

Research



Cite this article: Shiratsuru S *et al.* 2023
When death comes: linking predator–prey
activity patterns to timing of mortality to
understand predation risk. *Proc. R. Soc. B* **290**:
20230661.
<https://doi.org/10.1098/rspb.2023.0661>

Received: 21 March 2023

Accepted: 21 April 2023

Subject Category:

Ecology

Subject Areas:

behaviour, ecology, ecosystems

Keywords:

predator–prey, diel activity, time of predation,
predation risk, *Lepus americanus*, *Lynx*
canadensis

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Electronic supplementary material is available
online at <https://doi.org/10.6084/m9.figshare.c.6626115>.

When death comes: linking predator–prey activity patterns to timing of mortality to understand predation risk

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The assumption that activity and foraging are risky for prey underlies many predator–prey theories and has led to the use of predator–prey activity overlap as a proxy of predation risk. However, the simultaneous measures of prey and predator activity along with timing of predation required to test this assumption have not been available. Here, we used accelerometry data on snowshoe hares (*Lepus americanus*) and Canada lynx (*Lynx canadensis*) to determine activity patterns of prey and predators and match these to precise timing of predation. Surprisingly we found that lynx kills of hares were as likely to occur during the day when hares were inactive as at night when hares were active. We also found that activity rates of hares were not related to the chance of predation at daily and weekly scales, whereas lynx activity rates positively affected the diel pattern of lynx predation on hares and their weekly kill rates of hares. Our findings suggest that predator–prey diel activity overlap may not always be a good proxy of predation risk, and highlight a need for examining the link between predation and spatio-temporal behaviour of predator and prey to improve our understanding of how predator–prey behavioural interactions drive predation risk.

1. Introduction

The fact that predators can only kill prey when they overlap in space and time [1] has led to the belief that increased spatial [2,3] and temporal [4,5] overlap between predators and prey correlates with predation risk. For example, diel activity overlap between predator and prey is now increasingly used as a proxy of predation risk [6–8]. However, although this may be a reasonable starting assessment of perceived predation risk (e.g. high predator density or places and times where and when predators are more likely to be present and active), such overlap may not always be a good proxy of actual predation risk (the probability of predation). Assessment of predation risk in relation to behavioural predator–prey interactions requires simultaneous measures of the behaviour of predator and prey and predation rate, but such studies are still scarce (but see [9]).

Effects of predator–prey spatio-temporal overlap on predation can be confounded by various environmental factors. For example, habitat characteristics are potentially more important determinants of predation than predator–prey spatial overlap [10], or diel patterns of predation can be modified by anthropogenic disturbance while prey fail to adjust their temporal activity pattern in response to it [11]. It is well documented that prey show a wide

range of behavioural adjustments in response to high perceived risk [12,13]. More specifically, many previous studies have reported a reduction in the level of activity and foraging by prey as antipredator responses [12,14,15], leading to the assumption that prey activity/foraging increases predation risk which forms the basis of such fundamental concepts as predation–starvation trade-offs [16,17] and non-consumptive effects of predators [18,19]. However, it has been rarely tested whether and how the level of prey activity impacts the probability of predation (but see [9,20,21]). Additionally, given that predator–prey encounter rate is determined by both predator and prey activity and their relative importance is context-dependent [22–24], predator activity needs to be considered as well in examining the effect of prey activity on predation risk.

Identifying precise time of predation would help researchers tackle these knowledge gaps. First, knowing time of predation enables researchers to assess the validity of predator–prey diel activity overlap as a proxy of predation risk. Second, by linking time of predation to predator and prey behavioural data, researchers can directly test the effect of predator and prey activity on predation risk. With the advent of GPS-equipped radio transmitters there are studies that show where prey are killed [25,26], providing many empirical tests of whether predator–prey spatial overlap is a good proxy for spatial patterns of actual predation. However, as few studies have examined the fine-scale timing of predation, we have been limited in assessing if temporal activity overlap between prey and predator is a good proxy of predation risk. Vander Vennen *et al.* [9] tackled this knowledge gap by monitoring movement rates of wolves (*Canis lupus*) and moose (*Alces alces*) and identifying time of predation at relatively broad time scales (≥ 1 h) with GPS collars.

Recent development of tri-axial accelerometers now allows for continuous recording of different behavioural states at the scale of milliseconds in both predators and prey [27]. As such, simultaneous monitoring of prey and its predator with accelerometers provides a means for identifying precise timing of predation events [28,29] and activity of predator and prey [30]. We examined when predation on snowshoe hares (*Lepus americanus*) occurred relative to their activity level and to the activity of their primary predator, Canada lynx (*Lynx canadensis*). The snowshoe hare, a key prey species in the North American boreal forests [31,32], is a suitable species for the study because it is primarily active at night and inactive during the day (figure 1a) [33]. Hares are known to adjust foraging rates in response to perceived risk at various time scales [33–36], implying that hares perceive foraging as risky and thus a clear correlation between their activity and predation is expected. Hares are consumed by a diverse predator assemblage with different diel activity patterns [37–39] including diurnal northern goshawks (*Accipiter gentilis*) [40], nocturnal great horned owls (*Bubo virginianus*) [41], and diel-flexible (i.e. active throughout the diel cycle) Canada lynx (figure 1b) [42] and coyotes (*Canis latrans*) [43].

