SUMMER MOVEMENT ECOLOGY OF SNOWSHOE HARES (*LEPUS AMERICANUS*) DURING A POPULATION CYCLE

A Thesis Submitted to the Committee on Graduate Studies in Partial Fulfillment of the Requirements for the Degree of Masters of Science in the Faculty of Arts and Science

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ABSTRACT

summer movement ecology of snowshoe hares (*Lepus americanus*) during a population cycle

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I tracked summer movements and activity of snowshoe hares (*Lepus americanus*) in southwestern Yukon, Canada, during their population cycle (2015–2022) to assess the primary drivers of movement. Hares exhibited variable movement and activity during the cycle, exhibiting increased home range size and higher daily displacement during low population densities. Males exhibited more dramatic increases in their home ranges (>3-fold), and had greater and more variable movement rates and time spent travelling than females. The ratio of predators to hares was highest at low hare densities when hares were moving most, and seasonal activity of hares seemed unrelated to that of predators. Differences between sexes imply that reproductive activities likely were the main driver of hare movement variation rather than food availability. These findings reinforce that, even in highly variable environments, potential rewards associated with successful mate search and reproduction may outweigh the risks associated with reproductive behaviour.

Keywords: Snowshoe hare, *Lepus americanus*, home range, movement ecology, behaviour, predation risk, boreal forest, GPS telemetry

Preface

This thesis is written in manuscript format, as the second chapter will be published in a peer-reviewed journal. Chapter 2 is written as a stand-alone manuscript, and I am first author. This research could not have been possible without the help and contributions of a collaborative team and therefore the plural “we” is used throughout the text. Those people whose contribution to this work was significant are included as co-authors in the second chapter.

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Finally, thank you to the hares who made this research possible.

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Supplemental Materials

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Chapter 1: General Introduction

The factors driving animal movement dynamics are a central theme in ecology, with the causes and consequences of why and how animals move across the landscape relevant to virtually all aspects of individual, population, community, and ecosystem dynamics (Shaw 2020). Movement can vary from large- (i.e., dispersal, seasonal migration) to small-scale (i.e., foraging, predator chases, mating) behaviours (Stern 2009; Shaw 2020), and these patterns serve to determine survival and fitness and are inextricably linked to the environment in which animals live. Movement is elicited proximally by a variety of stimuli, as may arise when individuals: 1) search for mates (Mizumoto and Dobata 2018), 2) search for quality foraging areas (Owen-Smith et al. 2010), 3) avoid predators, 4) compete with conspecifics (Doherty and Ruehle 2020), and 5) minimize resistance to their movement (Balbi et al. 2019). Animals perceive their environment through a variety of sensory mechanisms, including olfactory cues, spatial memory, habitat structure, and visual/auditory cues (Finnerty et al. 2022). While animal movement is a well-studied component of ecology, it can be highly variable and sensitive to environmental variation, including temporal or spatial variations in risks and resources (Sergio et al. 2018). It follows that knowledge of animal movement and the mechanisms that drive it are essential for predicting how behaviours may change with a shifting environment, and this inference can help identify how these variations may reverberate throughout the ecosystem.

Dynamic animal movement

The success of free-ranging animals is often dependent on their ability to observe and respond to their surroundings. Environmental stressors such as predation risk, food limitation, inter- and intra-specific competition, and anthropogenic and abiotic factors can negatively affect an individual's survival if they do not respond appropriately (Jorge et al. 2011; Sergio et al. 2018). Animals can respond to stressors through dynamic changes in their movements and behaviours, physiology, changes in life history strategies, morphology, and even gene expression, depending on the type and scale of risk (Sergio et al. 2018). Understanding how animals respond to direct or perceived risks in their environment is important for understanding population dynamics and predicting how populations will respond to potential environmental or anthropogenic changes. For example, wildfires can alter mule deer (*Odocoileus hemionus*) movement as burned areas provide high-quality forage while also increasing susceptibility to predation (Ganz et al. 2022). Animals may reduce their movement during times of high predation risk to avoid detection (Schmitz et al. 1997) or increase their movement rates (Proffitt et al. 2009) to disperse olfactory cues or avoid predators. Additionally, anthropogenic linear features cause many species to increase their travel speed while also benefitting predator hunting efficiency (Dickie et al. 2019). While movement can be individual- and species-specific (Richmond et al. 2022), the underlying theory and drivers of animal movement tend to be generally applicable to most species.

Cyclic populations, which experience dramatic and reoccurring numerical fluctuations and related changes in their biotic features (e.g., mating opportunities, food availability, predation risk), offer a unique opportunity to test how animals may shift their movement patterns following large and rapid shifts in their environment. Like other populations, cyclic populations can face environmental stressors such as habitat loss, fragmentation and range shifts (King et al. 2020). On top of this, animals experience drastic shifts in conspecific density, predation risk, resource availability, and potential habitat availability during a population cycle (Krebs et al. 2018) and potential changes in cyclic amplitude (Krebs et al. 2014). Therefore, cyclic populations provide opportunities to observe how animals respond to dramatic shifts in their environment and population dynamics.

Quantifying movement and activity with bio-loggers

Advances in bio-logging technologies have opened a new world of opportunities in monitoring animal movement and behaviour. Specifically, miniaturization of bio-loggers allows the tracking of small animals with a high level of sensitivity and accuracy, thereby supplanting much cruder, traditional methods consisting of direct observation or conventional radiotelemetry (Crofoot et al. 2010). Likewise, repeated live trapping or camera trapping yield incomplete portraits of animal movements or behaviours. Further, many traditional methods are laborious and provide biased data (Priede and Swift 1992; Caravaggi et al. 2017). The recent advent of miniaturized GPS units allows ecologists to track and record animal movements continuously for weeks at a time, including smaller animals that cannot be instrumented with larger packages. Bio-logging can be further enhanced when combining GPS telemetry with accelerometers, which can inform researchers with not only where an animal is located but also its continuous patterns of activity. Using accelerometer-classified behavioural categories, animal activity types including foraging, hopping, sprinting, and resting can be quantified. For example, in snowshoe hares (*Lepus americanus*), the species used in my research, accelerometry-based behavioural classification has an 88% accuracy, distinguishing sprinting, foraging, hopping, and stationary behaviours (Studd et al. 2019). While some limitations to biologging technology are recognized (e.g., lost GPS signal in dense canopy; Wing and Eklund 2007), limited sample size due to costs of units (Hebblewhite and Haydon 2010)), these technologies can open many new opportunities for innovative and impactful research in animal movement dynamics (Williams et al. 2019). Notably, radio-transmitters used in my MSc thesis research on hares included GPS trackers, accelerometers, and VHF-telemetry trackers (for active tracking and survival monitoring; Fig. 1). Collectively, these units provided real-time information on hare survival, movements, and behaviour.

Figure 1 Radio-transmitter collar combining GPS, accelerometer, and VHF unit for monitoring movements and classifying behaviours of snowshoe hares. Photo credit: H. Miller.

Snowshoe hares and the boreal forest

Snowshoe hares are a keystone prey species in the boreal forest, representing over 50% of available herbivore biomass at peak densities (Krebs et al. 2001). Hares experience population cycles with 9–11-year periodicity, with densities fluctuating 20 to 30-fold, on average (Krebs et al. 2014). Hares have been studied in the Kluane region in Yukon, Canada for >40 years (Krebs et al. 2018), which is where I conducted my research. The breeding season for hares in southwestern Yukon extends from May to September, with hares typically producing two to four litters per breeding season (Stefan and Krebs 2001). Breeding is controlled by photoperiod (Severaid 1945; Davis and Meyer 1972) and is typically synchronous across the hare population (Stefan and Krebs 2001). Like other hare species, the mating system of snowshoe hares is either polygynous or promiscuous (Burton 2002; Knipe et al. 2013), with males being mainly responsible for mate searching. Pregnancy rates are highest at the beginning of the breeding season and decrease with successive litters (100% pregnancy rates early in the season, declining up to 20% in the last gestation period; Stefan and Krebs 2001). Pregnancy rates can also be phase-specific, with higher productivity during periods of population increase (Cary and Keith 1997). Hares exhibit immediate postpartum breeding (Keith et al. 1966; Bittner and Rongstad 1982), returning to their leverets once per day to nurse (Rongstad and Tester 1971).

Hares are subject to high predation from a variety of predators in the boreal food web (Fig. 2), with the two main terrestrial predators being Canada lynx (*Lynx canadensis*) and coyote (*Canis latrans*), which also exhibit cyclic population fluctuations that lag 1-2 years behind the hare cycle (Boutin et al. 1995). Predation is the proximate cause of death for most hares, ranging from 85-100% of mortalities across the cycle (Murray et al. 1997; Krebs et al. 2018). The increasing threat of predation during population declines can trigger physiological (increased cortisol and glucose levels; Boonstra et al. 1998; Sheriff et al. 2011) and behavioural (altered energy expenditure; Sheriff et al. 2011) changes in hares, although more recent findings question the role of non-consumptive predator effects on hare population cycles (Lavergne et al. 2021).

