Behavioural responses of Canada lynx (*Lynx canadensis*) to cyclic declines in the snowshoe hare (*Lepus americanus*)

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ABSTRACT

Behavioural responses of Canada lynx (*Lynx canadensis*) to cyclic declines in the snowshoe hare (*Lepus americanus*), by Rachael Derbyshire

Population cycles are characterized by predictable temporal oscillations in population size and are influenced by densities of both predators and prey. These oscillations are influenced by the predator functional response, i.e. the influence of prey density on predator kill rate. The Canada lynx (*Lynx canadensis*) is a predatory mammal with cyclic northern populations driven by snowshoe hare (*Lepus americanus*) density. Despite some understanding of the drivers of lynx cycles, we lack understanding of how lynx hunting behaviour, including kill site selection, is influenced by the spatio-temporal distribution of prey. These concepts are explored in chapter one of this thesis.

In chapter two, we (coauthors and I) built on work in Kluane region of the Yukon where lynx and hare populations have been tracked through several population cycles. Over six winters, we deployed GPS collars on >40 individual lynx, some of which were fitted with satellite transmitters, accelerometers, and audio recorders. We validated the use of these technologies for identifying hare kills with an accuracy of >87%. This validation is the foundation for chapter three of this dissertation.

In chapter three, we investigated the drivers of spatial variation in lynx kills. Using snow track transects through four winters of declining hare density, we developed a robust model of habitat-specific hare abundance over time. Using model predictions, in combination with lynx Utilization Distributions derived from GPS locations and related habitat associations, we determined the importance of hare abundance, lynx spatial use, and landscape characteristics such as vegetation density in determining patterns of lynx kills and space use. Lynx kill sites were most strongly predicted by lynx space use, followed by the relative abundance of hares, an index of tree cover density, and elevation. Lynx space use itself was not strongly predicted by hare relative abundance, but rather by a shift to the use of more open habitats when hares were abundant to higher use of denser habitats as hare populations declined; this apparently corresponded to temporal changes in hare distribution. This thesis helps to disentangle the drivers of spatio-temporal variation in predator foraging behaviour, with important implications for understanding predator-prey dynamics.

Keywords: animal behaviour, accelerometer, biologging, Canada lynx, foraging, functional response, habitat selection, *Lepus americanus*, *Lynx canadensis*, population cycles, predator-prey dynamics, snowshoe hare

Preface

Each data chapter (Chapter 2 and 3) is written in manuscript format, either because it has been published in a peer-reviewed journal (Chapter 2) or because the manuscript is in preparation for publication (Chapter 3). Therefore, these chapters are written and formatted according to the style of the journal, but with references for all chapters presented at the end of Chapter 4. Chapter 2 was published in *Methods in Ecology and Evolution* in 2021. It was co-first-authored by me and two other collaborators, Dr. Emily Studd and Dr. Allyson Menzies, who were both PhD Candidates at the time. This co-authorship reflects the significant contributions of all three lead authors to the manuscript; a further explanation of the differing contributions is provided at the beginning of the chapter. Chapter 3 is in preparation for submission to a peer-reviewed scientific journal, and I will be listed as first author on this manuscript. Because all my research has been in collaboration with others, I have used the plural “we” throughout the text of the data chapters and have included the names of all co-authors at the beginning of each chapter.

Acknowledgments

I am truly grateful to a host of people, without whom I would not have been able to complete this dissertation. First and foremost, I would like to extend a huge thank you to my Trent University supervisor, Dr. Dennis Murray. Dennis provided consistent and thoughtful mentorship throughout this entire project, and was invaluable to the development of research questions, methods, and manuscripts, among many other aspects of the dissertation. Under the guidance of Dennis and my co-supervisor, Dr. Stan Boutin (University of Alberta), I was able to execute this comprehensive and collaborative project from a few scraps of ideas floating around in my head. I would also like to thank the third member of my advisory committee, Dr. Jim Shaefer, who always offered insightful feedback and whose kind words and encouragement were incredibly valuable throughout my journey through this PhD.

Outside of my advisory committee, I had tremendous support from several people and organisations that are worth noting here. I would like to thank my fellow “lynx-ologists” Dr. Emily Studd and Dr. Allyson Menzies from McGill University (at the time), who showed me the ropes and helped jump-start my research. They have been important sources of knowledge, wisdom, and friendship along the way. Jacob Seguin provided invaluable support and guidance in the field, and I will never forget our lynx-trapping days in the Yukon. Vital field support was also provided by Heather Sterling, Will Bennett, Emina Ida, Liam Horne, Liam Cowan, Clare Murphy, and Michelle Mjolsness. Assistance with data processing was provided by Carly Scott, Charly Blais, Clare Murphy, Éliane Miranda, Emina Ida, Heather Sterling, Hannah Miller, Holly Faithfull, Jenilee Gobin, Jenna Knight, Jordan Reynolds, Kaitlyn Courchesne, Lee Scholl, Liam Cowan, Liam Horne, Markus King, Megan Brownlee, McGill Casault, Michelle Mjolsness, and Sean Hudson. The Yukon Government, the Champagne and Aishihik First Nations, and the Kluane First Nations provided permissions to work in Kluane and logistical support. While in the

Yukon, I also received assistance and encouragement from Lance Goodwin and Peter Upton. Both amazing men became good friends during my time in the north, and both have since passed away. I can only hope that their work and dedication is reflected in some small way within the pages of this dissertation.

I would like to thank all Murray Lab members, especially Carly Scott, Jenilee Gobin, Melanie Boudreau, Sam Sonnega, and Tucker Cambridge for their friendship, emotional support, and scientific assistance over the last 6 years. I also want to remember and thank Sean Hudson, an incredible person and scientist who was taken from this world far too soon. I miss you, dear friend.

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And finally, to my loving partner, Bruce. You moved with me to Peterborough in 2018 so I could start this PhD, and over that time we have gone from common-law partners, to an engaged couple, and finally to husband and wife. You have supported and buoyed me every step of the way, and for that I am eternally grateful. I truly couldn't have done it without you.

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Chapter 1: General Introduction

Predator-prey dynamics are an integral component of ecological studies since they directly influence population dynamics and the flow of energy through ecosystems (Berryman 1992, Layman et al. 2015). Predators are thought to have a particularly important role in ecosystem dynamics because they can reduce populations of other consumers and exert a “top-down” effect on food webs via numerical and functional responses (Wallach et al. 2010, Amiraux et al. 2023, Zhang et al. 2023). At a fine scale, several aspects of predator behaviour can influence the structure and function of ecosystems through processes such as behavioural responses of prey to predators (Hik 1995, Kauffman et al. 2007, Teckentrup et al. 2018, Mondal and Samanta 2021), prey switching (O’Donoghue et al. 1998a, Kjellander and Nordström 2003, Chan et al. 2017), and apparent competition (Kjellander and Nordström 2003, Ehlers et al. 2016).

In part because of the importance of predators in ecosystem dynamics, there has been longstanding interest in disentangling the drivers of predator behaviour, particularly foraging behaviour. The dynamic nature of prey abundance across the landscape and prey behavioural responses to predators can have a profound impact on predator foraging behaviour such as space use and habitat selection. For example, prey display behavioural tactics that decrease the probability of predation, such as occupying structural or spatial refuges that are difficult to access for predators (Sih 1984, Kauffman et al. 2007, Atwood et al. 2009). When this occurs, predators may not be able to effectively exploit patches of high prey density. Conversely, the need for food and other resources may preclude some prey animals from such refuge use (Hik 1995, Samelius et al. 2013), and per-capita refuge availability may be low, particularly when prey population densities are high (Sih 1987). In these cases, predators may select hunting habitats that increase the ease of hunting regardless of, or even counter to, patterns of prey density, because they are able to meet their energetic requirements without hunting in less accessible patches (Quinn and Cresswell 2004, Balme et al. 2007, DeCesare 2012, Zabihi-Seissan et al. 2022). Landscape characteristics that influence the vulnerability of prey to predation can also mediate predator responses to prey abundance, with many predators selecting landscapes that increase movement rates and/or encounters with prey (Bergman et al. 2006, Dickie et al. 2017, Smith et al. 2019, Zabihi-Seissan et al. 2022). Shifting patterns of prey vulnerability over time can lead to concurrent shifts in predator foraging behaviour, for example, shifting from habitat selection based on prey vulnerability to a tactic that maximizes prey encounter rate (Rayl et al. 2018). Kill site selection may even be decoupled from patches of both high prey density and vulnerability, if the behavioural response race between predators and prey “cancel each other out” (i.e., the response of one actor substantially weakens the efficacy of the behavioural tactics of the other; Sih 1987), or if behavioural shifts related to one predator increase vulnerability to another. For example, Atwood et al. (2009) found that landscape characteristics mediated predation risk for elk (*Cervus elaphus*) by wolves (*Canis lupus*), but landscapes that decreased vulnerability to wolves increased elk vulnerability to cougar (*Puma concolor*) predation. Inherent differences between predator species, even when relying on the same prey, can also play a role in variation in predator responses to fluctuations in prey abundance (O’Donoghue et al. 1998a, Peers et al. 2020, Warret Rodrigues and Roth 2023).

Despite the consequences of predator behaviour for ecosystem dynamics, until relatively recently we had limited understanding of the behaviour of predators in the wild. Before the advent and widespread use of transmitter technology such as VHF and GPS collars, field observations of predator behaviour were logistically challenging and required many person-hours, meaning that sample sizes were often low (Murray et al. 1995, O’Donoghue et al. 1998a). With increased use of GPS transmitters came a more thorough understanding of wildlife behaviour and how it relates to theoretical predictions (Hebblewhite et al. 2005, Hopcraft et al. 2005, Balme et al. 2007, Podgórski et al. 2008), but these field studies were initially limited to larger-bodied animals that could carry the weight of biologging equipment (Cagnacci et al. 2010, Thompson et al. 2012). Thus, inferences drawn from these studies do not necessarily reflect the unique challenges of small or medium-sized predators (mesocarnivores), which have different energetic requirements (Menzies et al. 2022), experience higher levels of intraguild competition and predation (Linnell and Strand 2000, Avrin et al. 2023, Davis et al. 2023, Latafat et al. 2023), and generally consume smaller prey, making it difficult to determine kill behaviour using conventional GPS techniques (Vogt et al. 2018). Moreover, we have a paucity of data on the ecological role of most mesocarnivores (Easter et al. 2020), making it critical to test whether patterns of predator behaviour are consistent across size guilds if we are to build a mechanistic framework for predator behavioural ecology across systems.

The drivers of predator behaviour may be particularly challenging to disentangle in cyclic systems, where large population fluctuations of both predators and prey can obscure the drivers of such behaviour without direct experimentation (Krebs et al. 2018). Population cycles play an important role in ecosystem function by influencing energy flow through food webs and sustaining predator-prey dynamics (Ims et al. 2008, Gilg et al. 2009, Krebs et al. 2018). Importantly, cyclic population changes can influence multiple aspects of animal behaviour such as predator diet (O'Donoghue et al. 1998a, Kjellander and Nordström 2003, Slade et al. 2022), prey behaviour (Hik 1995, Krebs et al. 2001), and predator movements (Mowat et al. 2000). However, we still have a limited understanding of how population dynamics in cyclic systems govern spatial patterns of predator hunting behaviour in the wild. Despite these challenges, population cycles can also provide opportunities to test many questions in the field of foraging ecology using the extremes in population density as a natural experiment.

Study System

The Canada lynx (*Lynx canadensis*; hereafter lynx) is a medium-sized (~10 kg) predatory mammal found throughout the North American boreal forest (Mowat et al. 2000). In the northern part of their range, lynx undergo population cycles that are driven by those of snowshoe hare (*Lepus americanus*; hereafter hare), their primary prey (Slough and Mowat 1996). Lynx are also known to rely on other prey, namely red squirrel (*Tamiasciurus hudsonicus*), during periods of low hare availability (O'Donoghue et al. 1998a). Hares are a keystone species in North American boreal forests, and multiple predators besides lynx including coyote (*Canis latrans*) and great-horned owls (*Bubo* *virginianus*) exhibit population cycles that mirror those of hare in the northern part of their range (Boutin et al. 1995). Moreover, hares have been hypothesized to occupy spatial refuges in the form of dense vegetative cover when predator densities are high, although the efficacy of these refuges may differ depending on the ecology of the predator, e.g. aerial vs. terrestrial predators (Wolff 1980, Hik 1995, Rohner and Krebs 1996).

Previous work suggests that patterns of lynx occupancy, habitat use, and habitat selection are associated with intermediate to high hare abundance, which tend to correlate with regenerating forests and high stem density (Fuller et al. 2007, Squires et al. 2022). Although these studies are useful for understanding lynx behaviour, they do not provide insight into fine-scale hunting behaviours such as kill site selection, which may be distinct from coarser patterns of habitat selection (Bouyer et al. 2015). Since Canada lynx kills cannot be identified with GPS data, rarely has kill site occurrence or spatial patterns of kill site selection been investigated in this species. In studies where kill sites were identified, this was accomplished through snow tracking; thus, individual lynx could not be reliably differentiated, and sample sizes of hare kills were relatively low (Murray et al. 1995: N = 95 kills; O'Donoghue et al. 1998: N = 252 kills over 8 winters; Maletzke et al. 2008: N = 17 kills). Moreover, these studies revealed somewhat ambiguous results about kill site selection, with Murray et al. (1995) suggesting that lynx select open spruce habitat, O'Donoghue et al. (1998) demonstrating a shift in kill habitat from dense to more open habitats as hare populations declined, and Maletzke et al. (2008) concluding that lynx hunt hares in the patches of highest relative hare abundance, which coincided with high stem densities (but note that this conclusion was based on only 17 kills). Our understanding of predator behavioural shifts in this predator-prey system therefore remains incomplete.

Thesis Objectives

In this thesis, I examine the relationships between lynx, snowshoe hare, and the environments in which these predators and prey interact within the context of a cyclic decline in snowshoe hare density. The interactions between predators, prey, and their environment are complex. I contribute to our understanding of these complexities by investigating the foraging behaviour of an elusive mammal, for which limited data on kill behaviour are available. In Chapter 2, I characterize hunting behaviour in Canada lynx by developing and validating classification models to identify hare kills using biologging technologies, including acoustic recorders and accelerometers. In Chapter 3, I use this classification system to identify >1000 hare kills by collared lynx over four winters of declining hare density. I also estimate the relative abundance of snowshoe hares across the study area coincident with this decline, then use this spatiotemporal map of hare abundance, in conjunction with landscape covariates (e.g., vegetation type) and lynx spatial behaviour, to disentangle the drivers of kill sites and patterns of space use in the Canada lynx. I synthesize my findings in Chapter 4, where I explore the wider implications and applications of my work.

Chapter 2: The Purr-fect Catch: using accelerometers and audio recorders to document kill rates and hunting behaviour of a small prey specialist.

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Running Headline: Biologging kill rates of predators.

AUTHORS' CONTRIBUTIONS: E.K.S. and M.M.H. conceived the initial idea of capturing hunting behaviour with accelerometers and S.B. suggested the use of acoustics; all the authors contributed to developing those ideas and provided comments on earlier drafts; E.K.S., A.K.M. and R.E.D. developed the field-based methods and collected the data; E.K.S., J.F.S. and R.E.D. completed the analyses; E.K.S., R.E.D. and A.K.M. wrote the paper.

Abstract

1. Characterizing variation in predator behaviour and, specifically, quantifying kill rates is fundamental for parameterizing predator-prey and food web models. Yet, current methods for recording kill rates of free-ranging predators, particularly those that consume small-bodied (< 2 kg) prey, present several associated challenges.

2. In this paper, we deployed custom-adapted acoustic recorders and tri-axial accelerometers on free-ranging Canada lynx (*Lynx canadensis*) to assess the capacity of biologging devices to continuously document individual kill and feeding behaviour, including prey species consumed and kill rates, on a predator that specializes on prey weighing <2 kg.

3. Classification of acoustic recordings captured 87% of snowshoe hare kills that were identified through snow-tracking (26 of 31 kills). Classification of detailed acceleration recordings summarised over 28 minutes per feeding event captured consumption of snowshoe hare (*Lepus americanus*), but not smaller species, at high accuracy (F1 [a score that combines precision and recall] = 0.96).

4. By summarizing acoustic and accelerometer data for a subset of lynx, we demonstrate the capacity of these devices to document within- and between-individual variation in diet composition (ranging from 40 - 80% snowshoe hares) and daily feeding bouts (ranging from 0 to 3.5 bouts per day).

5. We suggest that acoustic recorders provide a promising method for characterizing several aspects of predator hunting behaviour including prey selection and chase outcomes, while broad-scale accelerometer-based behavioural classifications provide

hare kill rates and fine-scale non-hunting behavioural information. Combined, the two technologies provide a means to remotely document both kills and meals of small-bodied prey, allowing for individual-based exploration of functional responses, predator-prey interactions, and food web dynamics at temporal scales relevant to environmental change.

Keywords: Acoustics, biologging, Canada lynx, hunting behaviour, kill rates, *Lynx canadensis*, predator-prey ecology, tri-axial accelerometer

Introduction

Predator kill rates are an important element of many fundamental theories in ecology. Whether the interest is in documenting functional responses, predator-prey interactions, or population and food web dynamics, understanding and estimating kill rates and hunting success is a necessary component (Lima 2002, Kalinkat et al. 2013, McGhee et al. 2013). In addition to kill rates, estimates of hunting success, kleptoparasitism, and scavenging in natural systems are key to predator energy budgets (Pagano et al. 2018), species interactions (Gorman et al. 1998, Peers et al. 2020), and food web dynamics (Wilson and Wolkovich 2011, Focardi et al. 2017). While current methodological approaches have provided estimates of kill rates and predator behaviour summarized at the population level and over seasonal time frames (O’Donoghue et al. 1998a, Lake et al. 2013), there is considerable interest in documenting predator responses to environmental change at the individual level across short temporal scales, e.g., days, weeks (Bolnick et al. 2011, Pettorelli et al. 2015).

Kill rates are traditionally measured through direct observation, which is restricted to species that are observable from one location thanks to small home ranges, e.g., invertebrates (Uiterwaal et al. 2017), or open habitats (Honer et al. 2002). Tracking is also common but is labour-intensive, and often only produces an average population kill rate across a season or year (O’Donoghue et al. 1998b). A recent major advancement that reduces the need for direct observation involves identifying kill sites through spatial and temporal clustering of GPS locations (Merrill et al. 2010). Although an improvement, this approach still requires visits to kill sites to confirm and identify prey, even after the technology has been validated (McPhee et al. 2012). Additionally, cluster analyses only identify large prey kill sites where the predator spent more time at the site (e.g., hours to days) than other locations (Bacon et al. 2011). This results in missing small prey kills and an overrepresentation of large prey items in predator diets (Jansen et al. 2019, Leighton et al. 2020). Thus, to date, there is no available method for quantifying individual kill rates of small-prey specialists beyond intense field effort (e.g., direct observation, kill site investigations, scat collection).

Recent advances in biologging technology provide opportunities to remotely record behaviour, including hunting, of free-ranging organisms. Accelerometers, which can record acceleration multiple times per second, have been used to generate activity-time budgets of cryptic carnivores, e.g., pumas (Williams et al. 2014), calculate energetic costs (Masello et al. 2017), and aid in quantifying kill rates (Petroelje et al. 2020). However, two major issues impede the widespread application of accelerometers for quantifying kill rates. First, classifications of acceleration work best for behavioural states consisting of repetitive motions, like walking or wing beats (Shepard et al. 2008). But, when a carnivore is feeding, the only clear, repetitive motion comes from movement of the jaw (Iwata et al. 2012). As such, attempts at classifying feeding behaviour with accelerometers are often associated with high error (e.g., 0.34 sensitivity in bobcats, Petroelje et al. 2020; 0.68 precision in polar bears, Pagano et al. 2017). Second, automated classifications often require species- and context-specific observational data to train the models (Campbell et al. 2013, Pagano et al. 2017), which for many cryptic species is not attainable.

In addition to accelerometers, camera collars can capture an individual's behaviour, but the size of battery needed to power these units limit their application to large animals and brief observations (e.g., 1.1 kg collars record 10 sec every 5 min: Thompson et al. 2012; 2.0 kg collars record 5-10 days: Pagano et al 2018). Acoustic recorders, which require less power to operate, might serve a similar purpose for smaller species (5.5 g record 24 hr; Couchoux et al. 2015). While stationary remote acoustic monitoring has provided novel approaches for documenting species presence, distribution and abundance (Hannay et al. 2013), activity levels (Lawson et al. 2019), and conspecific interactions (Welch et al. 1992, Manna et al. 2014), recent attachment or recorders directly to animals has provided novel approaches for recording individual behaviour (Lynch et al. 2013, Ilany et al. 2013, Couchoux et al. 2015) including that of predators (Wijers et al. 2018) and humans (Mirtchouk et al. 2016). As such, acoustic recorders hold great potential to circumvent challenges associated with other methods (Wijers et al. 2018, Studd et al. 2019), and to directly measure hunting behaviour of small – medium-sized predators.

Here, we assess the capacity of small acoustic recorders and accelerometers to characterize the hunting success and kill rates of Canada lynx (*Lynx canadensis*, hereafter lynx), a boreal, small-prey specialist. Lynx (average ~10 kg within our study system) occupy large (~2500 ha) home ranges in densely forested habitats, making them difficult to observe in the wild. In the northern part of their range, their diet is primarily composed of snowshoe hares, a relatively small-bodied prey (< 2 kg), along with smaller red squirrels (*Tamiasciurus hudsonicus*, 200 g) and birds, for example grouse (*Bonasa* *umbellus* and *Canachites canadensis)* and Canada Jays (*Perisoreus canadensis*, < 550 g; O'Donoghue et al. 1998b). The short handling times required to consume these prey preclude the use of GPS cluster analysis to identify kill sites as most clusters are located at resting or grooming sites. But lynx provide an ideal species to test these technologies thanks to the ease at which kill sites can be found through snow-tracking. Thus, lynx present an interesting and important case study for the usefulness of biologging technologies to document kill rates and hunting success of free-ranging predators. If these devices prove useful for identifying kills of small prey by a medium-sized carnivore, they could enable a more complete picture of predatory behaviour and diet for predators of all sizes.

Methods

This research conformed to the guidelines of the American Society of Mammalogists (Sikes and the Animal Care and Use Committee of the American Society of Mammalogists 2016) and was approved by the McGill University, University of Alberta, and Trent University Animal Care and Use Committees, and by the Yukon Government Scientists and Explorers and Yukon Government Wildlife Research Permits (Appendix A1.1)

Biologger Deployment

Canada lynx were live-trapped in southwestern Yukon (61°N, 138°W) between November and April (period corresponding to snow cover) over five winters (2015-2020) in conjunction with a 45-year long-term monitoring and ecological research project

(Krebs et al. 2018). We used custom-made box traps (Kolbe et al. 2003) baited with meat (e.g., road kill), scented lures (e.g., castor, skunk essence), and visual attractants (e.g., tinsel, compact discs). Once captured, lynx were transferred to a wooden crate and transported to a local veterinary clinic (~ 45 km away) where they were chemically immobilized (Appendix A1.2). For all lynx over 6.5 kg (mean mass = 10.1 kg), standard body measurements were taken, and a GPS collar (Telemetry Solutions remote download model [350 g; n = 5]) or Followit Iridium GPS [245 g; n = 34]) with externally mounted self-powered accelerometer (Technosmart Axy 3 or 4; 8 g; n = 39) and acoustic recorder (EDIC-mini tiny E60-1200h, 35 g, n = 27; or SOROKA-14E, 28 g, n = 12) was attached (see Appendix A2.1, Figures A-A1, A-A2 for collar design). Assembled collars were less than 5% of the weight of each animal (Telemetry Solutions: ~393 g, ~4%, mean lynx = 10.0 kg; Followit: ~281 g, ~3%, mean lynx = 10.2 kg)

Snow-tracking

To confirm that biologger-identified hunting behaviour was capturing real events, each winter we visited GPS locations from the previous 2-days (iridium collars only due to the ability to download locations via satellite; approximately 100 – 200 locations per lynx were downloaded at a time) and recorded whether lynx were feeding, travelling, sitting, or bedded down according to the tracks or prey remains in the snow. At kills, we identified prey species according to fur or feathers that remained, and whether it was a fresh kill (only fresh tracks, signs of a chase), or scavenging event (older or other predator tracks). Locations were labelled as unknown when tracks/behaviour were not discernible. For analysis, we categorized each GPS location as “kill” or “no kill” and combined all the consecutive locations of each individual within each category as a single “snow-tracking event”.

Acoustic Data

Two models of acoustic recorders (EDIC-mini or SOROKA-14E) were used over the study with slightly different recording settings (see Appendix A1.1). At selected settings and battery size, EDIC-mini recorded for up to 25 days and SOROKA-14E recorded for up to 49 days. Acoustic data were downloaded in 600 MB - 2GB .wav files for analysis.

Classification and processing of audio files involved multiple steps (Figure 1). We first listened to and transcribed a subset of lynx audio files (n = 18, 24.75 days, from 5 lynx; Figure 1: A1). This established that feeding (bone crunching sounds; Supplementary Materials 4) and chases (Appendix A5, A6) generated unique and distinguishable sounds (Figure 1: A2). We confirmed that our interpretation of feeding sounds was correct with video of free-ranging lynx (Appendix A7) and correlation with kill sites identified by snow-tracking (Appendix A2.2; Figure 1: A3).

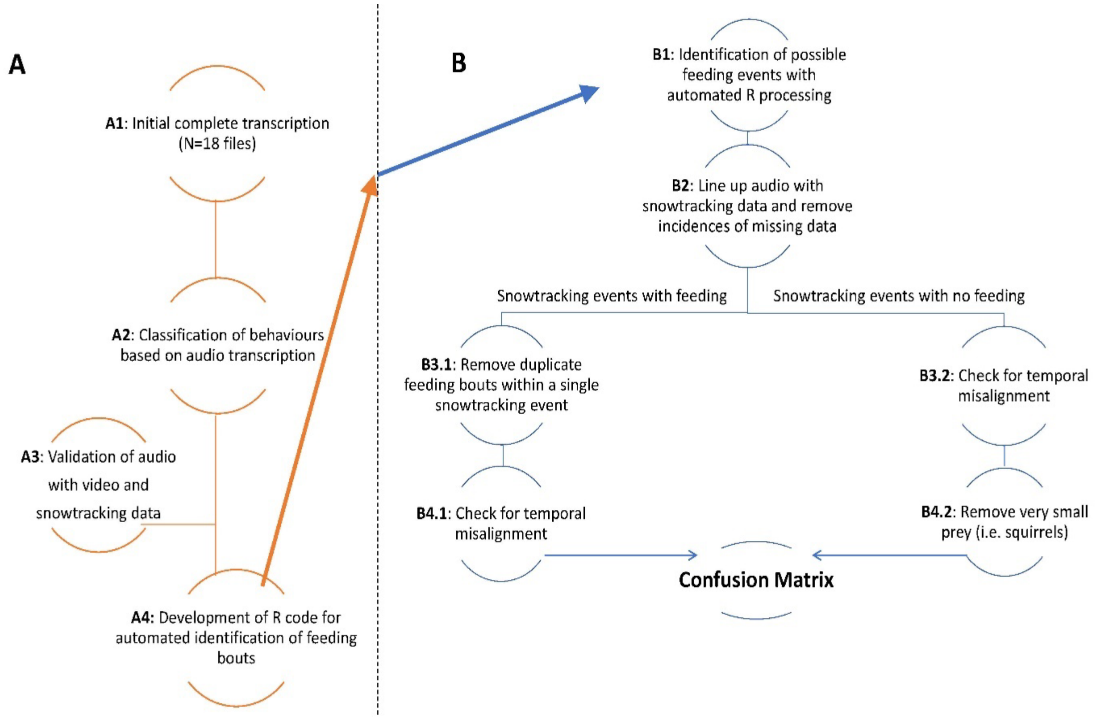

Figure 1: Methodological approach to generating an automated classification of snowshoe hare meals from acoustic data.

