The effect of the Covid-19 lockdown on the spatial ecology of moose in an area with high recreational activity

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Swedish University of Agricultural Sciences, SLU Department of Wildlife, Fish, and Environmental Studies Management of Fish and Wildlife Populations
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Abstract

In diverse landscapes, the coexistence of wildlife habitat requirements and human land use often leads to conflicts, posing challenges for sustainable species management. Recreational activities, especially in sparsely populated areas, frequently disturb wildlife behavior, necessitating a comprehensive assessment of anthropogenic impacts on habitats.

The global COVID-19 pandemic in 2020 and 2021 drastically reduced human activities, notably travel, resulting in improved environmental conditions and a resurgence of wildlife in urban areas. This study explores the pandemic's impact on large ungulates, with a focus on moose (*Alces alces*) in a northern Swedish region (67°51'N, 19°0'W) heavily influenced by nature tourism.

Utilizing GPS data from 20 tagged adult moose over a four-year span, I investigated temporal and spatial changes in moose behavior before, during, and after the COVID-19 lockdown. The study concentrated on two valleys with varying levels of human activities. Surprisingly, the results indicate that moose did not significantly respond to the reduction in recreational activity during the lockdown. There were no discernible changes in habitat use, moose activity, or proximity to human infrastructure associated with the lockdown. This unexpected outcome may be attributed to Sweden's pandemic policy, where increased free time and a sharp decline in foreign tourism sustained the appeal of local nature use, mitigating the anticipated decrease in tourism levels. Local biological and ecological factors further complicated the distinction between natural and anthropogenic influences on moose behavior.

Future research could investigate visitor numbers and weather influences in Nikkaluokta to gain a more nuanced understanding for formulating management strategies aimed at minimizing interactions between recreational use and the moose population. For example, when expanding recreational areas in moose habitats, more consideration can be given to the needs of the moose.

Keywords: *Moose, Alces alces, habitat selection, tourism, human disturbance, activity, movement, speed, seasons, Covid-19, pandemic*

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List of abbreviations

$^{1/3}$Trail proximity	Cube Root transformed trail proximity
e.g	Latin for "for example"
hr	hour
i.e	Latin for "that is"
iSSF	integrated Step Selection Function
GPS	Global Positioning System
log-m/hr	log-transformed movement rate
LME	linear mixed models
m	meter
m.a.s.l	meter about sea level
SLU	Swedish University of Agricultural Sciences

1. Introduction

The emergence of the COVID-19 pandemic in December 2019 in China and its subsequent global impact presented an unprecedented disruption to modern human societies (Buder *et al.,* 2020). As the virus, officially named COVID-19 or SARS-CoV-2, rapidly spread, the World Health Organization (WHO) declared it a public health emergency of international concern (WHO, 2020). By March 11, 2020, the WHO declared COVID-19 a pandemic, with Europe emerging as a significant epicenter, reporting over 40 % of the world's confirmed cases (Hass & Arsanjani, 2021). In response to the escalating crisis, the member states of the European Union implemented various measures to limit the virus's impact, including travel warnings, border controls, and even closures of both internal and external borders (Chinazzi *et al.,* 2020).

These measures aimed primarily at safeguarding public health but had profound consequences on the free movement of people within the European Union and, consequently, alterations in interactions between humans and the surrounding environment and wildlife, including daily, working, and touristic activities. Travel restrictions, especially during the initial waves of the pandemic in spring 2020 and autumn/winter 2020/2021, significantly curtailed travel within and among different EU countries (Neumayer *et al.,* 2021). However, the imposition of these restrictions was not uniform across EU member states, leading to a disparity in responses to the global crisis.

Notably, Sweden stood apart from many other EU countries during the initial wave of the pandemic in spring 2020. While other nations implemented strict and restrictive measures, Sweden's response was characterized by more moderate recommendations from its Public Health Agency, which encouraged reduced travel and socialization without explicit prohibitions (Hiselius & Arnfalk, 2021). Consequently, Sweden experienced a reduction in overall tourism (Manakov *et al.,* 2021), but its inhabitants increasingly turned to local nature for recreation during the restrictions (Hansen *et al.,* 2022).

Tourism is pivotal in Sweden's economy, contributing 8.2 % to its GDP (Gross domestic product) in 2019 (Manakov *et al.,* 2021). With 7.4 million predominantly European tourists visiting the country (Ide, 2021), international events substantially affect its tourism market. This impact, however, varies regionally due to Sweden's geographical shape and location (Manakov *et al.,* 2021). Southern Sweden, bordering Germany and Denmark, is the primary gateway for international tourists (Manakov *et al.,* 2021).

The region of northern Sweden, with its diverse landscapes and natural attractions, has long been a magnet for international tourists (Jacobsen, 2015). Remarkably, the northernmost Swedish province of Norrbotten experienced a surge in tourism prior to the pandemic, recording a 24.7% increase in visitor numbers in 2018 compared to the previous year, while national tourism increased by only 7.4% (Affärer i Norr, 2020). This remarkable increase has been attributed to the exponential growth of nature tourism (hiking, skiing) in Nordic areas (Fredman & Tyrväinen, 2010; Marjavaara & Müller, 2022), possibly leading to seasonal mass tourism (Rantala *et al.,* 2019; Müller *et al.,* 2020).

Intensification of nature-based recreational activities is increasingly encroaching on wildlife habitats (Fredman & Heberlein, 2003), affecting animals' behavior, stress levels, energy use (Creel *et al.,* 2002; Taylor & Knight, 2003; Stankowich, 2008; Lischka *et al.,* 2018), and vegetation (Cole, 2004; He, 2019).

Regular human disturbances of wildlife, even when non-lethal, can significantly influence habitat use behavior (Gaynor *et al.,* 2018). Studies propose that habituation may occur under specific conditions, wherein animals become accustomed to inevitable disruptions (Thompson & Spencer, 1966). For instance, Reimoser (2012) observed a decrease in the reactions of roe deer (*C. capreolus*) to disturbances caused by horses in a confined environment, suggesting potential habituation towards the end of the study. Nevertheless, the degree of habituation varied among stimuli, indicating that animals may adjust more readily to some disturbances than others. Borkowski *et al.* (2006) found that bison (*B. bison*) and elk (*C. canadensis*) in Yellowstone National Park exhibited reduced responses to snowmobile disturbances compared to findings in other research areas. This difference might signify habituation, possibly influenced by the consistently high snowmobile traffic in the park. Disturbances that animals can predict in terms of time and location, such as those near human infrastructure, often elicit fewer escape reflexes in response to unforeseen disruptions (Stankowich, 2008).

In contrast, experimental studies by Neumann *et al.* (2010) and Cassirer *et al.* (1992) revealed no habituation in GPS-tracked moose (*A. alces*) in Sweden and elk in the United States when exposed to off-trail skiers. Cassirer *et al.* (1992) identified potential habituation in the most frequented area, where animals exhibited weaker responses to predictable human disturbance and stronger reactions to unexpected disturbances. Similarly, Sibbald *et al.* (2011) found no consistent habituation effect on hikers in red deer (*C. elephus*), and Moen *et al.* (1982) observed no habituation to snowmobiles in white-tailed deer (*O. virginianus*).

These inconsistent findings underscore the challenges in the literature arising from varied experimental designs, leading to different responses among species and even within populations. Despite observing a reduction in response intensity (e.g., escape distance) in repeated experiments (Malo *et al.,* 2011; Parker *et al.,* 1984; Borkowski *et al.,* 2006), caution is urged in interpreting it as habituation. Visible behavior may not always mirror underlying physiological processes. Furthermore, apparent behavioral adaptations to regular disturbances may still result in adverse effects, including changes in condition, stress, or breeding success (Tarlow & Blumstein, 2007).

The COVID-19 pandemic offers a unique opportunity to investigate the repercussions of declines in anthropogenic activities on wildlife, particularly in areas characterized by high levels of tourism activity (Driessen, 2021; Corlett *et al.,* 2020). This impact can manifest in various ways, given that humans are integral to most ecosystems (Liu *et al.,* 2007). Understanding how the environment and wildlife respond to sudden reductions in human impact, such as those triggered by the pandemic, is a novel and relatively under-researched area of study (Anderson *et al.,* 2023). Past studies suggest that there is a return of wildlife with reduced anthropogenic use in previously heavily anthropogenic areas (Cassirer *et al.,* 1992; Gagnon *et al.,* 2007); in contrast, other studies indicate that persistent low levels of disturbance can hinder the return to previously used areas (Kuck *et al.,* 1985), leading to permanent shifts in habitat use (Rowland *et al.,* 2005).

Wildlife can respond in various ways to this sudden change in human presence. For example, wildlife sightings increased in metropolitan areas during the 2020 lockdown (Zellmer *et al.,* 2020; Bar, 2021), suggesting exit restrictions positively influenced wildlife species' temporal and geographical activity (Rutz *et al.,* 2020). Additionally, the substantial reduction in anthropogenic disturbances may have reshaped the human-induced landscape of fear (Ciuti *et al.,* 2012; Bleicher, 2017; Lodberg *et al.,* 2019). This landscape describes the spatial and temporal variations in prey animals' perception of predation risk and their subsequent anti-predator behavior (Laundré *et al.,* 2014; Gaynor *et al.,* 2019).

This complex interplay between humans, wildlife behavior, and the environment is particularly evident in areas where increased recreational activities overlap with wildlife habitats. One example of such overlap is the region around Kebnekaise, Sweden's highest mountain and its mountain station. The Ladtjo valley, which is heavily frequented by recreationists, is the gateway to Kebnekaise. Here, moose, an important wildlife species, are confronted with disturbance from various human activities (e.g., hiking, cross-country skiing, snowmobiling). Höög (2020), for example, observed that moose in the Ladtjo valley changed their habitat use pattern in response to human disturbance and avoided open areas during the main visiting seasons in summer and winter.

The extreme decline in Swedish tourist numbers in 2020-2021 due to COVID-19 restrictions (Grech *et al.,* 2020) provided a unique opportunity to investigate how reduced human recreational activities might affect the space use and movement activities of moose in northern Sweden in an area where nature tourism and moose habitats overlap.

This complex interplay between human activities, wildlife responses, and environmental changes highlights the need to investigate the dynamics of such interactions in the context of the COVID-19 pandemic and its effects on wildlife behavior and habitat use.

1.1 Aims and purposes

This study aims to delve into the intricate interplay between human-induced disturbances, with a specific focus on tourism, and their impact on the spatial behavior of moose. The primary goal is to uncover how different intensities of nature tourism shape free-ranging moose's movements and habitat preferences. A comparative analysis will be conducted, examining moose spatial behavior before, during, and after periods of heightened tourism activity. Two distinct valleys, the Ladtjo valley, known for its substantial tourism linked to the hiking trail leading to Kebnekaise Mountain Station, and the Vistas valley, characterized by a comparatively lower tourism level, will be scrutinized. Extensive datasets on animal locations collected across the pre-, during, and post-COVID-19 pandemic periods will be leveraged to ensure a comprehensive investigation. This temporal breadth facilitates a thorough examination of moose responses to diverse human disturbances over time and in different spatial contexts. Additionally, the study seeks to identify behavioral changes in moose attributable to the unique circumstances of the pandemic.

The insights gained from this research can contribute to developing informed strategies for coordinating wildlife management and recreational use. Based on previous research, I hypothesize the following:

1. Moose habitat selection will differ between the valleys with high (Ladtjo) and low (Vistas) tourist activity. I expect that moose in the Ladtjo valley will more often select suboptimal habitats during times of high touristic activity (à peak season and during pre/post covid).

2. Moose will change their activity pattern in relation to human activity. I expect moose in the Ladtjo valley will be more active (meter per hour) during nighttime during times of high touristic activity (à peak season and during pre/post covid), whereas I do not expect a change for moose in the Vistas valley.

3. Moose will avoid the proximity of humans. I expect moose to select for a closer distance to the hiking trail during the lockdown of the Covid period (2020-2021) and during periods of low human activity in the Ladtjo valley compared to years (2019 or 2022) and seasons with high human activity. I do not expect any change on trail proximity among seasons and years for moose in the Vistas valley.

4. I assume that moose show temporal adaptations in relation to human activity patterns. I expect moose to stay closer to trails in the Ladtjo valley during night compared to daytime in years/season with high human activity, whereas I do not expect such day/night pattern for moose in the Vistas valley.

2. Methods

2.1 Study area

The study area is located northwest of Nikkaluokta (470 m.a.s.l), a mountain village in the Gällivare municipality, Norrbotten province, Sweden (67°51'N, 19°0'W). Nikkaluokta is a tourist center that serves as a starting point for various recreational activities along the well-known long-distance hiking trail "Kungsleden" and the highest mountain in Sweden, Kebnekaise (2097 m.a.s.l). Mountain birch forest (*Betula pubescens*) describes large parts of the study area below the tree line (about 800 m), whereas above the tress line, treeless tundra vegetation dominates. Above 1000 to 1200 m, the vegetation is particularly sparse due to the northern latitude, and the soils consist mainly of scree and bare rock. This unique landscape makes Nikkaluokta one of Sweden's most visited mountain areas, attracting over 50,000 hikers annually (Jägerbrand *et al.,* 2015), as well as 2,000-3,000 summit ascents (Holmlund & Holmlund, 2019) of Kebnekaise. Due to limited tree vegetation at higher elevations, moose are commonly found in the Ladtjo and Vistas valleys (see Figure 3) in deciduous forests that visitors explore to varying degrees. With the beginning of the vegetation period, many moose follow an altitudinal migration to track the green wave along valley slopes (Singh *et al.,* 2012).