The main diet of hares consists of white spruce (*Picea glauca*), soapberry (*Shepherdia canadensis*), willow (*Salix* spp.), and bog birch (*Betula glandulosa*), as well as forbs and grasses in summer, and white spruce, willow, and birch twigs in winter. Due to the magnitude with which hare populations fluctuate, hare foraging can affect both the abundance and growth of vegetation (Sinclair et al. 1988; Dlott and Turkington 2000). While there is no evidence suggesting summer food limitation for hares in the Yukon, they may experience winter food limitation in response to population density and snow conditions (Sinclair et al. 1988; John and Turkington 1995). Accordingly, effects of winter food limitation for hares may spill over into spring/early summer as it does for other herbivores (e.g., Cook et al. 2004) and, not surprisingly, hares can exhibit greater foraging rates and related activity during spring green-up when forage quality is greatest.

Hares are a crepuscular species, with greatest movement rates between 1800 and 0800 (Feierabend and Kielland 2014). They spend approximately 50% of their time foraging, with the rest of their time spent not moving (Studd et al. 2019). These behaviours are meant to reduce predation risk while still meeting basic needs. While the effects of predation risk and food availability on hare movement have been explored in an experimental setting (Hodges 1999), this analysis focused solely on the low phase of the cycle and does not reflect the considerable temporal fluctuations in predator abundance, food availability, or hare density through a more complete cycle. More importantly, previous research on the determinants of hare movements (Hodges 1999) relied on VHF telemetry and triangulation to measure winter and summer travel distances, but this approach is not suited for assessing fine-scale movements or their behavioural correlates. Further, Hodges (1999) predicted that hares would reduce movements in response to predation risk (as is known for other small mammals; e.g., Lima and Dill 1990), but, contrary to expectation, hares moved more under higher risk. It is unknown whether the coarse movement measurements or experimental setting of the study contributed to these findings, but regardless, much uncertainty remains in understanding the determinants of hare movements during the phases of their population cycle. More broadly, neither the Hodges (1999) study, nor most other studies on small mammal movements (e.g., Schoepf et al. 2015) considered the potential effect of reproductive activities and mating on movement patterns. Yet, given the recognized importance of such activities on animal movements in general, and the marked change in number of prospective mates faced by hares across population densities, it seems plausible that searching for mates and reproductive opportunities may be a primary driver of hare movement dynamics.

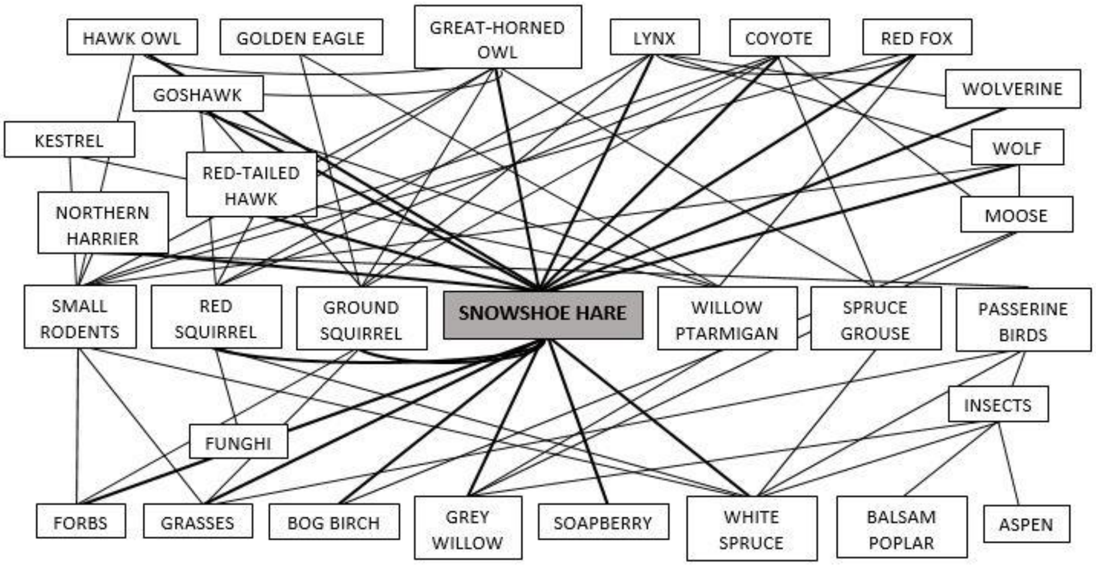

Figure 2. Food web for the boreal forest in the southern and central Yukon, with food web links to snowshoe hare highlighted (adapted from Krebs et al. 2022).

Thesis overview

The overall objective of this thesis is to explore the determinants of hare movement and activity and assess whether hares exhibit dynamic movement through their population cycle. I addressed this research objective by collecting location and accelerometer data from collared free-ranging snowshoe hares in the Kluane region of Yukon, Canada, over 8 years (2015–2022). This study period follows the increase, peak, decline, and low phases of the snowshoe hare population cycle. Using location data collected via GPS-telemetry, I calculated home range and core use areas as well as other movement metrics including daily displacement, hourly movement, and tortuosity (linearity). Using accelerometry, I quantified time that hares were engaged in travel-related behaviours. With these metrics of space use and behaviour, I assessed whether hares exhibit inter-annual and inter-sex variability in their movement and activity patterns. Thus, this thesis addresses the following research questions:

- Do snowshoe hares exhibit dynamic space use and activity during their population cycle?

  Animals adjust their movements in response to their environment. During a population cycle, hares experience dramatic shifts in population density, predation risk, and potentially food availability. Therefore, it is expected that hares will exhibit dynamic space use and activity in response to these changes.

- Are predation risk, food availability, or reproductive activity the main influences of hare space use and activity?

  Predation risk, food availability, and mate search (primarily by males) and care of offspring (by females) are all considered as drivers of movement of polygynous mammals. However, it is unclear what is the relative influence of each factor, and how this relevance may shift through the hare population cycle.

To answer these questions, I tracked the summer movements of 112 and activity of 80 snowshoe hares over 8 years corresponding to all phases of their population cycle.

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Chapter 2: Inter-annual variability in summer movement ecology of snowshoe hares (*Lepus americanus*) during a population cycle

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Abstract

Animals exhibit dynamic movement and activity in response to variation in their environment, including spatial and temporal variation in reproductive opportunities, predation risk, or food availability. To date, it remains unclear which of these factors is predominant in affecting animal movement, and whether the relative importance of these is consistent through time and variations in population density. We tracked May-September movements and activity of snowshoe hares (*Lepus americanus*) in southwestern Yukon, Canada, during a hare population cycle (2015–2022), and documented whether changes in home range features and movement activity corresponded with variation in population density and mating opportunities, predator densities, or per capita food availability. Across our 8-year study, hare density varied 25-fold, with numbers peaking in fall 2017 and low numbers persisting through 2020–2022. Hares exhibited strong inter-annual variability in their movements and activity, with both sexes increasing home range size and daily displacement 4-fold during low hare density; these changes were especially notable among males (2–3-fold greater than females). Both sexes retained similar core use isopleths and tortuosity of movements, but the movement rates and time spent travelling by males were greater and more temporally variable than females. Based on trail camera observations, the ratio of Canada lynx (*Lynx canadensis*) and coyotes (*Canis latrans*) to hares was highest during the cyclic low when hares moved most, and seasonal variation in hare activity did not correspond to changes in predator abundance. Although hares were consistently more active during May-June when they experienced greatest nutritional restriction, differences in movements between sexes indicate that reproductive activities are likely the main driver of movement dynamics.

Thus, potential fitness rewards associated with successful mate search and reproduction may outweigh risks associated with this behaviour, even in highly variable environments where costs of prioritizing production-related activities may be notably high and variable.

Introduction

Animals exhibit dynamic movement and activity in response to changes in their surroundings. Decisions related to space use, chosen paths, and movement trajectories can be driven by variation in four main factors: food, fear, intra-specific competition, and reproduction (Dill 2017; Finnerty et al. 2022). Decisions about when, where, and how much to invest in movement are determined by the balance of information received from these four factors (Forsman and Kivelä 2021; Shaw 2020). Distribution of food resources or mates can establish basic patterns of movement and space use (Owen-Smith et al. 2010; Lassis et al. 2022), but such decisions are typically weighed against constraints of predation risk and competition (Erlinge et al. 1990; Laundre et al. 2010; Doherty and Ruehle 2020). Movement are not fixed but rather can vary through space and time, so individuals must continuously assess environmental variation and the risks and benefits associated with their behaviour to make corresponding adjustments that increase their survival and productivity (Finnerty et al. 2022; Shaw 2020). Despite these straightforward principles in animal movement ecology, there is limited evidence that animal movement dynamics closely reflect environmental variation and the corresponding changes in risks and rewards (Shaw 2020).

