



UiT The Arctic University of Norway

Department of Arctic and Marine Biology

Red Fox (*Vulpes vulpes*) movement on the northern edge of range expansion

[Insights from Accelerometry in Varangerhalvøya]

Stanley Bryce Cates Jr

Master's thesis in Biology, BIO-3950, November 2024

Table of Contents

1	Abstract	4
2	Background	1
2.1	Introduction to Wildlife Movement	1
2.2	The Arctic Ecosystem: A Changing Landscape.....	2
2.3	Red Fox Expansion in the Arctic: Interspecific Competition and Predatory Dynamics.....	3
2.4	Research Questions and Hypotheses.....	5
3	Materials and Methods	6
3.1	Study site.....	6
3.2	Lotek collars and ODBA.....	7
3.3	Zoo Observations and Ground-Truthing	8
3.4	Fox trapping	9
3.5	Data Integration and Consolidation with Environmental variables	11
3.6	Statistical Analysis	13
4	Results	15
4.1	Zoo Observations and Ground-Truthing	15
4.2	Overview of Field Data	15
4.3	Model Choice	16
4.4	Total Daily Activity	17
4.4.1	Total Daily Activity in the presence and absence of snow cover.	17
4.4.2	Total Daily Activity with Continuous Snow Depth.....	20
4.5	Daily Proportion Active	21
4.5.1	Daily Proportion Active with Binary Snow Presence	21
4.5.2	Daily Proportion Active with Continuous Snow Depth.....	23
5	Discussion	24
5.1	Framing of the Findings	24

5.2	Environmental Interactions and Seasonal Variability	25
5.3	Role of Vegetation Density in Activity and Foraging.....	27
5.4	Human Influence	27
5.5	Precipitation and Behavioral Adaptations.....	28
5.6	Future Research Directions	30
5.7	Conclusions and Management Implications	31
	Works cited	34
	Appendix	46

List of Tables

Tabell 1	Total Daily Activity (Snow present/not present)	17
Tabell 2	Total Daily Activity (Snow continuous).....	20
Tabell 3	Daily Proportion Active (Snow present/not present).....	21
Tabell 4	Daily Proportion Active (Snow continuous).....	23

List of Figures

Figur 1	Varanger peninsula with tracks for three foxes Biret (red), Thorsen (green), and Reinart(yellow). Purple points are trap locations.....	6
Figure 2:	Thorsen with collar. Photo: Svein Johannessen	8
Figur 3	Red fox at trap	10
Figur 4	Camera position at trap.....	10
Figur 5	Light seasons with ODBA.....	12
Figur 6	Raw counts of zoo data.....	15
Figur 7	Combined counts of zoo data	15
Figur 8	Predicted mean ODBA (mean temp:snow presence)	18
Figur 9	Predicted mean ODBA (Area use intensity:snow presence)	18
Figur 10	Predicted mean ODBA (vegetation:snow presence)	19
Figur 11	Predicted mean ODBA (precipitation:snow presence).....	19
Figur 12	Interaction (snow depth:vegetation on mean ODBA).....	21
Figur 13	Predicted proportion of active ODBA (precipitation:snow presence).....	22

Figur 14 Predicted proportion of active ODBA (temperature:snow presence)..... 22
Figur 15 Interaction (mean temperature:precipitation of daily activity)..... 23

1 Abstract

Red foxes (*Vulpes vulpes*) are expanding into Arctic regions, altering predator-prey dynamics and intensifying competition with native species such as the Arctic fox (*Vulpes lagopus*). This study examines the activity patterns of red foxes in Varanger, Norway, at the forefront of their Arctic range expansion, focusing on the effects of environmental factors (e.g., snow depth, temperature, precipitation) and human influence on their behavior. Using GPS and accelerometry data (Overall Dynamic Body Acceleration, ODBA), integrated with environmental variables, we analyzed red fox activity across 1,085 fox-days from four individuals.

Results revealed that snow presence significantly reduced overall daily activity but did not affect the proportion of time spent active, indicating behavioral adjustments to energy conservation during winter. Vegetation biomass consistently correlated with increased activity, highlighting its role as both a resource and a sheltering habitat. Human land-use intensity influenced activity patterns, with foxes exhibiting reduced activity near human infrastructure during snow-free periods but increased presence in these areas during winter, likely due to resource availability.

These findings underscore the complex interplay between environmental factors and anthropogenic influences in shaping red fox behavior. The results also have implications for conservation management, suggesting that targeted vegetation control and reductions in human-mediated food subsidies could mitigate the red fox's impact on Arctic ecosystems. By improving our understanding of red fox behavioral adaptations, this study contributes to broader efforts to balance species management and ecosystem conservation in dynamic, climate-affected landscapes.

2 Background

2.1 Introduction to Wildlife Movement

Animal movement is a dynamic and multifaceted phenomenon shaped by an interplay of intrinsic and extrinsic factors. Understanding animal movement offers insights into the ecology of individual behavior and landscape dynamics. Movement ecology, an emerging paradigm, integrates four core components—internal state, external factors, motion capacity, and navigation capacity—that collectively drive animal movement decisions (Nathan et al., 2008). This approach considers diverse determinants of behavior, from environmental gradients like topography, vegetation (Bailey et al., 1996), and the adaptive behaviors of animals in heterogeneous or dangerous landscapes (Morales et al., 2005; Fortin et al., 2005), to cognitive aspects of spatial memory and path integration mechanisms within the brain (McNaughton et al., 2006). Additionally, individual-specific behaviors can shape activity patterns and responses to environmental variability (Tang & Bennett, 2010). By considering these perspectives, researchers can investigate broad determinates forming a comprehensive framework for understanding animal movement ecology (Turner & Gardner, 2015).

Advances in bio-logging technologies, such as GPS tracking and accelerometry, have revolutionized ecological research and enable researchers to explore diverse hypotheses by tracking real-world animal movements, energy expenditures, and interactions across multiple scales (Gleiss et al., 2011; Wilmers et al., 2015). By capturing movement along three axes (X, Y, and Z), accelerometers generate a metric called Overall Dynamic Body Acceleration (ODBA), a unitless, directionless index that effectively proxies for activity level and energy expenditure (Nathan et al., 2012; Qasem et al., 2012; Wilson et al., 2020). Accelerometry and ODBA have been validated across various species and habitats enabling continuous data collection on animal activity levels with and without direct observation, demonstrating reliability as a generalizable measure for assessing energy costs and activity in free-ranging animals (Ropert-Coudert and Wilson 2005; Brown et al., 2013; Patterson et al., 2018).

These methods allow researchers to deduce behavioral states and energy expenditure, providing valuable insights into how environmental factors influence activity levels and movement strategies in species such as polar bears (*Ursus maritimus*) (Pagano et al., 2019), mountain lions (*Puma concolor*) (Dunford et al., 2020), and dingoes (*Canis lupus dingo*) (Tatler et al., 2021) even with limited sample sizes. In Germany, machine learning algorithms

applied to datasets including ODBA accelerometry successfully classified behaviors in red foxes (*Vulpes vulpes*), linking specific activity patterns to energy expenditure in wild subjects (Rast et al., 2020).

Combining accelerometry with Geographic Information Systems (GIS) and meteorological data deepens our understanding of animal-habitat interactions, enabling models that reveal climate-driven adaptations in activity and energy use. GPS biologging of beluga whales (*Delphinapterus leucas*) shows for instance that climate-driven delays in sea-ice formation shift migration timing with implications for marine traffic (Hauser et al., 2016). Similarly, arctic ground squirrels (*Urocitellus parryii*) equipped with body temperature loggers demonstrate behavioral flexibility by prolonging hibernation during late snow events (Williams et al., 2011). Accelerometry data from giant pandas (*Ailuropoda melanoleuca*) revealed seasonal adjustments: increased movement in spring for nutrient-rich bamboo and frequent rest-foraging cycles in winter to conserve energy (Zhang et al., 2018). These examples illustrate how tracking environmental and physiological responses contributes valuable insights for predicting and mitigating climate impacts on biodiversity and ecosystem health—insights that are increasingly relevant in highly seasonally dynamic ecosystems like the Arctic, where species face accelerating ecological changes.

2.2 The Arctic Ecosystem: A Changing Landscape

In the Arctic, climate-driven ecological changes occur faster than in other biomes, severely impacting species at population and community levels (Post et al., 2009). These transformations are characterized by habitat alterations such as tundra greening: warming temperatures promoting growth of grasses and mosses in the tundra (Myers-Smith et al., 2011); shrubification: shrubs like willow (*Salix spp.*) and birch (*Betula spp.*) spreading into tundra areas, altering soils and snow cover (Tape, Sturm, & Racine, 2006); and borealization: the northward expansion of boreal species like spruce (*Picea spp.*) and red foxes into Arctic ecosystems, introducing new competitive dynamics (Elmhagen et al., 2015). Arctic amplification exacerbates these issues with warming at twice the global average (Serreze & Francis, 2006), driving widespread species' range shifts poleward at an average rate of 6.1 km per decade, with spring seasonal events advancing by 2.3 days per decade (Parmesan & Yohe, 2003).

These shifts are altering habitats, resource availability, and seasonal cycles, forcing animals to adapt their foraging and activity strategies to survive. This is particularly true for animals at the leading edge of an expanding range, like the red fox in the circumpolar north, which may experience more challenging periods with harsher climates and lower resource availability despite conditions having become more benign, requiring adaptation to activity patterns. For instance, red foxes in the High Canadian Arctic have been observed to expand their home ranges and venture onto sea ice during winter, untypical behaviors for the species likely driven by the need to meet energetic demands in a resource-scarce environment (Lai et al., 2022).

These habitat alterations can create and/or alter bottom-up effects in Arctic food webs, as vegetation shifts impact habitat quality for primary consumers like rodents (*Rodentia spp.*) and ungulates (*Alces spp.*; *Rangifer spp.*), with cascading effects on multiple trophic levels (Elmhagen et al., 2000; Killengreen et al., 2007).

2.3 Red Fox Expansion in the Arctic: Interspecific Competition and Predatory Dynamics

The red fox, one of the most widespread carnivorous species in the Northern Hemisphere, is renowned for its remarkable adaptability and opportunistic behavior (Hersteinsson & Macdonald, 1992). Its northward expansion across the circumpolar region is facilitated by various factors, including behavioral flexibility in response to changing resource availability (Baker et al., 2000), and physical adaptations like larger feet for better mobility in deep snow and elongated snouts for efficient prey capture in the subnivean zone (Murray & Larivière, 2006; Yuk et al., 2024). Additionally, anthropogenic food subsidies, such as reindeer (*Rangifer tarandus*) carcasses and waste from human settlements, have further facilitated this expansion by providing consistent food sources in both European and North American Arctic landscapes (Killengreen et al., 2007; Gallant et al., 2019). While temperature has been considered a limiting factor for red fox expansion in Eurasia (Pasanen-Mortensen et al., 2007), shifts in circumpolar conditions and global climate patterns (Parmesan & Yohe, 2003; Gallant et al., 2019) have weakened this constraint, allowing red foxes to thrive in traditionally Arctic fox-dominated areas such as the Varanger peninsula and other areas of arctic tundra. The red fox is now found on every continent except Antarctica. This exceptional range size, adaptability, and broad generalized niche makes the species an excellent candidate

for studying climatic and landscape factors in movement ecology across many ecosystems (Iossa et al., 2008).

The red fox is now present year-round on the Varanger Peninsula, marking the Arctic's southern and western edge in Europe. While red foxes have long existed in Varanger, their numbers and inland presence have increased (Ims et al., 2017). This expansion carries significant ecological consequences, particularly intensifying competition with the native Arctic fox, with which the red fox shares some aspects of its ecological niche (Elmhagen et al., 2017). The red fox's larger size provides a competitive advantage over Arctic foxes in direct encounters, often excluding them from productive territories or central foraging sites like carcasses. Red foxes may also predate adult Arctic foxes, though predation on pups at dens is more common (Tannerfeldt et al., 2002; Rodnikova et al., 2011; Hamel et al., 2013).

However, Arctic foxes have evolved to thrive in the resource scarcity of low-productive Arctic winters, even in years with low rodent abundance, giving them an indirect competitive edge in such conditions. However, the broader prey range of the red fox, especially in years of lower lemming numbers, enables it to adapt more flexibly to changing food conditions. If food availability increases at a landscape scale, red fox dominance could intensify further, disrupting the region's predator-prey dynamics (Elmhagen et al., 2002; Hamel et al., 2013).

Research by Killengreen et al. (2011) illustrates this possibility, showing that concentrated food sources—such as seabirds, marine mammals, and reindeer carrion—provide marine and terrestrial (anthropogenic) subsidies that disproportionately benefit red foxes. Even low densities of red foxes significantly hinder Arctic fox recolonization (Hamel et al., 2013), posing a serious threat to the survival of the critically endangered Arctic fox in Fennoscandia for which considerable conservation efforts, including captive breeding, reintroduction programs, supplementary feeding, and red fox culling, are underway (Landa et al., 2017). Managing red fox populations can thus directly support Arctic fox conservation.

This research aims to reveal how red foxes adjust their activity during energetically challenging periods as well as periods of higher production on the northern edge of their range expansion in Europe. This information may also reveal areas where interventions may be more effective at controlling further increases in the Varanger red fox population to aid in the Arctic fox's recovery (Hamel et al., 2013; Ims et al. 2017). Modern tracking technologies, such as GPS and GIS, provide essential tools for understanding movement ecology and

informing management strategies. For example, they allow researchers to assess effectiveness in control measures like sterilization, relocation, and targeted culling (Dunford et al., 2020; Wilson et al., 2020), enabling an adaptive management approach.

2.4 Research Questions and Hypotheses

Effective and humane management of red fox populations in Varanger requires a detailed understanding of their behavior. This study examines how environmental and human pressures influence red fox activity in Varanger, specifically addressing three key questions: How do daily changes in temperature, snow depth, and precipitation affect red fox activity? How does vegetation productivity correlate with activity? And how does human use intensity influence red fox activity in Varanger's varied landscape?

Studies on other carnivoran species provide insights into potential drivers of red fox behavior. Research on coyotes indicates that temperature and prey availability shape activity and foraging strategies (Gese et al., 1996a, 1996b), while findings on raccoon dogs in Finland show reduced activity with increasing snow depth and colder temperatures (Selonen et al., 2024), pointing to snow depth as a key factor in mesopredator behavior. Additionally, studies in Svalbard reveal that human disturbances, such as snowmobile traffic, increase nocturnal activity in Arctic foxes (Fuglei et al., 2017), suggesting that human factors can also impact daily and seasonal activity patterns.

I hypothesize that these environmental factors will influence red fox activity in complex ways. Regarding daily weather impacts, colder temperatures may increase activity due to higher thermoregulatory demands, while deep snow could hinder activity and limit foraging efficiency. Precipitation might have varying effects: light rain may not significantly alter activity, but heavy precipitation could reduce activity by limiting travel ease and foraging..

Seasonal and photoperiod factors may add further complexity to red fox behavior. During the polar day, which coincides with the breeding season, red foxes may exhibit reduced activity levels and shorter activity periods, potentially due to extended daylight limiting hunting cover and/or the demands of pup rearing. Conversely, during the polar night, red foxes may increase both the intensity and duration of activity as they shift to foraging and survival-focused behaviors; the extended low-light conditions may further support their nocturnal habits.

