predictive models (e.g., Griesberger et al., 2022) could help managers anticipate deer displacement patterns, informing decisions on seasonal access restrictions or rotating harvest zones. These strategies would avoid repeated targeting of high-suitability refuges.

For areas with denser road networks, mitigation strategies should focus on deer activity centers near forest edges, where high activity levels have been observed before the hunting season. Strategies such as wildlife crossings, road signage, and speed limit reductions should be implemented to mitigate the risk of vehicle collisions during high-movement months (August–October) (Meisingset et al., 2014; Meisingset et al., 2013). Additionally, crop protection measures, such as fencing or repellents, should be applied during peak activity periods to reduce the impact of deer on agricultural areas (Olaussen & Mysterud, 2012).

Although Svanøy's unique characteristics, a small island with no natural predators and a low human population, reduce human-wildlife interaction intensity compared to mainland areas, these findings have broader implications. In larger, more complex landscapes, similar behavioral patterns and habitat preferences may be observed. The interaction between red deer and other species, along with more intense human activity, must be considered. The observed preference for forested and edge habitats suggests that similar management strategies could be applicable in other regions with seasonal hunting pressures, making these recommendations relevant for broader landscapes. For multi-use landscapes, the findings should be adapted to account for species interactions, human infrastructure, and varying disturbance levels.

# Conclusion and synthesis

In this study, I investigated the habitat selection of red deer on Svanøy throughout the year, focusing on seasonal and sex-specific patterns. The results highlight the flexibility of red deer in both *habitat* and *spatial use,* with a clear preference for areas offering cover, such as forested regions and their edges, while also utilizing more open habitats like infield pastures and arable land. The absence of significant sex-based differences in habitat selection suggests that red deer employ a generalized strategy for balancing cover with accessibility, adapting to a variety of environmental conditions. A key finding of my study was the decline in red deer *activity* immediately following the onset of the hunting season. This response likely reflects a combination of decreased use of disturbed areas and shifts in activity patterns aimed at reducing human exposure, despite hunting being concentrated on only two of the ten days during the observation period. This suggests relatively low hunting pressure on Svanøy. These behavioral changes highlight the importance of incorporating such shifts into management strategies, particularly during critical periods like calving and rutting when red deer are especially vulnerable.

From a management standpoint, preserving key habitat types, particularly forested and edge habitats, is essential. Additionally, refining hunting practices to minimize disturbance during sensitive periods can help mitigate negative impacts on red deer behavior. Strategies such as rotating hunting pressure and aligning monitoring efforts with undisturbed activity windows will not only enhance data accuracy but also reduce the long-term effects of human disturbance on red deer populations.

Looking ahead, further research should examine how different levels of hunting exposure influence red deer behavior, particularly focusing on whether females with calves exhibit distinct responses to risk compared to males or sub-adults. Moreover, understanding how repeated exposure to hunting affects avoidance behaviors over time is crucial for developing sustainable management practices. Long-term monitoring combined with behavioral observations will provide deeper insights into how red deer adapt to human disturbances, offering more precise guidance for effective conservation strategies.

While this study is focused on Svanøy, its findings have broader implications for managing red deer in human-dominated landscapes. By emphasizing the dynamic, behavior-driven nature of habitat selection, future management approaches can be more adaptive, ensuring the sustainable conservation of red deer populations across both small and larger systems.

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# Appendices

## Appendix 1. Hunting pressure during the hunting period

**Table A1.** A number of hunting events were the response, ranging from 0 to 8 per day, with days since the start of the hunting period (1$^{st}$ of September) as the predictor. The hunting pressure (hunting events per day) shows a non-significant descending trend through September.

| Predictor | Estimate (Std. Error) | t-value | p-value |
|---|---|---|---|
| (Intercept) | 3.06 (0.54) | 5.65 | <0.001 |
| Days_since_start | -0.01 (0.008) | -1.79 | 0.086 |