Animal movement-related decisions are multi-faceted and should vary proximally according to animal priorities and perceptions of the environment. If predation risk varies spatiotemporally (Kauffman et al. 2007; Mayer et al. 2019), risk avoidance behaviour may be dynamic and thereby affect a variety of features related to movement. Likewise, if animals face food shortage or limited mating opportunities, they should exhibit movements that increase access to these resources (McIntyre and Wiens 1999; Guyer et al. 2012). However, balancing risks and rewards over space and time can be challenging especially for animals in highly dynamic environments.

Across much of their range in the boreal forest, snowshoe hares (*Lepus americanus*) experience cyclic population fluctuations every 9–11 years (Krebs et al. 2001). Hare cycles lead to rapid changes in, not only hare density, but also the hare : predator ratio, and thus, corresponding changes to hare predation risk (Boutin et al. 1995). Likewise, per capita availability of herbaceous and woody foods also varies according to cyclic dynamics (Boutin et al. 1995; Krebs et al. 2001, 2018). Given that hare densities can vary 20–30-fold over the span of a few years (Krebs et al. 2014), variation in hare density also influences the number and distribution of prospective mates and mating opportunities. While snowshoe hare mating structure is poorly understood, like other hares (Knipe et al. 2013), female hares engage in multiple paternity and are the sole care-givers of offspring (Burton 2002). Thus, males should be more active in mate searching. There is no evidence that hares exhibit defensive behaviours or territoriality (Boonstra et al. 1998; Krebs et al. 2018), meaning that their dispersion patterns across the landscape probably are not the result of competition among conspecifics.

We studied factors driving summer movements of snowshoe hares in southwestern Yukon, Canada, during a hare population cycle (2015–2022). We tracked hares intensively to test whether changes in mating opportunities, predation risk, or food availability are correlated with hare space use and movement patterns. We predicted that if mating and reproductive activities drove hare space use and movement (i.e., search for mates by males, tending leverets by females), then i) males would exhibit greater home range size and movement compared to females, especially when hare densities were low and mating opportunities may be limited. During the most intensive period of the hare breeding season (May-June), ii) males would exhibit increased travel in search of mating opportunities while females may restrict travel in favour of foraging within a smaller space to provide maternal care. In contrast, if predation risk drove hare movement, iii) all hares in the population would reduce movements and travel when predator-hare ratios were high; and iv) hare movement patterns would be inversely correlated with monthly variation in predator activity. Although hares are not known to be food-limited during summer (Sinclair et al. 1988; John and Turkington 1995), in temperate environments herbivore food limitation may arise during winter and herbivores can experience carry-over effects into the spring-summer seasons (Cook et al. 2004). Therefore, if food availability drove hare movement, v) all hares would exhibit increased movement and travel during years when winter food availability per capita was low following peak hare densities, with hares also exhibiting vi) greater travel in May-early June, before spring green-up. To summarize, if mating and reproductive behaviour were the primary determinants of hare movements, then responses should vary between sexes and be strongly associated with hare density. In contrast, if intense predation or food limitation were the main determinants, then both sexes should exhibit similar seasonal variation in behaviour that corresponded with temporal changes in either factor.

Methods

Study Site

We studied hares in the Kluane Lake region of southwestern Yukon Territory, Canada (61°58’N, 138°12’W) on six sites 6–37 ha in size, spanning ~20 km along the

Alaska Highway. Average summer (June-August) and winter (November-February) temperatures within the region were 12˚C and -17°C, respectively, with an average of ~275 mm of precipitation (~70% rain) annually (ECCC 2022). The forest is dominated by white spruce (*Picea glauca*) and includes trembling aspen (*Populus tremuloides* Michx.) and balsam poplar (*Populus balsamifera* L.), with understory composed of gray willow (*Salix glauca*), bog birch (*Betula glandulosa*), soapberry (*Shepherdia canadensis*) and other herbaceous plants (Krebs et al. 2001). Anthropogenic disturbance in this area is minimal.

Hare populations have been monitored on site since 1976 (Krebs et al. 2001, 2018), with variation in hare density ranging 20–30-fold, on average (Krebs et al. 2014). The breeding season extends from May-September, with most mating and maternal activity greatest at the beginning of the breeding season (Stefan and Krebs 2001). Our study spans 8 years during which average hare densities varied from 0.06–1.52 hares/ha, representing the increase, peak, decline and early low phases of the hare population cycle in the region (Krebs et al. 2022; Fig. 1). In our study area, terrestrial mammals like Canada lynx (*Lynx canadensis*) and coyotes (*Canis latrans*) are major predators (O'Donoghue et al. 2001) and their densities vary substantially through the hare cycle, with predator numbers fluctuating in tandem with hare numbers with a 1–2-year lag (Krebs et al. 2023).

Live Trapping and Collaring

From May to September 2015–2022, we live trapped hares (Tomahawk Live Trap Co., Tomahawk, WI, USA), ~six nights/month from 2015–2017 and ~14 nights/month from 2018–2022, in response to the decrease in hare density. We baited traps overnight with apple, rabbit chow, and alfalfa, and checked traps within 8–10 hours of setting. On first capture, hares were ear-tagged (National Band and Tag Co., Newport, KY, USA), weighed, and sexed. Adult hares (>1000 g) were equipped with radio-collars consisting of a VHF transmitter with mortality and activity sensors (Wildlife Materials, Murphysboro, IL, USA), a GPS unit (GiPSy 5) and an accelerometer (Axy-3; Technosmart, Guidonia, Rome, Italy). We collared only the animals that were repeatedly live trapped on site (>2 times), increasing the chance that collared hares were non-dispersers that could be recaptures reliably. GPS units were programmed to obtain a location every hour (2015–2018) or every 15 minutes (2019–2022). Collars were deployed for three-week periods and were collected and redeployed upon hare recapture. All live-trapping and handling procedures followed specific guidelines (Sikes et al. 2011), which were approved by the Trent University Animal Care Committee (protocols 23373, 25243, 28019).

We assessed GPS fix success and locational accuracy of our transmitters via field trials involving placing transmitters (stationary or in motion) in known locations within different landcover types across the study area including dense understory, open forest, and no cover. Stationary collars were placed in a location for 4-8 hours at a time, while collars in motion looked at relocations of collars as they were moved at least 250m from one location to another. For stationary transmitters we observed negligible variation in locational accuracy according to transmitter fix rates (15 minute: 10.6 ± 10.0 m [SD], n = 4; hourly: 11.3 ± 11.9 m, n = 4) or transmitter location (beneath dense understory: 9.2 ± 10.8 m, n = 8; open forest: 8.4 ± 9.9 m, n = 8; open sky: 5.7 ± 9.9 m, n = 8). We found that stationary vs. nonstationary transmitters provided similar accuracy (stationary: 8.0 ± 10.4, n = 8; non-stationary: 9.6 ± 14.8, n = 8). We filtered GPS data to remove implausible points (consecutive locations with distances moved >500 m/hr; Bjørneraas et al. 2010; Stark et al. 2017).

From May-September 2015–2022, we collected GPS and accelerometer data from 112 and 80 hares, respectively. Median GPS collar deployment per individual was 27 days (95% BCa CI: 21–32 days; n = 70 hares) for females and 25 days for males (20–30; n = 42), whereas median duration of individual accelerometer data collection was 35 days (22–36; n = 55) for females and 41 days (27–57; n = 25) for males.

Summer Home Range and Core Use

We estimated May-September home range size for hares using kernel density estimation (95% KDE) with a plug-in bandwidth. This method is preferable to other home range estimators for species with relatively low mobility and restricted ranges, especially when looking at seasonal habitat use with infrequent exploratory movements (Walter et al. 2011). We determined that 50–100 locations were required to reach an asymptote in home range size (Girard et al. 2002). Thus, we censored hares with <50 locations from home range analyses, and defined home range boundaries as the 95% isopleths (Kie et al. 2010; Walter et al. 2011; Garitano-Zavala et al. 2013). We defined core use area by fitting an exponential regression to a plot of utilization distribution (UD) area against UD volume (isopleth value) and identifying the isopleth value where the regression slope was equal to one (Vander Wal and Rodgers 2012). We created seasonal home range and core use isopleths using the Kernel Smoothing (ks) R package (Duong

2022) in R 4.2.1 (R Core Team 2022). Home range area and core use area had high correlation (r = 0.99, P = <0.001, n = 109) and thus could not be considered independent measures. Instead, we used core use isopleth values (IV) to assess the proportion of ranges used intensively, which had low correlation with home range area (r = -0.16, P = 0.10, n = 109) and thus were considered as independent measures of total area occupied and the percentage of the home range that is used intensively, respectively.

