Seasonal changes in the movements rates and activity patterns of Canada lynx

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Abstract

In Subarctic and Arctic environments, daily patterns of activity and space-use are strongly influenced by interplay between seasonal abiotic factors and the corresponding responses of the biotic environment. Here we combined accelerometry with GPS telemetry of Canada lynx (*Lynx canadensis* (Kerr, 1792), *n*=12) in northern Alaska to test the hypotheses that lynx activity would peak during twilight throughout the year, coinciding with activity of their preferred prey, and that individuals with larger home ranges would have greater spatial displacement and expend more energy on movement. Lynx activity occurred throughout the 24h day and peaked during twilight, but variation among individuals was high and diel rhythms were sometimes only detectable using the finer resolution accelerometer data. Surprisingly, home range size was not correlated with movement costs estimated via acceleration, but step length and acceleration were correlated in a positive curvilinear fashion. However, step length was sometimes disproportionately lower than predicted by acceleration. Such intervals of high activity with low spatial displacement were often followed by periods of rest, suggesting they may be indicative of hunting in a restricted patch of habitat. We conclude that accelerometers can provide additional information to supplement GPS data, providing a more complete picture of animal behavior.

Keywords: Canada lynx, *Lynx canadensis*, accelerometer, diel activity, seasonal activity, VeDBA, hunting behavior

Introduction

Biotelemetry and biologging, which involve the use of miniature tags for logging and/or relaying data on an animal's movement, behavior, physiology and/or environment, have become critical tools to study free-living animals in their natural environment. These technologies have proven to be particularly useful in the study of rare, cryptic, or otherwise not easily observable species (Rutz and Hayes 2009). For example, biologging has proven invaluable in quantifying the strong seasonality of activity patterns and movement parameters in species that occupy Subarctic and Arctic landscapes (e.g., Studd et al. 2019, Ware et al. 2020). Carnivores in particular exhibit widespread plasticity in their diel activity patterns, which are shaped by the interplay between abiotic and biotic factors (Heurich et al. 2014). Perhaps the most widely used biologging technology in free ranging animals is GPS telemetry, which has proven effective for examining a variety of facets of a species biology, including activity patterns (Hertel et al. 2017), migrations (Sawyer et al. 2005), habitat use (Tucker et al. 2008), resource selection (Chetkiewicz and Boyce 2009), feeding behavior (Cristescu et al. 2015), and parturition timing (Cameron et al. 2018, Nicholson et al. 2019).

Although GPS transmitters are capable of recording data with high temporal resolution, battery life is inversely proportional to the frequency of GPS relocations (fix rate hereafter), which leads to significant tradeoffs between device fix rate and device life span (Hebblewhite and Haydon 2010). For smaller taxa that require lightweight devices, researchers often sample at a lower temporal resolution that can limit the ability to resolve fine scale behavior or address certain research questions. The spatial displacement between consecutive GPS locations (step length hereafter) is often used to investigate patterns of activity and other aspects of spatial movement. However, low fix rates can substantially underestimate distance traveled (Dewhirst et al. 2016) and costs of transport (Wang et al. 2017) because long intervals between GPS fixes fail to capture the tortuosity of movement paths (Kramer and McLaughlin 2001, Hodges et al. 2014, Liu et al. 2015). By contrast to conventional GPS transmitters, accelerometers are lightweight biologgers that can collect very high frequency (beyond 64 Hz) body movement data over relatively long periods. The incorporation of high-resolution accelerometer data with lower temporal resolution GPS location data facilitates the construction of more fine-scale time budgets (Ware et al. 2020), which may allow for better characterization of the temporal niche occupied by free-living animals. Further, accelerometry has proven to be a particularly useful proxy for energy expenditure associated with movement in terrestrial animals, allowing researchers to estimate how behavior influences movement costs over short and long time-scales (Gleiss et al. 2011, Halsey et al. 2011).

We combined accelerometry with GPS data to investigate seasonal changes in the daily activity patterns of Canada lynx (*Lynx canadensis* (Kerr, 1792)) at the northern extent of their range in Alaska. Canada lynx ("lynx" hereafter) are an iconic species of the boreal forests in North America that prey predominantly on snowshoe hares (*Lepus americanus* (Erxleben, 1777)) during all seasons and throughout all phases of the hare cycle (Mowat et al. 1999, O'Donoghue et al. 2010). We hypothesized that lynx activity would peak during twilight throughout the year, coinciding with the initiation of the daily activity of their preferred prey (Feierabend and Kielland 2014, Studd et al. 2019).

Near the southern extent of their range (~46-47°N), lynx have been found to exhibit bimodal crepuscular activity patterns in the summer that shift to a unimodal activity pattern in winter with peak activity occurring around dusk (Parker et al. 1983, Kolbe and Squires 2007); diurnal activity in winter may allow them to search for alternative diurnal prey, such as American red squirrels (*Tamiasciurus hudsonicus* (Erxleben, 1777)), and/or hunt for hares by spotting or flushing inactive hares (Kolbe and Squires 2007). Because the sun does not rise above the horizon during mid-winter at our study site (>67°N), we predicted that in winter, lynx would be particularly active during the mid-day twilight. This prediction was based on the reliance of lynx on snowshoe hares; although lynx successfully hunt hares throughout the diel cycle (Kolbe and Squires 2007, Shiratsuru et al. 2023), hares are potentially more vulnerable to lynx predation under twilight conditions as felids are visual predators with vision well adapted for low light conditions (Ewer 1998, Malmström and Kröger 2006, Studd et al. 2019).

In addition to using accelerometry and GPS to examine seasonal diel activity patterns of lynx, we investigated the relationships between body movement (Vectorial Dynamic Body Acceleration, VeDBA hereafter), step length, and metrics of habitat use (i.e., home range size and core area use). The incorporation of auxiliary triaxial accelerometers is somewhat novel method, but is seeing increased use among researchers, yet often with computationally demanding analytical methods that require training datasets of observed animals (Brown et al. 2013, Pagano et al. 2017). Considering that such training sets are difficult to obtain, we sought to examine how a comparison of simple summary statistics between GPS and accelerometer derived data would provide insight into the relationship between energy expenditure and spatial displacement, and if there was any seasonal variation in this relationship. We hypothesized that animals that occupy larger home ranges would experience concordantly higher movement costs. As such, we predicted that animals with larger home ranges would have greater mean daily step length and expend more energy on movement (i.e., have higher mean daily VeDBA).

Finally, we further investigated the potential utility of GPS and accelerometer-derived summary statistics by examining the relationship between mean hourly VeDBA and step length (measured hourly). We subsequently used that relationship to make inferences about lynx behavior. Because body movement can become uncoupled from step length during tortuous travel, we expected to find instances of lower estimated step length than predicted by body movement. We lacked direct observations of lynx to verify whether intervals of high acceleration associated with short estimates of travel distances equated to hunting behavior. However, low movement/activity has previously been shown to be associated with prey handling and consumption that occurs following successful hunts in carnivores (Schmidt 1999, Studd et al. 2021). Therefore, we examined whether intervals in which VeDBA was uncoupled from step length were followed by periods of low activity as described by accelerometer data, which would be consistent with prey capture and handling after a successful hunt.

Methods

Study area

The study area was roughly 250 km^2 along the Dalton Highway in the Brooks Range of northern Alaska, USA (Figure 1). The small community of Wiseman (67.4100° N, 150.1075° W) is located near the center of the study area and the western edge of the study area falls within Gates of the Arctic National Park. The study area is bisected by the North Fork of the Koyukuk River and by the Dietrich River, whose tributaries flow from bottomland bogs and montane lakes throughout the area. The southern boundary of the study site is approximately 100 km north of the Arctic Circle. The vegetation is predominantly an open spruce-lichen woodland, but river corridors create a mosaic of early successional habitats dominated by willow (*Salix spp.*) and alder (*Alnus spp.*), and the highest elevations consist of alpine tundra habitats.