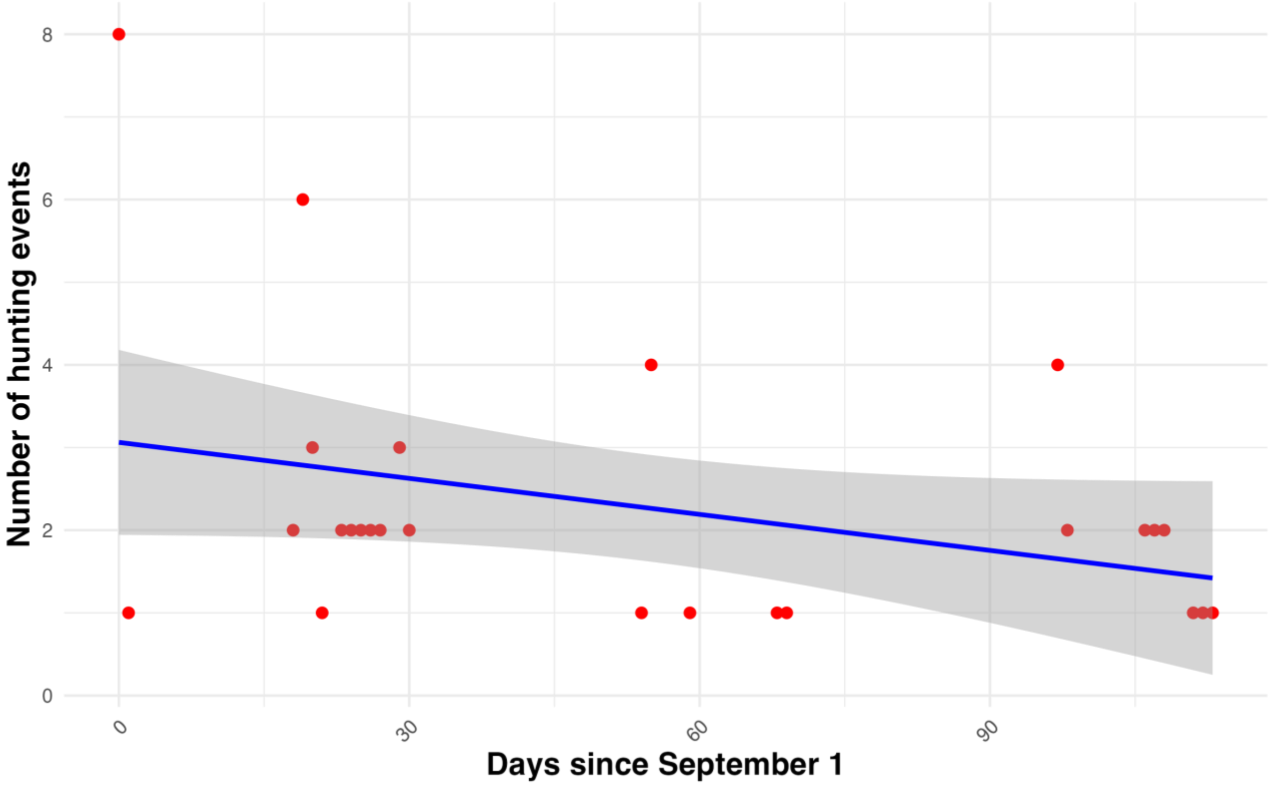


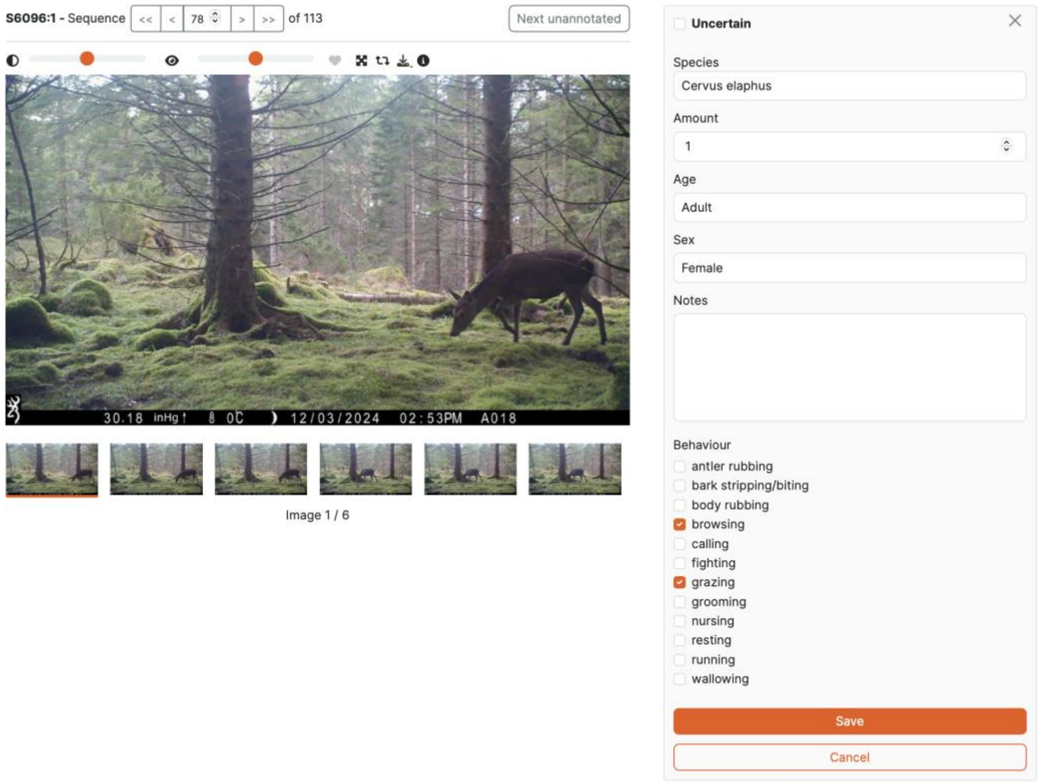
**Fig A1.** The hunting pressure (hunting events per day) shows a descending trend over time, but this is non-significant (β = -0.01, SE = 0.008, p-value = 0.086). A regression line with a slight downward slope indicates a weak but non-significant negative relationship between the number of hunting events and days since the start of the hunting period.

## Appendix 2. Road and trail network on Svanøy

Leaflet | Tiles © Esri — Source: Esri, i-cubed, USDA, USGS, AEX, GeoEye, Getmapping, Aerogrid, IGN, IGP, UPR-EGP, and the GIS User Community

**Fig A2.** Road and trail network on the study island displayed over Esri World Imagery. Red lines represent the mapped road network (roads.sf), and pink lines represent trails (trails.sf) extracted from spatial data in R.

## Appendix 3. Annotation of camera sequences from camera trap stations in Agouti



☐ **Uncertain**

Species: Cervus elaphus

Amount: 1

Age: Adult

Sex: Female

Notes:

Behaviour

☐ antler rubbing
☐ bark stripping/biting
☐ body rubbing
☑ browsing
☐ calling
☐ fighting
☑ grazing
☐ grooming
☐ nursing
☐ resting
☐ running
☐ wallowing

**Fig A3**. Set up on the Agouti website, with the option to choose species, how many individuals, age, sex, and behavior on 12 levels, as well as additional notes important for the sequence.

## Appendix 4. Camera photographic detection adjusted for effort

**Table A2**. Detection effort from 66 camera traps deployed across four arealtypes, adjusted for effort (active days). While fewer cameras were placed in arable land, infield pastures, and mire, these sites generally had longer deployment durations or yielded more detection events, resulting in higher effort per camera. Forest had the highest number of cameras, but the effort was more evenly distributed when standardized.

| Arealtype | Cameras | Total effort (days) | Mean effort per camera (days) |
|---|---|---|---|
| Arable land | 2 | 673 | 337 |
| Infield pasture | 4 | 1335 | 334 |
| Forest | 55 | 17172 | 312 |
| Mire | 5 | 1580 | 326 |