Movement and Activity Metrics

We measured hare movement patterns using: 1) daily displacement (m/day; extent = day, resolution = day); 2) hourly movement rate (m/hr; extent = hour, resolution = hour), 3) daily tortuosity of movements, and 4) daily movement rate (m/day; extent = day, resolution = hour). For all movement analyses, we addressed any potential bias from differences in temporal resolution by standardizing the data across the study period to a 1-hour fix rate, and created our metrics excluding data gaps. To address non-normal distributions of data, we used the median value of these metrics for each individual in our visualization. We define daily displacement as the distance between two GPS fixes, 24 hours apart, each at approximately 0000 hours. We calculated hourly movement rate using GPS data filtered to include only consecutive fixes. To assess changes in movement through the season, we calculated daily movement rate (DMR; m/day) as the cumulative distance moved in a 24-hour period. We calculated tortuosity using a straightness index (dE/L), defined as the Euclidean distance between two points divided by the total path length, to determine linearity of an individual’s path in 24-hours using a 1-hour fix rate (Batschelet 1981; Signer et al. 2011). All movement parameters were calculated using R

4.2.1 (R Core Team 2022) and the Animal Movement Tools (amt) package (Signer et al. 2011).

Accelerometers can classify snowshoe hare behaviour into hopping, sprinting, foraging, and resting with 88% accuracy (Studd et al. 2019). In our study, hare behaviours were recorded continuously during a radio-collar deployment, and we focused our analysis on time spent traveling per day, which comprised hopping and sprinting behaviours.

Hare Population Estimation

In addition to monitoring instrumented hares, we conducted a biannual census to estimate hare density on three 36-ha study areas (Krebs et al. 2018). Briefly, in spring and fall, capture-mark-recapture surveys were conducted over 2-4 trap nights for each area (depending on recapture rates), using 86 livetraps deployed at fixed locations on each grid. Hare numbers were estimated via spatially explicit capture-recapture models (Efford 2009). This census allowed us to calculate post-winter and post-breeding hare population density estimates for the larger study region.

Average hare population density estimates on our three monitoring sites were intermediate at the beginning of the study (2015) and reached a peak in fall 2016 (Fig. 1). Thereafter, numbers declined 25-fold by 2020 and remained comparably low until the study ended (2022).

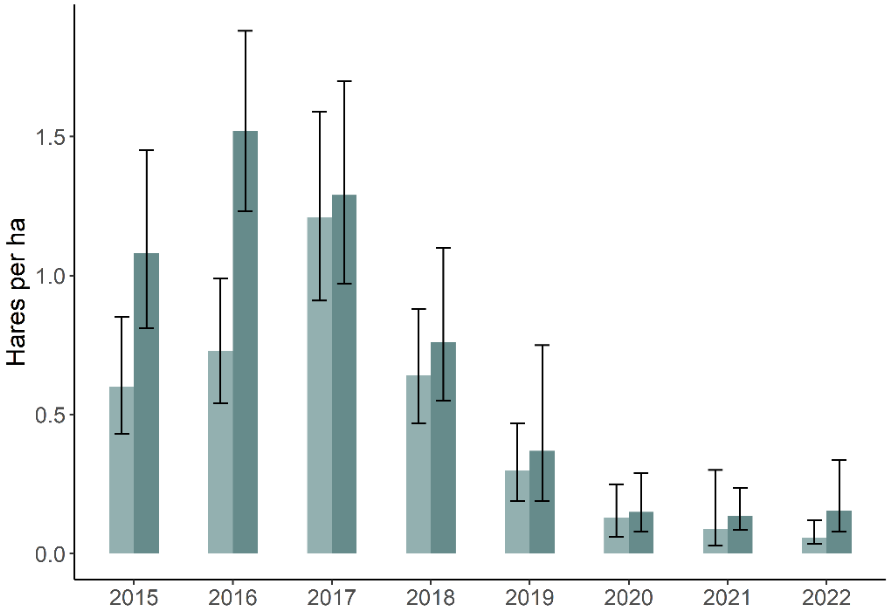

Figure 1 Snowshoe hare densities in southwestern Yukon, Canada (2015–2022; ± 95% CI), derived from capture-mark recapture estimates on control study areas during spring (light blue) and fall (dark blue) of each year (Krebs et al. 2023).

Relative Abundance of Hares and Predators

We used footage from twenty-seven trail cameras that were deployed within a 10 km buffer area of our hare study areas to index hare abundance and monthly activity as well as that of its main predators, Canada lynx (*Lynx canadensis*) and coyote (*Canis latrans*). Cameras were posted on trails or other animal travel routes with >1 km separation to establish independence between observations (Kenney et al. 2024). Camera site selection ensured a reasonable field of view and that cameras could be readily accessed by road or trail system. Cameras were mounted ~43 cm (range = 24 to 70 cm) above ground level, as this provided the best coverage of all species and the largest field of view (Kenney et al. 2024). We measured species abundance using hit rate, which is defined as number of times a species is detected divided by number of camera days of camera operation. One "hit" was recorded for each species within a 2-minute window, regardless of how many photos were taken (Kenney et al. 2024). Cameras were operational year-round, but we calculated hit rates only for the May-September study period.

Statistical Analysis

To examine the role of select covariates on hare movement and activity, we used generalized linear models (GLM) and generalized linear mixed models (GLMM) and assembled candidate sets of models *a priori* (Murray et al. 2020). We included year, sex, and their interaction as predictors, to test between our stated predictions. Our response variables included home range size and core use isopleths, for which we used year and sex as fixed effects; for daily displacement, tortuosity and time spent traveling, we used year and sex as fixed effects, but added calendar week and hare ID as random effects to calibrate our analysis according to potential seasonal changes. We used year, sex, week, and diel period (dawn, day, dusk, night; calculated using package ‘suncalc’; Thieurmel and Elmarhraoui 2022) to determine hourly movement rate, with week and hare ID included as random effects. Additionally, we used GLMMs with our camera data to examine how year and month affect detection of hares and their main terrestrial predators, lynx and coyotes (hits per 1000 days); camera ID was included as a random effect. Models were fit with Student’s t distribution (Pearson type VII distribution) using package ‘glmmTMB’ (Brooks et al. 2017) in R (ver. 4.2.1; R Core Team 2022). When appropriate given our *a priori* understanding of the snowshoe hare system, we added interaction terms for year and sex. We centered and scaled response variables and all continuous predictor variables prior to modelling (Schielzeth 2010). To address potential multicollinearity, we calculated variance inflation factors (VIFs) in the R package ‘performance’ (Lüdecke et al. 2021) and ensured low correlation between covariates in the same model (all VIF < 2.0). We used Akaike’s information criterion corrected for small sample sizes (AICc) to select the best model from each candidate set, with models with ΔAICc ≤ 2.0 considered indistinguishable (Burnham and Anderson 2002). We calculated model weights (w_i) to aid in interpretation and evaluated effect sizes based on regression coefficients. We calculated McFadden’s Pseudo-R^2 to measure model fit, with values between 0.2–0.4 indicating strong fit (package ‘piecewiseSEM’; Lefcheck 2016). When random effects were included in models, we used Conditional Pseudo-R^2 to measure model fit, to account for both fixed and random effects (Lefcheck 2016). We used 95% confidence intervals as an index of the magnitude of effect of independent variables and deemed that confidence intervals overlapping zero were not significant. Our data typically exhibited skewness that deviated from a normal distribution, so we used the median and 95% bias-corrected and accelerated (BCa) confidence intervals (calculated using package ‘rcompanion’; Mangiafico 2023) to describe raw data.

Results

Summer Home Range and Core Use

Hares exhibited variable summer home range size through the 8-year study period, with median ranges of 3.9 ha (3.4–4.4 [95% BCa CI]) during 2015-2019 and increasing more than 3-fold to 13.3 ha (10.1–16.1) during 2020–2022. Home range size was largely comparable between sexes, although during 2021–2022 male ranges were notably larger (2–3-fold; Fig. 2 & 3). The best-fit model of hare home range size included main effects of Year and Sex, with a Year × Sex interaction (Table 1). Model coefficients indicated a general increase in home range size with year and larger ranges for males than females (Table 2). Notably, confidence intervals for the Year × Sex interaction term did not overlap zero (Table 2), reinforcing the observation that males had larger ranges than females only during the low phase of the hare cycle (2021–2022) when range size differences between sexes were 2–3-fold (Fig. 1).

Core use isopleth values were largely consistent across years, with a median of 68% (range: 60–88%) from 2015–2022. Isopleth values were comparable between sexes throughout the study period (Fig. 2 & 3). Hare core use was comparably explained by three models (ΔAICc <2.0): Sex only, Null, and Year and Sex (Table 1), but given the poor fit of models (Table 1) and model coefficients overlapping zero (Table 2), we infer that core use isopleths are not influenced by either year or sex.