Lynx capture & tagging

We captured lynx throughout 2019 using home-made cage traps constructed from PVC pipes and chicken wire (Kolbe et al. 2003) and modified Fremont fox foot snares (The Snare Shop, Lidderdale, IA, USA). Modified Victor soft catch #3 traps (Victor-Oneida, Cleveland, OH, USA) were used in place of snares for trapping efforts in warm, snowless conditions. Traps were placed 200-1000 meters from the road along prominent lynx travel corridors and were outfitted with VHF trap transmitters (TBT-550, Telonics, Mesa, AZ) which were monitored daily. Trap locations were visited every 3-5 days to ensure proper functioning.

Upon capture, we chemically immobilized the animals with Telazol™ (3 mg Kg^{-1}) delivered intramuscularly via jab stick syringe. During anesthesia we monitored body temperature, heart rate, and respiration and recorded morphometric data (mass, body length, tail length, chest girth, neck circumference, head circumference, hind foot length, wrist circumference, ear tuft length, canine tooth length, and width between canines). We classified lynx age as juvenile or adult based on body size and ear tuft length (Stephenson and Karczmarczyk 1988).

We fit captured lynx with Telonics (Mesa, AZ, USA) and Lotek (Newmarket, ON, CA) Iridium GPS collars. Telonics collars had a 4-hour fix rate whereas Lotek collars had a 1-hour fix rate. During the late winter and early spring 2019, we affixed axy-4 triaxial accelerometers (TechnoSmart Europe srl., Rome, Italy) to select GPS collars (*n*=21). Lynx that were known to be residents from previous capture efforts (Kielland, unpublished data) were prioritized for accelerometer deployment, as it was necessary to recapture individuals to recover the accelerometer data and individuals that left the study area would not be available for recapture. During fall and early winter 2019, most accelerometers were affixed to Lotek collars with a remote drop off mechanism so devices could be recovered without recapturing the animal. We successfully recovered 12 (9 affixed to Lotek collars and 3 affixed to Telonics collars) of the 21 triaxial accelerometers deployed. Accelerometers sampled at 10 Hz with 8 *g* sensitivity (1 *g* is the value of the Earth's gravitational field), 8-bit resolution. At their heaviest configuration with accelerometers and drop off mechanisms, the mass of Lotek collars was 292 gtams, while the mass of Telonics collars fitted with accelerometers was 247 grams. Collar mass was less than 3% of the body mass of any lynx on which they were deployed. All collars had VHF radio transmitters allowing us to locate mortalities and recover collars with drop off mechanisms.

Animal ethics statement

Animal capture and handling was approved by University of Alaska Fairbanks Institutional Animal Care and Use Committee (protocol 135202-42) and Alaska Department of Fish and Game (scientific permit #19-071). University of Alaska Fairbanks Institutional Animal Care and Use Committees follow the international animal care guidelines described by the Guide for the Care and Use of Laboratory animals.

Data preparation

From the raw accelerometry data, we calculated Vectorial Dynamic Body Acceleration (VeDBA), a metric for overall body movement that is correlated with travel speed and energy expenditure in terrestrial mammals (Bidder et al. 2012, Qasem et al. 2012). VeDBA was used for all subsequent analyses. Collars can sometimes shift on an animal while deployed, and VeDBA is less sensitive to changes in the orientation of the accelerometer than Overall Dynamic Body

Acceleration, which is a similar metric for body movement that also aggregates information from the three axes of acceleration (Bidder et al. 2012). The equation for VeDBA is as follows:

$$VeDBA = \sqrt{(A_x^2 + A_y^2 + A_z^2)}$$

A_x, A_y, and A_z are the dynamic accelerations of each axis of the accelerometer, measured in *g*. We calculated dynamic acceleration for each axis by subtracting the 3-second rolling mean, which approximates the gravitational force with respect to body angle, also known as static acceleration, from the raw acceleration for each of the corresponding axes (Wilson et al. 2006, Bidder et al. 2012).

Daily activity pattern models

Binomial behavioral classifications at the ten-minute scale were assigned using a k-means clustering approach (Hartigan and Wong 1979). A k-means cluster analysis with K=3 (3 clusters) was performed on 10-minute mean VeDBA of each individual lynx using the package *stats* in R (R Core Team 2022). The K value was selected by using the “elbow method” on K values from 1-10 (Li and Zoltàn 2017). The cluster with the lowest mean VeDBA was classified as inactive, while the other two clusters (low activity and high activity) were subsequently grouped and classified as active (Figure 2). We also performed the same K-means clustering approach with $K = 3$ on higher resolution 1-min mean VeDBA data; results of this clustering revealed that animals grouped into the “low activity” cluster from 10-minute interval data were typically only active for a small portion of the 10-minute interval (Figure 2). Additionally, the duration of each resting bout was calculated based on the number of consecutive 10-minute intervals classified as “inactive”.

To assess diel activity patterns, we implemented binomial general additive mixed models (GAMMs) with cyclic circular splines. The dependent variable in these models was activity (i.e., inactive or active) based on the mean 10-minute VeDBA data. We chose this binomial approach because residuals from models that used raw values were not normally distributed, based on Q-Q plots. We elected to use cyclic splines to account for diel rhythms because they allow the data to freely determine the shape of the daily waveform. Models also included a three-step autoregressive moving average process to control for temporal autocorrelation. Because we lacked continuous acceleration data across the year, we subset the dataset prior to analyses into four separate month-long sampling intervals for which we had data from multiple individuals for all or a portion of the sample interval. Hereafter, we refer to these sampling intervals as Spring (Mar 14 to Apr 14, *n* =5, Accelerometer (Axy hereafter) lynx days =112), Summer (May 16 to June 16, *n* =2, Axy lynx days =64), Fall (Oct 5 to Nov 5, *n* =4, Axy lynx days =114), and early Winter (Nov 12 to Dec 12, *n*= 4, Axy lynx days =113). Each individual lynx was modeled separately during each sampling interval to examine whether individuals differed in their temporal patterns of movement (e.g., crepuscular *vs.* nocturnal activity) as well as together to compare overall lynx activity among and between seasons. For lynx F05, we only characterize the rhythm between March 24 and April 14, as this animal was arrhythmic before March 24. We also excluded lynx M12 from the spring GAMM analyses as we had insufficient data to test for rhythmicity. The sample size for Spring (*n*=4) accelerometer derived GAMMs consisted of 91 lynx days.

We constructed additional GAMMs with cyclic circular splines with activity defined by 1-hour step length, using the same k-means method, as the dependent variable to investigate whether analyses of lower resolution GPS data would be useful in identifying diel activity patterns detected based on high-resolution accelerometer data. Models included a one-step autoregressive moving average process to control for temporal autocorrelation. We excluded 2 of the 14 accelerometer-equipped lynx in our GPS diel activity analyses because they were equipped with collars on 4-hour fix rates. All GPS data was filtered for a Dilution of Precision (DOP) value of less than 4 before analysis to eliminate low quality fixes. The sample sizes were accordingly: Spring (*n* =4, GPS lynx days = 91), Summer (*n* =2, GPS lynx days = 64), Fall (*n* =4, GPS lynx days = 82), and early Winter (*n* = 4, GPS lynx days = 82). We also investigated whether individuals exhibited consistent daily patterns of activity over time by creating actograms in R using the *rethomics* package (Geissmann et al. 2019) with 10-minute averaged VeDBA values and 1-hour GPS step length.