I hypothesize that higher vegetation density will correlate with increased activity, offering cover and hunting resources. In contrast, low-vegetation areas could either function as travel corridors, thereby increasing activity, or limit foraging opportunities, potentially resulting in lower activity levels.

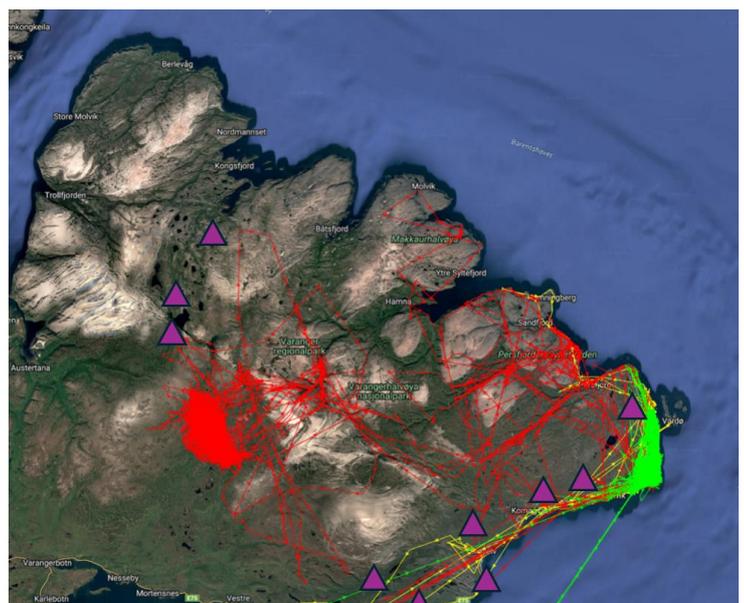
Research indicates that high human footprint areas correlate with reduced mammal movement (Tucker et al., 2018), suggesting that red foxes in Varanger may similarly adapt to human disturbance. The Varanger Peninsula, with its high recreational use and national park designation, highlights the need to consider human impact on red fox behavior. I hypothesize that red foxes will exhibit higher activity periods in low human-use areas but lower activity intensity near cabins or settlements where human subsidies ease energy demands.

These hypotheses collectively aim to illuminate red fox behavioral adaptations to the changing landscape in Varanger. This study combines zoo and field data to address red fox activity. ODBA values were calibrated using accelerometer data from a captive fox. These thresholds were then applied to GPS and ODBA data from wild foxes, integrated with climate and environmental data, to examine activity using acceleration as a proxy.

3 Materials and Methods

2.53.1 Study site

The Varanger Peninsula (70–71°N, 28–31°E) in Northern Norway lies at the western fringe of the Eurasian Arctic tundra, at the transition between the sub-Arctic and bioclimate subzone E (Walker et al. 2005). Coastal areas, influenced by the North Atlantic current, experience relatively mild winters (mean temperatures around -6°C in January) and cool summers (averaging 10°C), while inland highlands, reaching up to 600 meters, endure harsher conditions with annual temperatures often below freezing and sporadic permafrost (Farbrot et al., 2008; Ims



Figur 1 Varanger peninsula with tracks for three foxes Biret (red), Thorsen (green), and Reinart (yellow). Purple points are trap locations.

et al., 2017). Annual precipitation varies between 400 and 1000 mm, with significant snowfall during the extended winter months (COAT, 2023). Spatial heterogeneity is high, and the snowpack is strongly affected by wind.

Vegetation in Varanger is characterized by strong altitudinal gradients. Heaths of dwarf shrub extend through the low alpine tundra zone giving way to alpine vegetation and snow beds with mosses, graminoids, and lichen at higher elevations. Steep, fertile, river valley riparian zones are interspersed throughout the peninsula composed of lush forbes and graminoid rich meadows and willow thickets around 2-3 meters high (COAT science plan, willow thickets, and scattered birch forests in the warmer southwestern lowlands (July temperatures 11–13°C) (Walker et al., 2005; Killengreen et al., 2007). The region serves as summer pasture for Sámi reindeer herding, with some reindeer remaining in winter, providing vital carrion for mesopredators (Killengreen et al., 2011) . In addition to Varangerhalvøya national park and outdoor recreation activities; hiking, hunting, and holiday homes, other human uses in the area include sheep and cattle farming, permanent roads, windfarms, and human settlements and industry; notably fishing and fish processing along the coast. Key wild fauna includes small rodents—grey-sided voles (*Myodes rufocanus*), tundra voles (*Microtus oeconomus*), and Norwegian lemmings (*Lemmus lemmus*)—mountain hare (*Lepus timidus*) — mammalian mesopredators such as the red fox, Arctic fox — a single large predator, the wolverine (*Gulo gulo*); other large predators, brown bears (*Ursus arctos*), wolves (*Canis lupus*), and lynx (*Lynx lynx*) being absent by management decisions. Diverse bird species including ptarmigans (*Lagopus* spp.), waders, corvids, skuas, and raptors— and ungulates; semi-domestic reindeer (*Rangifer tarandus*), and moose (*Alces alces*) are also present (Killengreen et al. 2007; Killengreen et al. 2011; Ims et al. 2017).

Varanger serves as a key site for ongoing Arctic fox conservation efforts, notably intensive hunting, and culling efforts for the last 20 years (Ims et al., 2017; Fjellrevmodul COAT Finnmark: Rapport for 2023).

2.63.2 Lotek collars and ODBA

Lotek Iridium Litetrack 150 collars (170g); hereafter “collar”, have been used to monitor red foxes on the Varanger Peninsula since 2021. Collars were programmed record GPS fixes every three hours, plus every 20 minutes for three hours approximately every other day (14 bursts per month) distributed to cover all periods of the day, and capture acceleration data every 10

seconds as overall dynamic body acceleration (ODBA). An onboard accelerometer converts tri-axial (X, Y, Z) readings into ODBA values, providing an index of activity.

ODBA formula:

$$ODBA = |A_X - \overline{A_X}| + |A_Y - \overline{A_Y}| + |A_Z - \overline{A_Z}|$$

Where:

- A_X, A_Y, A_Z represent the acceleration along the respective axes as spot samples
- $\overline{A_X}, \overline{A_Y}, \overline{A_Z}$ represent the acceleration along the respective axes averaged over the previous 2 seconds.

GPS positions are transmitted over the iridium satellite network and can be downloaded from Lotek, but acceleration data must be retrieved from the collar by euthanizing the animal. Acceleration data is retrieved from the collar using Lotek software PinPoint Host version 2.15.17.0

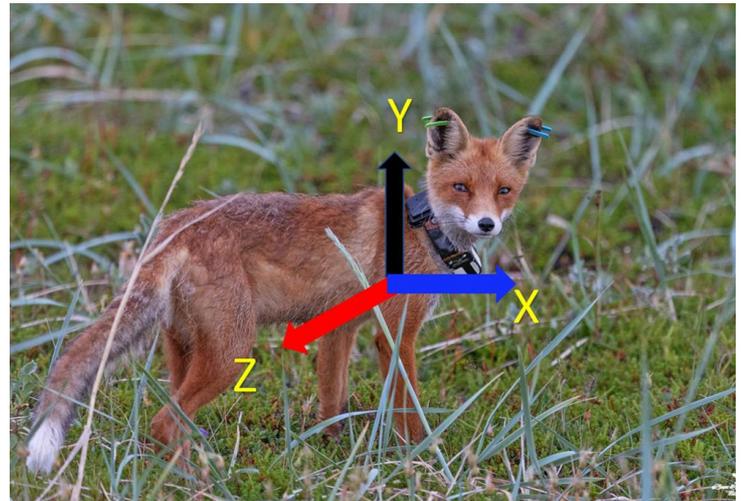


Figure 2: Thorsen with collar. Photo: Svein Johannessen

2.73.3 Zoo Observations and Ground-Truthing

To validate collar-based ODBA measurements against specific activity states, I conducted a lab to field ground-truthing study at Tangen Dyrpark in Tangen, Norway. The park houses a skulk of four red foxes in a spacious enclosure surrounded by a chain-link fence. The enclosure features an S-shaped slope with mixed terrain, including dirt, rocky areas, and vegetation. It also contains large boulders, medium-sized trees, and small dog houses that serve as dens for the foxes.

For this study, park staff selected two foxes, Johnny, and Franky, based on their accessibility. Johnny, a melanistic morph and the most habituated fox at the park, was prioritized due to his easily distinguishable appearance. Franky, a typical red morph, was more challenging to sedate safely, so I proceeded with collaring Johnny only. At approximately eleven years old, Johnny was sedated with an oral dose of acepromazine (21 mg at 2.5 mg/kg) and

dexmedetomidine (0.15 mg at 0.018 mg/kg) to facilitate collar placement. After securing the collar, I administered atipamezole (1.5 mg intramuscularly) as a reversal agent. Johnny's recovery was monitored for 30 minutes, during which he exhibited normal behavior and movement without any signs of discomfort. He was then given an overnight acclimation period before data collection began. All animal handling procedures were conducted in collaboration with the park's veterinarian to ensure safety and animal welfare.

Data were collected using a collar programmed with the same settings as those used for wild foxes. I positioned stationary cameras outside the enclosure in high-traffic areas, identified based on fox activity patterns and recommendations from the animal keepers. To ensure accurate synchronization of observational data with ODBA readings, I displayed a synchronized timestamp at the start of each filming session using the AtomicClock app linked to the time.nist.gov server.

I scored the footage using DaVinci Resolve software (version 18.6.2), embedding timestamps to align with ODBA readings. Whenever Johnny was visible, I categorized his behavior into one of five categories: Resting, Standing/Sitting/Shifting, Walking, Running, or Other, based on 10-second intervals. Initially, ODBA readings were classified into four activity levels: Resting, Standing/Sitting/Shifting, Walking, and Running. However, due to significant overlap between Walking and Standing/Sitting/Shifting, I combined them into a single Low Active category, resulting in three final activity levels: Inactive, Low Active, and High Active.

Because ODBA is meant to be a broad characterization of body movement there can be high variability and overlap between behavioral categories as well as between study species. To address this, I developed a decision tree model using the `rpart` package (Therneau et al., 2023) in R (R Core Team, 2024), with RStudio (Version 2024.04.2+764; RStudio Team, 2024), to classify these activity levels based on ODBA values. The model identified an ODBA threshold of 94.5 to distinguish Inactive from Active states; see results section for more information.

2.83.4 Fox trapping

Wild red foxes were trapped using large wooden double-entry traps (Värmlandsk tunnelfelle) baited with a variety of baits. Seven traps were situated near the coast between Vadsø and

Vardø with an additional three traps situated inland in the northwest of the peninsula. The traps were left on the study sight permanently with the doors locked open outside of the trapping season to habituate foxes to their presence. The traps were monitored remotely by cameras triggered automatically by motion or manually by SMS command. Traps were checked at least every six hours by SMS. Trapped red foxes were fitted with a collar without the use of sedation using an established protocol. Other animals found in the trap were released. All animal handling procedures were approved by Mattilsynet (FOTS ID 30085)

Between May of 2021 and November of 2023, a total of nine foxes were fitted with tracking collars. As of this study, six collars have been retrieved. Two collars were too damaged to retrieve acceleration data. Therefor a total of four individuals are used in this study.



Figur 3 Red fox at trap



Figur 4 Camera position at trap

2.93.5 Data Integration and Consolidation with Environmental variables

I employed custom R functions to integrate GPS and ODBA data; see appendix. Time stamps from the ODBA files, recorded in Arc/Info Data File (ADF) format, provided Greenwich Mean Time (GMT) timestamps for each observation of ODBA. GPS data, retrieved from the Lotek webserver, also recorded positions with specific GMT times. Using a nearest neighbor method, I matched ODBA and GPS timestamps by calculating absolute time differences and identifying the closest matches. Missing GPS data were filled with the nearest available coordinates, and the GPS coordinates were converted to Universal Transverse Mercator (UTM) coordinates to enable spatial integration with environmental data at a later step. The data were then aggregated by minute, calculating mean values for ODBA.

Activity state — Active or Inactive — was initially assigned solely by whether the ODBA value was above or below the 94.5 threshold established previously. To stabilize classifications and prevent momentary fluctuations — e.g., a fox moving in its sleep — from incorrectly triggering state changes, I implemented a Five-Minute Rule using a custom R function; see appendix. State transitions were confirmed only when supported by five consecutive one-minute observations or when the current observation and the following four one-minute observations consistently indicated a new state.

Meteorological data — snow depth in cm, mean daily temperature (C), and precipitation in mm — were sourced from seNorge’s THREDDS Data Server as gridded NetCDF files provided by the Norwegian Meteorological Institute (2021-2024). These NetCDF files provide daily values on a square grid over the whole of Norway at a 1km spatial resolution with the center of each gridded square as a reference point using UTM coordinates. Using a custom R function these values were extracted for each minute-aggregated GPS integrated ODBA timestamp; (see appendix for script). The UTM coordinates were first rounded to match the nearest gridded square center point. If the value for that gridded square center point returned NA — e.g., because the center point was in a body of water — the function referred to the next nearest center point to the coordinates in an adjacent square.

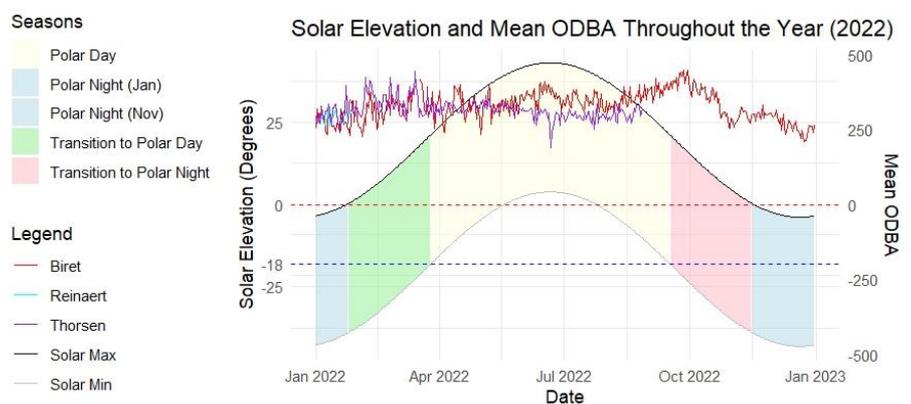
Raster data provided additional spatial context on area use intensity and vegetation at a resolution of ~182 meters per pixel. The area-use intensity dataset, “arealbruksintensitet,”

measures the degree of human influence over time. It classifies land use into a continuous gradient of four levels: 1) Low land use intensity, 2) Built-up areas, 3) Dense housing, and 4) City, reflecting variations from natural areas with minimal human impact to highly urbanized regions (Artsdatabanken, 2024). Vegetation data, represented by the Enhanced Vegetation Index (EVI), was derived from a national dataset of phenological state variables processed from Moderate Resolution Imaging Spectroradiometer (MODIS)(Tveraa et al., 2013). EVI quantifies vegetation greenness and is more sensitive and has reduced atmospheric effects compared to Normalized Difference Vegetation Index (NDVI). This dataset provides the mean of maximum EVI from 2000 to 2021, which was used to characterize vegetation for the study area (NINA, 2024). As for meteorological data, these data were assembled with the activity data based on spatial proximity.

