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# Shifts in diel activity of Rocky Mountain mammal communities in response to anthropogenic disturbance and sympatric invasive white-tailed deer

Persia Khan<sup>a,b,\*</sup>, Laura Eliuk<sup>b</sup>, Sandra Frey<sup>b,c</sup>, Christopher Bone<sup>a</sup>, Jason T. Fisher<sup>b</sup>

<sup>a</sup> Department of Geography, University of Victoria, PO Box 1700 STN CSC, Victoria, BC V8W 2Y2, Canada

<sup>b</sup> School of Environmental Studies, University of Victoria, PO Box 1700 STN CSC, Victoria, BC V8W 2Y2, Canada

<sup>c</sup> Ministry of Water, Land and Resource Stewardship, 525 Superior Street, Victoria, BC V8V 1T7

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## ABSTRACT

Coexistence mechanisms such as temporal niche partitioning among sympatric wildlife species may be impacted by continued human disturbance and invasive species. White-tailed deer expansion in North America, a product of landscape and climate change, may alter other species' diel activity and have implications for conservation of native species. We asked: 1) To what degree does invasive white-tailed deer temporal activity overlap with other ungulate species (mule deer and moose) in landscapes with high human disturbance, versus landscapes with low human disturbance? 2) To what degree does invasive white-tailed deer and predator activity (wolves, grizzly bears, and coyotes) overlap in landscapes with high human disturbance versus landscapes with low human disturbance? Using detection data from infrared remote cameras, we compared a high-disturbance (2019–2020) and a low-disturbance (2009–2010) landscape in the Canadian Rocky Mountains. We used activity pattern analysis to quantify temporal overlap between sympatric mammal species and white-tailed deer. We found that contrary to our hypotheses, sympatric ungulate species maintained activity and temporal overlap with white-tailed deer in both landscapes. Predators did not match the temporal activity of white-tailed deer in the high-disturbance landscape as closely as in the low-disturbance landscape. We conjecture ungulates may be prioritizing periods of optimal foraging or reducing predation risk rather than temporal niche partitioning from invasive-white-tailed deer. Predator species may be more sensitive to anthropogenic disturbance than ungulates and adjust their temporal activity in high-disturbance landscapes. Native ungulates' lack of diel activity adaptation to white-tailed deer invasions is an important piece of the behavioural puzzle about how western Nearctic systems change with anthropogenic disturbance and human-mediated range shifts.

## 1. Introduction

Anthropogenic landscape change has been pervasive globally in the last centuries, with multiple outcomes including habitat loss (Powers and Jetz, 2019), fragmentation (Fahrig, 2003) and the spread of invasive species (Didham et al., 2007). The last includes human-caused species introductions as well as the more nuanced range expansion of anthropophilic species (Davies et al., 2009; Pacifici

\* Corresponding author at: Department of Geography, University of Victoria, PO Box 1700 STN CSC, Victoria, BC V8W 2Y2, Canada.  
E-mail address: [persiakhan@uvic.ca](mailto:persiakhan@uvic.ca) (P. Khan).

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et al., 2020). For example, white-tailed deer (*Odocoileus virginianus*) have been expanding across North America since the 1900s, becoming the most widely-distributed and abundant ungulate on the continent (Heffelfinger, 2011; Laliberte and Ripple, 2004) with profound impacts to ecological communities (Côté, 2011). As an ungulate species originally native to temperate regions of eastern North America and limited by winter severity, white-tailed deer now occupy a vast array of landscapes across the Nearctic, extending into boreal and mountain systems.

The recent success of white-tailed deer in those northern systems has been a focus of extensive investigation (Lesage et al., 2000; Rouleau et al., 2002; Dawe et al., 2014; Laurent et al., 2021). Their expansion has mainly been attributed to two non-mutually-exclusive hypotheses: land use change and climate change – the former of which has been notable in landscapes dominated by petroleum extraction and forestry activity in the western boreal plains. Satellite telemetry (Darlington et al., 2022), camera-trap research (Fisher and Burton, 2020; Fisher et al., 2020; Fisher et al., 2021), and resource selection analysis from aerial survey data (Fuller et al., 2022) shows deer invasion is facilitated by the increasing density of anthropogenic linear features (e.g., seismic lines, cut lines, road verges) and polygonal features (forest harvest cutblocks, well sites, industrial sites), all of which provide widespread subsidies of early seral vegetation as forage.

Increased white-tailed deer abundance causes overbrowsing which can lead to alterations of ecosystems and initiate trophic cascades (Côté et al., 2004; Côté, 2011). This influx of ungulate biomass can also alter predator-prey interactions. For example in the western boreal forest, invading deer populations bolster wolf (*Canis lupus*) populations which predate Threatened-listed woodland caribou (*Rangifer tarandus*; Latham et al., 2011). This is the proposed mechanism of ongoing caribou declines (Boutin et al., 2012; Hervieux et al., 2014; Serrouya et al., 2019) via apparent competition: when prey species  $x$  increases thus increasing abundance of their common predator, prey species  $y$  decreases due to increased predation (Holt, 1977). Apparent competition can have numerical or functional responses for the shared prey species, decreasing in abundance or altering behaviour to avoid increased risk (Holt and Kotler, 1987). If white-tailed deer alter wolf-caribou dynamics, deer may likewise affect other ungulates, such as native mule deer (*O. hemionus*), moose (*Alces alces*), and elk (*Cervus canadensis*). Mule and white-tailed deer, in particular, share similar temporal and dietary niches, and an increase in individuals of one species may substantially alter community dynamics (Berry et al., 2019). White-tailed deer are primarily preyed upon by wolves (*Canis lupus*), coyotes (*Canis latrans*), and black bear (*U. americanus*), depending on life stage (Hewitt, 2011). We conjectured that early signs of shifting predator-prey-dynamics may manifest as shifts in diel activity and temporal niche partitioning among these sympatric ungulate species.