The Ladtjo valley is a popular route to the Kebnekaise Mountain Station, which offers year-round activities such as helicopter and summer boat transfers from Nikkaluokta, gastronomic service, and well-maintained trails, some of which are barrier-free. In addition, a snowmobile runs regularly on the trail in winter. In contrast, the Vistas valley is an alternative route to the "Kungsleden" trail but is less popular and frequently used. The two valleys are similar regarding vegetation (Figure 1, Appendix 4) and climatic conditions but differ significantly in the level of human activity.

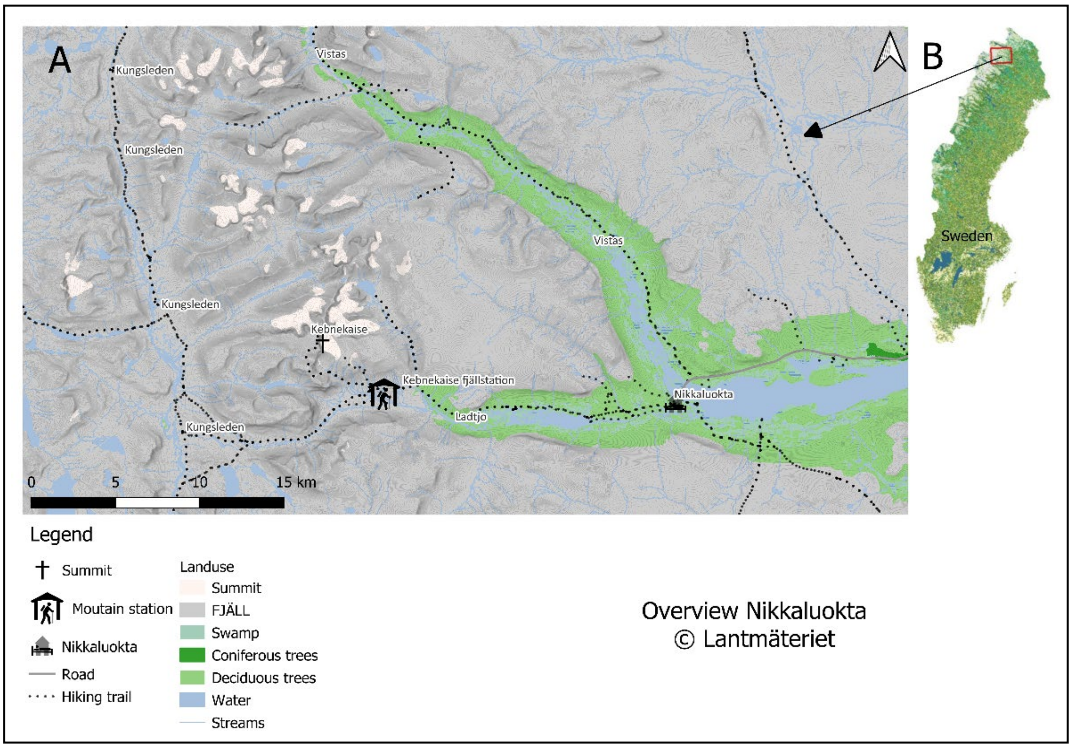

Figure 1. (A) Maps showing the study area. Distribution of the trail system (black dotted lines) and tree vegetation (green color) in the Nikkaluokta area and along the valleys, Ladtjo and Vistas. The marked trails in winter do not differ significantly from the marked trails in summer. In (B), the box outlined in red shows where in Sweden the study area is.

2.2 Data collection

2.2.1 Moose data and movement activity

Studying wildlife dynamics and interactions in natural environments, particularly within remote and extensive animal populations, the collection of accurate and reliable data is remotely crucial. This often involves immobilizing animals and equipping them with data loggers to be able monitor them remotely in space over time (Kays *et al.,* 2015). In the case of moose in Nikkaluokta, trapping operations are conducted by helicopter in winter (March) when snow and light conditions favorable, using CO2-powered dart guns to administer a combination of etorphine and xylazine, following to established protocols (Arnemo & Kreeger, 2003; Arnemo & Kreeger, 2007; Evans *et al.,* 2012; Græsli *et al.,* 2020b; Lian *et al.,* 2014). Strict compliance with the certification standards set by the Swedish Animal Welfare Agency and the Swedish Ministry of Agriculture is crucial for all employees handling moose.

All procedures for capturing, handling, and tagging the animals were carried out with the approval of the national administrative authority, the Animal Welfare Commission of Umeå (DNR A 11-2020). During handling, the animals were observed by trained personnel until the removal of the anesthesia. During capture, chasing time with the helicopter was minimized to avoid possible side effects such as hyperthermia. Given the low weight of the collars (<2 % of body weight), it is assumed that the collars do not significantly affect locomotion and behavior.

The moose are equipped with GPS collars provided by Vectronic Aerospace GmbH, Berlin, Germany. To save battery power, these collars are programmed to calculate the position every 3 hours during the annual cycle, except during the calving and rutting period, where the tracking device calculates a position every 30 minutes. The collected data is regularly transmitted to the Wireless Remote Animal Monitoring (WRAM) database at SLU using the method described by Dettki *et al.* (2014), allowing for near real-time monitoring.

In preprocessing the initial dataset of 30 tagged animals, I undertook a series of filtration steps to enhance data accuracy. Initially, I excluded inaccurate positions, such as those falling outside the defined study area, and eliminated data from individuals that did not contribute any information throughout the designated study period from 2019 to 2022. Subsequently, the dataset underwent additional refinement, focusing on capturing positional information at six-hour intervals, precisely four times a day on the hour. Notably, all half-hourly data points were excluded from the analysis.

As a result of these filtration processes, a final dataset emerged, comprising a total of 81,765 meticulously curated locations. This dataset encapsulated the movement patterns of 20 distinct moose, showcasing a division between the Ladtjo valley and the Vistas valley. Specifically, the Ladtjo valley featured nine individuals, all of which were female, while the Vistas valley comprised 11 moose—nine females and two males. This refined dataset forms the foundation for the subsequent analyses and insights presented in this thesis.

To study moose responses in relation to human activities and habitat features, I linked the locations of each moose to a set of environmental data (see more details below). However, it is imperative to note that linking animal movements to the environment may introduce biases due to differences in the environmental data's size, accuracy, and precision (Neumann *et al.,* 2015; Remelgado *et al.,* 2018).

2.2.2 Tourism data and study period

In the Norrbotten province, a significant trend known as 'arctification' has emerged, showcasing the growing popularity of northern destinations for tourism (Bohn & Varnajot, 2021; Lundmark *et al.,* 2020). This transformation has brought about significant changes, emphasizing the commercialization of nature-based activities to attract international and affluent travelers (Varnajot & Saarinen, 2022).

A notable indicator of this evolution is the substantial increase in overnight stays in Norrbotten province, rising from 2.1 million in 2012 to 2.7 million in 2018 (Tillväxtverket, 2023). This growth sets the province of Norrbotten apart from other Arctic regions in neighboring countries (Varnajot, 2020).

Despite the global impact of the COVID-19 pandemic and its associated lockdown on tourism, both domestically and internationally (Ide, 2021), tourism in the Norrbotten province has sustained – even though at a lower level - and avoided complete collapse during the lockdowns, as depicted in Figure 2.

In 2020, the province of Norrbotten recorded approximately 380,000 overnight stays, marking a significant 77% decrease compared to the pre-pandemic year of 2019 (Manakov *et al.,* 2022). The municipality of Gällivare, housing the study area, experienced a relatively moderate decline in tourist overnight stays, with a 34% decrease below the regional average. The reduction in European tourists in the municipality of Gällivare was less pronounced than in other municipalities within the Norrbotten province, with foreign tourist stays dropping from 30,000 in 2019 to 12,000 in 2020.

To address my four hypotheses, I analyzed the moose location dataset from January 1, 2019, to December 31, 2022, designating 2019 as the pre-COVID year, 2020 and 2021 as the during-COVID period, and 2022 as the post-COVID phase. This timeframe is crucial for analyzing both moose and tourism data. Information from Höög (2020) and overnight data from Tillväxtverket (2023) were used to identify high and low recreational tourism periods. This results in four seasons with varying levels of tourism activities, two peak and two low seasons of touristic activity (Table 1), and different climatic seasons. It is essential to note that the number of overnight stays is estimated and not the exact number of people in the study area.

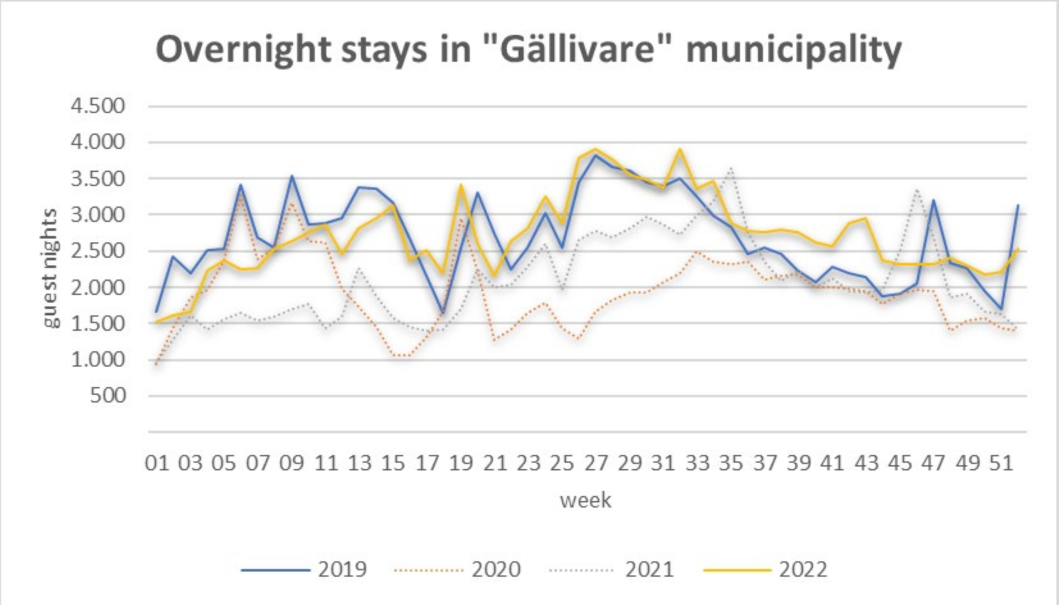

Figure 2. Overnight stays in the municipality of Gällivare (Tillväxtverket, 2023), where the study area is situated. The X-axis represents weeks per year, while the Y-axis represents the number of overnight stays. The solid lines represent the years without travel restrictions in 2019 and 2022, the dotted lines represent the years with travel restrictions in 2020 and 2021.

Table 1. Temporal division into the four seasons of touristic impact in the study area, with the dating depending on visitor frequency according to Höög, 2020 and Tillväxtverket, 2023 (see Figure 2).

Period name	Week start	Week end
Winter Peak	4 (start of Feb)	15 (mid. of March)
Spring Low	16 (end of March)	25 (end of Jun)
Summer Peak	26 (start of July)	35 (end of Aug)
Autumn Low	36 (start of Sep)	3 (end of Jan)

2.2.3 Environmental data

Human activity exhibits temporal variations throughout the day, leading to adjustments in wildlife behavior (Frid & Dill, 2002). In response to human presence, wildlife often shifts towards nocturnal activity (Gaynor *et al.,* 2018). Above the Arctic Circle, the duration of sunlight undergoes significant fluctuations, resulting in weeks of continuous daylight during summer and weeks of darkness in winter. Despite these variations, leisure time organization remains minimally affected (Dupuis, 2004). Acknowledging the substantial daylight changes, I define the period from 6 am to 9 pm as "day" for analysis purposes throughout the year, regardless of actual daylight, while considering the period from 9.01 pm to 5.59 am as "night," representing a presumed lower visitor activity period.

The study area experiences freezing temperatures between September and May, covering it in snow for approximately half of the year. This condition significantly influences regional vegetation and its utilization for leisure activities, such as cross-country skiing and snowmobiling in winter and hiking during the vegetation period. Helicopter transportation is prevalent in both seasons. Conversely, summer temperatures, reaching up to 25 °C, impact the local ecosystem, influencing wildlife behavior, such as reduced movement activity in moose with higher ambient temperatures (Ericsson *et al.,* 2015). In mountainous areas, moose migrate from higher-altitude summer habitats (600-850 m.a.s.l) to the bottom of valleys (250-400 m.a.s.l) during winter when snow depth increases (Singh *et al.,* 2012; Bunnefeld *et al.,* 2011). This migration typically begins in November/December, with the spring migration occurring in April/May (Singh *et al.,* 2012; Allen *et al.,* 2016).