Here, we used a 4-year accelerometry-based dataset of snowshoe hare activity and mortalities, and a 6-year accelerometry-based dataset of lynx activity and predation on hares, to test the effects of hare and lynx activity on the probability of predation at four different temporal scales. First, we explored if the probability of predation differs among diel phases and if diel activity patterns of hares and lynx and

their diel activity overlap are correlated with diel patterns of predation. Second, at a weekly scale, we examined if hare kill rate by lynx is positively related to hare and lynx activity rate. Third, at a daily scale, we tested if hare mortality rate is positively affected by hare and lynx activity rate. Finally, at an immediate scale, we assessed if hare activity in the minutes prior to death increases the probability of predation. Combined, we test whether predator–prey diel activity overlap is a valid proxy of predation risk and if prey and predator activity increase predation risk. By producing one of the first quantifications of the timing of predation in a terrestrial vertebrate at a very fine time scale, we aim to deepen our understanding of mechanisms by which predator–prey behavioural interactions drive predation risk.

2. Methods

(a) Study area/species

This study was conducted in the Kluane region, southern Yukon, Canada (61°N, 138°W) over 6 winters (November–April) between 2015 and 2021. Canopy cover in this area primarily consists of white spruce *Picea glauca*, with a shrub understory of bog birch *Betula glandulosa* and grey willow *Salix glauca* [44]. Snowshoe hares during this study were most commonly killed by lynx (59.4% of deaths where the predator could be identified) or coyote (25.5%) and occasionally by northern goshawk (9.4%) and great horned owl (5.7%) [39]. The two most important predators of hares, lynx and coyotes, are similar in body size and weight and both are highly dependent on hares as their main prey source throughout the 10-year hare cycle [45], but their morphological difference (= foot-load) results in different habitat preference and hunting behaviour [46]. Lynx is a stalk-and-ambush predator and prefers deep-snow habitat, while coyote is a cursorial predator and selects shallower and harder snow for movement and hunting in winter [46–48]. This study occurred during an increase, peak and decline of the snowshoe hare cycle in this region [35,49]. Procedures of handling and collaring hares were approved by the University of Alberta Animal Care and Use Committee and permitted by the Government of Yukon. Procedures of handling and collaring lynx were approved by the McGill University and Trent University Animal Care and Use Committees and permitted by the Government of Yukon.

(b) Identification of mortality time and estimation of activity rate of snowshoe hares

We trapped hares over four winters (2015–2019) using Tomahawk live-traps (Tomahawk Live Trap Co., Tomahawk, WI, USA) on five trapping grids (600 m \times 600 m) within a 10 km² area in the Shakwak Trench. For each captured hare, we recorded individual ID (using ear-tags), body mass and sex, and attached VHF collars (less than 40 g) with mortality sensors (Model SOM2380, Wildlife Materials Inc., USA, or Model MI-2M, Holohil, Canada) and AXY-3 accelerometers (Technosmart Europe Srl., Rome, Italy) to hares heavier than 1100 g. We monitored survival daily with ground-based telemetry throughout the winter. When a mortality signal was emitted, we located the individual to determine cause of mortality by investigating the carcass remains and predator tracks in the snow [38]. Accelerometers recorded body acceleration along three axes (dorsoventral, anterior–posterior and lateral) at 1 Hz frequency and $\pm 8 g_{\text{forces}}$ resolution. We monitored 173 hares (2015–2016: $n = 55$, 2016–2017: $n = 61$, 2017–2018: $n = 60$, 2018–2019: $n = 53$) for 16 356 days, of which 75 were killed by predators while accelerometers were functioning. A subset of females ($n = 40$) were part of an individual-targeted food supplementation

