Norwegian
University of
Life Sciences

Master's thesis 2025 45 ECTS
Faculty of Environmental Sciences and Natural Resource Management

The impact of anthropogenic disturbance on the interaction between brown bears (*Ursus arctos*) and semi-domesticated reindeer (*Rangifer tarandus*) during the calving period in mountainous habitat

Regine Marie Didriksen

Master of Science in Natural Resource Management

Picture from Långfjället.
Photo: Regine Marie Didriksen

Master’s thesis in Natural Resource Management

Faculty of Environmental Sciences and Natural Resource Management

NMBU Spring 2025

Norwegian Institute for Nature Research

Norwegian University of Life Sciences

40 år Skandinaviska Björnprojektet

Acknowledgements

I would like to sincerely thank my supervisor Ole-Gunnar Støen and Idre Nya Sameby for the opportunity to carry out a unique and rewarding fieldwork with cluster searches, GPS-data retrieval and handling of automatic people counters. Furthermore, also for Ole-Gunnar's valuable feedback and constructive guidance throughout the writing process. I am also truly grateful to my supervisor Inger Maren Rivrud, for her invaluable assistance with statistical analyses, insightful comments on drafts, and for patiently answering countless questions. This would not have been possible without your support. Huge thanks also go to my supervisor, Vegard Gundersen, for his direction and encouragement, and for participating in fieldwork and generously lending equipment. I am also grateful to Erik Stange for taking the time to explain the Strava-dataset in detail.

I would also like to thank the R-club for their ongoing help with statistics, with extra appreciation to Pierre Dupont for his patience and clear explanations. Many thanks as well to my friends Pauline and Ylva for reading through the final draft.

Finally, I want to thank all my fellow students for five memorable years, my partner for his steady support and encouragement, my parents for always believing in me, and my roommate Kaja for the many good conversations and dinners shared, I could not have done this without all of you!

Ås June 10, 2025

Regine Marie Didriksen

Regine Marie Didriksen

Abstract

Human recreational activity in natural landscapes has increased in the past decades. Combined with other land-use interests, this has placed significant pressure and disturbances on natural areas, along with impacts on ecosystems and interactions between species. Semi-domesticated reindeer (*Rangifer tarandus*) are a vital part of Sámi culture and livelihoods, and are especially sensitive to human disturbance during the calving period. In some areas can predators such as brown bears (*Ursus arctos*) cause economic losses to owners by preying on their livestock. This study aimed to assess whether human recreational activity in mountain calving grounds affects the habitat selection of brown bears and semi-domesticated reindeer during the calving period, and whether this in turn influences brown bear predation patterns.

Data utilized in this study included GPS-data from brown bears and semi-domesticated reindeer, carcass locations from reindeer killed by GPS-collared bears and human activity data. Both species' habitat selection was modelled through Resource Selection Functions (RSFs) with a use-availability design. The final model was used to develop habitat suitability and co-occurrence maps, which helped to identify suitable areas for each species and visualize where carcasses have been found.

Results showed that human recreational activity influenced both brown bears and semi-domesticated reindeer habitat selection, but at varying degrees. Brown bears consistently avoided areas with high human activity, while reindeer exhibited avoidance mainly in the early part of the calving period. Brown bears entered the mountain mostly during the night to predate on semi-domesticated reindeer, when human activity was low. Certain trails in the study area were more used by humans than others, offering guidance for visitor management. Human activity did not appear to influence brown bear predation patterns and may even act as a deterrent to bears if strategically managed.

This study highlights how human recreational activity affects the habitat selection of both species. Understanding these dynamics is crucial for future natural resource and visitor management, especially as human pressure on natural areas continues to grow. With informed management, a better coexistence between outdoor recreationists, wildlife and local livelihoods can be achieved.

Sammendrag

Friluftslivsaktivitet, også kalt rekreasjonsaktivitet, har økt i naturen de siste årene. I kombinasjon med andre arealinteresser skaper dette et økende press og forstyrrelser på naturområder. Den økte menneskelige tilstedeværelsen påvirker både økosystemer, dyreliv og tradisjonelle husdyrhold. Tamrein (*Rangifer tarandus*) er en sentral del av samisk kultur og næringsgrunnlag, og er særlig sensitiv for menneskelig forstyrrelser i kalvingsperioden. I tillegg kan rovdyr som brunbjørn (*Ursus arctos*) forårsake økonomiske tap for reineiere når de tar livet av reinsdyrene. Målet med dette studiet var å undersøke hvordan menneskelig rekreasjonsaktivitet i fjellområder påvirker valg av habitat hos tamrein og brunbjørn i kalvingsperioden, og om dette i sin tur påvirker brunbjørnens predasjonsmønster.

GPS-data fra tamrein, brunbjørn og tamreinkadaver ble kombinert med data på menneskelig aktivitet. Dataene ble brukt til å modellere habitatseleksjon gjennom en ressursutvelgelsesfunksjon (RSF) med et bruk-tilgjengelig design. Resultatene fra modellene ble også brukt til å lage habitat-egnethetskart for bjørn og tamrein, samt et kart for sannsynlig sameksistens mellom artene hvor kadaverlokasjonene også ble plottet for visualisering.

Studien viser at brunbjørn konsekvent unngår områder med høy menneskelig aktivitet, mens tamrein viser mest unngåelse i den tidligere delen av kalvingsperioden. Bjørnene benytter seg av fjellområdene på nattestid mens menneskelig tilstedeværelse er lav. Enkelte stier var tydelig mer brukt av mennesker enn andre, noe som gir verdifull innsikt for besøksforvaltning. Menneskelig aktivitet virket ikke til å påvirke predasjonsmønsteret til brunbjørn, og kan i noen tilfeller fungere som en barriere mot bjørn hvis det nyttes riktig.

Studien fremhever at menneskelig rekreasjonsaktivitet påvirker valget av habitat for både brunbjørn og tamrein. For å sikre god sameksistens mellom mennesker, dyreliv og tradisjonelt husdyrhold er det viktig med kunnskapsbasert natur og besøksforvaltning. Dette blir stadig mer aktuelt ettersom menneskelig press på naturen øker. Med riktig forvaltning kan en finne en bedre løsning for sameksistens mellom friluftslivsaktiviteter, tradisjonell samisk næring, lokalsamfunn, natur og dyreliv.

Table of contents

1. Introduction

Understanding how human recreational activity and disturbance affect both wildlife and traditional land use is becoming increasingly important as human pressure on natural areas increases. As the human population grows, so do the demands placed upon natural landscapes, putting these under pressure from multiple interests, such as recreational activities, forestry or infrastructure development (IPBES, 2019). Outdoor recreation activity is a central part of the Scandinavian identity and have together with nature-based tourism grown extensively over the past 20 years, contributing to environmental, cultural and economic changes in natural areas (Bell et al., 2009; Fredman & Tyrväinen, 2010; IPBES, 2019). Increasing numbers of people now seek nature-based experiences in national parks and nature reserves, engaging in activities such as hiking, fishing and enjoying solitude in scenic landscapes (Fredman & Tyrväinen, 2010; IPBES, 2019).

While nature-based activities offer health benefits to participants, the increasing use of natural landscapes adds pressure on ecosystems, local communities and indigenous cultural practices (Bell et al., 2007; Bell et al., 2009; Fredman & Tyrväinen, 2010; Gundersen & Rybråten, 2022). Natural areas are vital for wildlife conservation, but increasing human recreational use can displace wildlife from preferred habitats, disrupt natural behaviors and raise energy expenditure (Doherty et al., 2021). In an increasingly human-dominated world, understanding how human activity affects species interactions is essential for natural resource and visitor management (Doherty et al., 2021; Gaynor et al., 2021). This includes recognizing the indirect effects humans may have on predator-prey dynamics.

Predators influence prey not only through direct predation, but also by shaping their movement, distribution and behavior in response to perceived risk, a concept known as the "landscape of fear" (Lima & Dill, 1990; Brown et al., 1999; Laundré et al., 2010; Scoyoc et al., 2023). Humans are often described as a "super predator", given that our long history of hunting wildlife may evoke similar avoidance responses in wildlife, with recreational activity potentially perceived as a predation threat (Frid & Dill, 2002; Darimont et al., 2015). One species likely influenced by both natural predators and human activity is the semi-domesticated reindeer (*Rangifer tarandus*).

Semi-domesticated reindeer are primarily descendants of the European wild reindeer (*Rangifer tarandus tarandus*), which today exists only in southern Norway in small, isolated mountain populations (Rolandsen et al., 2022; Rolandsen et al., 2023). Semi-domesticated reindeer are herded free-ranging populations, and similar effects of human disturbance can be observed for these herds as for wild reindeer (Nieminen, 2013; Gundersen et al., 2022). Frid & Dill (2002) defined disturbance as animal avoidance responses towards humans or human-related infrastructure. During the calving period, female reindeer form larger herds and migrate to remote areas to avoid predators, while males follow separate strategies and are generally more tolerant of disturbance (Skarin & Åhman, 2014). Female reindeer are particularly sensitive to disturbances during the calving period, and this may lead them to perceive humans engaging in recreational activities as predators, responding with avoidance (Anttonen et al., 2011; Skarin & Åhman, 2014; Gundersen et al., 2022). This is a common anti-predator strategy among large mammals as they have been hunted for centuries (Frid & Dill, 2002; Helskog & Indrelid, 2011).

Semi-domesticated reindeer are expected to prefer open mountain habitat during calving where they have a better overview of potential threats (Skarin & Åhman, 2014). Previous studies of semi-domesticated reindeer have shown that their behavioral response to human disturbance is influenced by a range of factors. These include season, year, herd size, handling by herders, the population's adaptability, previous exposure to humans, the frequency and type of human activity, and the availability of opportunities for avoidance (Skarin, 2006; Vistnes & Nellemann, 2008; Skarin et al., 2010; Anttonen et al., 2011; Skarin & Åhman, 2014; Sivertsen et al., 2016; Gundersen et al., 2022). Semi-domesticated reindeer may respond to human recreational activity with either habituation or avoidance, leading to displacement from preferred habitats (Hammitt et al., 2015; Gundersen et al., 2022). Disturbances during the sensitive calving period may also reduce parental care, disrupt feeding and increase predation risk, as females are likely to flee when disrupted (Vistnes & Nellemann, 2001; Anttonen et al., 2011; Skarin & Åhman, 2014; Hammitt et al., 2015).

Many of the Sámi people, recognized as indigenous, rely on semi-domesticated reindeer husbandry as a central part of their livelihood (Ravna et al., 2024). This practice developed in the 1500s-1600s and has since remained a fundamental part of the Sámi tradition and economy. Reindeer herding depends on large open landscapes, and the animals roam freely for parts of the year, making them vulnerable to human disturbance, predation and habitat loss (Røed et al., 2014; The International Centre for Reindeer Husbandry, s.a.). Research from forested reindeer herding districts in Sweden has shown that brown bears (*Ursus arctos*) can be significant predators of semi-domesticated reindeer, accounting for 39-62% of calf mortality, and causing substantial losses for herders (Støen et al., 2022; Tallian et al., 2023). To expand this understanding to mountainous terrain the Norwegian Institute for Nature Research (NINA) conducted a six-year study in Idre Sámi reindeer herding district, where calving takes place in mountain habitat. Although mountain areas are less preferred by brown bears, short distances between forest and mountain habitats allows bears to detect and access reindeer if conditions are favorable (Støen et al., 2025).

The brown bear has been present in Scandinavia since the last ice age and was among the first animals to follow the wild reindeer when the ice retreated (Sørensen, 2012). Brown bears are omnivorous and prefer coniferous forest and remote terrain where they are less exposed and can hide in vegetation (Ordiz et al., 2011; Bevanger, 2021). Historically, improved weaponry and bounty hunting brought the species close to extinction before protective measures were introduced (Swenson et al., 1995; Bischof et al., 2019). Previous studies have shown that GPS-collared brown bears typically avoid areas with high human activity, reduce daytime movement, increase nocturnal activity, and move away or seek cover in dense vegetation in response to human presence (Ordiz et al., 2011; Ordiz et al., 2013; Ordiz et al., 2019). Brown bears have also been found to utilize the same areas as humans when human activity is low, e.g. at nighttime (Martin et al., 2010; Ordiz et al., 2016). This demonstrates a clear anti-predator strategy, where humans are related to the risk of mortality and these behavioral adaptations allow bears to persist in human-dominated landscapes (Martin et al., 2010; Ordiz et al., 2011; Ordiz et al., 2013; Ordiz et al., 2019).

Human-wildlife interactions between carnivores and livestock are well documented, controversial and conflict ridden, as predation causes economic losses for herders (Frank & Glikman, 2019; Linnell & Kaltenborn, 2019; IUCN, 2022). However, the effect of human recreational activity on interactions between predators and livestock, and potentially predation patterns, is understudied. The responses of each species depend on factors such as human activity type, timing, frequency, and predictability, as well as species-specific and individual tolerance levels (Hammitt et al., 2015; Gundersen et al., 2022). Increased human presence may displace semi-domesticated reindeer into smaller more predictable areas, limiting their ability to evade predators and potentially increasing spatial overlap with brown bears and thus enhancing predation risk (Vistnes & Nellemann., 2008; Hammitt et al., 2015; Scoyoc et al., 2023). This suggests that human presence may indirectly increase predation risk by altering habitat selection.

On the other hand, semi-domesticated reindeer are somewhat accustomed to humans through supplemental feeding, calf-marking and herding, and may habituate to human disturbance over time (Skarin, 2006; Skarin et al., 2010; Anttonen et al., 2011; Nieminen, 2013; Skarin & Åhman, 2014). If reindeer could tolerate nearby recreationists, human presence could act as a buffer, deterring brown bears that generally avoid humans (Muhly et al., 2011; Ordiz et al., 2013; Ordiz et al., 2019; Scoyoc et al., 2023). Understanding how both species respond to human recreational activity and disturbance is crucial for evaluating potential impacts on predation, and informing management strategies in areas with similar challenges (Hammitt et al., 2015).

This study aimed to assess whether human recreational activity in mountainous terrain affects the habitat selection of both brown bears and semi-domesticated reindeer, and whether this, in turn, influences brown bear predation patterns. Based on previous findings, the following hypothesis and predictions were posed.

I hypothesize (H1) that human recreational activity influences both brown bear and semi-domesticated reindeer habitat selection within mountain calving areas, because both species avoid humans as part of an anti-predator strategy (Ordiz et al., 2011; Ordiz et al., 2013; Skarin & Åhman, 2014; Ordiz et al., 2019). In support of (H1), I predict the following:

(P1) Brown bears and semi-domesticated reindeer will show avoidance of areas with high human trail density and show selection for areas with low trail density.

(P2) Brown bears and semi-domesticated reindeer will show avoidance of areas with higher levels of human recreational activity compared to those with lower levels.

(P3) Brown bears and semi-domesticated reindeer will show selection for mountain habitat closer to the forest/tree line rather than habitat further away where they are more exposed.

(P4) Brown bears and semi-domesticated reindeer will show selection for areas with a greater distance to trails and buildings, and show avoidance for areas nearby these features as they are associated with human activity.

(P5) There is a higher probability of co-occurrence between semi-domesticated reindeer and brown bears near the forest. Because reindeer may be displaced to areas close to the forest to avoid human disturbance during calving, while brown bears favor areas close to forest.

Secondly, I hypothesize (H2) that human recreational activity in mountain calving grounds increases brown bear predation on semi-domesticated reindeer as both reindeer and bears avoid human presence during the calving period, leading them to co-occur in areas where reindeer are more vulnerable to predation (Mills & Harris, 2020; Scoyoc et al., 2023). In support of (H2), I predict the following:

(P6) Semi-domesticated reindeer carcasses will be more frequently located in areas of higher predicted probability of co-occurrence, i.e. where spatial overlap between reindeer and brown bears is expected to be greater and thus also the probability for brown bear predation on reindeer.

2. Materials and methods

2.1 Study area

This study was conducted in Idre, within Älvdalens municipality in the northwestern parts of Dalarna County in Sweden (Figure 1). Idre Nya Sameby, Sweden's southernmost Sámi reindeer herding community, has its herding area here. A Sámi reindeer herding community (Sameby) refers to a defined geographical area, and to an economic union of Sámi herders who hold the legal right to practice reindeer husbandry. The study area is in the transition between the alpine and boreal zones and is found between 440 and 1193 meters above sea level, with the highest peak at Storvätteshågna, standing 1204 meters above sea level. Pine forest dominates the landscape below the mountains and is home to wildlife such as moose (*Alces alces*) and hare (*Lepus timidus*) (Støen et al., 2025; Länsstyrelsen Dalarnas län, s.a.).

NINA's research project was conducted within a broader study area encompassing several protected areas, including Städjan-Nipfjället Nature Reserve, Töfsingdalen National Park and Långfjället Nature Reserve consisting of both forest and mountain habitat. Beyond the protected areas are large sites of actively managed forest, resulting in numerous clear-cut areas and an extensive network of forest roads. The landscape is also shaped by tourism, with the presence of skiing facilities, hotels, cabins and numerous hiking and skiing trails (Støen et al., 2025). Långfjället nature reserve along with Grövelsjön mountain station and Södra Kungsleden trail are popular mountain destinations for outdoor recreation and nature-based tourism. Numerous winter and summer trails start from cabin areas at Lövåsen and Grövelsjön mountain station, with destinations at rental cabins at the lake Hävlingen or the mountain peak Storvätteshågna (Figure 2). The reserve lies within Idre Sámi herding community's traditional lands and is used for reindeer husbandry year-round (Länsstyrelsen Dalarnas län, s.a.).

Reindeer herding in Idre has been practiced for centuries and follow the reindeer's seasonal movements between different grazing areas (Støen et al., 2025). Some remnants of older Sámi settlements, as well as historic trapping pit systems can still be found throughout the reserve, and the landscape includes some fences and herder huts. The Sámi herders are allowed to have up to 2700 animals in the winter herd (Støen et al., 2025; Länsstyrelsen Dalarnas län, s.a.). The specific study area of this thesis lies within Långfjället Nature Reserve and covers 178 km² of mountain habitat above the tree line (Figure 2). This is the core area where most of the semi-domesticated reindeer, hereafter referred to as reindeer, give birth during the calving period, and where many people go skiing or hiking along marked trails (Støen et al., 2025).