## Appendix 5. Correlation matrix for spatial covariates

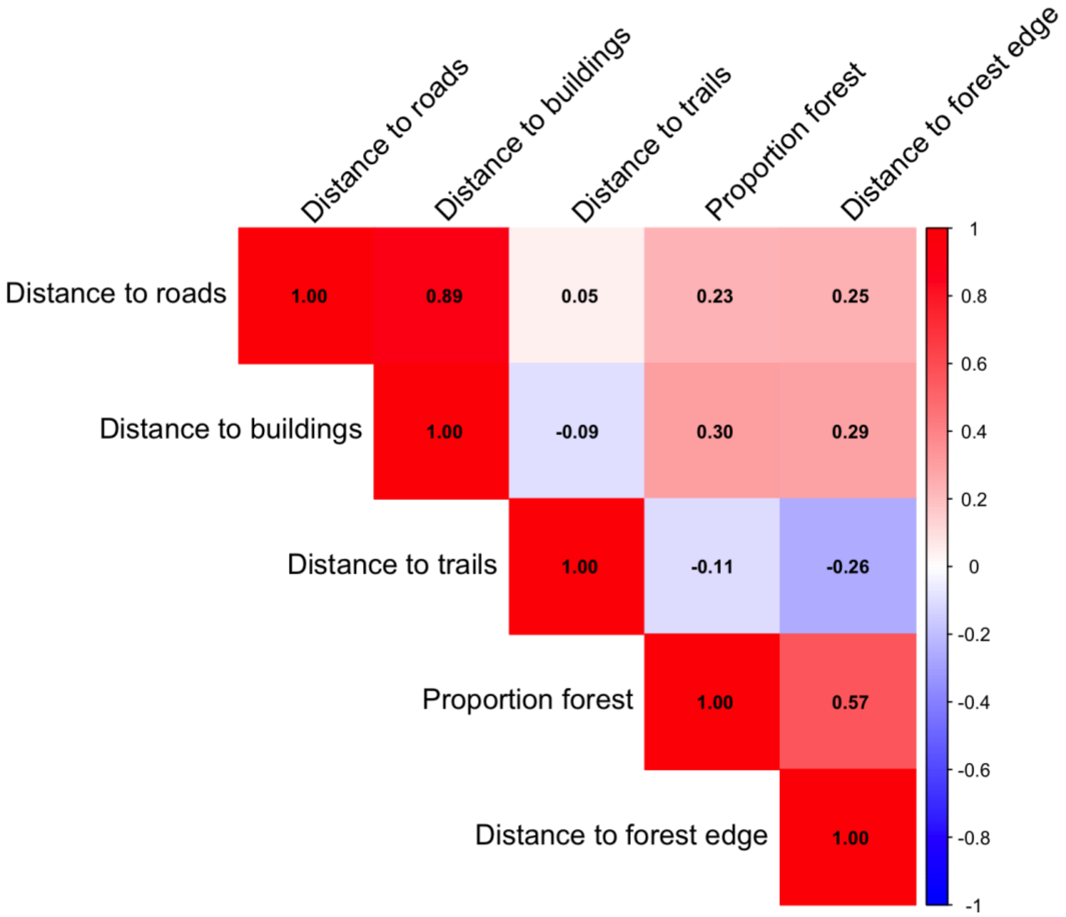


**Fig A4.** Results from the correlation test between the spatial covariates distance to road, distance to buildings, distance to trail, the proportion of forest, and distance to the nearest forest edge. There were strong correlations between the distance to the road and the distance to buildings, the proportion of forest, and the distance to the nearest forest edge.