The importance of understanding animals' diel activity derives from niche theory, which dictates that the differential exploitation of resources primarily determines ecological segregation within a community (Case and Gilpin, 1974). If time is considered a resource that a given species can exploit, then it, in theory, must be partitioned by sympatric species to facilitate coexistence (Kronfeld-Schor and Dayan, 2003). Temporal niche partitioning may have associated costs (Brown and Kotler, 2004) in terms of suboptimal foraging, increased energetic demands, and increased risk of predation, however, it may be necessary for coexistence when resources are restricted, or competition is pronounced (Cunningham et al., 2019; Sovie et al., 2019). Niche partitioning via spatial segregation has often been explored spatially (Fisher et al., 2013; Davis et al., 2018; Owen-Smith, 2019). The importance of temporal niche partitioning, however, is increasingly being investigated in the literature and can provide new ecological insights across rapidly changing landscapes (Frey et al., 2017). Emerging global trends indicate that temporal activity for mammals has experienced directional shifts as a product of increased anthropogenic disturbance (Gaynor et al., 2018). The direction of activity shifts in response to human disturbance is commonly toward nocturnal activity (Lamb et al., 2020), however, the details are more complex: changes in temporal activity in dominant predators can spur subsequent temporal avoidance by subdominant competitors, thus shifting diel activity patterns of communities (Lendrum et al., 2017; Frey et al., 2020; Sévêque et al., 2022).

We used serial detection data from remote cameras to evaluate the impacts of anthropogenic disturbance and invasive white-tailed deer occurrence on the diel activity patterns of sympatric ungulate and predator species in the Canadian Rocky Mountain mammal community. Remote cameras monitor the activity of multiple sympatric species over large spatial and temporal scales (Frey et al., 2017; Lashley et al., 2018; Gracanin and Mikac, 2022). We investigated the difference in temporal activity patterns between two landscapes: one impacted substantially by resource extraction, and one largely protected from development. We asked: To what degree does invasive white-tailed deer temporal activity overlap with other native ungulates, and primary predators, in high-disturbance landscapes versus low-disturbance landscapes? We hypothesized that other ungulates would decrease temporal overlap with white-tailed deer in the high-disturbance landscape – relative to the low-disturbance landscape – to avoid short-term behaviourally-mediated apparent competition (via opportunistic predation from wolves) (Holt and Kotler, 1987) with the greater density of white-tailed deer on this landscape. We also hypothesized that predators would shift to nocturnality in high-disturbance landscape – relative to the low-disturbance landscape – to avoid human activity and perceived risk from anthropogenic disturbance (Gaynor et al., 2018; Frey et al., 2020). Finally, we hypothesized that predator species would have increased temporal overlap with white-tailed deer in the high disturbance landscape relative to the low-disturbance landscape: as anthropogenic disturbance facilitates white-tailed deer range expansion (and population densities) through forage subsidies, predators will match their activity to those white-tailed deer as a predation strategy.

## 2. Methods

### 2.1. Study area

Our sampling frame is the Canadian Rocky Mountains of the western Nearctic; within this frame, we studied, respectively, a high disturbance and low disturbance landscape in Alberta, Canada (Fig. 1): the Willmore Wilderness Area (WW) and the Bighorn

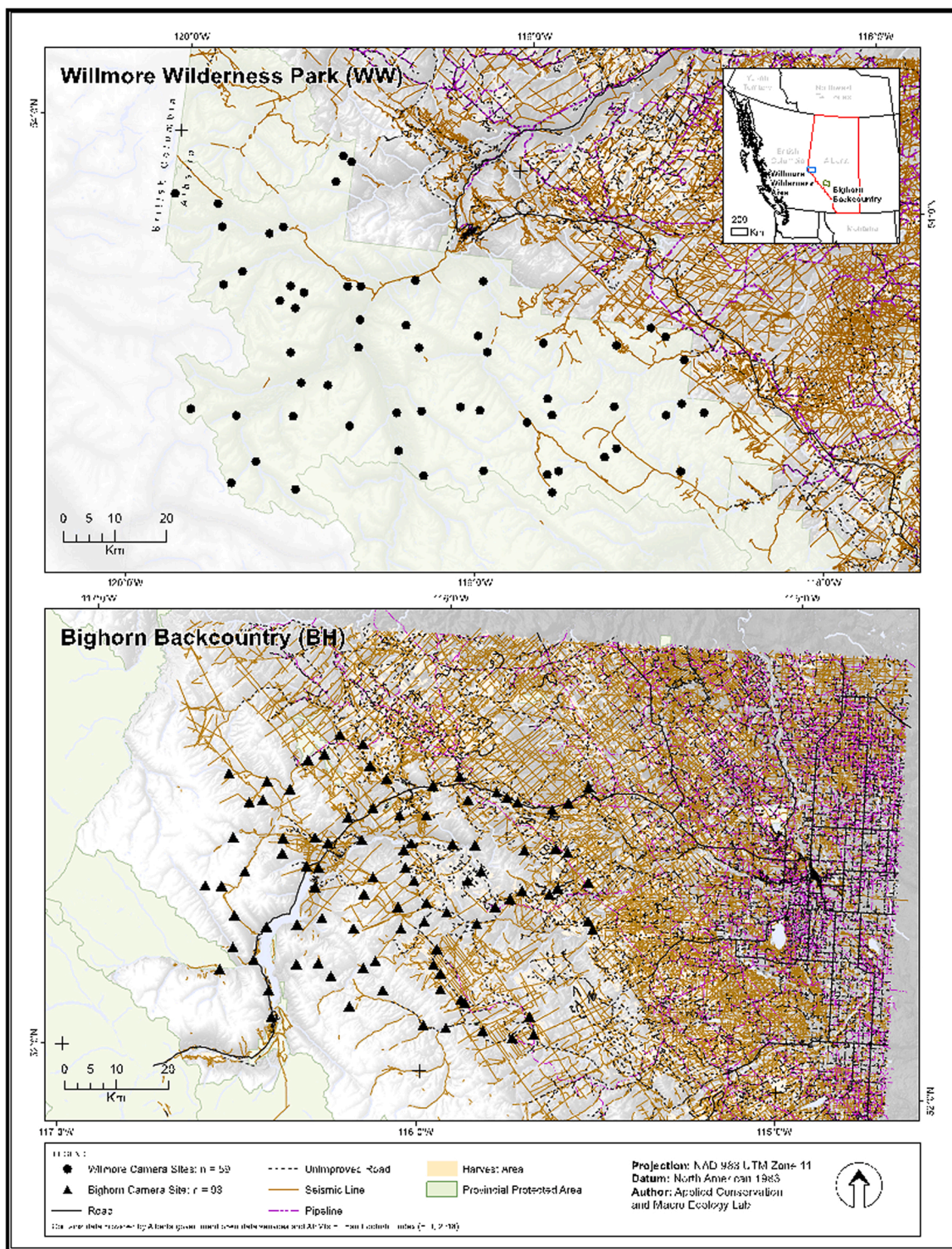


Fig. 1. Wildlife camera locations in both study areas in the Canadian Rocky Mountains: the Willmore Wilderness (WW) representing the low-disturbance landscape, and the Bighorn Backcountry (BH) in the high-disturbance landscape. Contains publicly available data provided by the Alberta Government and the Alberta Biodiversity Monitoring Institute (2010–2019).