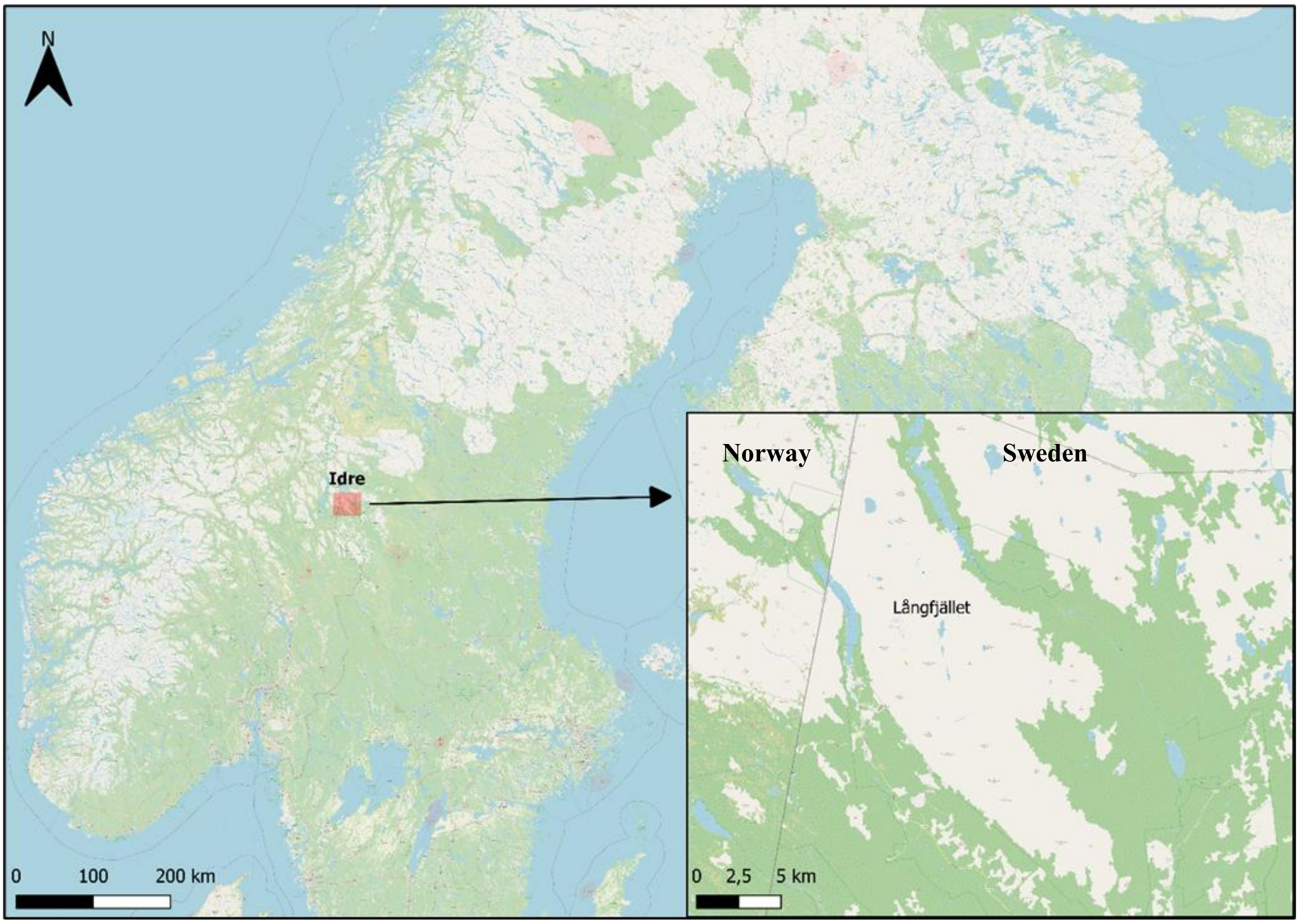

Figure 1: Location of Idre with a closer view of the study area in mountain Långfjället, situated within Idre Sámi reindeer herding district, Dalarna County, Sweden.

2.2 Data collection

Most of the datasets used in this study, including reindeer carcass-data and GPS-data on both brown bears and reindeer, were collected by NINA as a part of their larger research project in Idre (Støen et al., 2025). In addition to NINA's datasets, this study incorporates data on human activity collected from automatic people counters, hereafter called counters, as well as data from the Strava Metro database and the web-based visualization tool Strava Global Heatmap. This study focuses specifically on the calving period, utilizing data collected within the mountain calving grounds between May 1 and June 20, which is the period from the calving starts until the reindeer are gathered for calf-marking (Støen et al., 2025).

2.2.1 GPS-data and carcass data collected by NINA

During NINA's research project, thirty-three brown bears (12 females and 21 males) were immobilized from helicopter and equipped with pre-programmed GPS-collars (Vertex Plus collars, VECTRONIC Aerospace GmbH, Germany). Captures were conducted in accordance with protocols of the current Scandinavian brown bear research project and under permits from the relevant authorities in Sweden and Norway (Arnemo & Evans, 2017; Støen et al., 2025). For each GPS-collared individual, a position was recorded every five minutes from May 1 to June 20 while the bear remained within a virtual fence, hereafter referred to as the spring polygon. The spring polygon was defined based on traditional knowledge of calving areas used by reindeer and encompassed an area of 855 km² surrounding the core mountain area of focus in this study (Figure 2; Støen et al., 2025).

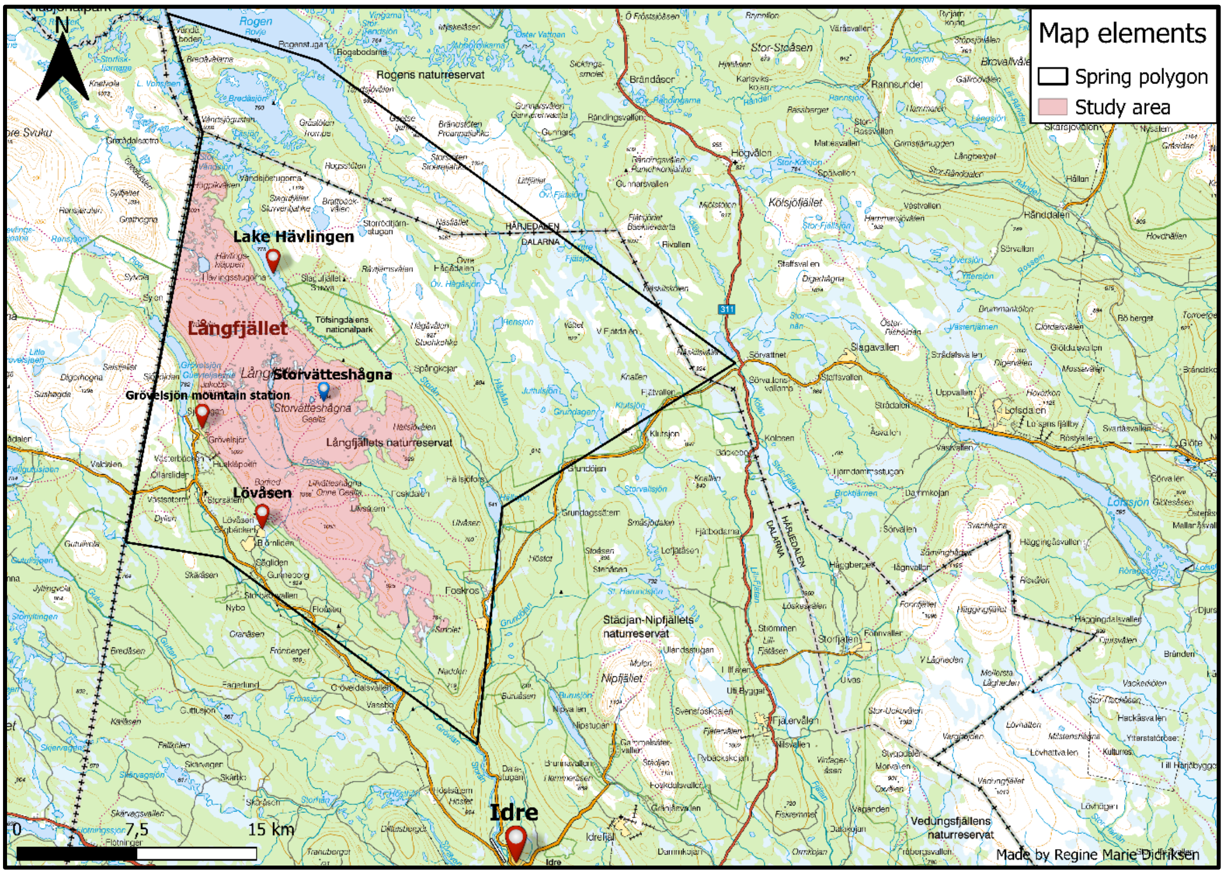

Figure 2: Overview of the study area located inside the spring polygon used for cluster searches during the study period (May 1 – June 20). The spring polygon is marked with a black line from the Norwegian border, whereas the study area is marked in light red color and represents the mountain habitat of Långfjället nature reserve.

Based on the recorded GPS-data, potential predation sites, hereafter referred to as cluster sites, were identified according to the movement behavior of the GPS-collared brown bears inside the spring polygon. Cluster sites were defined as locations where a brown bear remained within a radius of 30 m for more than ten minutes (i.e. at least 3 consecutive GPS-positions; Støen et al., 2025). Each morning, GPS-data were retrieved from the Swedish Wireless Remote Animal Monitoring (WRAM) system (https://wram.slu.se/public), processed in R, and visualized in Quantum Geographic Information System (QGIS) to locate new cluster sites. Each cluster site was assigned to a field team, consisting of a researcher from NINA and a representative from Idre Sámi reindeer community.

The aim was to visit cluster sites as early as possible after detection, but not until the bear was at least one kilometer away and moving away from the site, to minimize disturbance and avoid influencing behavior. Typically, the cluster sites were visited within 1-2 days after the bear had left the site (Støen et al., 2025). The field team used handheld Garmin GPS-devices to navigate to the cluster sites and investigate signs of brown bear activity, such as feces, fur or resting sites. If a carcass was found (Figure 3), the researcher secured the GPS-coordinates and conducted a detailed examination, documenting the species, sex, age, carcass condition, freshness and the likely cause of death on a standardized field form (Støen et al., 2025).

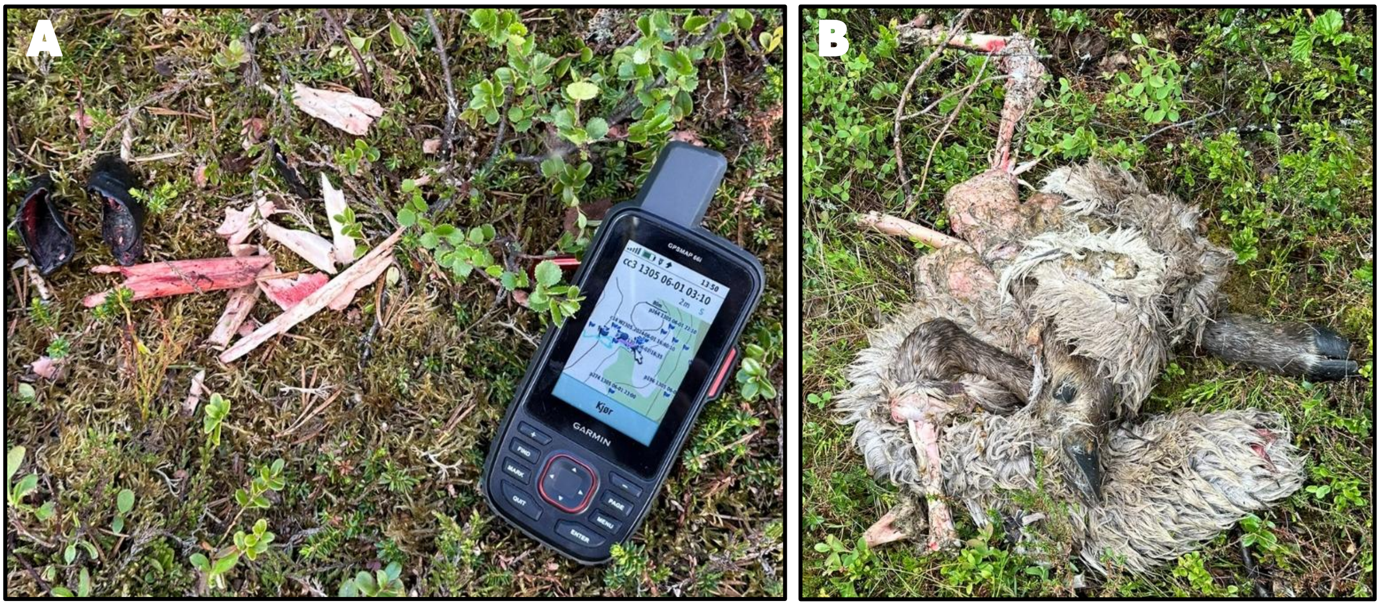

Figure 3: Remains of semi-domesticated reindeer carcasses found during cluster searches in June 2024. The images illustrate the range of findings encountered in the field. Photo A shows how minimal the remains can be by the time a researcher arrives at the site.

In addition to GPS-monitoring and cluster site investigations of brown bears, GPS-data were also collected from reindeer to document their movement patterns and habitat use during the calving period. Only GPS-data from female reindeer was analyzed in this study, as the focus was on the calving period when females and males live in separated groups (Bevanger, 2015). Approximately 25 female reindeer were fitted with GPS-collars (Followit AB, Lindesberg, Sweden) each year during NINA's research project, with a total of 143 individuals over the course of the study. The GPS-collar was pre-programmed to record two locations per day by default. However, collars with sufficient battery capacity recorded one position per hour, which made it possible to follow daily movement and determine the time of calving for GPS-collared individuals (Støen et al., 2025).

2.2.2 Data collection on human recreational activity

Data on human spatiotemporal recreational activity was collected by a combination of the following data: counters, crowdsourced data from Strava Metro and Strava Global Heatmap, marked trail networks from a public map, and local knowledge. Eight counters were deployed along well-known skiing and hiking trails within the study area. Since recreational use of the landscape shifts with seasonal changes in snow cover and trail availability, from skiing in spring to hiking in early summer, the calving period was divided into two sub-periods for the analysis. This division of periods was informed by local insight regarding both seasonal change in snow cover and dominant type of recreational use of the area. Period 1 (May 1 to 23) represents skiing season, while period 2 (May 24 to June 20) represents hiking season.

Strava Global Heatmap and Strava Metro

Crowdsourced data from the training app, Strava, were used to describe the spatial network of recreational use, through the sources of Strava Global Heatmap (http://strava.com/maps; only visualization on map) and Strava Metro (downloaded spatiotemporal data on recreational use). Strava is a free fitness tracking app that tracks the user's activity (route, distance, pace, time) using the phone's inbuilt GPS, and uploads the data to the central platform called Strava Metro (Venter et al., 2023).

Strava Global Heatmap is a publicly available web-based visualization tool, which is used in this study for two purposes. The heatmap visualizes aggregated, anonymized data from the Strava app users, using color intensity to indicate activity levels (Figure 4). Users of the heatmap can filter the map by activity and season, making it a valuable tool for identifying popular trails across different areas (Venter et al., 2023; Stange et al., 2024; Barton et al., 2025). Firstly, the heatmap was examined prior to fieldwork to identify strategic locations for positioning the counters, in combination with local insight regarding entry and exit points to the mountain. Secondly, it was used during the analysis to determine the most frequently used trails in the mountain area.

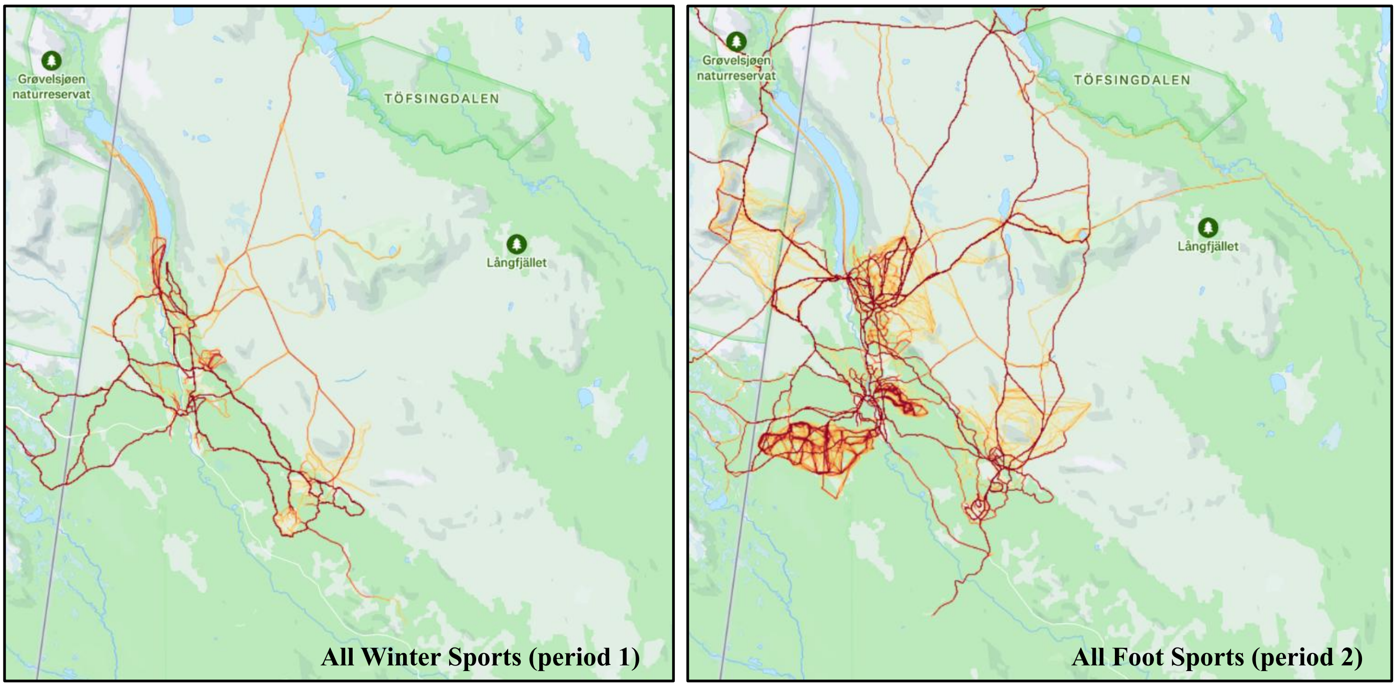

Figure 4: Excerpts from Strava Global Heatmap showing human recreational activity patterns within and near the study area, based on users tracking their movements with Strava. The left map displays "All Winter Sports" activity, while the right map shows "All Foot Sports" activity, both using the orange heat intensity setting. Darker colors indicate areas with higher levels of use while fainter colors indicate lower levels of use.

Strava Metro is a data-sharing platform that provides aggregated human activity data from Strava app users. Access to downloading data is granted to research institutes and public agencies that have agreements with Strava Metro. The dataset includes numerous trail segments that vary greatly in length, from just a few meters to several kilometers. This means that one trail distance can consist of either a few or many segments (Stange et al., 2024). In this study, segments categorized as "All Foot Sports" activities (walking, running, hiking) were downloaded from Strava Metro in August 2024, covering monthly data from 2019 to 2024. However, the dataset lacked several segments from June 2024 and did not include winter-sport activity as originally intended (as showed visually in Strava Global Heatmap, Figure 4), because Strava administration restricted data access to “All Foot Sports”.

Therefore, spatial segments were used without their associated human activity data. Instead, each trail segment was manually assigned a human activity value based on counter registrations, and incorporated into the statistical analysis. Additionally, the trail network was imported into QGIS (version 3.34.14) for visualization purposes (QGIS.org, 2025).

Automatic people counters (counters)

Temporal human recreational activity was recorded by eight counters (A-H). These were installed along various skiing and hiking trails within the study area in Långfjället nature reserve (Figure 5). The counters used were the Eco Twin model (EcoCounter) with a pyroelectric sensor that is sensitive to infrared radiation released by human bodies. These counters were selected because of their ability to record and store data at 15-minute intervals, operate across a wide range of temperatures and are waterproof (Andersen et al., 2013). The counters were mounted inside a carved wooden box to hide the sensor and the equipment and positioned as discreetly as possible for the people passing on the trails (Figure 5). Each counter was buried approximately one meter into the snow, next to a tree or a trail sign and secured with steel wire, to ensure stability and secure placement. This approach is aimed at preventing individuals from altering their movement patterns upon noticing the devices, and to reduce the risk of tampering or interference (Kaltenborn, 2012). The sensor was placed approximately 0.7 meters above the trail surface.

When a person passes the counter, the lens detects the radiation and determines their direction, at the same time as people remain anonymous. Under normal conditions the counters have a margin of error at ± 5%, with somewhat higher uncertainty in wintertime. The sensor sensitivity was set to one, as this is recommended for less crowded areas and lower temperatures (Kaltenborn, 2012; Andersen et al., 2013).