In order to characterize light conditions for each observation solar elevation for each GPS integrated ODBA timestamp was calculated using established astronomical formulas; see appendix (Meeus, 1998; Duffie & Beckman, 2013; Reda & Andreas, 2004; Michalsky, 1988). Light conditions were categorized by solar elevation angle as Day ($\alpha > 0$), Twilight ($0 \geq \alpha > -18$), and Night ($\alpha \leq -18$) (Bikos and Kher). At the high latitude of the study site, civil, nautical, and astronomical twilight were combined into a single Twilight category due to their brevity or absence during portions of the year.

Following integration of data for each fox, datasets were aggregated to the day structured around a "fox day"; defined from one solar noon to the next, to capture the foxes' predominantly nocturnal activity patterns

comprehensively; see appendix. For each fox day, I calculated daily totals and summary statistics for activity metrics—mean ODBA of active periods, proportion of time spent active— as well as mean daily values for all other variables; snow depth, mean daily temperature, precipitation, anthropogenic area use intensity, and vegetation data. Spatial variables were averaged over the places the fox used during that day. Mean ODBA is meant to represent the total daily activity exhibited by a fox



Figur 5 Light seasons with ODBA

on a given day, while the proportion of active ODBA represents the proportion of time the fox spent being active on a given day, daily proportion active.

Processed datasets from each fox were then pooled for comprehensive group-level analysis retaining the individual fox as a categorical variable; “fox ID.” Each fox day was categorized into one of four seasons—Polar Night (sun continuously below the horizon, 0 degrees), Transition to Polar Day, Polar Day (sun continuously above -18 degrees), or Transition to Polar Night—based on solar transitions, providing a framework for considering seasonal variations; see appendix.

2.103.6 Statistical Analysis

All statistical analysis and plotting of data were performed in R with a variety of packages; nlme (Pinheiro et al., 2023), dplyr (Wickham et al., 2023), AICcmodavg (Mazerolle, 2023), ggeffects (Lüdtke, 2023), ggplot2 (Wickham, 2023), broom.mixed (Bolker & Robinson, 2023), gridExtra (Auguie, 2023), ggcorrplot (Kassambara, 2023), patchwork (Pedersen, 2023), lubridate (Grolemund & Wickham, 2023), and tidyr (Wickham & Henry, 2023).

To ensure the data were appropriate for linear mixed models (LMM), I first visualized the distributions of mean ODBA and the proportion of active ODBA (>94.5), using histograms, checking for skewness. I then ran preliminary linear models with these activity metrics as dependent variables and environmental predictors, including snow depth, mean temperature, precipitation, area use intensity, and vegetation data as independent variables.

I assessed the key model assumptions by examining diagnostic plots. These included checks for the normality of residuals, homoscedasticity (constant variance of residuals), and the absence of multicollinearity among predictors. The residuals were approximately normally distributed, variances were consistent across levels of the predictors, and no significant multicollinearity was detected. These results confirmed that the data met the necessary assumptions, supporting the suitability of LMM for further analysis.

To examine the influences of environmental variables on red fox activity, I used linear mixed-effects models (LME) with an autoregressive structure of order 1 (AR(1)) to account for temporal autocorrelation and avoid statistical pseudo-replication. The modeling process

involved constructing a series of candidate models for each activity metric, evaluating them based on statistical performance and biological plausibility.

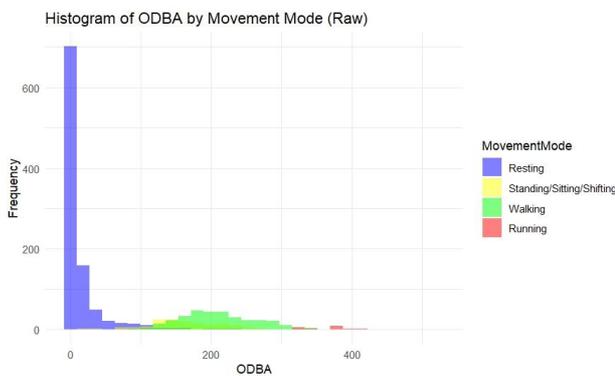
Snow depth and temperature were categorized into binary variables to reflect ecologically relevant thresholds in order to compare broadly the effects of snow presence and absence on the landscape as well as the difference between temperatures above and below freezing. Snow depth was classified as present when it exceeded 0.5 cm, and temperature was categorized as above or below 0°C. Therefore two sets of models were constructed and selected from for each dependent variable which represented the effect of snow on the landscape and the effects of the depth of snow on the landscape respectively. Continuous predictors, including snow depth, temperature, precipitation, area use intensity, and vegetation density, were standardized to a mean of 0 with a standard deviation of 1 to ensure comparability of effect sizes of the different variables.

Each candidate model included some or all fixed effects for predictors and their interactions. The chosen interactions capture key environmental factors affecting red fox behavior and habitat use. I included Mean Temperature \times Precipitation to address how temperature-dependent precipitation (rain vs. snow) influences habitat conditions. Snow Depth \times Vegetation Density captures how winter conditions and snow type impact prey visibility and fox mobility. Finally, Area Use Intensity \times Vegetation Data examines how human land use and altered vegetation influence prey availability and fox navigation in modified landscapes. See model selection table #. Random intercepts for fox ID and season were incorporated to prevent statistical pseudo-replication from individual variations in behavior, as well as seasonal variability in light conditions that might befall otherwise similar environments. Models were ranked using Akaike Information Criterion (AICc), which facilitated the selection of parsimonious models that provided the best balance between goodness of fit and model complexity. This process ensured that the chosen models appropriately captured relationships that were both statistically sound and biologically meaningful.

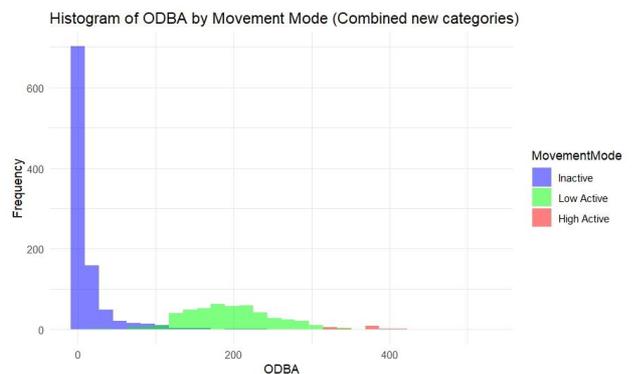
3.4 Results

3.14.1 Zoo Observations and Ground-Truthing

In total, 253 minutes of footage from the zoo trial was used to make 1519 10-second interval scorings of behavior for four categories: resting (n=997), standing/sitting/shifting (n=160), walking (n=332), and running (n=30); figure 6. Two of these categories (standing/sitting/shifting, and walking) were combined to a single low active category; figure 7. The model identified an ODBA threshold of 94.5 to distinguish Inactive from Active states and 313.5 to separate Low Active from High Active activity; see appendix. Due to the limited observations of running behavior, I used only the 94.5 threshold in subsequent analyses to differentiate between Inactive and Active states in wild foxes.



Figur 6 Raw counts of zoo data



Figur 7 Combined counts of zoo data

3.24.2 Overview of Field Data

In total, 1085 fox-days were considered in this study from four foxes. Thorsen was tracked from May 24th, 2021, to August 31st, 2022; fox-days= 460 and had a high fidelity for the eastern coast near Vardø. Reinaert was tracked from November 11th, 2021, to January 27th, 2022; fox-days= 79 and had preference for the eastern coast moving between Vardø and Vadsø along the main roadway; where he was eventually struck by a vehicle and killed. Uhcci Biret was tracked from October 11th, 2021 to February 2nd, 2023; fox-days=460 and initially had habitat preferences for the eastern coast before later moving further inland. Geir was tracked from October 14th, 2023, to January 8th, 2024; fox-days=87 with a preference for the western inland of the peninsula; Geir was unfortunately prematurely harvested by a hunter. Carcass examination showed that the foxes were in generally good health at the time

of their deaths with fat indexed between 3 and 4 and no noted abnormalities (Dorothee Ehrich; unpublished data).

3.34.3 Model Choice

For model selection, mod2va was chosen as the best model for analyzing total daily activity with snow presence/absence, as it consistently showed robust performance across various candidate model lists. This model incorporates all environmental variables and interactions with snow presence, providing a comprehensive yet explanatory fit. Mod0va was also evaluated but ultimately excluded due to an insignificant temperature-precipitation interaction effect, despite being within two AIC points.

For the snow depth analysis during snow-present conditions, mod3v was selected as the most suitable model for total daily activity. Although mod3va was considered for consistency across models, area use intensity was insignificant, favoring mod3v's simpler structure. For daily proportion active, mod0va was chosen due to its strong support (delta AIC ~10 compared to mod2va), reflecting time-budgeting dynamics potentially distinct from activity efforts. Here, the interaction between temperature and precipitation was deemed relevant to decisions to move versus the efforts required. However, mod0a or mod0v could also be reasonable choices due to their parsimony and AIC proximity.

In the continuous snow depth models for daily proportion active, mod3 was selected as it remained within 1 AIC point of mod3a and excluded non-significant area use effects, suggesting that a narrower set of factors influences activity periods during the snow season, likely due to seasonal changes in vegetation cover and reduced human activity. Ultimately, the selected models are mod2va for binary total daily activity, mod3v for snow depth total daily activity, mod0va for binary daily proportion active, and mod3 for snow depth daily proportion active. See appendix for AIC tables

3.44.4 Total Daily Activity

3.4.14.4.1 Total Daily Activity in the presence and absence of snow cover.

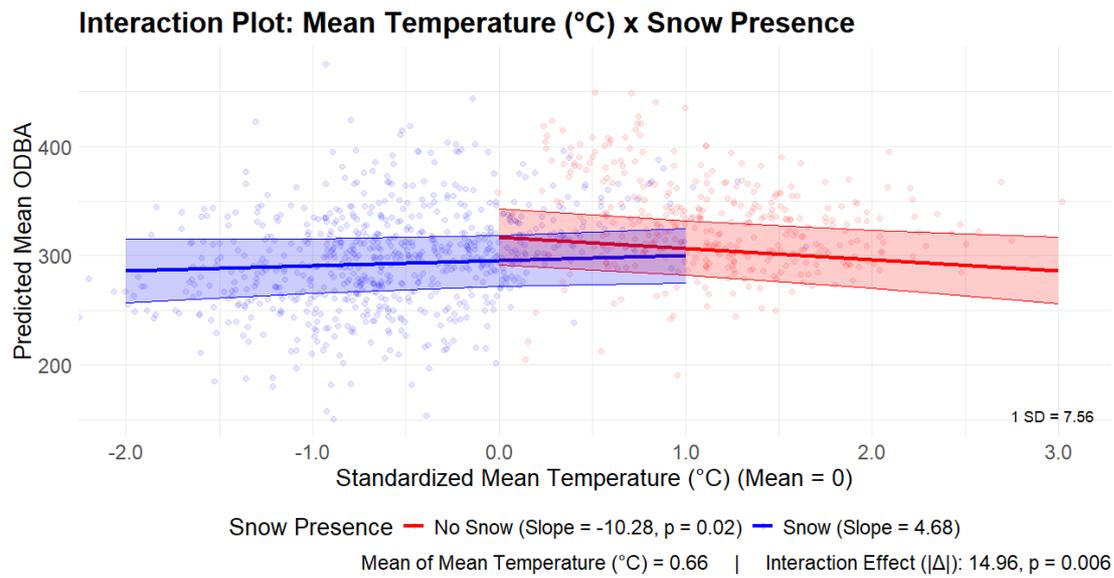
Model Summary: Total Daily Activity with Snow Present/Absent (mod2va)

Term	Estimate	Std. Error	Statistic	P-value
Intercept	317.344	13.306	23.850	0.000
Snow Presence (Yes)	-21.915	6.658	-3.292	0.001
Scaled Mean Temperature	-10.283	4.408	-2.333	0.020
Scaled Precipitation	2.175	1.063	2.046	0.041
Scaled Vegetation Data	6.468	2.907	2.225	0.026
Scaled Area Use Intensity	-10.942	2.849	-3.840	0.000
Snow Presence × Mean Temperature	14.959	5.433	2.754	0.006
Snow Presence × Precipitation	-6.319	1.705	-3.706	0.000
Snow Presence × Vegetation Data	-1.847	3.215	-0.575	0.566
Snow Presence × Area Use Intensity	9.699	3.255	2.980	0.003

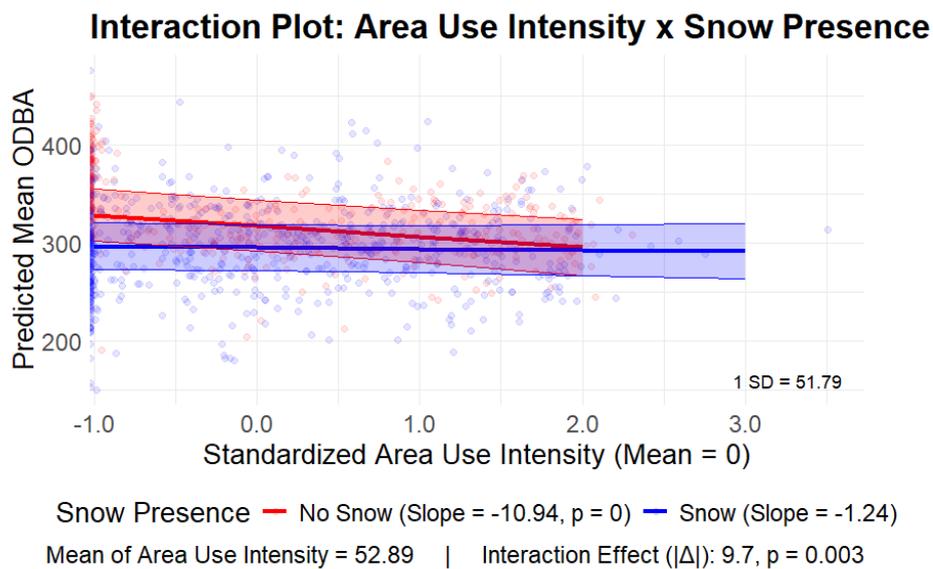
Tabell 1 Total Daily Activity (Snow present/not present)

The presence of snow significantly reduced average activity level by 21.92 in terms of mean ODBA (standard error SE = 6.66, $p = 0.001$). In the absence of snow, mean temperature also had a slight negative effect on average activity level (SE = 4.41, $p = 0.020$; effect size = -10.28), meaning that for every one standard deviation (7.56 degrees) increase in mean temperature, average activity level decreased by 10.28 in ODBA; figure 8. Foxes were also less active in areas with high area use intensity when snow was absent ($p < 0.0001$; effect size = -10.94); figure 9. Conversely, increased vegetation was associated with slightly higher average activity level (SE= 2.9, $p = 0.026$; effect size = 6.47); figure 10, as was increased

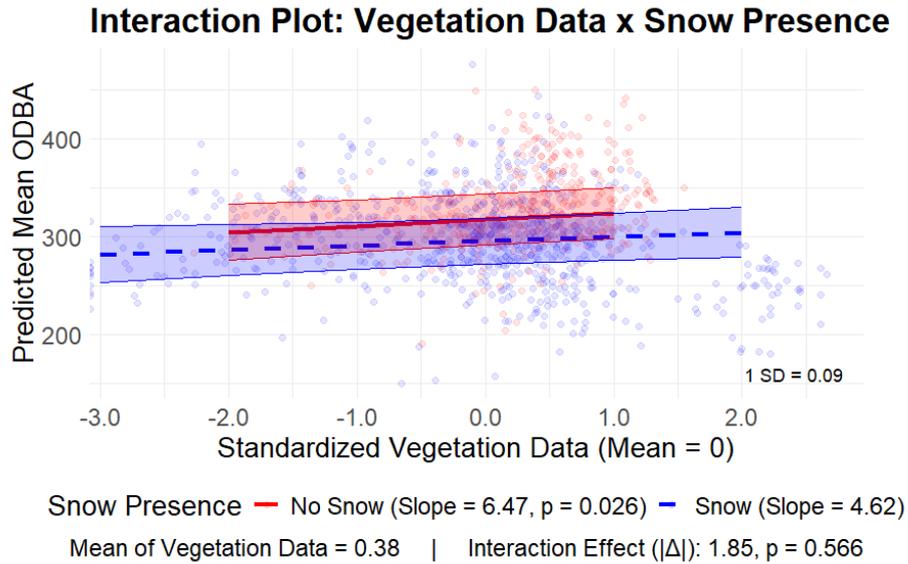
precipitation (SE = 1.06, p = 0.04; effect size = 2.18); figure 11.