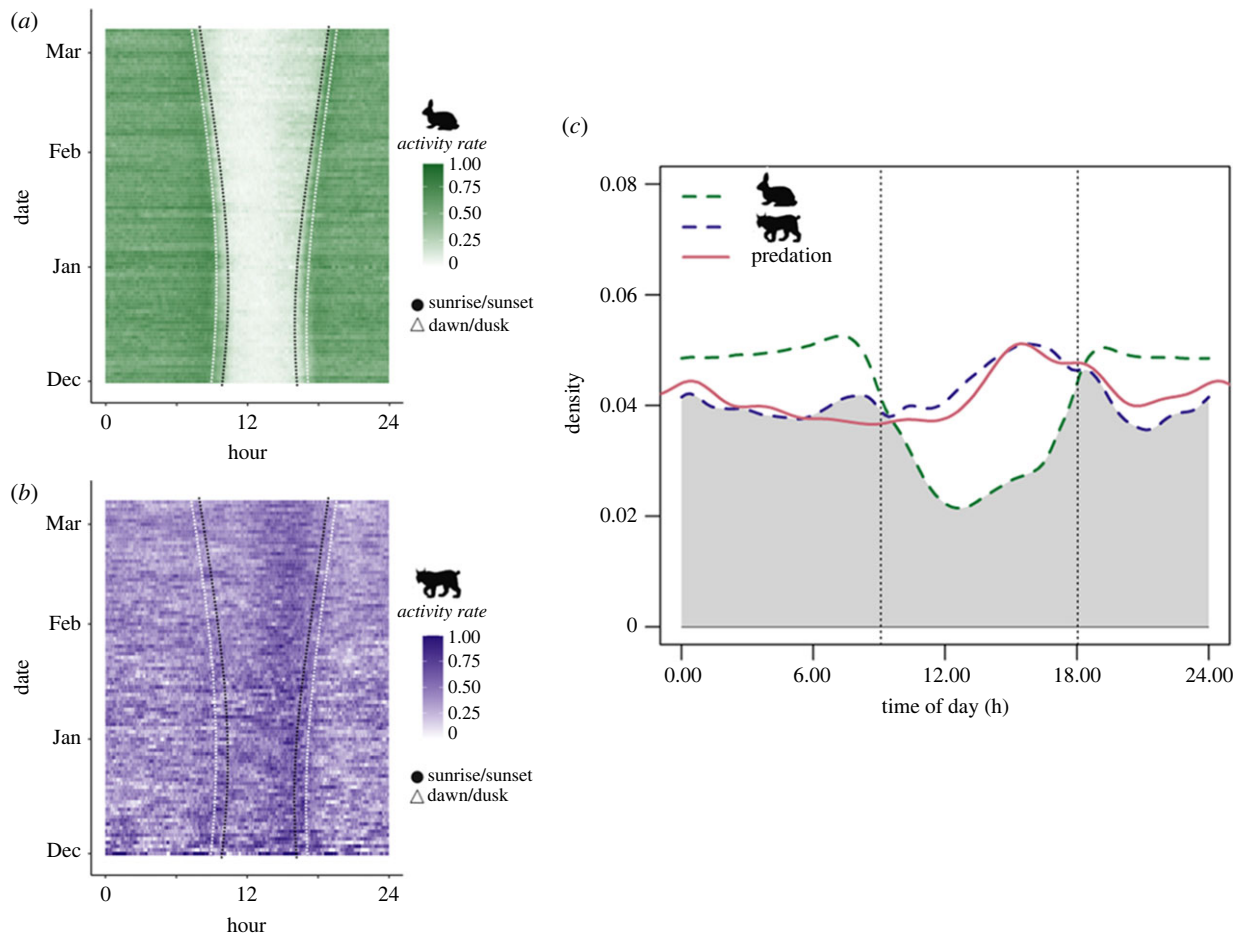


Figure 1. Winter (Dec–Mar) diel activity patterns of (a) snowshoe hares and (b) Canada lynx, and (c) diel density curves of hare and lynx activity and lynx predation on hares in the Kluane Lake region, Yukon, Canada. Average activity was calculated from accelerometer data collected on hares ($n = 161$) and lynx ($n = 36$). For lynx predation on hares ($n = 1926$), the data on hare mortalities caused by lynx ($n = 26$) and the data on hare kills by lynx ($n = 1900$) were combined. Activity rate was defined as the proportion of the population that was doing any behaviour other than inactivity at a given time with a darker colour representing a higher proportion of the population that is active. Times of the start of dawn and end of dusk (white triangles) and sunrise and sunset (black circles) are overlaid on the activity data. Shaded area in (c) represents diel activity overlap between hares and lynx. In (c), time of day was scaled relative to the mean sunrise and sunset times across the winter weighted by the number of data points on each date, and vertical lines represent the mean sunrise and sunset times across the winter.

experiment examining the effect of food availability on survival and reproduction of hares and were provided with commercial rabbit chow (crude protein 17%, crude fat 2%, and 2320 kcal kg⁻¹) ad libitum within their home range [35]. Therefore, our collared animals were skewed towards females.

To identify the time of death, we used a suite of metrics calculated from the collar temperature and acceleration data to create an automated identification process in R [50]. This involved three different criteria: changes in collar temperature (from body temperature to ambient), activity and collar orientation (see electronic supplementary material, methods S1, for details).

We calculated behaviour of the hares using a previously validated hierarchical decision tree that classifies accelerometer data into four behavioural categories (not moving, hopping, sprinting and foraging) with a 93.1% accuracy (see electronic supplementary material, methods S1, for details) [33]. For this study, activity rate was defined as the proportion of time spent hopping, sprinting, and foraging (as defined in [33]). As the foraging category represents approximately 95% of all movement [33], we considered hare activity as primarily related to foraging in this study.

(c) Identification of time of hare kills by lynx

We trapped lynx each winter from Nov 2015 to Apr 2021 using custom-made box traps (similar to [51]) baited with meat (road kill) and scent (castor, skunk essence) and outfitted with visual

attractants (e.g. hanging CDs). Traps were placed along roads and trails within a 300 km² area that overlapped the hare trapping grids (see electronic supplementary material, methods S2, for details).

Acceleration data for lynx ($n = 2271$ days) were converted into 4 behavioural states (not moving, chewing, grooming and travelling) using a previously validated random forest algorithm in Python [29] (see electronic supplementary material, methods S2, for details). Similar to hares, we defined lynx activity rate as the proportion of time spent chewing, grooming, and travelling. Following Studd *et al.* [29] we defined kills of hares by lynx as consecutive occurrences of chewing with no gaps greater than 10 min and a total duration ≥ 15 min (0.93–0.97 accuracy [29]; see electronic supplementary material, methods S3, for details).

For all analyses, we used the start of the feeding event as the time of the kill as lynx primarily consume their prey immediately after killing (less than 5 min), and only rarely cache whole hares (personal observation from snow tracking).

(d) Diel patterns of predation

To quantify temporal patterns in hare mortality, we assessed the diel patterns in our two datasets: deaths of collared hares (hereafter ‘mortalities’) from Nov to Apr and hare kills from the lynx collars (hereafter ‘kills’) from Nov to Mar. We assigned diel phases (day, night, and civil dawn/dusk) to each mortality and kill using timing of light phases for the study site from the

maptools package in R [52] (lat = 60.5716, long = -138.0145), and then conducted Chi-square goodness-of-fit tests to examine if the observed diel patterns of mortalities or kills deviated from random. We considered *p*-values of less than 0.05 statistically significant. To determine the expected random values of mortalities or kills for the goodness-of-fit test, we calculated the proportion of time that hares (16 356 days for 173 hares) or lynx (2271 days from 36 lynx) were monitored with accelerometers during each light phase (day = 142 930.3 h, night = 222 208.4 h, and dawn/dusk = 3618.6 for hares and day = 20 720.9 h, night = 30 164.5 h and dawn/dusk = 3618.6 h for lynx). On average, 34%, 59% and 7% of the 24-h diel cycle fell into day, night and dawn/dusk, respectively, over the study.