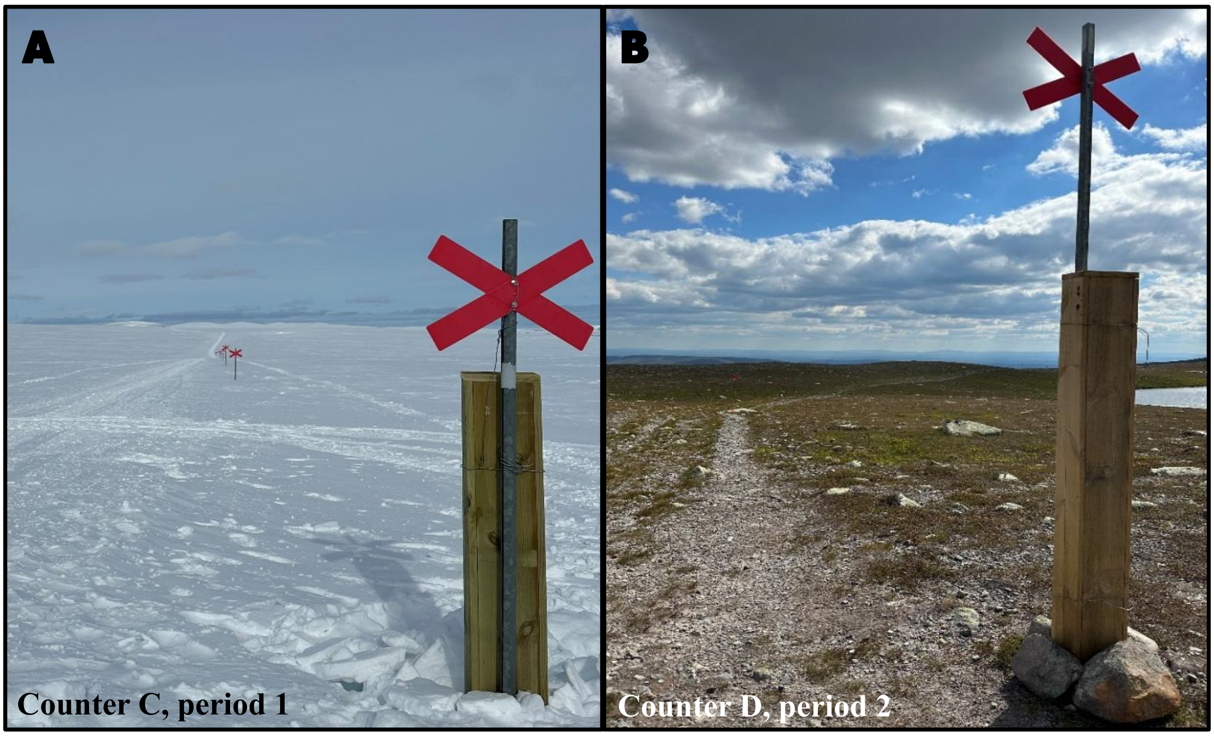

Figure 5: Counter C and D in the study area attached to a trail sign. A: Counter C in period 1 beside a ski trail, buried one meter into the snow. B: Counter D in period 2 beside a hiking trail.

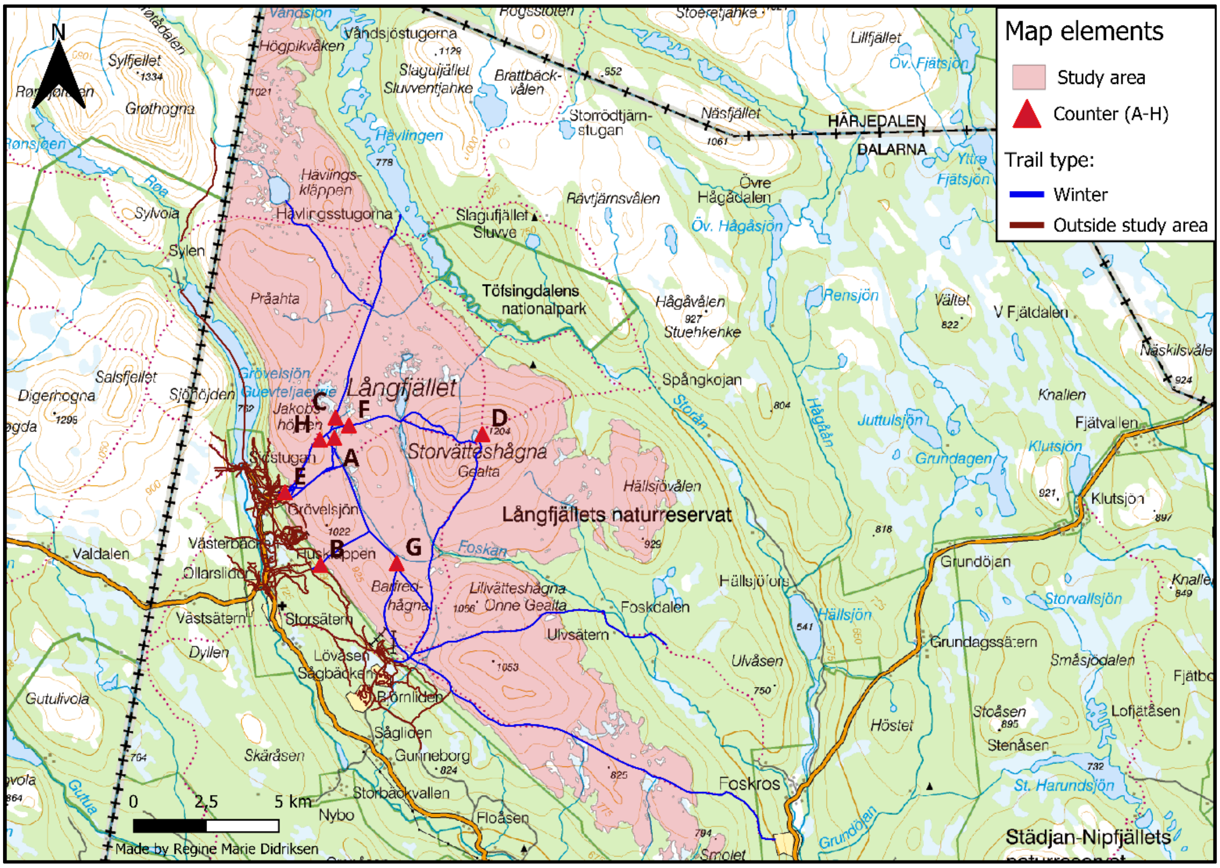

Figure 6: Map of study area in period 1, with trails and positions of each counter (A-H), as red triangles. Blue trails represent winter trails, brown trails represent trails outside the study area.

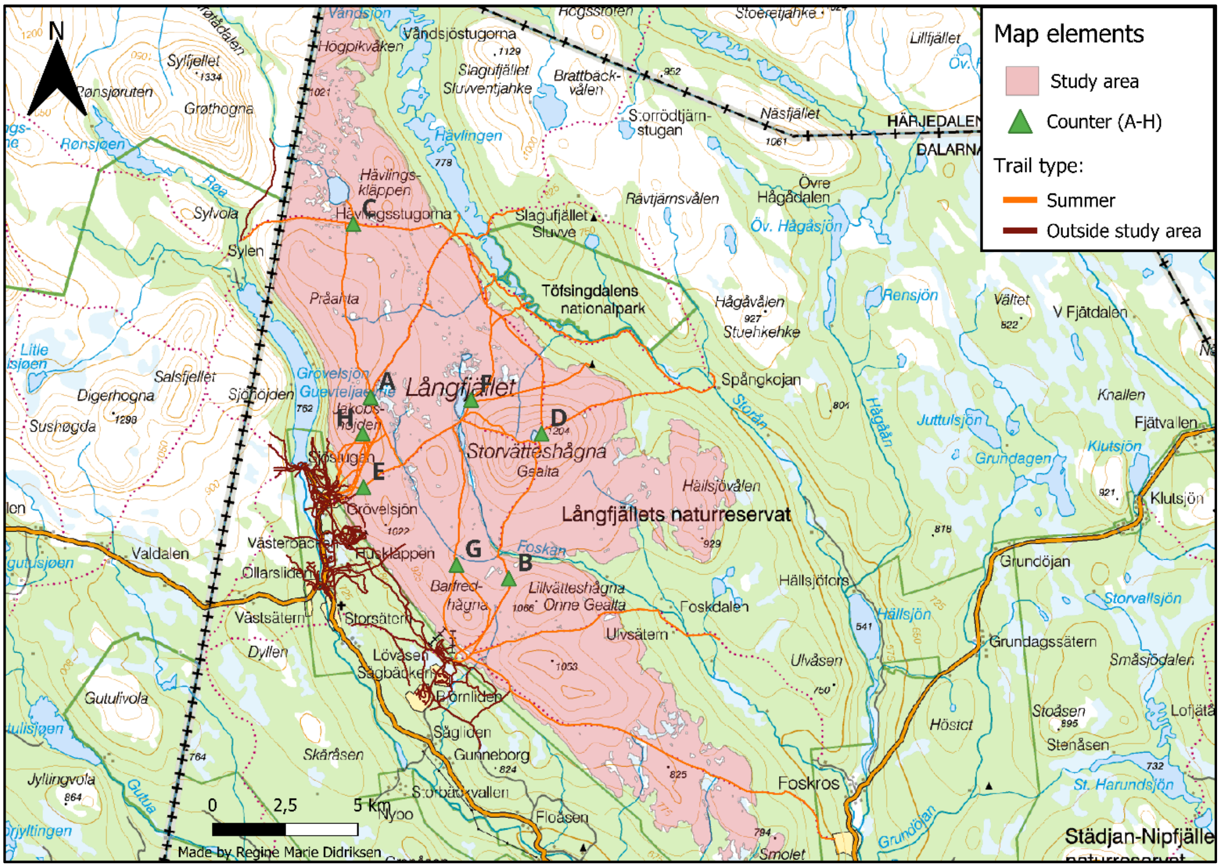

Figure 7: Map of study area in period 2, with trails and positions of each counter (A-H) as green triangles. Orange trails represent summer trails, brown trails represent trails outside the study area.

The counters were strategically placed next to ski trails (period 1) and hiking trails (period 2) (Figure 6, Figure 7). At the end of period 1 (May 23), counter A, C, F, and H were relocated to hiking trails, while counter G was relocated on the 27 of May (due to time constraint). Counter D and B remained at their original site because of its strategic location including both ski and hiking trails. Counter E was excluded from this study as the data could not be retrieved due to a technical error.

2.3 Data handling and preparations

2.3.1 Data filtering

The extensive raw dataset of brown bear GPS-positions from NINA's research project included 627 452 positions. The dataset was cleaned and filtered to include only positions recorded within the study area and calving period (May 01 to June 20), reducing it to 3380 brown bear GPS-positions from 16 individuals (4 females and 12 males). NINA's dataset on female reindeer GPS-positions included 158 310 positions. Following the cleaning and filtering the final dataset included 73 981 reindeer GPS-positions from 142 individuals. In addition, NINA's carcass dataset initially contained 418 carcasses of various species and causes of death. For this study, only carcasses of reindeer killed by a GPS-collared brown bear within the study area and study period were included, resulting in 58 carcasses.

The raw dataset from the counters included the number of individuals moving in both directions past each counter, as well as a total count. To address the potential counting errors, all daily records where more than 50 passings were recorded in one direction but 0 in the other were flagged as invalid and manually corrected. The 50-passings threshold was based on contextual knowledge of recreational activity in the area along with comparisons to counts from other nearby counters on the same day. Invalid values (x=44, 20.3%) were replaced with estimated counts derived from the same day in the previous week for period 1, and the following week for period 2, assuming week-to-week variation would be limited. This estimation method was based on an established standard method used internally at NINA.

Estimations based on previous and following weeks were made to ensure accurate counts for each counter at its correct location, as most counters were relocated on May 23. Counter D, G and H showed some abnormally high counts between May 14 and May 23, and these were replaced with estimated counts (Table 1). Estimations were also necessary for the days when the counters were relocated, as they continued recording during transportation, producing inaccurate data.

Table 1: The number of days for each counter in both periods where human counts were adjusted by standard method, along with the percentage of days with adjusted human counts in the total study period. The count range shows the range of daily human passings recorded by each counter during the study period.

Counter	Estimated days Period 1	Estimated days Period 2	Estimation percentage	Count range
A	2	0	1%	0 – 64
B	0	5	2.5%	0 – 16
C	2	0	1%	0 – 26
D	10	0	5.1%	0 – 148
F	1	0	0.5%	0 – 90
G	10	3	6.6%	0 – 70
H	11	0	5.6%	0 – 111

2.3.2 Estimation of human activity per trail

The study area contained numerous trails used for human recreational activity. Due to the high number of trails, it was not feasible to install counters at every route. Period and trail specific human activity levels were estimated using a combination of data from the installed counters, Strava Global Heatmap, local knowledge and a public map showing an overview of trails in the area (Gränslandet, s.a.). All trails within the study area were manually classified as either winter or summer trails. Trails located beyond the study area in a 2 km buffer were classified as outer trails (Figure 6, Figure 7). The 2 km buffer was included to account for the fact that large mammals can be affected by human activity beyond the immediate proximity of trails (Skarin & Åhman, 2014).

For trails equipped with a counter, an average daily trail count value (mean passings per day) was assigned to the full length of the corresponding trail for each period (Figure 8, Figure 9, Table 3). Although the exact number of passings was known only for the specific counter location, the same value was applied to the entire trail route (consisting of multiple trail segments) to ensure consistency across the full trail. For trails without a counter, a default value of 1 person per day was assigned (Figure 8, Figure 9). This estimate was based on supporting evidence from the Strava Global Heatmap, local insight, and the public map, which indicated human use even when exact counts were unavailable.

This estimation approach (with a default value of 1) was applied to all trails in cabin areas outside the study area (e.g., Lövåsen, Björnliden, Sågbäcken, Huskläppen, Västerbäcken, Grövelsjön Fjällstation) where human presence was known but not quantified. Additionally, the trail from the tourist hotel Fjällstugan to the lake Övre Fosksjön in period 2 (red trail, Figure 9) was assigned an estimated count value based on the combined counts from counter F and D, as data from counter E which originally was positioned along this trail were not obtainable. All estimated count values were later used in the statistical analysis to construct the Human Activity Intensity (HAI) index.

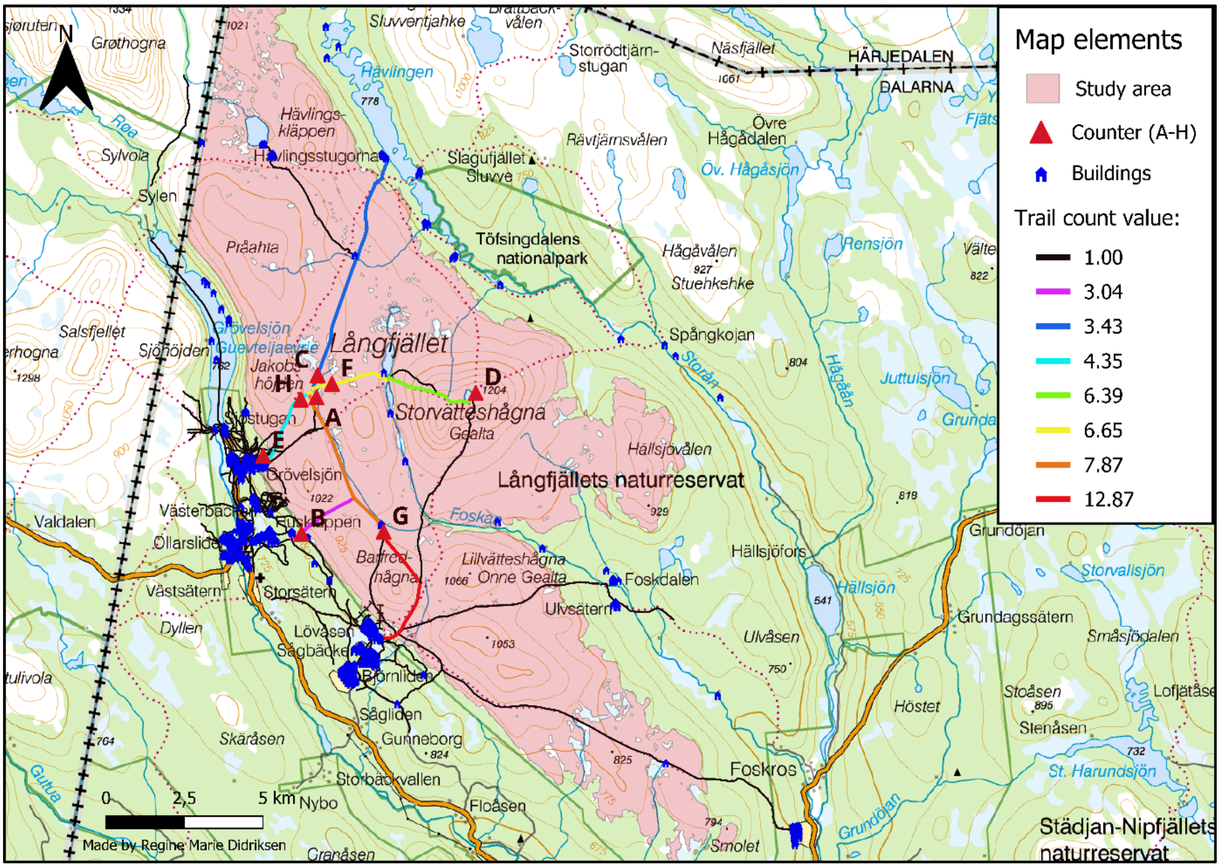

Figure 8: Trail count values (mean passings per day) in period 1 (May 1 - 23). Clusters of blue buildings outside the study area represent mostly cabins/houses, while structures within the study area include a mix of shelters and huts. Trails are colored based on daily count values from counters, with counter locations marked as red triangles. Black trails indicate known trails with unknown usage intensity and were assigned a default value of 1.

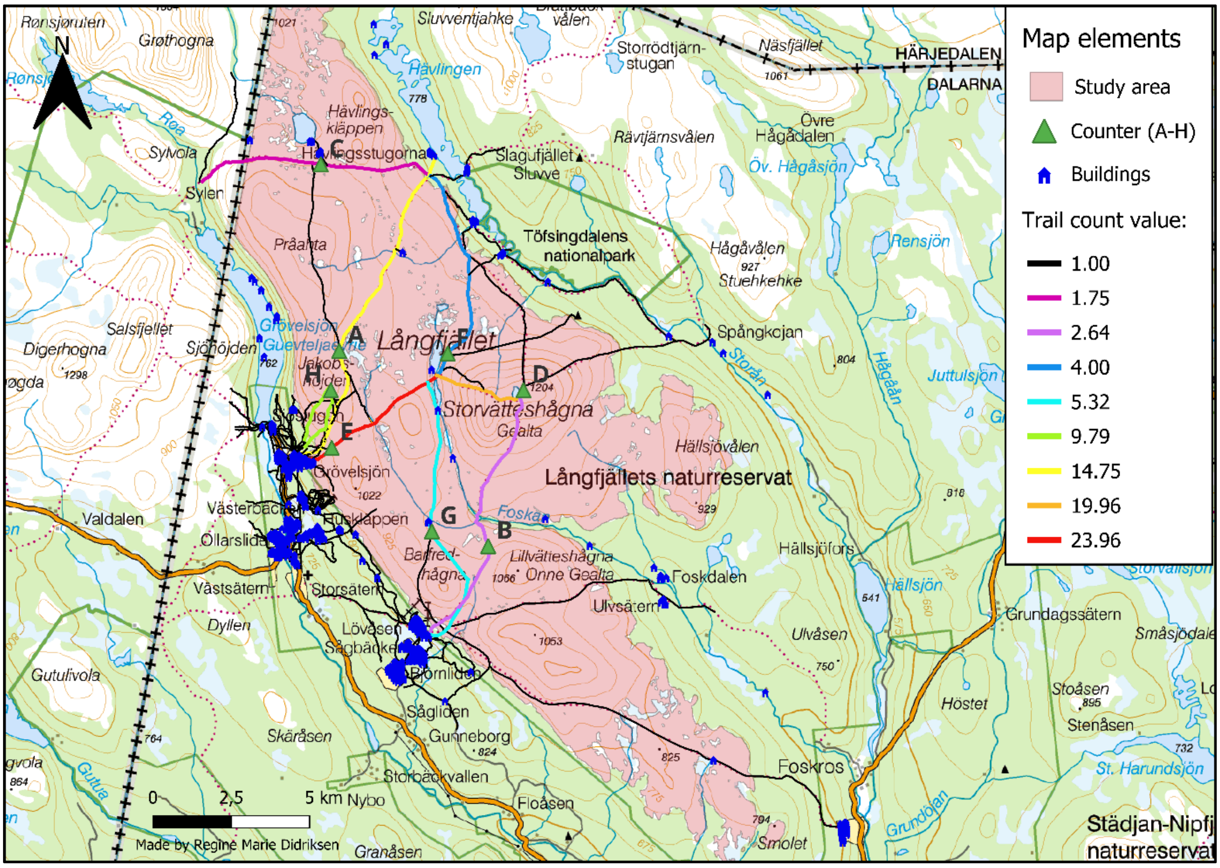

Figure 9: Trail count values (mean passings per day) in period 2 (May 24 - June 20). Clusters of blue buildings outside the study area represent mostly cabins/houses, while structures within the study area include a mix of shelters and huts. Trails are colored based on daily count values from counters, with counter locations marked as green triangles. Black trails indicate known trails with unknown usage intensity and were assigned a default value of 1.