Backcountry (BH). These landscapes have similar natural landscapes (Table 1): both have steep mountainous topography characterized by Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*); Douglas fir (*Pseudotsuga menziesii*), trembling aspen (*Populus tremuloides*), lodgepole pine (*Pinus contorta*), and white spruce (*Picea glauca*). However, the two landscapes have notably different human footprints (Fig. 1). WW is mean elevation ca. 2000 m, encompasses roughly 4600 square kilometers of protected area, and hosts a relatively small human footprint (Table 1), with disturbance limited to deforested linear features at park boundaries and public access limited to foot or horseback at the time of data collection. Disturbances have markedly accumulated over the last two decades. In contrast BH has a mean elevation of 1500 m, and is an actively industrialized 6000 km<sup>2</sup> area with extensive forestry, mining, and energy extraction, generating linear features and polygonal features (Table 1) that are still frequently used by industry and by recreationalists.

WW and BH support similar mammal communities, facilitating a cross-landscape comparison. A diverse predator community is made up of grizzly (*Ursus arctos*) and black bear, grey wolf, cougars (*Puma concolor*), wolverine (*Gulo gulo*), coyote and red fox (*Vulpes vulpes*) as well as an abundance of ungulate species, including white-tailed deer, mule deer, moose, and elk.

## 2.2. Sampling design

In both BH and WW, infrared remote cameras were deployed using a systematic sampling design that captured both the gradients of disturbance across landscapes (Table 1) in the Canadian Rocky Mountains, as well as the distribution of mammalian communities (Fisher et al., 2011; Fisher and Bradbury, 2014). In the WW, arrays were based on a 12 × 12-km hybrid design (Fisher et al., 2014): half the sites were deployed systematically and half allocated to three strata (mid-elevation conifer forest, low elevation valley bottoms, high elevation alpine). Minimum distance between cameras is 6 km, maximum is 12 km. In the BH arrays were established using a 6 × 6-km systematic design (min. spacing = 2-km, max = 6 km) The sampling design was more spatially dense in the BH, but sites remained independent (i.e., site spacing > home-range size, with temporal data generated by multiple individuals within the sampled population). Within each grid cell, one camera was deployed on an active game trail to maximize species detection (WW: n = 59, 2009–2010; BH: n = 93, 2019–2020). We assume that there were no substantial changes in large mammal communities during this time, as they are generally slow to mature and reproduce. Wolves were subject to government population control measures adjacent to the WW landscape, and persecuted around the BH, for context. White-tailed deer did not appreciably change in density in the mountains through that period (<https://www.alberta.ca/aerial-wildlife-survey-reports.aspx>) so we assumed these samples are suitable for spatial comparisons.

In both study sites, *Reconyx* infrared-triggered digital cameras (models PC900 and Hyperfire 2X; Holmen, WI, USA) were deployed in combination with scent lure (O’Gorman’s Long Distance Call; Broadus, MT, USA) positioned 6–10 m from the camera (Fisher and Bradbury, 2014). Cameras were positioned 0.5–1.5 m off the ground and set to high sensitivity to reduce the number of false triggers.

We focused on six species with sufficiently frequent occurrence to allow analysis: white-tailed deer, mule deer, moose, grey wolf, grizzly bear, and coyote (Fig. 2). Ungulate species are generally crepuscular as this is an optimal foraging period, though both mule-deer and moose can be active during other temporal periods depending on disturbance and predation (Frey et al., 2022). For predators, wolves have been shown to decrease diurnal activity in the presence of disturbance and co-occurrence with humans, trending towards nocturnality (Oriol-Cotterill et al., 2015). As a mesopredator, coyotes exercise temporal niche partitioning to reduce competition amongst predator species, often leading to sub-optimal foraging. Grizzly bears are typically active during the day and crepuscular periods, and are opportunistic omnivores (Schwartz et al., 2010).

**Table 1**

Summary of land cover similarities and differences in the Willmore Wilderness Park (WW) and Bighorn Backcountry (BH), Alberta, Canada, in 2010 and 2019. The mean proportion (± SE) for natural, abiotic, and disturbance features within a 5000-m buffer surrounding camera sites in WW and BH. The “ratio” refers to the relationship between the mean of BH to the mean of WW features.

Covariate	Description	WW (Low Disturbance) Mean (± SE)	BH (High Disturbance) Mean (± SE)	Ratio
<b>Natural features</b>				
Conifer	< 30 % to > 70 % crown closure; > 80 % coniferous forest	53.4 (± 0.55)	73.50 (± 1.67)	1.38
Shrub	> 25 % shrub cover, < 6 % tree cover	7.11 (± 0.23)	4.50 (± 0.27)	0.63
Herb	< 25 % shrub cover, < 6 % tree cover	6.17 (± 0.11)	2.47 (± 0.23)	0.40
<b>Abiotic features</b>				
Ruggedness	Average elevational differences in each area using Topographical Ruggedness Index (TRI)	12.80 (± 1.20)	9.76 (± 0.70)	0.76
<b>Disturbance features</b>				
Block industrial	Percentage cover of forest harvest cut blocks and well sites	0.05 (± 0.01)	8.62 (± 1.06)	172.4
Linear industrial	Percentage cover of linear industrial features (seismic lines, transmission lines, pipelines, and roads)	0.06 (± 0.01)	1.15 (± 0.07)	19.2