To examine the relationship between the diel pattern of lynx predation on hares and hare/lynx diel activity patterns, we quantified the average activity rate of hares and lynx, the degree of hare-lynx activity overlap, and the total number of lynx kills of hares for each hour of the 24-h diel cycle. To account for variation in day-length, we first transformed clock time of all datasets to solar times relative to the mean sunrise and sunset times over the study period by the average double anchoring method (see [53] for details) using the *transtime* function in the *activity* package in R [54]. Then across the 24 h of the day, we fitted a von Mises kernel density function to the hare and lynx accelerometer data averaged over 5-minute time windows with the *overlapPlot* function of the *overlap* package in R [55] using the default smoothing parameter, and extracted a density estimate of each species' activity for each 5 min window using the argument *n.grid* = 288 (12/h * 24 h). We defined the degree of activity overlap as the area under both of the hare and lynx activity density curves [55], and thus calculated an hourly index of hare-lynx activity overlap with the *AUC* function in the *DescTools* package [56] using the 12 minimum values of the two activity density functions that we had for each hour (1 per 5 min). For the amount of predation each hour, we summed the data on hare mortalities caused by lynx (*n* = 26) with the hare kills by lynx (*n* = 1900). Finally, to test if hourly activity of hares, lynx, or hare-lynx activity overlap correlates with predation, we calculated a Pearson correlation coefficient for each activity metric.

(e) Effect of short-term activity rates on predation

(i) Weekly lynx kills

To test if weekly hare kill rates by lynx increased with an increase in population mean of hare activity rate or individual lynx activity rates, we used hurdle-gamma generalized linear mixed effects models (GLMMs). For each week from 1 November to 30 March over the 4 winters, we calculated number of kills/hour for each collared lynx, by dividing the number of kills during day and night by number of hours of day and night that the lynx was monitored over the week. For each week, we only included lynx with ≥ 3 full days of accelerometer data in the analysis, which resulted in 277 lynx-weeks of data from 31 lynx. As the main predictor variables, for each week we used the population mean activity rate (i.e. proportion of time active) for day and night of all the hares monitored by accelerometers, and the mean activity rate for day and night of each individual lynx. To account for potential effects of multi-annual variations in lynx-hare density ratio on hare kill rate by lynx, we included year as a categorical fixed variable. In addition, we included individual lynx ID as a random intercept. All continuous fixed predictors were standardized by mean-centring and then dividing by their standard deviations. We only included an intercept in the zero-inflated model which modelled whether the response variable was zero or non-zero, and included all the above fixed and random effects in the conditional model which modelled non-zero response data. We constructed both hurdle-gamma GLMMs with gamma family and log link function, using *ghmmTMB* package in R [57]. We

assessed multicollinearity of the covariates for both models by using *performance* package in R [58], ensuring that none of the covariates had VIF values > 3 [59].

(ii) Daily hare mortality risk

To quantify the impact of individual hare activity rate on the probability of hare mortality we used semiparametric Cox proportional hazard (CPH) models using the *survival* package in R [59]. We adopted a staggered entry and right-censored framework at a daily scale (1 Nov is day 1 for each of the 4 winters). For each day, we averaged activity rate during day and night hours for each hare over the three previous days to establish a sufficiently representative time window of pre-mortality behaviour of hares. Using 15 312 hare-days of data from 166 hares (66 mortalities (day = 30, night = 31)), we constructed 'time-specific' CPH models for daytime and night-time mortalities separately given that the effect of activity rate on predation risk may differ between day and night. We included daytime and night-time activity as covariates in the daytime and night-time mortality models, respectively. Night-time and dawn/dusk mortalities were entered as censored observations in the daytime model, while daytime and dawn/dusk mortalities were treated as censored observations in the night-time model. Additionally, since survival rates of hares in our population are affected by food-supplementation and annual variation in predator-prey density ratio [35], we also included the treatment type ('control' and 'food-supplemented') and year (4 classes) in both models as categorical covariates to account for their effects. Activity rates were standardized by mean-centring and then dividing by their standard deviations. We confirmed that there was no violation of the proportional hazard assumption by assessing the scaled Schoenfeld residuals with the *cox.zph* function of the *survival* package in R [60], and that none of the covariates had VIF values > 3 [59].

(f) Hare activity immediately prior to predation

To examine whether being active increases the likelihood of predation, we compared activity rates of hares immediately prior to their death with the mean activity rate of all surviving hares during the same diel phase (daytime and night) on the same day. We calculated activity rate for four time windows, 0–1, 1–5, 5–10 and 10–15 min before predation, and conducted one-sided paired *t*-test for each window. We included in the analysis only those hares (daytime: *n* = 36, night: *n* = 33) for which there were ≥ 7 other hares being monitored by accelerometers on the day of mortality. We conducted this analysis for daytime and night-time mortalities separately and considered *p*-values of less than 0.05 to be statistically significant.

3. Results

(a) Diel patterns of predation

Hares showed strong diel activity patterns with high activity during the night ($57.5 \pm 15.0\%$ (s.d.) active) and dawn/dusk ($40.7 \pm 18.0\%$ active), and low activity during the day ($12.6 \pm 9.7\%$ active) (figure 1). Lynx showed comparatively less pattern in diel activity, with similar activity rates during the day ($46.1 \pm 20.1\%$ active), night ($38.2 \pm 16.8\%$ active) and dawn/dusk ($43.0 \pm 26.3\%$ active) (figure 1). These patterns led to diel activity overlap between hare and lynx being highest during the night and dawn/dusk and relatively lower during the day (figure 1).