Relationship between VeDBA and step length

We used quadratic regression models to both examine the correlation between 1-hour GPS step lengths and mean VeDBA per hour and to investigate if trends in the relationship of these two variables were indicative of discrete behaviors. Log transformed step length was the dependent variable in models and hourly mean VeDBA and hourly activity index were included as fixed effects. Hourly mean VeDBA for all lynx ranged from 0.0067 – 0.2667 *g*. The hourly activity index was assigned using a mean VeDBA breakpoint that allowed the relationship between VeDBA and step length to change, i.e., values above the break point received an index value of 1, and values below the break point were 0. Values assigned 0 represented a low level of activity for that hour, whereas 1 represented all other activity. For each lynx, we empirically assigned the VeDBA breakpoint by constructing models with breakpoints ranging from 0.01*g* up to 0.08 *g* in 0.01 *g* intervals and selecting the model with the lowest AIC score.

Models included a quadratic term for mean VeDBA to account for non-linearity and included the interaction of VeDBA and activity index. The regression lines were plotted piecewise by activity to show two separate lines for the levels of the hourly activity index. The regression equation was as follows:

$$\begin{gathered} ln\,(1 + Step\ length) \sim VeDBA\ + hourly\ activity\ index\ +\ VeDBA^2\ + \\ VeDBA * hourly\ activity\ index\ + VeDBA^2 * hourly\ activity\ index \end{gathered}$$

Although we found that GPS step length was correlated with VeDBA, we also noted many instances in which step length was shorter than predicted by the model (i.e., cases with large negative residuals, where activity was high but step lengths short). We subsequently examined whether negative residuals in one hour predicted movement (step-length) in the following hour – specifically, we created a generalized linear model to investigate the effect that lynx body movement and activity level in one hour has on its activity in the subsequent hour. We then used VeDBA in the next hour as the dependent variable, with VeDBA and the residuals from the quadratic model of points under “all other activity” as fixed effects, and lynx ID as a random effect. We used a gamma distribution in this model because residuals were not normally distributed, based on Q-Q plots.

Relationships among other acceleration and spatial metrics

We calculated seasonal mean values for several metrics of spatial habitat usage (i.e., home range and core area size) and examined how these metrics related to estimates of activity (i.e., mean VeDBA) and/or spatial displacement (i.e., mean step-length). We created separate linear models with mean VeDBA as a response variable and home range, core area, and mean step length as explanatory variables. We also constructed separate models with mean step length as the response variable and home range, core area, and proportion time active per day as explanatory variables. Models used a single explanatory variable to avoid collinearity between explanatory variables that were calculated using the same data (accelerometer or GPS derived). The home range of Lynx M46 was nearly four times as large as the next largest home range during the spring, eight times as large during the summer, and three times as large as the next largest overall home range. The core areas of M46 were similarly disproportionate. These outliers in home range and core area were excluded from models to prevent bias.

All spatial metrics and accelerometer-derived activities and were calculated using the same seasonal subsets employed in prior analyses. Home ranges and core use areas were calculated using 95% and 50% kernel density estimation, respectively, in R using default parameters in the package *adehabitatHR* (Calenge 2006).

Results

Seasonal changes in daily activity patterns

Both accelerometer and GPS data indicated that lynx shifted their daily activity cycles throughout the year such that peak activity occurred during twilight. Though most lynx were more active during twilight, there were no extended periods of inactivity. Rather, lynx tended to have several short rest bouts throughout each diel period (mean = 69 minutes, SD = 85 minutes). On average, lynx were active ~45% of the day (Table 1). However, despite the consistency between accelerometry and GPS data, the uncertainty regions around the patterns of daily activity cycles was substantially higher for step-length than for VeDBA (e.g., the confidence bands around the waveforms were wider: Figures 3-4). Due to this wider uncertainty region, we were unable to detect diel activity patterns from step length for 6 out of 12 individual lynx (see

F05, M08, F09, M19, F33, M36: Figure 3). Within each season, we detected significant cyclic time of day splines ($P < 0.001$ for all seasons) when all animals were included in the analysis. However, some individuals were arrhythmic at times and substantial variation among individuals was evident.

During Spring (*n* =4, Axy lynx days =112, GPS lynx days = 100), both GPS and accelerometer-derived models showed that lynx exhibited bimodal crepuscular-like activity patterns with activity peaking around sunrise and just before sunset. One exception during this sampling interval was lynx F09, who exhibited a more nocturnal activity pattern (Figure 4). Another lynx (F05) was arrhythmic during the first 10 days of the spring interval but exhibited a clear bimodal activity pattern with activity being highest during twilight for the last 24 days (Figure 4).

The activity patterns of the two animals sampled during Summer differed from one another, but with accelerometer and GPS-informed models showing similar results. Lynx M46 was relatively inactive during the afternoon and early evening, but active throughout the remainder of the diel cycle. By contrast, lynx F05 was less active during the late morning, but otherwise maintained a fairly constant activity level throughout the diel cycle. We note that this female birthed a litter of kittens during this summer. The difference in how these two animals changed their activity patterns between Spring and Summer because of this life history event is apparent in their accelerometer-derived actograms. Female 05 had an abrupt drop in activity level on 5/30/19 and this low level of activity persisted for 6 days (Figure 5). We assumed that this interval of low activity occurred following parturition as we later found 8 kittens at her den site. Interestingly, the denning period for this female was also indicated from an increase of missing GPS fixes during that same time period. We surmise that cover around her den and her body position while nursing prevented GPS fixes while at the den (Figure 5). This week-long interval of low activity was followed by an extended interval of high nocturnal activity for about 4 days, which gradually transitioned into medium-intensity activity over most of the 24-hour day with a brief period of inactivity before noon (Figure 5). Conversely, M46 did not abruptly change his activity pattern, but gradually delayed the onset of, and shortened the duration of daily activity across the summer and also shifted its period of inactivity to the early evening (Figure 6).

During Fall (*n* =4, Axy lynx days =114, GPS lynx days = 82), both accelerometer and GPS models showed that lynx were most active during the crepuscular windows, between dawn and sunrise, and sunset and dusk, and less active during mid-day and overnight. One exception, however, was F33, who exhibited very little change in either mean VeDBA or mean step length (Figures 3 & 4).

During the early Winter (*n* = 4, Axy lynx days =113, GPS lynx days = 82), accelerometer data indicated all animals were most active at midday, which coincides with twilight conditions at this high latitude. However, we were unable to detect significant diel patterns in hourly step length for 2 of 3 individuals. The shift from inactivity at midday during Fall to activity during midday in Winter was clearly illustrated in the actogram of M19, which maintained a bimodal crepuscular-like activity pattern in Fall with intervals of low activity during midday and overnight. This animal then switched to a more diurnal activity pattern in late October and continued this pattern into the winter through the remainder of device deployment until 2 December (Figure 6).

Relationship between VeDBA and hourly step length

We found significant non-linear relationships between 1-hour GPS step length and hourly mean VeDBA for all lynx. The two variables were positively related and large spatial displacements were almost always accompanied by high accelerometer values (Figure 7). Nevertheless, there were instances where short step lengths were associated with a high level of activity (i.e., where there were large negative residuals), when animals were active but exhibited low spatial displacement.

Consequently, we examined the effects of VeDBA and the residuals from the quadratic regression models on VeDBA) in the following hour. We found that VeDBA was positively correlated with VeDBA in the preceding hour (i.e., there was temporal autocorrelation; Figure 8a) and positively correlated with the residual values from the preceding hour (Figure 8b). In other words, large negative residuals, where VeDBA is disproportionately larger than step length, are likely to be followed by low mean VeDBA in the next hour. Functionally, this means that when animals have disproportionately high body movement relative to distance traveled (i.e., tortuous movement patterns indicative of prey searching behavior), they usually had low activity levels in the next hour.

Relationships between seasonal activity levels, spatial displacement, and metrics of habitat use

During the Spring, lynx home range sizes averaged 57 km^2 (range 9 – 161 km^2), but typically the animals concentrated their activities in an area less than a quarter this size (13 km^2, range 1-36 km^2). Home ranges and core use area sizes were similarly variable between individuals in the summer subset, with home ranges averaging 78 km^2 (range 18-138 km^2), and the core use area 21 km^2 (range 4-37 km^2). During Fall, home range sizes were substantially lower at 21 km^2 (range 18-26 km^2), and animals concentrated their activities in a 6 km^2 area (range 4-7 km^2). During the early Winter, home ranges averaged 27 km^2 (range 15-51 km^2), yet lynx spent most of their time in a 5 km^2 area (range 3-7 km^2) (Table 2).