2.3.3 Use of Artificial Intelligence (AI)

ChatGPT (version GPT-4o) and GitHub Copilot have been utilized for coding assistance in R, particularly with filtering the datasets, plotting, modelling, solving errors and warnings. Furthermore, ChatGPT has been used to find solutions to challenges in QGIS. Lastly, it has been used to identify suitable synonyms, enhance the readability of the text and improve academic writing. All modifications suggested by ChatGPT to the written text have been manually reviewed and adjusted.

2.4 Statistical analysis

All data processing and statistical analysis were performed using R version 4.4.2 (R Core Team, 2024; Posit team, 2025). Data handling and extraction from the raw datasets were primarily performed using functions from the "tidyverse" package (Wickham et al., 2019). Spatial datasets were visualized using the "mapview" package (Appelhans et al., 2023). The "sf" package was used for handling spatial vector data, and the "sp" package was used for handling spatial GPS-point data (Bivand et al., 2013; Pebesma, 2018).

2.4.1 Covariates

HAI index

The Human Activity Intensity (HAI) index was calculated based on the average trail count values assigned to each trail segment, as described in chapter 2.3.2. A grid of 1000 x 1000 m was overlaid the study area, then for each grid cell, the length of each trail segment and the corresponding count value within the cell were extracted. The HAI index for each grid cell was then calculated as the weighted average count value per unit trail segment length (m) within a cell. In this way, longer trail segment will contribute significantly more to the HAI index. HAI index was calculated as follows:

$$HAI = \frac{\sum_{i=1}^{n}(count\ value_i \times trail\ segment\ length_i)}{\sum_{i=1}^{n} trail\ segment\ length_i}$$

where **i** denotes a given trail segment, and **n** is the total number of trail segments within the cell. The HAI index was calculated separate for each period as trail usage and associated count values differed between periods, and rasterized for use in the modeling, using functions from the "terra" and "raster" packages (Hijmans et al., 2025a; Hijmans et al., 2025b). While the HAI index reflects the level of human presence on each trail, it does not necessarily indicate unique individuals, as a single visitor may traverse multiple trail segments in one day (Gundersen et al., 2021).

Trail density

Trail density (km/km^2) was calculated separately for each period using the corresponding trail network. A raster template with 1 km^2 resolution was created, and the total trail length within each grid cell was calculated. Trail length (in meters) was then converted to kilometers and divided by the area of each grid cell (1 km^2) to calculate trail density. A 1000 m resolution was selected as it maintained both spatial detail and interpretability.

Distance to trail

Distance to trail was calculated separately for each period using the corresponding trail network. A 2 km buffer zone around the study area was retained to include trails that could influence species' behavior beyond the immediate study boundary. For each GPS-point the Euclidean distance to the nearest trail was calculated, using functions from the "sf" and "tidyverse" package.

Distance to forest

Distance to forest was the same for each period, thus calculated only once. The tree line/forest was defined as the boundary of the mountain study area (Figure 2). For each GPS-point the Euclidean distance to the nearest tree line/forest was calculated using functions from the "sf" and "tidyverse" package.

Distance to buildings

Geographic data on buildings (cabins, houses, huts, sheds, shelters etc.) in the study area were obtained from the freely available "Topografi 50" vector layer downloaded from the Swedish Lantmäteriet website (Lantmäteriet, 2025). Buildings within the study area and a surrounding 5 km buffer were extracted and converted to a spatial vector using the "terra" package. Then, for each GPS-point the Euclidean distance to the nearest building was calculated using functions from the "sf" and "tidyverse" package.

2.4.2 Modelling and predictions

Resource Selection Functions (RSFs) with a use-availability design were used to analyze brown bear and reindeer habitat selection (Manly et al., 1993). The GPS-points logged by the individual collars were defined as use, and available points were sampled at a 1:1 ratio with the individual GPS-points used within the study area. This corresponds to third-order habitat selection (habitat scale within home range, where the mountainous area is defined as available area (Johnson, 1980)). The response variable was binary, with used GPS-positions coded as 1 and available as 0.

Five covariates were included to complete the dataset for modeling: Human Activity Intensity (HAI), trail density, distance to trails, distance to forest and distance to buildings. An interaction term between period (p1 and p2, categorical) and all covariates were included to test whether habitat selection varied between periods. Prior to model fitting, all covariates were checked for correlations. Generalized additive models were used to assess non-linearity, using the "mgcv" package (Wood, 2025). All covariates were scaled (mean-centered and divided by the standard deviation) prior to fitting the model, to facilitate model interpretation and convergence.

Brown bear habitat selection was analyzed fitting RSFs using a mixed-effects logistic regression model in the "lme4" package (Bates et al., 2015). A random effect for individual bear ID was included to account for individual variation in selection and to control differences in sample size per individual. In addition to the covariates described above, distance to trail and trail density was included as non-linear terms. To ensure model convergence and robustness, the optimizer "bobyqa" was applied.

Reindeer habitat selection was analyzed by fitting RSFs using a logistic regression model. Including individual reindeer ID's as a random effect did not improve model fit, and a mixed-effects model was thus not needed. In addition to the covariates described above, distance to trail, trail density and HAI were included as non-linear terms.

Backwards model selection was performed on both models, guided by likelihood ratio tests and Akaike's Information Criterion (AIC). Model predictions were visualized using the "ggplot2" package, and resulting plots were arranged into a single panel using the "ggpubr" package (Wickham et al., 2016; Kassambara, 2023).

2.4.3 Habitat suitability, co-occurrence and correlation

Habitat suitability for brown bears and reindeer was predicted using the final RSFs. The existing raster grids (period-specific where it was relevant) for HAI and trail density were used, and it was generated 10x10m raster for distance to trails, distance to buildings and distance to forest, as well as categorical raster for period (p1 and p2). Maps were scaled corresponding to the scaling of covariates in the modeling process. The resulting predictions were presented as raster maps of habitat suitability ranging between 0-1. Predictions were conducted using the "sf", "raster" and "lme4" packages.

To quantify spatial overlap between brown bear and reindeer habitat suitability, a pixel-wise multiplication of their habitat suitability raster's was conducted for each period. This process resulted in maps showing the probability of co-occurrence. Co-occurrence values across the study area and at carcass locations were extracted from these raster's and combined into a dataset using the "raster" package. The package "ggplot2" was used to produce a boxplot illustrating the distribution of co-occurrence probabilities across the study area and at carcass locations for both periods. A Welch two sample t-test was also utilized to assess whether the mean co-occurrence values differed significantly between carcass locations and across the study area.

Additionally, a Pearson correlation analysis was conducted using the "raster" package, to examine the relationship between habitat suitability for brown bear and reindeer, both across the study area and at carcass locations. Lastly, the distance from each carcass to the forest was calculated, and a Welch two sample t-test was used to assess whether the mean co-occurrence values and the carcass distance-to-forest differed significantly between the two periods.

3. Results

3.1 Temporal distribution of brown bear, semi-domesticated reindeer and carcass GPS-positions

Most brown bear GPS-positions within the study period and study area were recorded during nighttime hours, with 3265 positions registered at night compared to 619 positions during daytime (Figure 10).

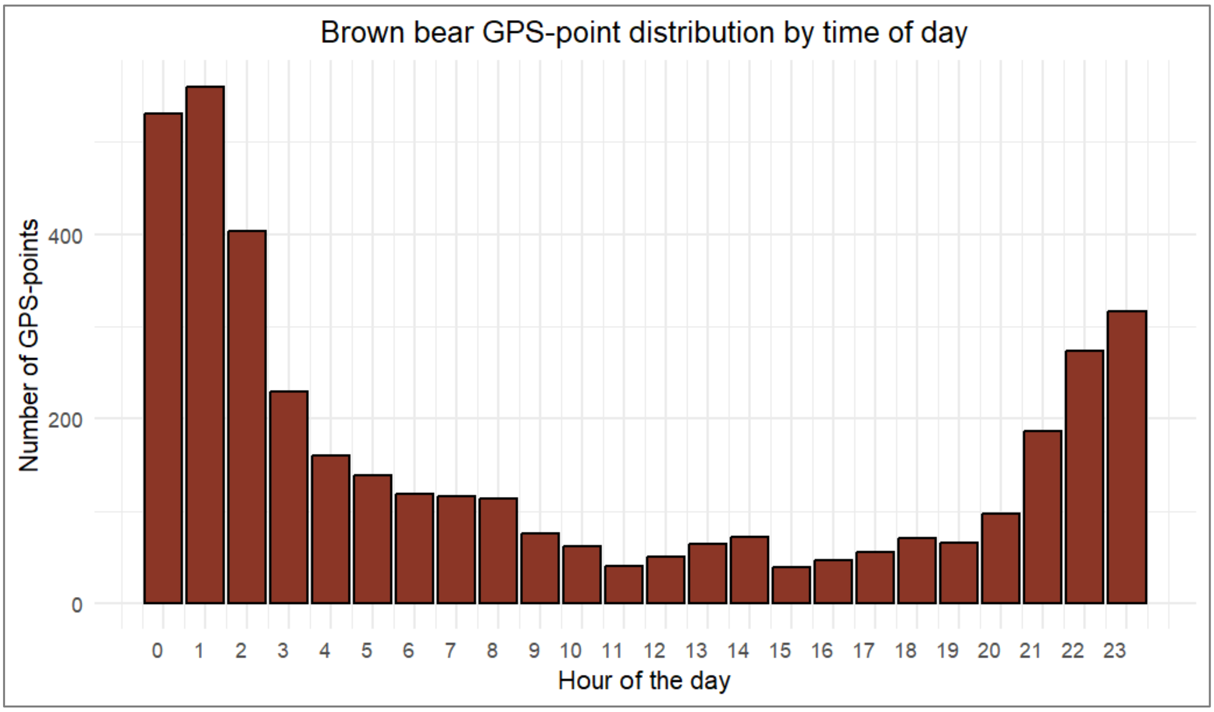

Figure 10: Temporal distribution of brown bear GPS-positions (n = 3884) by time of day, throughout the study period.

For reindeer, the temporal distribution of GPS-positions in mountain habitat showed relatively even use throughout the day, with 35 006 positions recorded during daytime and 38 963 positions at nighttime (Figure 11).

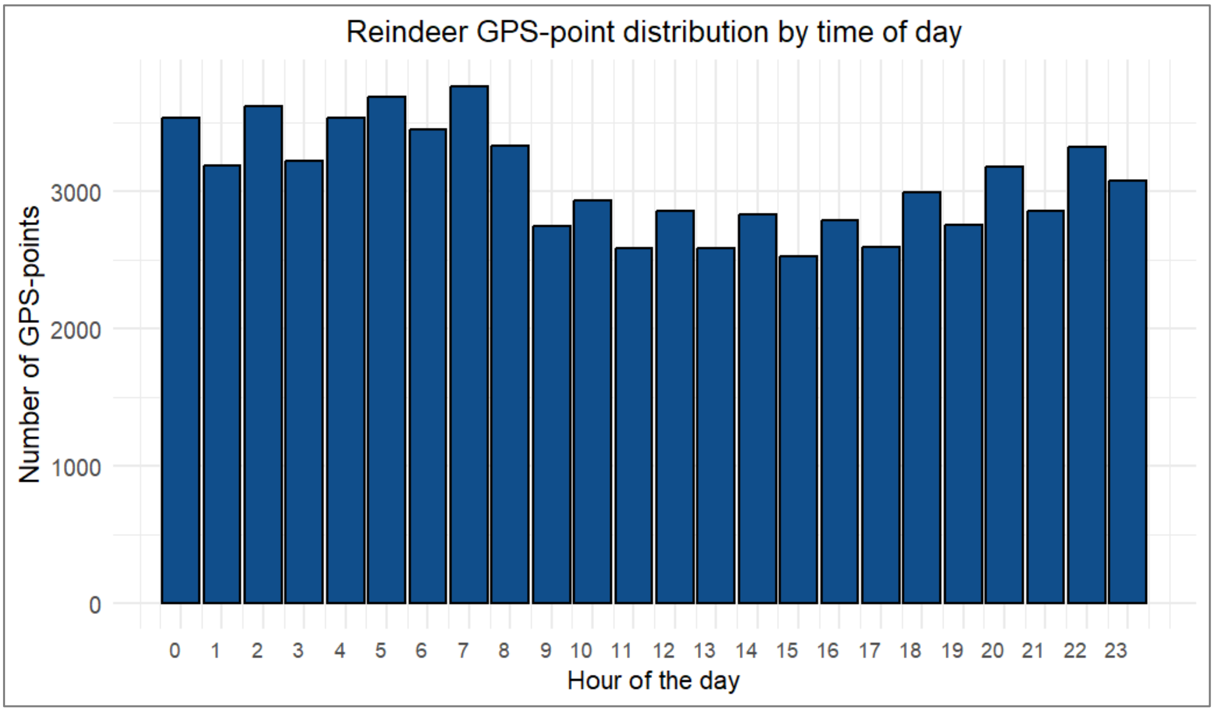

Figure 11: Temporal distribution of semi-domesticated reindeer GPS-positions (n = 73 969) by time of day, throughout the study period.

The temporal distribution of carcasses further supported the brown bear GPS-findings, that brown bears predominantly access mountain habitat to prey on reindeer during nighttime (Figure 12). Of the 58 carcasses found, 52 were registered at night and 6 during the day. The majority were calves, with 2 adult reindeer among the confirmed carcasses. Moreover, 20 carcasses were found in period 1 and 38 in period 2.

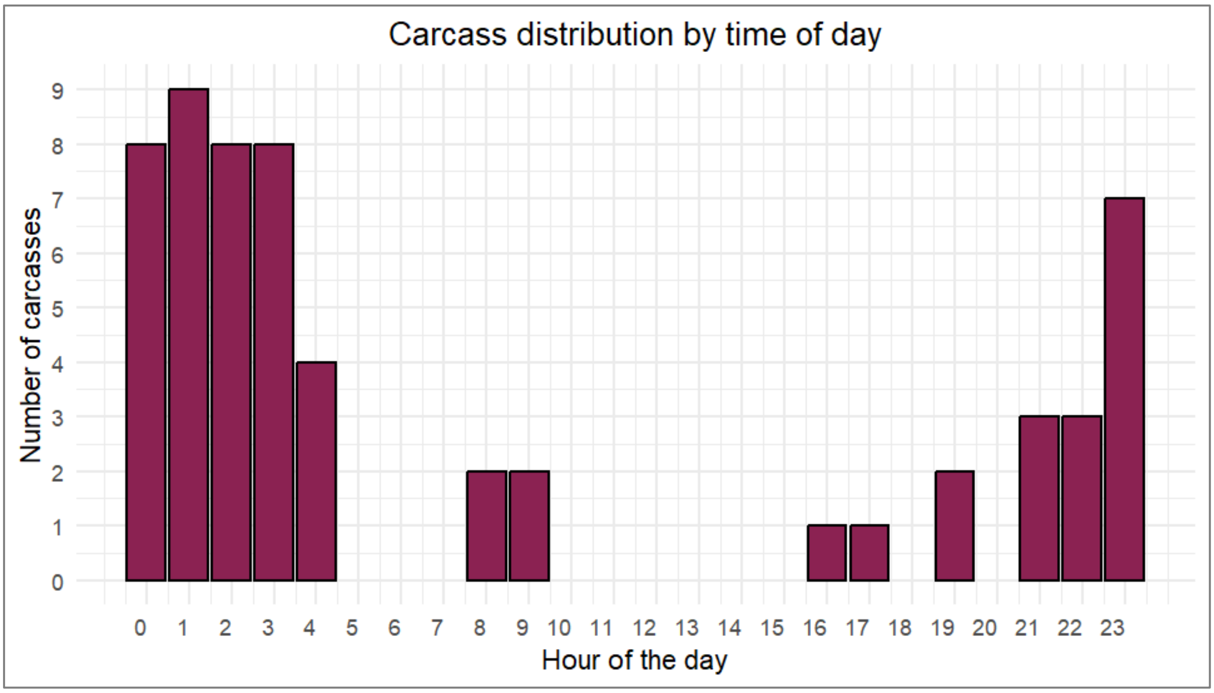

Figure 12: Distribution of carcasses based on the time the GPS-position of the brown bear entering the cluster was registered during the day.

3.2 Human recreational activity counts

The counters registered a total of 2656 human passings over the study period (Table 2). There were notable differences in the number of human passings recorded by each counter (Table 1, Table 2). Counter D registered the highest number of passings, with a total of 706 counts, while counter C recorded the lowest, with only 128 counts in total. Human activity varied not only between counters (Table 2, Table 3), but also between weekdays and weekends (Figure 13), and throughout hours of the day (Figure 14).

Table 2: The total number of people registered by the different counters within the calving period.

Counter	Period 1 (May 1-23)	Period 2 (May 24-June 20)	Total counts	Percentage
A	181	413	594	22.4 %
B	70	74	144	5.4 %
C	79	49	128	4.8 %
D	147	559	706	26.6 %
F	153	112	265	10.0 %
G	296	149	445	16.8 %
H	100	274	374	14.0 %
In total	1026	1630	2656	100%

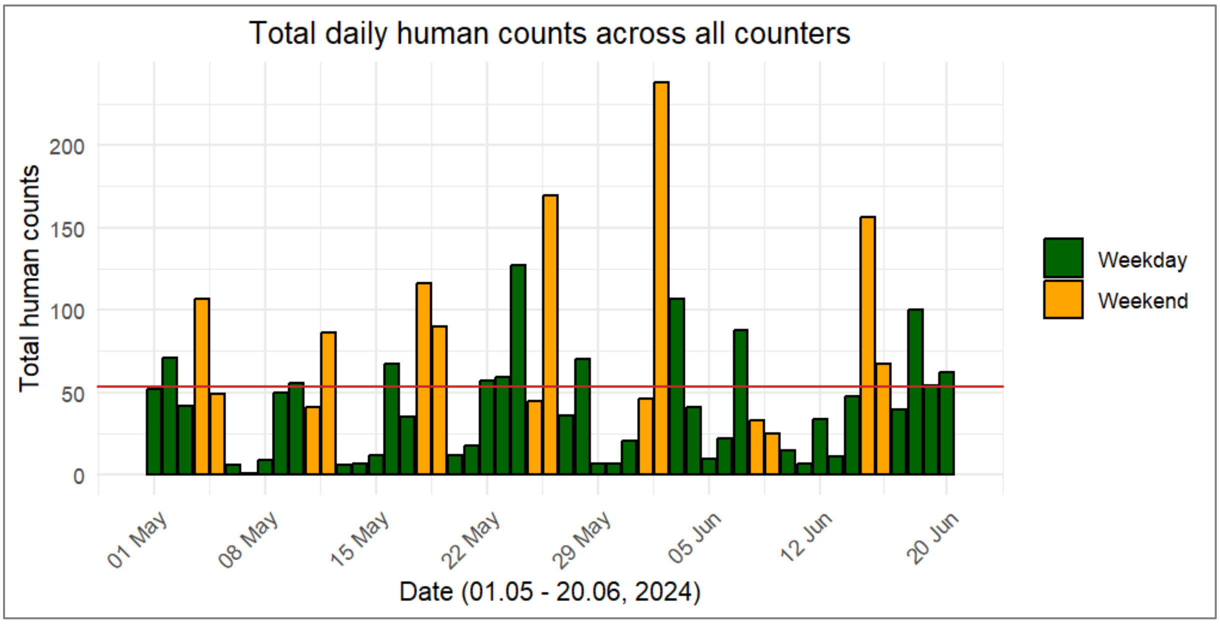

Figure 13: Total daily human counts recorded across all counters during the study period. The red line indicates the mean number of people recorded every day (52) across all counters. The green bars represent weekdays (Monday - Friday), whereas the yellow bars represent weekends (Saturday and Sunday).