Over 4 winters, we identified the time of mortality for 75 hares (male = 15, female = 60) killed by predators (figure 2a and electronic supplementary material, table S1). Mortalities caused by avian predators were rare (10.7% of mortalities)

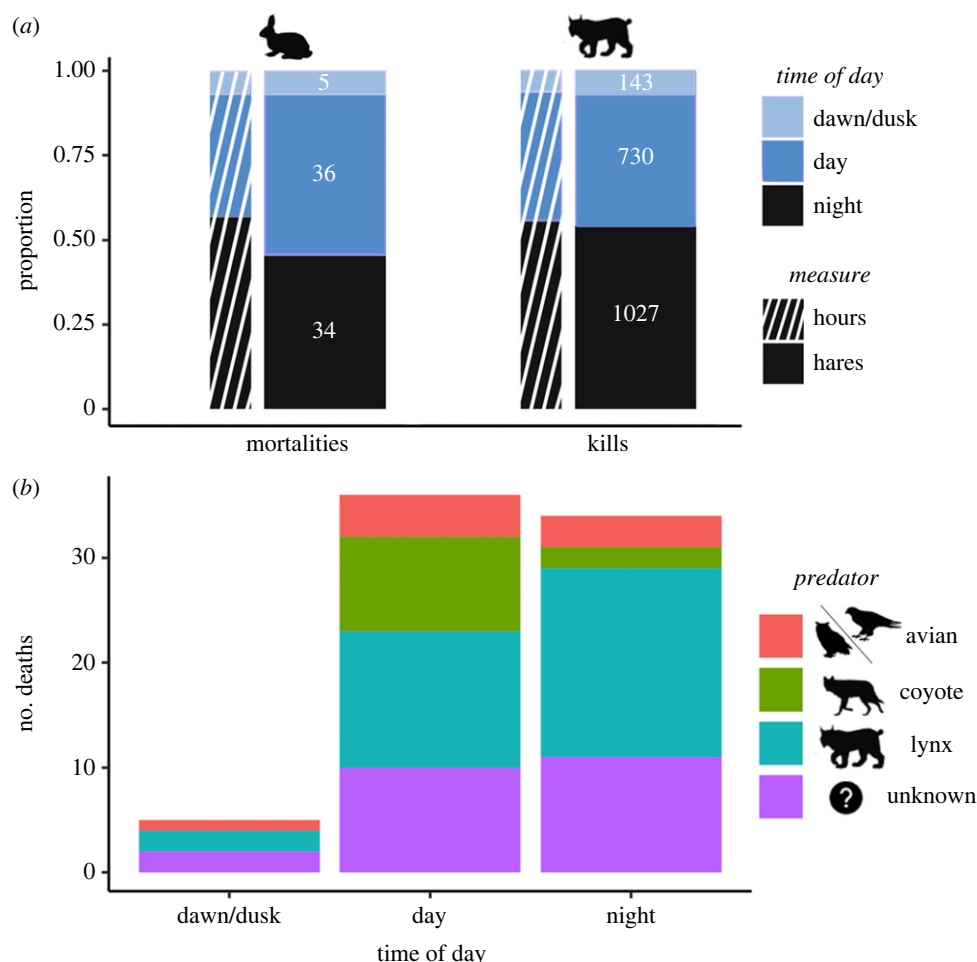


Figure 2. Temporal patterns of winter snowshoe hare mortalities and lynx kills from 2015 to 2021 in the Kluane Lake region, Yukon, Canada. (a) Proportion of hare mortalities and kills (wide solid bars) relative to the proportion of hours monitored (narrow striped bars) in each light phase. Data are shown for all mortalities of hares collared with accelerometers (left), and all kills made by lynx collared with accelerometers during the winter. Numbers in the histograms represent numbers of hare mortalities or lynx kills. (b) The number of hare mortalities by different predators (avian, lynx, coyote, unknown) in each phase of the day according to kill site investigations of collared hares.

with owls killing at night and goshawks during the day. Lynx predation occurred at all times (day = 39.4%, night = 54.5%) whereas coyote predation occurred primarily during the day (81.8%; figure 2b, electronic supplementary material, table S2). Hare mortalities did not occur more frequently during either of the diel phases when hares are active (night and dawn/dusk) than when they are inactive (day; $\chi^2 = 4.46$, d.f. = 2, $p = 0.11$). Similarly, there was no diel structure in the 1900 hare kills by lynx over 6 winters with kills occurring proportional to the number of monitoring hours in all diel phases ($\chi^2 = 2.91$, d.f. = 2, $p = 0.23$; figure 2a, electronic supplementary material, table S2).

There was no relationship between the degree of hare–lynx diel activity overlap and the diel pattern of lynx predation on hares (figure 1, figure 3a). There was a strong positive correlation between hourly lynx activity rate and the number of lynx predation on hares (figure 3b), whereas hourly hare activity rate was not correlated with the number of lynx predation on hares (figure 3c).

(b) Effect of short-term activity rates on predation

(i) Weekly lynx kills

Population mean hare activity rates did not positively affect weekly hare kill rates of lynx during the day ($\beta = -0.053$ [95% CI: $-0.117, 0.011$]) or night ($\beta = -0.046$ [$-0.111, 0.020$])

(electronic supplementary material, figure S2a,b and table S3). However, lynx activity rate positively affected hare kill rates during both the day ($\beta = 0.267$ [0.186, 0.348]) and night ($\beta = 0.224$ [0.140, 0.309]) (electronic supplementary material, figure S2c,d and table S3), and its effect size was more than four to five times as large as that of hare activity rate in both cases.