We did not find significant correlations between mean VeDBA and home range size, core area size, or mean step length in any season[1,2]. These observations suggest animals with larger home ranges and core use areas are not more active overall than animals with smaller home ranges and core areas, though our sample sizes are relatively small. One individual (M46), sampled in Spring and Summer, used a much larger core area and had a substantially larger home range compared to all other lynx in our sample[1]; although this individual was excluded from the analyses because he was an outlier in this respect, its mean activity levels (VeDBA) were not particularly large and he only had high mean step length during Spring. We also found that home range size, core area size, and proportion time active per day were not correlated with mean step length[2]. This lack of correlation between the variables examined here indicates that animals with larger home ranges and core areas do not typically move at greater speeds than those with smaller home ranges and core areas, and lynx with large step lengths are not more active throughout the day.

Discussion

We used a combination of accelerometer and GPS data to examine seasonal change in the temporal niche of lynx at the northern extent of their range. Regardless of what time of the year an individual lynx was sampled, we found they were active throughout the 24h day, with most individuals having peaks in both VeDBA and step length occurring during twilight conditions

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[1] Figure S1
[2] Table S1

We also investigated how activity, as measured by VeDBA, corresponded to step length over different temporal scales. Step length was correlated in a curvilinear fashion with mean VeDBA at the hourly scale. Instances where animals exhibited high VeDBA in conjunction with step length may be indicative of behaviors that involve more tortuous movement patterns, such as hunting. Additionally, we investigated the seasonal relationships between acceleration and space use metrics and found that home range size, core use area size, and mean daily step length were not correlated with mean daily VeDBA of lynx, suggesting that lynx with larger home ranges did not experience higher energetic costs associated with movement.

Diel activity

Recently, Menzies et al. (2022) reported that lynx in Canada’s Yukon Territory (~61°N) do not exhibit clear diel rhythms of activity or movement and, instead, individuals cycle between states of activity and inactivity without aligning their behavioral cycles to photoperiod or other environmental cues. This finding was surprising given that lynx at lower latitudes (~47°N) exhibit clear diel rhythms with peaks in activity at dusk and dawn (Parker et al. 1983, Kolbe and Squires 2007). Despite using similar accelerometry and GPS approaches to Menzies et al. (2022), we found that at our study site in northern Alaska (~67°N), lynx clearly shifted their activity patterns across the seasons such that peak activity was generally aligned with twilight conditions. There was also clear among-individual variability in the diel patterns exhibited by lynx – some individuals were most active during the night, rather than twilight (e.g., F09 in spring) and others had severely dampened rhythms at times without a clear crepuscular peak (e.g., F05 in Spring and Summer and F33 in Fall). The bimodal crepuscular-like activity pattern that we detected in most lynx during the Spring and Fall was followed by a phase shift to a unimodal pattern during Winter with activity peaking at mid-day. As days shorten in early Winter, the dawn and dusk windows in the Arctic converge into a single twilight period at mid-day when the sunrise/sunset cycle is lost. In contrast, during Summer, when photoperiod was either exceedingly long or, after June 1st, the sun did not set, individuals exhibited a peak in activity during the dimmest part of the 24h day. We suspect the difference between our results and that of Menzies et al. (2022) reflects methodological approaches, rather than population differences in activity patterns, as their diel activity analyses were more qualitative and did not account for individual or temporal autocorrelation in the data. However, our results otherwise aligned well with Menzies et al. (2022) in that individual lynx were frequently active at any time of the 24h day and individuals tended to lack extended bouts of rest.

Peaks in activity followed the temporal shift of the twilight window throughout the year, suggesting that light conditions are an important driver of lynx activity. We propose that these peaks in lynx activity coincide with favorable light conditions for hunting snowshoe hares, their preferred prey. Although snowshoe hares are nocturnal, they initiate activity at dusk (Mech et al. 1966, Feierabend and Kielland 2014, Studd et al. 2019) when their movement makes them potentially more vulnerable to visual predators. The reduction of activity that hares exhibit during full moons supports the notion that they are most vulnerable to predation during brighter conditions within their activity cycle (Griffin et al. 2005, Studd et al. 2019). Interestingly, Shiratsuru et al. (2023) report lynx kills of hares are as likely to occur during the day when hares are inactive as at night when hares were active. Lynx are likely particularly reliant on olfaction and hearing to hunt this cryptic prey species during the day. Feline vision is well adapted for low light and nocturnal conditions for hunting at night (Ewer 1998, Malmström and Kröger 2006, Kang et al. 2009). That said, felines have increased contrast sensitivity (i.e. the ability to distinguish objects from their background) with increased light (Kang et al. 2009), suggesting lynx should be most effective at hunting hares during the brightest period in which hares are active, which is during twilight.

Taking advantage of specific light conditions to increase hunting success is common among carnivore species (Hayward and Slotow 2010, Rockhill et al. 2013, Ditmer et al. 2021) and the differences in light conditions selected by similar Arctic species corroborates the importance of light in predatory behavior. Eurasian lynx (*Lynx lynx* (Linnaeus, 1758)) that occupy polar regions and hunt reindeer (*Rangifer tarandus* (Linnaeus, 1758)) remained least active during midday twilight conditions and most active in darker conditions in the evening and overnight during the winter period (Heurich et al. 2014). This nocturnal behavior is attributed to the light-dependent vulnerability of their preferred prey, reindeer, which at Arctic and subarctic latitudes have arrhythmic or only weakly rhythmic activity patterns (Heurich et al. 2014). Reindeer are likely less susceptible to predation under twilight conditions in winter as they can detect predators from a long distance due to seasonal restructuring of the retina that increases sensitivity to light (Stokkan et al. 2013). Differences in the daily timing of peak activity in these two Arctic lynx species indicates that their circadian chronotypes are not simply dictated by the direct effects of light conditions but are instead a complex function of the interaction between light and prey behavior.

Effect of reproduction on diel activity

We detected a GPS cluster for lynx F05 that was initiated on May 30, 2019, and confirmed on June 25, 2019 the presence of 8 kittens at a den site. Raising young has previously been shown to significantly alter behavioral patterns in lynx (Parker et al. 1983, Schmidt 1999, Kolbe and Squires 2007, Heurich et al. 2014), and the low amplitude unimodal activity pattern that we documented (Figure 4) is the similar to what Kolbe and Squires (2007) described in reproductive female lynx during the summer in Montana. Further study with a larger sample size during the Summer interval is warranted to better understand the effects of reproduction on the activity patterns of lynx in the low-Arctic.

The relationship between acceleration and step length

As predicted, body movement as measured by VeDBA and distance traveled each hour as measured by GPS were positively related. However, we recorded instances where body movement was disproportionally larger than distance traveled during a given hour (Figure 7) and suggest this ‘uncoupling’ between body movement and spatial displacement may be indicative of tortuous movements, possibly involving hunting behavior. Consistent with this hypothesis, we observed an increased likelihood of low activity in the hour following a period of high body movement but low spatial displacement. If tortuous movements indicate hunting behavior, these instances of low activity after tortuous movement could be indicative of prey handling and consumption associated with successful hunts. Studd et al. (2021) found that it can take more than 1 hour for a lynx to consume a snowshoe hare, though most feeding events last approximately 30 min. The lower acceleration associated with feeding could explain the low activity classification in the hour following potential hunt behavior, particularly if feeding events are lengthy.

Additional studies that focus on ground truthing these potential hunting events (e.g., Studd et al. 2021) are needed to discern whether the influence of the relationship between acceleration and step length relative to rest in the subsequent hour could be used to predict successful hunts and make conservative kill rate estimates.