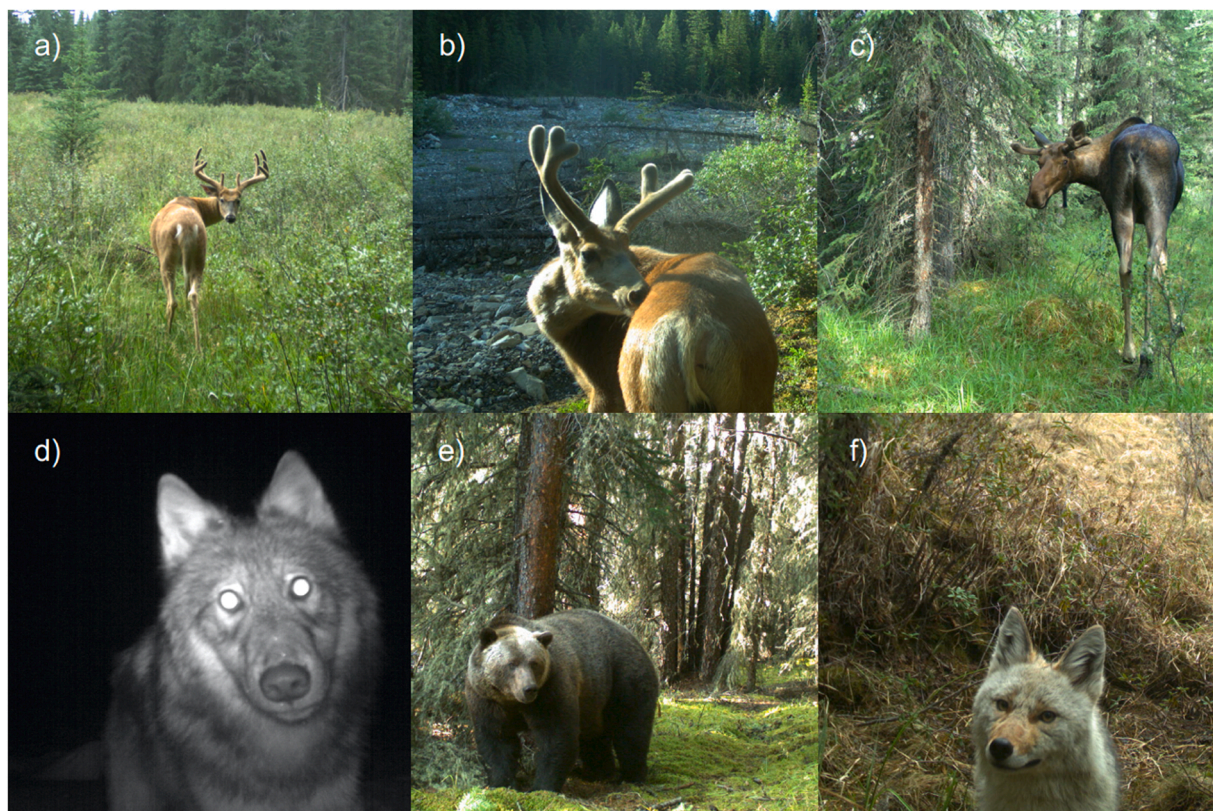
### 2.3. Temporal analysis

To analyze trends in diel activity patterns with increased white-tailed deer abundance, we compared species activity curves between high- (BH) and low-disturbance (WW) landscapes. From camera images, we recorded the date, time, and species present in Timelapse 2.0 image analyzer (Greenberg et al., 2019). The months of July through September yielded 7602 (WW) and 39,828 (BH) animal detections; to reduce temporal autocorrelation of consecutive detections, we used a 30-minute truncation to identify independent detections (not repeats of the same animal), yielding 768 (WW) and 1430 (BH) independent detections.

We pooled independent detections of our target species from each camera site to estimate species-specific diel activity across each landscape. We required a minimum of 10 detections per species for our statistical analysis (Lund et al., 2017). Using time of day as a circular variable, we applied non-parametric kernel density estimation methods (Ridout and Linkie, 2009) using the R package *overlap* (Meredith and Ridout, 2014) to generate species activity curves. The fitted curves use a von Mises kernel to estimate the circular distribution of the temporal data. We quantified overlap between species' activity curves using the coefficient of overlap ( $\Delta$ ) based on nonparametric estimators of  $\Delta$ . We used  $\Delta_1$  and  $\text{adjust} = 0.8$  for comparison when the smaller sample size was less than 50 independent detections, and  $\Delta_4$  and  $\text{adjust} = 1$  for comparison when the smaller sample size was greater than 75 independent detections (Ridout and Linkie, 2009; Meredith and Ridout, 2014). We then applied a bootstrap of 10,000 samples to  $\Delta$  to calculate a bootstrap mean (*BS*) and an estimated confidence interval. We used the Mardia-Watson-Wheeler (MWW) test in the R package *circular* (Lund et al., 2017) to test for significant differences among activity curves, wherein  $p > 0.05$  indicates different activity patterns. We then compared the overlap in estimated confidence intervals as well as statistical significance to investigate temporal activity overlap between mammal species as predicted by our hypotheses. We compared activity curves in two parts: first as species-pairs in each landscape, and finally as single-species comparisons between landscapes.

### 3. Results

We detected focal species in WW and BH respectively: coyote (19; 18), moose (57; 29), grizzly bear (57; 25), mule deer (10; 176), white-tailed deer (44; 685), and grey wolf (16; 10).



**Fig. 2.** The six species included in our analysis, identified from infrared remote camera arrays in both the Willmore Wilderness Area and the Bighorn Backcountry in the Canadian Rocky Mountains: a) White-tailed deer (*Odocoileus virginianus*); b) Mule deer (*Odocoileus hemionus*); c) Moose (*Alces alces*); d) Grey wolf (*Canis lupus*); e) Grizzly bear (*Ursus arctos*); and f) Coyote (*Canis latrans*).

### 3.1. Analysis of temporal niche partitioning within landscapes

Sympatric prey species exhibited stronger temporal overlap ( $\Delta$ ) than predator species (Table 2). Mule and white-tailed deer occupied similar temporal niches in both the low-disturbance and high-disturbance landscape. Both sympatric deer species exhibited bimodal activity with a pronounced density of activity during dawn and a separate, defined activity peak at dusk (Fig. 3a; Fig. 4a). Estimated overlap between the two deer species in the low-disturbance landscape ( $\Delta = 0.55$ ) was lower than in the high-disturbance landscape ( $\Delta = 0.82$ ).