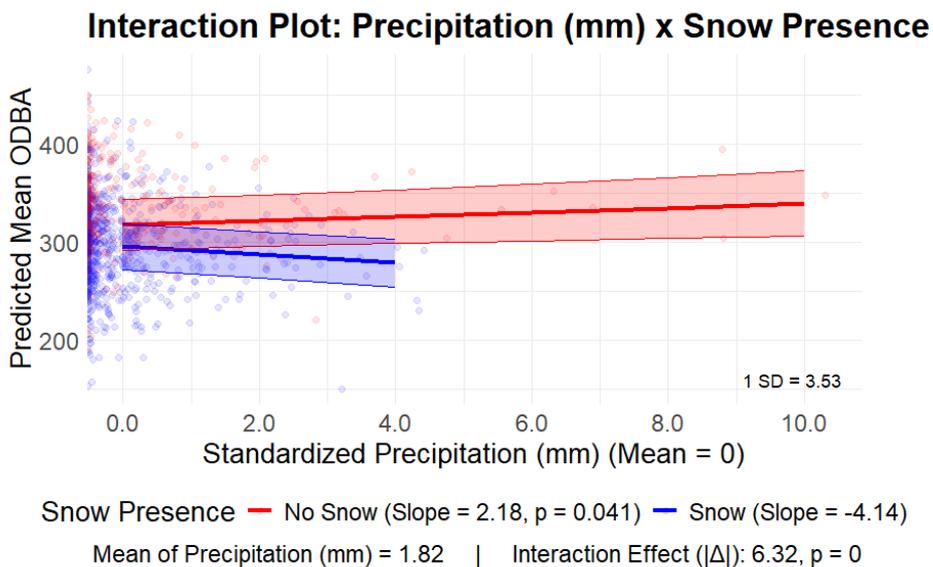
Figur 8 Predicted mean ODBA (mean temp:snow presence)



Figur 9 Predicted mean ODBA (Area use intensity:snow presence)



Figur 10 Predicted mean ODBA (vegetation:snow presence)



Figur 11 Predicted mean ODBA (precipitation:snow presence)

Several of these relationships were inverted in the presence of snow. The effect of temperature in this case was slightly positive (interaction 14.96, SE = 5.43, p=0.006), the effect of precipitation negative (p=0.0002) and the effect of area use intensity close to 0 (p=.003). Vegetation biomass did not show a significant interaction with snow presence, implying that vegetation's effect on activity was similar regardless of snow presence.

3.4.24.4.2 Total Daily Activity with Continuous Snow Depth

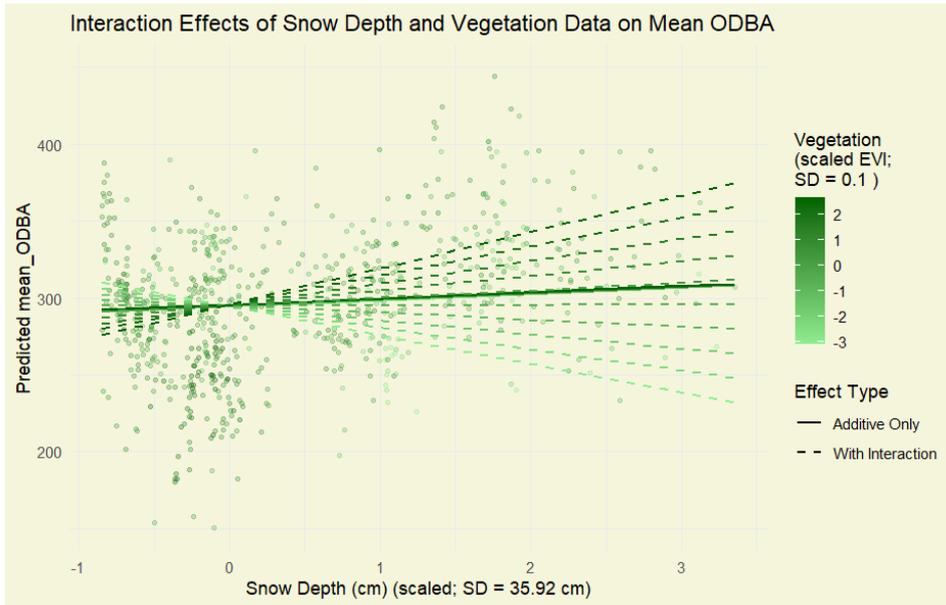
Model Summary: Total Daily Activity with Snow Depth (mod3v)

Term	Estimate	Std. Error	Statistic	P-value
Intercept	295.111	10.273	28.727	0.000
Scaled Snow Depth	4.050	3.287	1.232	0.218
Scaled Mean Temperature	3.728	3.464	1.076	0.282
Scaled Precipitation	-3.295	1.581	-2.084	0.038
Scaled Vegetation Data	0.215	1.887	0.114	0.909
Snow Depth × Mean Temperature	-2.640	3.501	-0.754	0.451
Snow Depth × Precipitation	-2.079	1.568	-1.326	0.185
Snow Depth × Vegetation Data	7.365	1.541	4.779	0.000

Tabell 2 Total Daily Activity (Snow continuous)

Looking only at periods with snow cover and considering snow depth as a continuous variable, I found no significant direct effect on average activity level ($p = 0.22$). However, precipitation was associated with a small but significant decrease in average activity level ($p = 0.0375$; effect size = -3.30), suggesting that snowfall but not snow depth effects activity during the snow-covered periods.

Despite snow depth having no effect on its own, I did find a significant positive interaction between snow depth and vegetation biomass (7.37 , $SE = 1.54$, $p < 0.001$); figure 12. This finding suggests that with increasing snow depth activity increased in areas with more vegetation ($p = < 0.0001$).



Figur 12 Interaction (snow depth:vegetation on mean ODBA)

3.54.5 Daily Proportion Active

3.5.14.5.1 Daily Proportion Active with Binary Snow Presence

Model Summary: Daily Proportion Active with Snow Present/Absent (mod0va)

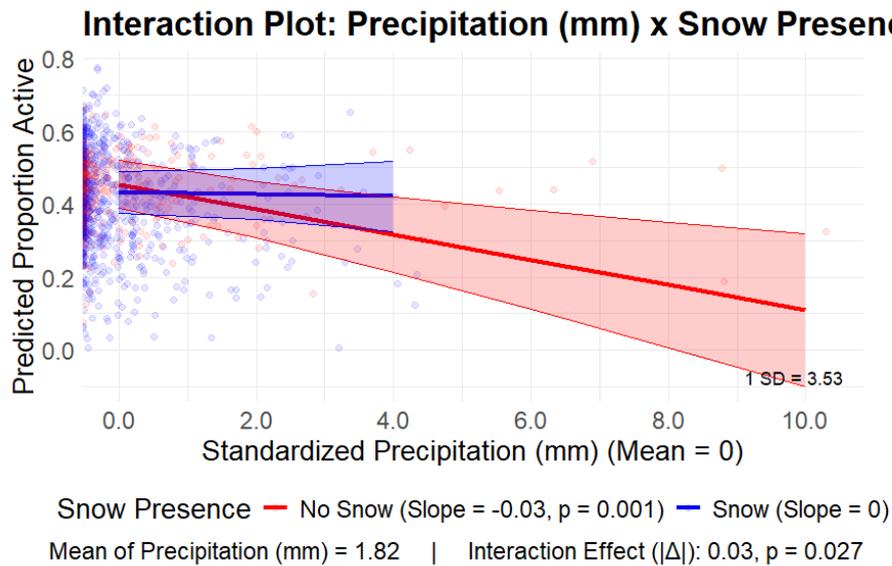
Term	Estimate	Std. Error	Statistic	P-value
Intercept	0.455	0.034	13.496	0.000
Snow Presence (Yes)	-0.022	0.018	-1.210	0.226
Scaled Mean Temperature	0.006	0.013	0.476	0.634
Scaled Precipitation	-0.035	0.010	-3.424	0.001
Scaled Vegetation Data	0.009	0.010	0.937	0.349
Scaled Area Use Intensity	0.001	0.009	0.064	0.949
Snow Presence × Mean Temperature	0.043	0.015	2.800	0.005
Snow Presence × Precipitation	0.032	0.014	2.211	0.027
Snow Presence × Vegetation Data	0.001	0.010	0.077	0.938
Snow Presence × Area Use Intensity	-0.016	0.009	-1.812	0.070
Temperature × Precipitation Interaction	0.024	0.007	3.461	0.001

Tabell 3 Daily Proportion Active (Snow present/not present)

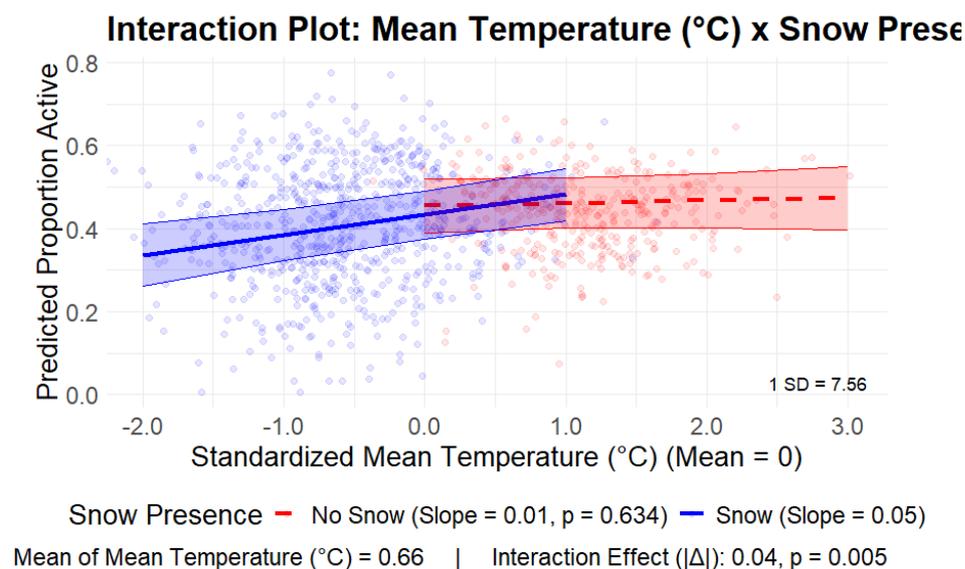
The intercept of the binary snow model for the proportion of active ODBA indicates that in the absence of snow, with other variables at their mean, foxes spend about half (45%) of the time in an active state. Snow presence did not significantly affect the proportion of time a fox

was active ($p = 0.23$). However, precipitation was significantly associated with a decrease in the proportion of time active ($SE = .01$, $p = 0.0006$; effect size = -0.0346); figure 13.

The presence of snow interacted with both mean temperature and precipitation to affect the proportion of time active. Snow presence combined with higher mean temperatures increased the proportion of time active ($SE = 0.015$, $p = 0.0052$; effect size = 0.04); figure 14.



Figur 13 Predicted proportion of active ODBA (precipitation:snow presence)



Figur 14 Predicted proportion of active ODBA (temperature:snow presence)

3.5.24.5.2 Daily Proportion Active with Continuous Snow Depth

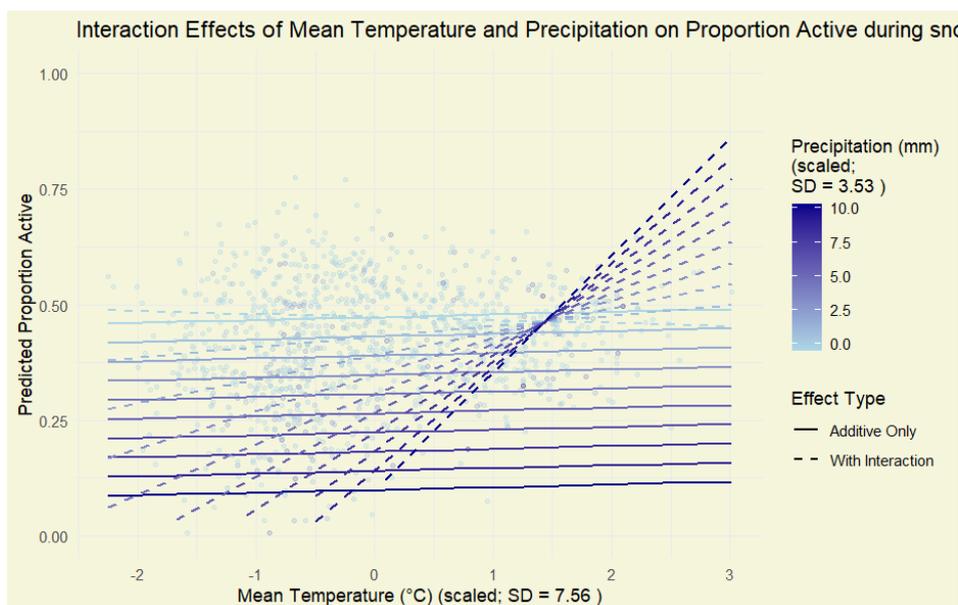
Model Summary: Daily Proportion Active with Snow Depth (mod3)

Term	Estimate	Std. Error	Statistic	P-value
Intercept	0.431	0.033	12.871	0.000
Scaled Snow Depth	0.002	0.008	0.285	0.776
Scaled Mean Temperature	0.045	0.011	4.221	0.000
Scaled Precipitation	-0.023	0.006	-3.591	0.000
Snow Depth × Mean Temperature	0.004	0.011	0.387	0.699
Snow Depth × Precipitation	0.012	0.006	1.839	0.066

Tabell 4 Daily Proportion Active (Snow continuous)

Like snow presence, snow depth did not significantly affect the proportion of time active ($p = 0.7758$). However, higher mean temperatures were associated with an increase in the proportion of time active ($SE = 0.01, p < 0.0001$; effect size = 0.0448), while precipitation had the opposite effect ($SE = 0.006, p = 0.0004$; effect size = -0.0227).