The data revealed a recurring pattern of increased activity on weekends, particularly throughout May, whereas midweek days tend to show fewer passings (Figure 13). Human activity peaked around 12:00, with a consistently higher percentage of people counted between 11:00 and 16:00. After 16:00, the percentage of recorded people declined sharply. A low percentage of people were counted between 22:00 and 07:00 (Figure 14).

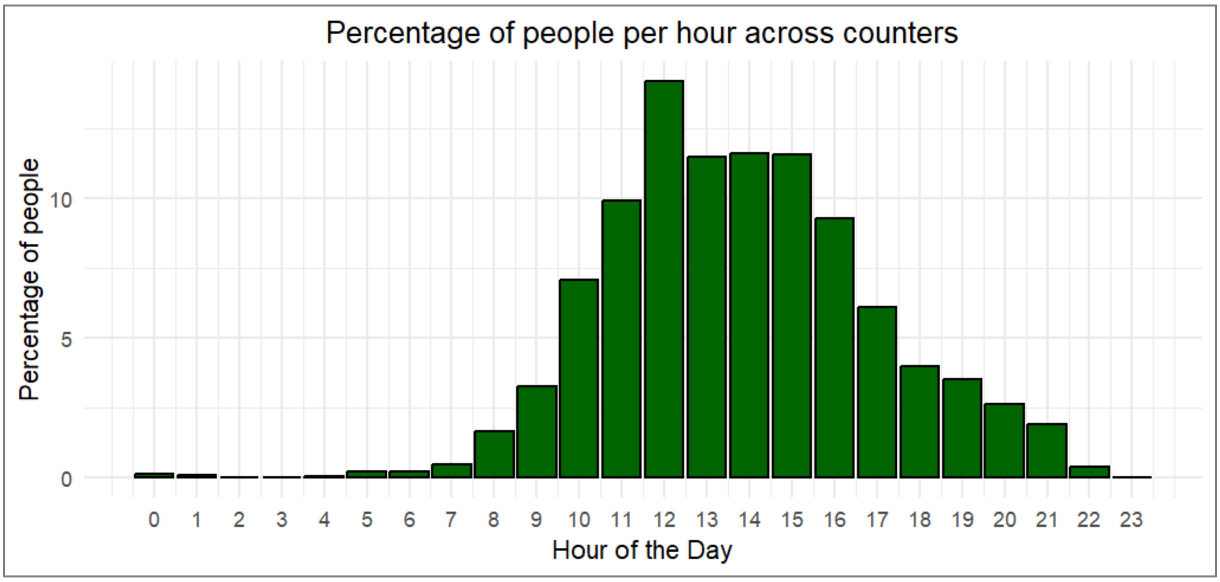

Figure 14: The percentage of people counted by hour across all counters, based on raw data from the full period the counters where deployed in the field (March 22 to June 26, 2024).

The estimated daily trail use (for use in development of the HAI index) varied between counter and within the calving period, with increased activity during period 2 compared to period 1. Some counters, particularly A, D and H, recorded a rise in passings in period 2 (Table 3).

Table 3: Estimated daily trail use recorded by each counter during the calving period. The values represent the average number of daily passings per counter and are visualized in Figure 8 and Figure 9. Estimation method described in chapter 2.3.2.

Counter	Period 1	Period 2
A	7.87	14.75
B	3.04	2.64
C	3.43	1.75
D	6.39	19.96
F	6.65	4.00
G	12.87	5.32
H	4.35	9.79

3.3 Brown bear habitat selection

The final model explaining brown bear habitat selection included all covariates, with trail density and distance to trail modeled as quadratic terms, and interaction with period (p1 and p2) included for distance to trail, distance to buildings and trail density (Table 4). The effect of Human Activity Intensity (HAI) and distance to forest did not vary between periods.

In support of H1, human recreational activity influenced spatial habitat selection by brown bears, as they consistently selected areas farther from human recreational activity-related features in both periods. While the effects of distance to forest and HAI remained consistent, the influence of trail density, distance to buildings, and distance to ski/hiking trails varied slightly between period 1 and period 2 (Table 4, Figure 15).

In line with P1, brown bear habitat selection showed a negative relationship with trail density, with selection decreasing as trail density increased in both periods. Brown bears avoided all areas with trails in period 1, whereas in period 2 there was a slight selection for trail densities lower than 3 km/km^2 while areas with higher densities were avoided (Table 4, Figure 15a).

Consistent with P2, a similar negative relationship was found with HAI, where higher HAI corresponded with lower habitat selection. In period 1, they avoided areas across all levels of human activity. In period 2, they selected areas with HAI values below 10 and avoided areas with higher activity levels (Table 4, Figure 15b).

Supporting P3, brown bear habitat selection showed a negative relationship with distance to forest, with selection decreasing as distance to forest increased. In period 1, bears selected areas within 500 m of forest and avoided areas farther away. In period 2, they selected areas up to 1500 m from the forest and avoided areas beyond that distance (Table 4, Figure 15c).

In support of P4, brown bear habitat selection showed a positive relationship with distance to buildings in both periods, and the distance to trails in period 1, with selection increasing as distance from these features increased (Table 4). In period 1, bears avoided all areas close to buildings, while in period 2, they clearly selected areas more than 1000 m away (Figure 15d). Moreover, in period 1, bears selected areas more than 2000 m from trails and avoided areas closer. In period 2, bears selected areas at intermediate distances (500-3500 m) and avoided both closer and more distant areas (Figure 15e).

Overall, the model results supported H1 and P1 to P4 and these findings confirm that human recreational activity influenced brown bear habitat selection, with a stronger effect in period 1 (Table 4, Figure 15).

Table 4: Parameter estimates from a logistic regression mixed-effects model explaining brown bear habitat selection in semi-domesticated reindeer calving grounds. All continuous variables are rescaled by mean centering and dividing by the standard deviation. The reference level for period = 1, and period = 2 is shown in the table. Individual bear ID was fitted as random intercept with st.dev = 0.232.

Parameter	Estimate	Std. Error	z-value	P-value
Intercept	-0.423	0.095	-4.417	<0.001
Distance to trail	76.054	5.193	14.644	<0.001
Distance to trail^2	9.281	4.740	1.958	0.050
Distance to buildings	0.182	0.054	3.350	<0.001
Distance to forest	-0.504	0.033	-14.852	<0.001
Trail density	-86.790	12.969	-6.692	<0.001
Trail density^2	-104.911	11.490	-9.130	<0.001
HAI	-0.328	0.036	-9.074	<0.001
Period (1 vs 2)	0.247	0.077	3.212	0.001
Distance to trail × period	-78.148	6.470	-12.078	<0.001
Distance to trail^2 × period	-43.705	6.253	-6.989	<0.001
Distance to buildings × period	0.344	0.063	5.400	<0.001
Trail density × period	64.019	13.406	4.775	<0.001
Trail density^2 × period	14.990	10.710	1.400	0.161

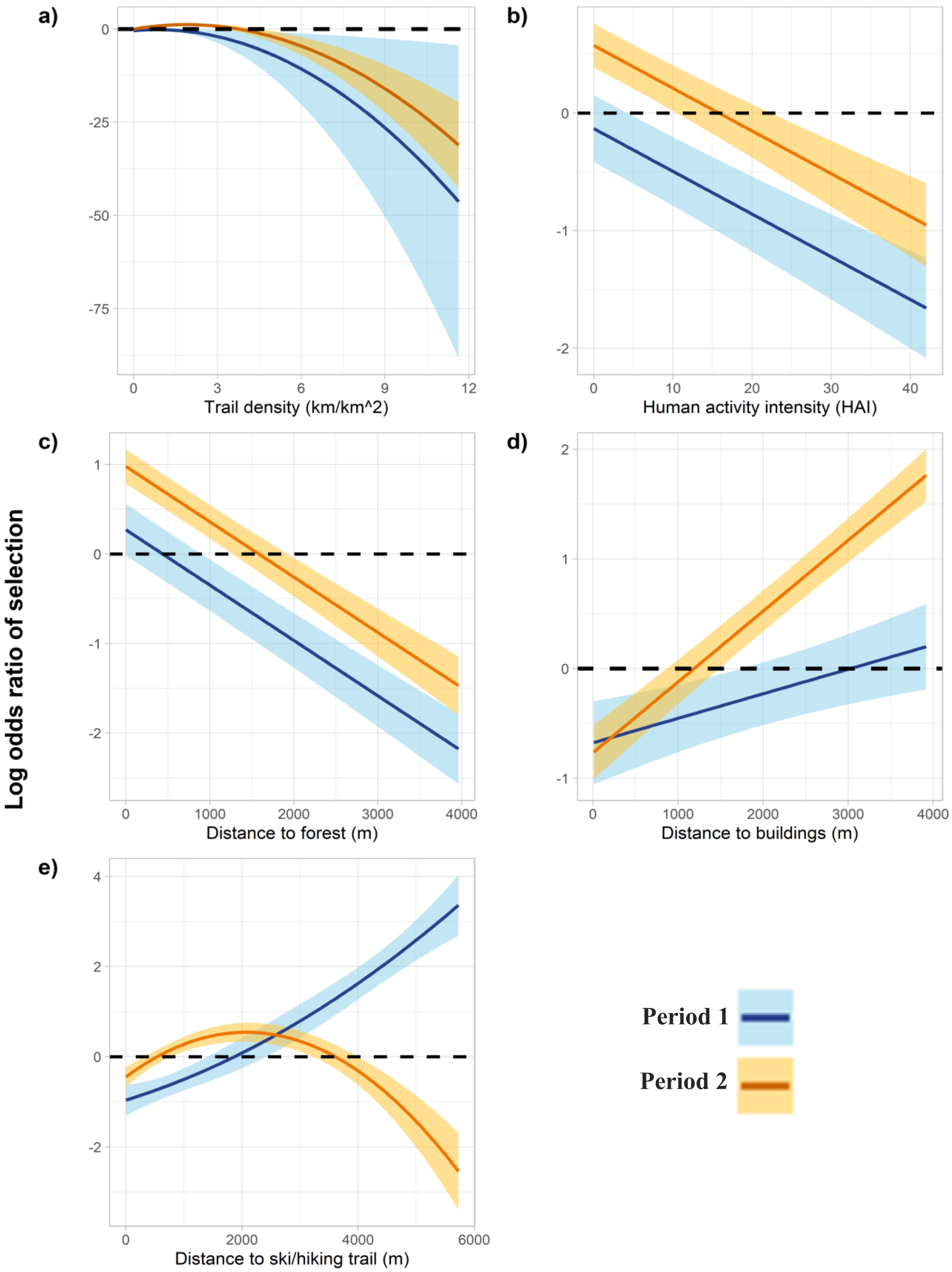

Figure 15: The predicted effect of covariates on brown bear habitat selection, shown as the log odds ratio of selection, based on a logistic regression mixed effects model. Colored lines show model predictions and represent the two different periods, blue for period 1 and orange for period 2. The shaded areas show 95% confidence intervals. The dashed horizontal line at 0 indicates no selection or avoidance, where the values above indicate selection and below indicates avoidance.

3.4 Semi-domesticated reindeer habitat selection

The final model explaining reindeer habitat selection included all the covariates, with trail density, distance to trail and HAI modeled as quadratic terms, and interactions with period (p1 and p2) for all covariates (Table 5). In support of H1, human recreational activity influenced the spatial habitat selection of reindeer, however, the strength of this effect varied throughout the calving period (Figure 16).

In support of P1, reindeer habitat selection showed a strong negative relationship with trail density in period 1, with selection decreasing as trail density increased. Reindeer avoided areas with values above 2 km/km^2 and showed a slight selection for areas with lower density. In contrast to P1, this relationship reversed in period 2, where reindeer showed selection across most trail density values, suggesting a reduced sensitivity to trail density later in the calving period (Table 5, Figure 16a).

In line with P2, reindeer habitat selection showed a negative relationship with HAI in period 1, with selection decreasing as HAI increased. Reindeer selected areas with HAI values up to 20 and avoided areas with higher human activity. In contrast to P2, reindeer habitat selection showed a positive relationship in period 2, with increasing selection as HAI increased and selection across all HAI values (Table 5, Figure 16b).

Contrary to P3, reindeer habitat selection in period 1 showed a positive relationship with distance to forest, with increased selection as distance to forest increases. In period 1, reindeer clearly avoided areas within 1000 m of the forest and selected open mountain areas farther away from the forest. However, in period 2 there was no effect of distance to forest on habitat selection (Table 5, Figure 16c).

Contrary to P4, reindeer habitat selection showed a negative relationship with distance to buildings, with decreased selection with increased distances to buildings (Table 5). In period 1, distance to buildings had a strong effect, with selection for areas within 3000 m and avoidance beyond that. In period 2, reindeer selected areas across all distances, indicating a diffuse effect of distance to buildings (Table 5, Figure 16d).

Partly supporting P4, reindeer showed avoidance at both short and long distances to trails, with selection at intermediate distances (1000-3500 m) in period 1. In period 2, reindeer selected areas 500-2000 m from trails and avoided areas closer than 200 m and beyond 2000 m (Table 5, Figure 16e).

These results indicate that reindeer were more sensitive to human recreational activity earlier in the calving period (period 1), particularly showing avoidance for higher trail density and HAI. Whereas in period 2, human recreational activity doesn't seem to influence reindeer habitat selection negatively.

Table 5: Parameter estimates from a logistic regression model explaining semi-domesticated reindeer habitat selection on calving grounds. All continuous variables are rescaled by mean centering and dividing by the standard deviation. The reference level for period = 1, and period = 2 is shown in the table.

Parameter	Estimate	Std. Error	z-value	P-value
Intercept	-0.198	0.0129	-15.280	<0.001
Distance to trail	58.45	4.479	13.049	<0.001
Distance to trail^2	-125.1	3.971	-31.495	<0.001
Distance to buildings	-0.079	0.008	-9.818	<0.001
Distance to forest	0.666	0.009	69.841	<0.001
Trail density	-96.82	12.26	-7.894	<0.001
Trail density^2	-129.7	16.46	-7.882	<0.001
HAI	-47.97	11.09	-4.327	<0.001
HAI^2	-23.63	8.433	-2.802	0.005
Period (1 vs 2)	0.169	0.015	11.144	<0.001
Distance to trail × period	-110.5	6.017	-18.368	<0.001
Distance to trail^2 × period	49.26	5.779	8.524	<0.001
Distance to buildings × period	0.038	0.011	3.341	<0.001
Distance to forest × period	-0.670	0.013	-52.536	<0.001
Trail density × period	148.1	12.64	11.716	<0.001
Trail density^2 × period	97.95	16.67	5.876	<0.001
HAI × period	65.25	11.46	5.693	<0.001
HAI^2 × period	26.46	8.878	2.980	0.003

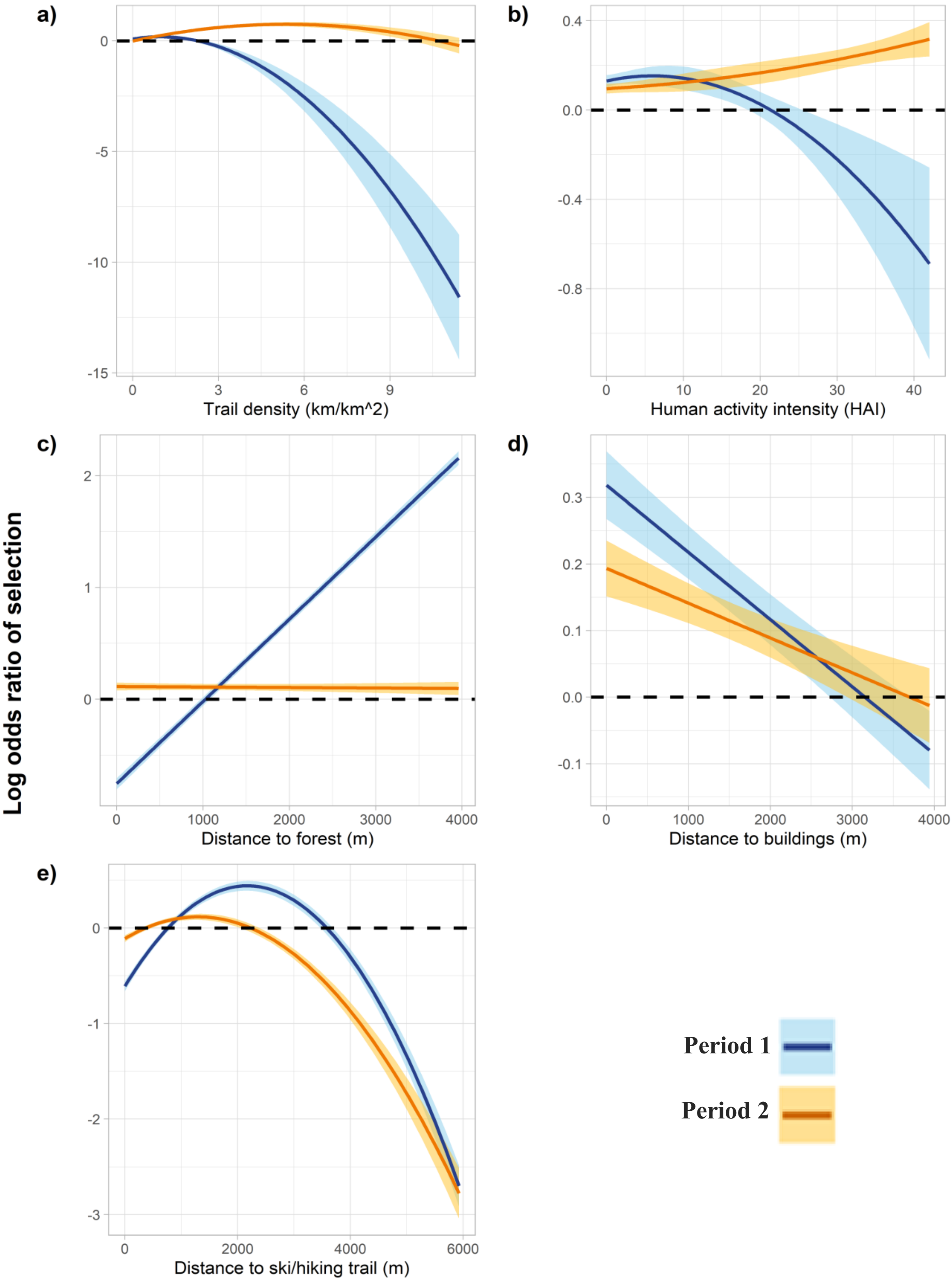

Figure 16: The effect of covariates on semi-domesticated reindeer habitat selection, shown as the log odds ratio of selection based on a logistic regression model. Colored lines show model predictions and represent the two different periods, blue for period 1 and orange for period 2. The shaded areas show 95% confidence intervals. The dashed horizontal line at 0 indicates no selection or avoidance, where the values above indicate selection and below indicates avoidance.