Moose were more nocturnal than white-tailed deer yet with similar bimodal activity, as demonstrated in the low-disturbance landscape ( $\Delta = 0.76$ ; CIs in Table 2), with moose activity peaking during dawn and at midnight and more diurnal white-tailed deer activity (Fig. 3b). These patterns are similar in the high-disturbance landscape ( $\Delta = 0.65$ ), however there is less overlap in evening activity peaks between the two species, with white-tailed deer activity peaking closer to dusk with a following peak in moose activity closer to midnight (Fig. 4b).

Predator species exhibited more temporal overlap with white-tailed deer in the low-disturbance landscape (Figs. 3c and 3d) versus the high-disturbance landscape (Figs. 4c and 4d). Grey wolves appeared to match white-tailed deer activity more closely in the low-disturbance landscape ( $\Delta = 0.80$ ) than in the high-disturbance landscape ( $\Delta = 0.65$ ). Like white-tailed deer, wolf activity in the low-disturbance landscape had bimodal peaks (Fig. 3c), whereas in the high-disturbance landscape wolf activity shifted diurnally (Fig. 4c). Grizzly bears and white-tailed deer had a high degree of temporal overlap in the low-disturbance landscape ( $\Delta = 0.82$ ) which was maintained in the high-disturbance landscape ( $\Delta = 0.78$ ), however grizzly activity peaked more notably after dusk, whereas deer activity had a higher density of activity at dawn and into morning hours (Supplementary Information, Fig. 1). White-tailed deer activity overlap with coyotes is more similar in the high-disturbance landscape (Fig. 4d) than in the low-disturbance landscape (Fig. 3d), as the activity in the latter is more ephemeral. However, the overlap coefficient is estimated to be the same in both landscapes ( $\Delta = 0.72$ ).

### 3.2. Analysis of activity pattern shifts between landscapes

The results from the second analysis, comparing single-species activity directly between the low-disturbance and high-disturbance landscapes, showed that prey species maintained their activity between landscapes compared to predator species who exhibited a directional shift in activity in the high-disturbance landscape (Table 3). White-tailed deer maintained activity between landscapes and had the highest overlap coefficient across all species in the analysis ( $\Delta = 0.88$ ; Fig. 5a). Mule deer activity patterns produced similar results across landscapes, with mule deer utilizing the same temporal window in both landscapes ( $\Delta = 0.71$ ; Fig. 5b). Likewise varying disturbance across landscapes did not affect diel activity of moose ( $\Delta = 0.80$ ). Of the three ungulate species, moose activity was the most nocturnal in both landscapes (Fig. 5c).

Predator species generally exhibited a directional shift in activity – either towards more diurnal or nocturnal activity – between low- and high-disturbance landscapes. Grey wolf activity was mainly nocturnal in the low-disturbance landscape and showed a directional shift towards diurnal activity in the high-disturbance landscape with a sharp peak in activity midday ( $\Delta = 0.59$ ; Fig. 5d). Grizzly bear activity patterns shifted to a lesser degree ( $\Delta = 0.74$ ; Fig. 5e) towards more nocturnality in the high-disturbance landscape than in the low-disturbance landscape. Coyotes remained cathemeral in both landscapes but with a sharpened activity peak around dawn in the high-disturbance landscape ( $\Delta = 0.68$ ; Fig. 5f).

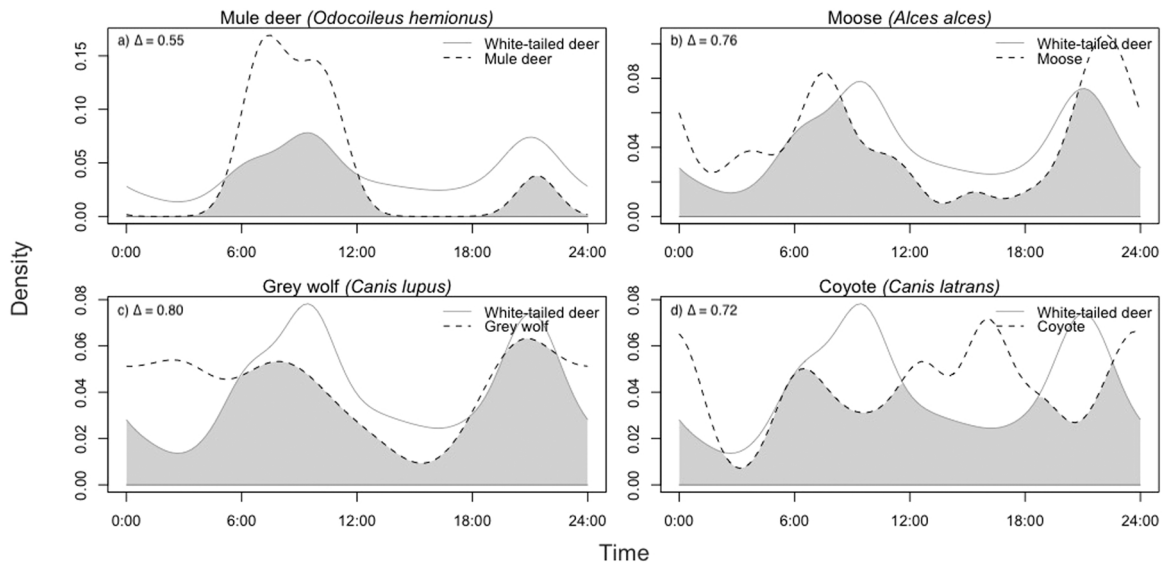
## 4. Discussion

Contrary to our hypotheses, our analysis did not reflect a shift in temporal activity of ungulate species in the face of either extensive landscape disturbance or co-occurrence with an increasing density of invasive white-tailed deer. In contrast, predator species shifted their activity in the high-disturbance landscape, but without matching prey activity. Despite potential impacts of white-tailed deer