We then developed in two steps an automated classification aimed at classifying all audio into feeding and not feeding (Figure 1: A4). First, we determined which acoustic metrics identified feeding from other behavioural states. Using 360 fifteen-second audio clips of feeding, grooming, walking, and not moving from 6 lynx (15 clips per behaviour per lynx) we calculated spectral properties, peak frequency, number of bursts, number of syllables, mean amplitude of syllables, mean amplitude of whole clip, and loudness using *seewave* and *soundgen* (Sueur et al. 2008, Anikin 2019) packages in R. Comparing these metrics between behavioural states revealed that clip loudness and mean amplitude could be used to isolate feeding (Appendix A, Figures A-A3, A-A4). Second, we used a larger sample of individuals (n = 11 x 3 days each) for which we had manually identified all meals (i.e., full feeding events, based on manual processing of audio data) to train a model to automate the identification of meals from the audio. Loudness and amplitude were calculated for every 15 seconds across the three days, and we built a classification algorithm around three criteria. For each acoustic recorder, a clip was labelled as feeding when 1) the loudness was in the *a* percentile or higher of all audio clips, and 2) the mean amplitude was in the *b* percentile or lower of all audio clips. Finally, 3) a meal required *c* audio clips within a 10-minute window to be classified as feeding. To determine which thresholds generated a classification model that best predicted training data, we calculated F1, precision, and recall for each of the 6408 models run across a range of values for *a* (0.5 – 0.95 by 0.05 increments), *b* (0.1 – 0.95 by 0.05 increments), and *c* (5 – 40 clips) parameters (Figure A-A5).

We tested the accuracy of our top model by assessing whether the modelled meals matched known kill sites from snow-tracking (Figure 1B). After lining up extracted feeding bouts with snow-tracking events using *fuzzyjoin* in R (Robinson 2020) and removing any cases where no tracks were found during snow-tracking, we divided snow-tracking events into two subgroups: those with identified feeding bouts, and those without (Figure 1: B2). For events with feeding bouts, we manually combined multiple feeding bouts that were associated with a single snow-tracking event (i.e., were all in the same location based on GPS data; Figure 1: B3.1) and adjusted false negatives caused by slight time misalignment (Figure 1: B4.1, Appendix A2.3). We checked for time misalignment of events with no feeding bouts (Figure 1: B3.2) and removed any kills (e.g., squirrels) that could not have been identified in our 10-minute window due to short feeding times (Figure 1: B4.2). Once data were cleaned we used a confusion matrix in package *caret* (Velez et al. 2007, Kuhn 2008) to calculate the proportion of predicted meals that correspond to true snow-tracking kills (recall); the proportion of predicted non-meals that correspond to non-feeding snow-tracking events (specificity); the proportion of snow-tracking kill events that the model predicted (precision); F1 and overall accuracy.

Lastly, to measure hunting success, we generated an automated classification of chases. Using the fully transcribed audio files as validation data, we determined that chases were distinguishable as the loudest sounds (Figure A-A3). Using *seewave*, we calculated the mean amplitude of sound over 2 seconds for each second of recording, and extracted all sounds that were louder than 30% (in all years except 2019-2020) or 20% (SOROKA recorders in 2019-2020 due changed microphone settings) of the maximum amplitude recorded in that file. This threshold tagged <1% of audio (~33 of 8931 hours) and captured 94.5 % of 109 chases in the scored audio files.

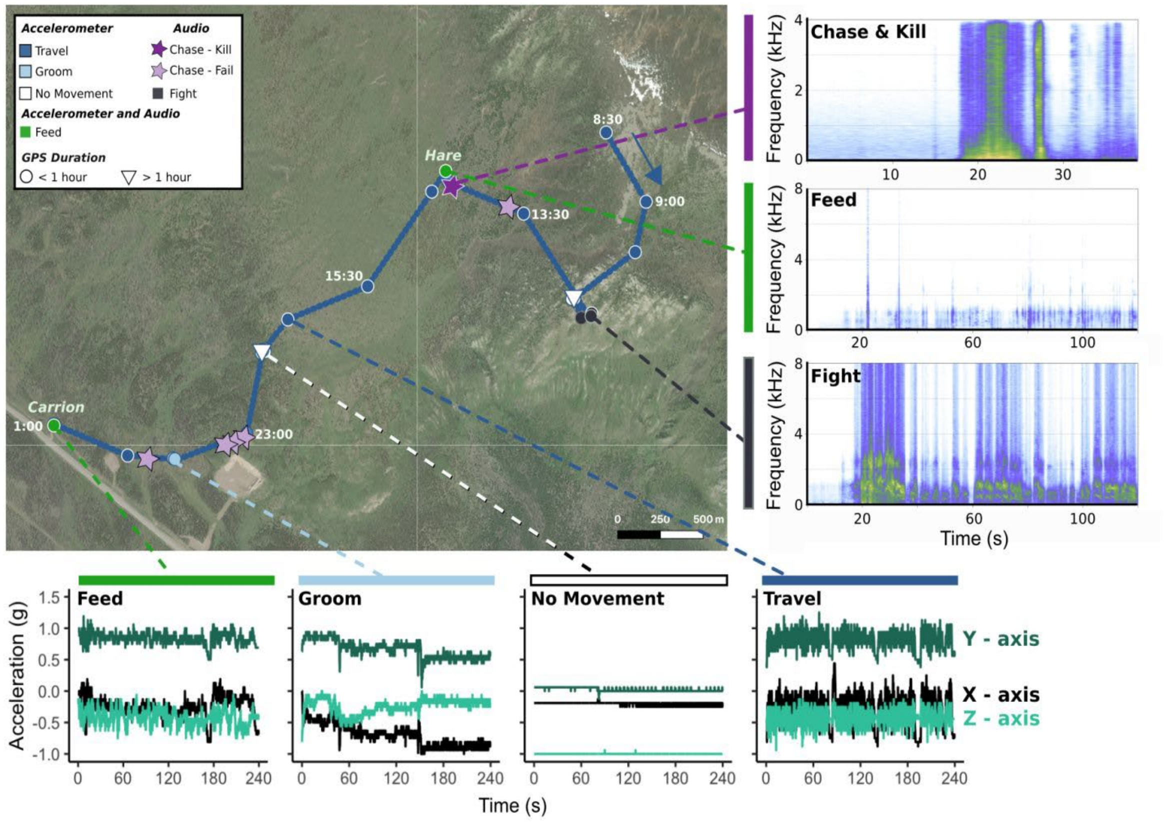

Figure 2: Example GPS track and behaviour of a male lynx over a day. Locations illustrate the acoustic (i.e., sonogram; right) and acceleration (i.e., fine-scale movement; bottom) signatures of each behaviour that is extractable from the biologging devices. For acceleration, signatures for the X (black), Y (dark teal), and Z (light teal) axes are shown.

Accelerometer Classification

Accelerometers recorded acceleration continuously at a 1 Hz (2015-2017) or 10 Hz (2017-2020) sampling frequency within a +/- 8g range. Prior to generating a model to identify meals, we used continuous behavioural observations of tagged free-ranging lynx to determine the most common behavioural states that needed to be included in the model to minimize misclassification. By locating and observing lynx (24 hours on 4 individuals) using very high frequency (VHF) telemetry, we determined that lynx spend 95% of their time in one of four states (feeding, not moving, grooming, and walking; see

Figure 2 for example accelerometer profiles), often expressing each state for 15 mins or longer at a time. For our classification model, we generated training data for these four behavioural states for 10 lynx (2300 - 3200 min per state) according to whether the individual was travelling (GPS) and the sound level on the acoustic recorders, denoting whether individuals were sleeping or active (Figure 3; Appendix A3.1 and A3.2 for clock drift correction). For our models, these training data were subsampled using a 2-minute sliding window with a stride of 1 minute. Direct observations were not used for training data as most lynx were not observable, and observations were inefficient for the volume of data needed.

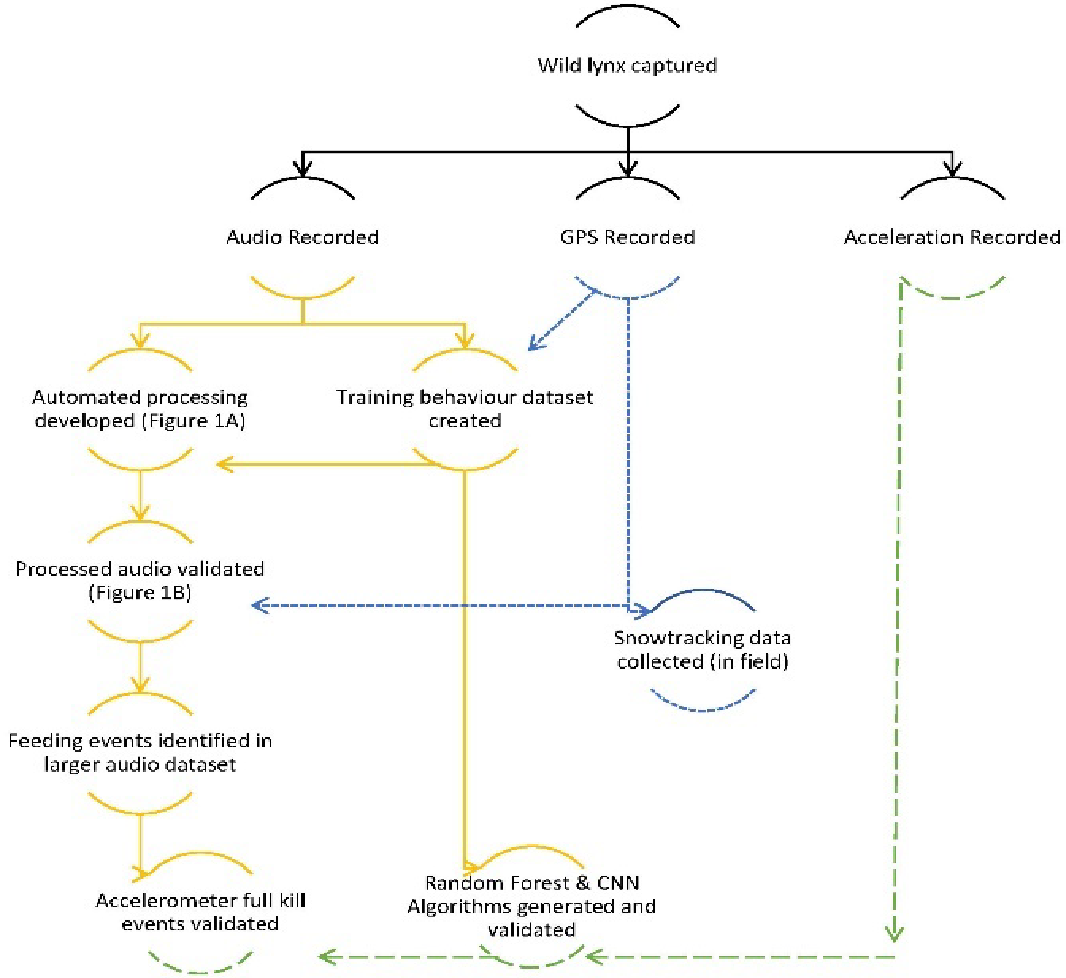

Figure 3: Schematic of the methodological workflow for extracting kill rates from accelerometers, acoustic recorders, and GPS collars deployed on free-ranging lynx.

For classification, we separated 1 Hz (n = 5 lynx) and 10 Hz (n = 5) accelerometer data and explored two different machine learning algorithms for each frequency using the Python programming language (Figure 3; green dashed line). One algorithm was a 1-dimensional convolutional neural network (1d-cnn) model implemented using the *keras* and *tensorflow* libraries that we ran on the raw data (see Appendix A3.3). The second was a random forest using the *scikit-learn* library (Pedregosa et al. 2011) that operated on a suite of time series features generated using the *tsfresh* library (Christ et al. 2018). We removed as many features as possible without compromising the cross-validation scores to minimize the computational cost of the model (see specifications in Appendix A3.3). We ran and compared classifications on only the heave axis (i.e., vertical movements) with those on all three axes. This revealed that those on only the one axis outperformed those that included multiple axes, especially with the 1d-cnn models (Appendix A3.5, Table A-A1). Thus, all reported classifications use only the heave axis. Performance of all classifications (n = 4; both algorithms for 1 and 10 Hz) was calculated using a "leave one lynx out" cross-validation method where the model was built using training data from all lynx but one and then validated on the training data from that remaining lynx.

Finally, for calculating kill rates, we validated the accelerometer classifications at the scale of complete meals instead of at the scale of the classification (i.e., 2-minute windows). We defined a meal as consecutive feeding behaviour from the classification with no gaps greater than 10 minutes (see Appendix A3.4). Using all confirmed meals in the audio files (n= 269; mean per lynx =19) as known events, we calculated precision and recall of accelerometer-classified meals. We additionally tested if meal duration impacted the accuracy of classification by running an optimization analysis on the minimum feeding duration required to be considered a meal. Optimization consisted of calculating F1 scores across a range of minimum meal durations (2 to 24 minutes; Figure A-A6). This validation used the accelerometer classification that did not include training data for that lynx (i.e., leave one out), included meals in the audio that were not used for training accelerometer classification (training included 68 events; 43.3% all events used in validation; Figure 3), and included 4 lynx not used in training the classification algorithms.

Lynx hunting behaviour

To demonstrate potential ecological data that can be generated from the above classifications in addition to snowshoe hare kills, we processed all audio and accelerometer data for 13 lynx for which we had data from both devices. For each chase identified by our semi-automated classification, we recorded duration (<1 to 39s; mean = 6.0s), prey species from vocalization, and whether it was successful (Figure 4). Chases were successful if followed by a death-associated vocalization of the prey (66% of 331 successful chases; Figure A-A7; audio clip Appendix A5, A6), or if feeding occurred within 10 minutes with no subsequent chases (91% of 331 successful chases). We excluded non-sprint chases to minimize inclusion of running for other reasons, which resulted in a similar chase success rate as has been found previously with snow tracking (O'Donoghue et al. 1998a). Since we captured chases lasting less than one second (i.e., a pounce), we believe that this included most hunting attempts from ambush beds. For all meals, we recorded prey type (prey vocalization), meal duration, and whether the meal was a new kill (preceded by a chase), a stolen kill (preceded by vocalizations of other predators and no chase; Appendix A8), or scavenging (no chase or lynx vocalizations). We calculated the proportion of different prey types in lynx diets categorized as: snowshoe hare kill (hare vocalizations prior to feeding and/or any feeding longer than 15 minutes), red squirrel kill (squirrel vocalizations prior to feeding), stolen meals, scavenging, or other (unidentifiable prey vocalization, or no vocalization with feeding less than 15 minutes). We also calculated the average number of feeding bouts across 2-day periods from classified accelerometer data for every individual.

Results

Audio Data

Over the five seasons of the study, we collected 14470 hours (spanning 693 lynx-days) of audio data from 39 collars and 26 individual lynx. We visited 4682 lynx GPS points through snow-tracking and identified 129 kills (81% hare, 14% red squirrel, and 4% avian spp.). These points clustered into 158 snow-tracking events lasting 14-1020 minutes, but only 34 kills corresponded with audio due to faulty recorders (n=8 collars, n=5 individual lynx). Our automated model for feeding tagged 113 feeding bouts from 971 hours of audio. After aligning and cleaning (n=13 duplicates removed), 31 feeding bouts occurred during snow-tracking observations: 26 aligned with a snow-tracking kill, leaving 5 false positives. There were 46 snow-tracking events that did not correspond to a feeding bout in audio after cleaning (n=2 small prey removed; Figure 1: B4.2). This included 5 kill sites, all of which were females that were known to be travelling with another lynx. The overall accuracy of the confusion matrix was 0.87 with high recall (0.87), specificity (0.87), precision (0.87), and F1 (0.87). Our automated classification of chase behaviour tagged 16,745 sound clips, of which 1316 were unsuccessful chases, 331 were successful chases (i.e., ended in a kill), and 15098 were not chases.

Accelerometer Classification

Classification of accelerometer data into four behavioural states at 2-minute resolution produced an overall F1- score >0.80, but there was variation in accuracy between sampling frequencies and classification algorithms (Table A-A1; Appendix A3.5). Accuracy at classifying feeding at this 2-minute resolution was higher with the random forest (F1=0.82-0.90) than the CNN (F1=0.79-0.81) algorithm. At the scale of full meal events, the accuracy of the classification algorithm varied with the threshold for minimum meal duration (Figure A-A4). A classification that included all meals with durations greater than 2 min generated high incidences of false positives (meal events that did not exist in audio). Generally, increasing the minimum feeding duration threshold reduced false positives while increasing false negatives (meal events in audio that were missed). A minimum meal duration threshold of 15 minutes produced the highest F1 score when classifying all meals (F1=0.90; Figure A-A6a), only snowshoe hare meals (F1=0.93; Figure A-A6b), or only snowshoe hare meals with a duration equivalent or longer than the threshold (F1=0.97; Figure A-A6c). This threshold captured 90% of hare kills, stolen meals, and scavenging, but only 6% of red squirrel and other species kills (Figure A8). At this threshold 1 Hz and 10 Hz sampling frequencies were equally successful at identifying full hare meals (Table 1). The random forest models were more successful than the CNN models at identifying full meals both at the individual device level (Table A-A1) and across all devices (RF: F1=0.96; CNN: F1=0.78 - 0.80; Table 1).

Table 1: Performance metrics of accelerometer classification models at identifying meals with durations greater than 15 minutes for each model type and acceleration sampling frequency. Overall precision, recall, F1-scores, and sample size are presented, along with the range of F1-scores for individual lynx.

Model Type	*Frequency*	*Support*	*Precision*	*Recall*	*F1*	*F1 range*
Random Forest	1 Hz	108	0.99	0.94	0.96	0.92 - 1
	10 Hz	118	0.94	0.98	0.96	0.83 - 1
CNN	1 Hz	108	0.74	0.88	0.80	0.53 - 1
	10 Hz	118	0.69	0.91	0.78	0.54 – 0.96

Variation in Diet Composition and Feeding Rates

Both audio recorders and accelerometers provided individual data that captured variation in hunting behaviour (Figure 2). According to audio data of 13 individual lynx (6 female, 7 male), at the increase/peak phase of the snowshoe hare cycle, the individual proportions of meals involving hares ranged from 40% to 80% (Figure 4), while red squirrel kills ranged from 0% to 27%. If scavenging events or stolen prey are assumed to be snowshoe hares, as suggested from our snow-tracking and from lynx diet research in the study area (O’Donoghue et al. 1997), then meals comprised of snowshoe hares ranged from 70% to 100% of all meals consumed. Both audio and accelerometer data showed that lynx eat an average of 1.2 large (hare) meals per day (Figure 5). The variation was greater within individuals (2-day average ranging from 0 - 3.5 meals) than across individuals (individual means varied from 0.97 to 1.5 meals per day).

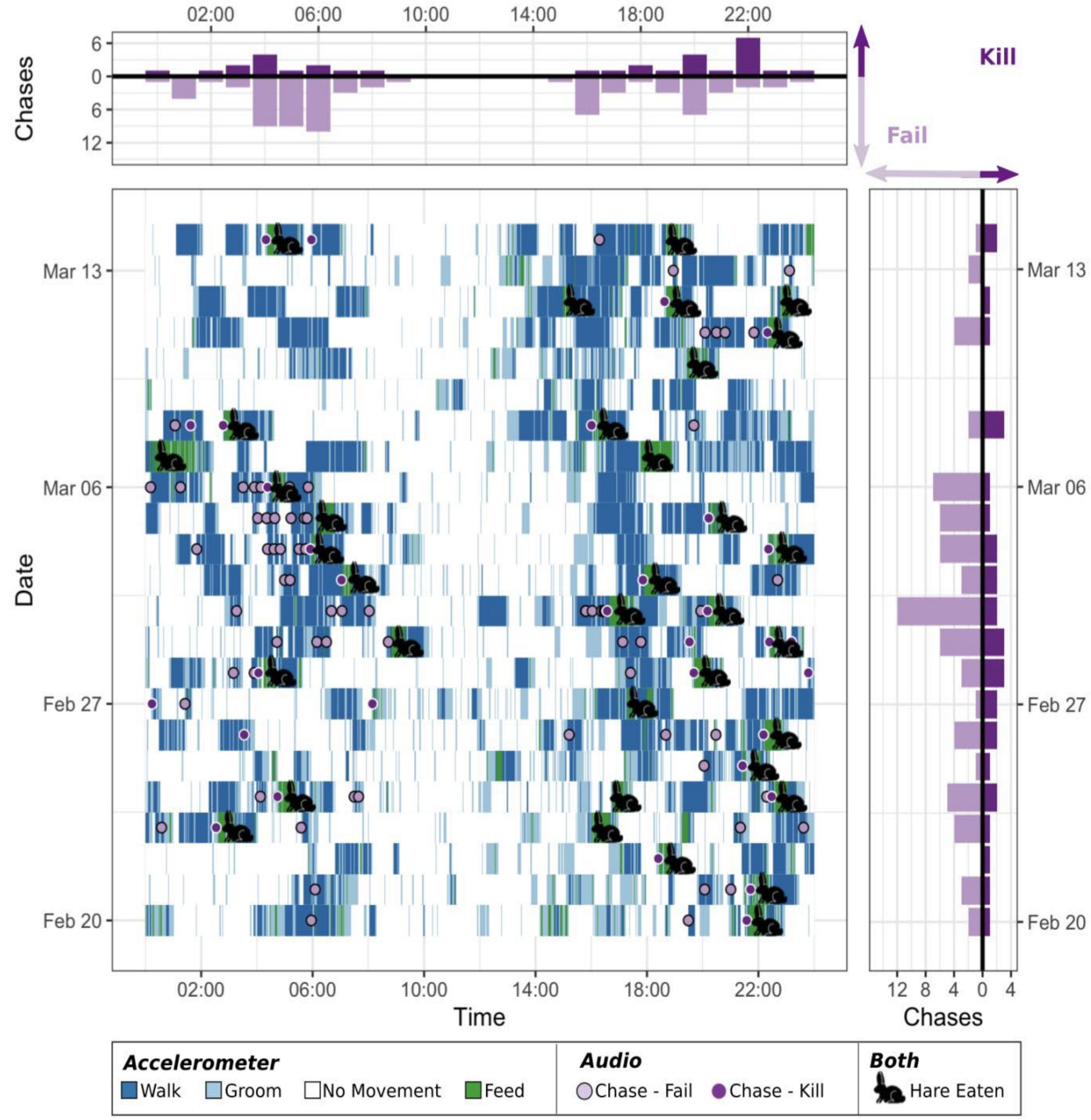

Figure 4: Example actogram (of a male lynx) illustrating continuous behavioural classification over one month from a combination of accelerometer and audio devices.

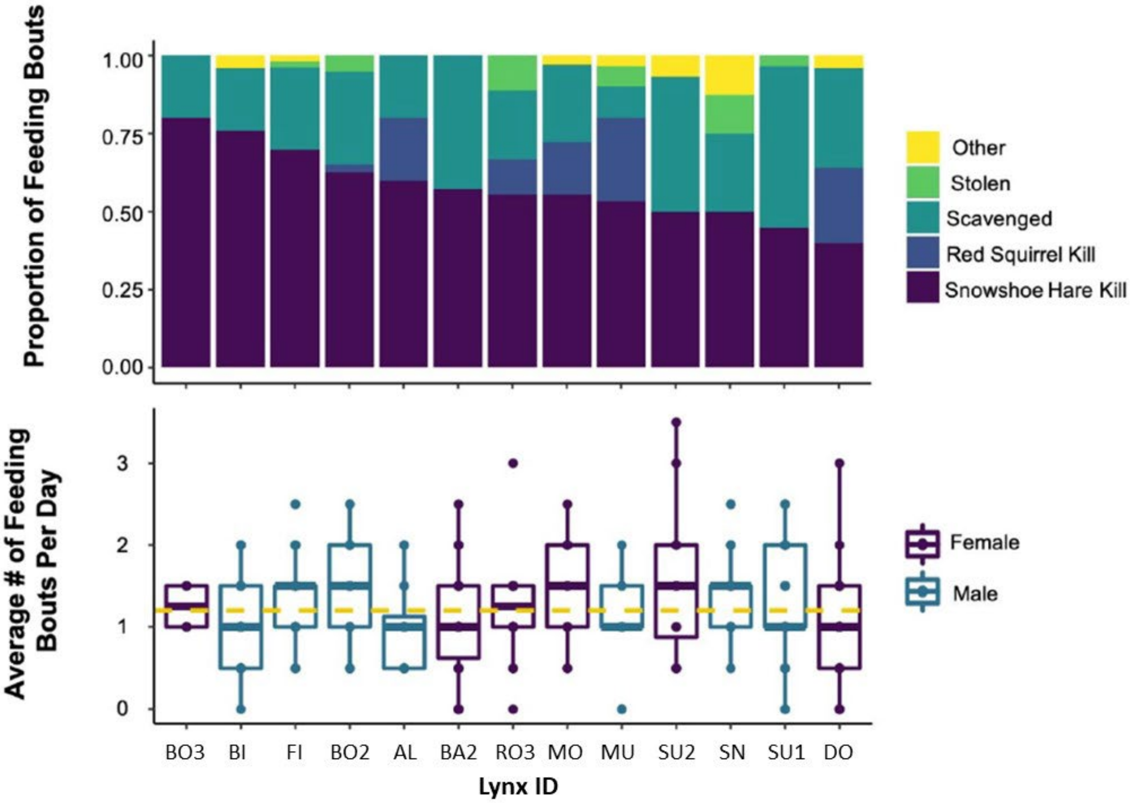

Figure 5: Variation in A) feeding composition and B) average number of feeding bouts per day for 13 individual lynx (6 females, 7 males) in winter. Feeding composition was determined through audio data. Average kills per day were calculated from both accelerometers and acoustic recorders across 2-day periods for individual male (blue) and female (purple) lynx along with the population average (1.2 kills per day; dashed line).

Discussion

Using audio recorders and accelerometers, we were able to document chases, kills, scavenging events, and meals of free-ranging Canada lynx, a cryptic mesocarnivore and small prey specialist of the boreal forest. Although similar behavioural metrics have been documented in larger carnivores using GPS cluster analyses (Williams et al. 2014), these key hunting metrics have remained unattainable for the majority of carnivores (71.9% are small prey specialists; calculated from Carbone et al. 1999) due to the limited time spent at a kill site (<1 hour) relative to other behavioural states (grooming: ~1 hour, sleeping: >1 hour). As such, predator studies have had low detection rates of short meals (25% chance of detecting GPS clusters less than 9 hours long, Vogt et al. 2018) which often leads to not considering prey <2 kg in their results (McLean et al. 2005, Svoboda et al. 2013). As such, the biologging methodologies presented here are a substantial advance in the capacity to continuously document kill rates and detailed hunting behaviour, even for mesocarnivores, without intensive field work related to kill site investigations or scat collection, but particularly for carnivores that specialize on small-bodied vertebrate prey.

We found that audio recorders accurately captured predator kill rates, while also providing additional information on prey type, hunting success, intraspecific aggression at kill sites, and post kill behaviour (although not quantified here). Audio recorders have been used to document feeding behaviour in herbivores (Kikuchi et al. 2014, Studd et al. 2019) and, here, we show that they are also well-suited for use on predators, although recording duration and battery size will depend on body size. In addition to chases and kills, we were often able to identify the prey species (for 66% of kills) according to prey vocalizations, which is a major advantage over GPS and accelerometer approaches that require kill site visits for prey information (McPhee et al. 2012). Another advantage of audio that we found is the ability to identify meals as scavenging or kleptoparasitism, or the potential to quantify the social dynamics (solitary or cooperative hunting), although not validated here, according to the presence of chases prior to feeding, and frequency and type of vocalizations between individuals. The capacity of audio recorders to provide these extra details improves quantification of predator hunting behaviour and provides new opportunities to explore the role of cooperation, competition, and scavenging in predator success and predator-prey interactions.