(ii) Daily hare mortality risk

Similarly, we did not find any evidence that individual activity rate of hares positively affected either daily daytime or night-time mortality risk of hares. Activity rate of hares did not influence mortality risk (i.e. 95% CIs of hazard ratio overlap with 1) during the day (hazard ratio = 0.81 [0.41, 1.63]), while increase in activity rate reduced mortality risk (i.e. upper 95% CI of hazard ratio < 1) during the night (hazard ratio = 0.61 [0.40, 0.93]) (electronic supplementary material, table S4).

(c) Hare activity immediately prior to predation

Hares that were killed during the day ($n = 36$) were generally inactive ($17.9 \pm 21.8\%$ s.d.; median = 7.7%) while those killed at night ($n = 33$) were generally active ($61.6 \pm 27.7\%$ s.d.; median = 66.9%) in the last 15 min prior to mortality. However, activity rates of killed hares increased in both day and

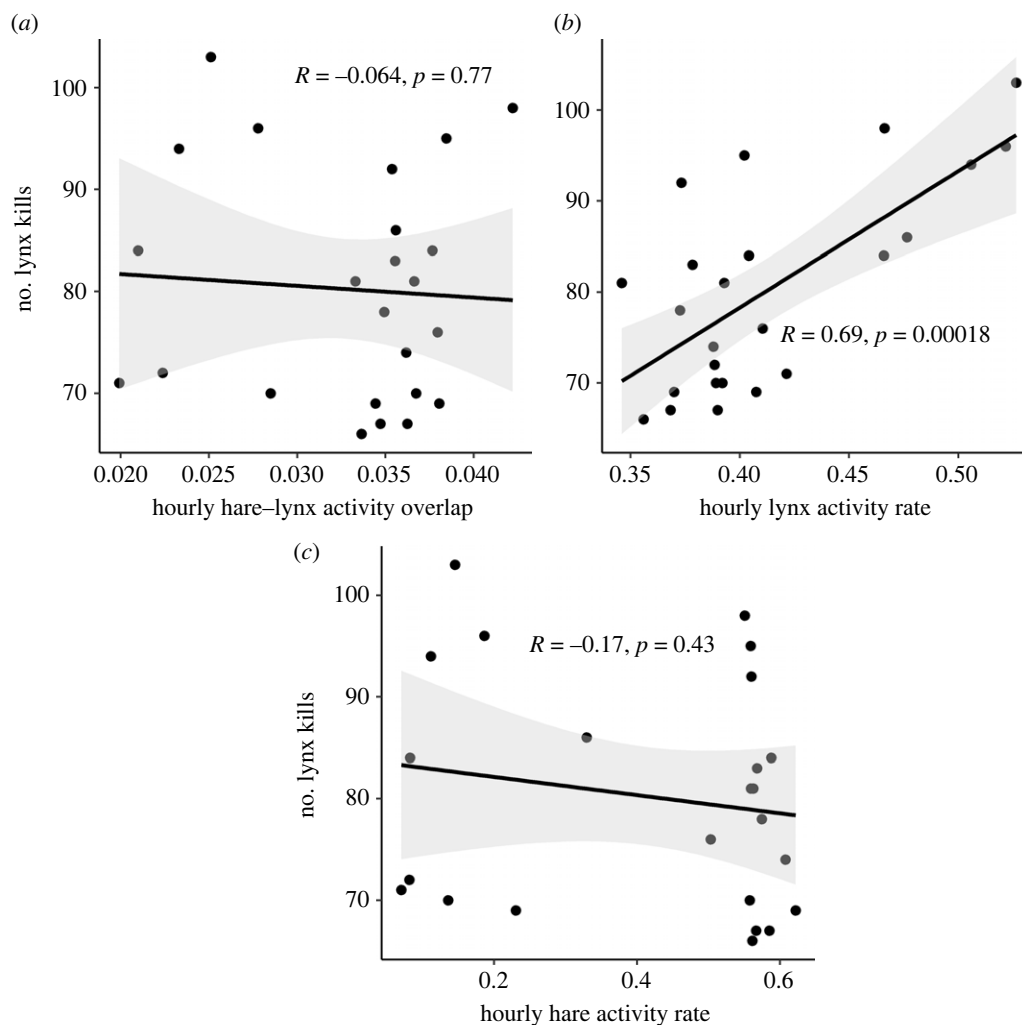


Figure 3. Relationship between lynx kills of hares per hour and (a) hare–lynx activity overlap, (b) lynx activity rate, and (c) hare activity rate in winter (Dec–Mar) in the Kluane Lake region, Yukon, Canada. Hourly rates were determined for each relative hour of the 24-hour diel cycle. The number of hare kills by lynx for each hour represents the total number of kills occurring in that relative hour from a total sample size of 1926 lynx predation on hares (hare mortalities caused by lynx ($n = 26$) plus hare kills by lynx ($n = 1900$)). Time of day was scaled relative to the mean sunrise and sunset times across the winter weighted by the number of data points on each date. Solid lines represent regression lines, and shadings represent 95% CIs.

night, and their activity rates were higher than the population-mean activity rate during 0–1 min prior to death (day: mean difference (md) = 0.18 [95% CI: 0.08, 0.28], $t = 3.62$, $p < 0.001$; night: md = 0.19 [0.09, 0.29], $t = 3.74$, $p < 0.001$). While the magnitude was not as great, activity rate was still higher than the population mean at 1–5 min prior to death (day: md = 0.11 [95% CI: 0.01, 0.21], $t = 2.01$, $p = 0.026$; night: md = 0.07 [−0.02, 0.16], $t = 1.54$, $p = 0.07$). Activity rate > 5 min before predation was not different from the population mean during both the day and night (figure 4; electronic supplementary material, table S5).