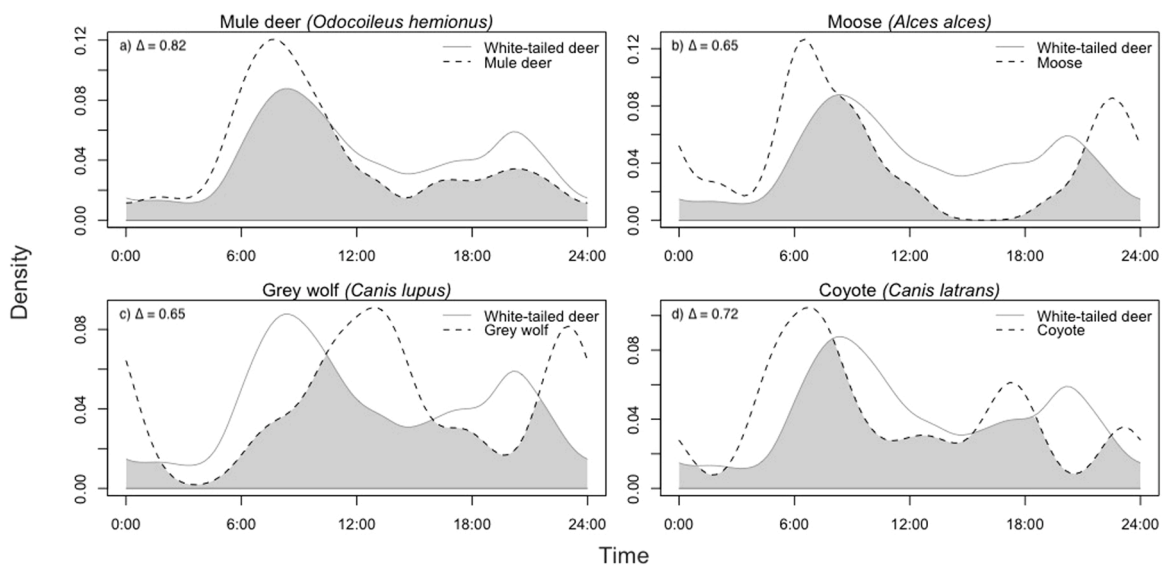
**Table 2**

Species-pair comparisons in the low-disturbance Willmore Wilderness (WW) landscape and the high-disturbance Bighorn Backcountry (BH) landscape. The coefficient of overlap ( $\Delta$ ), bootstrap mean (BS), 95 % confidence interval (CI) of the coefficient of overlap are presented; the p-value ( $p$ ) is the probability that the two curves are from equal distributions based on the Mardia-Watson-Wheeler test.

Landscapes	Species Pair	$\Delta$	BS	CI	$p$
Low disturbance (WW)	White-tailed deer vs. Mule deer	0.55	0.53	0.34–0.75	0.05
	White-tailed deer vs. Moose	0.76	0.74	0.62–0.88	0.02
	White-tailed deer vs. Grey wolf	0.80	0.70	0.62–0.95	0.34
	White-tailed deer vs. Grizzly bear	0.82	0.77	0.69–0.93	0.18
	White-tailed deer vs. Coyote	0.72	0.69	0.54–0.87	0.69
High disturbance (BH)	White-tailed deer vs. Mule deer	0.82	0.82	0.75–0.89	< 0.005
	White-tailed deer vs. Moose	0.65	0.65	0.52–0.78	< 0.005
	White-tailed deer vs. Grey wolf	0.65	0.62	0.42–0.84	0.67
	White-tailed deer vs. Grizzly bear	0.78	0.74	0.64–0.92	0.11
	White-tailed deer vs. Coyote	0.72	0.71	0.56–0.86	0.34



**Fig. 3.** Kernel density estimation plots of temporal activity curves and overlap for species (dashed line) compared against white-tailed deer activity (solid line) in the low-disturbance landscape, the Willmore Wilderness (WW). Activity overlap is represented by the coefficient of overlap ( $\Delta$ ) is represented by the shaded grey area and listed for each plot.  $\Delta = 1$  represents complete temporal overlap between species, and  $\Delta = 0$  represents no temporal overlap between species.



**Fig. 4.** Kernel density estimation plots of temporal activity curves and overlap for species (dashed line) compared against white-tailed deer activity (solid line) in the high-disturbance landscape, the Bighorn Backcountry (BH). Activity overlap, represented by the coefficient of overlap ( $\Delta$ ), is represented by the shaded grey area, and is listed for each plot.  $\Delta = 1$  represents complete temporal overlap between species, and  $\Delta = 0$  represents no temporal overlap between species.

expansion on sympatric species' diel activity, our results did not support decreasing temporal overlap between competitor species and increasing temporal overlap with predator species.

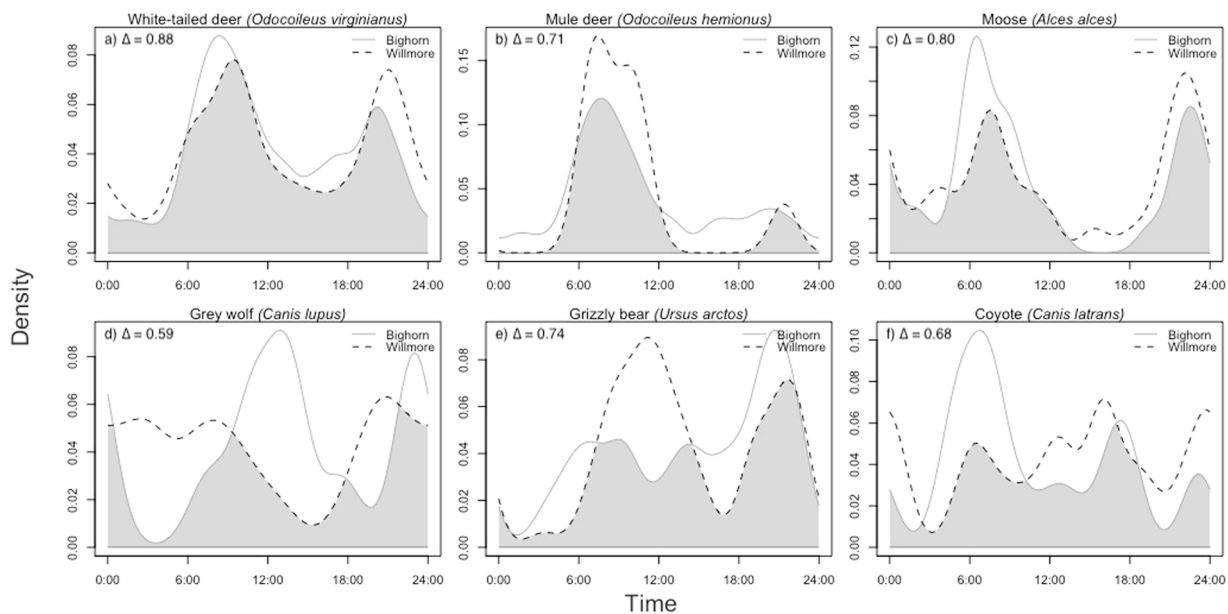
#### 4.1. Prey species maintain temporal activity across mountain landscapes