GPS and accelerometer seasonal movement and space use

We found a high degree of variability among individual lynx in home range size, core use area size, and mean step length in almost all seasons. We suspect this variation in home range and core area size might be attributable variables that we did not consider here, such as prey density, body size, nutritional demands, and breeding opportunities (McNab 1963, Sandell 1989, Herfindal et al. 2005). We investigated whether accelerometer-informed parameters, specifically mean VeDBA and mean proportion of the day active, could help explain some of this variation. Home range size, core use area size, and mean daily step length were not correlated with mean daily VeDBA of lynx, meaning that lynx with larger home ranges, core use areas, or step lengths were not more active as determined by body movement. Even the animal excluded from our statistical analyses because of its considerably larger home range and core area measurements (M46) did not have a mean daily VeDBA that reflected these colossal differences in spatial displacements observed by GPS[1]. Whereas mean daily VeDBA in terrestrial vertebrates is generally well correlated with movement-based energy expenditure (Halsey et al. 2009, 2011), our data are inconclusive regarding the energetic cost of maintaining larger home ranges in this population of lynx.

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[1] Figure S1

Value of supplemental accelerometer use with GPS data

Our study of lynx behavior at their northern range limit demonstrates the efficacy of supplementing GPS location data with accelerometer data. Compared to hourly GPS fix rates, the high-resolution data provided by lightweight accelerometers allowed for a higher degree of precision in estimating diel activity patterns using a relatively simple k-means clustering approach. Additionally, accelerometers do not suffer from poor quality or missing data which often plague GPS transmitters. The likelihood of missed and poor-quality GPS fixes increases in areas with variable terrain or dense vegetation (Hofman et al. 2019) and is also influenced by body position (D’Eon and Delparte 2005). This trend was clearly illustrated by the GPS actogram of lynx F05 during her denning period (Figure 5). The capacity of accelerometers to provide near continuous data regardless of environmental conditions is particularly useful when accompanying GPS devices are deployed in mountainous or dense forest terrain that could affect fix success. In addition, the relationship between spatial displacement and body movement may be useful in identifying behaviors that cannot be determined solely using GPS data. Accelerometry has also previously proven useful in classifying behavioral states of free ranging animals using more complex supervised and unsupervised machine learning approaches (Chimienti et al. 2016, Leos-Barajas et al. 2017, Glass et al. 2020). Whereas these methods are perhaps necessary for the identification of more discrete behavioral states, our approach does not require the training data from captive or observed animals needed for supervised approaches, nor the additional variables (dynamic acceleration of individual axes, body position, movement speed, etc.) needed for both unsupervised and supervised approaches. Our methods may share some of the uncertainties and anecdotal nature of unsupervised learning algorithms (Chimienti et al. 2016), but active/inactive is easily parsed through relatively simple k-means clustering approach. Future investigations that utilize this method with higher resolution GPS data could potentially parse more discrete behavioral states from the relationship of body movement and distanced traveled alone.

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Author Contribution Statement

M.C.K, K.K., and C.T.W formulated the ideas and designed the study and contributed to logistics of field research. K.K. and C.T.W. contributed to funding of research.

M.C.K. and K.K. captured lynx and collected data. M.C.K. organized and analyzed all field data and led the writing of the manuscript. G.A.B. provided guidance and advice on the statistical methods. All authors contributed to selection and refinement of analytical methods, interpretation of results, improvement of written drafts

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Data availability statement

Data generated or analyzed during this study are available in the following repositories:

Accelerometer data-[Dryad repository TBD]; R scripts-[gitub repository TBD]

Competing interests

The authors declare there are no competing interests

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Figures

Map data: Google © 2020, Image Landsat/Copernicus

Figure 1. Geographical location of study area (bounded region) in the Brooks Range of Alaska. Yellow line indicates the Dalton Highway.

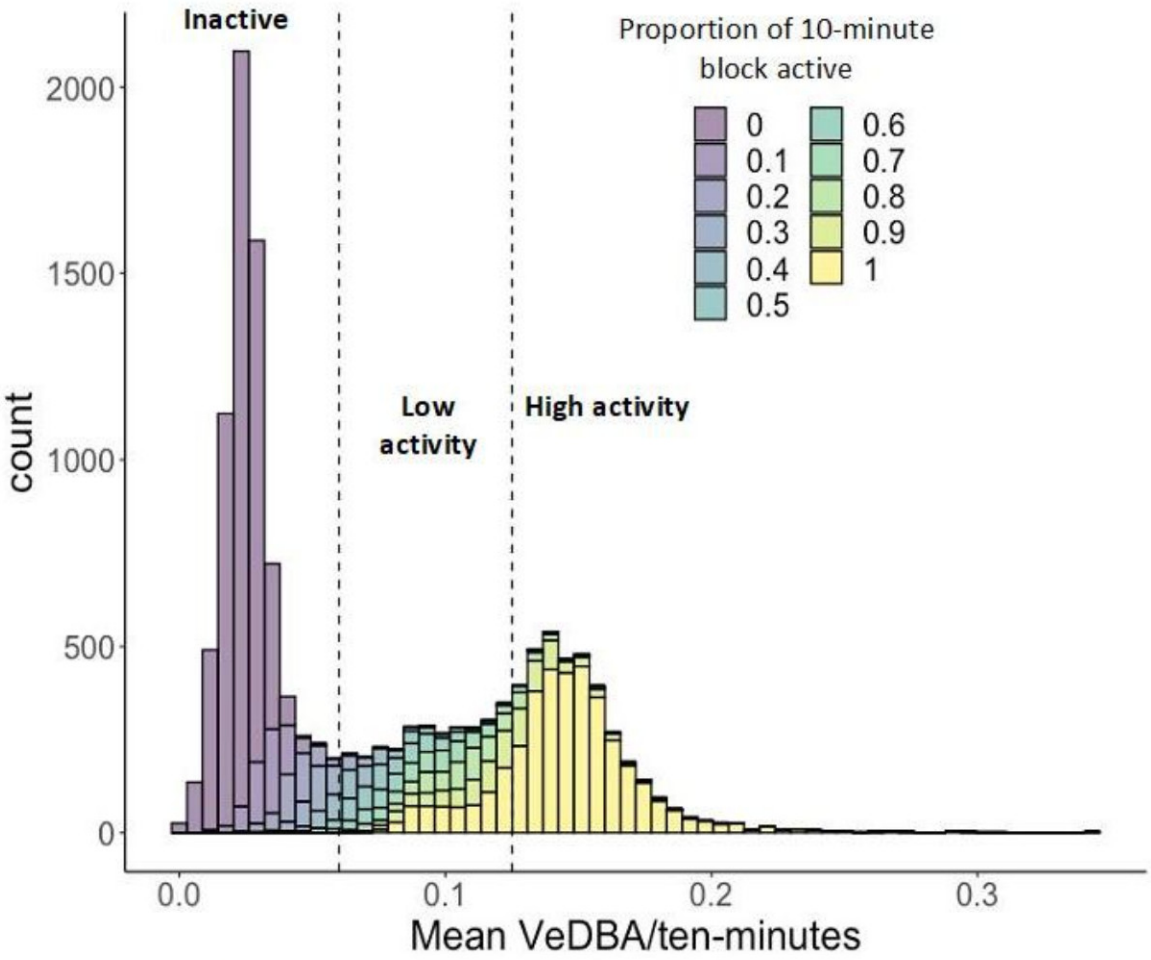

Figure 2. Distribution ten-minute mean VeDBA values of one male Canada lynx (*Lynx canadensis* over four-months. The dashed lines are the cluster divisions, and cluster of the lowest VeDBA values was classified as “inactive”, while the two other clusters (low and high activity) were grouped together as “active” for subsequent analyses. K-means clustering using higher resolution (1-minute mean VeDBA data) indicate that the middle cluster in the 10-minute data is comprised mostly of intervals where animals were only active for a proportion of the 10-minute window.