Nikkaluokta experiences an annual precipitation average of around 700 mm/year, limiting tree growth to lower valleys due to the area's northern latitude and extended frost periods. These valleys are predominantly covered with mountain birch trees (*Betula pubescens*) and serve as preferred moose habitats, offering cover and foraging areas (Allen *et al.,* 2016; Fohringer *et al.,* 2021). Wetlands, including lakes, rivers, and saline marshes, attract moose in summer due to the availability of preferred food sources, such as seedlings, buds, leaves, grasses, and aquatic plants. Notably, these valley bottoms favoured by moose align with significant recreational migration routes (see Figure 3).

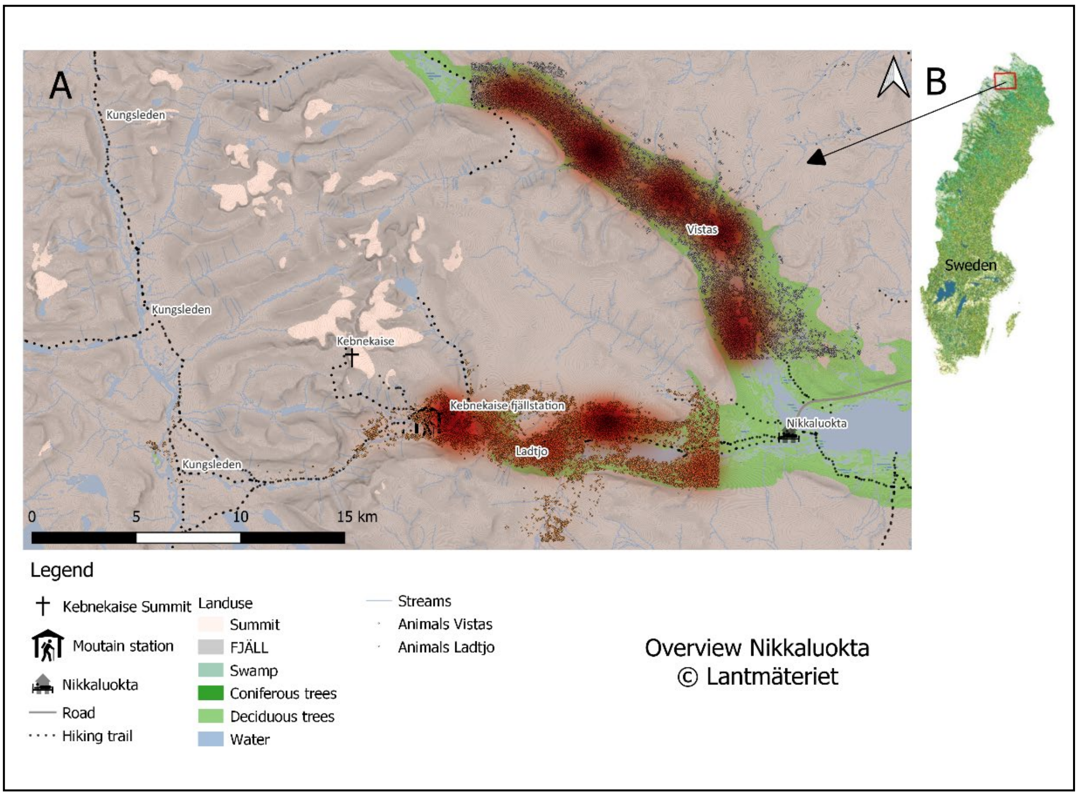

Figure 3. (A) Distribution of the trail system (black dotted lines) and tree vegetation (green color) and main moose distribution (orange dots in Ladtjo valley & blue dots in Vistas valley) in the Nikkaluokta area and along the valleys Ladtjo and Vistas (n=20 moose individuals). In (B), the box outlined in red shows where in Sweden the study area is.

2.3 Statistical analysis

2.3.1 Habitat selection in relation to human activity

To investigate moose habitat selection in response to environmental conditions, I utilized a conditional logistic regression approach, explicitly employing the integrated step selection function (*iSSF*) as Avgar *et al.* (2016) detailed. This method integrates moose telemetry data with habitat parameters obtained from the Swedish Land Survey Agency (www.lantmäteriet.se) at a spatial resolution of 10x10m, comparing habitats used by animals with available habitats. Various land cover types were categorized into five biologically relevant vegetation classes for moose: "open areas," "deciduous forests," "swamps," "water bodies," and "other" (refer to Appendix 1 for detailed categorization).

Using the R-package *amt* (Signer *et al.,* 2019), I computed moose movement steps based on positional data, calculating the length and rotation angle for each observed step. Each actual step was paired with five randomly generated steps (Thurfjell *et al.,* 2014), utilizing a gamma distribution for step length calculation and the Von Mises distribution for step angle calculation (Signer *et al.,* 2019). Subsequently, environmental data was extracted to the end of the stride for both the observed and randomly generated steps. The occurrence of vegetation classes between the observed steps and the corresponding set of five randomly generated steps was then compared using a probability equivalent.

This estimation method, employing a Cox proportional hazards model, evaluates the selection of animals (observed step) within a given vegetation class relative to their availability (random steps). All data analyses were conducted separately for the two geographically distinct valleys (Ladtjo and Vistas, Fig. 1), the seasons (Table 1), and the day/night distinction.

In northern latitudes, moose habitat uses, and diet exhibit significant seasonal variation (Allen *et al.,* 2016; Spitzer *et al.,* 2019). During snow-free periods, large herbivores display a preference for easily digestible and abundant broad leaves and herbaceous plants. Forage quality in more open areas, especially riparian zones, is higher than in closed forests (Alaback, 1982; MacCracken *et al.,* 1997; Stephenson *et al.,* 2006). Conversely, the less digestible branches of deciduous and coniferous trees present throughout the year contribute to diverse habitat use (Rettie & Messier, 2000; Bjørneraas *et al.,* 2011; Spitzer *et al.,* 2019). But temperature stress also plays a major role for moose and influences their choice of habitat. If the air temperature rises in spring, summer and autumn, moose are more likely to be found in thermal shelters (deciduous forest) (Dussault *et al.,* 2004).

Therefore, I hypothesized that moose have better access to forage in most open habitats than in closed forests and that closed forests provide more cover (vision and heat) than open habitats (Molvar & Bowyer, 1994; Bowyer *et al.,* 1998). I assumed that cover-rich deciduous forests are used more frequently due to visitor intensity and selected them as an intercept for statistical analyses. This assumption is further supported by Höög (2020), who found an increased selection of cover-rich habitats by moose during visitor peaks in Nikkaluokta.

2.3.2 Movement behavior in relation to human activity

To assess the impact of human activities on moose behavior, I conducted an analysis focusing on their movement speed (measured in meters per hour) and proximity to human infrastructure (measured in meters). As the study area lacked paved roads and permanent residences, the network of hiking trails (see Figure 1) was considered the primary human infrastructure, and moose proximity to these trails were calculated.

To discern seasonal variations, a linear mixed effects model was employed using the "*lme*" package in R (Pinheiro *et al.,* 2018). Given the non-normal distribution of the dependent variables—namely, "steps per hour" and "proximity to trail"—a transformation was applied to ensure normality.

The "moose ID" was included as a random effect in the analysis, incorporating random intercepts for each moose. This approach allowed for the consideration of individual differences and accounted for repeated measures in the analyses.

To maintain simplicity and avoid an excessive number of interaction terms, each season and each valley were examined separately. This strategy facilitated a nuanced examination and comparison of model outputs for each valley during every season over the study period.

All statistical analyses were performed using R version 4.3.2 (R Core Team 2023), with significance tests set at a p-value of < 0.05.

Table 2. The model set-up to address the four hypotheses. All models are run separately per season and valley. Model lme represent a linear mixed model and iSSF an integrated step-selection function.

Hypothesis	***Model***	***Response variable***	***Fixed effects***	***Data***
1	***iSSF***	***Habitat selection***	***Case[a] ~ (vegetation[b]) * year[c] + strata (step id)***	***two different valleys with 4 seasons each (8 data sets)***
2	***lme***	***Movement Speed***	***Log_stepmhr ~ day_night * year, random = ~1 | Object_ID[f]***	***two different valleys with 4 seasons each (8 data sets)***
3	***iSSF***	***Trail proximity***	***Case_ ~ Trail_proximity * year + strata (step_id)***	***two different valleys with 4 seasons each (8 data sets)***
4	***lme***	***Trail proximity***	$^{1/3}$***Trail_proximity[e] ~ day_night * year, random = ~1 | OBJECT_ID***	***two different valleys with 4 seasons each (8 data sets)*** ***only observed steps[d]***

Variables

[a]Observed or random step, binary

[b]Vegetation: categorical

[c]year: pre-, during-, post COVID, continuous

[d]Observed steps: categorical

[e]Euclidean distance to the nearest trail (m), continuous

[f]random Intercept→ Object ID

3. Results

Of the 20 adult and tagged moose available for my analysis, nine lived in the Ladtjo valley and 11 in the Vistas valley.

3.1 Hypothesis I: Habitat selection will differ with human impact

Throughout the study period, moose varied little in their habitat selection, including among periods of different human activity (i.e. before, during, and after the COVID-19 lockdown or among different tourist seasons). Contrary to hypothesis 1, I did not find an increased selection of "open" habitats during the pandemic or during periods with less visitor pressure (spring and autumn). However, moose in the Ladtjo valley (characterized by high recreational pressure) did show an increased selection of "open" habitats, particularly during spring (lower visitor pressure) and summer (high visitor pressure) seasons, but only in the first lockdown year, 2020, and after the pandemic in 2022.

A notable shift in habitat preference occurred during the *spring*, a period of low human activity spanning from 2019 to 2022 in both the Ladtjo and Vistas valleys (Table 3). In the year before the lockdown (2019), moose in both valleys preferred deciduous forests to "open" habitats (i.e. showed a higher selection for deciduous forests). However, in the first year of the COVID-19 lockdown (2020), there was an increasing preference for open areas, surpassing the preference for deciduous forests observed in the year before the lockdown.

While there were no discernible changes in habitat choice in the second year of the lockdown (2021), there was a shift in moose habitat choice in the year after the lockdown (2022). In the Ladtjo valley, moose increasingly chose open habitats, reminiscent of the first year of the lockdown (2020). In the less tourist-frequented Vistas valley, however, moose chose fewer swamp areas in the year after the lockdown (2022) than before the lockdown (2019).

Before the COVID lockdown, moose in both valleys preferred deciduous forests over "open" habitats in the *summer* of 2019, characterized by high human activity. Moose used significantly fewer open habitats in both valleys than in deciduous forests (Table 3). Interestingly, this phenomenon (increased use of deciduous forests) did not occur among moose in either valley during the lockdown (summer 2020). Moose in the Vistas valley tended to increase use of open habitats compared to deciduous forests (2019). During the second lockdown year (2021), moose in the Ladtjo valley chose more "open" habitats than deciduous forests in 2019, and moose in both valleys tended to choose more swamp areas. Similarly, after the Covid-19 restrictions were lifted (2022), moose in the Ladtjo valley chose more open habitats (Table 3).

In *autumn*, characterized by reduced anthropogenic recreational use, before the COVID-19 lockdown (2019), moose did not select any habitat more than deciduous forests, except for a tendency to exhibit a stronger preference for "open" and "water" habitats in the Ladtjo valley (Table 3). In contrast, moose in the Vistas valley select more for swampy habitats than deciduous forests during the pre-lockdown year, whereas they switched and selected significantly less for swampy habitats in the first year of the lockdown (2020). In the second COVID year (2021), there was also a significant decline in "other" habitats in Vistas (Table 3, Appendix 1). After the pandemic (2022), moose in the Ladtjo valley showed a trend towards increased selection of swampy habitats.

During the *winter* season, characterized by high recreational impact, moose exhibited similar habitat preferences before, during, and after the pandemic. Before the pandemic (2019), moose in the Vistas valley tended to use open habitats less than deciduous forests. During the first lockdown (2020), moose in the Vistas valley significantly reduced their usage of swamp areas compared to deciduous forests in 2019 (Table 3).

Table 3. The estimates and standard errors of moose habitat selection in relation to different levels of anthropogenic activity (pre, during and after COVID-19 lockdown and different tourism period) as given by the integrated step-selection function (i.e., conditional logistic regression), Nikkaluokta, 2019 to 2022. Deciduous forest serves as the intercept, and moose are assigned as a random factor. Significant differences are highlighted in bold. The years with reduced visitor numbers (COVID years) are presented in italics, as well as the seasons with lower anthropogenic impact. P-values between 0.05 and 0.1 indicate a trend and are marked with a dot and given in italics.