Despite these considerable advantages, there are some drawbacks to the use of acoustic data. The sound quality varied considerably between devices and across deployments, partially due to variation in re-housing and attachment to collars, but also from damage sustained post deployment. This contributed to some error in our automated classification of meals as the fit of our universal thresholds varied with the quality of the acoustic file, with some files generating more false positives than others. We also had five snow-tracking kills that were not captured by the classification. Manual listening of the audio revealed that one such incident had some evidence of feeding (although it was unclear), while four incidents included purring, grooming, and scratching. In all cases, these events stemmed from three female lynx that consistently hunted in a group (2-3 individuals), so we suspect the kill was primarily consumed by another individual. Thus, it seems that our classification was capturing all substantial meals of collared individuals. The major drawback for this technology is that extracting additional information like chase success or prey type required some manual processing, which was substantial for the information we wanted (~1 hour/day of audio). Moreover, because this technology is not currently produced commercially for wildlife applications, it required considerable troubleshooting with high device failure rates in the first couple of years; >50% of devices failed to record at all, or broke within the first 3 days of deployment, mostly due to water or physical damage from lynx claws.

Independent of the acoustic recorders, we successfully quantified kill rates using accelerometers with higher accuracy than has been previously achieved. Although behavioural classification of acceleration is becoming common practice in ecology, feeding has proven difficult to discern on terrestrial predators (Pagano et al. 2017, Wijers et al. 2018, Glass et al. 2020). Our success here results from considering behavioural signals over longer time periods (minutes) than are often used for classifications (seconds) (Nuijten et al. 2020). For lynx, we found that the clear and consistent distinction between feeding and grooming in our accelerometer classification was a result of posture; during feeding, lynx consistently maintained a crouched posture over the carcass (see Appendix A7), while during grooming, they adjusted posture every couple of minutes to reach different body parts. Although the boost in classification accuracy that we achieved for feeding over other studies may seem moderate (~10 %), such error in classification can translate into substantial over- or under-estimation of kill rates (i.e., a doubling) due to the rarity of meals in most large predators (< 5 % of the day in lynx).

However, the use of accelerometers to characterize hunting behaviour also had limitations. First, like audio, our classification was most accurate when using long time windows (2-minute), which reduced the ability to extract short meals (< 15 mins). Therefore, although these methods greatly improve what can be achieved through GPS clustering (Jansen et al. 2019, Leighton et al. 2020), our automated classifications still miss identifying consumption on the smallest prey (squirrels and birds; Figure A-A8). Second, accelerometer classification algorithms require considerable amounts of observational data for training. As use of captive animals or surrogate species often increases error in the classification (Campbell et al. 2013, Pagano et al. 2018), collecting data on the focal species, in the field, remains a major challenge. Here, because free-ranging lynx are difficult to observe (most individuals avoided observers), we had to infer behavioural states from a combination of GPS and audio data. While successful, the deployment of additional biologging technology increases costs, data management, and processing requirements. Finally, achieving sufficiently low error to accurately quantify kill rates is challenging. We attempted several combinations of statistics, time windows, and algorithms, of which only the two presented here produced promising results. A universal approach does not seem to exist, so each classification requires a considerable amount of time to determine the best metrics and algorithm to use. This time investment should be considered when selecting accelerometers, and biologgers in general, for studying behaviour.

Ultimately, we found that the combination of acoustics and accelerometry provided the best results. Although each technology, individually, generates unprecedented information about predator behaviour, we found that the most complete quantification was produced from a combination of the two. Audio data provided chase and prey details and accelerometers provided an efficient method for identifying hare kills. Despite the focus of this study on hunting behaviour, both devices also provide additional behavioural and environmental information, which can refine our understanding of predator behaviour, predator-prey interactions, and social dynamics. We documented substantial intraspecific variation in both prey selection and kill rates, something that has been unattainable for free-ranging, small prey specialists. We believe that the fine-scale (minute by minute) data that can be collected by these technologies continuously over long periods (weeks to months) will provide unprecedented insight about the lives of cryptic terrestrial species.

Chapter 3: Canada lynx kill sites and space use are differentially predicted by distinct spatio-temporal drivers during a decline in primary prey density

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A version of this chapter is in preparation for peer-reviewed publication

Abstract

Predator-prey dynamics are an integral component of ecological studies since they influence population dynamics and the flow of energy through ecosystems. Foraging theory predicts that predators should select habitats where they can achieve the highest rate of energetic return, but this can be shaped by various interacting factors such as the absolute abundance of prey and how prey respond to predator foraging activity, potentially making it difficult for predators to exploit high-quality foraging patches. To test how prey abundance interacts with other landscape-level variables to influence predator hunting behaviour and space use, we investigated the drivers of snowshoe hare (*Lepus americanus*) kill locations by Canada lynx (*Lynx canadensis*) during a drastic (8-fold) cyclic decline in hare density over four years. Using track count surveys over a range of habitat types, we first confirmed that hares preferentially used habitats with denser vegetation, potentially as a refuge from predation. Then, based on >1000 hare kills by 23 instrumented individual lynx, we found that lynx space use (i.e., utilization distribution probability surface) was the strongest predictor of kill site location, followed by hare relative abundance, vegetation density, and elevation. Lynx utilization distributions were best predicted by vegetation density and its interaction with *Year*, but with high variability across collar deployments, suggesting that lynx do not rely primarily on hare abundance when selecting habitat within their home range. Our work highlights that predator responses to prey may not be strictly driven by prey abundance or behaviour, and that even in systems with large fluctuations in prey abundance, predator behaviour may remain relatively stable over time.

Introduction

Ecologists have a longstanding interest in disentangling predator-prey interactions and documenting how these relationships may change through space and time. A re-occurring question relates to the balance between how and where predators hunt and kill prey and whether these patterns are driven simply by prey abundance or other factors, like predator movement behaviour or prey vulnerability (Brown et al. 1999, Wheatley et al. 2020). For example, individual predators may use different foraging strategies leading to variable kill rates, whereas prey may alter activity and movements to limit the risk of predation (Hugie and Dill 1994, Kauffman et al. 2007). Predator foraging strategy or anti-predator prey responses may change depending on predator or prey density, leading to corresponding variation in the frequency, distribution, and outcome of predator-prey encounters (Abrams 1994, Scoleri et al. 2023). These dynamics could lead to shifts in spatial patterns of predation and their corresponding drivers, but to date few efforts have addressed such variation in natural systems.

Predators and prey should be responsive to each other, with predators seeking areas where prey are abundant or easy to capture and prey using areas where predators are rare or have low hunting success. An important feature of this predator-prey conflict is the use of refuge habitat by prey, which often is composed of structural cover in the form of vegetation or other visual or locomotory obstruction that impedes prey detection and/or capture by predators (Wheatley et al. 2020, Scoleri et al. 2023). Conversely, in habitats where prey may be easily encountered and/or captured, prey are thought to be “vulnerable”, but these habitats may coincide with better food or other resources for prey (Petrunenko et al. 2016, Rayl et al. 2018). The relative vulnerability of prey to predation can be influenced by a range of structural characteristics within its habitat, including vegetation density and type, among other factors (e.g., predator type; Atwood et al. 2009).

Refuge habitat can play a crucial role in predator-prey interactions, but changes in the density of predators and prey are likely to influence the frequency and location of predator-prey encounters and kills. If prey abundance is low, a predator may concentrate hunting efforts in refuge habitats where prey densities are higher, even though this may incur a cost (e.g., energetic; Anderson 2001, Prokopenko et al. 2023). When prey abundance outside of refuge habitats is sufficient to meet energetic requirements, predators may hunt where prey are most vulnerable (Quinn and Cresswell 2004), or even kill prey opportunistically when encountered, irrespective of prey density or vulnerability (Cristescu et al. 2019). The current energetic needs of the predator may influence its foraging decisions, with hungrier predators taking more risks to hunt prey (Moran et al. 2021). Predator behaviours may therefore be dynamic in response to changing prey abundance and behaviour, particularly in environments with high variability in prey availability. Such behavioural shifts may accompany changes in movement or the location/size of the home range (Rayl et al. 2015, Warret Rodrigues and Roth 2023).

The Canada lynx (*Lynx canadensis*) is a medium-sized carnivore that occurs across the boreal forest of North America, and northern lynx populations undergo cycles that are driven by those of snowshoe hare (*Lepus americanus*), their primary prey

(Slough and Mowat 1996). Lynx are visual hunters that stalk and chase prey over short distances (O'Donoghue et al. 1998a, Squires et al. 2010). When lynx densities are high, hares may limit predation risk by occupying refuges comprised of dense vegetation (Hik 1995, Beaudoin et al. 2004). However, refuge availability may be limited on the landscape and its importance in reducing hare predation is not well known (Wolff 1980, Rohner and Krebs 1996, Aubry et al. 1999). Cyclical changes in hare density govern home range size, prey consumption, and movements of lynx (Ward and Krebs 1985, Slough and Mowat 1996), which could lead to variation in the frequency, distribution, and habitat association of lynx-hare encounters and predation events. Although there is limited evidence that lynx kill sites vary through the lynx-hare cycle (O'Donoghue et al. 1998a), it is not clear whether changes reflect variation in the absolute abundance of hares, temporal or spatial variation in the relative abundance of hares, or variation in areas used by lynx.

The cyclic nature of lynx and snowshoe hare populations offers an opportunity to study dynamic predator-prey interactions in a relatively simple boreal ecosystem with high variability in prey abundance. We investigated lynx predation determinants and kill site selection through a dramatic 4-year change (94.3% decline) in snowshoe hare density in the Kluane region of the Yukon (Krebs et al. 2022), using accelerometers and fine-scale GPS data from radio-collared lynx. First, we tested whether hares preferentially occupy habitats with denser structural cover, i.e., refuges (Wolff 1980, Hik 1995), particularly as hare populations decline and predator: prey ratios increase. We then explored five alternative predictions: lynx will kill hares 1) consistently in habitats with high relative hare abundance during all phases of the cycle (i.e., invariant selection for prey abundance); 2) increasingly in more open habitats as hare populations decline (progressive selection for prey vulnerability as hares shift to greater use of refuge habitat); 3) increasingly in habitats with high hare relative abundance as populations decline (progressive selection for greater prey relative abundance in refugia); 4) consistently in habitats with high hare vulnerability (i.e., more open habitats) during all phases of the cycle (invariant selection for vulnerability); or 5) based on general patterns of lynx habitat use, with no strong impact of either hare relative abundance or vulnerability. We also explored these five possibilities as they relate to lynx space use, in an effort disentangle the possible differential drivers of kill site selection and patterns of predator space use within the home range. We predict that if, as previously suggested (Wolff 1980, Hik 1995), hares shift to greater use of refugia as hare populations decline, the most likely responses of lynx relate to predictions 2 and 3, both of which invoke progressive use of refugia by hares and behavioural shifts by lynx as hare populations decline. If hare refugia are effective in reducing the likelihood of lynx predation, we expect a shift of lynx to the selection/use of more vulnerable habitats for hares; otherwise, lynx may progressively use hare refuge habitat to hunt as hares become less abundant.

Methods

Study area and habitat classification

We studied lynx and hares during 4 winters in the Kluane region of Yukon Territory (61°57'N, 138°12'W), where populations have been monitored intensively for >40 years (Krebs et al. 2018). The area is characterized as semiarid, with winter snowfall averaging ~25-60 cm (Peers et al. 2020). Vegetation is dominated by white spruce (*Picea glauca*) with stands of trembling aspen (*Populus tremuloides*) or balsam poplar (*Populus balsamifera*), and shrub-dominated patches (predominantly willow, *Salix sp.* and dwarf birch, *Betula glandulosa*; Dale et al. 2001, Krebs et al. 2014). Hare populations undergo dramatic 8-10 year population cycles with hare densities varying ~40-fold during the course of the cycle (Hodges et al. 1999). We delineated our study area (Fig. 1) as covering 216.5 km^2, which encompassed ~2 km around our hare track count triangles for estimating hare relative abundance (see below) and overlapped with 99% kernel density home range estimates for lynx monitored during this study. This area included 98.0% of the 1121 hare kill locations by radio-collared lynx that were detected during the study. Elevation ranges from 800 – 1500 m (mean = 959 m ± 115 [SD]), with most of the study area below 1000 m in elevation but with increasing elevation along the edges of the defined area and with increasing distance from the highway that bisects the study area (Fig. 1).

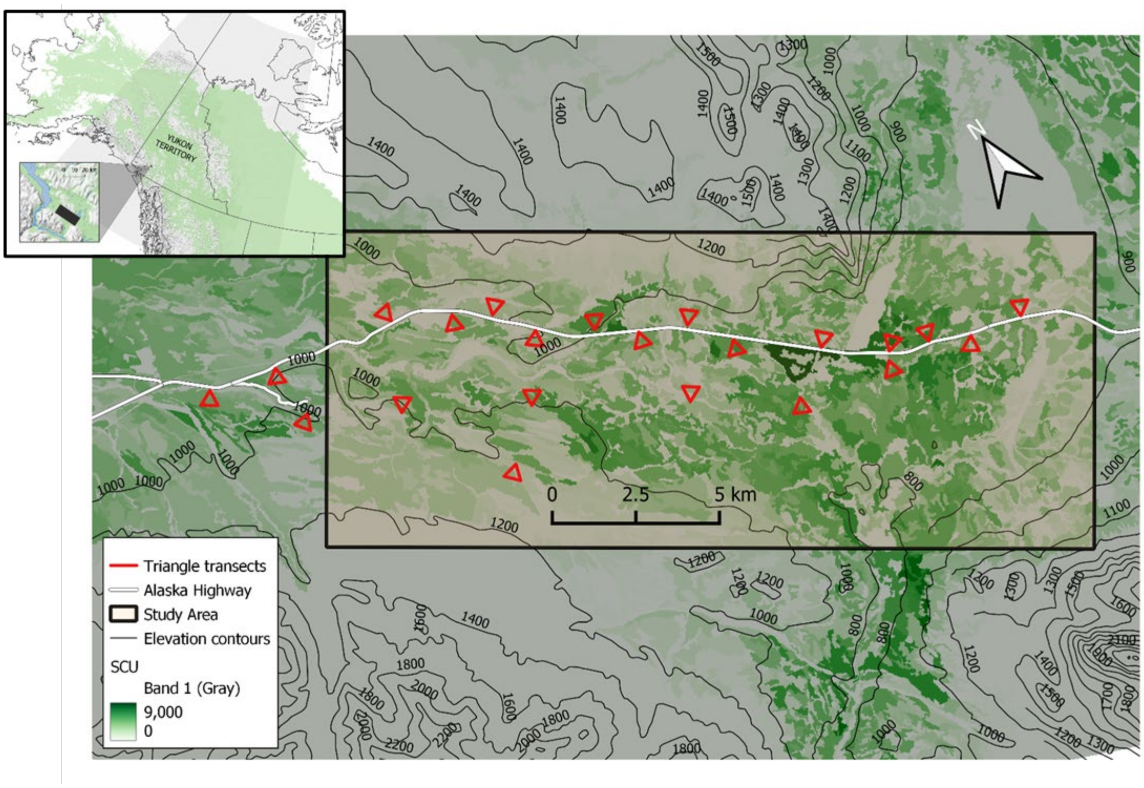

Figure 1: Lynx and hare study area in southwest Yukon, Canada. Contour lines and associated numbers represent elevation (m), while colours indicate Stem Cover Units (*SCU;* index of stem density that accounts for tree species: darker colours = higher values of *SCU*). The outlined area (~ 216 km^2) represents that for which hare relative abundance was estimated. Snowshoe hare track survey locations are represented as red triangles.

We mapped habitats available to lynx and hares using GIS layers developed by the Yukon Government Vegetation Inventory (YGVI) (Forest Management Branch, Dept. of Energy, Mines and Resources, Yukon Government 2014). Habitat categories were chosen to reflect the nature of the study area, which is almost exclusively spruce forest consisting of a range of tree densities, with most non-spruce habitat occurring as shrub-dominated patches in higher elevations along the edge of the study area (Fig. A-B1). GIS layers contain spatially referenced polygons with landcover type, vegetation, dominant tree species, and estimated stem density of the dominant tree species. Polygons were mapped and interpreted digitally at a 1:40,000 scale, and polygons range in size from <1 ha to ~690 ha within our study area (mean = 15.8 ha ± 32.6 [SD]). Ground-truthing and aerial checks occurred on permanent plots (~2% of our study area; YGVI 2014). We re-classified polygons according to vegetation type and stem density, which are primary determinants of hare occupancy (Litvaitis et al. 1985, Thornton et al. 2013, Richmond et al. 2022). Using the YGVI, we classified spruce-dominated polygons as *Spruce* (70.3% of study area). We considered *Shrub* (18.7% of study area) as any non-forested polygon with >20% shrub cover. Any other vegetated polygons were classified as *Other* (8.2% of study area). We included a fourth category, *Water*, to represent any polygons classified in the YVIM as water (2.9% of study area). This category was not used by hares and was excluded in our analysis of hare movement, hare relative abundance, or drivers of hare kill sites (see below); however, it was included as a category in our analysis of lynx home ranges, which sometimes included this habitat type.

Using the YGVI, we extracted stem density of the dominant tree species in each forested polygon. Although snow cover during the winter period (when we conducted the field study) may cause stem density to be functionally reduced in contrast to summer when the YGVI was conducted, the stem density variable is likely minimally influenced by snow cover since the average height of the dominant species (usually spruce) was 12.2 m (± 3.85 m [SD]), and 0.5% of forested polygons had an average height <4 m. To reflect different effects of spruce and deciduous stem density on cover available to hares, we calculated an index of Stem Cover Units (*SCU*). We used the two dominant tree species in each polygon to calculate *SCU* = *StemDen* (species 1) + *StemDen* (species 2), where *StemDen* = stem density (if the dominant tree species was deciduous) *OR* 3*stem density (if the dominant tree species was spruce; Fuller and Harrison 2013), since spruce trees are related to higher horizontal cover in winter (Litvaitis et al. 1985). This index only represents tree stem density (and not shrubs) and successfully predicts hare densities (Fuller and Harrison 2010, 2013). *SCU* ranged from 0 to 7200 in the study area (mean = 1615, skewness = 0.53, kurtosis = 2.41). The distribution of *SCU* values was right-skewed, with most values <1000 and higher values coinciding with lower elevations (Fig. 1). *SCU* was correlated to stem density as estimated by the YGVI (Fig. A-B2) ($r^2 = 0.51$) and accounted for deciduous patches which can be influential to hares. Mean *SCU* also varied with vegetation type (*Other*: 735.26 ± 50.43; *Shrub*: 137.34 ± 18.49; *Spruce*: 2289.80 ± 43.70). Finally, we rasterized maps (*Veg* and *SCU*) using a 30 X 30m grid size in the R package *raster* (Hijmans 2023).

Hare track transects for relative abundance estimates

From December-April 2017-21 (winters 2018, 2019, 2020, and 2021), we indexed hare abundance via 22 triangular track transects located across the study area (Fig. 1; Pellikka et al. 2005). Transects were equilateral triangles (500m per side) spaced >300m. Within 3 days of a snowfall, we followed each transect and recorded the number of hare tracks encountered each 30m; overlapping hare tracks were recorded as a run. Each 30m section where tracks were tallied was considered a “segment”. Transects were resurveyed opportunistically 1-5 times per winter season, with >4 days between visits. Of the 22 transects sampled *a priori*, 19 overlapped with lynx home ranges and were included in the delineated study area (Fig. 1). Transects covered *SCU* and elevation ranging from 0 to 6000 (mean 2601 ± 1553 [SD]; see Fig. A-B3 for sample distribution), and 826 m to 1036 m (mean 933 m ± 67 [SD]), respectively. Most transect segments (~85%) occurred in spruce forest, ~10% occurred in *Shrub*, and the remaining ~4% were classified as *Other*.

Hare movement

To quantify hare movement parameters for inclusion in track count models of relative abundance (see below), we used GPS data from a concurrent study of hares in our area (Majchrzak et al. 2022) to construct integrated Step Selection Functions (iSSFs; Avgar et al. 2016) and calculate habitat-specific step length (*SL*; distance between consecutive GPS points) and turn angle (*TA*; angle, in radians, between consecutive steps; *TA*) for each *Year* and *Season* (for full details of this analysis, see Appendix B1). Following steps outlined in Fieberg et al. (2021), we fit separate models for each hare collar deployment and calculated updated *SL* and *TA* distributions for each value of *SCU* (in increments of 100). Mean values of *TA* and/or *SL* from updated individual iSSFs were included in hare track models 5-7, 9-11, and 13-15 as possible predictors of track count (Table 1).

Table 1: Model specifications and AICc comparisons for the drivers of snowshoe hare track counts in Kluane region, Yukon (winters 2018-2021). In each model, triangle name (Table S1) is a random effect. Predictors include: time since snow (*TSS*), vegetation (*Veg: Other, Shrub,* and *Spruce*), hare step length (*SL*), hare turn angle (*TA*), Stem Cover Units (*SCU;* index of stem density that accounts for tree species), and elevation (*Elev*).

Model	*Parameters*	*K*	*AICc*	*Δ AICc*	*AICwt*
14	~Year + Season + TSS + SCU + Veg + TA	22	17808.45	0	0.88
15	~Year + Season + TSS + SCU + Veg + SL + TA	24	17812.47	4.02	0.12
12	~Year + Season + TSS + SCU + Veg	20	17825.62	17.17	0.00
16	~Season + TSS + SCU*Year	19	17828.08	19.63	0.00
13	~Year + Season + TSS + SCU + Veg + SL	22	17829.36	20.91	0.00

6	~Year + Season + TSS + SCU + TA	18	17836.82	28.37	0.00
7	~Year + Season + TSS + SCU + SL + TA	20	17838.35	29.90	0.00
4	~Year + Season + TSS + SCU	16	17864.86	56.41	0.00
5	~Year + Season + TSS + SCU + SL	18	17866.58	58.13	0.00
18	~Season + TSS + Veg*Year	24	17917.19	108.74	0.00
10	~Year + Season + TSS + Elev + TA	18	17986.22	177.77	0.00
11	~Year + Season + TSS + Elev + SL + TA	20	17989.54	181.09	0.00
9	~Year + Season + TSS + Elev + SL	18	18119.42	310.97	0.00
17	~Season + TSS + Elev*Year	19	18123.62	315.17	0.00
8	~Year + Season + TSS + Elev	16	18129.43	320.98	0.00
3	~Year + Season + TSS	14	18134.13	325.68	0.00
2	~Year + Season	12	18172.48	364.03	0.00
1	~1	4	19822.29	2013.84	0.00

Hare relative abundance and habitat use

We used model selection with zero-inflated negative binomial distributions to rank models of potential factors influencing relative hare abundance in our study area. Zero-inflated models are composed of a binomial (zero-inflated) model to explain drivers of hare occurrence (i.e., prevalence) and a second (conditional) model to explain number of observations when they occur (i.e., intensity; Ali et al. 2020). We defined “track count” as the number of hare tracks per 30m segment + 3*hare runs, assuming at least three sets of tracks will obscure individual tracks and be qualified as a “run” (R. Derbyshire, *unpubl.*). Each zero-inflated model was identical to the conditional model but with interaction terms removed. Transect ID (19 levels; Table A-B1) was specified as a random factor. The variable *Year* (2018, 2019, 2020, and 2021) was coded as a factor, and *Season* (*Early*: 1 Dec to 31 Dec; *Mid*: 1 Jan to 11 Feb; and *Late*: 12 Feb to 29 Mar) was coded as an integer. Time since last snow (*TSS;* range 0.49 to 3.05 days) was included as a covariate along with average hare *TA* and *SL* values for each *Year/SCU* combination (see above). *Veg* and *SCU* values were extracted from rasterized maps at the start point of each triangle census segment, and elevation (*Elev)* was extracted from the Yukon Government Map Service ("GeoYukon" n.d.). Variables that were correlated ($r^2 > 0.50$) were not included together in the same model (Table A-B2). All models were fit in R package *glmmTMB* (Brooks et al. 2017).

We reduced spatial autocorrelation in hare track models by calculating a distance-weighted autocovariate (*DWAC*) using package *spdep* (Bivand 2022a). We first calculated mean annual track count for each 30m segment, then sorted these values into a nearest-neighbour matrix. Next, we generated an autocovariate value (i.e., an index of the degree of spatial autocorrelation) for each segment using auto-logistic regression and an inverse weighting scheme (Bardos et al. 2015, Bivand 2022b). We confirmed that counts were positively spatially correlated by inspecting a plot of *track count* ~ *DWAC*, and then reduced potential bias from autocorrelated counts by including scaled *DWAC* (*sDWAC*) subtracted from 1 as the correlation structure in all models: $sDWAC = 1 - (DWAC - \min(DWAC))/(\max(DWAC) - \min(DWAC))$.

We compared 18 candidate models of hare abundance, with models selected *a priori* based on our understanding of the system and the need for parsimony (Murray et al. 2020). We used Akaike Information Criterion corrected for small sample size (AICc) to identify best-fit models (Burnham and Anderson 2004), then calculated Nakagawa's Pseudo-R^2 for generalized mixed-effect models in the R package *MuMin* (Nakagawa et al. 2017, Bartoń 2023). We assessed the covariates of the top model for evidence of hare refuge use, i.e., vegetation density in the top model (based on *SCU*) and a significant positive effect of this variable on hare track count. To investigate whether this relationship changed over time, we fit a series of curves (linear, then polynomial of degree 2, 3, 4, and 5) to the relationship between predicted track count from the model and vegetation density; we selected the simplest curve when the next highest polynomial did not improve the Pearson's R^2 by >0.01. Finally, using the conditional, unweighted predictions from our top model, we generated a series of maps of estimated relative abundance (hereafter *RelAb*) of hares across the study area (raster grid size = 30m x 30m), with spatially referenced values for each year and season (Fig. A-B4). For grid cells not predicted in the model because their unique combination of spatial covariates were not sampled with our transects, we imputed the mean *RelAb* value across a 510-by-510m area around the cell. These imputations averaged ~12-19% of the study area.

Lynx spatial behaviour and kills

During November-April 2017-2021, we live-trapped Canada lynx (N = 33) using custom-made box traps (Kolbe et al. 2003) baited with meat and lures. Captured lynx were transported to a local veterinary clinic (~45 km) for chemical immobilization and processing (see Chapter 2 for additional details on immobilization procedures). Lynx >6.5 kg (mean mass = 10.1 kg) were equipped with a GPS collar (either Telemetry Solutions ~350 g; N = 15; Followit Iridium ~245 g; N = 66) with externally mounted accelerometer (Technosmart Axy 3 or 4; 8 g) and acoustic recorder (EDIC-mini, 35g or SOROKA14E, 28g). Assembled collars were ~3-4 % of the body mass of each animal. Collars were deployed at a fix rate of 30 mins (N = 23), 15 mins (N = 54), or 5 mins (N =

4). Of the 77 collar deployments, we included in our analysis only those that had >5 days of GPS points and >3 days of continuous accelerometer data to calculate utilization distributions (*UD*) and identify hare kill sites. We further censored one lynx in early 2018 because it was an outlier due to unusual behaviour (spending several days in one place with very limited movement) and excessive influence on model parameters; our final sample therefore comprised of 49 collar deployments on 23 individual lynx (Table A-B3; Fig. A-B5).