## Appendix 6. Time windows assessing the sensitivity to the onset of hunting period

**Table A3**. Models assessing hunting pressure within a 15-day window. The response variable is "detection," and the models include multiple interactions between the predictor variables: Hunting, arealtype (habitat type), and demCat (demographic category). Additionally, several log-transformed distance variables (distance to road, trail, forest, and other factors) were incorporated into the models. The table presents the degrees of freedom (df), AIC (Akaike Information Criterion), ΔAIC (difference in AIC from the best model), and the model weight (relative likelihood of each model).

| Models for 15-day hunting window | df | AIC | ΔAIC | Weight (%) |
|---|---|---|---|---|
| detected ~ Hunting + arealtype + demCat + dist.road * dist.trail * cover * dist.edge | 23 | 3919.24 | 0.00 | 1.00 |
| detected ~ Hunting + demCat * arealtype + Hunting * dist.road + Hunting * dist.trail + Hunting * cover + Hunting * dist.edge | 25 | 4044.97 | 125.73 | 0.00 |
| detected ~ Hunting * arealtype + demCat + dist.road + dist.trail + cover + dist.edge | 15 | 4049.59 | 130.35 | 0.00 |
| detected ~ Hunting + demCat * arealtype + demCat * dist.road + demCat * dist.trail + demCat * cover + demCat * dist.edge | 33 | 4056.84 | 137.60 | 0.00 |
| detected ~ Hunting + arealtype * demCat | 17 | 4106.89 | 187.66 | 0.00 |
| detected ~ Hunting + arealtype + demCat | 8 | 4111.41 | 192.18 | 0.00 |
| detected ~ Hunting * arealtype + demCat | 11 | 4113.66 | 194.42 | 0.00 |
| detected ~ Hunting * arealtype + Hunting * demCat | 14 | 4119.18 | 199.95 | 0.00 |
| detected ~ Hunting * demCat * dist.road + dist.trail + cover + dist.edge | 40 | 4119.20 | 199.97 | 0.00 |

**Table A4**. Models assessing hunting pressure within a 20-day window. The response variable is "detection," and the models include multiple interactions between the predictor variables: Hunting, arealtype (habitat type), and demCat (demographic category). Additionally, several log-transformed distance variables (distance to road, trail, forest, and other factors) were incorporated into the models. The table presents the degrees of freedom (df), AIC (Akaike Information Criterion), ΔAIC (difference in AIC from the best model), and the model weight (relative likelihood of each model).

| Models 20-day hunting window | df | AIC | ΔAIC | Weight (%) |
|---|---|---|---|---|
| detected ~ Hunting + arealtype + demCat + dist.road * dist.trail * cover * dist.edge | 23 | 5149.01 | 0.00 | 1.00 |
| detected ~ Hunting + demCat * arealtype + Hunting * dist.road + | 25 | 5349.74 | 200.73 | 0.00 |

| | | | | |
|---|---|---|---|---|
| Hunting * dist.trail + Hunting * cover + Hunting * dist.edge | | | | |
| detected ~ Hunting * arealtype + demCat + dist.road + dist.trail + cover + dist.edge | 33 | 5353.22 | 204.20 | 0.00 |
| detected ~ Hunting * arealtype + demCat + dist,road + dist,trail + cover + dist,edge | 15 | 5357.03 | 208.02 | 0.00 |
| detected ~ Hunting + arealtype * demCat | 17 | 5431.68 | 282.66 | 0.00 |
| detected ~ Hunting + arealtype + demCat | 8 | 5439.30 | 290.29 | 0.00 |
| detected ~ Hunting * arealtype + demCat | 11 | 5441.46 | 292.45 | 0.00 |
| detected ~ Hunting * arealtype + Hunting * demCat | 14 | 5445.59 | 296.57 | 0.00 |
| detected ~ Hunting * demCat * dist,road + dist.trail + cover + dist.edge | 40 | 5457.77 | 308.76 | 0.00 |

## Appendix 7. Model output for seasonal habitat selection of red deer

**Table A5.** Summary of model estimates for red deer detection. This presents the estimated coefficients (log-odds) from the model examining red deer detections across different habitat types and seasons, considering demographic categories (subadult, female adult, and male adult) and environmental variables (dist.road = distance to roads, dist.trail = trails, and dist.edge = nearest forest edge, as well as cover = forest proportion).