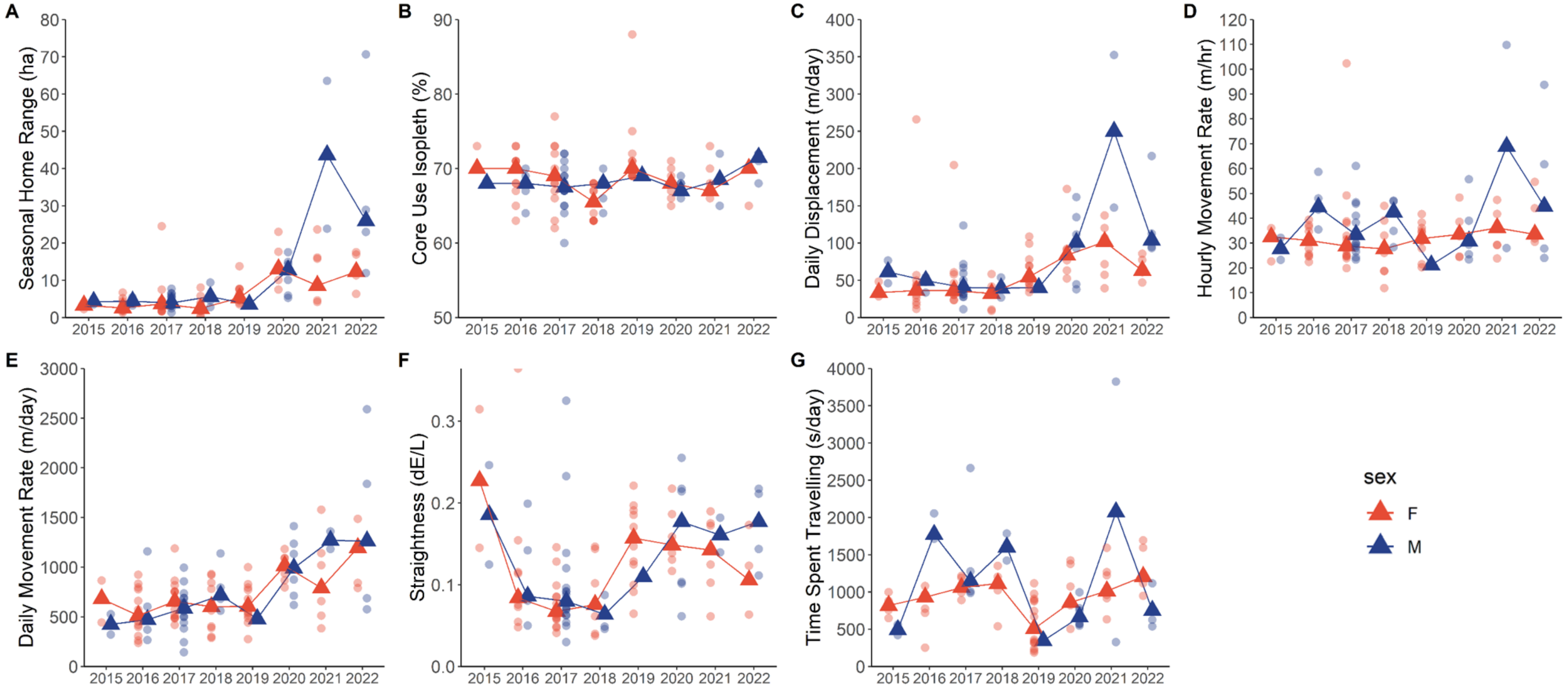

Figure 2 Annual variation in median (triangles) and individual (circles) movement metrics in snowshoe hares (*Lepus americanus*) during May-September in southwestern Yukon, Canada (2015–2022). **A.** home range size (95% isopleth), **B.** core use isopleths (%), **C.** daily displacement (m/day), **D.** hourly movement rate (m/hr), **E.** daily movement rate (m/day), **F.** Straightness (dE/L), **G.** daily time spent travelling (s/day). Male (blue) and female (red) snowshoe hares are depicted.

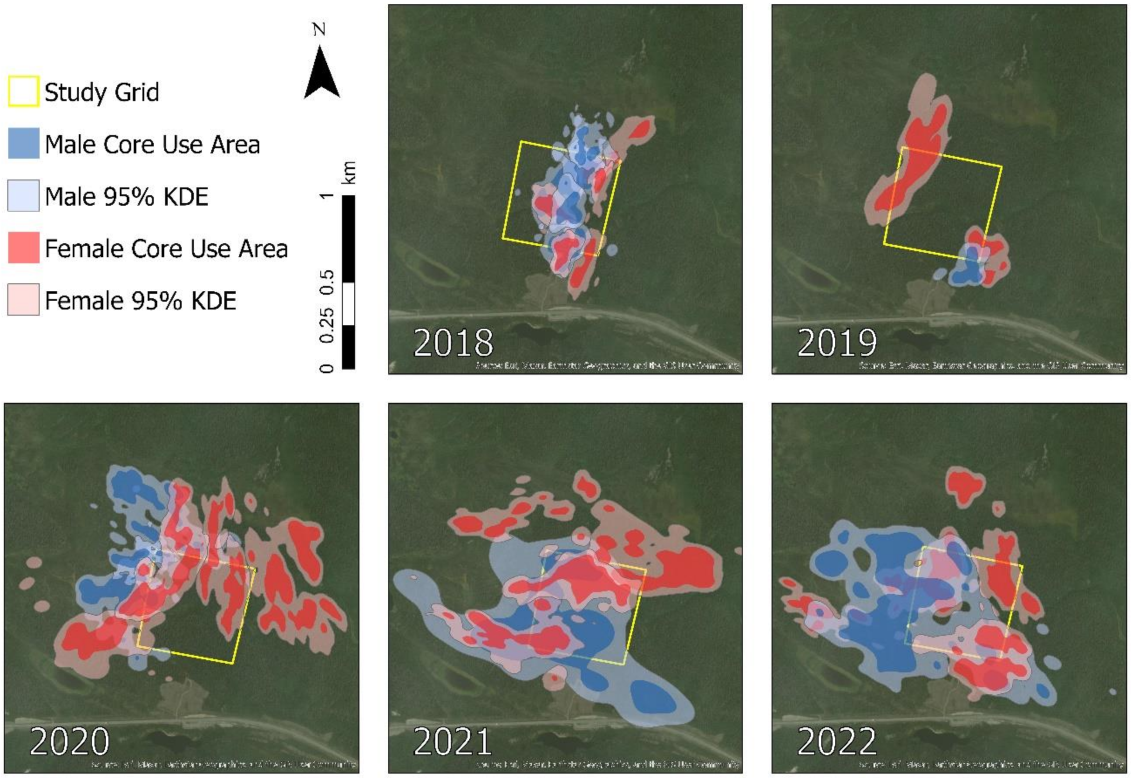

Figure 3 Seasonal home ranges (95% kernel density estimate) and core use areas (60-88% isopleths) of a sample of snowshoe hares monitored in southwestern Yukon, Canada (2018–2022; n = 11 [2018], n = 4 [2019], n = 4 [2020], n = 4 [2021], n = 5 [2022]).

Table 1 Best-supported models ($\Delta AIC_c \leq 2$) predicting snowshoe hare (*Lepus americanus*) movement and activity in southwestern Yukon, Canada (2015–2022). All continuous covariates were scaled prior to modelling.

	Model	**K**	**ΔAICc**	w_i	**LL**	**Pseudo-R^2**	**Conditional Pseudo-R^2**
Seasonal Home Range	Year × Sex	5	0.00	0.99	-121.75	0.27	-
Core Use Isopleth	Sex	3	0.00	0.35	-155.39	0.02	-
	Null	2	0.25	0.31	-156.57	0.00	-
	Year + Sex	4	1.88	0.14	-155.25	0.02	-
Daily Displacement	Year	5	0.00	0.44	-3814.37	-	0.23
	Year × Sex	7	0.67	0.31	-3812.69	-	0.23
	Year + Sex	6	1.20	0.24	-3813.96	-	0.23
Movement Rate	Year + Sex + Diel Period	8	0.00	0.70	-95900.47	-	0.09
	Year × Sex + Diel Period	9	1.73	0.30	-95900.33	-	0.09
Tortuosity	Null	4	0.00	0.37	-4567.58	-	0.11
	Year	5	1.01	0.22	-4567.08	-	0.11
	Sex	5	1.56	0.17	-4567.35	-	0.11
Time Spent Travelling	Year × Sex	7	0.00	1.00	-3645.87	-	0.59
Daily Movement Rate	Year × Sex + Week	7	0.00	0.56	-4252.88	-	0.32
	Year + Sex + Week	6	0.47	0.44	-4254.12	-	0.32

Table 2 Regression coefficients (± 95% CI) of best-supported models ($\Delta AIC_c \leq 2$) predicting snowshoe hare (*Lepus americanus*) movement and activity in southwestern Yukon, Canada (2015–2022). All continuous covariates were scaled prior to modelling. Coefficients where confidence intervals did not overlap zero are in bold.