4. Discussion

Here, using one of the first vertebrate datasets of the precise time of predation and simultaneously recorded fine scale (seconds to minutes) activity of both predator and prey, we tested (1) whether the degree of diel activity overlap between predator and prey is a reasonable proxy of predation risk and (2) whether prey and predator activity increase the chance of predation. We found that the diel pattern of predation in hares did not mimic the diel activity pattern of hares or hare–predator diel activity overlap, nor was predation

influenced by activity rate of hares at weekly or daily scales. However, we did find that predation by lynx was positively affected by lynx activity. Thus, the level of prey activity or diel activity overlap between prey and predators are not always good proxies of predation risk, highlighting that such assumptions are not universally true and riskiness of prey activity should be carefully assessed.

While the integration of VHF and GPS technologies over the past few decades into predator–prey research has opened the door for measuring predation in space [26,61,62], there has been a lack of methodological means for measuring predation in time. As such our understanding of the temporal aspects of predation remains poor [11] relative to the spatial aspects. The study of wolf–moose interactions by Vander Vennen *et al.* [9] is the only one, to our knowledge, which has ever directly tested predator and prey activity on the diel pattern of predation, but their estimated predation time was based on GPS-based predator movement data collected at 2.5 h intervals and their metrics of predator and prey activity were solely GPS-based movement rates calculated over ≥ 1 h. Here we show a novel approach of using accelerometers to accurately document the precise timing of (1) mortality in a small mammal and (2) predation by a medium sized predator at very fine time scales (at second-scale for prey and

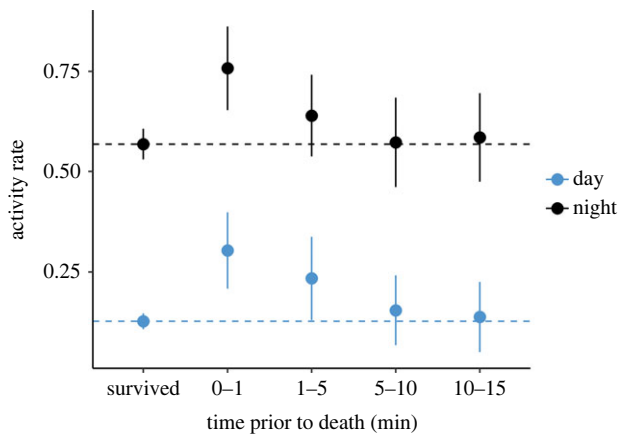


Figure 4. Comparison of activity rate of hares before predation (points and 95% CI) to the population-mean activity rate (dotted lines; day = 0.13, night = 0.57) on the same day, for daytime ($n = 36$) and night-time ($n = 33$) mortalities.

minute-scale for predator). The added bonus of this approach is that our accelerometer-based predator/prey data could be classified into activities, allowing more detailed exploration into whether predator and prey activity and their activity overlap are reasonable proxies of predation risk. By showing that prey activity and predator-prey diel activity overlap do not always increase the likelihood of predation, our findings highlight that our assumptions of the drivers of predation can be misguided, overly simplistic, and in need of actual testing. However, with the novel approach for precisely recording time of death, and the ability to easily combine this with spatial data (GPS-based) at high sampling rates, more researchers can, and should, begin to more carefully examine how spatio-temporal behaviours of predator and prey drive spatio-temporal patterns of predation at fine scales. This important advancement will allow for wide scale testing across species and systems of many long-held assumptions (e.g. predator/prey activity predicts predation) within predator-prey ecology helping to unravel the complexities that exist which in turn will lead to important theoretical advancements.

We acknowledge that a high degree of diel activity overlap with predators may still be perceived by hares as risky, but it appears that hares make behavioural adjustments such that activity overlap cannot be assumed to reflect actual predation risk. These behavioural adjustments may involve adjustments in vigilance or habitat selection which we did not study. Prey can probably mitigate predation risk without reducing foraging rate by adopting vigilance while foraging (routine vigilance) [63,64]. Riskiness of foraging can also vary among different habitats [18,65]. Previous studies have reported that hares are potentially trading off forage quality with protection from predators in habitat selection [35,66]. Our findings suggest that such behavioural adjustments may lead to actual predation risk not being correlated with activity overlap between predator and prey.

Alternatively, the risk of inactivity, especially sleep [67,68], is possibly equal to that of activity and thus may create opposing patterns that mask any relationship between foraging and predation that does exist. Although inactivity such as hibernation has been reported to increase prey survival potentially through reduced predation risk [69], sleep requires individuals to enter a state of reduced neural activity and

suspension of consciousness that results in a lack of awareness of, and responsiveness to, the environment [68]. Some organisms minimize the dangers of sleep by relying on communal resting [70,71] or using safe places or refuges for sleep [72], but not all environments provide refuges that completely eliminate risks. Indeed, numerous studies have demonstrated prey being targeted by predators while they sleep (e.g. [73–75]). Thus, it is possible that the dangers of sleep may outweigh the dangers of activity in some species leading to an asynchrony, or lack of relationship, between predator-prey interactions, mortalities and prey activity. This may be the case for hares, and thus both foraging and sleep may be equally risky given that hares are solitary and do not use a burrow or other physical refuge for rest. Such patterns create complexities in our ability to test basic assumptions in predator-prey ecology and raise questions in how to properly quantify the impact of risk on prey behaviour and whether predator avoidance or other mitigation strategies are being used to balance survival-growth trade-offs.