| Term | Estimate | Std. Error | z value | Pr(>\|z\|) |
|---|---|---|---|---|
| **(Intercept)** | **-3.90** | **0.31** | **-12.69** | **<0.0001** |
| **Sub-adult** | **-1.10** | **0.35** | **-3.11** | **0,002** |
| **Adult female** | **1.22** | **0.26** | **4.60** | **<0.0001** |
| Adult male | 0.21 | 0.29 | 0.75 | 0,456 |
| **Fall** | **-1.89** | **0.38** | **-5.02** | **<0.0001** |
| **Spring** | **-3.04** | **0.50** | **-6.11** | **<0.0001** |
| **Winter** | **-3.63** | **0.45** | **-8.01** | **<0.0001** |
| **Arable land** | **1.88** | **0.30** | **6.25** | **<0.0001** |
| **Infield pasture** | **1.31** | **0.27** | **4.80** | **<0.0001** |
| **Forest** | **1.25** | **0.25** | **4.94** | **<0.0001** |
| **dist.road** | **-0.18** | **0.03** | **-6.05** | **<0.0001** |
| **dist.trail** | **0.24** | **0.02** | **10.44** | **<0.0001** |
| **cover** | **1.48** | **0.25** | **5.82** | **<0.0001** |
| **dist.edge** | **-0.25** | **0.02** | **-10.59** | **<0.0001** |
| **Sub adult:Fall** | **1.17** | **0.15** | **7.98** | **<0.0001** |
| **Female adult:Fall** | **0.71** | **0.11** | **6.25** | **<0.0001** |
| **Adult male:Fall** | **1.35** | **0.12** | **10.85** | **<0.0001** |
| **Sub-adult:Spring** | **3.89** | **0.34** | **11.52** | **<0.0001** |
| **Adult female:Spring** | **3.24** | **0.33** | **9.98** | **<0.0001** |

| | | | | |
|---|---|---|---|---|
| **Adult male:Spring** | **3.14** | **0.33** | **9.43** | **<0.0001** |
| **Sub-adult:Winter** | **1.74** | **0.20** | **8.80** | **<0.0001** |
| **Adult female:Winter** | **1.48** | **0.16** | **8.97** | **<0.0001** |
| **Adult male:Winter** | **1.09** | **0.19** | **5.80** | **<0.0001** |
| Sub-adult:Arable land | 0.01 | 0.42 | 0.02 | 0,985 |
| Adult female:Arable land | -0.21 | 0.33 | -0.65 | 0,515 |
| Adult male:Arable land | 0.37 | 0.35 | 1.06 | 0,288 |
| Sub-adult:Infield pasture | 0.66 | 0.38 | 1.71 | 0,087 |
| Adult female:Infield pasture | 0.34 | 0.30 | 1,12 | 0,261 |
| Adult male:Infield pasture | -0.49 | 0.33 | -1.50 | 0,133 |
| Sub-adult:Forest | 0.18 | 0.35 | 0.50 | 0,616 |
| Adult female:forest | 0.07 | 0.27 | 0.26 | 0,796 |
| Adult male:forest | -0.32 | 0.29 | -1.11 | 0,267 |
| **Fall:Arable land** | **0.65** | **0.28** | **2.36** | **0,018** |
| Spring:Arable land | 0.45 | 0.27 | 1.66 | 0,097 |
| Winter:Arable land | 0.30 | 0.31 | 0.95 | 0,343 |
| **Fall:Infield pasture** | **0.62** | **0.23** | **2.67** | **0,008** |
| **Spring:Infield pasture** | **0.58** | **0.24** | **2.42** | **0,016** |
| Winter:Infield pasture | 0.19 | 0.25 | 0.75 | 0,454 |
| Fall:Forest | 0.37 | 0.23 | 1.58 | 0,115 |
| Spring:Forest | 0.09 | 0.23 | 0.38 | 0,702 |
| Winter:Forest | -0.24 | 0.25 | -0.95 | 0,345 |
| **Fall:dist.road** | **0.14** | **0.05** | **2.83** | **0,005** |
| Spring:dist.road | 0.01 | 0.05 | 0.16 | 0,873 |
| **Winter:dist.road** | **0.15** | **0.06** | **2.52** | **0,012** |
| Fall:dist.trail | -0.06 | 0.04 | -1.69 | 0,090 |
| **Spring:dist.trail** | **-0.14** | **0.04** | **-3.65** | **<0.0001** |
| Winter:dist.trail | 0.04 | 0.04 | 0.83 | 0,409 |
| Fall:cover | -0.17 | 0.39 | -0.45 | 0,656 |
| Spring:cover | -0.23 | 0.41 | -0.55 | 0,585 |
| **Winter:cover** | **1.01** | **0.48** | **2.08** | **0,037** |
| Fall:dist.edge | 0.02 | 0.04 | 0.60 | 0,547 |
| Spring:dist.edge | -0.05 | 0.04 | -1.34 | 0,181 |
| Winter:dist.edge | 0.00 | 0.04 | -0.06 | 0,954 |