Ungulate species maintained their temporal activity patterns between the low-disturbance and high-disturbance landscapes, with no support for our hypothesis that disturbance would shift ungulate activity. Moreover, instead of segregating temporal activity from the invasive and more abundant white-tailed deer as we hypothesized, moose and mule deer activity remained unchanged. The consistency in this pattern was unexpected but suggests that the diel behavioural strategy ungulates employ – presumably mitigating

**Table 3**

Statistics from the single-species comparison between the low-disturbance landscape, the Willmore Wilderness (WW) and the high-disturbance landscape, the Bighorn Backcountry (BH). For each comparison, the coefficient of overlap ( $\Delta$ ), bootstrap mean (BS), confidence interval of the coefficient of overlap, and p-value (p), wherein  $p > 0.05$  indicates different activity patterns. All parameters were estimated using the R package *overlap* (Meredith and Ridout, 2014) and the Mardia-Watson-Wheeler test in the R package *circular* (Lund et al., 2017).

Species	$\Delta$	BS	Confidence Interval	p
White-tailed deer ( <i>Odocoileus virginianus</i> )	0.88	0.83	0.78–0.97	0.51
Mule deer ( <i>Odocoileus hemionus</i> )	0.71	0.67	0.53–0.86	0.30
Moose ( <i>Alces alces</i> )	0.80	0.74	0.64–0.93	0.28
Grey wolf ( <i>Canis lupus</i> )	0.59	0.54	0.34–0.82	0.21
Grizzly bear ( <i>Ursus arctos horribilis</i> )	0.74	0.70	0.59–0.89	0.46
Coyote ( <i>Canis latrans</i> )	0.68	0.63	0.46–0.88	0.12



**Fig. 5.** Kernel density estimation plots comparing change in diel activity between the low-disturbance landscape (Willmore Wilderness (WW); dashed line) and the high-disturbance landscape (Bighorn Backcountry (BH); solid line) for each of the six species included in the analysis. Activity overlap, represented by the coefficient of overlap ( $\Delta$ ), is represented by the shaded grey area, and is listed for each plot.  $\Delta = 1$  represents complete temporal overlap between species, and  $\Delta = 0$  represents no temporal overlap between species.

predation pressure – is more important than interference competition from invasive deer or perceived risk from human activity and landscape change. To facilitate coexistence, it is possible that ungulates are occupying similar temporal niches but are partitioning other niche axes such as space-use and forage (Case and Gilpin, 1974; Beck and Peek, 2005).

We hypothesized sympatric ungulates would shift diel activity as a behavioural response to increased predation risk through disturbance-mediated apparent competition: increasing deer increase wolves, increasing risk to other ungulates (Holt, 1977; Holt and Kotler, 1987). A classic example of disturbance-mediated apparent competition is the reduction in caribou populations (*Rangifer tarandus caribou*) resulting from increasing density of alternative ungulate prey for wolves that subsequently increases wolf populations (DeCesare et al., 2010). However, we found no behavioural shift in our target ungulate species. Instead, these apparent competitors shared a similar temporal niche within both the low-disturbance and high-disturbance landscapes. There are a few hypothesized explanations for these outcomes. First, deer may induce no numerical response in wolves in this system, and hence there is no increased predation risk to other ungulates; wolf densities could not be estimated and presumed increases may not have occurred. Second, if there is increased predation risk, ungulate responses may manifest spatially rather than temporally. An increased density of linear features, commonly used as a proxy for the degree of human disturbance, can reduce refugia for prey species and create corridors for predators to travel more easily across the landscape (Dickie et al., 2017; Dickie et al., 2020). It is thus possible that ungulate movement or space-use (distribution) may change instead (Dickie et al., 2020). Future research on species co-occurrence will help further illuminate these dynamics.

A third potential explanation for the lack of difference in prey temporal activity between the two landscapes is the human shield hypothesis, which states that humans alter natural predator-prey spatial dynamics by acting as a buffer: predators spatially avoid humans, creating refugia for prey species (Berger, 2007; Shannon et al., 2014). Human activity is widespread and frequent in the high-disturbance landscape conducting industrial and recreational activities. The human shield hypothesis has been examined

spatially (Muhly et al., 2011; Sarmiento and Berger, 2017) but temporal shielding behaviour is a worthwhile hypothesis to explore and might explain ungulates' maintaining daytime activity.

Finally, it is possible that ungulates may express behavioural plasticity to temporally respond to novel risk (DeMars and Boutin, 2018). As the spatial and temporal scale of camera-trap sampling spreads – hopefully globally – future analyses can parse these alternatives (Steenweg et al., 2017). Perhaps if disturbance is perpetuated on this landscape through time, trends of temporal niche partitioning will emerge, and longitudinal studies have great value in further exploring temporal niche partitioning.

#### 4.2. Predators experience a directional shift in activity not exhibited by prey

We interpreted white-tailed deer expansion in the high-disturbance landscape as an opportunity for predator species to fulfill energetic requirements (Latham et al., 2011), and therefore hypothesized that predator species would capitalize on the increased abundance of prey by targeting temporal windows when white-tailed deer were most active. However contrary to our hypothesis, predators did not exhibit temporal prey matching in the high-disturbance landscape. Our hypothesis was structured around prey matching, where predators match the timing of their activity to that of their prey (Lang et al., 2019), though this was not observed.

Some hypothesized explanations warrant future testing. First, if there is temporal matching it may be seasonal, and we did not capture it. Of the predators, grey wolves are the most likely to prey on adult ungulates throughout the sampling period, whereas other predators such as the coyote or grizzly bear are more likely to hunt these prey species during fawning and calving season (Boertje et al., 1988; Higdon et al., 2019). Expanding our analyses to include these seasons may have allowed for further investigation of different predation strategies amongst the included predator species. Secondly, predators may structure diel activity in response to cues other than ungulates. This is supported by our finding that predator species' activity curves differed between disturbance levels.