While we found strong evidence that hare activity and hare-lynx activity overlap are poor predictors of predation risk, the obvious question is how generalizable are our results to other predator-prey systems? Research emerging from the realm of spatial overlap suggests that these findings may be quite common in the natural world. Theoretically, the movement of the organism that travels the greatest distance per time should be the main determinant of predator-prey encounter rates [22,23]. In many systems this tends to be the predator and not the prey. In which case often predator activity should be more important than prey activity, especially when movement rates of predators are higher than those of prey [22], exemplified by the wolf-moose interaction [9]. However, theoretically there are also situations where prey activity may become highly important in predicting predation. The first is where predators are less mobile than prey, as would be the case with some ambush hunters [24] or for sessile predators [76]. The second is where prey activity is correlated with accessibility as would be the case for prey that have daily migrations shifting between refuges from predators during inactivity and accessible locations during activity [77]. Therefore, while theoretically similar patterns to what we found should exist in other predator-prey systems, understanding the generalizability of our findings requires more empirical studies so that we can begin to decipher how predator and prey traits, and their combinations, drive the relationships between predator/prey activity and predation.

If the patterns we found are generalizable to other systems, then the lack of importance of prey activity for predation has important broader implications on our theoretical understandings of predator and prey activity. First, if predators do not have to match hunting to the diel activity patterns of prey as is the case with lynx, they become free to set activity in response to other factors like thermoregulatory costs [78], reproduction and competition. Similarly for prey, if predation is unaffected by the level of prey activity/foraging, as we found in hares, then things like thermoregulatory costs, reproductive opportunities and resource quality may be more important determinants of activity of prey than predator activity [79,80]. This suggests that we need to be careful of broad scale statements such as diel activity patterns in herbivores being top-down constrained and in carnivores being bottom-up constrained [78]. On the topic of antipredator behavioural responses to risk, our finding that activity of

hares only increased risk at an immediate temporal scale implies that short-term behavioural responses might be a more important driver of predation risk than long-term activity/foraging rates of prey [12,81]. While the significantly high activity rate 0–1 min before predation may be related to escape behaviour triggered by the presence of a predator, we still observed high activity rate 1–5 min prior to predation relative to the average activity rate. This suggests that in some systems, short-term reactive behavioural responses induced by perception of predator presence such as induced vigilance [13,63] or forgoing foraging [34] will be a more important determinant of predation risk than broad-scale or long-term behavioural patterns such as seasonal/weekly/daily activity or predator–prey spatio-temporal (e.g. home range or diel activity) overlap. Or, from the predator's perspective, this may imply that prey activity or movement increases the probability of predation potentially by increasing prey detectability rather than by increasing predator–prey encounter rate. While these are just a few of the implications from the findings of our study, they ultimately point out that in order to properly understand the link between activity and risk in predator–prey systems we need more empirical studies that actually test the drivers of activity and predation across temporal scales from immediate to long term.

Often in ecology we base interpretations of patterns on assumptions that have been minimally tested on only a handful of species and for which the universal applicability is unknown. Such is the case with temporal activity overlap between predator and prey being used as a measure of predator–prey interactions under the scarcely tested assumption that predation is highly correlated with both predator and prey activity (or foraging). However, given that this assumption failed to be supported by a commonly considered predator-driven prey species, snowshoe hares, highlights that more empirical studies that test basic assumptions in ecology are needed prior to broadly applying assumptions as the basic framework for studies. In terms of predator–prey research, we need to better explore the risk of each behavioural state for different species by monitoring behaviour of predator and prey with advanced biologging technologies such as accelerometers and GPS, and thereby

moving beyond the simple assumption of a positive relationship between activity or foraging and predation. Only then can we begin to appropriately use behaviour as a proxy of predator–prey interactions and accurately interpret the patterns of predation risk that exist across space and time.

Ethics. Procedures of handling and collaring hares were approved by the University of Alberta Animal Care and Use Committee (#AUP00001973) and permitted by the Government of Yukon (2015=#15-01, 2016=#16-02, 2017=#17-03, 2018=#18-01). Procedures of handling and collaring lynx were approved by the McGill University (#4728) and Trent University Animal Care and Use Committees (#26170), and permitted by the Government of Yukon (2015=#15-01, 2016=#16-02, 2017=#17-03, 2018=#18-01, 2019=#18-85, 2020=#19-82).

Data accessibility. Data and the R script used in this study are available in the Dryad Digital Repository: <https://doi.org/10.5061/dryad.sbcc2frc1> [82].

The data are provided in electronic supplementary material [83].

Authors' contributions. S.S.: conceptualization, data curation, formal analysis, methodology, writing—original draft; E.K.S.: conceptualization, data curation, formal analysis, methodology, writing—original draft; S.B.: conceptualization, funding acquisition, methodology, project administration, supervision, validation, writing—review and editing; M.J.L.P.: conceptualization, data curation, methodology, validation, writing—review and editing; Y.N.M.: data curation, writing—review and editing; A.K.M.: data curation, writing—review and editing; R.D.: data curation, writing—review and editing; T.S.J.: project administration, writing—review and editing; C.J.K.: writing—review and editing; R.B.: project administration, writing—review and editing; D.L.M.: project administration, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

Funding. This research was supported by the Natural Sciences and Engineering Research Council of Canada (NSERC), Northern Studies Training Program, the University of Alberta Northern Research Award programme, the Association of Canadian Universities for Northern Studies, the Wildlife Conservation Society Canada, the W. Garfield Weston Foundation, the Killam Laureates programme, Government of Yukon, Fur Institute of Canada and Earth Rangers.

Acknowledgement. We thank all the field technicians that contributed significantly to hare and lynx data collection. We also thank Agnes MacDonald and her family for long-term access to her trap line, and the Champagne and Aishihik First Nations for allowing us to conduct research within their traditional territory. We also would like to thank two anonymous reviewers for their helpful comments and feedback.

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