Our previous work (Chapter 2) fully details our approach in identifying hare kills; briefly, feeding events were identified through accelerometry as lasting ≥ 15 minutes and lined up with concurrent GPS data to identify feeding bout location. Kills that did not coincide with the GPS data were censored (e.g., if the accelerometer was working but not the collar), and collar deployment ID was specified as a random factor in kill site models. Therefore, lynx utilization distribution *(UD)* values reflect landcover use by individual lynx during the period associated with kills. Spatial covariates for kill locations were extracted from *Veg* and *SCU* maps; since < 8% of kills were within 10m of an edge between forested and non-forested vegetation types, we interpreted spatial covariates at the extracted kill location as representing actual conditions at the kill site (estimated error range of collars ~ 10.4m, R. Derbyshire, *unpublished data*). In 2019, a single collar (with faulty accelerometer) was deployed in the early part of the winter (before January) whereas in 2021, collars were deployed only in late winter (Table A-B3).

For each collar deployment, we calculated *UD* to describe the probability of lynx use at every pixel of the home range. We estimated the 99% fixed kernel density estimate for each collar (package *amt*, Signer et al. 2019) and used the *ad hoc* method for selecting bandwidth (Kie 2013). We determined the default value for grid size for each collar (grid size = max (extent$_{[max]}$ (lynx points)/100), then selected a grid size of 80x80m to encompass default values for most (88%) collar deployments. This grid size is consistent with the scale at which lynx respond to resource heterogeneity (lynx alter their movements within ~130m of the main road; R. Derbyshire, *unpublished data*) and ensures that home range estimates are contiguous (Kie 2013, Signer et al. 2019) and not sampled at a finer scale than our other spatial covariates. We calculated the probability density value for each grid cell, then included in the *UD* all cells that cumulatively contained ≥99% of density values.

To investigate how characteristics of lynx home ranges change over time, for each *UD* we calculated: i) area; ii) average *SCU* and *Elev*; iii) maximum probability density (*UD*) value; and iv) proportional *Veg* use based on probability density estimates from lynx *UD*s. For the latter, we summed *UD* values for each *Veg* type, then multiplied this by proportion of cells of that habitat within the *UD* (e.g., proportional density probability of *Spruce* habitat for a given *UD* = sum [probability$_{Spruce}$] * Number Cells$_{Spruce}$ / Number Cells$_{Total}$). These variables were each used as separate response variables in a series of linear mixed effects models fit using package *lmer*, with *Year*, *Season* and *Days* as predictor variables; we included number of days [*Days*] for each collar deployment to control for this variable in calculations of mean home range values. Individual *lynx ID* was included as a random factor in all models.

Drivers of hare kill sites and lynx UD

To investigate whether the distribution of kills across habitat types changed over time, we first calculated the number of kills for each *Veg* type in each *Year*, then specified this value as the response variable in a Poisson generalised linear mixed effects model with *Veg*Year* as the predictor variables and *lynx ID* as a random factor. To assess shifts in relative hare abundance and further understand possible drivers of lynx kills, we used the hare track model that specified an interaction between *Veg* and *Year* (model 18; Table 1). We repeated this analysis with kills/*SCU* and kills/*Elev* value. For hare tracks, we used the associated model for each predictor variable and its interaction with *Year* (*SCU*: track model 16; *Elev*: track model 17; Table 1) to predict shifts in relative abundance over time for each of these spatial covariates. These analyses were conducted to investigate how changes in lynx home range characteristics may relate to kill site characteristics and relative hare abundance and were intended to summarize overall changes in kill habitat over time.

We then employed a resource selection framework (use vs. availability) to compare kill site locations to available locations within each lynx home range (Northrup et al. 2022). We cropped lynx *UDs* to our study area (Fig. 1), which included 77.1% of lynx *UD*s. We plotted 100 random points in each cropped *UD* (ratio of used to available points = 1:4 for data pooled across all collar deployments). This number of random locations allowed us to sample a variety of habitat types within the study area while reducing the likelihood of poorly approximating the resource use model (Northrup et al. 2013). We specified 16 competing binomial mixed models in package *lme4* (Bates et al.

2023) to explain the locations of hare kills by lynx, with source of the point (kill or random point) as response variable and collar deployment ID as a random effect (i.e., each deployed collar was considered separately, regardless of lynx ID). First, we specified a null model (1) and two models including exclusively temporal covariates: ~ *Year* (2); and ~ *Year* + *Season* (3). These models allowed us to evaluate how changes in environmental variables over time, independent of hare abundance, may influence lynx kill behaviour. We included the models ~ *Veg* (4), and ~*Elev* (5) to assess the effect of these spatial covariates alone on kill location. To test prediction 1 (see Introduction; consistent lynx selection for habitats with high relative hare abundance), we specified model (6) as ~ *RelAb*. *Year* and *Season* were not included alongside *RelAb* in any models because of correlations between variables (*RelAb* and *Year*: r = -0.78; *RelAb* and *Season*: r = -0.57). To test prediction 2 (increasing selection for hare vulnerability), we specified two sets of models with interactions between either *SCU*RelAb* (7) and *SCU*Year* (8). To test prediction 3 (increasing selection for high relative abundance), we specified an interaction between *UD*RelAb* (9) and *UD*Year* (10). Models with an interaction with *Year* were included to test time-varying effects outside of changes in hare abundance alone. We tested prediction 4 (consistent selection for high hare vulnerability) with model (11) ~ *SCU,* and (12) ~ *Year + Season + SCU*. Prediction 5 (consistent effect of general lynx space use, irrespective of hare abundance or vulnerability) was tested with model (13) ~ *UD* and (14) ~ *Year + Season + UD*. Finally, we included two global models: model (15) ~ *RelAb + SCU + UD + Elev*; model (16) ~ *Year + Season + SCU + UD + Elev*; these models could not be combined because of correlations between variables. All numerical variables were scaled and centered prior to model fitting. We used AICc to rank models (Burnham and Anderson 2002) and assessed model fit of top models via Nakagawa et al.'s (2017) pseudo-R^2 in the R package *MuMin* (Barton 2022).

We investigated drivers of lynx *UD* values by exploring relative importance of spatial and temporal covariates using model selection. First, we extracted all spatial covariates at each grid point within each individual *UD*, then repeated the same model selection exercise as for kill sites but with *UD* as the response variable and using generalized linear mixed effects models for exponential distributions (Gamma family with a log link). We excluded *UD* as a predictor variable from all models. This resulted in a reduced model set of 12 competing models, which were compared using AICc.

Results

Hare abundance

Over the four winters of study, hare populations fell substantially, as evidenced by mean hare track count per survey segment (30 m) declining by roughly 90% (6.93 ± 0.18 [SE] in 2018, 2.98 ± 0.08 in 2019, 1.13 ± 0.056 in 2020, and 0.63 ± 0.045 in 2021). The prevalence of survey segments lacking hare tracks increased from 13.2% in 2018 to 82.3% in 2021 (180 of 1366 segments in 2018, 941 of 2373 in 2019, 1106 of 1725 in 2020, and 1686 of 2049 in 2021). Thus, our study coincided with a marked decline in hare abundance, as expected based on the cyclic stage of the snowshoe hare population cycle in this region (Krebs et al. 2021).

Hare relative abundance and refuge use

Of the 18 models explaining hare track count, our top model (model 14: AIC weight = 0.88, conditional pseudo-R^2 = 0.27, marginal pseudo-R^2 = 0.21; Table 1) showed that track counts were best predicted by all temporal covariates under consideration, as well as vegetation type, stem cover units, and hare *Turn Angle* (i.e., the best fit model included *Year*, *Season*, *Time Since Snow*, *Veg, SCU,* and *TA*). The second-best model (model 15; ΔAICc = 4.02) was identical to our top model but included one additional covariate (*SL*); we therefore used the top model (model 14) to predict hare relative abundance across the study area. Our top model did not include an interaction with *Year.* Track counts declined each year and over the course of each winter but increased with *Time Since Snow* (Table 2). *SCU* had a weak positive effect on predicted counts (β = 3.53e-05 ± 1.20e-04; Fig. 2). Hares were not more abundant in *Spruce* or *Shrub* habitat compared to *Other* based on the conditional model (*Shrub:* β = -0.015 ± 0.25; *Spruce:* β = 0.024 ± 0.14), although the number of 30 m segments with no hare tracks was higher in *Shrub* based on the zero-inflated binomial model (i.e., the component that modeled the presence and absence of tracks; β = 0.93 ± 0.41; Table 2). The highest number of hare tracks per segment (11.89 tracks/30 m) was predicted for *Early* 2018 in spruce-dominated habitat with high *SCU* (6000 stems/ha), whereas lowest number of tracks per segment was predicted in *Shrub* habitat in *Late* 2021 (0.039 tracks/30 m). Within *Veg* categories, predicted counts over the four winters of study declined at similar rates from 7.59 (± 0.022) to 0.36 (± 0.022) in *Other* (open and deciduous) habitats, 5.53 (± 0.15) to 0.14 (± 0.0052) in *Shrub*, and 9.35 (± 0.078) to 0.55 ± (0.0077) in *Spruce*. Predicted counts across the study area declined 11-fold from mean values of 6.71 (± 0.063) in 2018 to 0.61 (± 0.0089) in 2021.

Table 2: Incidence rate ratios for a zero-inflated negative binomial track count model (model 14) predicting hare track counts from triangular track surveys, identified by AICc as the top model (ΔAICc of second-best model = 4.02 and contained one additional covariate, hare step length; Table 1). In this model, hare track count (per 30m transect segment) was the response variable, triangle transect ID was included as a random factor, and counts were weighted by a spatial autocovariate to reduce possible bias from spatially correlated counts. Estimates (± SE) and p-values from the conditional and the zero-inflated components are presented (conditional = number of tracks when tracks were present; zero-inflated = presence (1) and absence (0) of tracks). Predictors include time since snow (*TSS*), vegetation type (*Veg*), hare turn angle (*TA*), and Stem Cover Units (*SCU*; index of stem density that accounts for tree species). Reference levels for factors are: *Year* = 2018, *Season* = *Early*, *Veg* = *Other* habitats.

	Conditional		***Zero inflated***	
	Estimate	**p**	**Estimate**	**p**
(Intercept)	1.90 [0.73, 3.08]	<0.01	−2.21 [−4.92, 0.51]	0.11
Year2019	−0.228 [−0.373, −0.083]	<0.01	2.6 [1.1, 4.2]	<0.01
Year2020	−0.927 [−1.075, −0.778]	<0.01	3.65 [1.98, 5.33]	<0.01
Year2021	−0.68 [−0.92, −0.43]	<0.01	5.1 [3.3, 6.9]	<0.01
Season	−0.32 [−0.42, −0.22]	<0.01	0.317 [0.137, 0.498]	<0.01
TSS	0.15 [−0.05, 0.35]	0.14	−0.55 [−0.75, −0.35]	<0.01
SCU	3.5e−05 [−2.0e−04, 2.7e−04]	0.77	−4.5e−04 [−8.4e−04, −6.2e−05]	0.02
Shrub	−0.015 [−0.504, 0.474]	0.95	0.93 [0.13, 1.73]	0.02
Spruce	0.024 [−0.254, 0.301]	0.87	−0.097 [−0.565, 0.371]	0.68
TA	−0.196 [−0.310, −0.082]	<0.01	0.320 [0.065, 0.576]	0.01

Our top model included a measure of vegetation density, *SCU*, which had a positive (albeit modest) influence on track counts. Based on our curve-fitting, a quadratic model best predicted track counts over the range of *SCU* values (Fig. 2, Table A-B4). Mean predicted track count was highest at intermediate *SCU* values in 2018 (mean = 8.74 tracks/segment at 2100 *SCU*), whereas in later years of the study, the highest counts were associated with high *SCU* (2019: mean = 3.98 tracks/segment at

6000 *SCU*; 2020: mean = 1.78 tracks/segment at 6000 *SCU*; 2021: mean = 1.43 tracks/segment at 5400 *SCU*).

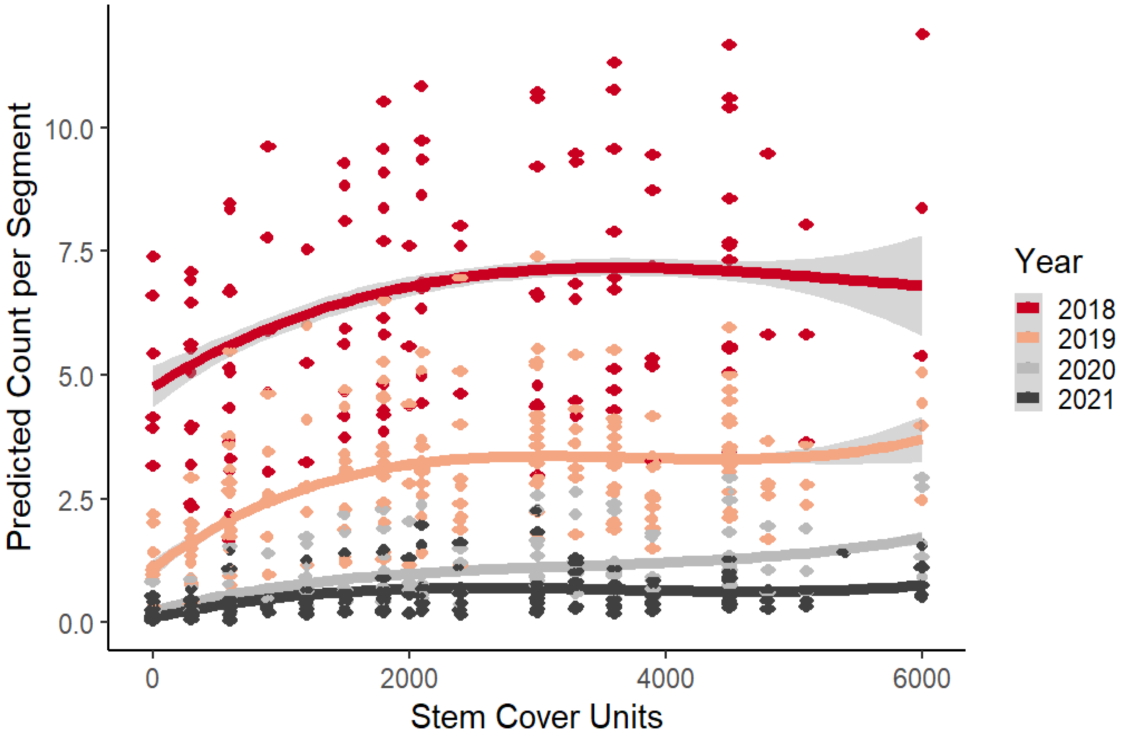

Figure 2: Predicted relative abundance of snowshoe hare tracks based on Stem Cover Units (index of stem density that accounts for tree species; see *Methods*) for winter snow track transects in southwest Yukon, Canada (2018-2021). Predicted counts refer to the estimated number of hare tracks per 30m survey segment predicted by our most-supported model (Table 1). Lines represent a quadratic model fit to the data for each year separately, ± SE.

Lynx spatial behaviour

Patterns of lynx space use changed very little over time, with consistent mean home range size (2018: 2152 ha, inter-quartile range (IQR) = 1358 - 2198; 2019: 2843 ha, IQR = 1900 - 2668; 2020: 2542 ha, IQR = 1792 - 3181; 2021: 3498 ha, IQR = 1906 - 4733; Fig. 3A-B). Further, neither mean *SCU* (2018: 2003, IQR = 1286 - 2685; 2019: 1938, IQR = 1486 - 2378; 2020: 2161, IQR = 1358 - 2855; 2021: 1818, IQR = 1651 - 1927; Fig. 3C-D) nor mean elevation (2018: 977 m, IQR = 899 - 1069; 2019: 989 m, IQR = 973 - 1063; 2020: 956 m, IQR = 876 - 1028; 2021: 974 m, IQR = 954 - 994; Fig. 3E-F) varied through time across lynx home ranges. Lynx did not proportionally use vegetation types within the home range differentially over the four years of the study (Fig. A-B6). Lynx also did not shift in their intensity of use within the home (maximum *UD* probability values remained constant across winters: 2018: 2.79e-7, IQR = 1.49e-7 – 3.10e-7; 2019: 1.99e-7, IQR = 1.46e-7 – 2.21e-7; 2020: 2.42e-7, IQR = 1.62e-7 – 2.58e-7; 2021: 2.43e-7, IQR = 1.30e-7 – 2.91e-7; Fig. A-B7).

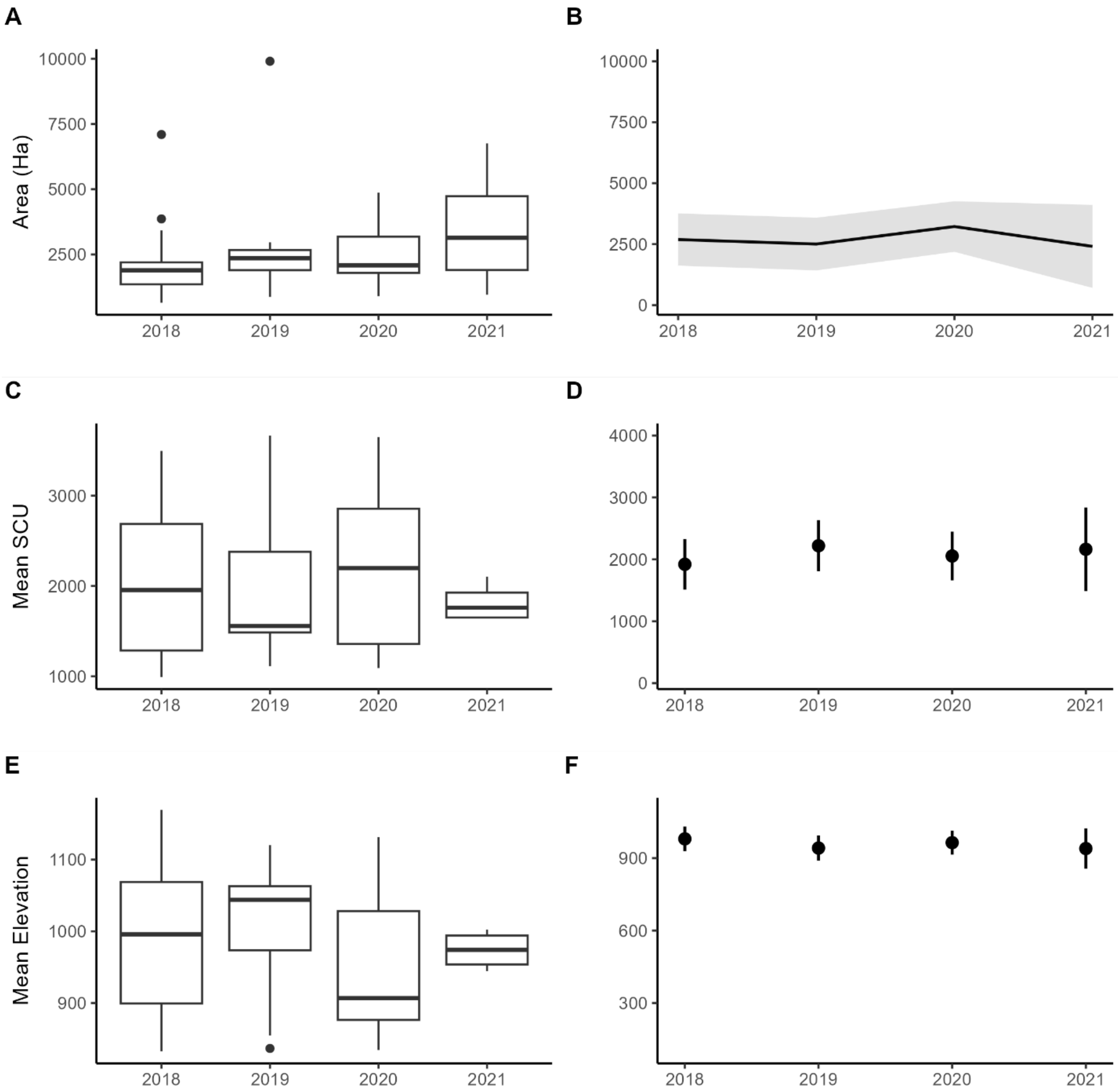

Figure 3: Changes in Canada lynx home range characteristics based on 99% kernel density estimates over four winters in the Kluane region of Yukon, Canada (home range area = A & B; Stem Cover Units = C & D; elevation = E & F). Left-hand plots display mean values calculated from raw home range data; right-hand plots display predictions from a linear mixed effects model that controlled for *Season* (*Early*, *Mid*, or *Late* winter), the number of days the collar was deployed, and a random effect of lynx ID. Sample sizes for mean values (A, C, and E) are as follows: 2018 = 19, 2019 = 11, 2020 = 15, 2021 = 4.

Drivers of hare kill sites and lynx UD

Most hare kills by lynx (56%) were detected during the first winter of study (2018: 588 kills from 19 collars; 2019: 212 kills from 11 collars; 2020: 221 kills from 15 collars; 2021:

50 kills from 4 collars). Lynx killed more hares in *Spruce* compared to other vegetation types (780 kills in *Spruce*, 164 in *Shrub,* and 127 in *Other*; β = 1.55 ± 0.12), but the degree of this difference declined qualitatively in the following years (Fig. 4A). However, based on our hare track model of the change in *Veg* effects through time (model 18, Table 1), there were no appreciable variation in relative hare abundance among habitats, although there were fewer zero counts in *Spruce* habitat (β = -0.44 ± 0.19 for zero-inflated model), and there was a *Veg* X *Year* interaction, with fewer hare tracks in *Spruce* compared to *Other* in 2020 ($Spruce_{[2019]}$: β = 0.064 ± 0.20; $Spruce_{[2020]}$: β = -0.83 ± 0.22; $Spruce_{[2021]}$: β = 0.32 ± 0.34; Fig. 4B). The number of hare kills was also lower in denser cover (i.e., higher *SCU:* β = -0.21 ± 0.044), and the degree of this effect was qualitatively larger in 2018 (i.e., the negative relationship between kills and *SCU* was strongest in 2018; Fig. 4C). Conversely, according to the hare track model of *SCU* effects through time (model 16, Table 1), hares were more abundant in denser cover (*SCU*: β = 1.40e-04 ± 3.02e-05), although the slope of this relationship decreased during the 4 years (Fig. 4D). There was no strong relationship between elevation and lynx kill sites (β = -0.028 ± 0.041), although in 2019 lynx killed more kills at higher elevation, and in 2021 this pattern was reversed ($Elev_{[2019]}$: β = 0.42 ± 0.082; $Elev_{[2020]}$: β = -0.12 ± 0.079; $Elev_{[2021]}$: β = -0.47 ± 0.16; Fig. 4E). Similarly, according to the hare track model of *Elev* effects through time (model 17, Table 1), elevation did not strongly influence hare abundance (β = -0.00011 ± 0.0011), but there was a slight increase in *RelAb* abundance at higher elevations in later years of the study (Fig. 4F).

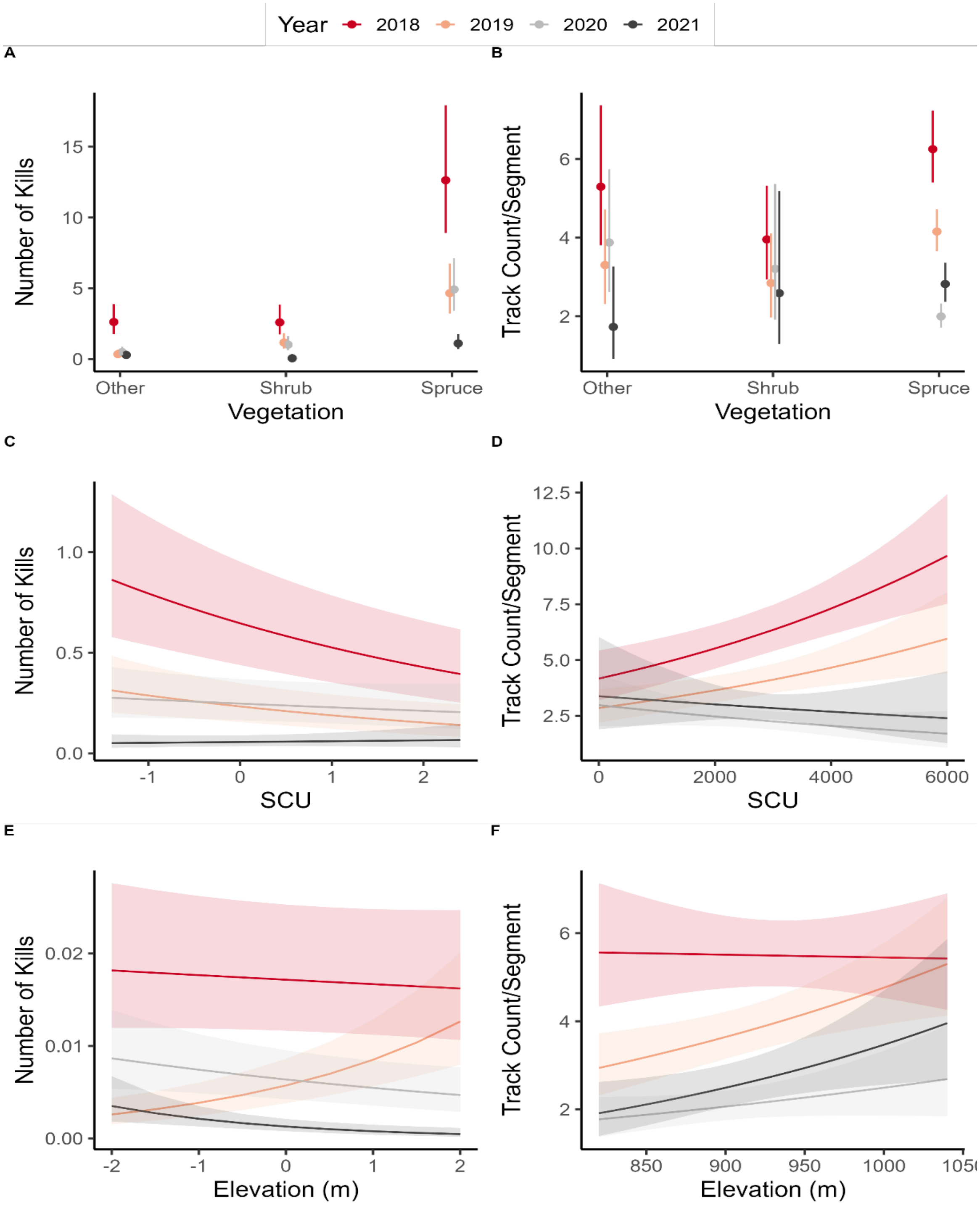

Figure 4: Changes in Canada lynx kill site characteristics and predicted hare track count in the Kluane region of Yukon, Canada (based on vegetation type, *SCU* (index of stem density that accounts for tree species), and elevation (m)). Left-hand plots display characteristics of lynx kill sites based on linear mixed models of the interactive effect of each spatial covariate with *Year* (*SCU* and *Elevation* values have been scaled and centred), while right-hand plots display the analogous hare track count predictions from zero-inflated negative binomial models (track models 16-18; Table 1). Lines represent model predictions ± SE.

Lynx kill site selection was best explained by the global model including lynx utilization distribution, hare relative abundance, elevation, and *Stem Cover Units* (model 14: ΔAICc = 0.00, AIC weight = 0.90, conditional pseudo R^2 = 0.29, marginal pseudo R^2 = 0.18; Table 3). The second-best model (model 16: ΔAICc = 4.51, AIC weight = 0.09) was identical to our top model, but with *Year* and *Season* substituted for hare *RelAb*; we selected the simpler top model (model 15) to explain patterns in kill site location. According to this model, lynx were more likely to kill hares in proportion to lynx habitat utilization (β = 0.81 ± 0.039) and relative hare abundance (β = 0.33 ± 0.080), with a weaker positive effect of vegetation density (*SCU*: β = 0.13 ± 0.042) and elevation (β = 0.18 ± 0.057) on kill probability (Table 4; Fig. 5). The mean *RelAb* value at kill sites was up to 23% higher than non-kill sites across years, with the degree of difference increasing over time (2018: 0% higher; 2019: 12% higher; 2020: 18% higher; 2021: 26%).