			Ladtjo				**Vistas**			
			Estimate	SE	z-value	Pr(>|z|)	Estimate	SE	z-value	Pr(>|z|)
Pre Covid 2019	*Spring low*	Open	**-0.35**	**0.10**	**-3.47**	**0.000*****	**-0.23**	**0.09**	**-2.62**	**0.008****
		Swamp	0.05	0.15	0.35	0.723	0.14	0.12	1.19	0.232
		Water	-0.45	0.28	-1.63	0.103	**0.33**	**0.14**	**2.27**	**0.023***
		Other	0.13	0.57	0.23	0.817	0.02	0.37	0.07	0.943
During Covid 2020	*Spring low*	Open	**0.26**	**0.12**	**2.07**	**0.038***	**0.28**	**0.11**	**2.37**	**0.017***
		Swamp	- 0.21	0.21	-1.02	0.307	-0.03	0.15	-0.20	0.835
		Water	- 0.52	0.48	-1.08	0.278	**-0.51**	**0.22**	**-2.28**	**0.022***
		Other	- 0.19	1.23	-0.15	0.876	-0.58	0.55	-0.97	0.332
During Covid 2021	*Spring low*	Open	0.15	0.13	1.30	0.229	0.17	0.11	1.46	0.142
		Swamp	0.10	0.21	0.50	0.614	-0.01	0.16	-0.03	0.950
		Water	0.29	0.33	0.88	0.375	-0.31	0.20	-1.51	0.131
		Other	0.41	0.83	0.83	0.619	-0.34	0.52	-0.66	0.506
Post Covid 2022	*Spring low*	Open	**0.35**	**0.13**	**2.53**	**0.011***	0.14	0.11	1.23	0.217
		Swamp	0.02	0.24	0.09	0.922	**-0.36**	**0.16**	**-2.22**	**0.026***
		Water	**0.85**	**0.41**	**2.06**	**0.038***	**-0.39**	**0.19**	**-2.00**	**0.045***
		Other	0.53	0.89	0.59	0.550	-0.36	0.57	-0.63	0.527
Pre Covid 2019	Summer peak	Open	**-2.24**	**7.95**	**-2.82**	**0.004****	**-0.16**	**0.06**	**-2.39**	**0.016***
		Swamp	-2.46	1.96	-1.25	0.208	**-0.28**	**0.14**	**-1.97**	**0.048***
		Water	**-7.48**	**3.44**	**-2.17**	**0.029***	*-0.38*	*0.22*	*-1.70*	*0.088.*
		Other	-7.38	1.05	-0.70	0.484	-0.23	0.33	-0.71	0.473
During Covid 2020	Summer peak	Open	1.57	1.09	1.44	0.148	*0.18*	*0.10*	*1.80*	*0.071.*
		Swamp	1.45	2.70	0.53	0.591	0.24	0.22	1.11	0.264
		Water	4.83	4.49	1.07	0.282	0.33	0.33	0.98	0.324
		Other	-2.31	1.28	-0.18	0.857	0.22	0.56	0.57	0.568
During Covid 2021	Summer peak	Open	**2.65**	**1.13**	**2.37**	**0.017***	0.05	0.09	0.57	0.568
		Swamp	*4.72*	*2.65*	*1.78*	*0.074.*	*0.39*	*0.21*	*1.87*	*0.061.*
		Water	6.84	5.21	1.31	0.189	0.15	0.31	0.48	0.627
		Other	-1.25	4.60	-0.02	0.978	0.73	0.45	1.60	0.108
Post Covid 2022	Summer peak	Open	**2.32**	**1.16**	**2.00**	**0.045***	0.03	0.10	0.30	0.761
		Swamp	3.77	2.47	1.52	0.127	0.06	0.20	0.31	0.750
		Water	3.77	4.23	0.89	0.372	0.36	0.31	1.18	0.236
		Other	1.06	1.12	0.94	0.345	0.16	0.51	0.32	0.742

			Ladtjo				Vistas			
			Estimate	SE	z-value	Pr(>|z|)	Estimate	SE	z-value	Pr(>|z|)
Pre Covid 2019	*Autumn low*	Open	*-9.67*	*5.62*	*-1.71*	*0.085.*	0.00	0.06	0.13	0.890
		Swamp	-1.76	1.38	-1.27	0.202	**0.23**	**0.07**	**3.11**	**0.001****
		Water	*-3.73*	*2.03*	*-1.83*	*0.067.*	0.02	0.09	0.30	0.760
		Other	-8.25	7.41	-1.11	0.265	0.13	0.28	0.49	0.619
During Covid 2020	*Autumn low*	Open	8.13	7.93	1.02	0.304	-0.05	0.08	-0.61	0.540
		Swamp	5.00	1.89	0.26	0.791	**-0.23**	**0.10**	**-2.12**	**0.033***
		Water	-2.53	3.80	-0.66	0.504	-0.07	0.14	-0.50	0.614
		Other	1.12	9.89	1.14	0.254	-0.04	0.39	-0.11	0.912
During Covid 2021	*Autumn low*	Open	-7.58	7.96	-0.09	0.925	0.08	0.09	0.92	0.355
		Swamp	-1.67	2.26	-0.73	0.461	0.01	0.10	0.10	0.917
		Water	3.48	3.01	1.15	0.247	0.06	0.14	0.44	0.659
		Other	-1.15	3.15	-0.03	0.974	**-1.17**	**0.59**	**-1.99**	**0.004***
Post Covid 2022	*Autumn low*	Open	-6.95	8.95	-0.07	0.938	-0.00	0.10	-0.01	0.989
		Swamp	*3.15*	*1.90*	*1.65*	*0.098.*	-0.11	0.14	-0.81	0.416
		Water	-6.72	4.33	-0.15	0.876	-0.10	0.20	-0.54	0.586
		Other	1.18	9.38	1.25	0.208	0.22	0.47	0.46	0.642
Pre Covid 2019	Winter peak	Open	-0.05	0.08	-0.66	0.506	*-0.09*	*0.05*	*-1.71*	*0.086.*
		Swamp	-0.03	0.14	-0.25	0.801	-0.07	0.09	0.83	0.405
		Water	-0.32	0.20	-1.57	0.114	-0.08	0.13	-0.62	0.532
		Other	0.61	0.42	1.45	0.145	-0.07	0.25	-0.31	0.752
During Covid 2020	Winter peak	Open	-0.05	0.10	-0.53	0.591	0.00	0.07	0.00	0.997
		Swamp	-0.10	0.17	-0.62	0.529	**-0.25**	**0.12**	**-2.01**	**0.044***
		Water	0.17	0.24	0.69	0.486	-0.12	0.19	-0.63	0.527
		Other	-1.10	0.89	-1.27	0.201	0.12	0.31	0.40	0.683
During Covid 2021	Winter peak	Open	-0.11	0.09	-1.13	0.258	-0.01	0.07	-0.20	0.836
		Swamp	-0.24	0.18	-1.29	0.196	0.08	0.12	0.66	0.508
		Water	-0.20	0.30	-0.66	0.507	-0.25	0.22	-1.10	0.267
		Other	-0.31	0.63	-0.49	0.620	-0.28	0.39	-0.72	0.466
Post Covid 2022	Winter peak	Open	-0.12	0.10	-1.12	0.259	0.03	0.07	0.42	0.667
		Swamp	0.12	0.20	0.61	0.541	-0.09	0.11	-0.76	0.425
		Water	0.39	0.30	1.30	0.191	0.18	0.16	1.08	0.276
		Other	-1.05	0.86	-1.21	0.224	0.24	0.30	0.81	0.414

3.2 Hypothesis II: Diurnal Activity pattern will differ with human activity

When examining moose day and night activity in Nikkaluokta across both valleys—Ladtjo (marked by high recreational use) and Vistas (characterized by less recreational use), similar movement and recreational use fluctuations were observed, as depicted in Figure 4. On average, moose exhibited lower nocturnal activity for all the years except the summer months than daytime in the year preceding the COVID-19 lockdown (2019).

However, when analysing the timeline (before, during, and after the lockdown), no significant difference in nighttime activity during 2020, 2021, and 2022, and daytime activity in the year before COVID-19 (2019) was observed, indicating no notable impact attributable to visitor pressure. Consequently, hypothesis 2 was not confirmed, suggesting increased nocturnal movement by moose in the Ladtjo valley during high visitor pressure periods and before & after the pandemic. The less anthropogenic-used Vistas valley showed no significant change.

During *spring*, characterized by reduced anthropogenic use, moose in the Ladtjo valley did not exhibit a significant difference between day and night activity. In contrast, moose in Vistas demonstrated a noteworthy reduction in night activity (t(1,4420)= -0.56, p=0.000). However, examining individual years, moose in Ladtjo valley used nighttime hours significantly less for movement during the first lockdown (2020) compared to spring 2019 (t(1,3232)= -0.37, p=0.026). In contrast, moose in Vistas valley increased nighttime activity in the second lockdown year (2021) and post-pandemic (2022) compared to spring 2019 (Figure 4, see Appendix 2 for details).

Both valleys showed a similar behavioral pattern in the *summer* season, with no significant difference in night and day activity compared to 2019. Post-COVID-19 restrictions and increased visitor pressure in 2022, moose in Ladtjo valley used nighttime hours more for movement than daytime in 2019 (t(1,4243)= 0.26, p=0.027).

During the less visitor-intensive *autumn* period, both valleys exhibited a reduction in average nighttime activity. In Ladtjo valley, moose used nighttime hours less for movement (t(1,8623)= -0.48, p=0.000), while in Vistas valley, daytime activity was higher than nighttime activity in 2019 (t(1,6776)= -0.58, p=0.000) (Figure 4, see Appendix 2 for further details).

In *winter*, frequented by cross-country skiers and snowmobile riders, both valleys significantly reduced nighttime activity compared to daytime in 2019. In the second year of the pandemic (2021) and after restrictions were lifted in 2022, moose in Vistas valley demonstrated a noteworthy reduction in nighttime activity compared to pre-pandemic daytime levels in 2019 (t(1,9332)= -0.17, p=0.010) (Figure 4, see Appendix 2 for further details).

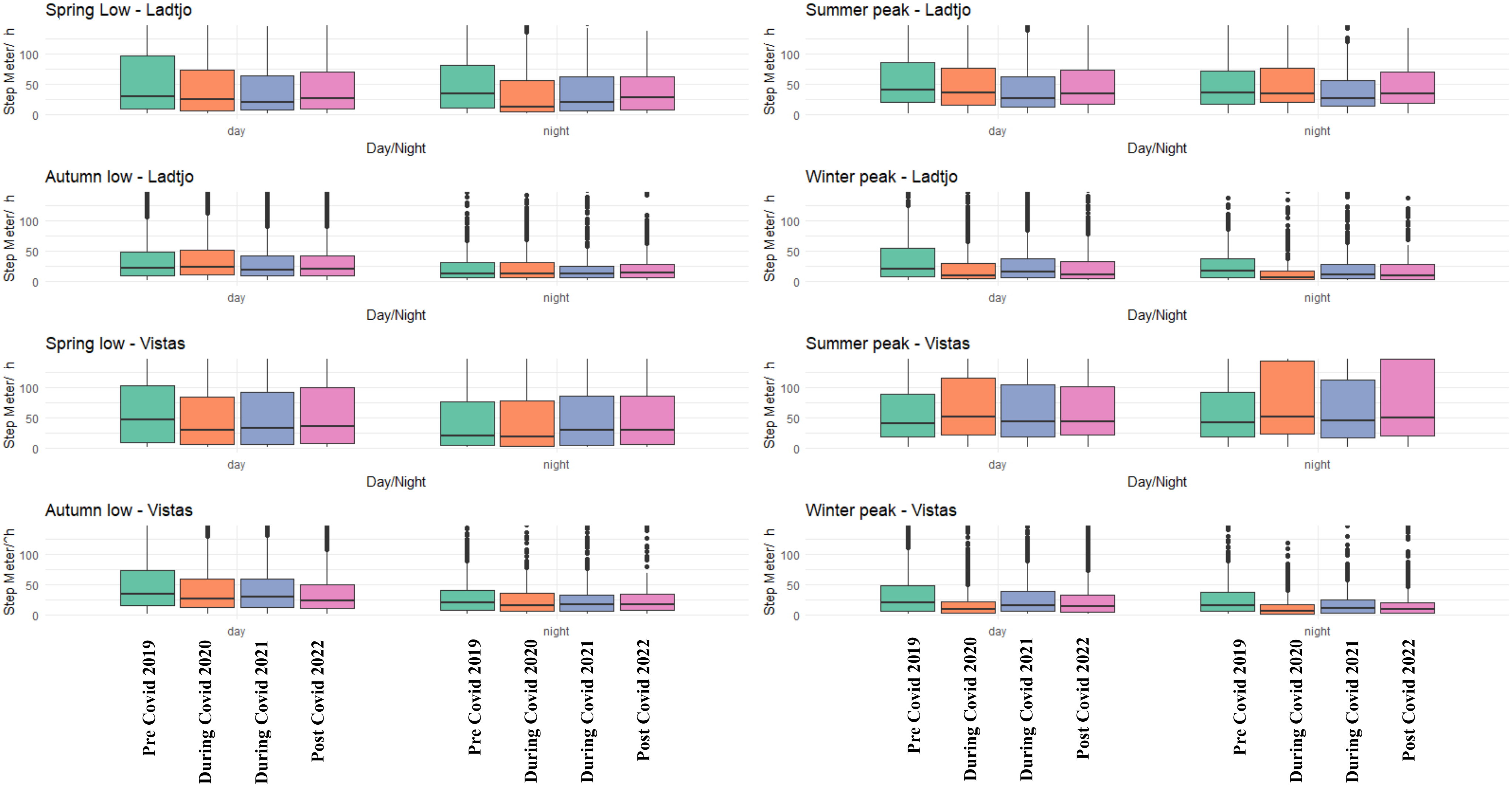

Figure 4. Moose diurnal movement activity (log -m/hr) before, during and after the pandemic lockdown in the study area of Ladtjo and Vistas vallay in different seasons of human activity, Nikkaluokta 2019-2022. The Y-axis represent the back-transformed estimates as given by the linear mixed model, while the X-axis denotes the years pre, during and after the lockdown and distinguishes between day and night. The intercept contains the time of day of the respective valley and the respective season in 2019.