3.5 Habitat suitability, co-occurrence and correlation

Predicted brown bear habitat suitability showed slight variation between the two periods. In both periods, the most suitable areas (green in Figure 17) were located near the edges of the study area, closer to forested zones and away from the open, exposed mountain terrain. The least suitable areas (white in Figure 17) were concentrated in the center, near trails and several buildings, or closer to the more populated areas with cabins around Lövåsen and Grövelsjön mountain station. In period 1, suitable habitat was more concentrated in two distinct areas without intersecting trails, while in period 2, suitability was more broadly distributed, including some areas with trail presence (Figure 17).

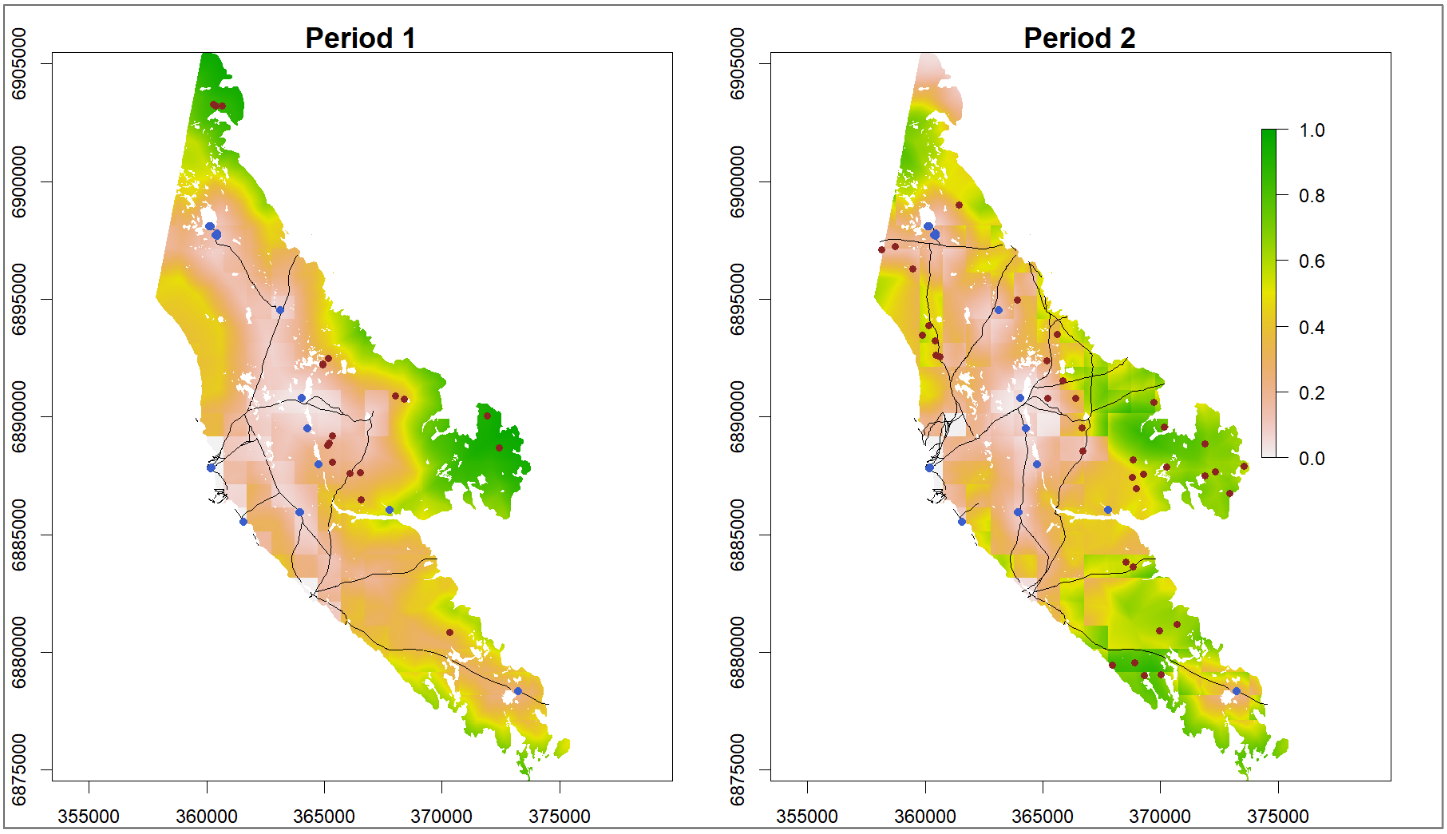

Figure 17: Predicted habitat suitability maps showing the combined effect of all covariates for brown bears across the study area within the calving period. Habitat suitability values ranging from 0 (low suitability, shown in light colors) to 1 (high suitability, shown in dark green). The axis represents UTM coordinates (Zone 33N), with eastings on the x-axis and northings on the y-axis. The black lines indicate trails, the red dots indicate carcasses, and the blue dots indicate buildings.

Predicted habitat suitability for reindeer differed notably within the calving period. In period 1, the most suitable habitat (green in Figure 18) was concentrated in the central part of the study area, within open mountain terrain and away from the forest. Habitat suitability decreased near the forest. In period 2, overall habitat suitability was less concentrated, with fewer zones of notable high or low suitability (Figure 18).

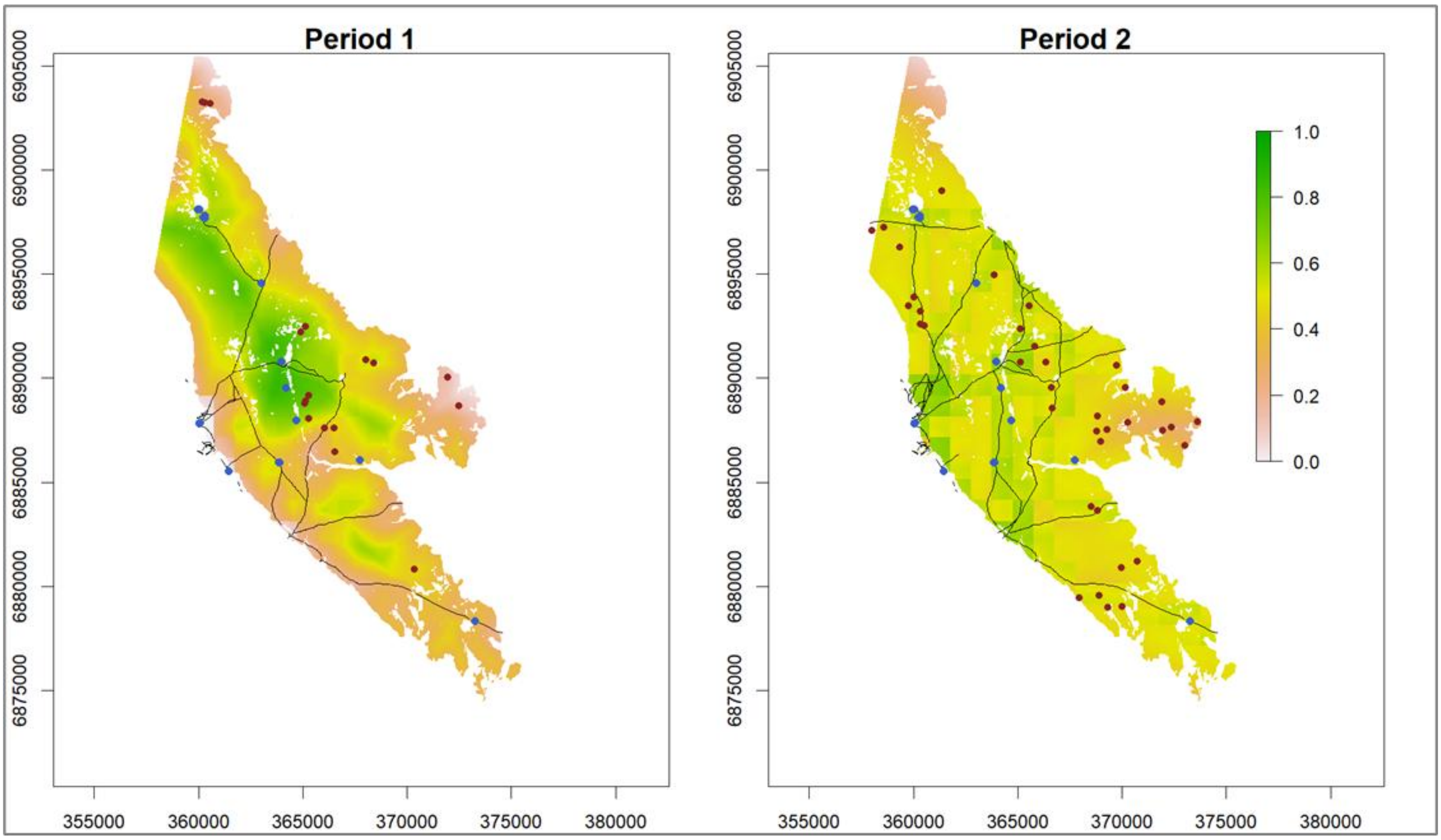

Figure 18: Predicted habitat suitability maps showing the combined effect of all covariates for semi-domesticated reindeer across the study area within the calving period. Habitat suitability values ranging from 0 (low suitability, shown in light colors) to 1 (high suitability, shown in dark green). The axis represents UTM coordinates (Zone 33N), with eastings on the x-axis and northings on the y-axis. The black lines indicate trails, the red dots indicate carcasses, and the blue dots indicate buildings.

Furthermore, Pearson's correlation matrix was used to compare habitat suitability between brown bear and reindeer across period 1 and period 2 (Table 6). The results revealed a negative correlation in habitat suitability between the two species, with r = -0,54 for period 1 and r = -0.31 for period 2, indicating that areas suitable for one species tend to be less suitable for the other. For reindeer, habitat suitability between periods showed a weak positive correlation (r = 0.25), suggesting notable variation in habitat preference across time. In contrast, brown bear habitat suitability showed a strong positive correlation between periods (r = 0.68), implying that bear spatial preferences remained relatively consistent across time (Table 6).

Table 6: Pearsons's correlation coefficient between predicted habitat suitability maps across the study area for semi-domesticated reindeer and brown bears across period 1 (p1) and period 2 (p2). Blue indicates a negative correlation and red indicates a positive correlation, with the intensity of the color reflecting the strength of the correlation.

Pearsons's correlation coefficient			
	Reindeer	Brown bear p1	Brown bear p2
Reindeer p1	0.25	-0.54	
Reindeer p2			-0.31
Brown bear p1			0.68

Predicted co-occurrence between brown bear and reindeer differed within the calving period. Notably, all high-overlap areas were located near the forest, while the central parts of the mountain consistently showed the lowest co-occurrence probabilities in both periods (Figure 19). In support of H1 and P5, human recreational activity contributed to a higher probability of co-occurrence between reindeer and brown bears near the forest, particularly in period 2 (Figure 19). In period 1, areas with high co-occurrence probability were fewer and more fragmented, whereas in period 2, these areas were larger and more continuous.

Contrary to H2 and P6, carcasses (red points) were not concentrated in areas with a high probability of brown bear and reindeer co-occurrence. Instead, carcasses were distributed in areas of low co-occurrence probability in period 1, while in period 2 they were more evenly spread across the full range of co-occurrence probabilities (Figure 19).

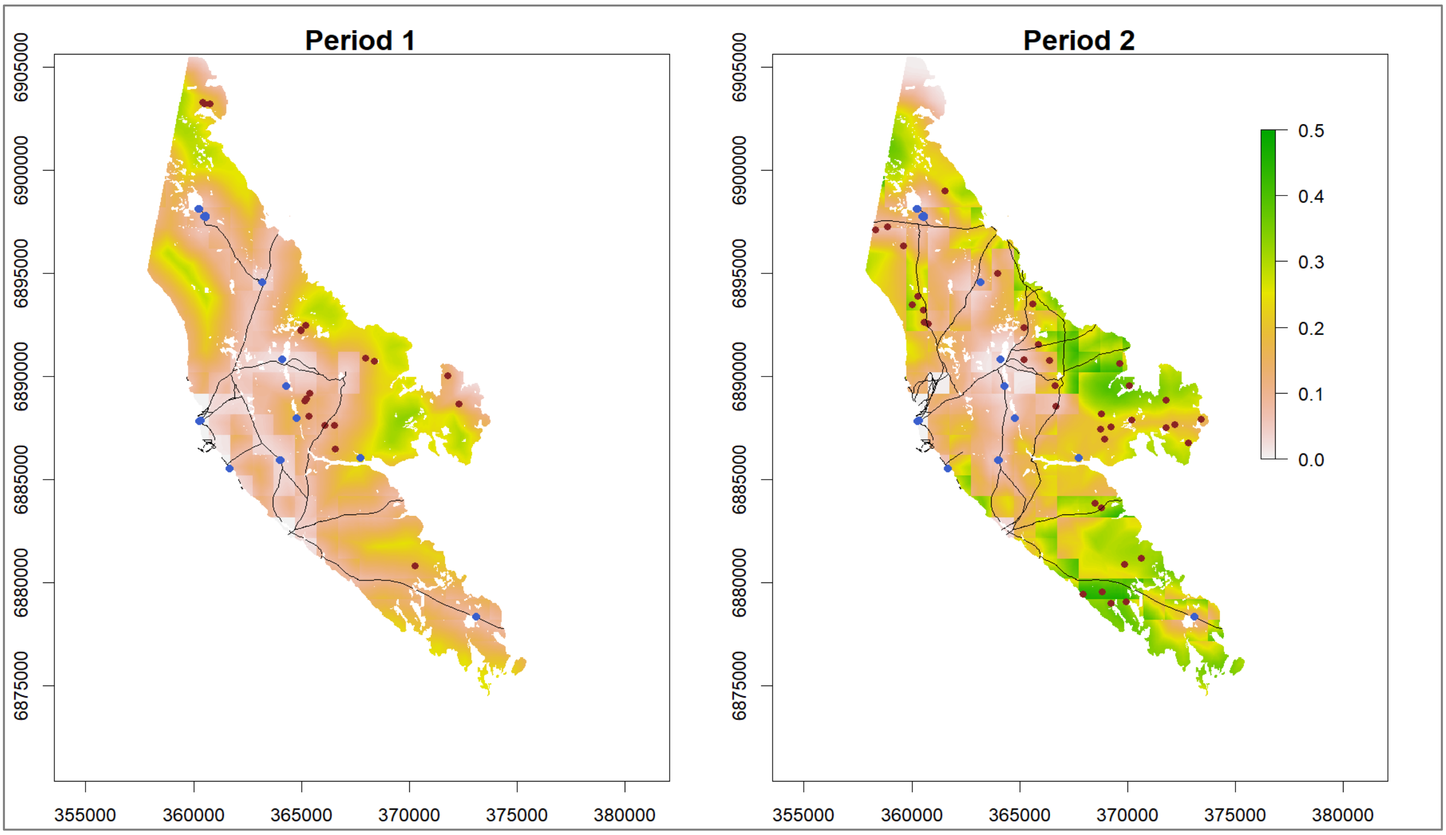

Figure 19: Predicted probability of co-occurrence for brown bear and semi-domesticated reindeer in both periods across the study area. Higher values indicate higher probability of co-occurrence. The brown points mark the locations of reindeer carcasses found in the study area during the study period. The axis represents UTM coordinates (Zone 33N), with eastings on the x-axis and northings on the y-axis. The black lines indicate trails, the red dots indicate carcasses, and the blue dots indicate buildings.

In addition to the habitat suitability maps, a Pearson's correlation test was performed to evaluate the relationship between brown bear and reindeer habitat suitability at carcass locations (see Figure 17, Figure 18 and Figure 19 for carcass locations). The correlation test revealed a strong and significant negative relationship between brown bear and reindeer habitat suitability at the carcass locations (r = -0.68, p < 0.001), indicating that carcasses are in areas suitable for one species but not suitable for the other species. This result contradicts H2, if human recreational activity increased predation, we would expect the carcasses to be found in habitats suitable for both species, as both species would prefer areas further away from human related features.

The probability of co-occurrence between brown bears and reindeer showed a slight variation at carcass locations compared to the broader study area, especially in terms of distribution in period 1, but the mean co-occurrence values did not differ significantly based on Welch's t-test (Figure 20).

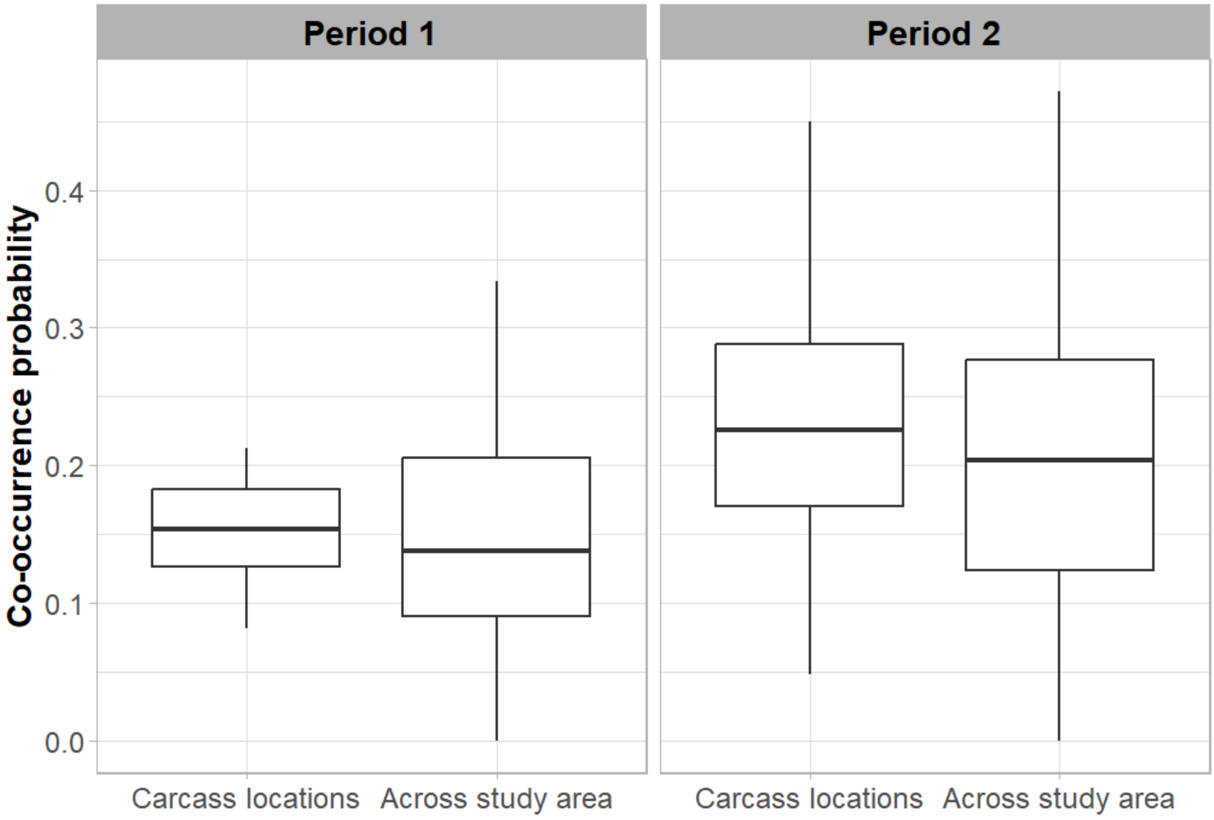

Figure 20: The probability of co-occurrence at carcass locations and across the study area in period 1 (left) and period 2 (right), based on resource selection functions.

In addition, a Welch t-test comparing average distances from carcass locations to the forest between period 1 and period 2 revealed no significant difference in mean distance, providing additional evidence against H2.