Despite having conflicting effects separately, during the snow free period, mean temperature and precipitation show a slightly positive synergistic effect ($SE = 0.006, p = 0.0006$; effect size = 0.024); figure 15.



Figur 15 Interaction (mean temperature:precipitation of daily activity)

4.5 Discussion

I asked how daily changes in temperature, snow depth, and precipitation affect red fox activity. In snow-free conditions, higher temperatures reduced activity, but temperature during snowy conditions did effect activity levels as I predicted. I hypothesized that colder temperature may increase activity levels, this was shown to be the case, but only mildly. My results reveal how snow presence and depth, along with other environmental factors, shaped red fox activity and behavior. As predicted, snow significantly reduced total daily activity. However, contrary to my hypothesis, snow depth was not important in this regard but instead the presence or absence of snow played the important role. I also asked how vegetation correlates with activity behavior. As I expected, increased vegetation biomass had a positive influence on both proportion of time spent active and overall activity. Snow depth positively interacted with vegetation biomass, leading to increased activity in vegetated areas, this result was not expected. Precipitation did not have the expected results, with foxes actually increasing overall activity in the presence of rainfall but decreasing during snowfall. I also asked how does human use intensity influence red fox activity? Human use intensity had varying effects. I hypothesized that increasing human use intensity would negatively affect the proportion of time foxes spent being active, but this was not supported by the results. I also hypothesized that human use intensity would have a negative impact on overall activity level, this was supported, however, it was only supported in the absence of snow. However, these relationships shifted with snow: higher temperatures offset snow's suppressive effect on activity, while precipitation further reduced it. Vegetation had a consistent positive effect regardless of snow presence. I hypothesized that these factors would influence activity in complex ways, and that certainly seems to be the case.

Snow presence did not significantly affect the proportion of time spent active, though precipitation reduced it. With snow, higher temperatures increased active time, while snow-free conditions showed a synergistic effect of temperature and precipitation. Overall, my findings illustrate the complex interplay between snow, temperature, precipitation, vegetation, and human use in influencing fox behavior across seasonal changes.

4.15.1 Framing of the Findings

This study captured the influence of snow, temperature, vegetation density, and human area-use intensity on red fox behavior across Varanger, shedding light on how these factors

interact across the landscape. While ODBA measurements can provide a useful proxy for activity levels, they do not capture the nuanced, moment-to-moment conditions each fox encounters. Thus, my results should be interpreted within a broader landscape-level context rather than as specific responses to precise conditions. For example, the presence of X cm of snow on the landscape serves as an indicator of general conditions that correlate with observed activity trends, rather than a direct predictor of fox behavior at that specific snow depth. This approach allows us to interpret red fox behavior as part of a larger ecological framework in response to seasonal shifts and changing landscape conditions.

4.25.2 Environmental Interactions and Seasonal Variability

The observed reduction in overall activity among red foxes during snow presence suggests an adaptive strategy to conserve energy under winter conditions. As a physical obstruction, snow imposes energetic costs for total daily activity, necessitating that animals either minimize travel or follow paths of least resistance to maintain energetic efficiency. This behavior is consistent with observations of red fox in other areas. Halpin & Bissonette (1988) documented that snow depth influenced habitat selection by red foxes in Maine, USA, by physically following fox trails over two winters without the benefit of electronic biologging. They noted that habitats with snow crust conditions were preferred by foxes, likely due to decreased snow sinking. Thus, their study sets a precedent in red fox research that snow depth alone does not tell a whole story. Indeed, my results seem to agree as the presence of snow had a negative effect on overall activity, but snow depth itself did not reflect significantly in the mean ODBA readings. If deep snow were consistently physically impeding fox total daily activities, I would expect overall activity to drop measurably with presence of snow on the landscape, but also increasingly with added snow depth. However, this expectation is complicated by the fact that in Varanger, snow depth is heavily influenced by wind, and it is difficult to relate the actual snow depth at any given point to the broad daily scale snow depth data at a 1 km grid. Finding that the landscape level snow depth had a different result than expected suggests that foxes behaviorally adjust to deal with deep snow at the landscape level; by choosing to travel along ridges where snow accumulation is less, for example. Similarly, Murray and Boutin (1991) found that coyotes in Yukon, Canada, exhibited stronger behavioral patterns to reduce locomotive costs than the more snow adapted lynx (*Lynx canadensis*) in sympatry by preferring areas with hard-packed or shallow snow at varying elevations and it is worth considering that foxes might make similar choices in Varanger.

Interestingly, despite the reduction in overall activity, the proportion of time red foxes spent being active (ODBA > 94.5) did not significantly change with either snow presence or depth. This suggests that while foxes may adjust their total daily activity strategies to contend with snowy conditions, they maintain something of a consistent time budget overall. This conflicts with my hypothesis that increased seasonal darkness associated with the snow season would increase the amount of time foxes spent being active in accordance with their typically nocturnal nature. However, given that the snow season only partially corresponds with the darkest periods in Varanger, with snow sometimes arriving later in fall and lingering well into spring. Additionally, foxes might only be as active as necessary based on seasonal needs, such as territory defense, mating, and pup-rearing, which could vary across both snowy and snow-free periods. These seasonal behaviors may reduce the effect of snow on overall activity.

This study did not investigate the specific composition of this active time. For example, how frequently foxes stop to rest in between periods of activity, or how long those individual periods of activity last were not addressed, and questions around circadian plasticity in foxes in Varanger remain. Kämmerle et al. (2020) highlight this type of circadian plasticity, observing that red foxes adjust their circadian patterns seasonally in response to human presence, showing increased daytime activity in winter when human disturbances decrease, leaving questions about polar night and polar days' influence on foxes in Varanger open for future investigation. An additional alternative to consider is that foraging might become more challenging with snow, which could theoretically demand higher activity levels; however, this study did not find evidence of increased activity during snowy periods, suggesting that snow did not substantially affect foraging difficulty. This capacity for adaptive reallocation of time means that red foxes may similarly optimize the composition of their active time in the presence of snow without changing the overall time budget.

Temperature further influences red fox activity by adding another layer of seasonal behavioral adjustment. In snow-covered conditions, warmer temperatures slightly increased overall activity without, suggesting that foxes move more freely on warmer snow-cover days than on colder snow-cover days perhaps to take advantage of lower thermoregulatory demands to increase foraging time across more territory during the relatively more resource scarce winters. Gosselink et al. (2003) noted increased home range sizes in foxes in Illinois, USA, during winter suggesting the need to cover more territory to compensate for resource scarcity. Conversely, in snow-free conditions, higher temperatures correlate with reduced activity, suggesting that foxes may decrease total daily activity to avoid potential overheating, even in

subarctic and arctic climates. These findings underscore the role of temperature and snow as complex and sometimes conflicting forces shaping red fox behavior across seasons.

4.35.3 Role of Vegetation Density in Activity and Foraging

The correlation between high dense vegetation and increased red fox activity suggests that vegetation serves as a multifaceted resource, providing benefits beyond direct access to prey. In winter, dense vegetation might serve as a buffer, offering relatively sheltered areas from wind and extreme conditions in Varanger's exposed landscape. Importantly, areas with dense vegetation are also likely to support a higher abundance of prey. For instance, tundra voles (*Microtus oeconomus*) frequently inhabit willow thickets, as highlighted by Henden et al. (2011), while willow thickets also attract ptarmigan and hare in winter, as shown by Ehrich et al. (2012). These vegetated patches, therefore, may provide foxes with improved hunting grounds in winter, aiding in their energy management by centralizing hunting efforts.

While vegetation had considerable influence on overall activity from vegetation. This interaction implies that vegetation acts as a conditional resource in the presence of deep snow. Ellington et al. (2020) found that coyotes alter their behavior and habitat selection at multiple temporal and spatial scales.

The complexity of these interactions reflects the adaptive strategies red foxes may employ to navigate seasonal challenges, suggesting that vegetation and temperature create dynamic opportunities for behavioral flexibility within snowy landscapes. Such plasticity likely enables red foxes to balance energy conservation with the need for total daily activity under fluctuating environmental conditions, showing how multiple factors work synergistically to shape their activity levels.

4.45.4 Human Influence

In snow-free conditions, red foxes in Varanger showed a significant decrease in activity levels in areas with high human use intensity, aligning with findings by Gorman et al. (2024) that carnivores, such as coyotes and bobcats (*Lynx rufus*), adopt species-specific spatial strategies to minimize disturbance in human-modified landscapes. However, it is worth noting that foxes in Varanger are not simply avoiding these areas; instead, as suggested by recent findings by Stijn Hofhuis (personal communication), they show a degree of positive selection for areas close to human infrastructure, even if their activity levels are reduced. This decrease

in activity might reflect an adaptive strategy to minimize direct encounters with humans during peak recreational periods, such as summer and early fall, when hiking, hunting, and holiday home use are at their height in Varanger and Norway in general. In contrast, during snow-covered periods, the effect of human use intensity on overall fox activity was nearly null, suggesting seasonal variation in their behavioral responses to human presence.

This seasonal difference may also be influenced by human-associated resources in Varanger. Alexandre et al. (2020) found that in places where foxes are sympatric with humans, human resources often drive their presence. Similarly, foxes in Varanger may be drawn to hunting camps and holiday homes at the beginning of the snow season, particularly if waste is not properly disposed of. Scavenging opportunities in these areas could draw foxes back even in the absence of humans, reinforcing site fidelity to locations offering food subsidies. Exploring this dynamic further, such as through camera trap studies in collaboration with holiday homeowners, could provide more nuanced insights into how foxes interact with human-modified landscapes and resources.

4.55.5 Precipitation and Behavioral Adaptations

The influence of precipitation on red fox activity patterns varied considerably across seasons, with distinct differences observed between snow-free and snow-covered periods. The surprising positive effect of precipitation on overall activity during snow-free periods, contrasting with its negative impact during snow-covered periods, suggests that red foxes respond differently to rainfall and snowfall.

During snow-free periods, precipitation correlated positively with mean ODBA, indicating that red foxes increase their activity despite, or perhaps because of, intermittent rainfall. This response could be related to changes in prey behavior or availability during rainy conditions. For example, light to moderate rainfall can stimulate activity in small mammal prey (Vickery & Bider 1981), potentially prompting foxes to exploit these windows of increased prey activity; suggesting that, under snow-free conditions, foxes use rainfall as an opportunity rather than an impediment. Here it is important to consider the temporal scale of the environmental data again. Weather conditions in Varanger can shift quite rapidly, and it is rare to have periods of rain for 24 hours. This means that foxes may be emerging in the

periods after rainfall as opposed to during the rainfall, while still taking advantage of the precipitation effects on prey.

Conversely, during snow-covered periods, precipitation had a negative effect on overall activity that was significantly different from the snow-free period, indicating reduced activity during snowfall specifically. Notably, when snow depth was modeled as a continuous variable, it had no significant effect on mean ODBA; this implies that the immediate effects of active snowfall on activity are more influential than accumulated snow depth alone in this regard. Research by Droghini and Boutin (2018) came to similar conclusions about gray wolves in Canada, finding that it was snowfall, and perhaps the soft conditions of fresh snow before it has been wind packed or crusted, and not snow accumulation per se that reduced total daily activity rates, though accumulation of snow on the animal itself probably has a thermoregulatory cost. Unlike rain, which may be exploited during snow-free times, snowfall is more likely to disrupt hunting success by obscuring prey trails and increasing energy expenditure for total daily activity (Patterson & Messier, 2001; Callaghan et al. 2012). The reduction in the proportion of time active during snow-covered periods with increased precipitation, despite temperature's positive influence, indicate that foxes prioritize energy conservation over activity during snowfall.

Temperature's influence on red fox activity varied between snow-free and snow-covered conditions as well. Mean temperature was not a significant predictor of activity during snow-covered periods, yet it positively affected the proportion of active time, suggesting that warmer temperatures within snowy periods encourage red foxes to remain active longer, potentially compensating for limited foraging success under colder, snowy conditions. Warmer conditions can reduce thermoregulatory costs, making extended activity less energetically taxing (Aublet et al., 2009). This pattern may be particularly important as red foxes face colder periods with decreased prey availability; the temperature effect implies an adaptive response where foxes attempt to maximize active time and forage when temperatures permit, despite overall challenging snow conditions. In snow-free conditions, the interaction of temperatures and precipitation slightly increased the proportion of time red foxes remained active. Similar to the effects of rainfall noted earlier, increased rodent activity as a result of rainfall may be that much more pronounced at warmer temperatures as small rodents are even more susceptible to heat loss than foxes due to basic surface area to volume principles. This

interaction suggests that, although temperature and precipitation individually have opposing effects, together they may create favorable foraging condition, thereby encouraging active behavior.

Overall, these results underscore the nuanced behavioral flexibility of red foxes in adapting to Arctic environmental conditions. This flexibility may serve as a crucial adaptive mechanism as Arctic climates experience increasingly variable precipitation patterns. The distinct responses to rain versus snow suggest that red foxes actively assess environmental cues, adjusting their behavior to maintain foraging efficiency and energy balance. Future studies could benefit from examining how shifting precipitation and temperature patterns, influenced by climate change, may affect the availability of prey, or alter the spatial distribution of favorable habitats for foraging, potentially further challenging red fox adaptability in these dynamic Arctic ecosystems.

4.65.6 Future Research Directions

This study's findings emphasize the need for biologging at finer spatial and temporal scales to capture more detailed insights into red fox total daily activity and habitat use in this landscape. Future research could benefit from gathering more frequent position data alongside additional environmental variables, such as wind speed and terrain models. Analyzing fox activity at sub-daily scales, even with the current data, could also provide valuable insights. For example, examining activity levels within a time window around each recorded position could reveal more immediate behavioral responses to fluctuating environmental conditions, such as sudden temperature drops or shifts in wind direction. This finer resolution would allow us to detect patterns in activity or rest periods in relation to specific terrain conditions such as vegetation density or terrain changes, such as foxes seeking shelter during wind events or moving more actively through particular topographies. Ultimately, such an approach would clarify how foxes adjust their activity decisions throughout the day.

Given the distinct seasonal light conditions in this study area, further exploration of circadian plasticity in red foxes would add valuable context to my findings. In this study, we used season as a random effect to account for extreme light cycles; however, a focused investigation into seasonal time budgeting and circadian adjustments, again using ODBA as a

proxy, could reveal how or if these animals adapt their activity in response to shifting photoperiods.

Using collar-mounted cameras presents an exciting opportunity to gain direct, real-time visual data on habitat use and behavior. This tool could reveal specific habitat features, foraging techniques, and potential interactions with human infrastructure. By complementing biologging data, these observations would deepen our understanding of how foxes navigate and respond to their environment, providing a more holistic view of their spatial decisions.