3.3 Hypothesis III: Moose proximity to trails will differ with human impact

When examining moose distance to human infrastructure (the proximity of hiking trails), distinct patterns emerged between moose in the Ladtjo and Vistas valleys (Ladtjo, characterized by high recreational use, and Vistas, characterized by less recreational use). In both valleys, moose exhibited a significant preference for selecting locations near hiking trails only during periods of lower visitor activity, such as in the spring and autumn, but only in the year before the lockdowns in 2019 (Table 5). Remarkably, there was even a significant aversion to trail proximity in the Vistas valley during the lockdown year (2020). Therefore, my results do not support my hypothesis 3, that moose in the Ladtjo valley would adjust their behavior to the level of recreational use and stay closer to the trail during lockdowns, compared to before or after the pandemic.

Before the global pandemic, in the *spring* of 2019 (a period with less visitor pressure), moose in the Vistas valley preferred locations near hiking trails compared to random steps. However, this preference for utilizing human infrastructure did not persist during the subsequent COVID-19 lockdown years (2020/21) or afterwards (2022). In contrast, moose in the Ladtjo valley did not vary their select locations in relation to the hiking trail over the years.

Before the COVID-19 lockdown in the *autumn* (a period with lower visitor pressure) of 2019, moose in the Ladtjo valley chose locations near hiking trails compared to random steps. However, this preference did not continue during the COVID-19 lockdown years or the following year. Moose in the Vistas valley exhibited a similar response during the same period in 2019. In the first COVID-19 lockdown in 2020, moose in the Vistas valley were selected against trail proximity. In contrast, during the second lockdown year and the year following COVID-19 restrictions (2021/22), moose in both valleys showed no significant preferences in trail proximity.

During peaks in the *summer* and *winter*, moose in both valleys showed no significant preferences in trail proximity compared to availability. Similarly, they behaved during the winter season, although a trend towards human infrastructure emerged (p-value > 0.05 - 0.1). Before the lockdown (2019), moose in the Vistas valley preferred trail proximity. In contrast, moose in the Ladtjo valley showed a trend of selecting locations near hiking trails during the lockdown years (2020/21).

Table 4. Estimates and standard errors of moose selection of locations in relation to proximity to hiking trails during different periods of anthropogenic activity based on an integrated step-selection function, Nikkaluokta, 2019 to 2022. The years with reduced visitor numbers (COVID years) are presented in italics, as well as the seasons with lower anthropogenic usage (i.e. low tourism periods). The intercept consists of moose selection in the year before the COVID 19 lockdown (2019) in the respective season. Analyses are done separately for each valley.

		Ladtjo				**Vistas**			
		Estimate	SE	z-value	Pr(>|z|)	Estimate	SE	z-value	Pr(>|z|)
Spring low	pre covid 2019	-1.69	1.35	-1.24	0.212	**-2.05**	**9.35**	**-2.18**	**0.024***
	during covid2020	-1.54	1.71	-0.09	0.928	1.10	1.08	1.01	0.308
	during covid2021	1.84	1.72	0.01	0.991	1.05	1.14	0.92	0.357
	post covid 2022	1.88	1.78	0.10	0.916	9.56	1.09	0.87	0.384
Summer peak	pre covid 2019	1.99	7.92	0.25	0.801	-1.14	6.28	-0.18	0.856
	during covid2020	-2.98	1.05	-0.28	0.777	-2.84	9.27	-0.30	0.759
	during covid2021	-3.32	1.03	-0.32	0.749	-4.02	8.39	-0.47	0.632
	post covid 2022	-6.32	1.11	-0.56	0.571	-7.20	9.13	-0.78	0.430
Autumn low	pre covid 2019	**-9.61**	**3.70**	**-2.53**	**0.011***	**-2.49**	**5.43**	**-4.59**	**0.000*****
	during covid2020	5.37	4.82	1.11	0.265	**1.60**	**7.18**	**-2.23**	**0.025***
	during covid2021	-1.50	5.82	-0.02	0.979	7.00	7.80	0.89	0.369
	post covid 2022	4.02	5.42	0.74	0.458	7.05	9.37	0.07	0.940
Winter peak	pre covid 2019	-1.68	7.29	-0.23	0.817	*-1.05*	*5.43*	*-1.93*	*0.052.*
	during covid2020	*-1.83*	*9.76*	*-1.88*	*0.060.*	8.70	6.30	1.38	0.167
	during covid2021	*-1.76*	*1.01*	*-1.73*	*0.083.*	-1.55	7.06	-0.02	0.982
	post covid 2022	-1.27	1.09	-1.11	0.265	5.71	6.74	0.84	0.396

3.4 Hypothesis IV: Moose will show temporal adaptations in proximity to infrastructure in relation to human activity patterns

When assessing alterations in diurnal behavior (proximity to human infrastructure) of moose in relation to varying recreational use intensity by visitors, no discernible deviations were observed in either the Ladtjo valley (characterized by high visitor intensity) or the Vistas valley (characterized by low visitor intensity). In 2019, moose generally exhibited a pattern of moving closer to human infrastructure during the night compared to the day, particularly during periods of heightened recreational activity in summer and winter, as well as during the less anthropogenically utilized spring period. However, when considering the years (pre-during-and post-lockdown), no significant difference in selection towards or away from human infrastructure at night compared to moose diurnal behavior in 2019 could be identified. Therefore, my proposed hypothesis 4 cannot be confirmed, as moose from both valleys exhibit similar responses to varying levels of anthropogenic use and do not adjust to the decline in the number of recreationists through temporal adaptations during the lockdown.

During the less frequented *spring* period by recreational users, moose in both the Ladtjo valley (t(1,3060)= -0.53, p=0.001) and Vistas valley (t(1,4246)= -0.42, p=0.011) showed a significant selection of habitats near anthropogenic infrastructure during the night over the years (Figure 5 & 6). However, this nocturnal proximity did not significantly change during the lockdown years (2020, 2021) or the subsequent year (2022) compared to the time before the pandemic (2019, see Appendix 3).

Moose were closer to human infrastructure at night during the heavily frequented *summer* period by recreationists, both in the less recreation-influenced Vistas valley (t(1,4532)= -0.67, p=0.000) and in the more frequented Ladtjo valley (t(1,3972)= -0.32, p=0.043). However, their nocturnal distance did not decrease in the years of the pandemic lockdowns (2020, 2021) and the following year (2022) compared to the distance observed before the pandemic during the day in 2019 (Figure 5 & 6, see Appendix 3).

In contrast to all other periods characterized by different intensities of recreational use, moose in the less frequented *autumn* period over the years showed no significant differences between the selection of habitats influenced by human infrastructure and the time of day, either day or night. Neither in the Ladtjo valley (t(1,8444)= -0.08, p=0.465) nor in Vistas valley (t(1,6410)= -0.09, p=0.417) was there a difference between day and night and a selection of moose toward or away from human infrastructure, nor a change among years. However, during the pandemic (2020/21), moose were not found closer to the trail at night compared to the day in 2019 (Figure 5 & 6).

Similar to the less frequented spring season, moose were closer to anthropogenic trails at night than during the day in both the Ladtjo valley (t(1.5530)= -0.38, p=0.011) and the Vistas valley (t(1.9063)= -0.27, p=0.014) in *winter* (high visitor pressure) (Figures 5 and 6). However, their proximity during the night remained unchanged in the years of the pandemic lockdown (2020, 2021) or the following year (2022) compared to the pre-pandemic period (2019, see Appendix 3).

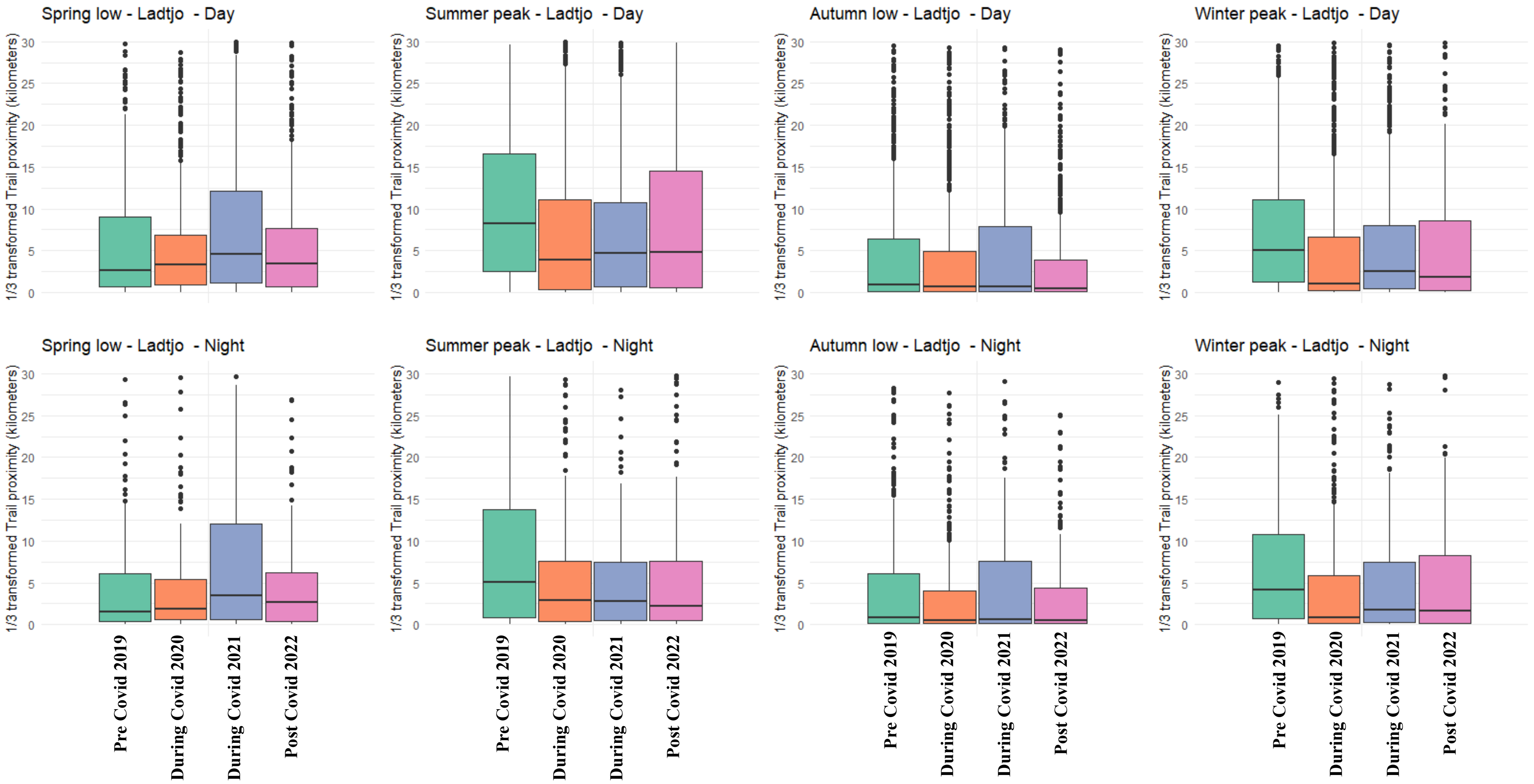

Figure 5. Moose trail proximity before, during and after the pandemic lockdown in the study area of Ladtjo across different seasons of human activity, Nikkaluokta 2019-2022. The Y-axis represent the back-transformed estimates (Trail proximity in kilometers) as given by the linear mixed model, while the X-axis denotes the different years and distinguishes between day and night.