	Model	**Year**	**Sex (M)**	**Year*Sex (M)**	**Time of Day (Day)**	**Time of Day (Night)**	**Week (Interval)**
Seasonal Home Range	**Year × Sex**	**0.34 (0.18 - 0.50)**	**0.39 (0.12 - 0.66)**	**0.50 (0.23 - 0.77)**	-	-	-
Core Use Isopleth Value	Sex	-	-0.29 (-0.66 – 0.08)	-	-	-	-
	Null	-	-	-	-	-	-
	Year + Sex	0.05 (-0.13 – 0.23)	-0.28 (-0.65 – 0.09)	-	-	-	-
Daily Displacement	**Year**	**0.18 (0.08 – 0.28)**	-	-	-	-	-
	Year × Sex	0.12 (0.00 – 0.24)	0.10 (-0.10 – 0.30)	0.16 (-0.04 – 0.36)	-	-	-
	Year + Sex	**0.18 (0.08 – 0.28)**	0.09 (-0.11 – 0.29)	-	-	-	-
Movement Rate	**Year + Sex + Diel Period**	**0.08 (0.04 – 0.12)**	**0.12 (0.02 – 0.22)**	-	**0.26 (0.24 – 0.28)**	**-0.08 (-0.13 - -0.02)**	-
	Year × Sex + Diel Period	**0.07 (0.01 – 0.13)**	**0.12 (0.02 – 0.22)**	0.02 (-0.08 – 0.12)	**0.26 (0.24 – 0.28)**	**-0.08 (-0.14 - -0.02)**	-
Tortuosity	Null	-	-	-	-	-	-
	Year	0.04 (-0.04 – 0.12)	-	-	-	-	-
	Sex	-	0.05 (-0.11 – 0.21)	-	-	-	-
Time Spent Travelling	**Year × Sex**	-0.14 (-0.34 – 0.06)	**0.61 (0.20 – 1.02)**	**-0.87 (-1.32 - -0.42)**	-	-	-
Daily Movement Rate	**Year × Sex + Week**	**0.32 (0.18 – 0.46)**	0.18 (-0.04 – 0.40)	0.17 (-0.03 – 0.37)	-	-	**-0.07 (-0.11 – -0.03)**
	Year + Sex + Week	**0.38 (0.28 – 0.48)**	0.19 (-0.03 – 0.41)	-	-	-	**-0.07 (-0.11 - -0.03)**

Movement Metrics

Hares exhibited variable daily displacement during the study period, and this pattern mirrored trends in summer home range size. During the increase, peak, and decline phases (2015–2019, Fig. 1), median daily displacement was 40.3 m/day (37.2–45.4), and this more than doubled to 92.8 m/day (71.7–107.0) during the low phase (2020–2022). Males and females showed some variation in daily displacement, especially during 2021–2022 when males traveled long distances and hare numbers were notably low (Fig. 2). The set of three best-fit models for daily displacement (ΔAICc <2.0) included Year alone, as well as interactive and additive models including both Year and Sex. All three models were within an acceptable range of goodness-of-fit (0.2–0.4 conditional Pseudo-R^2; Table 1) although only Year had confidence intervals that did not overlap zero (Table 2). On average, displacement distance increased as the study progressed, but variation between sexes was high.

Males exhibited variable hourly movement rates between years, with rates increasing from an average of 27.7 m/hr (23.2–27.7) in 2015 to 68.9 m/hr (28–68.9) in 2021 (Fig. 2). Females, however, showed little variability in hourly movement rates with median rates of 31.4 m/hr (29.1–32.9) from 2015–2022. The best-fit models included main effects of Year, Sex, and Diel Period, and Diel Period with a Year × Sex interaction (Tables 1 & 2). However, these models did not fall within an acceptable range of goodness-of-fit (Table 1) and had large confidence intervals (Table 2). The best-fit model of hare movement tortuosity was the Null model (Table 1 & 2), indicating that this movement metric was not clearly influenced by the factors under consideration. Therefore, we surmise that the hare movement metrics that we measured were affected by hare density and sex, with some differences appearing to vary according to cyclic phase and being accentuated during the low period (2020–2022) of the hare cycle.

Hares exhibited variable travel-related behaviour during the study period, with time spent travelling (hopping, sprinting) almost tripling from 434.0 s/day in 2019 (319.0–809.0) to 1116.0 s/day in 2022 (626.0–1401.0). Qualitatively, males exhibited more variation in travel-related behaviours between years than females (Fig. 2), and the best-fit model of time spent travelling included main effects of Year and Sex, with a Year × Sex interaction (Table 1 & 2). The model had high goodness of fit (Table 1), but notably only Sex and Year × Sex variables had confidence intervals that did not overlap zero, with males exhibiting greater travel-related behaviours than females (Table 2). Similarly, daily movement rates were best explained by two models that included main effects of Week, Year and Sex, with or without an interaction term (Table 1), with Year and Week variables having confidence intervals that did not overlap zero (Table 2). In both models, daily movement rate was positively related to year (Table 2), with daily movement rate increasing steadily during the study period (Fig. 2). Daily movement rate was negatively related to week, indicating a consistent decline in daily movement rate through the season. Male daily movement rates were highest in May (median = 679.0 m/day; 557.0–800.0) and lowest in July (median = 587.3 m/day; 472.0–731.0). In contrast, female daily movement rates were lowest in May (median = 578.0 m/day; 522.0–698.0) and highest in August (median = 737.0 m/day; 574.0–842.0). Because of these differences between sexes, we consider this finding in support of prediction ii (males exhibit greater movement than females in early summer in search of mating opportunities) rather than supporting prediction vi (all hares exhibit increased movement in May-June).

Predation Risk Responses

We assessed annual and seasonal (May-September) activity patterns for hares and predators via trail camera detections (hare: 16,435; lynx: 2,719, coyote: 1,340 detections 2016-2023). Annual rates of camera captures of hares (Fig. 4) closely followed population trends from the hare capture-mark-recapture dataset (Fig. 1; Kenney et al. 2024). Both hare : lynx and hare : coyote ratios were highest in 2020 (hare : lynx (1 : 0.39); hare : coyote (1 : 0.26)), at the onset of the low phase of the hare population cycle. Annual rates of camera captures for lynx and coyote followed a similar trend, with greatest abundance in 2017 and lowest in 2022 (Fig. 4). For hares, there was a qualitative decline in detections during June and a resurgence by August, whereas for lynx, detections were consistent through the spring-summer season (Fig. 4). Coyote detections declined qualitatively in June-July and increased in August-September (Fig. 4). The best-fit models for hare detections ($w_i = 0.65$, cond. pseudo $R^2 = 0.56$) and lynx detections ($w_i = 0.38$, cond. pseudo $R^2 = 0.32$) included Year and Month as predictors, had acceptable goodness-of-fit (cond. pseudo $R^2 > 0.2$; Supplemental Tables 1 & 2). Hare detections increased with month (0.04, 0.00–0.08). However, confidence intervals overlapped with zero for monthly detections of lynx (0.03, -0.03–0.09). Detection models for coyote had low goodness-of-fit (cond. pseudo $R^2 < 0.2$; Supplemental Tables 1 & 2). Accordingly, we infer that although hares varied their activity and movements during the population cycle (Fig. 2), seasonal changes in movements did not correspond to activity variation or relative abundance of their terrestrial predators.