4.75.7 Conclusions and Management Implications

While there was no single definitive driver of red fox behavior in my findings, vegetation biomass played a critical role, with higher vegetation levels correlating with increased fox activity, regardless of snow cover. The patterns observed in this data support the consensus that as the Arctic warms and vegetation proliferates, resource availability and suitable habitat may increasingly support red fox and other traditionally boreal species warranting further research into long-term impacts on Arctic ecosystems by climate change.

Given the findings, two key areas for management emerge: the effects of vegetation on fox activity and the influence of human area use intensity. Vegetation appears to play a stabilizing role in fox activity patterns, increasing activity even in snow-covered periods, and also interacting with other factors. Thus, strategies to limit vegetation cover could help to manage red fox presence.

Human area use also affects fox behavior significantly, particularly during the snow-free period. Foxes were less active in areas of high human activity, possibly due to two factors: either a decreased need for activity, as they may access human waste as a food source, or human avoidance. The human infrastructure index here includes a range of infrastructure types, from seasonal cabins to year-round structures such as roads, farms, and villages, which remain active throughout the year. In winter, however, foxes became more active around certain areas with infrastructure, potentially taking advantage of resources left unsecured after human departure from seasonal locations. These insights underscore the importance of securing waste and discouraging direct feeding of foxes, a known issue in Varanger and elsewhere. Efforts to reduce human-mediated food subsidies could mitigate some of the pressures contributing to red fox expansion.

In addition to general habitat management, targeted control efforts, such as culling, could be enhanced by focusing on areas where vegetation and other features facilitate high fox activity. For instance, identifying transit corridors and microhabitats with sufficient vegetation cover might improve the efficacy of such efforts. By refining management actions around these vegetation-linked activity hotspots, conservation measures can be more precise, potentially reducing the impact of red fox expansion on native Arctic species, like the Arctic fox, without broad disturbance to the tundra ecosystem.

Works cited

- Alexandre, Marta, Dário Hipólito, Eduardo Ferreira, Carlos Fonseca, and Luís Miguel Rosalino. 2020. "Humans Do Matter: Determinants of Red Fox (*Vulpes Vulpes*) Presence in a Western Mediterranean Landscape." *Mammal Research* 65(2): 203–14. doi:[10.1007/s13364-019-00449-y](https://doi.org/10.1007/s13364-019-00449-y).
- Aublet, Jean-François, Marco Festa-Bianchet, Domenico Bergero, and Bruno Bassano. 2009. "Temperature Constraints on Foraging Behaviour of Male Alpine Ibex (*Capra Ibex*) in Summer." *Oecologia* 159(1): 237–47. doi:[10.1007/s00442-008-1198-4](https://doi.org/10.1007/s00442-008-1198-4).
- Bailey, Derek W., John E. Gross, Emilio A. Laca, Larry R. Rittenhouse, Michael B. Coughenour, David M. Swift, and Phillip L. Sims. 1996. "Mechanisms That Result in Large Herbivore Grazing Distribution Patterns." *Journal of Range Management* 49(5): 386. doi:[10.2307/4002919](https://doi.org/10.2307/4002919).
- Baker, Philip J., Stephan M. Funk, Stephen Harris, and Piran C.L. White. 2000. "Flexible Spatial Organization of Urban Foxes, *Vulpes Vulpes*, before and during an Outbreak of Sarcoptic Mange." *Animal Behaviour* 59(1): 127–46. doi:[10.1006/anbe.1999.1285](https://doi.org/10.1006/anbe.1999.1285).
- Bartoń, Kamil A., and Andrzej Zalewski. 2007. "Winter Severity Limits Red Fox Populations in Eurasia." *Global Ecology and Biogeography* 16(3): 281–89. doi:[10.1111/j.1466-8238.2007.00299.x](https://doi.org/10.1111/j.1466-8238.2007.00299.x).
- Brown, Danielle D, Roland Kays, Martin Wikelski, Rory Wilson, and A Klimley. 2013. "Observing the Unwatchable through Acceleration Logging of Animal Behavior." *Animal Biotelemetry* 1(1): 20. doi:[10.1186/2050-3385-1-20](https://doi.org/10.1186/2050-3385-1-20).
- Bryce, Authors: Caleb M, Michael S Davis, Matthew E Gompper, Aimee Hurt, Jeremy M Koster, Greger Larson, Elaine A Ostrander, et al. 2021. "Biology's Best Friend: Bridging Disciplinary Gaps to Advance Canine Science." *Integrative and Comparative Biology*: icab072. doi:[10.1093/icb/icab072](https://doi.org/10.1093/icb/icab072).
- Bryce, Caleb M., Carolyn E. Dunford, Anthony M. Pagano, Yiwei Wang, Bridget L. Borg, Stephen M. Arthur, and Terrie M. Williams. 2022. "Environmental Correlates of Activity and Energetics in a Wide-Ranging Social Carnivore." *Animal Biotelemetry* 10(1): 1. doi:[10.1186/s40317-021-00272-w](https://doi.org/10.1186/s40317-021-00272-w).

- Butler, Andrew R., Bryn E. Evans, Alessio Mortelliti, and Remington J. Moll. 2023. "Forest and Snow Rather than Food or Foe Limit the Distribution of a Generalist Mesocarnivore in Winter." *Ecosphere* 14(11): e4706. doi:[10.1002/ecs2.4706](https://doi.org/10.1002/ecs2.4706).
- Calhoun, Adam J, and Benjamin Y Hayden. 2015. "The Foraging Brain." *Current Opinion in Behavioral Sciences* 5: 24–31. doi:[10.1016/j.cobeha.2015.07.003](https://doi.org/10.1016/j.cobeha.2015.07.003).
- Callaghan, Terry V., Margareta Johansson, Ross D. Brown, Pavel Ya. Groisman, Niklas Labba, Vladimir Radionov, Raymond S. Bradley, et al. 2011. "Multiple Effects of Changes in Arctic Snow Cover." *AMBIO* 40(S1): 32–45. doi:[10.1007/s13280-011-0213-x](https://doi.org/10.1007/s13280-011-0213-x).
- Carricondo-Sanchez, David, Gustaf Samelius, Morten Odden, and Tomas Willebrand. 2016. "Spatial and Temporal Variation in the Distribution and Abundance of Red Foxes in the Tundra and Taiga of Northern Sweden." *European Journal of Wildlife Research* 62(2): 211–18. doi:[10.1007/s10344-016-0995-z](https://doi.org/10.1007/s10344-016-0995-z).
- Carricondo-Sanchez, David, Barbara Zimmermann, Petter Wabakken, Ane Eriksen, Cyril Milleret, Andrés Ordiz, Ana Sanz-Pérez, and Camilla Wikenros. 2020. "Wolves at the Door? Factors Influencing the Individual Behavior of Wolves in Relation to Anthropogenic Features." *Biological Conservation* 244: 108514. doi:[10.1016/j.biocon.2020.108514](https://doi.org/10.1016/j.biocon.2020.108514).
- Charnov, Eric L. 1976. "Optimal Foraging, the Marginal Value Theorem." *Theoretical Population Biology* 9(2): 129–36. doi:[10.1016/0040-5809\(76\)90040-X](https://doi.org/10.1016/0040-5809(76)90040-X).
- Chmura, Helen E., Thomas W. Glass, and Cory T. Williams. 2018. "Biologging Physiological and Ecological Responses to Climatic Variation: New Tools for the Climate Change Era." *Frontiers in Ecology and Evolution* 6: 92. doi:[10.3389/fevo.2018.00092](https://doi.org/10.3389/fevo.2018.00092).
- Collins, Philip M., Jonathan A. Green, Victoria Warwick-Evans, Stephen Dodd, Peter J. A. Shaw, John P. Y. Arnould, and Lewis G. Halsey. 2015. "Interpreting Behaviors from Accelerometry: A Method Combining Simplicity and Objectivity." *Ecology and Evolution* 5(20): 4642–54. doi:[10.1002/ece3.1660](https://doi.org/10.1002/ece3.1660).
- Crooks, Kevin R., and Michael E. Soulé. 1999. "Mesopredator Release and Avifaunal Extinctions in a Fragmented System." *Nature* 400(6744): 563–66. doi:[10.1038/23028](https://doi.org/10.1038/23028).
- Davis, Grace H., Margaret C. Crofoot, and Damien R. Farine. 2022. "Using Optimal Foraging Theory to Infer How Groups Make Collective Decisions." *Trends in Ecology & Evolution* 37(11): 942–52. doi:[10.1016/j.tree.2022.06.010](https://doi.org/10.1016/j.tree.2022.06.010).

DeAngelis, Donald L., and Wolf M. Mooij. 2005. "Individual-Based Modeling of Ecological and Evolutionary Processes." *Annual Review of Ecology, Evolution, and Systematics* 36(1): 147–68. doi:[10.1146/annurev.ecolsys.36.102003.152644](https://doi.org/10.1146/annurev.ecolsys.36.102003.152644).

Dlugosz, Elizabeth M., Mark A. Chappell, Thomas H. Meek, Paulina Szafrńska, Karol Zub, Marek Konarzewski, James H. Jones, et al. 2013. "Phylogenetic Analysis of Mammalian Maximal Oxygen Consumption during Exercise." *Journal of Experimental Biology*: jeb.088914. doi:[10.1242/jeb.088914](https://doi.org/10.1242/jeb.088914).

Droghini, Amanda, and Stan Boutin. 2018. "The Calm during the Storm: Snowfall Events Decrease the Movement Rates of Grey Wolves (*Canis Lupus*)" ed. Joseph K. Bump. *PLOS ONE* 13(10): e0205742. doi:[10.1371/journal.pone.0205742](https://doi.org/10.1371/journal.pone.0205742).

Dunford, Carolyn E., Nikki J. Marks, Christopher C. Wilmers, Caleb M. Bryce, Barry Nickel, Lisa L. Wolfe, D. Michael Scantlebury, and Terrie M. Williams. 2020. "Surviving in Steep Terrain: A Lab-to-Field Assessment of Locomotor Costs for Wild Mountain Lions (*Puma Concolor*)." *Movement Ecology* 8(1): 34. doi:[10.1186/s40462-020-00215-9](https://doi.org/10.1186/s40462-020-00215-9).

Ehrich, Dorothée, John-André Henden, Rolf Anker Ims, Lilyia O. Doronina, Siw Turid Killengren, Nicolas Lecomte, Ivan G. Pokrovsky, et al. 2012. "The Importance of Willow Thickets for Ptarmigan and Hares in Shrub Tundra: The More the Better?" *Oecologia* 168(1): 141–51. doi:[10.1007/s00442-011-2059-0](https://doi.org/10.1007/s00442-011-2059-0).

Ellington, E. Hance, Erich M. Muntz, and Stanley D. Gehrt. 2020. "Seasonal and Daily Shifts in Behavior and Resource Selection: How a Carnivore Navigates Costly Landscapes." *Oecologia* 194(1–2): 87–100. doi:[10.1007/s00442-020-04754-1](https://doi.org/10.1007/s00442-020-04754-1).

Elmhagen, Bodil, Peter Hellström, Anders Angerbjörn, and Jonas Kindberg. 2011. "Changes in Vole and Lemming Fluctuations in Northern Sweden 1960–2008 Revealed by Fox Dynamics." *Annales Zoologici Fennici* 48(3): 167–79. doi:[10.5735/086.048.0305](https://doi.org/10.5735/086.048.0305).

Elmhagen, Bodil, Jonas Kindberg, Peter Hellström, and Anders Angerbjörn. 2015. "A Boreal Invasion in Response to Climate Change? Range Shifts and Community Effects in the Borderland between Forest and Tundra." *AMBIO* 44(S1): 39–50. doi:[10.1007/s13280-014-0606-8](https://doi.org/10.1007/s13280-014-0606-8).

Elmhagen, Bodil, Magnus Tannerfeldt, and Anders Angerbjörn. 2002. "Food-Niche Overlap between Arctic and Red Foxes." *Canadian Journal of Zoology* 80(7): 1274–85. doi:[10.1139/z02-108](https://doi.org/10.1139/z02-108).

- Elmhagen, Bodil, Magnus Tannerfeldt, Paolo Verucci, and Anders Angerbjörn. 2000. "The Arctic Fox (*Alopex Lagopus*): An Opportunistic Specialist." *Journal of Zoology* 251(2): 139–49. doi:[10.1111/j.1469-7998.2000.tb00599.x](https://doi.org/10.1111/j.1469-7998.2000.tb00599.x).
- Fortin, Daniel, Hawthorne L. Beyer, Mark S. Boyce, Douglas W. Smith, Thierry Duchesne, and Julie S. Mao. 2005. "WOLVES INFLUENCE ELK MOVEMENTS: BEHAVIOR SHAPES A TROPHIC CASCADE IN YELLOWSTONE NATIONAL PARK." *Ecology* 86(5): 1320–30. doi:[10.1890/04-0953](https://doi.org/10.1890/04-0953).
- Fuglei, Eva, Dorothee Ehrich, Siw T. Killengreen, Anna Y. Rodnikova, Aleksandr A. Sokolov, and Åshild Ø. Pedersen. 2017. "Snowmobile Impact on Diurnal Behaviour in the Arctic Fox." *Polar Research* 36(sup1): 10. doi:[10.1080/17518369.2017.1327300](https://doi.org/10.1080/17518369.2017.1327300).
- Gallant, Daniel, Nicolas Lecomte, and Dominique Berteaux. 2020. "Disentangling the Relative Influences of Global Drivers of Change in Biodiversity: A Study of the Twentieth-century Red Fox Expansion into the Canadian Arctic" ed. Marta Rueda. *Journal of Animal Ecology* 89(2): 565–76. doi:[10.1111/1365-2656.13090](https://doi.org/10.1111/1365-2656.13090).
- Gallant, Daniel, Brian G. Slough, Donald G. Reid, and Dominique Berteaux. 2012. "Arctic Fox versus Red Fox in the Warming Arctic: Four Decades of Den Surveys in North Yukon." *Polar Biology* 35(9): 1421–31. doi:[10.1007/s00300-012-1181-8](https://doi.org/10.1007/s00300-012-1181-8).
- Garay, József, Ross Cressman, Fei Xu, Mark Broom, Villó Csiszár, and Tamás F. Móri. 2020. "When Optimal Foragers Meet in a Game Theoretical Conflict: A Model of Kleptoparasitism." *Journal of Theoretical Biology* 502: 110306. doi:[10.1016/j.jtbi.2020.110306](https://doi.org/10.1016/j.jtbi.2020.110306).
- Garde, Baptiste, Rory P. Wilson, Adam Fell, Nik Cole, Vikash Tatayah, Mark D. Holton, Kayleigh A. R. Rose, et al. 2022. "Ecological Inference Using Data from Accelerometers Needs Careful Protocols." *Methods in Ecology and Evolution* 13(4): 813–25. doi:[10.1111/2041-210X.13804](https://doi.org/10.1111/2041-210X.13804).
- Gehrt, Stanley D., Chris Anchor, and Lynsey A. White. 2009. "Home Range and Landscape Use of Coyotes in a Metropolitan Landscape: Conflict or Coexistence?" *Journal of Mammalogy* 90(5): 1045–57. doi:[10.1644/08-MAMM-A-277.1](https://doi.org/10.1644/08-MAMM-A-277.1).