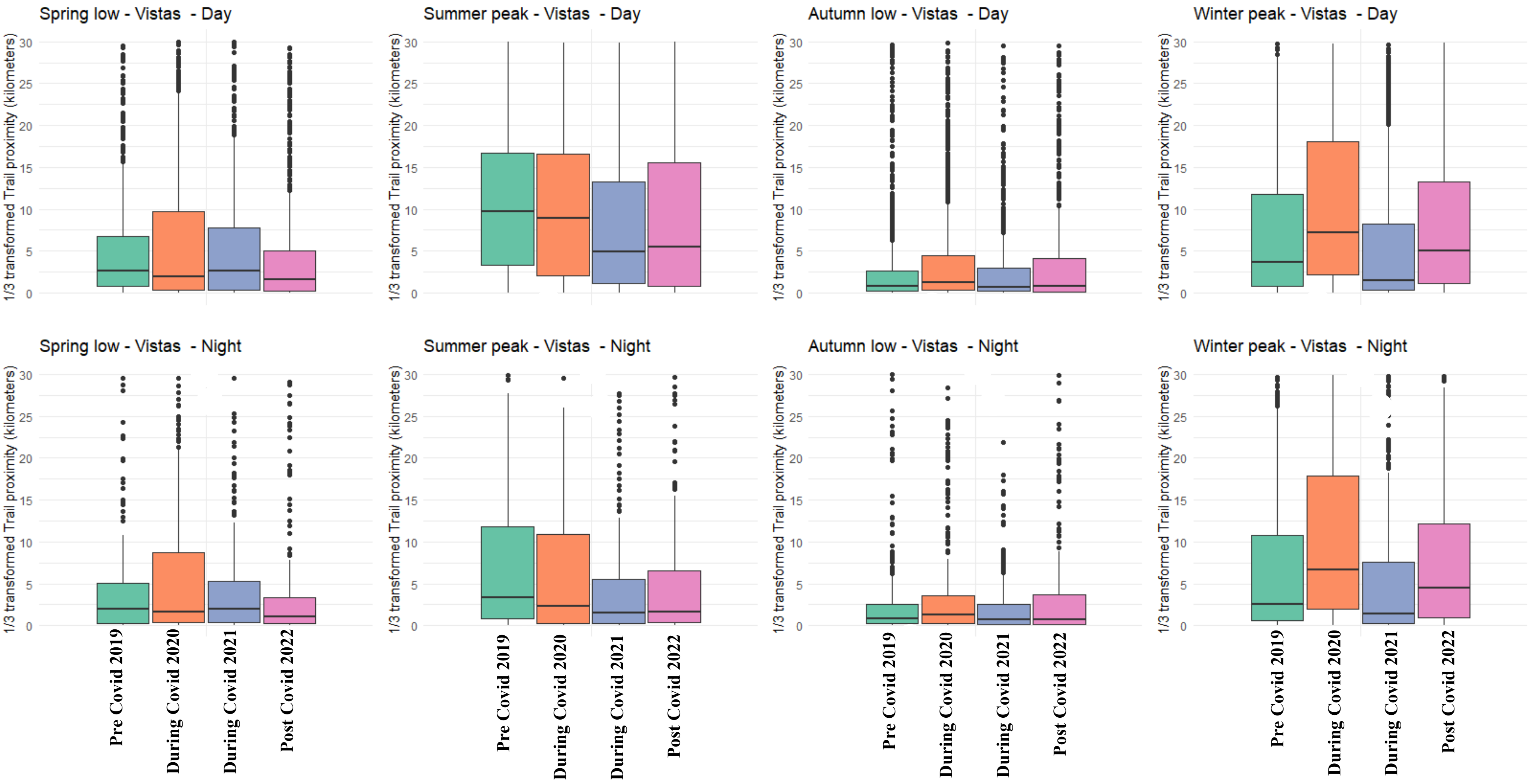

Figure 6. Moose trail proximity before, during and after the pandemic lockdown in the study area of Vistas across different seasons of human activity, Nikkaluokta 2019-2022. The Y-axis represent the back-transformed estimates (Trail proximity in kilometers) as given by the linear mixed model, while the X-axis denotes the different years and distinguishes between day and night

4. Discussion

The findings of my study can be encapsulated in four primary observations. Firstly, moose in both valleys demonstrated responses to human activities, but to varying extents. During and after the pandemic years, a preference for open habitats over deciduous forests was evident in both spring (low visitor activity) and summer (high visitor activity), while the moose's habitat selection remained unchanged in autumn (low visitor activity) and winter (high visitor activity). Therefore, my results substantiate my hypothesis only during the vegetation period (spring and summer from April to August). This indicates that moose opt for open habitats if these areas offer attractive food sources (e.g. herbs). The probability of encountering humans plays a rather subordinate role.

Secondly, moose in both valleys displayed altered daily patterns that fluctuated across seasons. Despite anthropogenic influences, this aligns with the natural activity behavior of moose (highest activity in May-July/lowest activity in February-March, Cederlund, 1989; Neumann *et al.,* 2012; Graesli *et al.* 2020). However, my results do not endorse my hypothesis that a reduction in nocturnal moose activity correlated with reduced human recreational activity.

Thirdly, before the lockdown (2019) moose selected for proximity to human infrastructure (hiking trails) only during off-tourist season (spring and autumn). However, during the pandemic (fewer recreational users), moose did not significantly shift their location towards hiking trails. Therefore, the results do not support my hypothesis that moose are closer to human infrastructure in times of less anthropogenic disturbance.

The fourth finding is that moose in both valleys reduced their distance from human infrastructure (hiking trails) during the night in spring (fewer visitors), summer and winter (many visitors). However, I could not detect any change during the pandemic (2020/21), so my hypothesis has to be rejected.

4.1. Implications of my results

4.1.1. Human impact on moose habitat selection (1st hypothesis)

Throughout my four-year observation period, encompassing periods of both high and low human impact, moose exhibited slightly altered multifactorial habitat preferences.

The vegetation period in seasonally influenced regions like Northern Sweden plays a crucial role in maintaining a positive energy balance for moose. During this time, moose adopt various browsing habits on deciduous trees, aquatic macrophytes, and herbaceous vegetation to meet the nutritional requirements for weight gain and development (Timmermann & McNicol, 1988; Spitzer, 2019). Fresh deciduous shoots with their high nutrient content are preferred during the vegetation season, and the protective structure of deciduous forests provides shade to heat-sensitive moose (Renecker & Hudson, 1986), serving as protection for female moose with offspring against predators (Poole *et al.,* 2007; Neumann *et al.,* 2020). In certain situations, the protective function even surpasses habitats with high-quality food (Gasaway *et al.,* 1983; Bowyer *et al.,* 1998).

The vegetation period 2018 was characterized by reduced precipitation (Appendix 5), widespread drought, wildfires (Krikken *et al.,* 2021), and subsequent tree mortality (Buras *et al.,* 2020). This led to degraded vegetation and lower food quality for moose, resulting in lower birth rates and poorer health conditions in the following year (Holmes *et al.,* 2021). As thermoregulatory behavior restricts the temporal-spatial food intake, it reduces body condition and energy reserves (Broders *et al.,* 2012). These deficits must be compensated for in the following year (2019), which could justify moose in both valleys (differing levels of recreational pressure) selecting deciduous forests during the vegetation season.

The selection of open habitats was observed during various pandemic phases and only during the vegetation period at non-elevated temperatures (Appendix 5). For instance, in the spring of 2020, during strict lockdowns across Europe, moose in both valleys preferred open habitats, which is possibly linked to the decline in tourism. Reducing the "landscape of fear" might have facilitated adapted foraging behavior in open areas during the vegetation period, associated with increased vulnerability to predators, humans, and adverse weather conditions (Barboza & Bowyer, 2000). In subsequent years, the selection of open habitats was only apparent in moose in the Ladtjo valley, extending beyond the lockdown period (2022), suggesting non-anthropogenic-driven behavior. Therefore, moose habitat requirements during the vegetation season are more influenced by foraging and thermal cover, which are subject to changes. Increased selection of open habitats at lower summer temperatures supports the hypothesis that moose can alter their selection in response to fluctuating environmental conditions. However, temperature-induced changes significantly influence habitat choice compared to the level of anthropogenic recreational pressure.

In contrast to the diverse food moose consume during the growing season, their diet in boreal areas in autumn and winter consists of over 75 % blueberries and pine twigs (Spitzer, 2019). Due to snow cover, trees and shrubs became the primary food source. Preferred species for moose in winter include rowan (*Sorbus aucuparia*), aspen (*Populus tremula*), willow (*Salix spp*.), juniper (*Juniperus communis*), and birch (*Betula spp*.) (Månsson *et al.,* 2007b). While pine (*Pinus sylvestris*) serves as a quantitative, if not qualitative, food source for moose in many regions of Sweden during this time (Spitzer, 2019), in the mountainous surroundings of Nikkaluokta, pine constitutes only 6 % of moose diet, with birch making up over 60 % of winter food (Fohringer *et al.,* 2021). The concentration of tree and shrub vegetation in valley bottoms means that moose in Nikkaluokta prefer these areas during the snowy period and move only to a limited extent to conserve resources (McCulley *et al.,* 2017; van Beest *et al.,* 2011). Climatic factors such as food availability, energy balance (Lundmark & Ball, 2008; Græsli *et al.,* 2020), and snow conditions (Lehning *et al.,* 2008) are crucial, restricting moose habitat choice during this critical winter period.

Moose habitat selection in autumn can also be influenced by biological factors other than food availability and heat stress. Aside from the rut, which already depletes a significant portion of moose energy reserves, additional human disturbances through hunting activities can trigger antipredator behavior, leading to changes in space use (Neumann & Ericsson, 2018; Fritz, 2009; Ericsson *et al.,* 2015; Graesli *et al.,* 2020b). During this time, moose tend to prefer habitats with closed canopies and ample cover, opting for good protection against the use of suitable feeding places, similar to the calving season (Bjørneraas *et al.,* 2011; Bonnot *et al.,* 2013; van Beest, 2010). This strategy appears more energy-efficient than a constant movement away from human disturbances, complicating the interpretation of moose habitat preferences. Zetterkvist (2020) noted significant differences in moose habitat selection during the rut.

While some studies suggest that multiple deer species avoid open areas during the hunting season to reduce predation risk (Bonnot *et al.,* 2013), others found that moose in Alaska prefer open and swampy areas during the rut to improve visibility, with food search playing a subordinate role (Jarnemo *et al.,* 2018; McCulley *et al.,* 2017).

The study's results support the hypothesis that moose habitat selection is subject to seasonal changes, emphasizing that biological preferences, including feeding, climatic conditions, and mating season, outweigh the influences of anthropogenic use. Therefore, I must reject the initial hypothesis that moose utilize less suitable habitats only during periods of high anthropogenic influence. The multifactorial nature of moose habitat selection suggests that a complex interplay of ecological, environmental, and biological factors determines their spatial behavior in different seasons.

4.1.2. Activity pattern in relation to human activity (2nd hypothesis)

When looking at day and night activity, the moose in the valleys did not differ significantly, but the activity of the moose depends on various factors. The personality of the animals (Gharnit *et al.,* 2020) can play a role, as can thermal conditions (Davimes *et al.,* 2017), interspecific competition (Cunningham *et al.,* 2019), anthropogenic disturbance (Ditmer *et al.,* 2020), food availability (Hut *et al.,* 2011) or biologically significant events (e.g. rutting, Reebs, 2002). The classification of day and night that I have chosen is independent of daylight and is based on the degree of recreational use (higher human activity during day). Hoofed animals, on the other hand, adapt their activity to the light conditions (i.e. during twilight, bimodal activity pattern, Neumann *et al.,* 2012, Ensing *et al.,* 2014; Græsli *et al.,* 2020), which is why there may be overlaps between the moose's activity and the nighttime defined by me, especially during the spring and summer period.

Over the entire observation period, I found that moose showed less nocturnal activity during the period of closed snow cover (November - April), while their activity did not differ between day and night in summer. This could be related to the length of daylight (Græsli *et al.,* 2020), but the seasonal differences in moose activity may also be temperature related. Higher ambient temperatures in the summer months can reduce movement activity (Ericsson *et al.,* 2015) and shift activity to cooler night hours (Montgomery *et al.,* 2019).

Moose in both valleys showed natural seasonal activity patterns (Cederlund, 1989) and restricted their nocturnal activity during the autumn and winter. This helps the animals conserve energy and optimize available resources during snowy and cold periods where energy supply is low (Græsli *et al.,* 2020). This diurnal behaviour appears to be unaffected by visitor activity in my study area outside the vegetation period.

Moose show a similar response to self-protection in summer. Moose react to higher ambient temperatures (e.g. first signs of heat stress at 14 °C in summer and -5 °C in winter, Renecker & Hudson, 1986) by shifting their movements and activities (Dussault *et al.,* 2004; Broders *et al.,* 2012) to the cooler night hours and thus reducing heat stress situations.

Behavior and environmental conditions can be harmonious by changing and adapting activities (Dunlap *et al.,* 2004). Favourable conditions, such as foraging can be exploited, or the adverse effects of anthropogenic use can be mitigated. These seasonal patterns are recognizable in my study. Nevertheless, the activity patterns found in this study are the result of biologically determined adaptations to heat stress, energy conservation measures and weather conditions such as snow, and not to anthropogenic disturbance, so I reject my hypothesis that increased anthropogenic utilisation and increased nocturnal activity are correlated.

4.1.3. Moose proximity to trails will differ with human impact (3rd hypothesis)

Before the pandemic (2019), moose were observed closer to the hiking trail in the less anthropogenically used Vistas valley during the low tourist season (spring and autumn). In the Ladtjo valley, proximity to the hiking trail in the autumn before the pandemic (2019) was also an isolated observation. Studies by Taylor & Knight (2003) and Wisdom *et al.* (2018) confirm an increase in escape behavior in ungulates the closer they are to trails.