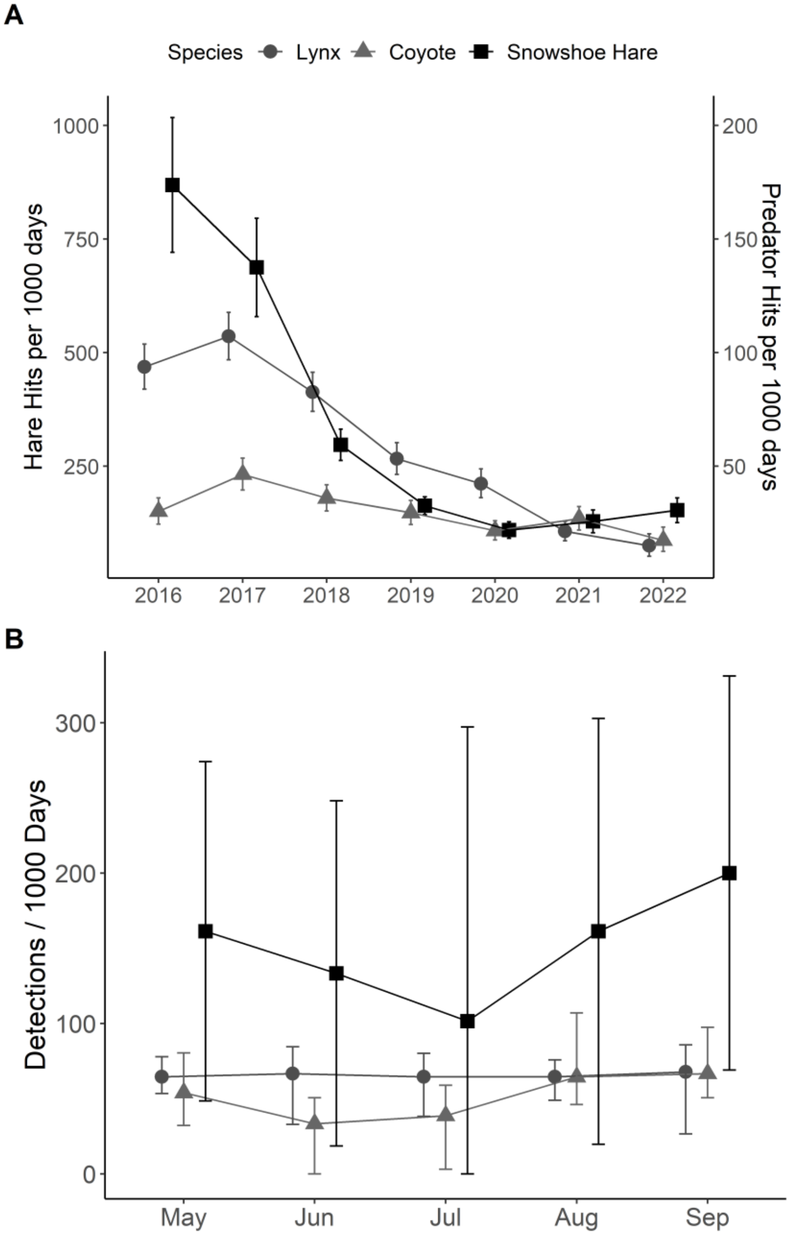

Figure 4 A. Median detections of snowshoe hare (black squares), lynx (dark grey circles), and coyote (light grey triangles) per 1000 days (± 95% BCa CI) in southwestern Yukon, Canada (2016–2022). **B.** Median detections (± 95% BCa CI) of snowshoe hare (black squares), lynx (dark grey circles), and coyotes (light grey triangles) per 1000 days from May-September (2016–2022) in southwestern Yukon, Canada.

Discussion

Our study revealed that snowshoe hares exhibit variable spring-summer movement and activity during their population cycle. While both males and females increased home range size and daily displacement in the low phase, males in particular exhibited a 2–3-fold increase in their range size compared to the high phase. During the cycle both sexes exhibited similar core use isopleths and movement tortuosity, but males also typically had greater and more variable movement rates and time spent travelling compared to females, typical of polygynous mating systems (Jones et al. 2012). Intra-season variation in hare movements were not closely associated with shifts in either predator activity and relative abundance or seasonal food availability. Collectively, our findings support the hypothesis that reproductive activities and mating opportunities are the primary drivers of hare movement during summer, as well as explaining inter-annual movement variation during their population cycle. More broadly, our findings reinforce that potential fitness rewards associated with successful mate search and reproduction may outweigh predation risks associated with greater movements, even in highly variable environments where costs of finding mates may be notably high.

Reproductive activities including dispersal, mating, and caring for offspring, are a major driver of animal behaviour and movements, including dispersal, mating and caring for offspring (Berec et al. 2018; Csányi et al. 2022). During dispersal and mating, animals may expand their non-breeding space use and take more risks in their movements and habitat selection (Keeley et al. 2017). Because home range size is often negatively related to population density (e.g., Trewhella et al. 1988; Dahle and Swenson 2003; Fauteaux and Gauthier 2022), lower population density may elicit increased mate search that is sex-specific depending on species' mating strategies (Kokko and Rankin 2006). In systems where males are primarily responsible for mate searching, mating limitations at low densities should require more expansive male ranges and movements (Berec et al. 2018). Snowshoe hare mating strategy is poorly understood but likely is polygynous or promiscuous (Burton 2002), implying that males actively search for mates, which could explain their more expansive movements compared to females during the period of low hare density. Because hares give birth to 2–4 litters per year (Cary and Keith 1979, Krebs et al. 2018), males may travel extensively during May-August in search of mating opportunities whereas females should most often be restricted by activities related to maternal care (O'Donoghue and Bergman 1992). Yet, inter-sex differences in movements may be more limited at lower population densities, when hares produce fewer litters (Stefan and Krebs 2001), leveret predation is higher (J. Gobin, unpubl.), and females may be less restricted by maternal duties. This speculation is supported by the similarity between male and female home range size and daily displacement during the low and increase phases of their population cycle, and the increase in home range and movements across both sexes during the decline period. The consistency in core use isopleths between sexes and throughout the cycle likely illustrates that hares' basic needs (food, cover) were consistently met at a smaller spatial scale.

Predation is the primary proximate cause of mortality in snowshoe hares (Murray et al. 1997; Krebs et al. 2018) and predation risk may be a driving force underlying hare population cycles and the extended cyclic lows in abundance (Boonstra et al. 1998). Yet, the lack of correspondence between hare movements and either annual changes in hare : predator ratio or May-September predator activity patterns implies that predation risk is not a primary driver of spring-summer hare movements. This inference was reinforced by differences in home range size and daily displacement between male and female hares, which should not arise if predation risk is a primary driver and given similar mortality rates between sexes (Murray et al. 1997). Of note, prey may sometimes increase their movements and home range size when under high predation risk as a means of diluting olfactory cues that are used by predators for prey detection (Frair et al. 2005; Finnerty et al. 2022). While there is evidence that prey may increase activity in response to predation pressure (Kauffman et al. 2007; Mayer et al. 2019), we showed previously that in our system lynx kill hares irrespective of hare activity shortly before their death (Shiratsuru et al. 2023). Thus, based on the dissimilarity in movement patterns between sexes as well as the generally weak correspondence between hare movements and our predator indices, we infer that predation risk was not an important driver of spring-summer hare movements.

We predicted that if carry-over effects of winter food limitation affect spring-summer movements, hares should be most active and wide-ranging during late May-early June when the sudden availability of leafy vegetation provide them with highly digestible food. Note that this prediction is not exclusive of that predicting higher mating activity during the same period. However, the lack of clearly higher hare activity and movements during this period refutes this prediction, even though in temperate environments annual switch to herbaceous vegetation in spring can play an important role in herbivore survival and nutrition (Cook et al. 2004). Regardless, if food limitation influenced hare movements, we predicted that travel would be higher during the peak in hare density, when any food limitation should have been at its highest and this was not the case, leading support to our conclusions.

We conclude that mating behaviour and population density are the primary factors driving hare movement dynamics in cyclic hare populations during summer. Nevertheless, movement dynamics can be shaped by multiple factors acting either alone or in tandem (Ganz et al. 2022), and the poor goodness-of-fit for several of our predictive models is an important reminder that other influences act to determine movement dynamics. Indeed, variation in population density may play a lesser role in determining movement patterns in non-cyclic snowshoe hare populations, whereas for other cyclic species factors like predation risk or food availability may play a more dominant role. Observations outside the breeding season could serve as a test of this hypothesis. Accordingly, a remaining challenge will be to develop general rules-of-thumb that predict movement dynamics in species across a range of ecological conditions, and to identify the circumstances where mating opportunities play an over-riding role in driving these variations in movement.

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Chapter 3: General Discussion

Thesis goals: Revisited

The aim of this thesis was to explore the determinants of hare movement and activity and assess whether hares exhibit dynamic movement during their population cycle. Indeed, I determined that both males and females increased their home range size and daily displacement in the low phase. Males exhibited larger increases in range size than females, likely due to increased effort and travel required for mate searching during low population densities. Both sexes exhibited similar core use isopleths and movement tortuosity. However, males typically showed greater and more variable movement rates and time spent travelling. Overall, my thesis supports the contention that reproductive activities and mating opportunities are the primary drivers of hare movement during the breeding season, and this provides explanation for variation in inter-annual movement during their population cycle. These findings reinforce that, even in highly variable environments, the benefits of mating and reproduction may outweigh the risks associated with mate searching behaviour.

Interactive effects of animal movement

Animal movement is driven by individual motivations and decision-making in response to perceptions of the surrounding environment (Bennett and Tang 2006). Decision-making in relation to movement can either be reactive (e.g., avoiding signs of predators; Mayer et al. 2020), or purposeful (e.g., increasing foraging despite greater predation risk; Brodin and Johansson 2004). These decisions are influenced by spatial memory (Fagan et al. 2013) and sensitivity to surrounding stimuli (Forsman and Kivelä 2021; Shaw 2020). An animal cumulates this information into a matrix of knowledge that influences behaviours such as movement, social interactions, risk avoidance, and ultimately, individual fitness. Therefore, while in my study I sought to assess snowshoe hare movement determinants individually, it is likely that multiple factors are involved and could have interactive (agonistic or synergistic) effects. Animals typically balance the costs of travel (e.g., exposure to threats/predation) against meeting and performing basic needs and functions (e.g., finding food and water, mating and caring for young). Balancing these factors may vary temporally, based on different internal and external factors. For example, elk (*Cervus elaphus*) may be attracted to quality forage but avoid areas with deep snow or use by predators, and the interaction between these factors is dependent on the spatial distribution of resources and threats (Bennett and Tang 2006). Additionally, interactions between internal factors (e.g., sex, age, body size) may also affect animal movement (Gutowsky et al. 2016). Ultimately, interactive effects between movement determinants can influence how animals interact with and move through the landscape. While my approach of assessing determinants independently is effective as a first step for comparing the relative significance of these factors, assessing interactive effects between these determinants, and others, would likely provide a more comprehensive understanding of animal movement determinants.