Gese, Eric M., Robert L. Ruff, and Robert L. Crabtree. 1996a. “Foraging Ecology of Coyotes (*Canis Latrans*): The Influence of Extrinsic Factors and a Dominance Hierarchy.” *Canadian Journal of Zoology* 74(5): 769–83. doi:[10.1139/z96-089](https://doi.org/10.1139/z96-089).

Gese, Eric M., Robert L. Ruff, and Robert L. Crabtree. 1996b. “Social and Nutritional Factors Influencing the Dispersal of Resident Coyotes.” *Animal Behaviour* 52(5): 1025–43. doi:[10.1006/anbe.1996.0250](https://doi.org/10.1006/anbe.1996.0250).

Gil-Fernández, Margarita, Robert Harcourt, Thomas Newsome, Alison Towerton, and Alexandra Carthey. 2020. “Adaptations of the Red Fox (*Vulpes Vulpes*) to Urban Environments in Sydney, Australia.” *Journal of Urban Ecology* 6(1): juaa009. doi:[10.1093/jue/juaa009](https://doi.org/10.1093/jue/juaa009).

Gleiss, Adrian C., Rory P. Wilson, and Emily L. C. Shepard. 2011. “Making Overall Dynamic Body Acceleration Work: On the Theory of Acceleration as a Proxy for Energy Expenditure.” *Methods in Ecology and Evolution* 2(1): 23–33. doi:[10.1111/j.2041-210X.2010.00057.x](https://doi.org/10.1111/j.2041-210X.2010.00057.x).

Gomo, Gjermund, Jenny Mattisson, Lars Rød-Eriksen, Nina E. Eide, and Morten Odden. 2021a. “Spatiotemporal Patterns of Red Fox Scavenging in Forest and Tundra: The Influence of Prey Fluctuations and Winter Conditions.” *Mammal Research* 66(2): 257–65. doi:[10.1007/s13364-021-00566-7](https://doi.org/10.1007/s13364-021-00566-7).

Gomo, Gjermund, Jenny Mattisson, Lars Rød-Eriksen, Nina E. Eide, and Morten Odden. 2021b. “Spatiotemporal Patterns of Red Fox Scavenging in Forest and Tundra: The Influence of Prey Fluctuations and Winter Conditions.” *Mammal Research* 66(2): 257–65. doi:[10.1007/s13364-021-00566-7](https://doi.org/10.1007/s13364-021-00566-7).

Gorman, Nicole T., Michael W. Eichholz, Daniel J. Skinner, Peter E. Schlichting, and Guillaume Bastille-Rousseau. 2024. “Carnivore Space Use Behaviors Reveal Variation in Responses to Human Land Modification.” *Movement Ecology* 12(1): 51. doi:[10.1186/s40462-024-00493-7](https://doi.org/10.1186/s40462-024-00493-7).

Gosselink, Todd E., Timothy R. Van Deelen, Richard E. Warner, and Mark G. Joselyn. 2003. “Temporal Habitat Partitioning and Spatial Use of Coyotes and Red Foxes in East-Central Illinois.” *The Journal of Wildlife Management* 67(1): 90. doi:[10.2307/3803065](https://doi.org/10.2307/3803065).

- Halpin, Margaret A., and John A. Bissonette. 1988. "Influence of Snow Depth on Prey Availability and Habitat Use by Red Fox." *Canadian Journal of Zoology* 66(3): 587–92. doi:[10.1139/z88-086](https://doi.org/10.1139/z88-086).
- Halsey, L. G., J. A. Green, R. P. Wilson, and P. B. Frappell. 2009. "Accelerometry to Estimate Energy Expenditure during Activity: Best Practice with Data Loggers." *Physiological and Biochemical Zoology* 82(4): 396–404. doi:[10.1086/589815](https://doi.org/10.1086/589815).
- Hamel, S., S.T. Killengreen, J.-A. Henden, N.G. Yoccoz, and R.A. Ims. 2013. "Disentangling the Importance of Interspecific Competition, Food Availability, and Habitat in Species Occupancy: Recolonization of the Endangered Fennoscandian Arctic Fox." *Biological Conservation* 160: 114–20. doi:[10.1016/j.biocon.2013.01.011](https://doi.org/10.1016/j.biocon.2013.01.011).
- Hauser, Donna D. W., Kristin L. Laidre, Kathleen M. Stafford, Harry L. Stern, Robert S. Suydam, and Pierre R. Richard. 2017. "Decadal Shifts in Autumn Migration Timing by Pacific Arctic Beluga Whales Are Related to Delayed Annual Sea Ice Formation." *Global Change Biology* 23(6): 2206–17. doi:[10.1111/gcb.13564](https://doi.org/10.1111/gcb.13564).
- Henden, John-André, Rolf Anker Ims, Nigel Gilles Yoccoz, Raymond Sørensen, and Siw Turid Killengreen. 2011. "Population Dynamics of Tundra Voles in Relation to Configuration of Willow Thickets in Southern Arctic Tundra." *Polar Biology* 34(4): 533–40. doi:[10.1007/s00300-010-0908-7](https://doi.org/10.1007/s00300-010-0908-7).
- Henden, John-André, Audun Stien, Bård-Jørgen Bårdsen, Nigel G. Yoccoz, and Rolf A. Ims. 2014. "Community-wide Mesocarnivore Response to Partial Ungulate Migration" ed. Matthew Hayward. *Journal of Applied Ecology* 51(6): 1525–33. doi:[10.1111/1365-2664.12328](https://doi.org/10.1111/1365-2664.12328).
- Hersteinsson, Pall, and David W. MacDonald. 1992. "Interspecific Competition and the Geographical Distribution of Red and Arctic Foxes *Vulpes Vulpes* and *Alopex Lagopus*." *Oikos* 64(3): 505. doi:[10.2307/3545168](https://doi.org/10.2307/3545168).
- Ims, Rolf A., and Eva Fuglei. 2005. "Trophic Interaction Cycles in Tundra Ecosystems and the Impact of Climate Change." *BioScience* 55(4): 311. doi:[10.1641/0006-3568\(2005\)055\[0311:TICITE\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2005)055[0311:TICITE]2.0.CO;2).
- Ims, Rolf A., Siw T. Killengreen, Dorothee Ehrich, Øystein Flagstad, Sandra Hamel, John-André Henden, Ingrid Jensvoll, and Nigel G. Yoccoz. 2017. "Ecosystem Drivers of an Arctic

Fox Population at the Western Fringe of the Eurasian Arctic.” *Polar Research* 36(sup1): 8. doi:[10.1080/17518369.2017.1323621](https://doi.org/10.1080/17518369.2017.1323621).

Iossa, Graziella, Carl D. Soulsbury, Philip J. Baker, and Stephen Harris. 2008. “Body Mass, Territory Size, and Life-History Tactics in a Socially Monogamous Canid, the Red Fox *Vulpes Vulpes*.” *Journal of Mammalogy* 89(6): 1481–90. doi:[10.1644/07-MAMM-A-405.1](https://doi.org/10.1644/07-MAMM-A-405.1).

Jahren, Torfinn, Morten Odden, John D. C. Linnell, and Manuela Panzacchi. 2020. “The Impact of Human Land Use and Landscape Productivity on Population Dynamics of Red Fox in Southeastern Norway.” *Mammal Research* 65(3): 503–16. doi:[10.1007/s13364-020-00494-y](https://doi.org/10.1007/s13364-020-00494-y).

Johnson, Devin S., Joshua M. London, Mary-Anne Lea, and John W. Durban. 2008. “CONTINUOUS-TIME CORRELATED RANDOM WALK MODEL FOR ANIMAL TELEMETRY DATA.” *Ecology* 89(5): 1208–15. doi:[10.1890/07-1032.1](https://doi.org/10.1890/07-1032.1).

Kämmerle, Jim-Lino, Suzon Rondeaux, and Ilse Storch. 2020. “Circadian Activity Patterns of Red Foxes (*Vulpes Vulpes*) in Montane Forests under Different Culling Regimes.” *Mammal Research* 65(3): 615–19. doi:[10.1007/s13364-020-00496-w](https://doi.org/10.1007/s13364-020-00496-w).

Killengreen, Siw T., Rolf A. Ims, Nigel G. Yoccoz, Kari Anne Bråthen, John-André Henden, and Tino Schott. 2007. “Structural Characteristics of a Low Arctic Tundra Ecosystem and the Retreat of the Arctic Fox.” *Biological Conservation* 135(4): 459–72. doi:[10.1016/j.biocon.2006.10.039](https://doi.org/10.1016/j.biocon.2006.10.039).

Killengreen, Siw T., Nicolas Lecomte, Dorothée Ehrich, Tino Schott, Nigel G. Yoccoz, and Rolf A. Ims. 2011. “The Importance of Marine vs. Human-Induced Subsidies in the Maintenance of an Expanding Mesocarnivore in the Arctic Tundra: *Importance of Subsidies to Mesopredators*.” *Journal of Animal Ecology* 80(5): 1049–60. doi:[10.1111/j.1365-2656.2011.01840.x](https://doi.org/10.1111/j.1365-2656.2011.01840.x).

Killengreen, Siw T., Elise Strømseng, Nigel G. Yoccoz, and Rolf A. Ims. 2012. “How Ecological Neighbourhoods Influence the Structure of the Scavenger Guild in Low Arctic Tundra.” *Diversity and Distributions* 18(6): 563–74. doi:[10.1111/j.1472-4642.2011.00861.x](https://doi.org/10.1111/j.1472-4642.2011.00861.x).

Kimmig, Sophia E., Joscha Beninde, Miriam Brandt, Anna Schleimer, Stephanie Kramer-Schadt, Heribert Hofer, Konstantin Börner, et al. 2020. “Beyond the Landscape: Resistance

Modelling Infers Physical and Behavioural Gene Flow Barriers to a Mobile Carnivore across a Metropolitan Area.” *Molecular Ecology* 29(3): 466–84. doi:[10.1111/mec.15345](https://doi.org/10.1111/mec.15345).

King, Andrew J., and Harry H. Marshall. 2022. “Optimal Foraging.” *Current Biology* 32(12): R680–83. doi:[10.1016/j.cub.2022.04.072](https://doi.org/10.1016/j.cub.2022.04.072).

Lacombe, Simon, Rolf Ims, Nigel Yoccoz, Eivind Flittie Kleiven, Pedro G. Nicolau, and Dorothee Ehrich. 2024. “Effects of Resource Availability and Interspecific Interactions on Arctic and Red Foxes’ Winter Use of Ungulate Carrion in the Fennoscandian low-Arctic Tundra.” *Ecology and Evolution* 14(4): e11150. doi:[10.1002/ece3.11150](https://doi.org/10.1002/ece3.11150).

Lai, Sandra, Chloé Warret Rodrigues, Daniel Gallant, James D Roth, and Dominique Berteaux. 2022. “Red Foxes at Their Northern Edge: Competition with the Arctic Fox and Winter Movements” ed. Michael Cherry. *Journal of Mammalogy* 103(3): 586–97. doi:[10.1093/jmammal/gyab164](https://doi.org/10.1093/jmammal/gyab164).

Landa, Arild, Øystein Flagstad, Veronika Areskoug, John D. C. Linnell, Olav Strand, Kristine Roaldsnes Ulvund, Anne-Mathilde Thierry, Lars Rød-Eriksen, and Nina E. Eide. 2017. “The Endangered Arctic Fox in Norway—the Failure and Success of Captive Breeding and Reintroduction.” *Polar Research* 36(sup1): 9. doi:[10.1080/17518369.2017.1325139](https://doi.org/10.1080/17518369.2017.1325139).

McNaughton, Bruce L., Francesco P. Battaglia, Ole Jensen, Edvard I Moser, and May-Britt Moser. 2006. “Path Integration and the Neural Basis of the ‘Cognitive Map.’” *Nature Reviews Neuroscience* 7(8): 663–78. doi:[10.1038/nrn1932](https://doi.org/10.1038/nrn1932).

Morales, Juan Manuel, Daniel Fortin, Jacqueline L. Frair, and Evelyn H. Merrill. 2005. “Adaptive Models for Large Herbivore Movements in Heterogeneous Landscapes.” *Landscape Ecology* 20(3): 301–16. doi:[10.1007/s10980-005-0061-9](https://doi.org/10.1007/s10980-005-0061-9).

Murray, D. L., and S. Larivière. 2002. “The Relationship between Foot Size of Wild Canids and Regional Snow Conditions: Evidence for Selection against a High Footload?” *Journal of Zoology* 256(3): 289–99. doi:[10.1017/S095283690200033X](https://doi.org/10.1017/S095283690200033X).

Murray, Dennis L., and Stan Boutin. 1991. “The Influence of Snow on Lynx and Coyote Movements: Does Morphology Affect Behavior?” *Oecologia* 88(4): 463–69. doi:[10.1007/BF00317707](https://doi.org/10.1007/BF00317707).

Nathan, Ran, Wayne M. Getz, Eloy Revilla, Marcel Holyoak, Ronen Kadmon, David Saltz, and Peter E. Smouse. 2008. “A Movement Ecology Paradigm for Unifying Organismal

Movement Research.” *Proceedings of the National Academy of Sciences* 105(49): 19052–59. doi:[10.1073/pnas.0800375105](https://doi.org/10.1073/pnas.0800375105).

Nathan, Ran, Orr Spiegel, Scott Fortmann-Roe, Roi Harel, Martin Wikelski, and Wayne M. Getz. 2012. “Using Tri-Axial Acceleration Data to Identify Behavioral Modes of Free-Ranging Animals: General Concepts and Tools Illustrated for Griffon Vultures.” *Journal of Experimental Biology* 215(6): 986–96. doi:[10.1242/jeb.058602](https://doi.org/10.1242/jeb.058602).

Pagano, Anthony M., Todd C. Atwood, George M. Durner, and Terrie M. Williams. 2020. “The Seasonal Energetic Landscape of an Apex Marine Carnivore, the Polar Bear.” *Ecology* 101(3): e02959. doi:[10.1002/ecy.2959](https://doi.org/10.1002/ecy.2959).

Parnesan, Camille, and Gary Yohe. 2003. “A Globally Coherent Fingerprint of Climate Change Impacts across Natural Systems.” *Nature* 421(6918): 37–42. doi:[10.1038/nature01286](https://doi.org/10.1038/nature01286).

Pasanen-Mortensen, Marianne, Markku Pyykönen, and Bodil Elmhagen. 2013. “Where Lynx Prevail, Foxes Will Fail – Limitation of a Mesopredator in E Urasia.” *Global Ecology and Biogeography* 22(7): 868–77. doi:[10.1111/geb.12051](https://doi.org/10.1111/geb.12051).

Patterson, Allison, Hugh Grant Gilchrist, Lorraine Chivers, Scott Hatch, and Kyle Elliott. 2019. “A Comparison of Techniques for Classifying Behavior from Accelerometers for Two Species of Seabird.” *Ecology and Evolution* 9(6): 3030–45. doi:[10.1002/ece3.4740](https://doi.org/10.1002/ece3.4740).