Table 3: Model parameters and AICc comparisons for drivers of kill site location. All models with ΔAICc < 100 are shown; all others are excluded for brevity (6 of 15 models are shown here). The response variable is kill location (vs. random point). The model considers each collar deployment separately, with 99% kernel density utilization distribution (*UD)* and cropped *UD* to the study area (Fig. 1). We include as predictors: hare relative abundance (*RelAb*), lynx utilization distribution (*UD*), Stem Cover Units (*SCU*), vegetation (*Veg*), and elevation (*Elev*).

Model #	*Parameters*	*K*	*AICc*	*Δ AICc*	*AICwt*
15	~SCU + RelAb + UD + Elev	6	4710.53	0.00	0.90
16	~Year + Season + SCU + UD + Elev	9	4715.04	4.51	0.09
9	~UD*RelAb	5	4722.44	11.91	0.00
10	~UD*Year	9	4724.65	14.12	0.00
14	~Year + Season + UD	7	4725.21	14.68	0.00
13	~UD	3	4734.10	23.57	0.00

Table 4: Coefficient estimates from top model for predicting lynx kill site locations. For each model, kill status (observed or random) was the response variable and lynx collar deployment ID was included as a random factor. We include as abbreviations of predictors: Stem Cover Units (*SCU;* index of stem density that accounts for tree species), hare relative abundance (*RelAb*), lynx utilization distribution (*UD*), and elevation (*Elev*).

	Est.	***p***
(Intercept)	−1.871 [−2.091, −1.650]	<0.001
RelAb	0.326 [0.169, 0.483]	<0.001
SCU	0.128 [0.045, 0.211]	0.003
UD	0.810 [0.733, 0.887]	<0.001
Elev	0.175 [0.063, 0.287]	0.002

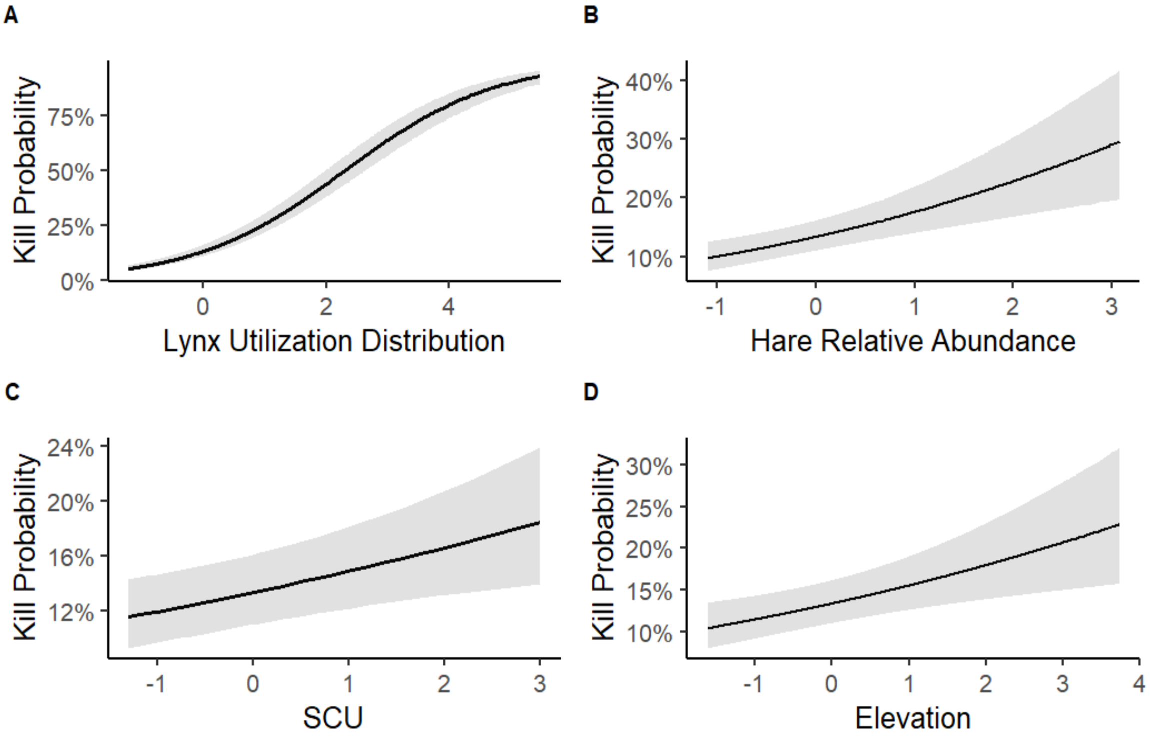

Figure 5: Model predictions for the top model (based on AICc: ΔAICc of second-best model = 4.51; Table 3) predicting lynx kill site locations of snowshoe hare using a use/availability framework. For each model, kill status (observed kill or random point) was the response variable and lynx collar deployment ID was included as a random factor. In all plots, the predictor variables were scaled and centred. The figure depicts kill probability as it is predicted by A) lynx utilization distribution; B) hare relative abundance; C) Stem Cover Units *(SCU;* index of stem density that accounts for tree species*)*; D) elevation (m). Shaded regions represent 95% confidence intervals of model estimates. See Methods for additional details.

Unlike kill site selection, lynx *UD* was best predicted by the model representing effects of vegetation density through time when accounting for the random effect of collar deployment ID (model 8: ΔAICc = 0.00, AIC weight = 1, conditional pseudo R^2 = 0.63, marginal pseudo R^2 = 0.019; Table A-B5). According to this model, lynx spent more time in denser habitats in the later part of the hare cycle (2020 and 2021), but this pattern was reversed in the earlier part of the cycle when they more frequently used more open habitats (Fig. 6, Table 5). However, the most important driver of lynx *UD* in this model was the random effect of collar deployment ID (Fig. A-B8), which increased model fit by 61% based on conditional/marginal R^2 values and identified that the response to *SCU* over time varied markedly across collar deployments. We conducted an ancillary analysis to further explore the effect of collar deployment ID on our results and the top model explaining *UD* remained the same (Appendix B2). Thus, we infer that variation in the local environment (i.e., differences in attributes between individual home ranges) had an over-arching effect on the space use of our study animals.

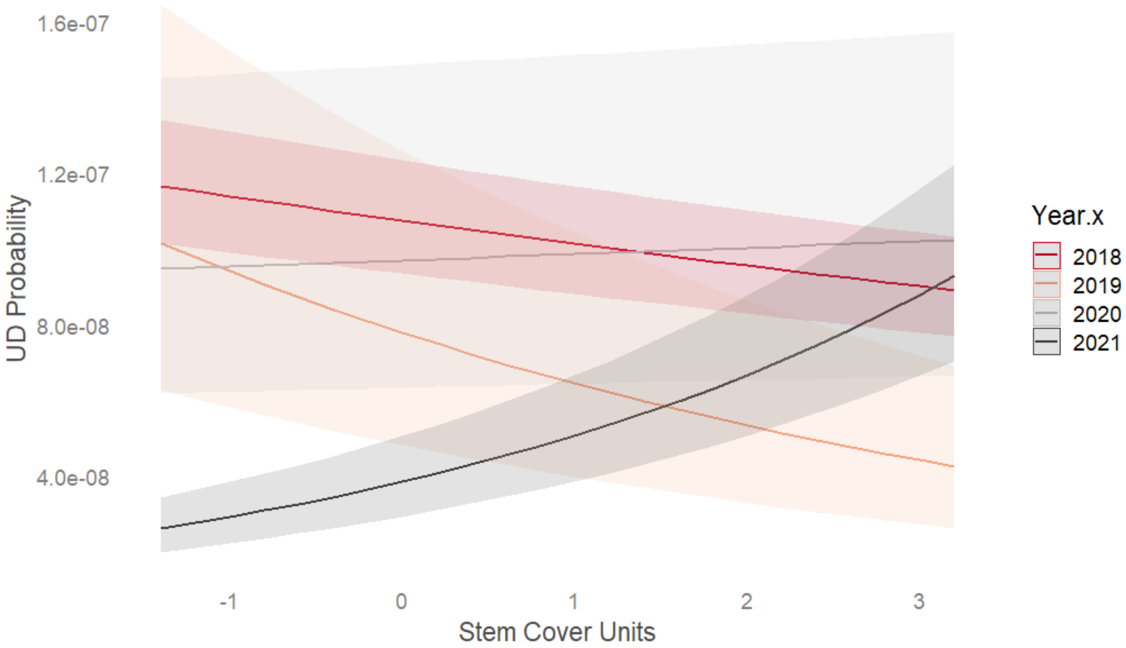

Figure 6: Model predictions for the top model (based on AICc: ΔAICc of second-best model = 770.62; Table A-B5) predicting lynx utilization distribution (*UD*) probability values. For this model, lynx *UD* was the response variable and lynx collar deployment ID was included as a random factor. *UD* probability values as they relate to Stem Cover Units (index of stem density that accounts for tree species) are plotted separately for each year. Shaded regions represent 95% confidence intervals of model estimates.

Table 5: Coefficient estimates from top model for predicting values of lynx utilization distributions (*UD*). For each model, *UD* probability at each pixel of individual lynx home ranges was the response variable and lynx collar deployment ID was included as a random factor. The variables Stem Cover Units (*SCU*; index of stem density that accounts for tree species) and *Year* (coded as a factor: reference level = 2018), as well as the interaction between the two, were included as predictor variables. See Methods for additional details.

	Est.	***p***
(Intercept)	−16.046 [−16.185, −15.907]	<0.001
SCU	−0.059 [−0.074, −0.043]	<0.001
Year[2019]	−0.322 [−0.814, 0.170]	0.200
Year[2020]	−0.102 [−0.529, 0.324]	0.638
Year[2021]	−1.028 [−1.272, −0.784]	<0.001
SCU × Year[2019]	−0.131 [−0.155, −0.107]	<0.001
SCU × Year[2020]	0.075 [0.054, 0.096]	<0.001
SCU × Year[2021]	0.334 [0.314, 0.354]	<0.001

Discussion

Our study revealed that lynx kill locations through a hare population decline were driven by a combination of lynx space use, hare relative abundance, and to a lesser extent, vegetation density and elevation. The strongest driver of kill site location was lynx space use, with kill probability exceeding 80% at the highest values of use probability (*UD*). Lynx killed hares more often in habitats with higher relative abundance of hares, with a weaker positive effect of vegetation density; this pattern mirrored our index of hare relative abundance which revealed higher track counts in denser cover (Fig. 2). Despite the 90% decline in hare relative abundance during the study, lynx kill site selection patterns did not shift appreciably. However, because lynx space use was best explained by vegetation density and this relationship changed with time, we surmise that lynx responded to interannual changes in relative hare abundance by spending more time in denser cover when hares were concentrated in that cover type. Together, we therefore interpret these results as support for prediction 1, namely that lynx kill hares in habitats with high relative hare abundance during all phases of the cycle, but with some (equivocal) support for prediction 3, that lynx may also shift to hunting in habitats with greater relative abundance of hares as populations decline. The strong effect of our hare *RelAb* variable on kill site selection and the increasing use of dense habitats by lynx (mirroring a similar shift by hares) support this interpretation. Indeed, previous work in Kluane showed that lynx hunting activity was concentrated in habitats with the highest abundance of hares (Murray et al. 1994, 1995) but that lynx used progressively denser cover during the late increase to the early decline phase of the hare cycle (O'Donoghue et al. 1998a).

Since hare kills were associated with patches of high hare abundance throughout the cycle, our results do not support assertions that hares can always reduce predation risk by occupying refuges in the form of dense vegetation (Wolff 1980, Hik 1995, Wirsing et al. 2002). However, it is notable that in other systems where hare refuges are thought to be important for protection against predation, stem densities are much higher than those in Kluane. In Maine, Canada lynx selected habitats with intermediate hare density and intermediate cover for hares, suggesting that lynx selected habitats where hares were more vulnerable to predation rather than where hares were most abundant (Fuller et al. 2007). However, stands in Maine with the highest hare abundance sometimes exceeded 14,000 tree stems/ha (or 52,000 *SCU*, based on trees protruding from the snowpack). This contrasts with our study area in Kluane, where stem densities rarely exceed 2000 stems/ha and these dense stands only account for 2% of our study area; maximum *SCU* was >7 times greater in Maine compared to Kluane. Similarly, in Montana, stem density averaged 700 stems/ha for trees >10 cm diameter at breast height [*dbh*] (2500 stems/ha for trees <10 cm *dbh*), and lynx tended to kill hares in habitats with dense vegetative cover (Squires et al. 2010). Therefore, it appears that *de facto* refuge habitat for hares in our study area is limited in availability and perhaps serves as an ineffective deterrent to lynx. This may have important implications for our understanding of lynx and hare interactions (and by extension population cycles), which have previously been hypothesized to be mediated by refuges (Wolff 1980, Chivers et al.

2014). If cycles are not reliant on the existence of a distinct spatial refuge based on habitat characteristics, other types of refuges (e.g., temporal, allee effect (McLellan et al. 2010)) may play a larger role than previously realized.

Importantly, despite our inclusion of a *Shrub* category with our *Veg* parameter, we did not account for the percentage of shrub cover within other vegetation categories, namely *Spruce*. Percent shrub cover likely has important consequences for hare occupancy and density because shrub can create dense understory cover (Wolff 1980, Litvaitis et al. 1985). However, we chose not to include this measure as a covariate for several reasons. First, shrub growth is known to be increasing with climate change, compared to trees which are experiencing reduced growth rates (Reid et al. 2022), and therefore percent shrub cover has likely changed more drastically than stem density since the YGVI was published in 2012. Moreover, shrub cover percentage seems to be negatively correlated with stem density, making these two measures possibly redundant (Fig. A-B9). We also confirmed that inclusion of shrub cover percentage in our track models did not change our top track count model (*unpublished data*). However, we recognize that our lack of inclusion of shrub cover percentage is an important limitation of our study and may explain why we did not find strong evidence of hares using a spatial refuge. Future work should attempt to measure contemporary levels of shrub cover in Kluane in an effort to address this question.

Surprisingly, patterns of lynx space use were not best explained by hare relative abundance alone and were instead described by time-varying effects of vegetation density. This is contrary to many studies on predator habitat use and its relation to prey availability. For example, coyote (*Canis latrans*) use of rabbit (*Sylvilagus* spp.) habitat remained consistent, even during a period of low rabbit abundance, despite a putative shift to alternate prey (Brunet et al. 2023). Similarly, puma (*Puma concolor*) utilization distributions correlated with the *UD* of their prey*,* although with a stronger correlation in less complex (more open) habitat (Smith et al. 2019). Although it is possible that the resolution of our utilization distribution analysis (based on a grid size of 80m by 80m) could have obscured patterns of use that were related to prey abundance, a companion analysis using a smaller grid size (60m by 60m, based on the average bandwidth calculated in *amt*) showed comparable results (Appendix B3). We note that the strong influence of collar deployment ID variable on lynx utilization distribution suggests that the availability of habitat within the home range may influence individual patterns of habitat use.

Our understanding of predator-prey ecology can be influenced heavily by scale (Hernandez 2020), and like virtually all ecological questions, our inferences are influenced by the spatial and temporal scales over which we collected data. Within the context of spatial scale, there are several considerations relating to hunting and habitat use behaviour that require further investigation. Although lynx are not considered cursorial predators and generally kill prey using a “sit and wait” tactic over distances of a few metres (*personal observation*; O’Donoghue et al. 1998a, Squires et al. 2010), we did not fully decouple prey encounter and prey kill locations in this study, which may be distinct and can have important implications for understanding the spatial drivers of predation (Hebblewhite et al. 2005, Gervasi et al. 2013). On larger spatial scales, we did not examine the drivers of habitat selection on the landscape scale, i.e., how lynx select and form home ranges; these decisions likely influence the relative availability of habitat types within the home range and therefore could impact hunting behaviour. Lastly, although we explicitly included a temporal component (*Year* and *Season*) in our models, our analyses failed to incorporate possible fine-scale temporal effects such as diel activity patterns which may influence lynx hunting behaviour (e.g., Fig. 4 in chapter 3 of this thesis; Kolbe and Squires 2007; but see Shiratsuru et al. 2023). Despite these limitations, we found strong spatial (e.g., *SCU*) and temporal (e.g., *Year*) influences on behaviour, supporting previous assertions that lynx can respond dynamically to large-scale environmental changes (Ward and Krebs 1985, Breitenmoser et al. 1993, O'Donoghue et al. 1997, Burstahler et al. 2016).

Our results highlight that predator responses to prey may not be strictly driven by either prey relative abundance or vulnerability, which is an important consideration for understanding the consequences of predator hunting behaviour. Importantly, we defined patterns of lynx space use within the home range (lynx *UD*) as a possible driver of kill site selection. Had we not done so we would have concluded erroneously that kill site selection was best explained by vegetation density, hare relative abundance, and their interaction. This conclusion would have conformed with prevalent theory and empirical studies identifying prey abundance and/or prey vulnerability (based on habitat) as the most important driver of kill sites (Hopcraft et al. 2005, Balme et al. 2007, Filla et al. 2017, Zabihi-Seissan et al. 2022; none of these studies used predator *UD* probability within the home range as a predictor variable in kill site models). The conflicting conclusions between our study and prevailing literature could therefore relate to the tendency to omit predator space use within the home range as a predictor of kill sites, leading to misleading inference about the determinants of spatial patterns of predation. Although some studies do include predator *UD* as an index of risk exposure for prey (Willems and Hill 2009, Thaker et al. 2011, Davies et al. 2016), when the drivers of predator *UD* are explicitly tested, they are often linked directly with prey space use and vulnerability. For example, Smith et al. (2019) compared how prey habitat selection and use influenced the space use patterns of puma through the lens of prey vulnerability and found that the correlation between predator and prey space use was heavily influenced by the relative vulnerability of prey (based on structural characteristics of habitat types). However, we show that spatial risk to prey (based on kill sites) and spatial use of predators can be driven by disparate factors.

If patterns of space use by predators are not consistently associated with prey abundance and/or vulnerability, this could have repercussions for our understanding of indirect effects of predators on prey, since the widespread assumption of a direct correlation between predator space use and risk (Willems and Hill 2009, Davies et al. 2016, Northfield et al. 2017, Kachel et al. 2023) may not always be valid. For example, in a review of methodologies for studying community ecology (Schmitz et al. 2017), the authors suggest that predator hunting and foraging behaviour can be effectively represented using predator utilization distributions; given that this assumption has rarely been tested (but see Thaker et al. 2011, Gervasi et al. 2013, Clermont et al. 2021), we propose that this recommendation be taken with caution.

The results of our study emphasize the need to test broad assumptions in predator-prey theory, such as the differential predictors of predator space use and kill site selection. Rather than viewing predator habitat use and hunting behaviour through the dichotomous lens of prey abundance or vulnerability, ecologists should have a more nuanced view of how these interactions play out in nature. Although some work has clearly begun in this regard by assessing predation determinants from the perspective of both predators and prey over varying spatial and temporal scales (Marzluff et al. 2007, Cresswell et al. 2010, Shiratsuru et al. 2023), our understanding of the validity of many assumptions in predator-prey theory is still incomplete. Without further tests assessing which assumptions are valid and generalizable across systems, and how these can be incorporated statistically into explicit evaluation of predictions, we risk perpetuating misleading inferences about how predators kill and how prey avoid being killed in complex ecosystems.

Chapter 4: General Discussion

Synthesis and Significance

The overarching goal of my thesis was to contribute to our understanding of the interactions between predators, prey, and their environment. To achieve this goal, I investigated how the foraging behaviour of an elusive mammal, the Canada lynx, was influenced by the abundance of their primary prey, the snowshoe hare, within the context of a drastic cyclic decline in snowshoe hare density. This investigation required accurate identification of lynx kill sites, which my colleagues and I achieved by developing and validating classification models using biologging technologies such as acoustic recorders and accelerometers. I then estimated relative abundance of snowshoe hares across the study area over time and used spatiotemporal maps of hare abundance (Fig. A-B4), in conjunction with landscape covariates (e.g., vegetation type) and lynx spatial behaviour, to disentangle the drivers of kill sites in Canada lynx.

Chapter 2: Accelerometer and acoustic-based kill site identification

In chapter 2, my colleagues and I developed and validated a classification system for identifying hare kills by Canada lynx, using both acoustic and accelerometer data. This work provided the foundation for my third chapter focused on predation events, but was also novel in its own right. Due to the limited time spent at a kill site (<1 hour) relative to other behavioural states (grooming: ~1 hour, sleeping: >1 hour), it was previously extremely difficult to identify kill sites by Canada lynx without rigorous and time-consuming snow-tracking in the field (O'Donoghue et al. 1998a). Moreover, >70%

of terrestrial carnivores consume small-bodied prey (Carbone et al. 1999), meaning that ecologists have historically missed a substantive piece of the puzzle of carnivore behaviour and kill rates. Even for predators that typically consume large-bodied prey, GPS cluster analysis to identify kill sites has equivocal accuracy, and different techniques or different species can lead to inconsistent results (e.g., Petroelje et al. 2020, Irvine et al. 2022, Lennox et al. 2023, Oliveira et al. 2023). Furthermore, large predators will sometimes consume smaller-bodied prey (Irvine et al. 2022, Freund et al. 2023), further highlighting that ecologists are missing parts of the bigger picture of predator behavioural ecology and kill rates. This research is therefore a significant contribution to the study of hunting behaviour in wild animals that consume medium-sized prey over relatively short periods. However, these techniques can be intensive in terms of both data processing and programming, and future work should prioritize the development of software (e.g., R packages) that can simplify these procedures.

Chapter 3: Drivers of kill sites in Canada lynx

In chapter 3, I used the classification system developed in chapter 2 as a basis to describe and investigate the drivers of kill site selection in Canada lynx. This research is important and original in several ways. First, the dataset was comprised of a large number of kills (>1000), which is rare in most field studies, even contemporary ones (e.g., Maletzke et al. 2008, Woodruff et al. 2018, Irvine et al. 2022, Zulla et al. 2022, Ghaskadbi et al. 2022, but see Dhakal et al. 2023, Oliveira et al. 2023 for recent examples of large sample sizes). In the context of a drastic decline of its primary prey, this allowed an unprecedented look into the foraging ecology of Canada lynx. Second, my model of relative hare abundance allowed for a spatially and temporally explicit depiction of the relative abundance of a keystone species across the entire study area (Fig. A-B4), an index which was missing for this study system (Krebs et al. 2022). Third, I showed that, despite the dichotomy often presented in the literature of “prey density vs. vulnerability” or “prey abundance vs. catchability” (e.g., Hopcraft et al. 2005, Balme et al. 2007, Petrunenko et al. 2016, Rayl et al. 2018, Zabihi-Seissan et al. 2022), these indices may not always be the strongest drivers of kill site selection. Lastly, I explicitly included patterns of lynx space use as a predictor of kill sites, a method that is generally not employed when examining spatial interactions between predators and prey (Schmitz et al. 2017; but see Barker et al. 2023). This allowed for a novel interpretation of patterns of hunting behaviour in this species, namely that kill site selection and space use patterns within the home range are driven by differing but complementary environmental factors as well as varying individual behavioural patterns.

Broader implications and conclusions

Globally, carnivores are under threat (Treves 2009, Ripple et al. 2014, Marneweck et al. 2021). Patterns of carnivore population decline are worrying given their importance in ecosystem structure and function (Frank 2008, Twining et al. 2022, Lu et al. 2023). It is therefore imperative that researchers and conservation practitioners understand and predict the effects of global change on carnivore behaviour, including foraging behaviour and kill rates. In particular, the measurement of kill rate is an essential component for calculating the functional response, which is itself a fundamental aspect of population dynamics and the study of food webs (Andersson and Erlinge 1977, Skalski and Gilliam 2001, Krebs 2022). In this context, ecologists have undertaken numerous studies to document accurate kill rates in the wild. This endeavour has been successful in large carnivores such as wolves (*Canis lupus*) and pumas (*Puma concolor*) that are large enough to carry GPS collars and consume large-bodied prey for which kill sites can be detected using aerial surveys and/or classified using GPS cluster analysis (Hebblewhite et al. 2005, Woodruff et al. 2018, Cristescu et al. 2019). However, many important carnivores are medium-sized (Warret Rodrigues and Roth 2023) and/or cryptic and elusive (Williams et al. 2014, Hertel et al. 2019), leaving an obvious gap in our knowledge of their interactions with prey. With the biologging technology described and validated here, scientists will be able to characterize hunting behaviour, as well as other components of behavioural ecology (Couchoux et al. 2015) in medium to small-sized animals with comparably-sized prey. Moreover, my work highlights the need to include multiple predictors of kill behaviour, including the space use of the focal predator itself, to paint a more complete picture of drivers of behaviour in ecologically-important terrestrial predators.

Future Research

Despite the gaps in knowledge addressed here, there continue to be relevant questions in the field of predator behavioural ecology. Within the Kluane system, I neglected to investigate the influence of alternate prey in my analyses, leaving much uncertainty about the role of prey switching (O’Donoghue et al. 1998a) in lynx foraging behaviour. The incorporation of spatiotemporal estimates of alternate prey abundance would allow us to better understand how the relative abundances of multiple prey species interact to influence predatory behaviour and the frequency and location of predation events. Moreover, although I have shown how patterns of lynx space use influence kill site selection, many unanswered questions remain about how lynx movement behaviours, sociality (O’Donoghue et al. 1998a), state-dependent behaviours (e.g., the effects of hunger), age, and individual differences/plasticity may interact to influence the drivers and outcomes of lynx space use and foraging behaviour. Integrating lynx movement patterns, spatially-explicit behavioural states, and the influence of other dynamic spatial covariates such as snow depth/hardness would help shed light onto the possible drivers of individual variation we see in this population, particularly as it relates to patterns of space use within the home range.

Looming questions remain about the effects of climate change on this system, which is characterised by population cycles of snowshoe hare, a keystone species in the North American boreal forest (Boutin et al. 1995, Krebs et al. 2014, 2018). Population cycles play an important role in ecosystem function (Ims et al. 2008, Gilg et al. 2009). However, climate change may pose a particular risk to lynx/hare cycles through a myriad of processes that have displayed pronounced shifts in northern ecosystems over the last several decades, such as plant growth (Myers-Smith and Hik 2018, Macander et al. 2022), fire regimes (Flannigan et al. 2000, Senici et al. 2010, Jones et al. 2022), and precipitation (Wickström et al. 2020, Reeve et al. 2023). Precipitation in the form of snow may have a particularly large effect on Canada lynx populations through influences on prey availability/detectability and lynx foraging tactics. The Canada lynx is a visual predator (Murray et al. 1995, O’Donoghue et al. 1998a), and snowshoe hares have evolved seasonal coat-colour change as a strategy to avoid visual detection by predators (Jones et al. 2020). However, changing snow conditions, particularly a reduction in the duration of snow cover, have led to a phenological mismatch between snow cover and hare pelage colour (Peltier et al. 2023), potentially leading to changes in hare survival, thermoregulatory costs, and behaviour (Kennah et al. 2023, Oli et al. 2023). The degree of this coat colour mismatch is expected to increase over the next century and may lead to declines in snowshoe hare abundance (Mills et al. 2013, Kumar et al. 2022). Moreover, changing snow conditions will differentially affect snowshoe hare, lynx, and other carnivores (e.g., coyotes) through interactions between snow depth, hardness, and species-specific foot-loading, leading to increased predator efficiency and reduced amplitude of snowshoe hare cycles (Peers et al. 2020). Beyond the winter season, climate change may impact lynx habitat availability through changing fire regimes which may have differential short- and long-term consequences for prey abundance (Vanbianchi et al. 2017, Olson et al. 2023) and influences on the seasonal pulses of energy through the food web. We know little about lynx behaviour outside of the winter months and how this may influence food web dynamics (Humphries et al. 2017).