## Appendix 8. Full model output for the effect of hunting on habitat selection for red deer

**Table A6.** Summary of parameter estimates from the generalized linear model (GLM) assessing the effects of hunting, demographic category (sex and age), habitat type (arealtype), and log-transformed environmental covariates (log_road = distance to road, log_trail = distance to trail, log_edge = distance to nearest forest edge, and cover = proportion forest), including interaction terms, on red deer presence. Estimates are on the logit scale.

| Term | Estimate | Std. Error | z value | Pr(>\|z\|) |
|---|---|---|---|---|
| **(Intercept)** | **-94.08** | **26.92** | **-3.49** | **<0.0001** |
| **HuntingTRUE** | **-0.28** | **0.11** | **-2.63** | **0,009** |
| **Arable land** | **3.67** | **0.65** | **5.68** | **<0.0001** |
| **Infield pasture** | **2.68** | **0.63** | **4.23** | **<0.0001** |
| Forest | 0.63 | 0.62 | 1.02 | 0,305 |
| Sub-adult | -0.33 | 0.19 | -1.72 | 0,085 |
| **Adult female** | **1.44** | **0.15** | **9.60** | **<0.0001** |
| Adult male | 0.27 | 0.17 | 1.61 | 0,108 |
| **dist.road** | **25.05** | **5.81** | **4.31** | **<0.0001** |
| **dist.trail** | **22.99** | **5.88** | **3.91** | **<0.0001** |
| cover | 20.99 | 56.24 | 0.37 | 0,709 |
| **dist.edge** | **66.34** | **13.03** | **5.09** | **<0.0001** |
| **dist.road log_trail** | **-6.22** | **1.25** | **-4.98** | **<0.0001** |
| log_road:log_cover | -17.69 | 10.94 | -1.62 | 0,106 |
| log_trail:log_cover | -14.50 | 11.83 | -1.23 | 0,220 |
| **log_road:log_edge** | **-15.57** | **2.75** | **-5.66** | **<0.0001** |
| **log_trail:log_edge** | **-15.55** | **2.66** | **-5.86** | **<0.0001** |
| **log_cover:log_edge** | **-71.76** | **19.71** | **-3.64** | **<0.0001** |
| log_road :log_trail: log_cover | 5.93 | 2.28 | 2.60 | 0,009 |
| **log_road :log_trail: log_edge** | **3.68** | **0.57** | **6.50** | **<0.0001** |
| **log_road :log_cover: log_edge** | **18.43** | **4.05** | **4.55** | **<0.0001** |
| **log_trail :log_cover: log_edge** | **18.48** | **4.11** | **4.50** | **<0.0001** |
| **log_road :log_trail + 1: log_cover:log_edge** | **-4.66** | **0.84** | **-5.51** | **<0.0001** |

## Appendix 9. Hunting activity during the 10-day of hunting

**Table A7.** Hunting activity during the 10-day period following the onset of the hunting season (1–10 September 2024).

| Hunting days | Number of hunting events |
|---|---|
| 2024-09-01 | 8 |
| 2024-09-02 | 1 |
| Daily hunting pressure = 0.9 hunting events | |

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