The degree of human contact (frequent or infrequent) and the type of recreational activities along trails can also influence risk avoidance strategies (Stankowich, 2008). An increased escape response has been observed when humans leave the trails (i.e. less predictable off-trail activities), especially during periods of low anthropogenic disturbance and human- ungulate encounters. This observation could provide a basis for interpreting my results, as increased habitat use near the trails was no longer observed during lockdown or in the tourist off-season.

Non-hunted ungulate populations are often more unaffected by human contact than hunted populations (Sytsma *et al.,* 2022) and can synchronize their activity pattern with human activity peaks due to predation avoidance. Large predators often avoid contact with humans, so these can be used as a spatial shield for ungulates (Gaynor *et al.,* 2018). However, the Fennoscandian moose population is heavily hunted (Lavsund *et al.,* 2003, Jensen *et al.,* 2020) and humans are the biggest mortality factor (Sand *et al.,* 2012), so it is doubtful that moose seek out proximity to humans in my study area. However, this behavior can also change over a longer period. In a long-term study over a period of around 60 years, Ciach & Pęksa (2019) demonstrated increased use of heavily anthropogenically influenced areas by chamois (*Rupicapra rupicapra tatrica)* in a now non-hunted population. The distance between chamois and hiking trails has systematically decreased over the last half-century, indicating a gradually increasing tolerance towards the almost constant presence of many people on hiking trails. Due to the comparatively short lockdown periods and the continued hunting, such a rapid adaptation is unlikely.

The results I obtained cannot confirm that moose avoid proximity to human infrastructure (hiking trails) and only use habitats close to human infrastructure in times of low visitor numbers. However, before COVID-19 (2019), I was able to observe that moose were closer to human infrastructure during the low tourist season. In the COVID years 2020/21 and the associated lockdown, this behavior was no longer observed and is more related to habitat preference than to escape from human disturbance. Due to the relatively short duration of the hard lockdowns (several weeks) and the continued use by the local population as well as the continued hunting, there was no shift towards human infrastructure (hiking trails) during the observation period.

4.1.4. Moose will show temporal adaptations in proximity to infrastructure in relation to human activity patterns (4th hypothesis)

During the night (fewer visitors), moose stayed closer to human infrastructure (hiking trail) than during the day, regardless of the valley (representative of human influence). Rogala *et al.* (2011) also observed this finely tuned interaction between humans and wildlife. Wisdom *et al.* (2004) also documented an increased movement speed and flight response in elk when recreational activity on the trail increased. These changes in environmental stimuli can induce behavioral plasticity in ungulate populations (Hall, 2000) and lead to increased activity at suboptimal times with higher predation risk, increasing energy requirements and fitness costs (Hall, 2000). Therefore, activity patterns in response to external stimuli (anthropogenic disturbances) can provide information on the degree of plasticity of species and the effects of different environmental factors (Frey *et al.,* 2018).

The trail network in my study area is mainly located in valley bottoms (see Figure 1), representing a seasonally attractive moose habitat (Dodd *et al.,* 2007). The greatest distance between the moose and the trail was observed during summer (high anthropogenic use). At this time, moose specifically use the high altitudes for foraging, as high-quality food (herbs) grows there (Singh *et al.,* 2012). This assumption is also supported by the results of my habitat analysis (Table 3, select open habitats during the vegetation period and not above average temperatures) and is less attributable to anthropogenic disturbances.

However, snow conditions, topography, individual behavior or changing environmental stimuli can lead to deviations in the selection of these habitats (Hebblewhite *et al.,* 2008). Previous studies have confirmed that wildlife avoid highly anthropogenic areas spatially and temporally (Ager *et al.,* 2003; Wisdom *et al.,* 2004; Keller & Bender, 2007), yet linear structures (trails) can be integrated into wildlife movement behavior (e.g. predators, Thurber *et al.,* 1994; Callaghan, 2002).

Therefore, moose must find a trade-off between suitable habitat and proximity to human infrastructure. The only exception to the observation that moose are closer to human infrastructure at night than during the day is the autumn season (fewer visitors) in both valleys. During this period (September - January), moose prefer forest-like structures, as the forage quality of the shady plants is relatively high (Hebblewhite *et al.,* 2008). The onset of snowfall towards the end of the autumn period also results in more forested habitats being selected as snow depth is often lower in these habitats, and thus movement costs are saved (Parker *et al.,* 1984). In contrast to the winter period, the reduced number of recreationists should also contribute to the fact that the animals move less away from the forested valley bottoms, where the trails are also located, at this time. Hunting by humans, which also takes place during the autumn period, can increase the use of habitats rich in cover. Brown *et al.* (2018) proved that moose prefer cover-rich areas during the hunting season, even if this is closer to hiking trails.

These results do not support my hypothesis that moose activity behavior adapts to the number of recreational visitors and reduces closer to human infrastructure at times of low human activity. The animals stay closer to human infrastructure at night (regardless of the number of visitors), but neither the pandemic (2020/21) nor a period with fewer recreational visitors (spring) has an impact on this behavior. The differentiated behavior in autumn is due to habitat preferences (food and shelter during the hunting season) and not to the level of recreational visitors.

4.2. Limitations and alternatives to my study

The primary limitation affecting the robustness of my results stems from the need for precise information regarding the number of recreational users in the Nikkaluokta area and their trail movements before, during, and after the lockdown years. The Swedish COVID-19 restrictions, characterized by more moderate recommendations compared to many other EU countries implementing strict lockdowns (Hiselius & Arnfalk, 2021), resulted in a substantial decline in foreign tourism (Manakov *et al.,* 2021). Concurrently, the Swedish population increased the local and regional use of nature (Hansen *et al.,* 2022). The reduced presence of foreign tourists, coupled with the consistently high number of wildlife-vehicle collisions in rural areas (Dörler & Heigl, 2021; Driessen, 2021; Bíl *et al.,* 2021), suggests that the nature around Nikkaluokta witnessed fewer foreign tourists but potentially an average or higher number of Swedish recreationists. However, obtaining an accurate estimate of the number of visitors to Nikkaluokta remains challenging. The reported number of overnight stays in the municipality of "Gällivare" by the Swedish Agency for Economic and Regional Growth is a rough estimate and does not account for visitors staying in tents, for instance.

Wildlife cameras could be explored to enhance our understanding of trail visitor patterns. These cameras can capture human activities and environmental conditions, offering valuable insights into recreational activities and wildlife distribution (Ahumada *et al.,* 2011; Steenweg *et al.,* 2017). They can even record environmental variables such as vegetation conditions (Hofmeester *et al.,* 2020), although this approach was beyond the scope of my study.

Alternatively, a theoretical approach involving spatially, and temporally individual modeling could be considered as proposed by Musiani *et al.* (2010). Such models partition human infrastructure based on the frequency of use (e.g., trails and roads), and moose movements are determined by the spatial distribution of resources and threats, as well as internal motivation and activity. This modeling approach could simulate fluctuations in visitor numbers and predict moose responses, assuming constant environmental variables.

Another potential avenue is incorporating mobile GPS data from Nikkaluokta visitors into a citizen science project. This approach can generate large-scale, temporally extensive datasets (Bela *et al.,* 2016; Tewksbury *et al.,* 2014). However, the unstructured sampling design may introduce biases, such as uneven spatial and temporal data distribution, potentially leading to erroneous conclusions.

Despite these limitations, my study revealed minimal behavioral changes in moose in response to the pandemic situation. This could be attributed to the shift in leisure behavior among Swedes, with a preference for outdoor recreation and nature over indoor cultural activities or crowded cities (Östh *et al.,* 2023). Surveys indicated that 90 % of the population desired to spend more time in nature, leading to increased demand for outdoor services (Josefsson, 2021). Swedish holiday homes in remote or rural areas were quickly booked out, and less populated areas were utilized for recreation. This is further supported by overnight stay data from the municipality of Gällivare, where my study area is located. Compared to other municipalities in northern Sweden, the number of visitors is not declining as sharply, suggesting that the demand for leisure time activities remains robust (Figure 2).

Similar observations of non-significant effects on ungulate behavior during lockdown have been made in other studies, further confirming the limited effects on nature use and, in some cases, even suggesting an increase in tourist numbers (Cukor *et al.,* 2021; Derks *et al.,* 2020; Venter *et al.,* 2020).

For example, Tucker *et al.* (2023) examined the movement patterns of 43 terrestrial mammal species and found no change in average movements or avoidance of anthropogenic infrastructure, which is likely due to differences between countries in terms of COVID restrictions. However, with strict lockdown measures (which did not exist in Sweden), an increase in landscape permeability and thus less avoidance of human infrastructure was found.

4.3. Conclusion

In conclusion, the COVID-19 pandemic exerted a profound impact on global nature tourism dynamics, ushering in shifts in the utilization of natural areas. While numerous countries witnessed a decline in tourism to remote locales due to travel restrictions, Sweden, with comparatively lenient COVID measures, experienced sustained interest in both local and distant natural areas.

Spanning a four-year period from 2019 to 2022, encompassing the pre-pandemic, pandemic, and post-pandemic phases, this study delved into the activity and habitat selection behavior of 20 adult moose in the mountainous region around Nikkaluokta in northern Sweden. My comprehensive data collection, covering the entire annual cycle, explored two valleys with similar habitats but varying degrees of human use, guided by prior studies and overnight data to gauge human impact intensity.

Results unveiled an increase in moose use of open habitats during the growing season, seemingly driven more by food preferences and mild temperatures than direct correlations with recreational user numbers. Importantly, no discernible alterations in moose activity patterns or proximity to human infrastructure were attributable to anthropogenic disturbance. The habitat preferences and spatial distribution observed in the study area appear primarily biologically determined, influenced by factors like food availability, rearing of young, and climatic conditions.

Despite a subtle spatio-temporal avoidance pattern, wherein moose maintained greater distances from human infrastructure during daytime disturbances, this behavior persisted during the pandemic, indicating a link to seasonal and intraspecific preferences rather than pandemic-induced shifts in human activities. Further precision on temporal and spatial distribution, along with absolute numbers of recreational users in the study area, would enhance our understanding of the observed behavior.

While the results suggest a decrease in recreational users, the extent is not substantial enough to evoke noticeable changes in moose behavior. Future studies honing in on nature use in Nikkaluokta during the pandemic hold the potential for invaluable insights, offering a pathway for continued exploration and understanding of the complex interplay between wildlife and human activities in these unique natural environments.

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Appendix 1

Table 5. Reclassification table of the landcover classes.

Grid code	**Class**	**Reclassified to:**
111	Pine forest not on wetland	Other
112	Spruce forest not on wetland	Other
113	Mixed coniferous forest not on wetland	Other
114	Mixed forest not on wetland	Other
115	Deciduous forest not on wetland	Deciduous
116	Deciduous hardwood forest not on wetland	Deciduous
117	Deciduous forest with deciduous hardwood forest not on wetland	Deciduous
118	Temporarily non-forest not on wetland	Other
121	Pine forest on wetland	Other
122	Spruce forest on wetland	Other
123	Mixed coniferous on wetland	Other
124	Mixed forest on wetland	Other
125	Deciduous forest on wetland	Deciduous
126	Deciduous hardwood forest on wetland	Deciduous
127	Deciduous forest with deciduous hardwood forest on wetland	Deciduous
128	Temporarily non-forest on wetland	Other
2	Open wetland	Swamp
3	Arable land	Other
41	Non-vegetated other open land	Open
42	Vegetated other open land	Open
51	Artificial surfaces, building	Other
52	Artificial surfaces, not building or road/railway	Other
53	Artificial surfaces, road/railway	Other
61	Inland water	Water
62	Marine water	Water
0	Outside mapping area	Other

Appendix 2

Table 6. Estimates and standard errors of moose resulting from the linear mixed model in terms of movement speed (m/hr) during different periods of anthropogenic activity, Nikkaluokta, 2019 to 2022. The years with lower visitor numbers (COVID years) are shown in italics, as are the seasons with lower anthropogenic use (i.e. periods with lower tourism). The intercept consists of the speed of movement during the day in the year before the COVID-19 lockdown (2019) in the respective season. The analyses are carried out separately for each valley. Significant differences are highlighted in bold.