Climate change has already been identified as a potential risk to the persistence of Canada lynx and other lynx species through multiple interacting effects including prey availability (Fordham et al. 2013, Yan et al. 2013), and is expected to restrict the geographical range of Canada lynx in North America through impacts on prey (Peers et al. 2014). Thus, we must continue to disentangle the consequences of climate change on lynx foraging behaviour if we are to predict its effects on cycle attenuation or disappearance and on population persistence. This is a promising area of research within the Kluane system and beyond.

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Appendix A: Supplementary materials for Chapter 2

Appendix A1. *Permits and Capture/Handling Procedures*

A1.1 Animal Care and Yukon Permits:

McGill University Animal Care and Use Committees (#4728)

Trent University Animal Care and Use Committees (#26170)

Yukon Government Scientists and Explorers (2015 = #15-01, 2016 = #16-02, 2017 = #17-03, 2018 = #18-01, 2019 = #18-85, 2020 = #19-82)

Wildlife Research Permits (2015/16 = #0156, 2016/17 = #0174, 2017/18 = #0215, 2018/2019 = #0299, 2019/2020 = #0317)

A1.2. Capture and Handling

Lynx were trapped using home-made wire mesh box traps (adapted from Kolbe et al. 2003) baited with scent lures and visual attractants. Traps were checked at a minimum once every 24 hours when temperatures were above -20°C or every 12 hours when temperatures were between -20°C and -30°C, meaning that lynx were in traps for a maximum of 24 hours. All traps were closed when temperatures dropped below -30°C. When a lynx was captured, they were transferred to a wooden handling crate and transported, while awake, to a nearby veterinary clinic (~ 40km) for immobilization. Upon arrival, lynx were chemically immobilized with 6 mg/kg ketamine hydrochloride (Ketalar, 50 mg/mL, I.M.), 0.07 mg/kg medetomidine (Domitor, 1 mg/mL, I.M.) or 0.01 mg/kg dexmedetomidine (Dexdomitor, 0.5 mg/mL, I.M.), and 0.07 mg/kg midazolam (Versed, 5 mg/mL, I.M.) based on visual mass estimation. To administer drugs, lynx was pushed to the front of the handling crate (the back wall of the handing crate disconnected and slid forward, gently squeezing the lynx), and the drugs were hand-injected into the gluteal or quadriceps muscle using a ½ inch, 21-gauge needle. After injection, animals were kept in the crate in a quiet location until a sufficient level of sedation was achieved (i.e., recumbent, decreased response to stimuli). Once sedated, the animal was placed in the prone position, eye lubricant was applied, and eyes were covered. Heart rate, respiration rate, rectal temperature, and mucus membrane colour were monitored and recorded every 5 minutes throughout immobilization. Pure oxygen was delivered at 200mL/kg/min via a face mask

Once handling was complete, monitors and intravenous fluids were discontinued and a reversal drug, Atipamezole, administered (0.35 mg/kg, I.M.) to partially reverse the effects of the (dex)medetomidine sedation. The animal was then transferred back into the handling crate, provided with Nutrical® (a high-calorie dietary supplement) on the fur of their front paw, and monitored until they moved their head. At this point, lynx was left in a warm, dark, quiet room until they were standing, alert, and responsive (from 30 minutes to 2 hours), at which time we transported them back to the location of their capture where they were released.

Appendix A2. Audio Settings and Validation

A2.1. Device settings

EDIC-mini recorders were programmed to record continuously at either 16000 Hz with 2-bit compression, or 8000 Hz with 4-bit compression. These devices were removed from original plastic casing, covered in connector coating (MG Chemicals 4229), and an external battery (CR17450ER lithium, 3V, 2200 mAh) was attached. Sokora recorders were programmed to record for 23 hours each day at 8000 Hz with u-Law compression. In our final season (2019-2020), we reduced the sensitivity of the microphone by 6 dB as preliminary analyses revealed that clipping was occurring during louder events. An external battery (Saft Primary Lithium Battery, 3.6V, 3600 mAh) was attached to these devices but the main recorder remained in its original metal housing. Both types of recorders and batteries were covered in a layer of Sugru (FormFormForm Ltd., London, UK) and attached to the collar beside the GPS battery with Sugru and heat shrink tubing.

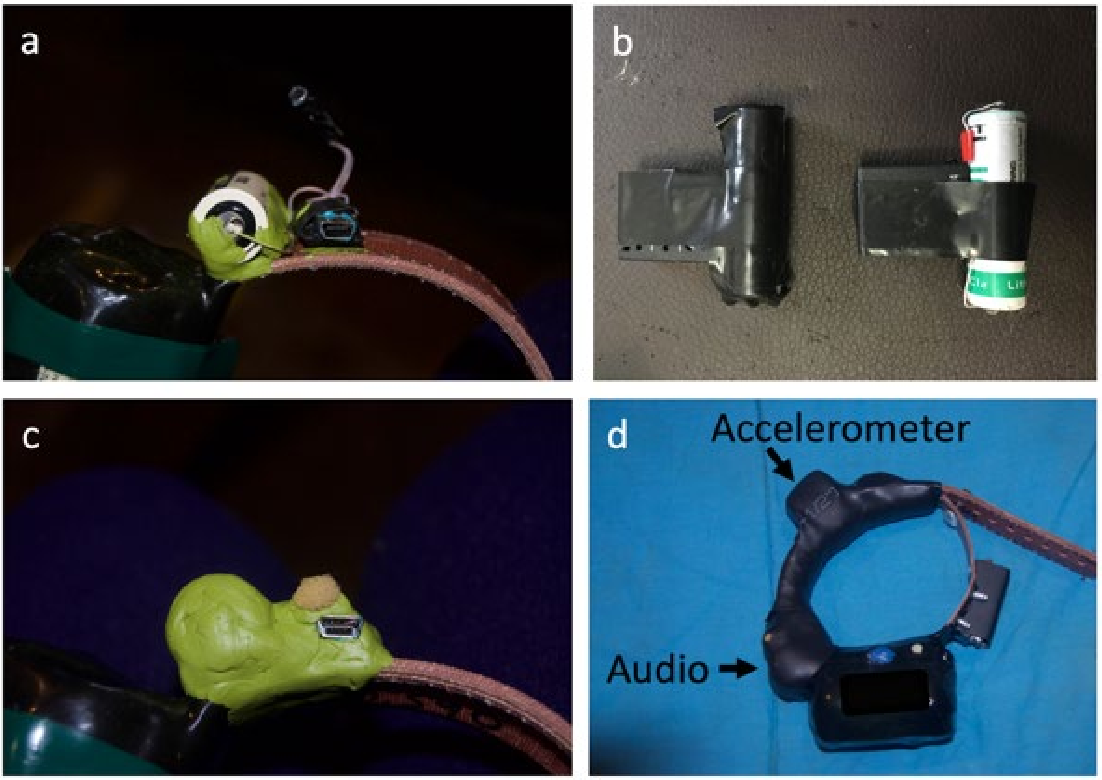

Figure A-A1. Attachment of audio recorders to GPS collars. a) EDIC-mini removed from original casing and rewired. b) SOROKA-14 with external battery wired. c) attachment of audio recorder to collar and d) final collar design with accelerometer and audio recorder covered in heat shrink.

Figure A-A2: Location of audio recorder attachment when deployed on Canada lynx. The recorder sits just above the battery for the GPS unit (red circle). In this photo, the collared lynx is exiting a lynx trap.

A2.2 Audio Validation (chewing sounds)

Prior to generating an automated classification of feeding, we confirmed that the sounds thought to be chewing were in fact chewing. We listened to all audio files that overlapped with snow-tracking and identified all chewing sounds. We created a confusion matrix for how this manual listening aligned to snow tracking kill and non-kill events. This alignment had a 0.98 accuracy, 1.00 recall, 0.93 specificity, 0.97 precision, and 0.99 F1-score, confirming that what we were tagging through manual listening as chewing is chewing.

A2.3 Audio Validation (time misalignment)

In some cases, no feeding event was identified within the audio data at a kill site (N = 12), or a feeding event was identified for a snow-tracking event where no kill site was found (N = 14). We then re-checked the audio data and found several cases of slight time misalignment. These errors occurred because feeding events sometimes took place shortly before or after the GPS points which were checked via snow-tracking. For example, all the points from a given morning (00:00 - 12:00) may have been checked via snow-tracking, and a kill site recorded for 00:00 - 03:00, but the kill event and feeding actually occurred at. 23:30 the previous day, meaning that the feeding event for this kill occurred slightly outside the time of the validated snow-tracking event. Any cases of slight time misalignment (<= 1 hour) were corrected accordingly for the final analysis.

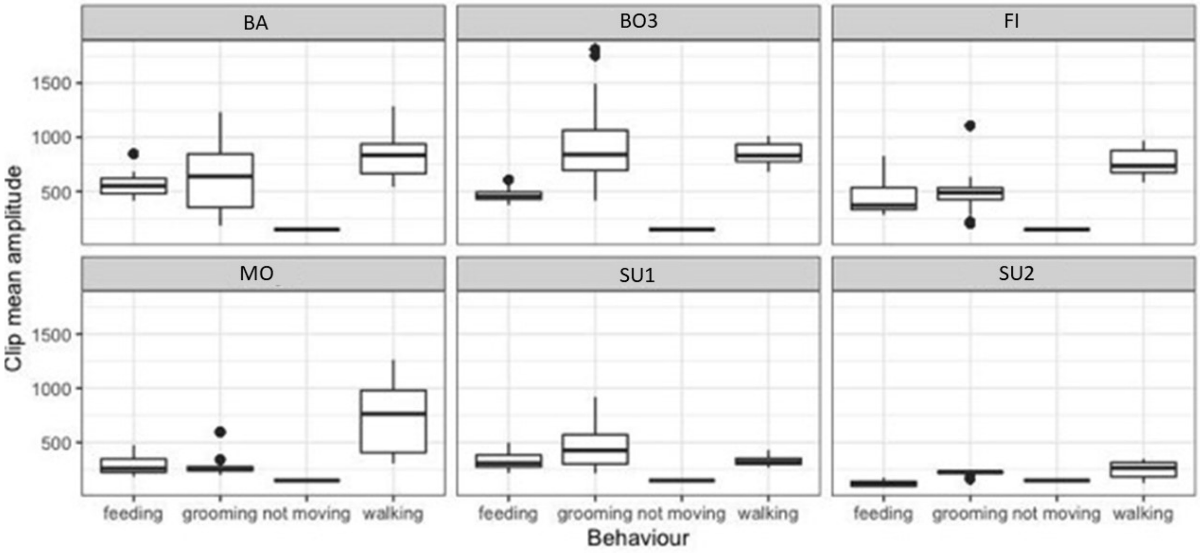

Figure A-A3: Mean amplitude of different behavioural states over 15 second audio clips for 6 different acoustic recorders deployed on free ranging lynx.

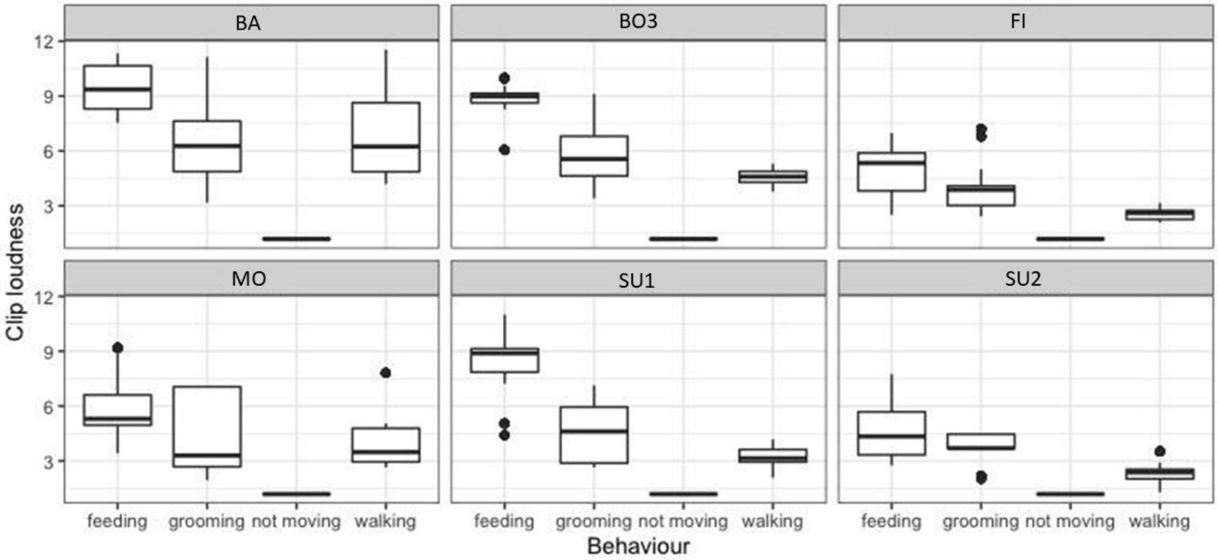

Figure A-A4: Mean loudness of different behavioural states over 15 second audio clips for six acoustic recorders deployed on free ranging lynx.

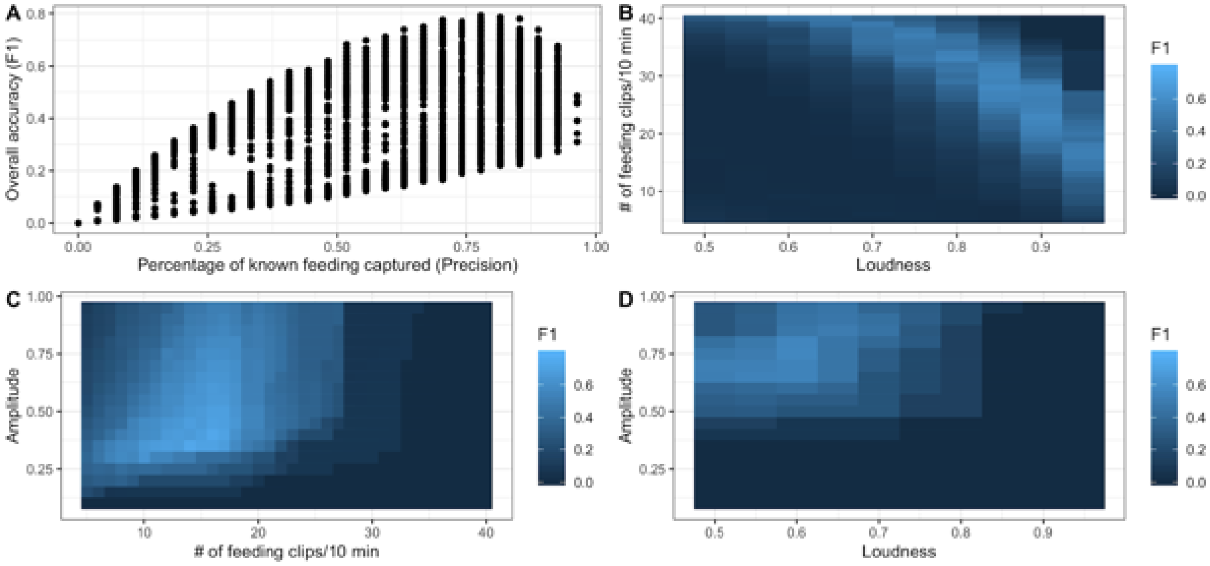

Figure A-A5: Accuracy of 6408 models at identifying feeding events across varying threshold values for clip loudness, amplitude, and number of clips labelled as chewing per 10 minutes. F1-score varied across models relative to the percentage of known feeding events correctly identified in training data (precision; A), driven by different combinations of threshold values for # chewing clips per 10 min, loudness, and amplitude (B, C, and D).

Appendix A3. Accelerometer Validation

A3.1 Known Behaviour Extraction

To convert acceleration into behavioural states, we generated a known behaviour dataset using GPS and acoustic recorders that were deployed on the same lynx as the accelerometer. We then extracted known behaviour for 10 lynx according to the following conditions. Not moving (n=147; 3292 min) was defined as continuous bouts of silence (acoustic amplitude < 10% max) lasting a minimum of 20 minutes in duration. This length of time was chosen so that we could be certain that the lynx was truly stationary and not just pausing amidst its other activities. Periods of walking (n=174; 3012 min) were bouts of sound (amplitude > 10% max) of > 5 minute duration with no pauses longer than 5 seconds that corresponded with lynx travelling at an average speed of 13 – 30 m/min between consecutive GPS fixes. Feeding (n=85; 2351 min) consisted of sounds of bones crunching (i.e., chewing) of > 5 min duration with no pauses longer than 5 seconds. Grooming (n=172; 2876 min) consisted of continuous bouts of sound (amplitude > 10% max) lasting > 5 minutes that did not consist of chewing and occurred when lynx travelled at a speed of < 1 m/min between consecutive GPS fixes. To account for the +/- 2 min error in time alignment between the acoustic and acceleration data, we removed the first and last 3 mins of each behavioural bout from all analyses. From observations and audio listening we found that when lynx partake in a behaviour they generally express that behaviour for long periods of time (i.e. 15 mins). As such, we extracted training samples of each behaviour using a 2-min sliding window with a stride of 1 min from the above dataset.

A3.2 Time Alignment

To control for the fact that clocks on different devices ran at different speeds, we realigned the time on the audio devices to that of the accelerometers and assumed that accelerometers were real time. To realign, we averaged acceleration and acoustic amplitude for each minute and visualized the waveforms. Using transitions from long naps to bouts of moving as identifiable points in both data forms, we determined the time difference between devices at a minimum of 3 points (max=18) per 2GB audio file (16 - 32 hours) and calculated the rate at which time drifted between the two devices with a regression. This regression was then applied to the audio files to match audio time with accelerometer time. Despite this, we assumed there was still an error of +/- 2 minutes in the alignment of the two devices.

A3.3 Model Specifications

For both 1 Hz and 10 Hz Convoluted Neural Network models.

Input shape for 1hz: (120, 1)
Input shape for 10hz: (1200, 1)

```
model = Sequential ()
model.add (Conv1D (filters=32, kernel_size=3, strides=2, input_shape=input_shape))
model.add (Activation('relu'))
model.add (MaxPooling1D(pool_size=2))
model.add (Conv1D (filters=32, kernel_size=3))
model.add (Activation('relu'))
model.add (Dropout (0.2))
model.add (Flatten ())
model.add (Dense (32, activation='relu'))
model.add (Dense (n_outputs, activation='softmax'))
```

Used Adam optimizer.
Learning rate set to 0.00015.
Used 'categorical_crossentropy' loss function.
Trained for 12 epochs with batch size of 8.

For both 1 Hz and 10 Hz Random Forest models.

Tsfresh parameters were:

```
settings = {
  'mean_abs_change': None,
  'abs_energy': None,
  'augmented_dickey_fuller': [ {'attr': 'pvalue'}],
  'number_crossing_m': [ {'m': 0}],
  'agg_linear_trend': [ {'f_agg': 'var', 'chunk_len': 10, 'attr': 'stderr'},
                        {'f_agg': 'max', 'chunk_len': 5, 'attr': 'stderr'}],
  'quantile': [{'q': 0.9}, {'q': 0.7}],
  'cid_ce': [{'normalize': False}],
  'ratio_value_number_to_time_series_length': None,
  'approximate_entropy': [{'r': 0.1, 'm': 2}],
  'number_peaks': [{'n': 3}],
  'agg_autocorrelation': [{'f_agg': 'var'}],
  'change_quantiles':
  [
     {'qh': 0.4, 'ql': 0.0, 'f_agg': 'mean', 'isabs': True},
     {'qh': 0.4, 'ql': 0.0, 'f_agg': 'var', 'isabs': False},
     {'qh': 0.4, 'ql': 0.0, 'f_agg': 'var', 'isabs': True},
     {'qh': 1.0, 'ql': 0.0, 'f_agg': 'mean', 'isabs': True},
     {'qh': 1.0, 'ql': 0.0, 'f_agg': 'var', 'isabs': True},
     {'qh': 1.0, 'ql': 0.8, 'f_agg': 'mean', 'isabs': True},
     {'qh': 1.0, 'ql': 0.8, 'f_agg': 'var', 'isabs': True}
  ],

  'absolute_sum_of_changes': None,
  'partial_autocorrelation': [{'lag': 6}]
}
```

Sklearn random forest was:

```
model = RandomForestClassifier (n_estimators=50, min_samples_split=4, min_samples_leaf=3)
```

A3.4 Acquiring feeding events

The process of acquiring feeding events is as follows. First, a full accelerometer file was processed by the classifier model to generate prediction windows of length 2 minutes at a stride of 1 minute. This resulted in a prediction file with timestamps 1 minute apart and likelihoods for walking, chewing, grooming, and resting. The likelihoods for 'chewing' are extracted and thresholded to be 0 or 1 using a threshold of 0.5. An average+threshold process was then repeated twice. The average+threshold process consists of applying a 3-minute running average filter followed by a threshold to 0/1 using a threshold of 0.5. The effect of the average+threshold process was to smooth noisy predictions to better reflect neighbouring predictions. For example, a solitary chewing prediction would be smoothed to its surrounding and not be counted and, likewise, a brief non-chewing prediction in the middle of a multiple chewing behaviour would be smoothed to become a chewing prediction. The average-threshold process only affects neighbours 0 or 1 minute away from a chewing prediction. We then merged successive 1 predictions together into a singular event with calculated start and end times. Our final feeding events consisted of any group of chewing that were separated by 10 minutes or less.

A3.5 Accelerometer classification results

We classified accelerometer data into four behavioural states at 2-minute resolution with an overall F1- score greater than 0.80, but there was variation in accuracy between sampling frequencies and classification algorithms (Table A-A1). Generally, the random forest algorithm operated better (F1 = 0.85 - 0.91) than the convolutional neural network (F1 = 0.30 - 0.84), with the CNN working better when using only the heave axis (F1 = 0.81 -0.84) than all three axis (F1 = 0.30 - 0.47). There was no discernible difference between the heave and all axis with the random forest (Table A-A1). A 10 Hz frequency sampling had a higher F1 accuracy in classifying the four behavioural states at the scale of minute-to-minute (F1 = 0.84 - 0.91) than the 1 Hz sampling frequency (F1 = 0.81 - 0.85). Of the four behavioural states, the models had the lowest success at correctly classifying grooming (F1 = 0.67-0.82), followed by chewing (F1 = 0.79-0.90), walking (F1 = 0.79-0.94), and resting (F1 = 0.96-0.98).

Table A-A1: Average performance of different accelerometer classification models at identifying feeding, grooming, walking, and not moving (rest) behavioural states at 2 minute resolution using a leave one lynx out cross-validation. Random forest and convolutional neural network models were generated using all three axis and heave only axis of 1 Hz and 10 Hz acceleration data using known behavioural states inferred from GPS and acoustic data. F1-scores are the average model performances on each lynx with 1 Hz (n=5) or 10 Hz (n=5) acceleration data.

Model Type	Axis	Frequency	Overall F1	Feed F1	Groom F1	Walk F1	Rest F1
Random Forest	Heave	1 Hz	0.85	0.82	0.75	0.86	0.98
		10 Hz	0.91	0.90	0.82	0.94	0.98
	All	1 Hz	0.86	0.82	-	-	-
		10 Hz	0.90	0.90	-	-	-
CNN	Heave	1 Hz	0.81	0.79	0.67	0.79	0.96
		10 Hz	0.84	0.81	0.72	0.92	0.97
	All	1 Hz	0.30	0.37	-	-	-
		10 Hz	0.47	0.42	-	-	-

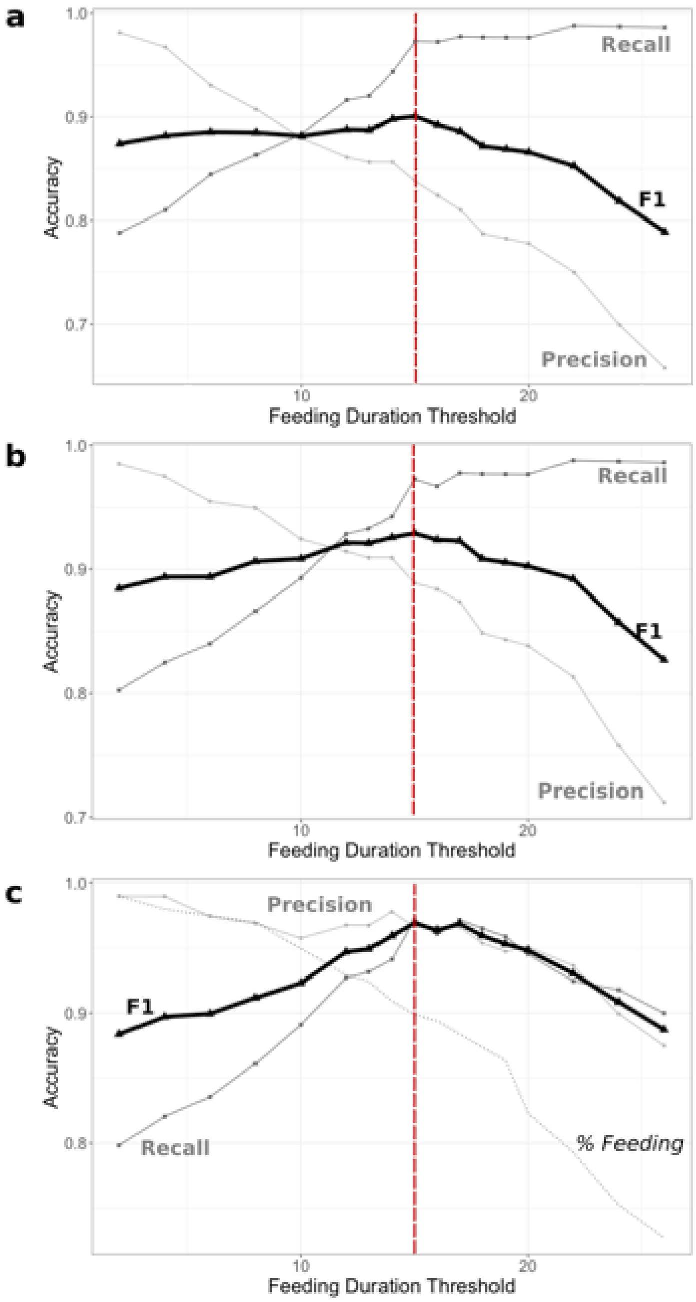

Figure A-A6: Precision, recall, and F1- scores for different feeding duration thresholds applied to accelerometer classification of feeding events in free-ranging Canada lynx . Panel a) is across all feeding events regardless of duration or prey species. Panel b) is across all feeding events on snowshoe hares regardless of duration. Panel c) is across feeding events on snowshoe hares with durations equivalent or longer than the threshold. Dotted grey line in this panel represents the percentage of all hare feeding events that had that duration or longer. Red dotted line represents the threshold value that produced the highest F1-score and was selected as the threshold value in the classification.