Predators showed a directional shift in diel activity in response to landscape disturbance. Predator species matched their activity more closely to prey in the low-disturbance landscape and showed greater activity shifts in response to disturbance than did prey species. Human disturbance in the form of land use change can be advantageous to predator species, as linear corridors and reduced forest cover present new opportunities to detect prey and travel across the landscape (Stewart and Komers, 2017; Finnegan et al., 2018; Dickie et al., 2020). However, humans also represent a direct mortality risk and likely a perceived mortality risk to wolves and other predators (Treves et al., 2016; Frey et al., 2022). Despite the potential advantages of disturbed landscapes, the observed diel activity shifts in predators suggests that human disturbance may temporally displace predators, a consequence of a 'landscape of fear' (Laundré et al., 2010; Ciuti et al., 2012). The surprising outcome is that – contrary to our hypothesis and previously observed shifts to crepuscular or nocturnal activity in the presence of humans (Theuerkauf, 2009; Frey et al., 2020) – here wolves shifted activity to peak at midday. This presents opportunity for further investigation, and we have no current explanation for this conclusion, which is subject to some caveats.

#### 4.3. Caveats

Remote cameras allowed for continuous detections over a 24-hour window throughout our sampling period with opportunities for novel insights across large spatial scales (Burton et al., 2015; Frey et al., 2017). Temporal analyses of this kind require many repeated detections. We had the required minimum detections for the Mardia-Watson-Wheeler test (Lund et al., 2017), and we used the  $\Delta$  recommended for small sample sizes (Ridout and Linkie, 2009; Meredith and Ridout, 2014). However, a comparison of radio-telemetry activity tags and camera traps showed  $\Delta$  estimate error between the two methods increases with decreasing sample size (Lashley et al., 2018) as is true for most statistical populations (Krebs, 1989). Lashley et al. was not a sensitivity analysis for camera-trap sample sizes but illustrates a challenge: wolves are rare on these landscapes with low detections and hence sample sizes, but low sample sizes (and attending large error) should hinder our ability to detect differences among landscapes (Type II error). That we observed temporal shifts despite low sample sizes suggests a strong signal exceeding noise.  $N$  also varies spatially: for example, white-tailed deer had much lower detections in the low-disturbance landscape ( $n = 44$ , occupancy at 28 % of sites) vs. the high-disturbance landscape ( $n = 685$ , occupancy at 89 % of sites) (Supplementary Information, Table 1). Thus, diel activity estimates are formed from a smaller population and distribution in each landscape – something to consider for multi-landscape comparisons in the future.

Sampling between the two landscapes was conducted in different time periods (2009-2010 and 2019-2020) so the observed differences could be concluded to be spatial (as we did) or spatiotemporal reflecting changes in space and time. We had no reason to believe large mammal populations changed appreciably in a decade, but there is substantial research to support the spatial changes – hence our conclusions. However the temporal differences among pooled arrays will be a challenge for future synthetic analyses and a scaled-up global camera-trap network (Steenweg et al., 2017). Finally, our study was also limited to summer months. In this period human activity includes heavy recreational and industrial land-use, but no direct harvest. A shift in activity mediated by predation risk from humans may be more pronounced during the autumn hunting season, or during periods of resource scarcity in winter.

We interpreted anthropogenic disturbance to encompass resource extraction features left behind by development, actively being developed, and actively used by recreationists; this was useful in generalizing our broad scale trends in temporal activity between predators and prey, but also affects our ability to attribute ecological processes to the phenomena observed in our data. We also did not investigate direct or lethal disturbances, such as active wolf culling in Alberta, which may have impacted predator and prey densities within both study areas (Hervieux et al., 2014; Latham et al., 2011). Pulses of disturbance in the form of human presence may have also been a factor in the during the summer of 2020, as recreation pressures surged due to the novel Coronavirus. Different types of disturbance may be mediating different responses in the wildlife community.

Finally, we focussed on diel activity behaviour as the scope for our research. Species however can partition space, or resources

within the same space, to allow coexistence. It is possible that spatial segregation among ungulates and their shared predators may be occurring, and that is worth future research.

## 5. Conclusions

In unexpected ways, the marked anthropogenic landscape change on the east slopes of the western Cordillera have influenced the diel activity of predator but not ungulate species. A shift in daily activity by predators may have cascading effects for community assemblages, as competition and predation will be affected (Frey et al., 2020). Behavioural changes in response to landscape change and invasive species are much more subtle than population declines and range contractions but may presage these bigger problems. As global landscape change continues apace (Maxwell et al., 2016) in hand with invasive species spread (Clavero and García-Berthou, 2005), areas of high-intensity change such as the Canadian Rocky Mountains prompt conservation managers to consider behavioural shifts as a potential “distant early warning” signal of impacts to animal populations and communities induced by human disturbance.

## CRedit authorship contribution statement

Persia Khan: Conceptualization (lead); data curation (equal); formal, analysis (equal); investigation (lead); methodology (lead); writing-original, draft (lead); writing-review & editing (equal), Sandra Frey: Conceptualization (supporting); data curation (equal); formal, analysis (equal); investigation (supporting); methodology (supporting), writing-review & editing (equal), Laura Eliuk: Data curation (lead); investigation (supporting), methodology (supporting), writing-review & editing (supporting), Christopher Bone: Conceptualization (supporting); investigation (supporting), methodology (supporting); writing-review & editing (supporting), Jason T. Fisher: Conceptualization (lead); funding acquisition (lead); investigation (lead), methodology (supporting); project administration (lead); writing-review & editing (lead).

## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

## Data Availability

Data and code is available at Borealis, the Canadian Dataverse Repository, <https://borealisdata.ca/>.

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## Research ethics

Alberta Environment and Parks Research and Collection Permit No: 20–335. All research was done in consultation with the University of Victoria’s Animal Care Committee.

## Animal ethics

This research was reviewed and approved by InnoTech Alberta’s Animal Care and Use Committee and University of Victoria’s Animal Care Committee.

## Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.gecco.2022.e02355](https://doi.org/10.1016/j.gecco.2022.e02355).

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