			Ladtjo				**Vistas**			
			Estimate	SE	t	p	Estimate	SE	t	p
2019	*Spring low*	Intercept	**3.51**	**0.09**	**36.5**	**0.000*****	**3.46**	**0.09**	**34.9**	**0.000*****
		Night	0.03	0.13	0.26	0.790	**-0.56**	**0.12**	**-4.68**	**0.000*****
2020		Night 20-Day 19	**-0.37**	**0.17**	**-2.21**	**0.026***	0.25	0.15	1.57	0.115
2021		Night 21-Day 19	-0.11	0.17	-0.68	0.495	**0.44**	**0.16**	**2.74**	**0.006***
2022		Night 22-Day 19	-0.07	0.18	-0.40	0.683	**0.45**	**0.15**	**2.86**	**0.004***
2019	Summer peak	Intercept	**3.74**	**0.06**	**59.6**	**0.000*****	**3.67**	**0.12**	**30.4**	**0.000****
		Night	-0.16	0.08	-1.87	0.061	0.04	0.08	0.55	0.578
2020		Night 20-Day 19	0.16	0.11	1.34	0.178	0.10	0.11	0.91	0.358
2021		Night 21-Day 19	0.12	0.11	1.06	0.284	-0.03	0.11	-0.34	0.731
2022		Night 22-Day 19	**0.26**	**0.12**	**2.19**	**0.027***	0.06	0.11	0.50	0.613
2019	*Autumn low*	Intercept	**3.16**	**0.10**	**30.5**	**0.000*****	**3.39**	**0.07**	**44.1**	**0.000*****
		Night	**-0.48**	**0.05**	**-8.54**	**0.000*****	**-0.58**	**0.05**	**-9.81**	**0.000*****
2020		Night 20-Day 19	-0.05	0.07	-0.68	0.493	0.01	0.08	0.18	0.855
2021		Night 21-Day 19	0.05	0.08	0.65	0.513	-0.08	0.09	-0.88	0.378
2022		Night 22-Day 19	0.09	0.08	1.07	0.280	0.22	0.10	2.08	0.037
2019	Winter peak	Intercept	**3.28**	**0.13**	**23.8**	**0.000*****	**2.93**	**0.08**	**34.3**	**0.000****
		Night	**-0.32**	**0.09**	**-3.28**	**0.001****	**-0.17**	**0.06**	**-2.56**	**0.010***
2020		Night 20-Day 19	-0.09	0.12	-0.74	0.450	-0.08	0.09	-0.98	0.324
2021		Night 21-Day 19	0.02	0.12	0.24	0.807	**-0.20**	**0.09**	**-2.11**	**0.034***
2022		Night 22-Day 19	0.05	0.13	0.43	0.660	**-0.23**	**0.09**	**-2.55**	**0.010***

Appendix 3

Table 7. Estimates and standard errors of moose resulting from the linear mixed model in relation to proximity to trails during different periods of anthropogenic activity, Nikkaluokta, 2019 to 2022. The years with lower visitor numbers (COVID years) are shown in italics, as are the seasons with lower anthropogenic use (i.e. periods with little tourism). The intercept consists of moose selection in the year before the Covid 19 lockdown (2019) in the respective season. The analyses are carried out separately for each valley. Significant differences are highlighted in bold.

			Ladtjo				**Vistas**			
			Estimate	SE	t	p	Estimate	SE	t	p
2019	*Spring low*	Intercept	**7.71**	**0.64**	**11.9**	**0.000*****	**8.40**	**0.57**	**14.6**	**0.000*****
		Night	**-0.53**	**0.16**	**-3.23**	**0.001***	**-0.42**	**0.16**	**-2.54**	**0.011***
2020		Night 20-Day 19	-0.01	0.20	-0.05	0.957	0.23	0.22	1.06	0.287
2021		Night 21-Day 19	0.17	0.21	0.83	0.401	0.16	0.22	0.74	0.456
2022		Night 22-Day 19	0.19	0.22	0.87	0.384	0.03	0.21	0.18	0.856
2019	Summer peak	Intercept	**9.48**	**0.62**	**15.1**	**0.000*****	**10.2**	**0.59**	**17.0**	**0.000****
		Night	**-0.32**	**0.16**	**-2.02**	**0.043***	**-0.67**	**0.12**	**-5.50**	**0.000****
2020		Night 20-Day 19	0.16	0.22	0.73	0.464	-0.17	0.17	-0.97	0.329
2021		Night 21-Day 19	0.19	0.21	0.91	0.361	-0.03	0.17	-0.19	0.843
2022		Night 22-Day 19	0.01	0.22	0.04	0.963	-0.10	0.18	-0.58	0.559
2019	*Autumn low*	Intercept	**7.66**	**0.97**	**7.84**	**0.000*****	**8.16**	**0.66**	**12.3**	**0.000****
		Night	-0.08	0.11	-0.73	0.465	-0.09	0.11	-0.81	0.417
2020		Night 20-Day 19	0.03	0.16	0.19	0.844	-0.03	0.16	-0.21	0.828
2021		Night 21-Day 19	0.04	0.16	0.27	0.780	-0.02	0.17	-0.13	0.896
2022		Night 22-Day 19	0.09	0.17	0.56	0.570	-0.02	0.20	-0.12	0.904
2019	Winter peak	Intercept	**8.80**	**0.70**	**12.4**	**0.000*****	**8.60**	**0.38**	**22.4**	**0.000****
		Night	**-0.38**	**0.15**	**-2.52**	**0.011***	**-0.27**	**0.11**	**-2.45**	**0.014***
2020		Night 20-Day 19	0.14	0.18	0.79	0.428	0.17	0.14	1.22	0.220
2021		Night 21-Day 19	0.01	0.18	0.08	0.934	0.10	0.15	0.68	0.493
2022		Night 22-Day 19	0.20	0.19	1.00	0.313	0.14	0.14	1.00	0.317

Appendix 4

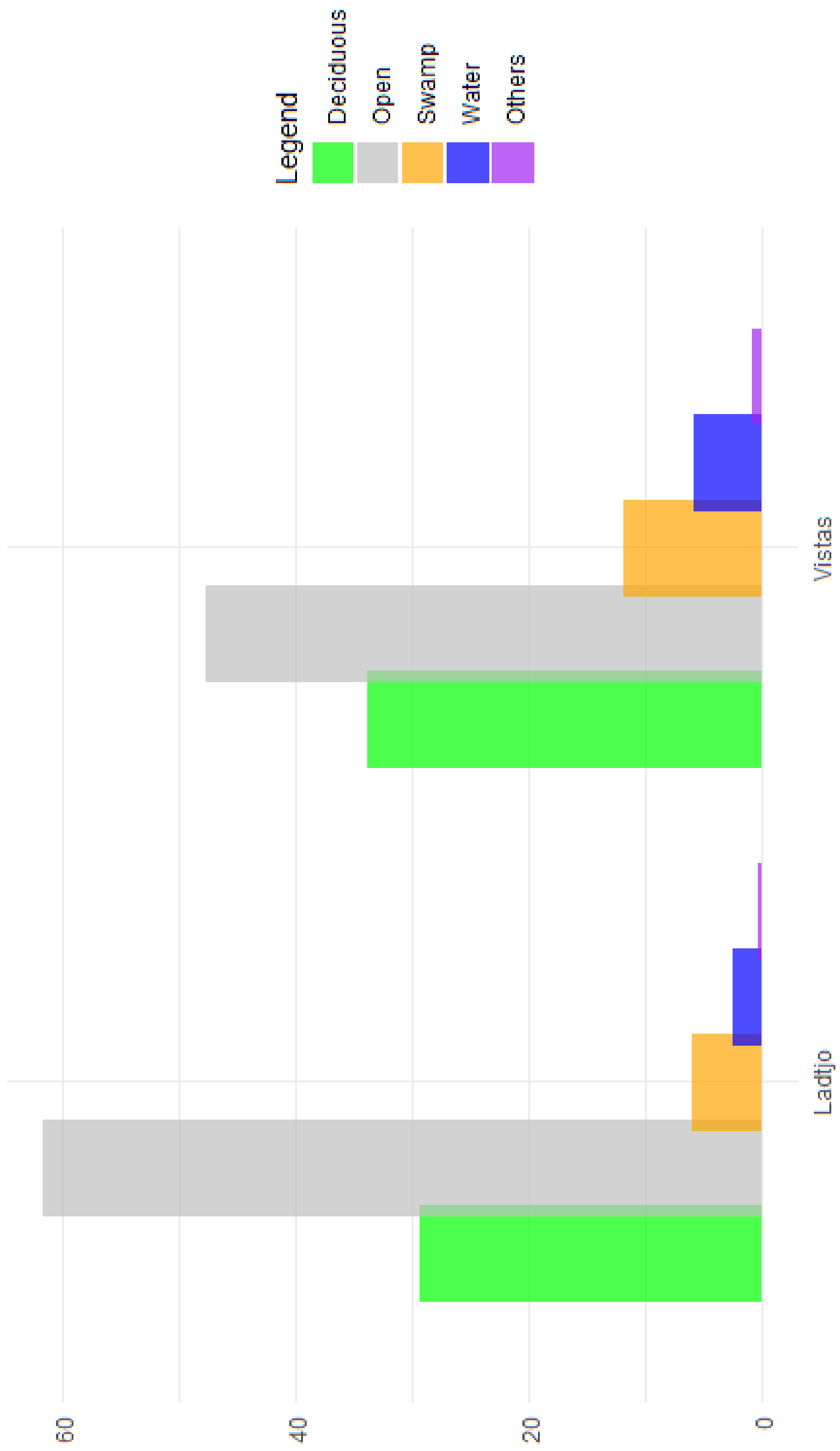

Figure 7. Distribution of moose positions (in %) among the available habitat classes, Nikkaluokta 2019 to 2022 in the Ladtjo and Vistas valleys.

Appendix 5

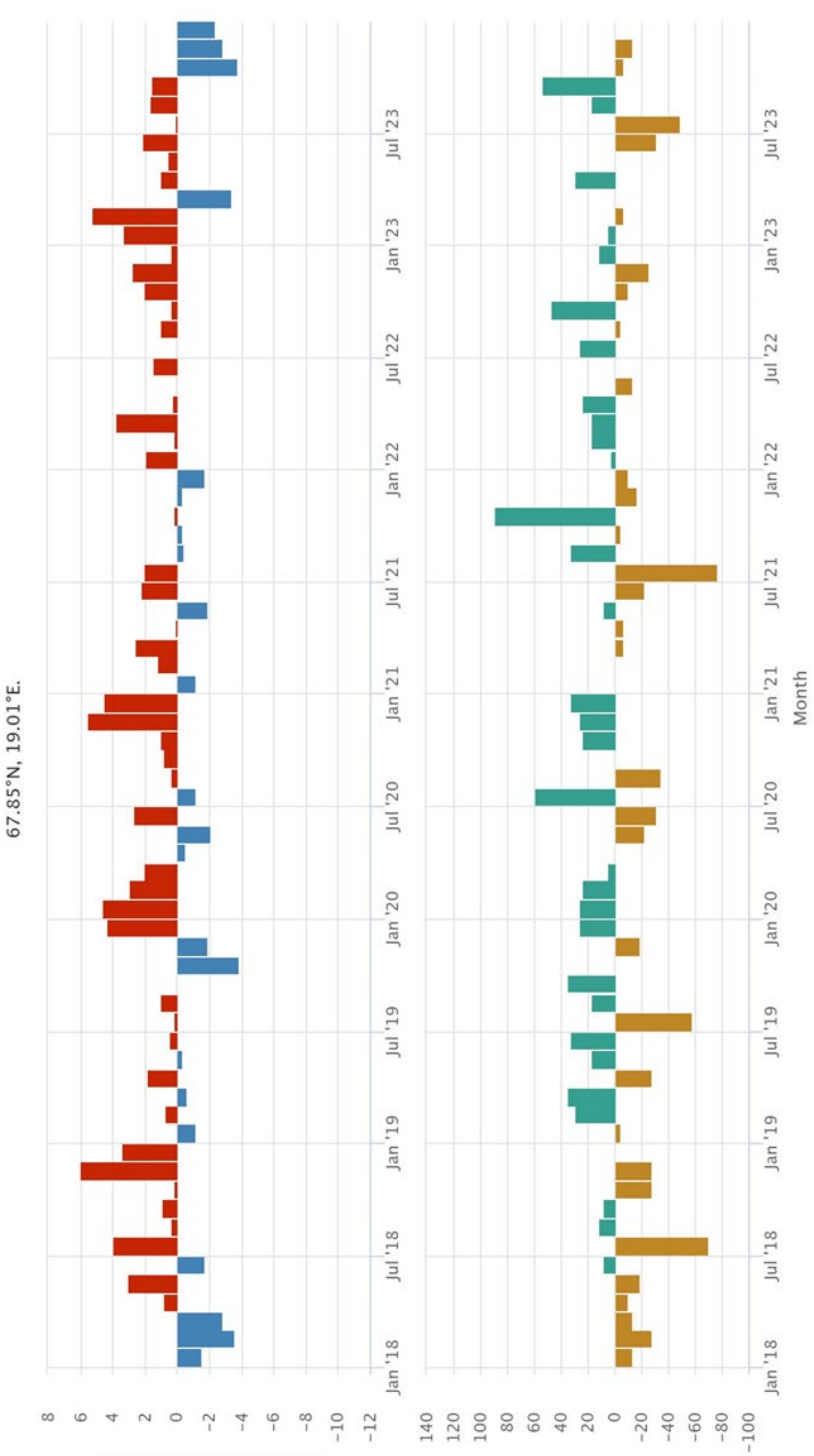

Figure 8. The top chart illustrates the temperature anomaly for each month in Nikkaluokta, 2018-2023. The anomaly reflects the deviation from the 30-year climate average spanning 1980-2010, with red indicating warmer and blue representing colder months compared to the norm. The subsequent chart depicts the precipitation anomaly for each month in Nikkaluokta during the same period. This anomaly signifies whether a month experienced more or less precipitation than the 30-year climate average from 1980-2010, with green denoting wetter and brown indicating drier months than usual. Data source: https://www.meteoblue.com/en/climate-change/nikkaluokta_sweden_2689715?month=10