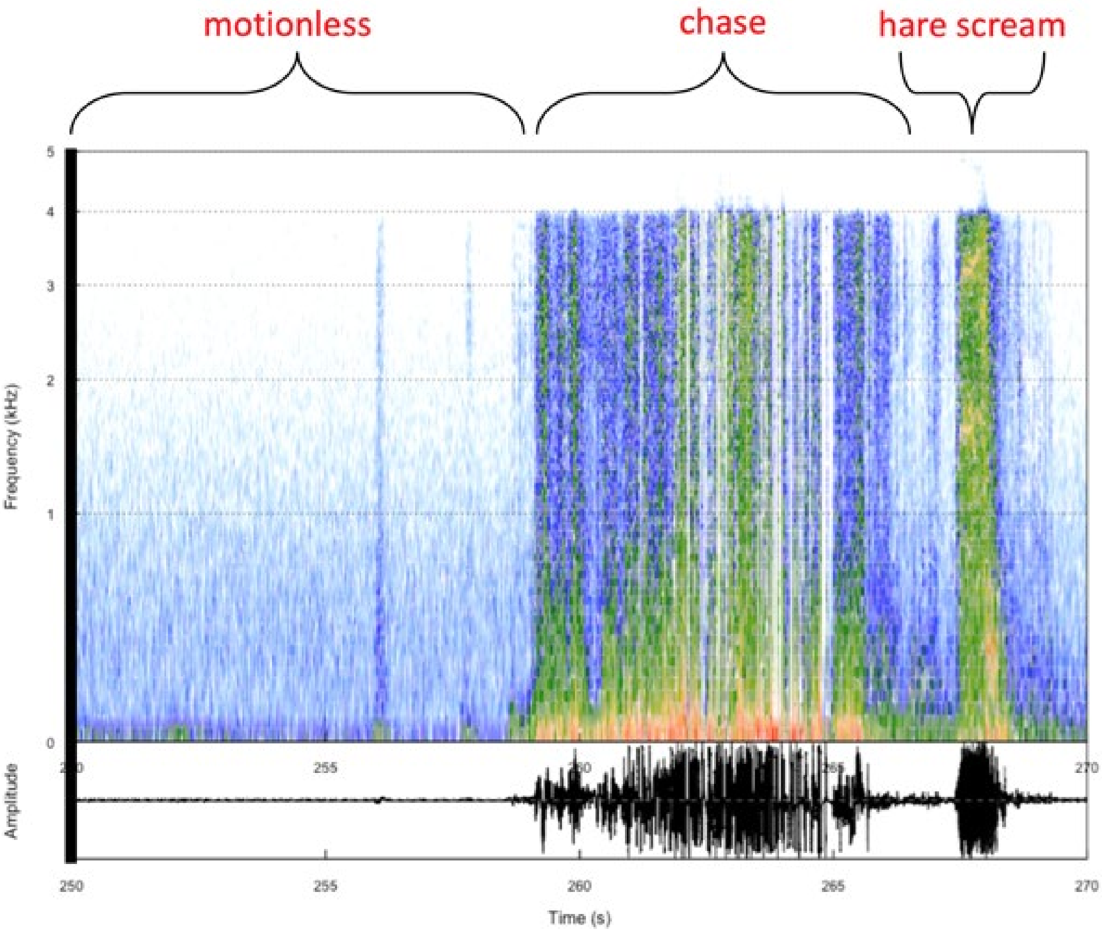

Figure A-A7: Spectrogram of audio clip of lynx hunting and killing a snowshoe hare (harecall.wav).

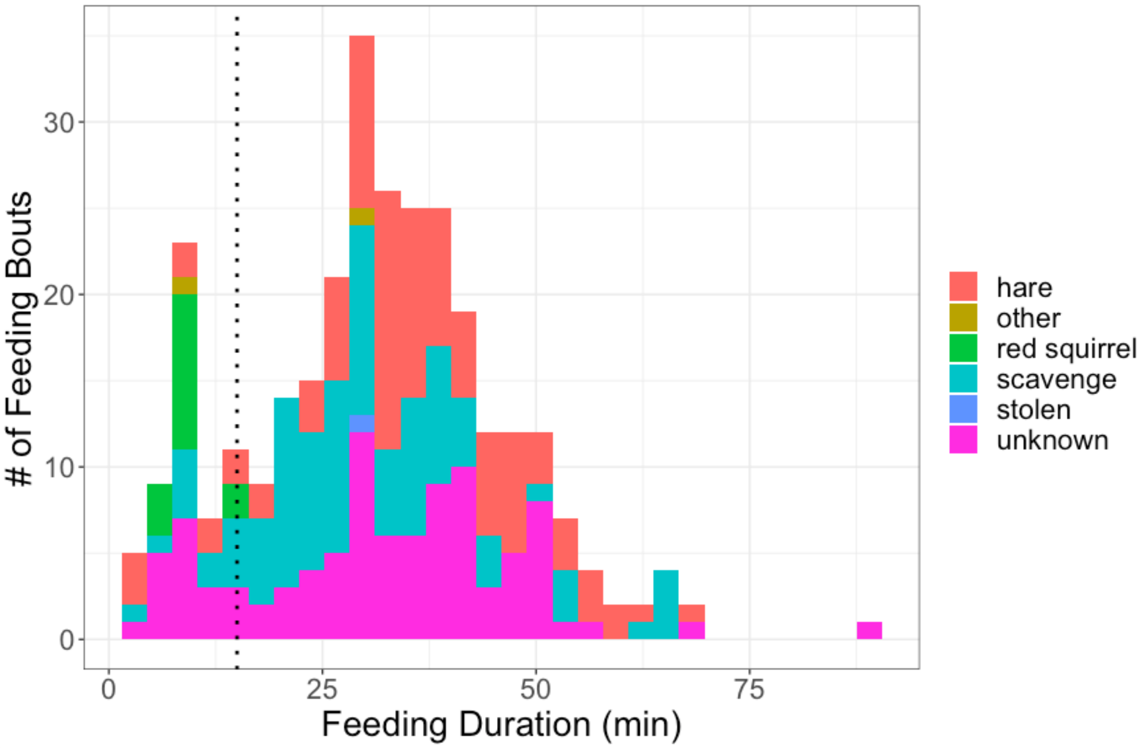

Figure A-A8: Feeding durations of different prey types consumed by free-ranging Canada lynx as measured using audio devices. Dotted line represents the feeding duration threshold applied to accelerometer behavioural classification for identifying feeding events. Hare, red squirrel, and other (avian spp.) are feeding events preceded by a chase and an identifiable prey vocalization. Scavenge are feeding events not preceded by a chase or any hunting behaviour. Unknown are feeding events preceded by a chase but not prey vocalization.

Appendix A4 – A8

The following Appendices can be found at https://besjournals-onlinelibrary-wiley-com.proxy1.lib.trentu.ca/doi/full/10.1111/2041-210X.13605 and are labelled on the website as Supplementary Materials.

Appendix A4 (Supplementary Materials 4): Feeding (feeding.wav)

Appendix A5 (Supplementary Materials 5): Chase and hare kill (harecall.wav)

Appendix A6: (Supplementary Materials 6): Squirrel kill (squirrel_kill_feed.wav)

Appendix A7: (Supplementary Materials 7): Lynx feeding (lynx_feeding.mp4)

Appendix A8: (Supplementary Materials 8): Audio clip of kleptoparasitism (klepto_feed.wav)

Appendix B: Supplementary materials for Chapter 3

Appendix B1

Hare movement

As part of a concurrent study of hares in our area (Majchrzak et al. 2022), we deployed 129 collars on 72 hares between November 15, 2017, and March 19, 2021, over four winter seasons (2017-18, 2018-19, 2019-20, 2020-21). These collars were set at a fix rate of 2-4 fixes per hour and were deployed for a range of 1 to 115 days. Collars were retrieved upon recapture or after the death of the animal due to predation. Sample sizes for collared hares varied over each year of the study; in particular, the cyclical decline in hare abundance led to relatively lower sample sizes in the latter years of the study (n = 32 for 2017-18; n = 27 for 2018-19; n = 7 for 2019-20; n = 6 for 2020-21). For three individuals (two in 2019-20 and one in 2020-21), models could not be fit due to low sample size and problems with convergence.

Using GPS data from these hares, we used integrated Step Selection Functions (iSSFs; Avgar et al. 2016) to calculate habitat-specific step length (distance between each consecutive GPS point; *SL*) and turn angle (angle, in radians, between each consecutive step; *TA*) values for hares. Step selection functions are similar to classic resource selection functions, but define available habitat based on the location and movement speed of the animal; these models can be further modified (i.e., integrated) by updating the *SL* and *TA* parameters based on the initial fit of the model (Avgar et al. 2016). We first pooled all hare data within a year, sampled 15 random steps for each observed step, and fitted iSSFs in R package *amt* (Signer et al. 2019). Our analysis of pooled data suggested that hare *SL* and *TA* may be influenced by stem cover units (*SCU)*; i.e., pooled data for each winter revealed that in all 2019 and 2020, hares selected habitats with higher *SCU* (Table A-B6). In 2018, hares took longer steps in habitats with higher *SCU*, but this effect was not apparent in 2020, and the effect was opposite in 2019 and 2021 (effect of *SL*SCU* in 2018: β = 4.13e-06 ± 1.55e-06, p = 0.008; 2019: β = 1.92e-06 ± 9.25e-07, p = 0.038; 2020: β = 1.03e-06 ± 7.14e-07, p = 0.15; 2021: β = 1.24e-04 ± 5.04e-06, p = 0.011). There did not seem to be an effect of *SCU* on the directionality of hare movement (*TA*; Table A-B6).

Following steps outlined in Fieberg et al. (2021), we then fit separate models for each collar deployment and calculated updated *SL* and *TA* distributions separately for each value of *SCU* (in increments of 100). Averaged model coefficients and updated movement parameter distributions across individual hare iSSFs revealed very little variation in step lengths over the four winters of the study, although the variance of estimates appeared greater in 2021 compared to other winters (Fig. A-B10). Although *TA* decreased with *SCU* in 2018, there was a slight positive relationship between *TA* and *SCU* in 2019, and this positive relationship became more pronounced over each successive year of the study (Fig. A-B10), suggesting that hares began exhibiting more tortuous movement patterns in dense vegetation as lynx: hare ratios increased.

Appendix B2

Random effects for UD model

Based on our analysis of lynx utilization distribution (*UD*), individual collar deployment ID was the strongest predictor of patterns of lynx space use (inclusion of deployment ID increased model fit by 61%; see *Results*). To further explore possible drivers of *UD* and confirm that the strength of the effect of deployment ID was not confounded with other potential variables such as *Year* or *Season,* we conducted an ancillary model selection exercise to test how Year and Season, specified as random factors, may influence model fit. We fit our series of 12 models for explaining *UD*, then fit an identical set of models with either *Year* or *Season* fit as additional random factor. This resulted in 36 competing models consisting of the original models (models 1-12), original + 1|*Year* (models 13-24), and original + 1|*Season* (models 25-36). We compared these models using AICc and found that the same top model was supported as our original analysis (model 8), followed by model 8 + 1|*Season* (ΔAICc = 2.00) and then by model 8 + 1|*Year* (ΔAICc = 2.00; Table A-B7). Based on this result, we were confident that the strong effect of collar deployment ID on patterns of *UD* was not an artifact of a nuisance parameter such as *Year* or *Season*.

Appendix B3

Analysis of grid size for UD analysis

To determine grid size for calculating lynx utilization distributions (*UD*), we used the *ad hoc* method as described by Kie (2013) to select a grid size of 80m^2, which encompassed the calculated grid size for 88% of the lynx in our study (grid sizes as calculated using this *ad hoc* method varied from 36 – 137 across collar deployments). Caution must be exercised when selecting grid size for *UD* analyses, as this selection can have important implications for the shape of *UD* probabilities across the home range (Kie 2013). To investigate whether our choice of grid size influenced the results of our model selection for drivers of lynx *UD*, we repeated the analysis but selected a smaller grid size of 60m^2 based on the mean value across collar deployments (mean = 61.26). We ran an identical set of models using the updated *UD* calculations and found that the top model was still the same as in our original analysis (Table A-B8). We were therefore confident that our selected scale for grid size was not too conservative for interpreting the drivers of *UD*.

Appendix B4

Power analysis for kill site selection

To investigate whether our low sample size of kills in 2021 relative to other years impacted our ability to disentangle any possible interactive effects with *Year*, we conducted a power analysis in package *pwr* (Champely 2020). We were interested in testing whether the difference in mean spatial values at kill site locations between years could be adequately detected based on the kill sample size in each year (2018: n = 588; 2019 = 212; 2020 = 221; 2021: 50), specifically for the covariates in our top model. For this analysis, we selected the spatial covariate in the kill site model with the strongest correlation with *Year*, *RelAb,* then calculated the mean scaled values for this parameter in each year. We then sequentially subtracted the mean values across each combination of 2 years (2018 – 2021; 2018 – 2020; 2018 – 2019; 2019 – 2021; 2019- 2020; 2020 - 2021), and used these differences, as well as the total annual sample size for kills, to compute power for two samples (different sizes) based on a t-test of means with the alternative hypothesis that *RelAb* is greater in earlier years. This analysis revealed variable power between years (Table A-B9), but the mean calculated value was 0.86, and the median was 1, suggesting that we had adequate power to test for differences between years.

CHAPTER 3 APPENDIX TABLES AND FIGURES

Table A-B1: Number of surveys conducted for each triangular transect ("Triangle" column) over each winter of the study (2018-2021). Each triangular survey consisted of three side, each measuring 500m. Triangular transects were located across the study area (Fig.1 in main text). Triangles were sampled within three days of a fresh snowfall and were only re-sampled if >4 days had elapsed since the last visit.

Triangle Name	*2018*	*2019*	*2020*	*2021*
B10	0	0	3	3
B14	3	5	3	3
B22	0	2	2	2
B28	0	3	2	2
B2	0	0	0	1
B34	0	0	0	1
B42	1	3	2	2
B8	3	3	3	3
C20	3	5	3	3
C25	0	0	0	1
C32	1	3	1	2
C38	0	0	0	1
C5	0	0	0	1
D23	3	4	3	3
D33	3	3	2	2
D41	2	3	2	2
E10	3	4	3	3
E16	3	4	3	3
F35	2	2	0	0

Table A-B2: Pearson correlation coefficients (r^2) for predictor variables used in zero-inflated negative binomial models for predicting hare track count across the study area. Parameter values are associated to 30m track transect segments.

Parameter	Year	Season	Time Since Snow	Mean Step Length	Mean Turn Angle	Stem Density	Stem Cover Units	Vegetation Type	Elevation
Year		0.37	0.10	-0.0063	0.033	-0.012	0.018	-0.028	0.025
Season			-0.030	-0.016	-0.030	-0.021	-0.068	0.039	0.23
Time Since Snow				-0.0090	-0.22	-0.025	-0.21	-0.12	0.19
Mean Step Length					-0.15	-0.22	-0.19	-0.11	-0.13
Mean Turn Angle						0.15	0.26	0.091	0.057
Stem Density							0.50	-0.22	-0.11
Stem Cover Units								0.42	-0.20
Vegetation Type									0.081
Elevation									

Table A-B3: Number and timing of collar deployments, as well as number of hare kills, associated with each individual lynx included in the study ("Lynx ID"; each alpha-numeric code represents a different individual). Seasons within each year were defined as follows: *Early*: Dec 1-31; *Mid*: 1 Jan to 11 Feb; and *Late*: 12 Feb to 29 Mar.

Lynx ID	*Number of collars*	*Year and Season*	*Number of kills*
AL	4	Early, late 2018; mid 2020 (2 collars)	77
AR	1	Mid 2019	22
AU	3	Mid, late 2018; late 2020	59
BA1	1	Mid 2018	6
BA2	1	Mid 2020	22
BO1	2	Late 2019; late 2020	19
BO2	2	Early 2018; late 2019	45
BU	2	Early 2018; late 2019	69
DO	1	Late 2021	17
FI	8	Early, mid, late 2018; late 2019 (2 collars); mid, late 2020; late 2021	170
GA	1	Late 2019	8
LI	4	Late 2018; mid 2019; early, late 2020	106
LU	1	Late 2020	14
RA	2	Mid, late 2021	25
RO1	1	Early 2020	26
RO2	1	Late 2019	23
RO3	2	Early, late 2018	76
SE	1	Mid 2018	2
SN	3	Mid 2018; early, late 2020	95
SU1	5	Late 2018 (2 collars); mid, late 2019; late 2020	76
SU2	1	Early 2018	43
TH	1	Mid 2020	19
TO	1	Late 2018	48

Table A-B4: Adjusted R^2 for a series of curves (linear to polynomial degree 5) fit to predicted hare track counts over a range of Stem Cover Units (*SCU*) values, for each year separately and for all years combined. We selected the best-fitting curve for all years combined that did not improve model fit by >0.01.

	linear	*^2*	*^3*	*^4*	*^5*
R^2: 2018	0.057	0.081	0.081	0.083	0.084
R^2: 2019	0.12	0.18	0.20	0.20	0.20
R^2: 2020	0.19	0.19	0.21	0.21	0.21
R^2: 2021	0.070	0.12	0.15	0.18	0.19
R^2: all years	0.012	0.025	0.025	0.025	0.025

Table A-B5: Model parameters and AICc comparisons for drivers of lynx utilization distribution (*UD*). The response variable is the UD probability for each pixel of the home range; home ranges (99% kernel density utilization distribution) were calculated for each collar deployment separately. We include as predictors: hare relative abundance (*RelAb*), Stem Cover Units (*SCU*), vegetation (*Veg*), and elevation (*Elev*).

Model #	*Parameters*	*K*	*AICc*	*Δ AICc*	*AICwt*
8	~SCU*Year	10	-5182570	0.00	1.00
7	~SCU*RelAb	6	-5181870	699.82	0.00
11	~SCU + RelAb + Elev	6	-5180914	1656.10	0.00
4	~Veg	4	-5180857	1712.98	0.00
9	~ SCU	4	-5180782	1788.11	0.00
10	~Year + Season + SCU	8	-5180776	1793.66	0.00
12	~Year + Season + SCU + Elev	9	-5180776	1794.02	0.00
6	~RelAb	4	-5180776	1794.19	0.00
1	~1	3	-5180608	1961.94	0.00
5	~Elev	4	-5180608	1962.20	0.00
2	~Year	6	-5180604	1965.67	0.00
3	~Year + Season	7	-5180602	1967.49	0.00

Table A-B6: Model coefficients from integrated Step Selection Functions (iSSF) using pooled hare data for each year. Shortforms are defined as follows: *SCU* = Stem Cover Units; *Veg* = vegetation type (reference = *Othe*r, 2 = *Shrub*, 3 = *Spruce*), *SL* = hare step length, *TA* = hare turn angle. *Start* and *end* notations describe whether the covariate was extracted at the beginning or end of a step. An explanation of each covariate is provided in *Methods*.

	iSSF2018			***iSSF2019***			***iSSF2020***			***iSSF2021***		
	Est.	**S.E.**	**p**	**Est.**	**S.E.**	**p**	**Est.**	**S.E.**	**p**	**Est.**	**S.E.**	**p**
SCUend	4.5e−05	4.3e−05	0.30	5.4e−05	4.1e−05	0.19	0.00011	0.00005	0.03	0.00018	0.00022	0.43
VegEnd	0.16	0.12	0.17				0.083	0.113	0.46			
SL	−0.0088	0.0062	0.16	0.0058	0.0039	0.14	−0.0046	0.0040	0.24	0.027	0.015	0.06
Log(SL)	−0.083	0.068	0.22	0.17	0.10	0.11	0.048	0.070	0.50	−0.27	0.21	0.18
Cos(TA)	−0.85	0.07	<0.01	−0.80	0.11	<0.01	−0.551	0.099	<0.01	−1.06	0.22	<0.01
SL × SCUstart	4.1e−06	1.5e−06	<0.01	−2.3e−06	1.6e−06	0.14	4.7e−07	1.4e−06	0.74	−7.6e−06	4.5e−06	0.09
Log(SL) × SCUstart	2.8e−05	2.0e−05	0.16	6.5e−05	2.8e−05	0.02	2.1e−06	2.8e−05	0.94	7.6e−05	6.3e−05	0.23
Cos(TA) × SCUstart	6.4e−06	2.1e−05	0.76	2.1e−06	3.3e−05	0.95	2.8e−05	4.1e−05	0.50	2.3e−05	6.6e−05	0.72
VegEnd2				0.81	0.43	0.06				0.53	0.99	0.59

RMSE	*BIC*	*AIC*	*Num.Obs.*	*Cos(TA) × VegStart3*	*Cos(TA) × VegStart2*	*Log(SL) × VegStart3*	*Log(SL) × VegStart2*	*SL × VegStart3*	*SL × VegStart2*	*VegEnd3*
0.14	13537.1	13459.5	120299							
0.17	6584.4	6456.2	38090	0.037	−0.65	−0.40	−0.37	0.00071	−0.032	0.42
				0.168	0.34	0.14	0.24	0.00679	0.026	0.19
				0.82	0.06	<0.01	0.12	0.92	0.22	0.02
0.21	11022.3	10901.3	42143	−0.11	−0.017	−0.056	−0.15	0.0057	−0.0024	
				0.20	0.190	0.135	0.12	0.0073	0.0084	
				0.58	0.93	0.68	0.23	0.43	0.78	
0.17	4139.0	4066.2	24015							−0.53
										0.91
										0.56

Table A-B7: Model selection results for testing additional random factors in the analysis of drivers of lynx *UD*. The 36 competing models consist of the original 12 models for understanding the drivers of lynx *UD*, (models 1-12; Table A-B5), original + 1|*Year* (models 13-24), and original + 1|*Season* (models 25-36).

Modnames	*K*	*AICc*	*Delta_AICc*	*ModelLik*	*AICcWt*	*LL*	*Cum.Wt*
8	10	-5179284	0	1	0.576153	2589652	0.576153
32	11	-5179282	2.000293	0.367826	0.211924	2589652	0.788076
20	11	-5179282	2.000294	0.367825	0.211924	2589652	1
7	6	-5178513	770.621	4.59E-168	2.64E-168	2589263	1
19	7	-5178511	772.6212	1.69E-168	9.73E-169	2589263	1
31	7	-5178511	772.6212	1.69E-168	9.73E-169	2589263	1
4	4	-5177552	1732.193	0	0	2588780	1
16	5	-5177550	1734.193	0	0	2588780	1
28	5	-5177550	1734.193	0	0	2588780	1
11	6	-5177521	1763.24	0	0	2588766	1
23	7	-5177519	1765.24	0	0	2588766	1
35	7	-5177519	1765.24	0	0	2588766	1
9	4	-5177466	1818.524	0	0	2588737	1
33	5	-5177464	1820.524	0	0	2588737	1
21	5	-5177464	1820.524	0	0	2588737	1
10	8	-5177460	1824.134	0	0	2588738	1
12	9	-5177459	1824.866	0	0	2588739	1
22	9	-5177458	1826.134	0	0	2588738	1
34	9	-5177458	1826.134	0	0	2588738	1
36	10	-5177457	1826.866	0	0	2588739	1
24	10	-5177457	1826.866	0	0	2588739	1
6	4	-5177369	1915.166	0	0	2588688	1
18	5	-5177367	1917.166	0	0	2588688	1
30	5	-5177367	1917.166	0	0	2588688	1
5	4	-5177284	1999.554	0	0	2588646	1
1	3	-5177284	1999.866	0	0	2588645	1
17	5	-5177282	2001.555	0	0	2588646	1
29	5	-5177282	2001.555	0	0	2588646	1
25	4	-5177282	2001.866	0	0	2588645	1
13	4	-5177282	2001.866	0	0	2588645	1
2	6	-5177280	2003.6	0	0	2588646	1
3	7	-5177279	2005.481	0	0	2588646	1
14	7	-5177278	2005.601	0	0	2588646	1
26	7	-5177278	2005.601	0	0	2588646	1
15	8	-5177277	2007.482	0	0	2588646	1
27	8	-5177277	2007.482	0	0	2588646	1

Table A-B8: Model selection results using a smaller grid size (60m x 60m) in the analysis of drivers of lynx *UD*. All models are identical to the original 12 models for testing the drivers of lynx *UD* (see *Methods*), but *UD* values were calculated using a 60 x 60m grid rather than the original 80 x 80m.

Modname	*K*	*AICc*	*Delta_AICc*	*ModelLik*	*AICcWt*	*LL*	*Cum.Wt*
mm_8	10	-1.8E+07	0	1	1	8810714	1
mm_7	6	-1.8E+07	1385.612	1.31E-301	1.31E-301	8810018	1
mm_11	6	-1.8E+07	1423.932	6.273e-310	6.27e-310	8809998	1
mm_12	9	-1.8E+07	1447.009	6.11e-315	6.11e-315	8809990	1
mm_9	4	-1.8E+07	2056.395	0	0	8809680	1
mm_10	8	-1.8E+07	2061.591	0	0	8809682	1
mm_5	4	-1.8E+07	3461.415	0	0	8808978	1
mm_6	4	-1.8E+07	4438.797	0	0	8808489	1
mm_4	4	-1.8E+07	4683.995	0	0	8808366	1
mm_1	3	-1.8E+07	4688.112	0	0	8808363	1
mm_2	6	-1.8E+07	4691.437	0	0	8808365	1
mm_3	7	-1.8E+07	4693.198	0	0	8808365	1

Table A-B9: Results of power analysis used to detect differences in mean hare relative abundance (*RelAb)* values of kill sites between years using the difference in mean *RelAb* values for each combination of years, based on a one-sided t-test with variable sample sizes and a significance value of 0.05.

Years	*Difference in means*	*Difference in sample size*	*Power*
2018-2021	1.966278	538	1
2019-2021	0.5300779	162	0.9571
2020-2021	0.1542779	171	0.2539
2018-2020	1.812	367	1
2019-2020	0.3758	-9	0.9880
2018-2019	1.4362	376	1

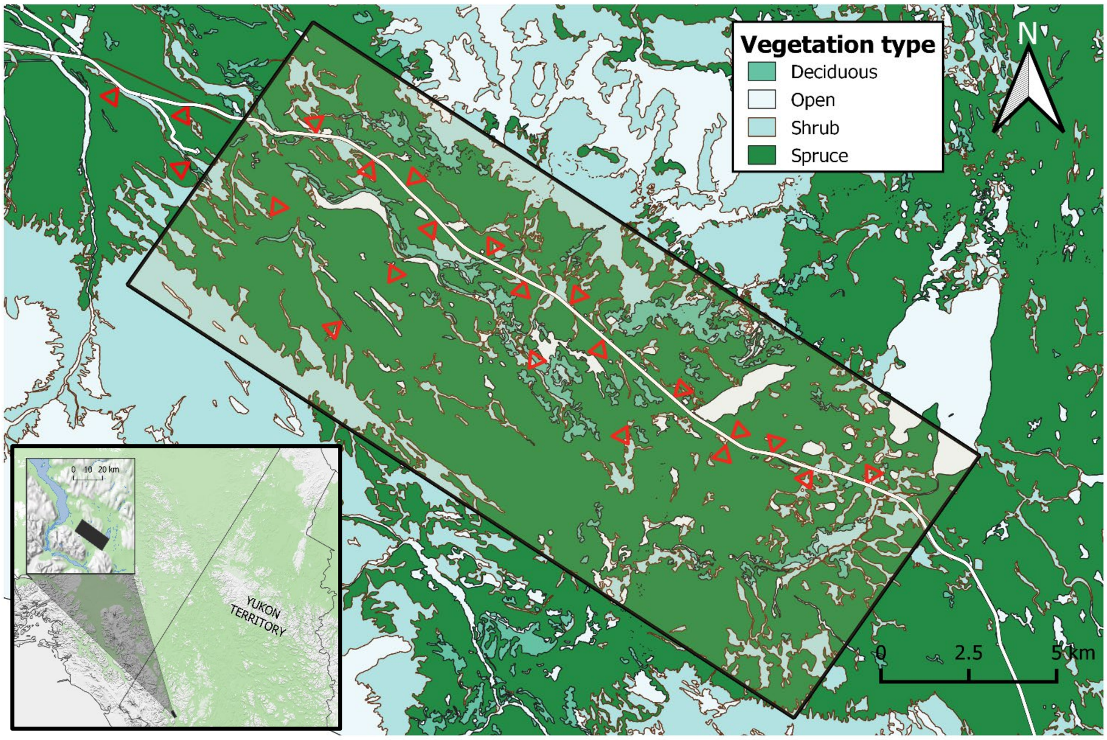

Figure A-B1: Lynx study area in southwest Yukon, Canada (see inset for location within Yukon Territory). The outlined area (~ 216 km^2) represents the area for which hare relative abundance was estimated. Snowshoe hare track survey locations are represented as red triangles. Of the 22 surveys selected a priori based on coverage of habitats within the study area, 19 were included in our final delineated study area (black rectangle). Vegetation types are depicted as colours (see legend).