Level of analysis

Movement patterns can vary significantly among populations, individuals in the same population, or even within an individual over time (Shaw 2020). These variations reflect seasonal activities (e.g., breeding), life stage, interactions with conspecifics, interactions with other species, and changes in the environment (Tang and Bennett 2010). While individual variability was factored into my analysis as a random effect, the focus of this thesis was ultimately at a population level. Individual movement can be driven by factors acting at the individual, population, community, and ecosystem level (Shaw 2020). Assessing determinants at an individual level should capture factors acting at these different scales, therefore providing the most complete picture of movement and activity patterns. Additionally, assessing movement at an individual level allows the opportunity to explore additional determinants at a finer spatial scale. For example, one could incorporate factors such as habitat type, forage patches, and potential inter- and intra-species interactions within an individual's home range. However, while assessing movement and activity patterns at an individual level is the best practice, there are many potential challenges to consider with this scale of analysis. The data necessary to assess animal movement at the individual level may be difficult to collect, costly, or not accessible in remote landscapes. These challenges can affect the number of individuals monitored, as well as the scale at which potential external factors are assessed (e.g., GPS accuracy too low for fine-scale habitat assessment). Additionally, assessing movement at an individual level may result in high levels of variability, from which it may be difficult to make solid inferences. As such, while efforts should be made to assess animal movement at an individual level when possible, assessing animal movement at a population level is still effective for determining the proximate factors of movement.

Conclusions and future research

My findings emphasize that, in the case of snowshoe hares, mating availability and reproductive activities are the major determinant of movement. From a life history and fitness perspective, the potential rewards associated with successful mate search and reproduction may outweigh risks, especially when costs of finding mates are notably high and variable. However, it is important to note that there are many determinants of movement and there are likely many factors not considered in this thesis. Therefore, a promising avenue for researchers would be to focus on movement and activity patterns throughout an individual's lifetime, in combination with other habitat, weather and inter/intraspecific factors to capture a more complete picture of movement determinants. Further investigation should incorporate potential interactive effects of these factors, as well as additional environmental factors (habitat type, available food, intra- and inter-species interactions). These efforts are especially important in highly variable and dynamic environments to assess how animals react to changes in their environment. In summary, my thesis identifies the importance of mating and reproduction in driving the movement and behaviour of snowshoe hare through their population cycle and provides a strong foundation for future research on the determinants of animal movement and activity patterns.

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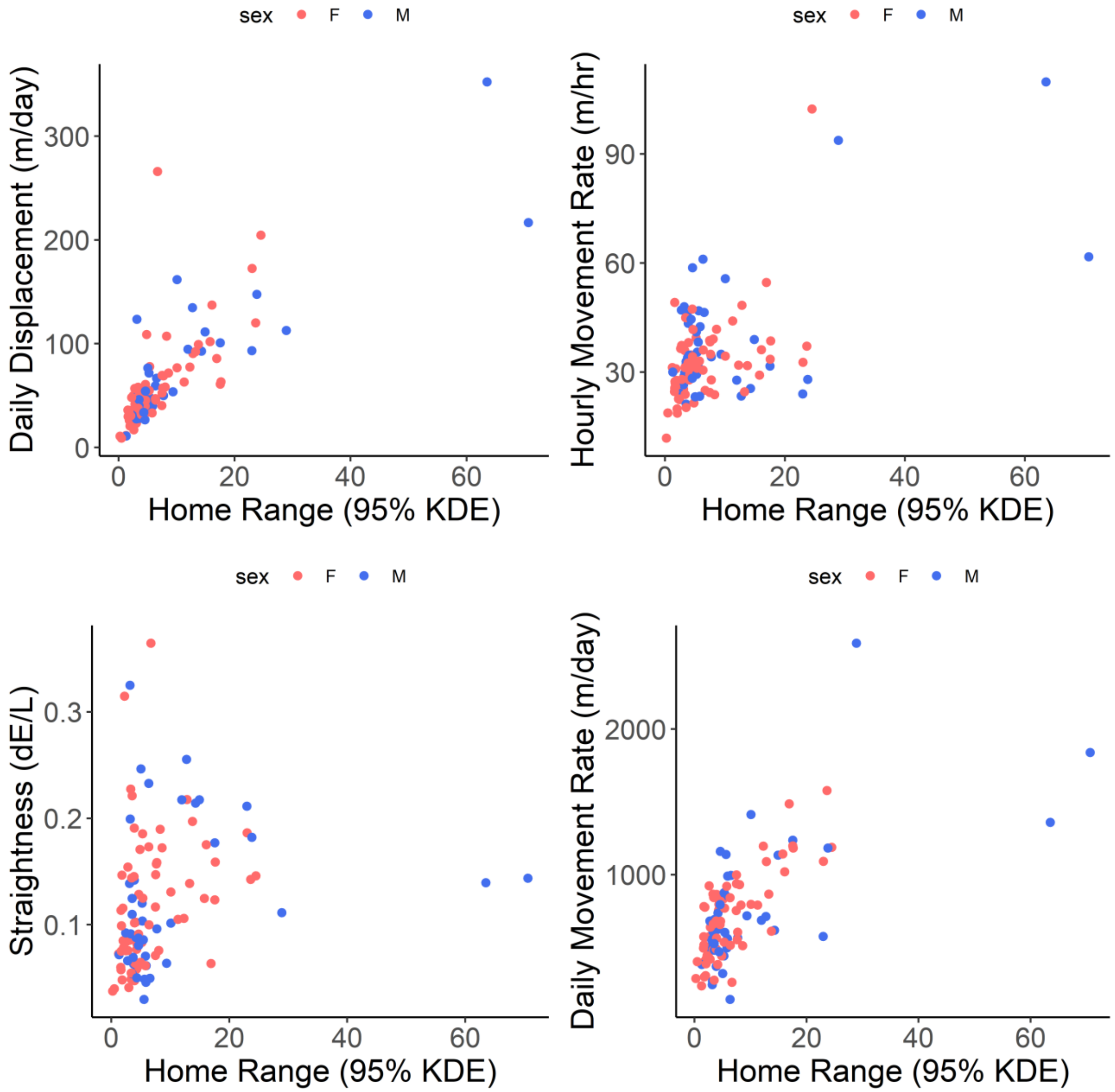
Supplementary Materials

Supplemental Figures



Supplemental Figure 1. Movement metrics compared to seasonal home ranges (95% KDE) of snowshoe hare (*Lepus americanus*) during 2015-2022 in southwestern Yukon, Canada.

Supplemental Tables

Supplemental Table 1 Best-supported models ($\Delta AIC_c \leq 2$) of camera detections (hits per 1000 days) of snowshoe hare (*Lepus americanus*), Canada lynx (*Lynx candensis*) and coyote (*Canis latrans*) May-September in southwestern Yukon, Canada (2016-2022; Kenney et al. 2024).

Species	**Model**	**K**	**ΔAICc**	w_i	**LL**	**Conditional Pseudo-R^2**
Snowshoe hare	Year + Month	5	0.00	0.65	-775.21	0.56
	Year	4	1.25	0.35	-776.85	0.56
Lynx	Year	4	0.00	0.62	-669.49	0.31
	Year + Month	5	0.95	0.38	-668.95	0.32
Coyote	Month	4	0.00	0.40	-511.42	0.14
	Year + Month	5	0.24	0.36	-510.51	0.15

Supplemental Table 2 Regression coefficients (± 95% CI) of best supported models ($\Delta AIC_c \leq 2$) predicting snowshoe hare (*Lepus americanus*), Canada lynx (*Lynx canadensis*) and coyote (*Canis latrans*) camera detections (hits per 1000 days) May-September in southwestern Yukon Territory, Canada (2016-2022; Kenney et al. 2024). Coefficients where confidence intervals did not overlap zero are in bold.

Species	**Model**	**ΔAICc**	**Year**	**Month**
Snowshoe hare	Year + Month	0.00	**-0.25 (-0.31 - -0.19)**	**0.04 (0.00 – 0.08)**
	Year	1.25	**-0.25 (-0.31 - -0.19)**	**-**
Lynx	Year	0.00	**-0.31 (-0.37 - -0.25)**	**-**
	Year + Month	0.95	**-0.30 (-0.37 - -0.25)**	0.03 (-0.03 – 0.09)
Coyote	Month	0.00	**-**	**0.10 (0.00 – 0.20)**
	Year + Month	0.24	-0.07 (-0.17 – 0.03)	**0.10 (0.00 – 0.20)**

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