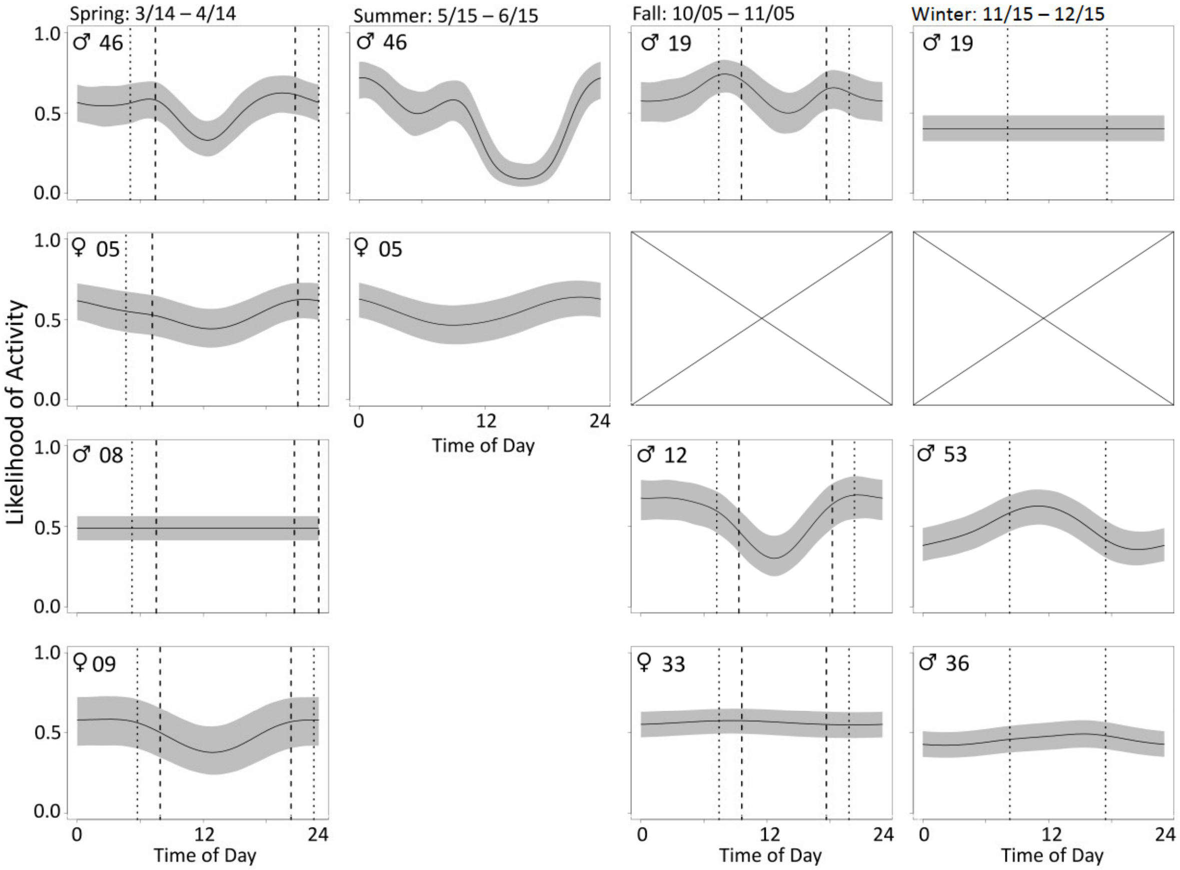

Figure 3. Canada lynx (*Lynx* canadensis) diel activity patterns described using 1-hour GPS step length. Each plot represents an individual lynx in a given seasonal sampling period, and the GAMM generated circular cubic splines show probability that an animal is active (y) at any given time of day (x). Dashed lines represent mean sunrise start and sunrise end for each sampling period, dotted lines represent mean nautical dusk and dawn, and the shaded area is the 95% confidence interval. Boxes with x's correspond with lynx that had greater than a 1-hour GPS fix rate and were excluded from this analysis.

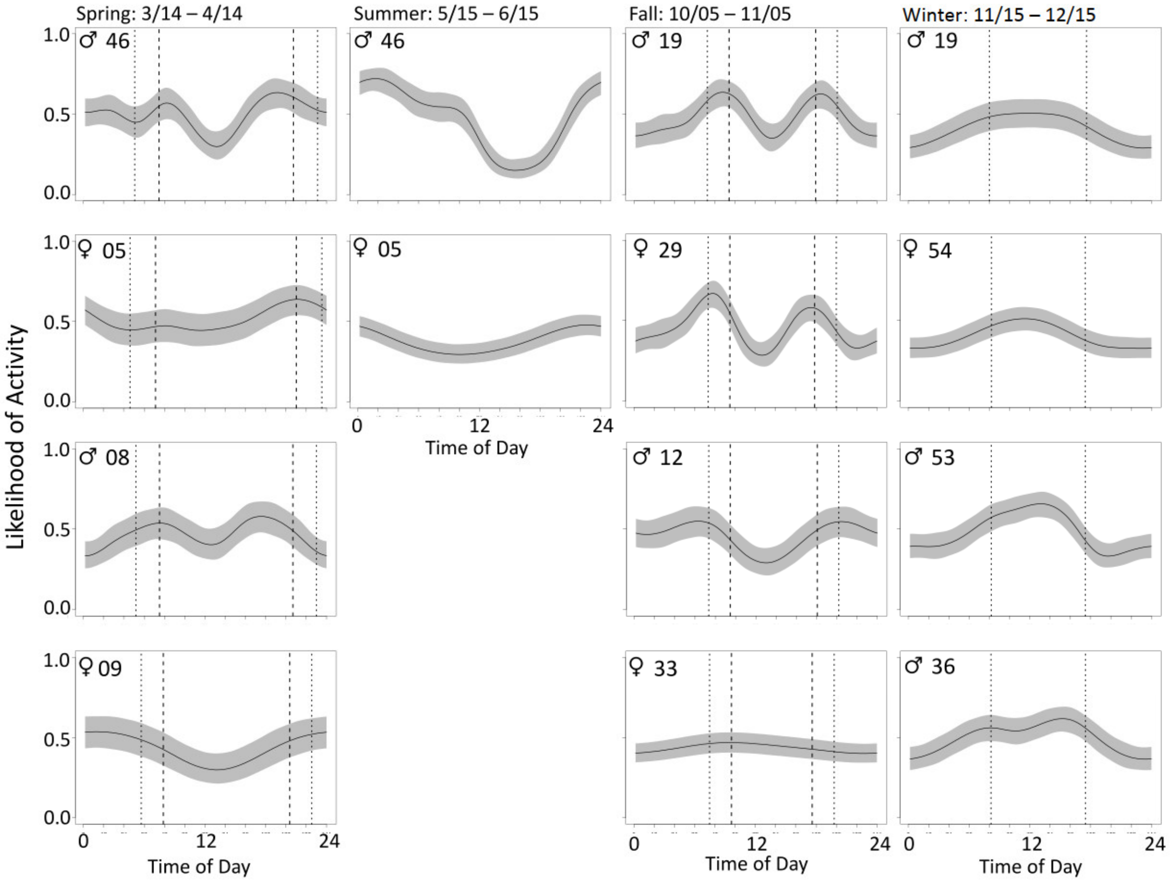

Figure 4. Canada lynx (*Lynx canadensis*) diel activity patterns described using triaxial accelerometers. Each plot represents an individual lynx in each seasonal sampling period, and the GAMM generated circular cubic splines show probability that an animal is active (y) at any given time of day (x). Dashed lines represent mean sunrise start and sunrise end for each sampling period, dotted lines represent mean nautical dusk and dawn, and shaded area is the 95% confidence interval.