Patterson, B. R., and F. Messier. 2001. “Social Organization and Space Use of Coyotes in Eastern Canada Relative to Prey Distribution and Abundance.” *Journal of Mammalogy* 82(2): 463–77. doi:[10.1093/jmammal/82.2.463](https://doi.org/10.1093/jmammal/82.2.463).

Post, Eric, Mads C. Forchhammer, M. Sydonia Bret-Harte, Terry V. Callaghan, Torben R. Christensen, Bo Elberling, Anthony D. Fox, et al. 2009. “Ecological Dynamics Across the Arctic Associated with Recent Climate Change.” *Science* 325(5946): 1355–58. doi:[10.1126/science.1173113](https://doi.org/10.1126/science.1173113).

Qasem, Lama, Antonia Cardew, Alexis Wilson, Iwan Griffiths, Lewis G. Halsey, Emily L. C. Shepard, Adrian C. Gleiss, and Rory Wilson. 2012. “Tri-Axial Dynamic Acceleration as a Proxy for Animal Energy Expenditure; Should We Be Summing Values or Calculating the Vector?” ed. Yan Ropert-Coudert. *PLoS ONE* 7(2): e31187. doi:[10.1371/journal.pone.0031187](https://doi.org/10.1371/journal.pone.0031187).

- Rast, Wanja, Sophia Elisabeth Kimmig, Lisa Giese, and Anne Berger. 2020. "Machine Learning Goes Wild: Using Data from Captive Individuals to Infer Wildlife Behaviours" ed. Christopher M. Danforth. *PLOS ONE* 15(5): e0227317. doi:[10.1371/journal.pone.0227317](https://doi.org/10.1371/journal.pone.0227317).
- Rød-Eriksen, Lars, Siw T. Killengreen, Dorothee Ehrich, Rolf A. Ims, Ivar Herfindal, Arild M. Landa, and Nina E. Eide. 2023. "Predator Co-occurrence in Alpine and Arctic Tundra in Relation to Fluctuating Prey." *Journal of Animal Ecology* 92(3): 635–47. doi:[10.1111/1365-2656.13875](https://doi.org/10.1111/1365-2656.13875).
- Rodnikova, Anna, Rolf A. Ims, Alexander Sokolov, Gunhild Skogstad, Vasily Sokolov, Victor Shtro, and Eva Fuglei. 2011. "Red Fox Takeover of Arctic Fox Breeding Den: An Observation from Yamal Peninsula, Russia." *Polar Biology* 34(10): 1609–14. doi:[10.1007/s00300-011-0987-0](https://doi.org/10.1007/s00300-011-0987-0).
- Rohner, Christoph, and Charles J. Krebs. 1996. "Owl Predation on Snowshoe Hares: Consequences of Antipredator Behaviour." *Oecologia* 108(2): 303–10. doi:[10.1007/BF00334655](https://doi.org/10.1007/BF00334655).
- Ropert-Coudert, Yan, and Rory P. Wilson. 2005. "Trends and Perspectives in Animal-Attached Remote Sensing." *Frontiers in Ecology and the Environment* 3(8): 437–44. doi:[10.1890/1540-9295\(2005\)003\[0437:TAPIAR\]2.0.CO;2](https://doi.org/10.1890/1540-9295(2005)003[0437:TAPIAR]2.0.CO;2).
- Selonen, Vesa, Pyry Toivonen, and Elina Tuomikoski. 2024. "Invasion in Cold: Weather Effects on Winter Activity of an Alien Mesopredator at Its Northern Range." *European Journal of Wildlife Research* 70(4): 74. doi:[10.1007/s10344-024-01824-0](https://doi.org/10.1007/s10344-024-01824-0).
- Serreze, Mark C., and Jennifer A. Francis. 2006. "The Arctic Amplification Debate." *Climatic Change* 76(3–4): 241–64. doi:[10.1007/s10584-005-9017-y](https://doi.org/10.1007/s10584-005-9017-y).
- Sturm, Matthew, Charles Racine, and Kenneth Tape. 2001. "Increasing Shrub Abundance in the Arctic." *Nature* 411(6837): 546–47. doi:[10.1038/35079180](https://doi.org/10.1038/35079180).
- Tang, Wenwu, and David A. Bennett. 2010. "Agent-based Modeling of Animal Movement: A Review." *Geography Compass* 4(7): 682–700. doi:[10.1111/j.1749-8198.2010.00337.x](https://doi.org/10.1111/j.1749-8198.2010.00337.x).
- Tannerfeldt, Magnus, Bodil Elmhagen, and Anders Angerbjörn. 2002. "Exclusion by Interference Competition? The Relationship between Red and Arctic Foxes." *Oecologia* 132(2): 213–20. doi:[10.1007/s00442-002-0967-8](https://doi.org/10.1007/s00442-002-0967-8).

Tape, Ken, Matthew Sturm, and Charles Racine. 2006. “The Evidence for Shrub Expansion in Northern Alaska and the Pan-Arctic.” *Global Change Biology* 12(4): 686–702.

doi:[10.1111/j.1365-2486.2006.01128.x](https://doi.org/10.1111/j.1365-2486.2006.01128.x).

Tatler, Jack, Shannon E. Currie, Phillip Cassey, Anne K. Scharf, David A. Roshier, and Thomas A. A. Prowse. 2021. “Accelerometer Informed Time-Energy Budgets Reveal the Importance of Temperature to the Activity of a Wild, Arid Zone Canid.” *Movement Ecology* 9(1): 11. doi:[10.1186/s40462-021-00246-w](https://doi.org/10.1186/s40462-021-00246-w).

Tucker, Marlee A., Katrin Böhning-Gaese, William F. Fagan, John M. Fryxell, Bram Van Moorter, Susan C. Alberts, Abdullahi H. Ali, et al. 2018. “Moving in the Anthropocene: Global Reductions in Terrestrial Mammalian Movements.” *Science* 359(6374): 466–69. doi:[10.1126/science.aam9712](https://doi.org/10.1126/science.aam9712).

Turner, Monica G., and Robert H. Gardner. 2015. *Landscape Ecology in Theory and Practice: Pattern and Process*. New York, NY: Springer New York. doi:[10.1007/978-1-4939-2794-4](https://doi.org/10.1007/978-1-4939-2794-4).

Tveraa, Torkild, Audun Stien, Bård-J. Bårdsen, and Per Fauchald. 2013. “Population Densities, Vegetation Green-Up, and Plant Productivity: Impacts on Reproductive Success and Juvenile Body Mass in Reindeer” ed. Gil Bohrer. *PLoS ONE* 8(2): e56450. doi:[10.1371/journal.pone.0056450](https://doi.org/10.1371/journal.pone.0056450).

Vickery, W. L., and J. R. Bider. 1981. “The Influence of Weather on Rodent Activity.” *Journal of Mammalogy* 62(1): 140–45. doi:[10.2307/1380484](https://doi.org/10.2307/1380484).

Walker, Donald A., Martha K. Raynolds, Fred J.A. Daniëls, Eythor Einarsson, Arve Elvebakk, William A. Gould, Adrian E. Katenin, et al. 2005. “The Circumpolar Arctic Vegetation Map.” *Journal of Vegetation Science* 16(3): 267–82. doi:[10.1111/j.1654-1103.2005.tb02365.x](https://doi.org/10.1111/j.1654-1103.2005.tb02365.x).

Wilkinson, Caitlin, Jan Vigués, Marianne Stoessel, Mikael Vinka, Anders Angerbjörn, and Karin Norén. 2024. “Phase-dependent Red Fox Expansion into the Tundra: Implications for Management.” *The Journal of Wildlife Management* 88(4): e22569. doi:[10.1002/jwmg.22569](https://doi.org/10.1002/jwmg.22569).

Williams, Cory T., Michael J. Sheriff, Joel A. Schmutz, Franziska Kohl, Øivind Tøien, C. Loren Buck, and Brian M. Barnes. 2011. “Data Logging of Body Temperatures Provides Precise Information on Phenology of Reproductive Events in a Free-Living Arctic

Hibernator.” *Journal of Comparative Physiology B* 181(8): 1101–9. doi:[10.1007/s00360-011-0593-z](https://doi.org/10.1007/s00360-011-0593-z).

Williams, Hannah J., Mark D. Holton, Emily L. C. Shepard, Nicola Largey, Brad Norman, Peter G. Ryan, Olivier Duriez, et al. 2017. “Identification of Animal Movement Patterns Using Tri-Axial Magnetometry.” *Movement Ecology* 5(1): 6. doi:[10.1186/s40462-017-0097-x](https://doi.org/10.1186/s40462-017-0097-x).

Williams, Terrie M., Lisa Wolfe, Tracy Davis, Traci Kendall, Beau Richter, Yiwei Wang, Caleb Bryce, Gabriel Hugh Elkaim, and Christopher C. Wilmers. 2014. “Instantaneous Energetics of Puma Kills Reveal Advantage of Felid Sneak Attacks.” *Science* 346(6205): 81–85. doi:[10.1126/science.1254885](https://doi.org/10.1126/science.1254885).

Wilmers, Christopher C., Barry Nickel, Caleb M. Bryce, Justine A. Smith, Rachel E. Wheat, and Veronica Yovovich. 2015. “The Golden Age of Bio-logging: How Animal-borne Sensors Are Advancing the Frontiers of Ecology.” *Ecology* 96(7): 1741–53. doi:[10.1890/14-1401.1](https://doi.org/10.1890/14-1401.1).

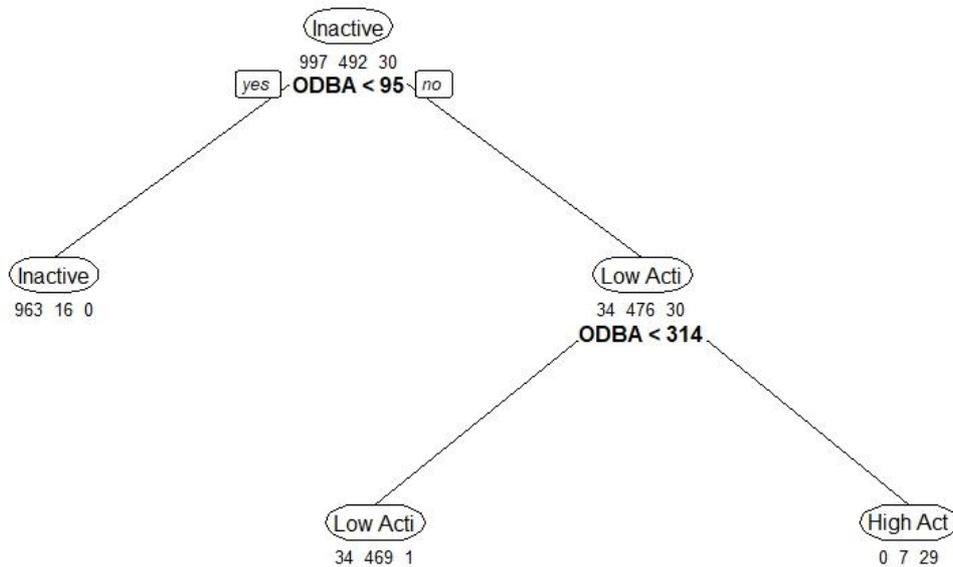
Wilson, Rory P., Luca Börger, Mark D. Holton, D. Michael Scantlebury, Agustina Gómez-Laich, Flavio Quintana, Frank Rosell, et al. 2020. “Estimates for Energy Expenditure in Free-living Animals Using Acceleration Proxies: A Reappraisal” ed. Jean-Michel Gaillard. *Journal of Animal Ecology* 89(1): 161–72. doi:[10.1111/1365-2656.13040](https://doi.org/10.1111/1365-2656.13040).

Yuk, Jisoo, Anupam Pandey, Leena Park, William E. Bemis, and Sunghwan Jung. 2024. “Effect of Skull Morphology on Fox Snow Diving.” *Proceedings of the National Academy of Sciences* 121(19): e2321179121. doi:[10.1073/pnas.2321179121](https://doi.org/10.1073/pnas.2321179121).

Zhang, Jindong, Vanessa Hull, Zhiyun Ouyang, Liang He, Thomas Connor, Hongbo Yang, Jinyan Huang, et al. 2017. “Modeling Activity Patterns of Wildlife Using Time-series Analysis.” *Ecology and Evolution* 7(8): 2575–84. doi:[10.1002/ece3.2873](https://doi.org/10.1002/ece3.2873).

Zhang, Victor Y, Calypso N Gagorik, Lara J Brenner, Christina L Boser, Tad C Theimer, and C Loren Buck. 2022. “Interspecific Asymmetries in Behavioral Plasticity Drive Seasonal Patterns of Temporal Niche Partitioning in an Island Carnivore Community.” *Integrative And Comparative Biology* 62(4): 998–1011. doi:[10.1093/icb/icac113](https://doi.org/10.1093/icb/icac113).

Appendix



Determination of Solar Declination:

The solar declination, which is the angle between the rays of the sun and the plane of the Earth's equator, was computed using the following formula:

$$\delta = \frac{180}{\pi} \times 0.409 \times \sin\left(\frac{2\pi \times \text{day_of_year}}{365} - 1.39\right)$$

where *day_of_year* is the day number within the year.

(Meeus, 1998; Duffie & Beckman, 2013)

Equation of Time:

The equation of time, which accounts for the discrepancy between solar time and clock time, was calculated using:

$$EoT = 229.18 \times (0.000075 + 0.001868 \cos\left(\frac{2\pi \times \text{day_of_year}}{365}\right) - 0.032077 \sin\left(\frac{2\pi \times \text{day_of_year}}{365}\right) - 0.014615 \cos\left(\frac{4\pi \times \text{day_of_year}}{365}\right) - 0.040849 \sin\left(\frac{4\pi \times \text{day_of_year}}{365}\right))$$

(Reda & Andreas, 2004)

Time Correction Factor :

The time correction factor, which adjusts for the equation of time and the geographical longitude, was computed as:

$$TC = 4 \times \text{longitude} - 60 \times \text{timezone} + EoT$$

(Reda & Andreas, 2004)

Local Solar Time:

Local solar time was derived from the time correction factor and the observed time in GMT:

$$LST = \text{hour}(t) \times 60 + \text{minute}(t) + \frac{\text{second}(t)}{60} + \frac{TC}{60}$$

where t is the timestamp of the observation.

(Meeus, 1998)

Hour Angle:

The hour angle, which represents the solar time in degrees, was determined by:

$$H = 15 \times \left(\frac{LST}{60} - 12\right)$$

(Michalsky, 1988)

Solar Elevation Angle:

Finally, the solar elevation angle was calculated using the following trigonometric relation:

$$\alpha = \arcsin\left(\sin\left(\frac{\pi}{180} \times \text{latitude}\right) \times \sin\left(\frac{\pi}{180} \times \delta\right) + \cos\left(\frac{\pi}{180} \times \text{latitude}\right) \times \cos\left(\frac{\pi}{180} \times \delta\right) \times \cos\left(\frac{\pi}{180} \times H\right)\right) \times \frac{180}{\pi}$$

where α is the solar elevation angle, *latitude* is the geographical latitude of the observation, δ is the solar declination, and H is the hour angle.

(Meeus, 1998; Michalsky, 1988)