4. Discussion

4.1 Influence of human recreational activity on habitat selection and predation

Human activity in the mountain influenced the spatial habitat selection of both brown bears and reindeer, but with some differences between species. Brown bears were influenced negatively, with consistent avoidance related to human recreational activity throughout the reindeer calving period. For reindeer, the effect was more variable. In period 1, recreational activity had a negative influence on habitat selection leading to avoidance, while in period 2, the effect was more diffuse and not necessarily leading to avoidance (Figure 15 and Figure 16). There was not found a notable effect of human recreational activity in the mountain on brown bear predation pattern during the calving period.

As hypothesized (H1) and predicted in P1 to P4, brown bears generally selected areas further away from human activity and human-related features in both periods (Figure 15). This is consistent with the findings in Ordiz et al. (2013), which show that brown bears generally avoid humans. Furthermore, the results reveal no habituation towards humans between periods, and brown bears seem to actively avoid human encounters across the study period, in line with the findings of Ordiz et al. (2019). The bear and carcass GPS-positions recorded in the mountain were primarily logged at night, suggesting a temporal avoidance behavior, where brown bears use human-disturbed areas during nighttime when human activity is low. This trend has also been observed in previous studies, where Martin et al. (2010) and Ordiz et al. (2016) observed increased nocturnal behavior in bears exposed to higher levels of human disturbance. Brown bears typically rest in dense vegetation during the day to avoid humans (Ordiz et al., 2011), and even at night, when human presence is minimal, they still avoid highly disturbed areas in the mountain (Figure 15).

Moreover, the level of avoidance varied slightly between periods, with stronger avoidance observed in period 1. This increased influence of human activity in period 1 might be explained by snow early in the season (Støen et al., 2025), when snow cover could limit bear movements and alter behavior, as it has been found to do so with other species (Parker et al., 1984; Murray & Boutin, 1991).

In support of P1, P2 and H1 in period 1, reindeer avoided areas with higher levels of HAI and trail density (Figure 16). This may be linked to a high sensitivity early in the calving period, as the mean calving was May 9th (Støen et al., 2025). This finding is consistent with previous findings of Reimers et al. (2003), Anttonen et al. (2011) and Skarin & Åhman (2014) where female reindeer tend avoid human related features in late winter and spring when they are in a negative energy balance and calves are more vulnerable to predation. In contrast, during period 2, this was reversed, reindeer appeared to select areas with higher HAI and trail density, contradicting P1 and P2 (Figure 16).

One possible explanation is that reindeer may partially habituate to human presence as a trade-off for benefits like improved forage quality or insect relief, consistent with previous research findings (Skarin, 2006; Skarin et al., 2007; Skarin et al., 2010). In addition, Skarin et al. (2004) found that the reindeer in Idre used mountain habitat alongside tourists in summer to avoid insects, and Skarin (2006) argue that the effect of hiking trails during summer is small. This indicates potential for habituation, which may explain reindeer selection of areas near human-related features in period 2. However, these two studies were not from the calving period, and many factors influence reindeer's avoidance of human activity. The findings of avoidance in one population may not be applied to all reindeer populations, as found in Skarin et al. (2010).

Another explanation than habituation is that reindeer use historical movement routes and select better forage opportunities. According to local herders in Idre the reindeer move frequently between forest and mountain areas in period 2, searching for high-quality food and favorable conditions. Furthermore, many of the marked trails in Långfjället, used by humans today, are likely situated in landscapes which coincide with historical migration routes for wildlife. This includes traditional reindeer migration corridors, which the herds still use once the calf is strong enough to follow. Local herders have also observed that reindeer tend to use areas and trails associated with high human activity during early mornings or late evenings when human presence is minimal, and these areas coincide with the most suitable habitat in period 2 (Figure 18). This suggests that selection for human-related features in period 2 may be more temporally flexible and primarily influenced by traditional reindeer migration routes and vegetation rich habitat (Figure 18; Idre Nya Sameby, pers.comm.). Additionally, because humans move more slowly and predictably on foot during period 2, than on skis during period 1, they may also be perceived as less threatening, leading to reduced avoidance behavior (Gundersen et al., 2022).

The strongest effect on reindeer habitat selection was observed for distance to forest. Supporting P3, reindeer clearly selected areas far from the forest in period 1. This coincides with reindeer tending to select areas with good visibility and less tree cover during calving to reduce the risk of predation on newborn calves (Lima & Dill, 1990; Skarin & Åhman, 2014; Støen et al., 2025). In contrast, distance to forest had no effect in period 2, contrary to P3 (Figure 16). This shift may partly result from herding practices, as herders actively keep the reindeer on the mountain early in the calving period using snowmobiles, to reduce predation risk in forested areas. Disturbance from snowmobiles triggers avoidance behavior in reindeer, helping to keep them in the open mountain terrain (Reimers et al., 2003). The active herding along the outer edges of the herd typically ceased between May 15 and June 02, depending on snow cover (Støen et al., 2025).

Few studies have investigated how humans may influence the habitat selection of both predator and prey simultaneously, thereby influencing predation patterns. Mills & Harris. (2020) studying carnivores and ungulates in West Africa found that human presence caused a behavioral shift in prey activity, making them more accessible to predators during nighttime and increasing predation risk. On the other hand, areas associated with human activity may also act as refuges, as found in Canada, where the abundance of prey species was higher and predator species were lower on trails with high human activity compared trails with lower activity (Muhly et al., 2011). However, this study found that, contradicting H2 and P6, human recreational activity did not influence brown bear predation patterns. This contrasts with the findings from Neilson & Boutin (2017), who found that predation on moose by wolves (*Canis lupus*) increased in areas near human activity and disturbance.

Despite increased human activity in period 2 (Table 2, Table 3), the carcass location showed no clear spatial pattern, and their mean distance to forest did not differ significantly between periods. This indicates that predation is not strongly shaped by either of the species' spatial response to human recreational activity, as measured in this study. Most carcasses were in areas with high reindeer, but low bear habitat suitability, suggesting that brown bears move outside their preferred habitats to access reindeer (Figure 17, Figure 18), supported by a strong negative correlation in habitat suitability at carcass locations.

At the same time, the study found support for H1 and P5, suggesting that human recreational activity resulted in a higher probability of co-occurrence between the species near the forest (Figure 19), however no support for increased predation in these areas was found. Figure 19 and Figure 20 further show that carcasses were not concentrated in zones of high species overlap. If human activity increased predation by pushing both species toward the forest due to mutual human-avoidance, as suggested to be an alternative outcome of human activity in Scoyoc et al. (2023), more carcasses would be expected in areas with high co-occurrence. Yet this pattern was not observed.

4.2 Study limitations

Automatic people counters can be affected by environmental factors like snow, sunlight, moisture, or animals leading to false counts (Kajala et al., 2007; Kaltenborn, 2012). Period 1 had more invalid counts needing estimation than period 2 (Table 1), likely due to sunlight reflecting off snow. The exact causes remain unclear due to the lack of field observations, but errors were addressed using the estimation methods described in chapter 2.3.2. Estimating invalid counts using data from adjacent weeks was not feasible due to counter relocations which hindered cross-week comparability. Still, with an expected error rate of approximately 5% (Andersen et al., 2013) and only 0.5 – 6.6% of days per counter requiring count adjustment (Table 1), the overall impression of human activity remains robust. Furthermore, applying counts from 2024 across the study period may lead to inaccurate estimates, as daily trail use can vary with season, weather, holidays and events (Andersen et al., 2013; Gundersen et al., 2021). However, although the total number of trail users may vary between years, the relative difference in use between trails is assumed to remain consistent, and thus the avoidance effect is expected to be comparable across years.

The estimation of trail count values (mean passings per day) may underestimate actual human recreational activity, as individuals engaging in off-trail activities such as downhill skiing or fishing are not captured by the counters, and therefore not accounted for. However, the default value of 1 remains robust, as trails acquiring this value were likely less used than trails with a counter. Furthermore, the use of Strava Global Heatmap to guide counter placement and assess trail usage has limitations, as trail patterns and color intensity can vary (Stange et al., 2024). To improve reliability, local knowledge and a public trail map were used for cross-validation. This approach proved effective, and the HAI and trail density covariates aligned well with local observations and served as reliable relative indices for human activity. However, future research would benefit from access to complete Strava Metro trip-count data, enabling extrapolation of human recreational activity on trails without counters and across years.

Additionally, deploying counters over multiple years and across trails with varying levels of expected use would further allow spatiotemporal comparisons and improve the understanding of habitat selection in relation to human activity, as highlighted by Flydal et al. (2019).

While this study provided valuable insight into habitat selection, some additional variables could have further improved the analysis and interpretation of species behavior. To better understand temporal use of areas near human-related features by reindeer, time of day could have been included as a covariate in the statistical analysis. Additionally, including a vegetation covariate could have improved understanding of reindeer habitat suitability by helping to assess whether vegetation quality was the key driver of habitat selection. This might have clarified why reindeer appeared to select areas closer to human-related features in period 2, as it is not clear if this is due to habituation or better forage in those areas. Lastly, incorporating snow cover could provide insight into how snow conditions affect brown bear movement and possibly predation patterns. Since snow cover may restrict bear mobility and limit their ability to escape quickly, it is possible that brown bears avoid exposed areas under such conditions. However, this was beyond the scope of this study, focusing on human presence and infrastructure, but future studies could benefit from broadening the analyses in this direction.

4.3 Implications for natural resource management and visitor management

The result from this study informs both natural resource and visitor management, and are applicable to other reindeer herding districts with similar habitat conditions. The findings indicate that human recreational activity in mountain habitat influences habitat selection by both focus species (Figure 15, Figure 16). Furthermore, the results reveal a contradiction, while human presence may benefit reindeer by deterring predators, it can also cause disturbance during the most sensitive time of the calving period. However, there was no indication that predation patterns were impacted by human recreational activity.

Effective visitor management requires a detailed understanding of the natural area and strategies to reduce recreation related impacts while balancing the public right of access and local interests (Miljødirektoratet, 2023). Management approaches include a range of strategies, from restrictive to informative (Bell et al., 2009; Hammitt et al., 2015). Temporal trail closures can reduce disturbance to reindeer with a minor impact on recreational users, though such measures may be perceived as controversial (Kaltenborn et al., 2001; Gundersen et al., 2015; Whittington et al., 2019). In Sweden the public right of access is strongly valued and legally protected, granting people the freedom to access and travel through nature regardless of land ownership, but with certain responsibilities (Sténs & Sandström, 2014; Bengtsson, 2023; Waaler, 2023).

In Långfjället nature reserve, measures are already in place to reduce disruption to reindeer during the calving period. Disturbing reindeer is prohibited, and several snowmobile routes are closed from late April. Furthermore, from April 24 to June 14 (2025), five fishing waters were closed to minimize disruption and possible calf abandonment (Reimers et al., 2003; Vistnes & Nellemann., 2008; Länsstyrelsen Dalarnas län, s.a.). The local tourism company, Experience Grövelsjön, offers courses and guided experiences in the area, but refrains from promoting mountain activities during the calving period out of respect for the reindeer (Experience Grövelsjön, pers.comm.).

Because the public right of access is so deeply rooted and local herders report increasing pressure from recreationists on reindeer, place-specific management strategies are needed as found in Gundersen et al. (2024). A dynamic approach involving local tourism companies and members of Idre Nya Sameby can potentially ensure good visitor experiences while further minimizing disturbance on reindeer. If a temporal trail closure in May is an alternative, the yellow and green trails from Jakobshöjden to Storvätteshågna, and the blue trail crossing the mountain from Jakobshöjden to the cabins at lake Hävlingen are most relevant for evaluation (Figure 8). These trails had intermediate use levels, meaning the most popular trails could remain open, minimizing disruption for most visitors. Simultaneously, redirecting visitors and promoting alternative trails along the outer edges of the calving grounds, closer to the forest, may reduce disturbance while potentially deterring brown bears. Additionally, improving awareness through guiding, informational signs, and outreach through social media platforms can influence visitor behavior and further support coexistence between recreationists, local herders and wildlife (Kuba et al., 2018; Gundersen & Rybråten, 2022; Gundersen et al., 2024; Selvaag, 2025).

Managing brown bear predation on reindeer is challenging and there might not be any effective measure to prevent predation, especially since bears primarily enter mountain areas at night, limiting herders' ability to intervene. If a clear predation pattern had been found, it might have supported recommendations to keep reindeer away from certain areas, however this was not found. Strategies to reduce predation, like fencing or relocation of the herd have been attempted, but have proved unsuccessful due to high costs, reduced reindeer welfare and predators following the herd (Tallian et al., 2023; Idre Nya Sameby, pers.comm.). Alternative nighttime deterrence strategies like patrolling, installing floodlights and sound-based devices near the forest may hold potential, as sound deterring devices proved successful in deterring mountain lions (*Puma concolor*) in the Santa Cruz Mountains (Suraci et al., 2019) and seals in Scotland (Götz & Janik, 2016). Yet, the effectiveness of such measures remains uncertain and practical challenges subsist.

5. Conclusion

This study demonstrates that human recreational activity influenced both brown bear and semi-domesticated reindeer habitat selection, though to varying degrees. Brown bears consistently avoided human-related features. Reindeer showed avoidance primarily during the most sensitive part of the calving period, when calves are newly born, struggle to move with the herd and are at increased risk of predation. Later in the season, reindeer habitat selection appeared to be less negatively affected by human recreational activity. While past studies suggest that reindeer may habituate to human presence as a trade-off for other benefits, local herders emphasize that reindeer follow traditional migration routes to seek better forage, using human-affected areas primarily during times of low human presence.

The strongest predictor of reindeer habitat selection during the early calving period was distance to forest, likely influenced by selection of more remote areas during calving and active herding by Sámi reindeer herders, something that may reduce predation. No evidence was found that human recreational activity increased brown bear predation on reindeer. Still, temporary trail closures in May, along with existing management measures, may further reduce disturbance on reindeer during calving. Visitor management through communication and other strategies that support both recreation, reindeer herding and conservation of natural areas is key to coexistence in an increasingly human-dominated world. As biodiversity and indigenous livelihoods are facing growing threats from habitat loss, understanding the interactions between recreationists, traditional land use and wildlife is becoming increasingly important.

6. References

Andersen, O., Gundersen, V., Wold, L. C. & Stange, E. (2013). Monitoring visitors to natural areas in wintertime: issues in counter accuracy. *Journal of Sustainable Tourism*, 22 (4): 550-560. Doi: 10.1080/09669582.2013.839693

Anttonen, M., Kumpula, J. & Colpaert, A. (2011). Range Selection by Semi-Domesticated Reindeer (*Rangifer tarandus tarandus*) in Relation to Infrastructure and Human Activity in the Boreal Forest Environment, Northern Finland. *Arctic*, 64 (1): 1-14. Available at: https://www.jstor.org/stable/23025661

Appelhans, T., Detsch, F., Reudenbach, C., Woellauer, S., Forteva, S., Nauss, T., Pedesma, E., Russel, K., Summer, M., Darley, J., Roudier, P., Schratz, P., Marburg, E. I. & Busetto, L. (2023). *Mapview: Interactive Viewing of Spatial Data in R*. Available at: https://cran.r-project.org/web/packages/mapview/index.html (accessed: 18.05.2025).

Arnemo, J. M. & Evans, A. L. (2017). *Biomedical Protocols for Free-ranging Brown Bears, Wolves, Wolverines and Lynx.* Inland Norway University of Applied Sciences report 2017. Available at: https://brage.inn.no/inn-xmlui/bitstream/handle/11250/2444409/Biomedical%20Protocols%20Carnivores%202017.pdf?sequence=1 (accessed: 10.02.2025).

Barton, D. N., Clappe, S., Gundersen, V., Hansen, J. E., Korkou, M., Rød, J. K. & Venter, Z. S. (2025). *Metodeutvikling for kartlegging og verdsetting av friluftslivsområder*. NINA Rapport 2539. Available at: https://brage.nina.no/nina-xmlui/bitstream/handle/11250/3184748/ninarapport2539.pdf?sequence=6&isAllowed=y (accessed: 28.05.2025).

Bates, D., Mächler, M., Bolker, B. & Walker, S. (2015). Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software*, 67 (1): 1-48. Doi: 10.18637/jss.v067.i01

Bell, S., Simpson, M., Tyrväinen, L., Sievänen, T. & Pröbstl, U. (2009). *European forest recreation and tourism – a handbook.* Abingdon: Taylor & Francis.

Bell, S., Tyrväinen, L., Sievänen, T., Pröbstl, U. & Simpson, M. (2007). Outdoor Recreation and Nature Tourism: A European Perspective. *Living Reviews in Landscape Research,* (1). Doi: 10.12942/lrlr-2007-2

Bengtsson, B. (2023). *Allemannsrätten – Vad säger lagen?* Naturvårdsverket report 11/2023. Available at: https://www.naturvardsverket.se/4aced1/globalassets/media/publikationer-pdf/8900/978-91-620-8902-3.pdf (accessed: 02.04.2025).

Bevanger, K. (2015). *Rein Rangifer tarandus (Linnaeus, 1758).* Available at: http://www.artsdatabanken.no/Pages/179491 (accessed: 05.03.2025).

Bevanger, K. (2021). *Brunbjørn Ursus arctos Linnaeus, 1758*. Available at: http://www.artsdatabanken.no/Pages/180928 (accessed: 22.02.2025).

Bischof, R., Milleret, C., Dupont, P., Chipperfield, J., Brøseth, H. & Kindberg, J. (2019). *RovQuant: Estimating density, abundance and population dynamics of bears, wolverines and wolves in Scandinavia*. MINA fagrapport 63. Available at: https://nmbu.brage.unit.no/nmbu-xmlui/handle/11250/2649424 (accessed: 27.02.2025).

Bivand, R. S., Pebesma, E. & Gómez-Rubio, V. (2013). *Applied Spatial Data Analysis with R*. 2nd ed. Springer. Available at: https://asdar-book.org/ (accessed: 18.05.2025).

Brown, J. S., Laundré, J. W. & Gurung, M. (1999). The Ecology of Fear: Optimal Foraging, Game Theory and Trophic Interactions. *Journal of Mammalogy*, 80 (2): 385-399. Doi: doi.org/10.2307/1383287

Darimont, C. T., Fox, C. H., Bryan, H. M. & Reimchen, T. E. (2015). The unique ecology of human predators. *Science*, 349 (6250): 858-860. Doi: 10.1126/science.aac4249

Doherty, T.S., Hays, G. C. & Driscoll, D. A. (2021). Human disturbance causes widespread disruption of animal movement. *Nature ecology & evolution*, 5: 513-519. Doi: 10.1038/s41559-020-01380-1

Flydal, K., Tsegaye, D., Eftestøl, S., Reimers, E. & Colman, J. E. (2019). Rangifer within areas of human influence: understanding effects in relation to spatiotemporal scales. *Polar Biology*, 42: 1-16. Doi: 10.1007/s00300-018-2410-6

Frank, B. & Glikman, J. A. (2019). Human-Wildlife Conflicts and the Need to Include Coexistence. In Frank, B., Glikman, J. A. & Marchini, S. (ed.) *Human-Wildlife Interactions*, pp. 1-19. Cambridge: Cambridge University Press.

Fredman, P. & Tyrväinen, L. (2010). Frontiers in Nature-Based Tourism. *Scandinavian Journal of Hospitality and Tourism,* 10 (3): 177-189. Doi: 10.1080/15022250.2010.502365

Frid, A. & Dill, L. (2002). Human-caused Disturbance Stimuli as a Form of Predation Risk. *Conservation Ecology*, 6 (1). Available at: https://www.jstor.org/stable/26271862

Gaynor, K. M., Mclnturff, A. & Brashares, J. S. (2021). Contrasting patterns of risk from human and non-human predators shape temporal activity of prey. *Journal of Animal Ecology*, 91 (1): 46-60. Doi: 10.1111/1365-2656.13621

Gränslandet. (s.a.). *LÅNGFJÄLLET NATURRESERVAT*. Available at: https://www.graenslandet.se/sv/nio-skyddade-naturomraden/rogen/14-kartor/kartor/128-langfjaellet (accessed: 23.03.2025).