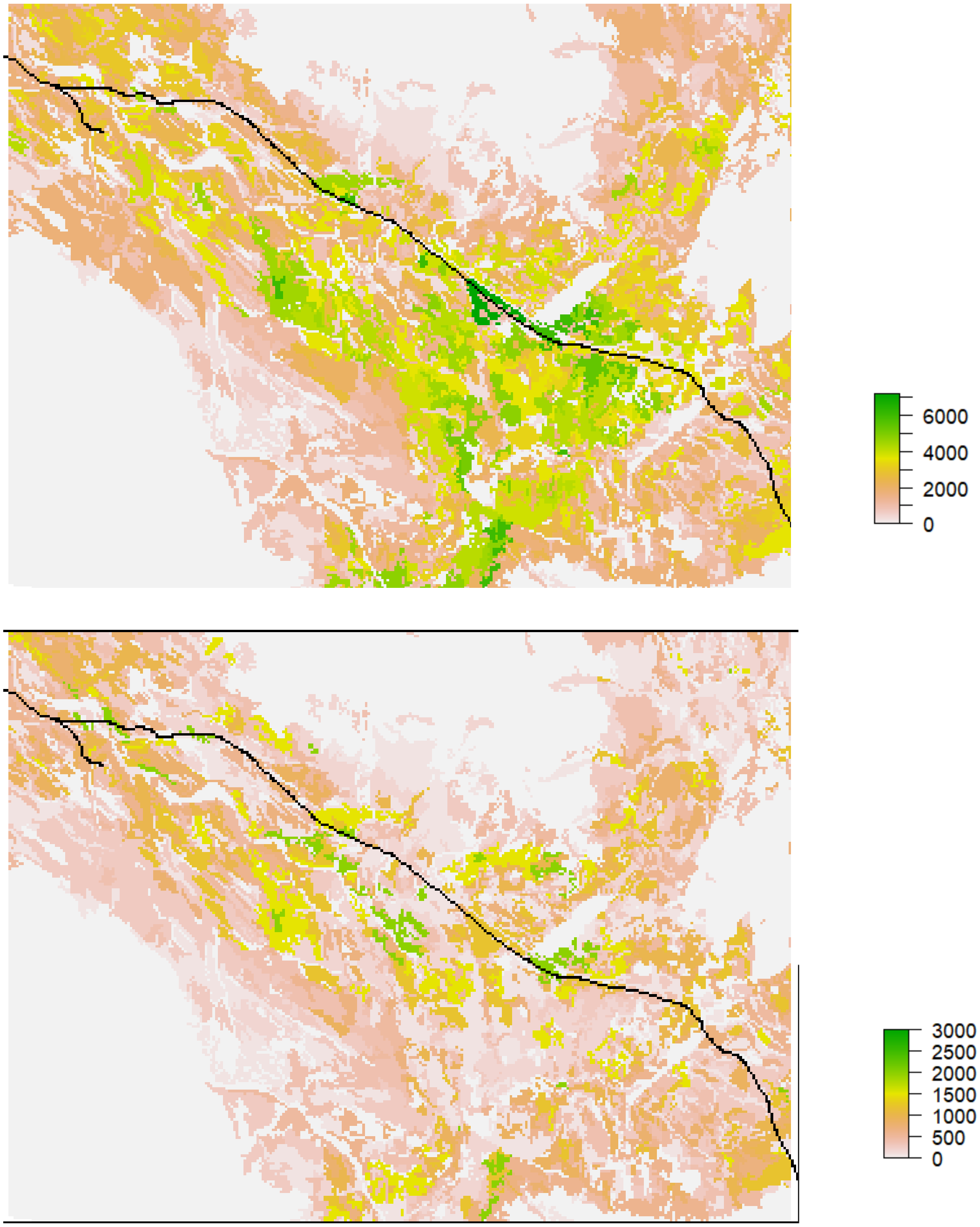

Figure A-B2. Stem Cover Units *(SCU,* an index of tree stem density that accounts for differing horizontal cover between species*;* top) and tree stem density per hectare (bottom) of the Kluane region, Yukon. The black line represents the highway. Higher values of both *SCU* and stem density are shown in darker colours, with the value of each colour depicted in the legend to the left of each plot. There was a positive correlation between stem density and *SCU* across the study area (r^2 = 0.51).

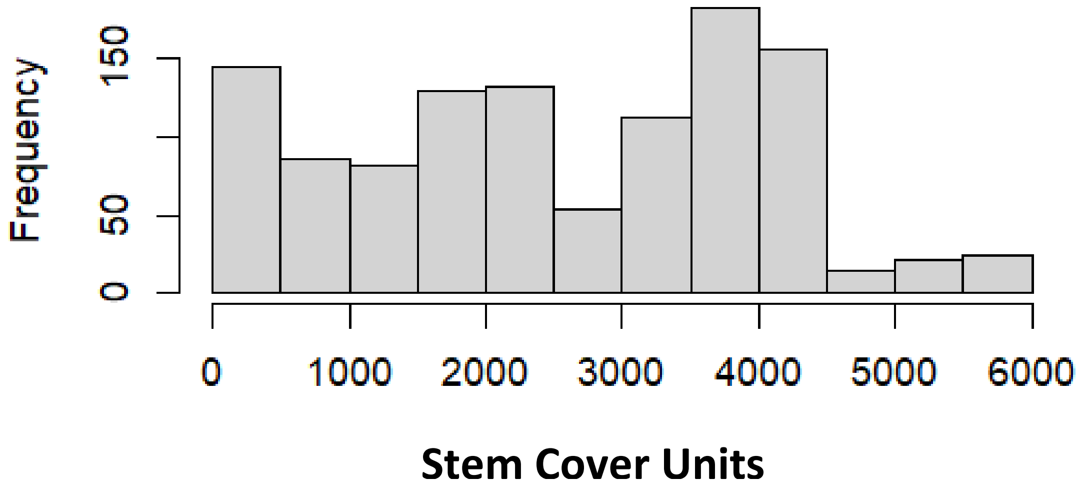

Figure A-B3: Sample distribution of Stem Cover Units *(SCU,* an index of tree stem density that accounts for differing horizontal cover between species) for 30m triangle transect segments used in models of relative abundance of snowshoe hares in Kluane, Yukon.

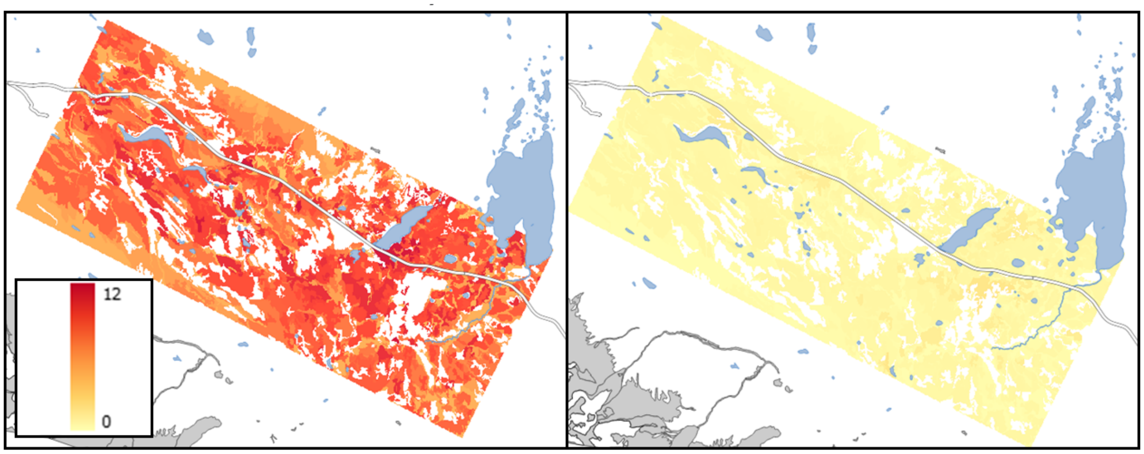

Figure A-B4: Examples of hare relative abundance maps calculated from track count model predictions from early 2018 (left) and late 2021 (right). Darker colours represent higher relative abundance of hares (inset bottom-left).

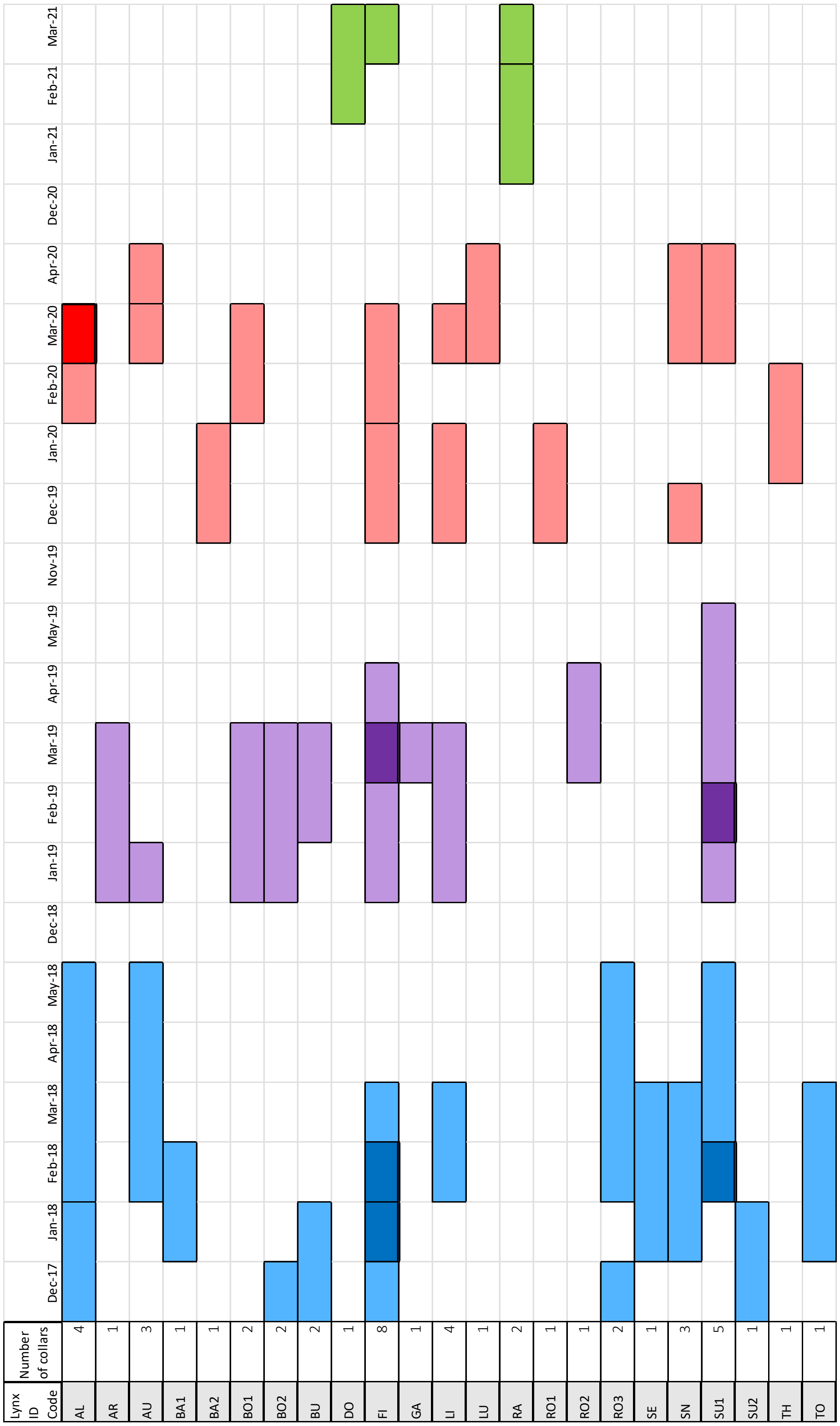

Figure A-B5: Number and timing of collar deployments for each individual lynx included the study ("Lynx ID Code"; each alpha-numeric code represents a different individual). Each block represents a separate collar deployment, with dates (by month) along the y-axis and overlapping deployments shown in darker shades. Colours depict the Year of the deployment (blue = 2018; purple = 2019; red = 2020; green = 2021).

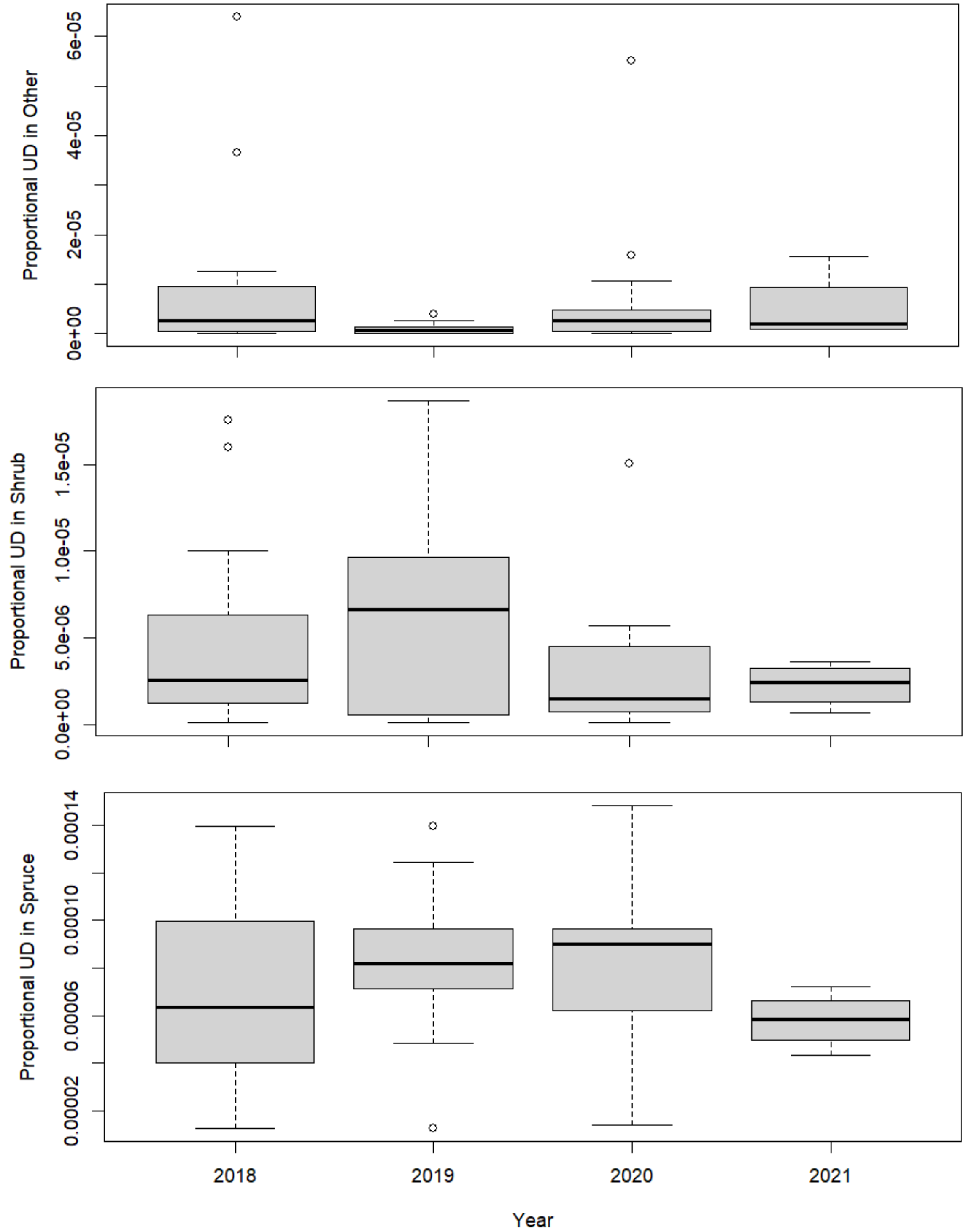

Figure A-B6: Proportional values of lynx utilization distribution (*UD)* in different vegetation types across years. In each plot, the y-axis depicts the proportional vegetation use of each vegetation type (top = *Other*, middle = *Shrub*, bottom = *Spruce*) based on the sum of lynx *UD* values divided by the proportional availability of that vegetation type in the home range (number of grid cells for that vegetation type / total number of cells in home range).

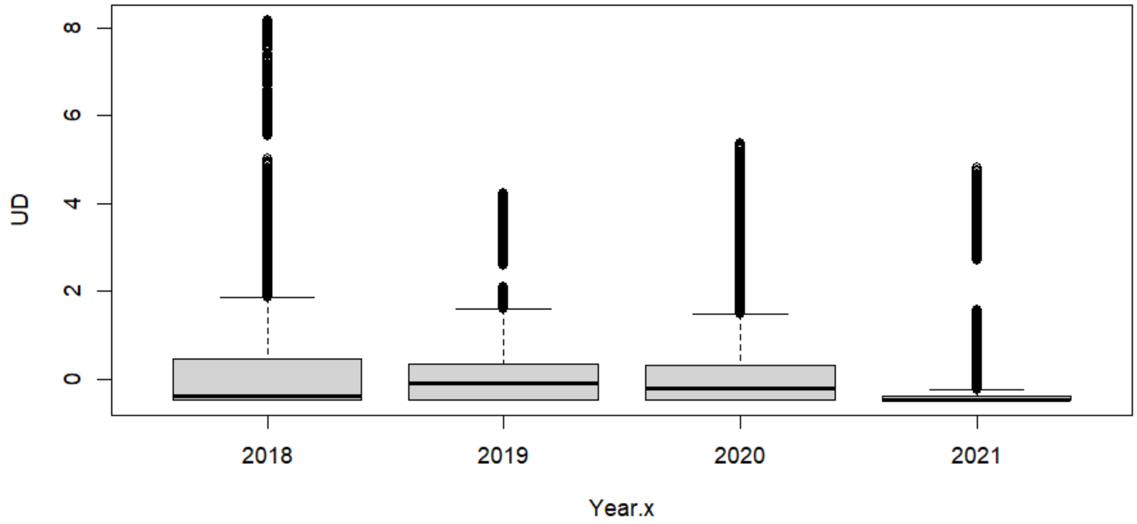

Figure A-B7: Values of lynx utilization distribution (*UD)* across years. Box plots present mean values (middle line) and 1st and 3rd quartiles (bottom and top of boxes, respectively); whiskers represent data within 1.5 * interquartile range, and outliers beyond this range are displayed as single points. *UD* values were scaled and centered prior to plotting.

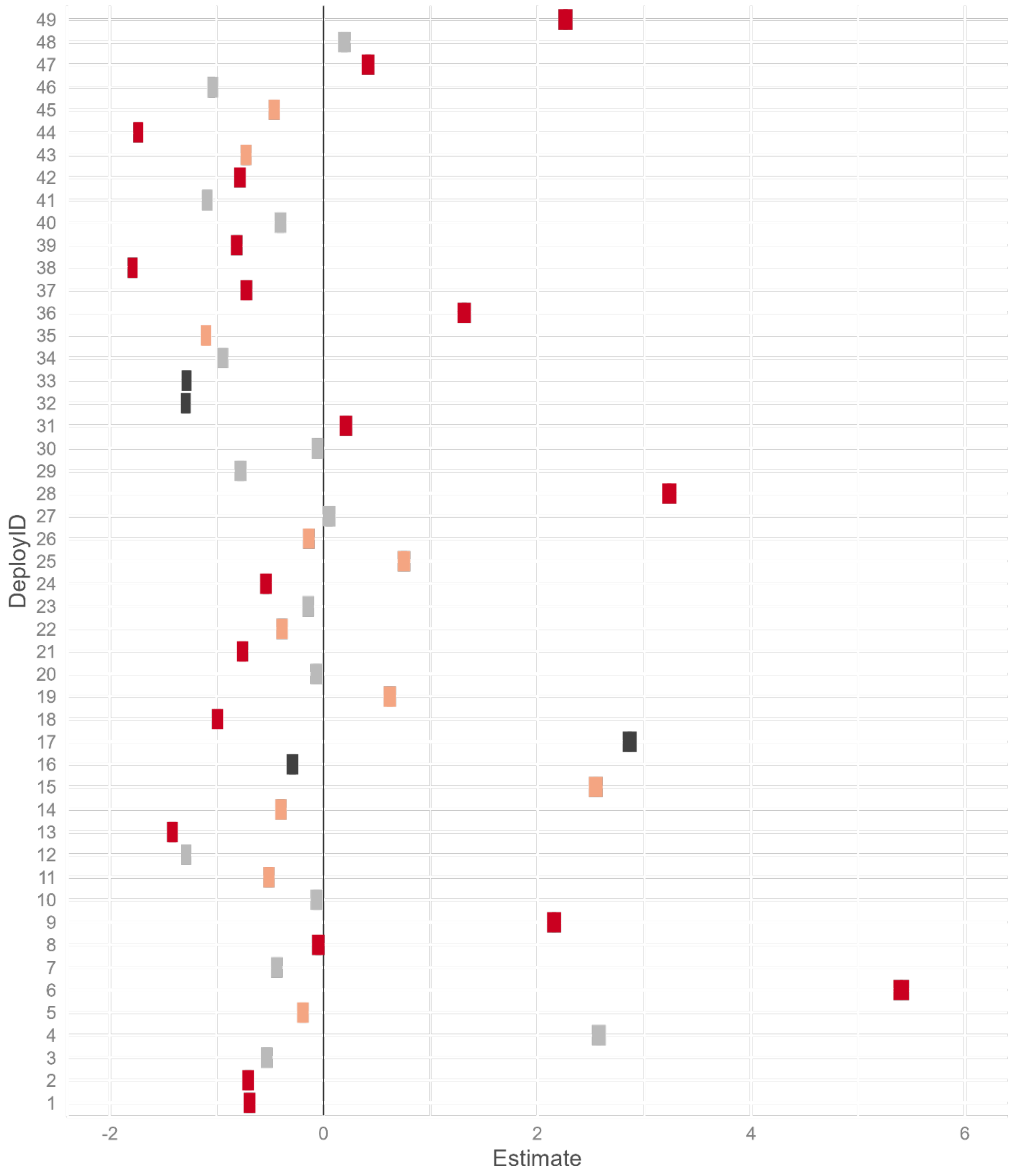

Figure A-B8: Variation in random intercept values across 49 levels of collar deployment ID in our top model of drivers of lynx utilization distribution. The y-axis depicts the numeric value of the deployment ID, while the x-axis depicts the random intercept calculated for that collar deployment. Colours depict the *Year* of the deployment (red = 2018; pink= 2019; grey = 2020; black = 2021) and the width of the rectangle depicts the 95% confidence interval for the estimate.

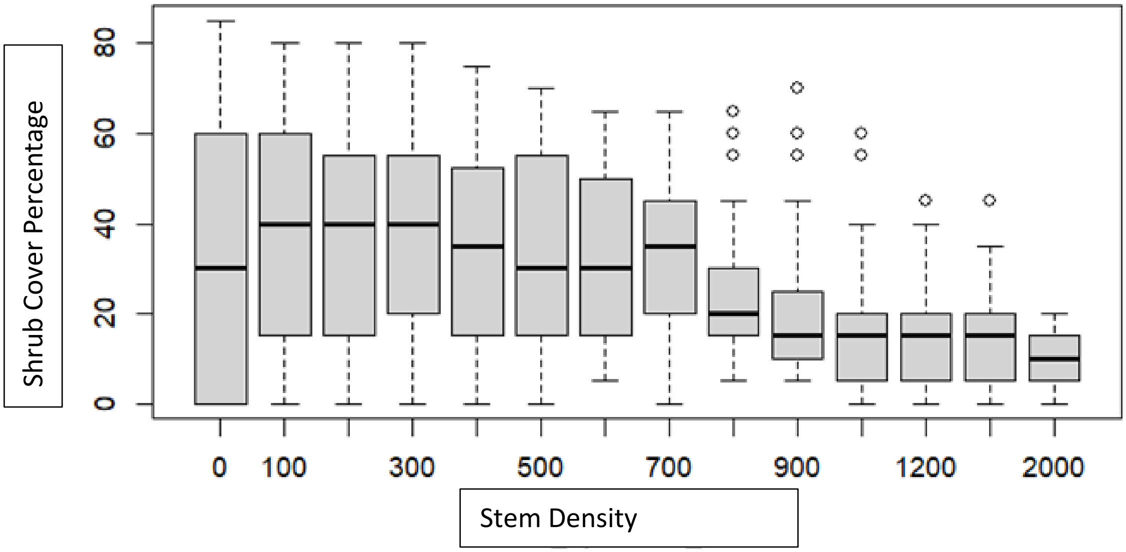

Figure A-B9: Relationship between stem density (stems per ha, in increments of 100) and shrub cover (% cover of shrub vegetation in forested plots, estimated in 5% increments) in Kluane according to the Yukon Vegetation Inventory (2014).

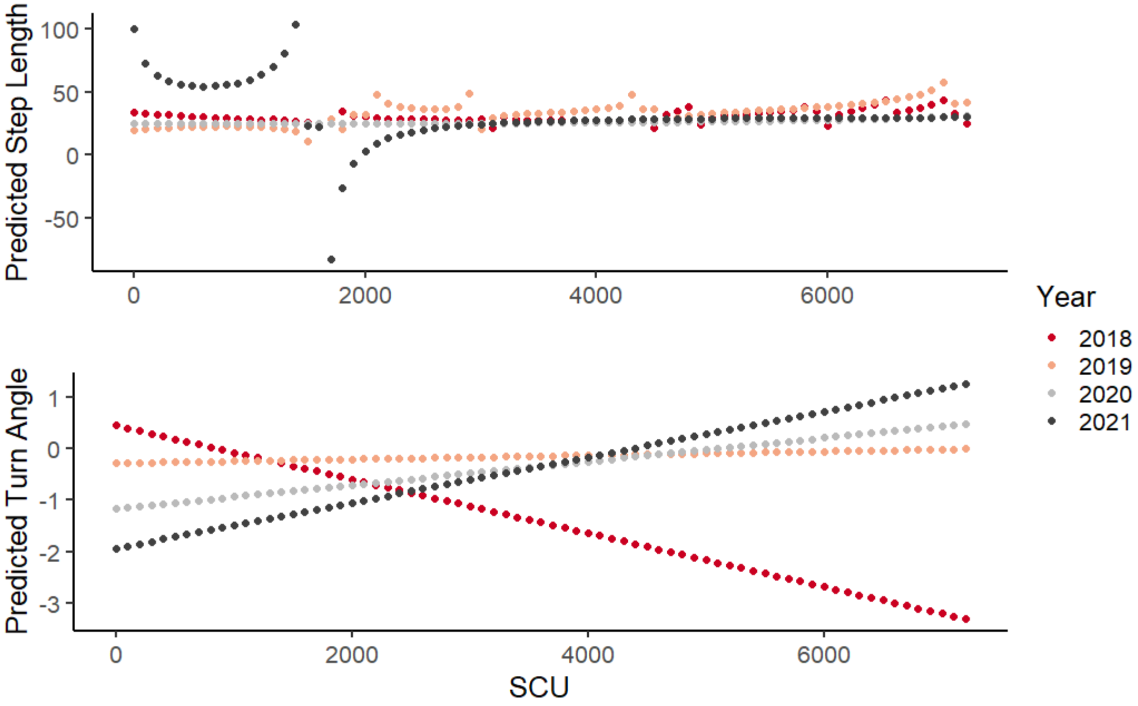

Figure A-B10: Mean hare step length (top) and turn angle (bottom) calculated from updated individual hare movement distributions using integrated Step Selection Functions (see Appendix B1), over a range of Stem Cover Units (an index of stem density that accounts for tree species; see *Methods*). Colours depict the year of the deployment (red = 2018; pink= 2019; grey = 2020; black = 2021).