126

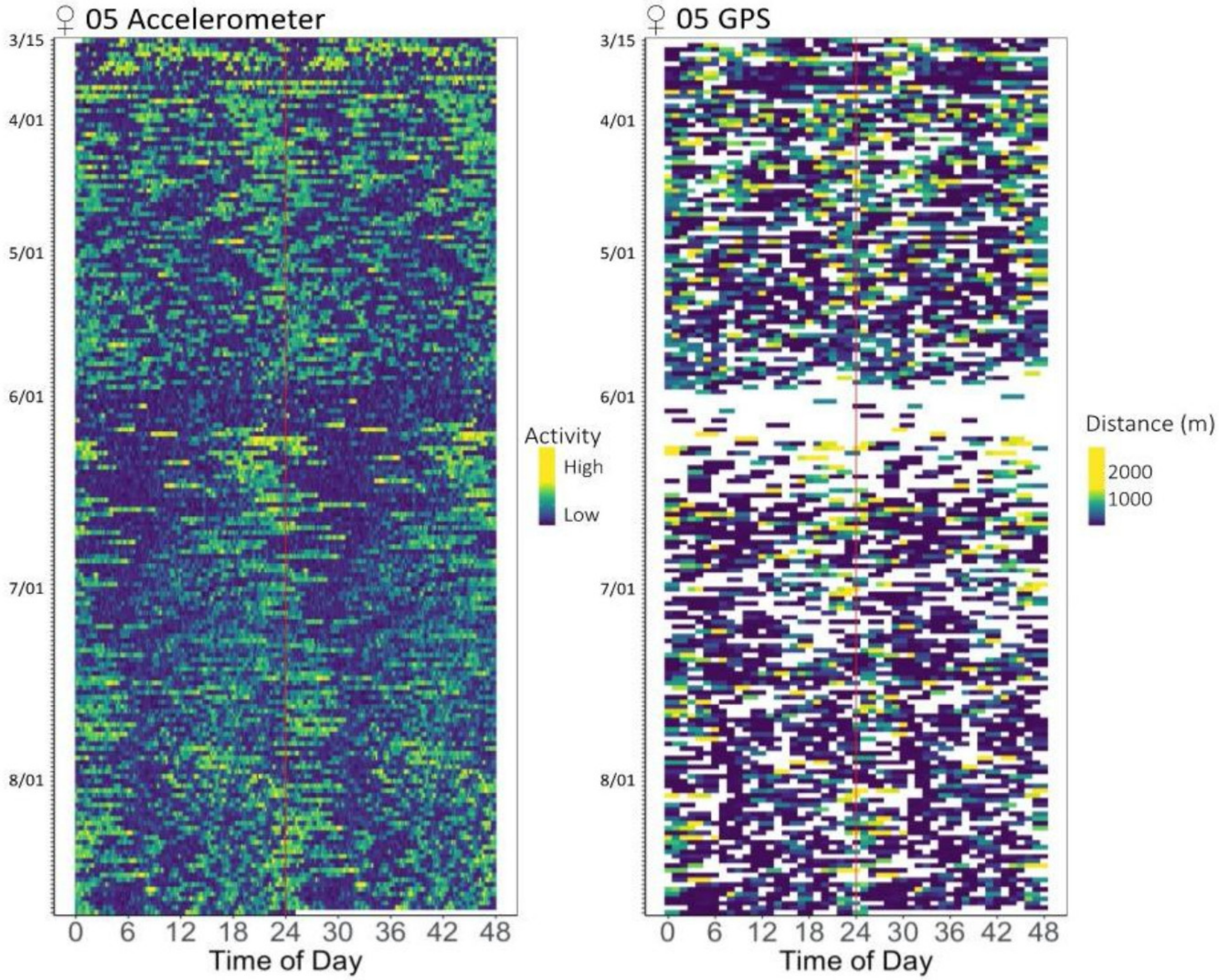

Figure 5. Accelerometer and GPS actograms of female Canada lynx (*Lynx canadensis*) 05. Each line of each actogram represents a 48-hour period. The second 24 hours is repeated at the start of the second line to more easily visualize trends that occur overnight. Actograms are displayed over 48 hours in order to more clearly visualize patterns that occur overnight. In the left panel, dark colors represent low activity and bright colors represent high activity. The activity index is determined by 10-minute mean VeDBA. In the right panel, dark colors represent short step lengths, and the color brightens with increasing step length. White boxes are missing GPS data, or data that did not meet the precision requirements for analysis.

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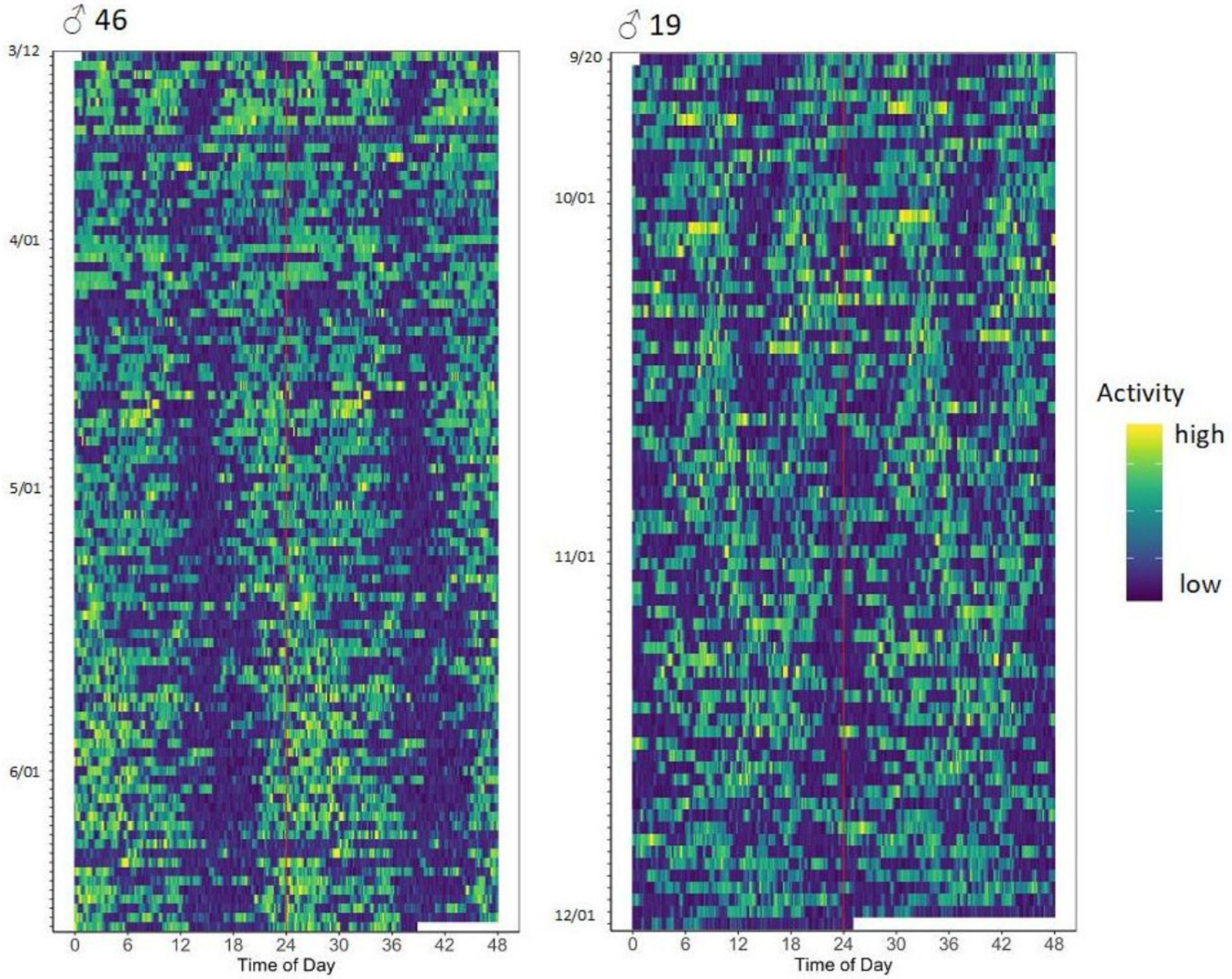

Figure 6. Actograms of 2 Canada lynx (*Lynx canadensis*) during periods of seasonal change. Each horizontal line of each actogram represents a 48-hour period. The second 24 hours is repeated at the start of the second line to more easily visualize trends that occur overnight. Actograms are displayed over 48 hours in order to more clearly visualize patterns that occur overnight. Dark colors represent low activity and bright colors represent high activity. Activity index is determined by 10-minute mean VeDBA.