Gundersen, V. & Rybråten, S. (2022). Differing perceptions and tensions among tourists and locals concerning a national park region in Norway. *Journal of Rural Studies*, 94: 477-487. Doi: 10.1016/j.jrurstud.2022.07.017

Gundersen, V., Myrvold, K. M., Kaltenborn, B. P., Strand, O. & Kofinas, G. (2022). A review of reindeer (*Rangifer tarandus tarandus*) disturbance research in Northern Europe: towards a social-ecological framework? *Landscape Research*, 47 (8): 1100-1116. Doi: 10.1080/01426397.2022.2078486

Gundersen, V., Mehmetoglu, M., Vistad, O. I. & Andersen, O. (2015). Linking visitor motivation with attitude towards management restrictions on use in a national park. *Journal of Outdoor Recreation and Tourism*, 9: 77-86. Doi: 10.1016/j.jort.2015.04.004

Gundersen, V., Myrvold, K. M., Rauset, G. R., Selvaag, S. K. & Strand, O. (2021). Spatiotemporal tourism pattern in a large reindeer (*Rangifer tarandus tarandus*) range as an important factor in disturbance research and management. *Journal of Sustainable Tourism*, 29 (1): 21-39. Doi: 10.1080/09669582.2020.1804394

Gundersen, V., Selvaag, S. K., Junker-Köhker, B. & Zouhar, Y. (2024). Visitors relations to recreational facilities and attractions in a large vulnerable mountain region in Norway: Unpacking the roles of tourists and locals. *Journal of Outdoor Recreation and Tourism*, 47. Doi: 10.1016/j.jort.2024.100807

Götz, T. & Janik, V. M. (2016). Non-lethal management of carnivore predation: long-term tests with a startle reflex-based deterrence system on a fish farm. *Animal Conservation*, 19 (3): 212-221. Doi: 10.1111/acv.12248

Hammitt, W. E., Cole, D. N. & Monz, C. A. (2015). *WILDLAND RECREATION, Ecology and Management, Third Edition*. Chichester: WILEY Blackwell.

Helskog, K. & Indrelid, S. (2011). Humans and reindeer. *Quaternary International*, 238 (1-2): 1-3. Doi: 10.1016/j.quaint.2011.03.018

Hijmans, R. J., Barbosa, M., Bivand, R., Brown, A., Chirico, M., Cordano, E., Dyba, K., Pebesma, E., Rowlingson, B. & Sumner, M. D. (2025a). *Terra: Spatial Data Analysis*. Available at: https://cran.r-project.org/package=terra (accessed: 18.05.2025).

Hijmans, R. J., Etten. J., Sumner, M., Cheng, J., Baston, D., Bevan, A., Bivand, R., Busetto, L., Canty, M., Fasoli, A., Forrest, D., Ghosh, A., Golicher, D., Gray, J., Greenberg, J. A., Hiemstra, P., Hingee, K., Ilich, A., Karney, C., Mattiuzzi, M., Mosher, S., Naimi, B., Nowosad, J., Pebesma, E., Lamigueiro, O. P., Racine, E. B., Rowlingson, B., Shortridge, A., Venables, B. & Wueest, R. (2025b). *raster: Geographic Data Analysis and Modeling*. Available at: https://cran.r-project.org/package=raster (accessed: 18.05.2025).

IPBES. (2019). *Global assessment report of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services*. Available at: https://doi.org/10.5281/zenodo.3831673 (accessed: 28.02.2025).

IUCN. (2022). *Human-wildlife conflict*. Available at: https://iucn.org/resources/issues-brief/human-wildlife-conflict#7043 (accessed: 25.02.2025).

Johnson, D. H. (1980). The Comparison of Usage and Availability Measurements for Evaluating Resource Preference. *Ecology*, 61 (1): 65-71. Doi: 10.2307/1937156

Kajala, L., Almik, A., Dahl, R., Dikšaitė, L., Erkkonen, J., Fredman, P., Jensen, F. Søndergaard., Karoles, K., Sievänen, T., Skov-Petersen, H., Vistad, O. I. & Wallsten, P. (2007). *Visitor monitoring in nature areas – a manual based on experiences from the Nordic and Baltic countries* (TemaNord 2007:534). Stockholm: Swedish Environmental Protection Agency.

Kaltenborn, B.P. (2012). *Bruk og vern i utmarksområder: Sluttrapport. Strategisk instituttprogram for perioden 2009-2011.* NINA Temahefte 50. Available at: https://www.nina.no/archive/nina/pppbasepdf/temahefte/050.pdf (accessed: 14.02.2025).

Kaltenborn, B. P., Haaland, H. & Sandell, K. (2001). The Public Right of Access &#x2013; Some Challenges to Sustainable Tourism Development in Scandinavia. *Journal of Sustainable Tourism*, 9 (5): 417-433. Doi: 10.1080/09669580108667412

Kassambara, A. (2023). *ggpubr: 'ggplot2' Based Publication Ready Plots*. Available at: https://cran.r-project.org/package=ggpubr (accessed: 15.05.2025).

Kuba, K., Monz, C., Bårdsen, B.-J. & Hausner, V. H. (2018). Role of site management in influencing visitor use along trails in multiple alpine protected areas in Norway. *Journal of Outdoor Recreation and Tourism*, 22: 1-8. Doi: 10.1016/j.jort.2018.02.002

Lantmäteriet. (2025). *Topografi 50 Nedladdning, vektor*. Available at: https://geotorget.lantmateriet.se/dokumentation/GEODOK/76/latest.html#kort-om-produkten (accessed: 14.05.2025).

Laundré, J. W., Hernández, L. & Ripple, W. J. (2010). The Landscape of Fear: Ecological Implications of Being Afraid. *The Open Ecology Journal*, 3: 1-7. Available at: https://www.predatordefense.org/agencies/docs/research_LandscapeOfFear_Laundre_2010.pdf

Lima, S. L. & Dill, L. M. (1990). Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology*, 68 (4): 619-640. Doi: 10.1139/z90-092

Linnell, J. D. C. & Kaltenborn, B. P. (2019). The Case of Large Herbivores and Large Carnivores in Europe. In Frank, B., Glikman, J. A. & Marchini, S. (ed.) *Human-Wildlife Interactions*, pp. 288-310. Cambridge: Cambridge University Press.

Länsstyrelsen Dalarnas län. (s.a.). *Långfjället.* Available at: https://www.lansstyrelsen.se/dalarna/besoksmal/naturreservat/langfjallet.html?sv.target=12.382c024b1800285d5863a87f&sv.12.382c024b1800285d5863a87f.route=/&searchString=&counties=&municipalities=&reserveTypes=&natureTypes=&accessibility=&facilities=&sort=none (accessed: 23.05.2025).

Manly, B. F. J., McDonald, L.L. & Thomas, D. L. (1993). *Resource Selection by Animals: Statistical design and analysis for field studies*. Springer Dordrecht. Available at: https://link.springer.com/book/10.1007/978-94-011-1558-2 (accessed: 18.05.1015).

Martin, J., Basille, M., Moorter, B., Kindberg, J., Allainè, D. & Swenson, J. E. (2010). Coping with human disturbance: spatial and temporal tactics of the brown bear (*Ursus arctos). Canadian Journal of Zoology*, 88 (9): 875-883. Doi: 10.1139/Z10-053

Miljødirektoratet. (2023). *Hva er besøksforvaltning?* Available at: https://www.miljodirektoratet.no/ansvarsomrader/friluftsliv/naturvennlig-ferdsel/besoksforvaltning-i-mye-besokte-naturomrader/hva-er-besoksforvaltning/ (accessed: 07.04.2025).

Mills, K. L. & Harris, N. C. (2020). Humans disrupt access to prey for large African carnivores. *eLife*: Doi: 10.7554/eLife.60690

Muhly, T. B., Semeniuk, C., Massolo, A., Hickman, L. & Musiani, M. (2011). Human Activity Helps Prey Win the Predator-Prey Space Race. *PLOS ONE*, 6 (3). Doi: 10.1371/journal.pone.0017050

Murray, D. L. & Boutin, S. (1991). The influence of snow on lynx and coyote movements: does morphology affect behavior? *Oecologia*, 88: 463-469. Doi: 10.1007/BF00317707

Neilson, E. W. & Boutin, S. (2017). Human disturbance alters the predation rate of moose in the Athabasca oil sands. *Ecosphere*, 8 (8). Doi: 10.1002/ecs2.1913

Nieminen, M. (2013). Response distances of wild forest reindeer (*Rangifer tarandus fennicus* Lönnb.) and semi-domestic reindeer (R. *t. tarandus* L.) to direct provocation by a human on foot/snowshoes. *Rangifer*, 33 (1): 1-15. Doi: 10.7557/2.33.1.2614

Ordiz, A. Moen, G. K., Sæbø, S., Stenset, N., Swenson, J. E. & Støen, O.-G. (2019). Habituation, sensitization, or consistent behavioral responses? Brown bear responses after repeated approaches by humans on foot. *Biological Conservation,* 232: 228-237. Doi: 10.1016/j.biocon.2019.01.016

Ordiz, A., Støen, O.-G., Delibes, M. & Swenson, J. E. (2011). Predators or prey? Spatio-temporal discrimination of human-derived risk by brown bears. *Oecologia*, 166: 59-67. Doi: 10.1007/s00442-011-1920-5

Ordiz, A., Støen, O.-G., Sahlén, V., Pedersen B. E., Kindberg, J. & Swenson, J. E. (2013). Lasting behavioural responses of brown bears to experimental encounters with humans. *Journal of Applied Ecology*, 50 (2): 306-314. Doi: 10.1111/1365-2664.12047

Ordiz, A., Sæbø, J., Kindberg, J., Swenson, E. & O.-G. Støen. (2016). Seasonality and human disturbance alter brown bear activity patterns: implications for circumpolar carnivore conservation. *Animal Conservation*, 20 (1): 51-60. Doi: 10.1111/acv.12284

Parker, K. L., Robbins, C. T. & Hanley, T. A. (1984). Energy Expenditures for Locomotion by Mule Deer and Elk. *The Journal of Wildlife Management*, 48 (2): 474-488. Doi: 10.2307/3801180

Pebesma, E. (2018). Simple Features for R: Standardized Support for Spatial Vector Data. *The R Journal*, 10 (1): 429-446. Doi: 10.32614/RJ-2018-009

Posit team. (2025). *Download Rstudio IDE*. Posit software PBC. Available at: https://posit.co/downloads/ (accessed: 15.05.2025)

QGIS.org. (2025). *QGIS Geographic Information System*. QGIS Association. Available at: http://qgis.org

Ravna, Ø., Benjaminsen, T. A. & Jernsletten, K. (2024). Reindrift. In *The Great Norwegian Encyclopedia*. Available at: https://snl.no/reindrift (accessed: 25.05.2025).

R Core Team. (2024). *The R Project for Statistical Computing*. Available at: https://www.r-project.org/ (accessed: 15.05.2025).

Reimers, E., Eftestøl, S. & Colman, J. E. (2003). Behavior Responses of Wild Reindeer to Direct Provocation by a Snowmobile or Skier. *The Journal of Wildlife Management,* 67 (4): 747-754. Doi: 10.2307/3802681

Reimers, E., Miller, F. L., Eftestøl, S., Colman, J. E. & Dahle, B. (2006). Flight by feral reindeer *Rangifer tarandus tarandus* in response to a directly approaching human on foot or on skis. *Wildlife Biology*, 12 (4): 403-413. Doi: 10.2981/0909-6396(2006)12[403:FBFRRT]2.0.CO;2

Rolandsen, C. M., Tveraa, T., Gundersen, V., Røed, K. H., Tømmervik, H., Kvie, K., Våge, J., Skarin, A. & Strand, O. (2022). *Klassifisering av de ti nasjonale villreinområdene etter kvalitetsnorm for villrein: Første klassifisering – 2022*. NINA Rapport 2126. Available at: https://hdl.handle.net/11250/2991315 (accessed: 03.06.2025).

Rolandsen, C. M., Tveraa, T., Gundersen, V., Røed, K. H., Tømmervik, H., Våge, J., Skarin, A., Strand, O. & Hansen, B. B. (2023). *Klassifisering av 14 ikke-nasjonale villreinområder etter kvalitetsnorm for villrein: Første klassifisering – 2023*. NINA Rapport 2372. Available at: https://hdl.handle.net/11250/3106763 (accessed: 03.06.2025).

Røed, K. H., Bjørnstad, G., Flagstad, Ø., Haanes, H., Hufthammer, A. K. Jordhøy, P. & Rosvold, J. (2014). Ancient DNA reveals prehistoric habitat fragmentation and recent domestic introgression into native wild reindeer. *Conservation Genetics*, 15: 1137-1149. Doi: 10.1007/s10592-014-0606-z

Scoyoc, A. V., Smith, J. A., Gaynor, K. M., Barker, K. & Brashares, J. S. (2023). The influence of human activity on predator-prey spatiotemporal overlap. *Journal of Animal Ecology*, 92 (6): 1124-1134. Doi: 10.1111/1365-2656.13892

Selvaag, S. K. (2025). *Fostering pro-environmental behavior through communication: managing outdoor recreation in national park settings.* PhD thesis. Ås: Norwegian University of Life Sciences. Available at: https://hdl.handle.net/11250/3196196 (accessed: 02.06.2025).

Sivertsen, T. R., Åhman, B., Steyaert, S. M. J. G., Rönnegård, L., Frank, J., Segerström, P., Støen, O.-G. & Skarin, A. (2016). Reindeer habitat selection under the risk of brown bear predation during calving season. *Ecosphere*, 7 (11). Doi: 10.1002/ecs2.1583

Skarin, A. (2006). *Reindeer Use of Alpine Summer Habitats*. PhD thesis. Uppsala: Swedish University of Agricultural Sciences. Available at: https://res.slu.se/id/publ/13605 (accessed: 07.04.2025).

Skarin, A. (2007). Habitat use by semi-domesticated reindeer, estimated with pellet-group counts. *Rangifer*, 27 (2): 121-132. Doi: 10.7557/2.27.2.167

Skarin, A., Danell, Ö., Bergström, R. & Moen, J. (2004). Insect avoidance may override human disturbances in reindeer habitat selection. *Rangifer*, 24 (2): 95–103. Doi: 10.7557/2.24.2.306

Skarin, A., Danell, Ö., Bergström, R. & Moen, J. (2010). Reindeer movement patterns in alpine summer ranges. *Polar Biology*, 33: 1263-1275. Doi: 10.1007/s00300-010-0815-y

Skarin, A. & Åhman, B. (2014). Do human activity and infrastructure disturb domesticated reindeer? The need for the reindeer's perspective. *Polar Biology,* 37: 1041-1054. Doi: 10.1007/s00300-014-1499-5

Stange, E., Gundersen, V., Simensen, T. & Frassinelli, F. (2024). *Ferdsel fra hytter i villreinområdet Norefjell-Reinsjøfjell: Analyse av Strava data, villreinens arealbruk og tomtereserve*. NINA Rapport 2462. Available at: https://brage.nina.no/nina-xmlui/handle/11250/3134123 (accessed: 14.02.2025).

Sténs, A. & Sandström, C. (2014). *Allemansrätten* in Sweden: A Resistant Custom. *Landscapes*, 15 (2): 106-118. Doi: 10.1179/1466203514Z.00000000029

Støen, O.-G., Sivertsen, T. R., Tallian, A., Rauset, G. R., Kindberg, J., Persson, L.-T., Stokke, R., Skarin, A., Segerström, P. & Frank, J. (2022). Brown bear predation on semi-domesticated reindeer and depredation compensations. *Global Ecology and Conservation*, 37. Doi: 10.1016/j.gecco.2022.e02168

Støen, O.-G., Thorsen, N. H., Andersson, P., Jonsson, M., Segerström, P., Tveraa, T., Riverud, I. M., Kopatz, A., Jonsson, B., Andersson, M., Renhuvud, E., Jonsson, A., Moorter, B. V., Kindberg, J., Kleven, O., Tallian, A. & Mattison, J. (2025). *Bjørnens predasjon på tamrein – Sluttrapport fra Bjørn- og tamreinprosjektet i Idre, Sverige*. NINA Rapport 2585. Available at: https://brage.nina.no/nina-xmlui/handle/11250/3183569 (accessed: 29.03.2025).

Suraci, J. P., Clinchy, M., Zanette, L. Y. & Wilmers, C. C. (2019). Fear of humans as apex predators has landscape-scale impacts from mountain lions to mice. *Ecology Letters*, 20 (10): 1578-1586. Doi: 10.1111/ele.13344

Swenson, J. E., Wabakken, P., Sandegren, F., Bjärvall, A., Franzén, R. & Söderberg, A. (1995). The near extinction and recovery of brown bears in Scandinavia in relation to the bear management policies of Norway and Sweden. *Wildlife Biology*, 1 (1): 11-25. Doi: 10.2981/wlb.1995.005

Sørensen, O. J. (2012). *I BJØRNENS FOTSPOR - Kunnskapsstatus, biologi og historie*. Trondheim: Akademika Publishing.

Tallian, A., Støen, O.-G., Immerzeel, B., Kindberg, J., Ordiz, A., Persson, L. T., Segerström, P., Skarin, A., Stokke, R., Tveraa, T., Åhman, B. & Frank, J. (2023). Large carnivore conservation and traditional pastoralism: A case study on bear-reindeer predation mitigation measures. *Ecosphere*, 14 (6). Doi: 10.1002/ecs2.4564

The International Centre for Reindeer Husbandry (ICR). (s.a.). *What is Reindeer Husbandry?* Available at: https://reindeerherding.org/what-is-reindeer-husbandry (accessed: 09.03.2025).

Venter, Z. S., Gundersen, V., Scott, S. L. & Barton, D. N. (2023). Bias and precision of crowdsourced recreational activity data from Strava. *Landscape and Urban Planning*, 232. Doi: 10.1016/j.landurbplan.2023.104686

Vistnes, I. & Nellemann, C. (2001). Avoidance of Cabins, Roads, and Power Lines by Reindeer during Calving. *The Journal of Wildlife Management*, 65 (4): 915-925. Doi: 10.2307/3803040

Vistnes, I. & Nellemann, C. (2008). The matter of spatial and temporal scales: a review of reindeer and caribou response to human activity. *Polar Biology*, 31: 399-407. Doi: 10.1007/s00300-007-0377-9

Waaler, R. (2023). Friluftsliv. In *The Great Norwegian Encyclopedia*. Available at: https://snl.no/friluftsliv (accessed: 02.04.2025).

Wickham, H., Averick, M., Bryan, J., Chang, W., McGowan, L.D., Francois, R., Grolemund, G., Hayes, A., Henry, H., Hester, J., Kuhn, M., Pedersen, T. L., Miller, E., Bache, S. M., Müller, K., Ooms, J., Robinson, D., Seidel, D. P., Spinu, V., Takahashi, K., Vaughan, D., Wilke, C., Woo, K. & Yutani, H. (2019). Welcome to the Tidyverse. *Journal of Open Source Software*, 4 (43): 1686. Doi: 10.21105/joss.01686

Wickham, H., Chang, W., Henry, L., Pedersen, T. L., Takahashi, K., Wilke, C., Woo, K., Yutani, H., Dunnington, D. & Brand, T. (2016). *ggplot2*. (R-package). Available at: https://ggplot2.tidyverse.org/ (accessed: 15.05.2025).

Whittington, J., Low, P. & Hunt, B. (2019). Temporal road closures improve habitat quality for wildlife. *Scientific Reports*, 9. Doi: 10.1038/s41598-019-40581-y

Wood, S. (2025). *mgcv: Mixed GAM Computation Vehicle with Automatic Smoothness Estimation*. Available at: https://cran.r-project.org/package=mgcv (accessed: 27.05.2025).

Norges miljø- og biovitenskapelige universitet
Noregs miljø- og biovitenskapelege universitet
Norwegian University of Life Sciences

Postboks 5003
NO-1432 Ås
Norway