144

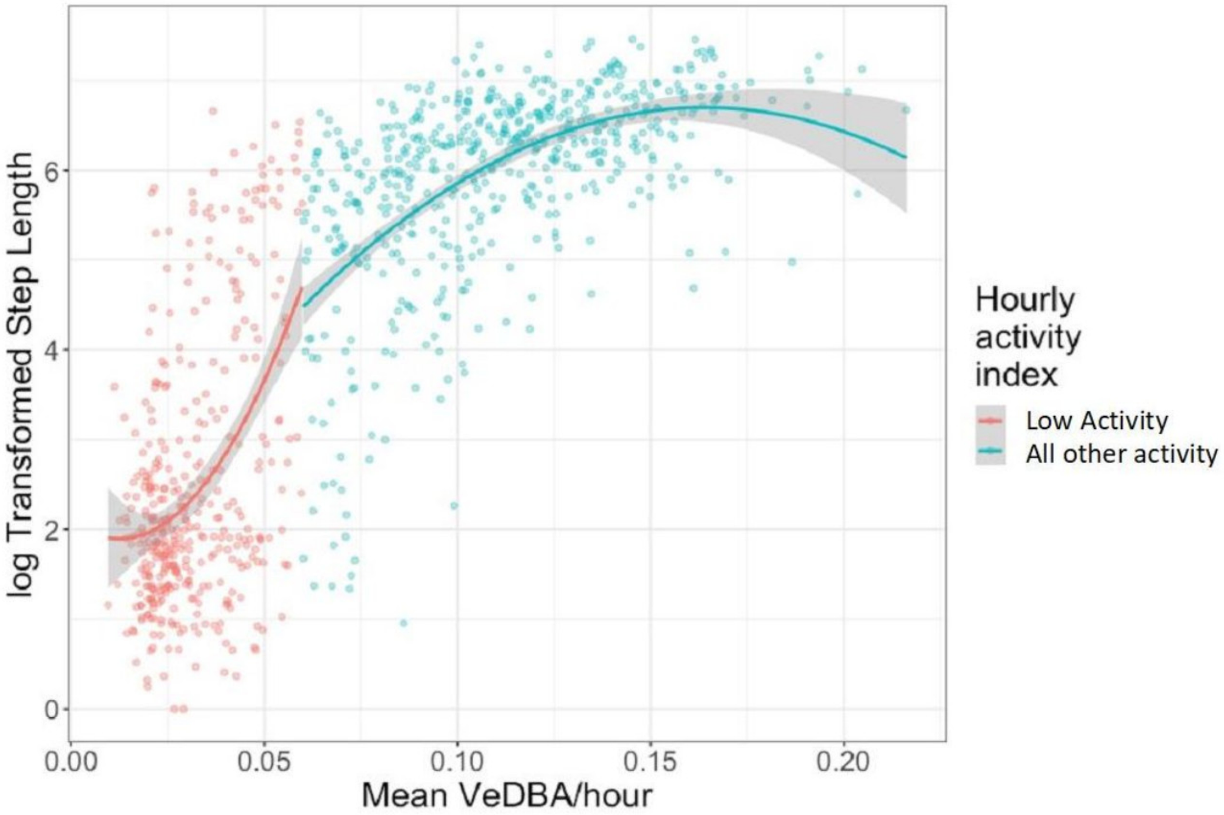

Figure 7. Piecewise quadratic model predictions of log transformed GPS step length based on mean VeDBA per hour of one individual Canada lynx (*Lynx canadensis*) over 53 days. Points representing raw data values and quadratic curves are separated by hourly activity index values: red is low activity, and blue is all other activity. Figure illustrates that GPS step length and mean VeDBA per hour are positively correlated.

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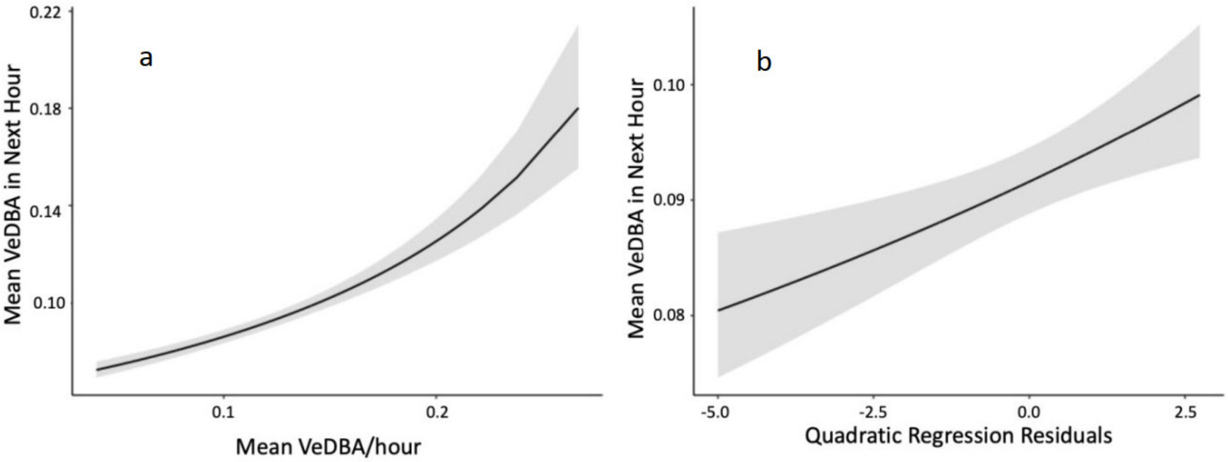

Figure 8. Generalized linear model predictions of activity level (measured by mean VeDBA) in next hour. Panel a shows VeDBA is positively correlated with VeDBA in the next hour, and panel b shows that residuals from the quadratic regression comparing 1-hour GPS step length and VeDBA are positively correlated with VeDBA in the subsequent hour.

Tables

Table 1. Seasonal values for mean VeDBA, mean rest bout, and mean proportion time active/day of Canada lynx (*Lynx canadensis*) as informed by accelerometer data. Values are means (±Standard Deviation).

Season	Axy *n*=	mean VeDBA	mean rest bout (minutes)	mean proportion time active/day
Spring	5	0.0778 (±0.0098)	67 (±77)	0.48 (±0.14)
Summer	2	0.0681 (±0.0078)	74 (±98)	0.42 (±0.11)
Fall	4	0.0755 (±0.0095)	68 (±83)	0.47 (±0.10)
Winter	4	0.0689 (±0.0079)	72 (±84)	0.44 (±0.12)

Table 2. Seasonal values for Canada lynx (*Lynx canadensis*) mean home range, mean core area, and mean step length as informed by GPS data. Values are means (±Standard Deviation).

Season	GPS *n* =	mean home range (km²)	mean core area (km²)	mean step length (*m*)
Spring	4	57 (±71)	13 (±16)	490 (±141)
Summer	2	78 (±85)	21 (±23)	359 (±96)
Fall	3	23 (±4)	6 (±1)	424 (±172)
Winter	3	27 (±20)	5 (±2)	209 (±76)