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Research

Move to nocturnality not a universal trend in carnivore species on disturbed landscapes

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Sandra Frey, J. P. Volpe, N. A. Heim, J. Paczkowski and J. T. Fisher

S. Frey (https://orcid.org/0000-0001-9847-835X) ✉ (safrey@uvic.ca), J. P. Volpe and J. T. Fisher, Univ. of Victoria, School of Environmental Studies, PO Box 3060, STN CSC, Victoria, British Columbia, V8W 3R4, Canada. JTF also at: InnoTech Alberta, Victoria, BC, Canada. – N. A. Heim and J. Paczkowski, Alberta Environment and Parks, , Alberta, Canada.

Anthropogenic landscape change is a leading driver of biodiversity loss. Preceding dramatic changes such as wildlife population declines and range shifts, more subtle responses may signal impending larger-scale change. For example, disturbance-induced shifts to species' activity patterns may disrupt temporal niche partitioning along the 24-h time axis, compromising community structure via altered competitive interactions. We investigated the impacts of human landscape disturbance on species' activity patterns and temporal niche partitioning in the Canadian Rocky Mountain carnivore guild using camera trap images collected across two regions encompassing a wide gradient of human footprint. Applying kernel density estimation techniques, we tested for carnivore species' activity shifts 1) between a low versus high disturbance landscape, and 2) in relation to site-scale disturbance. To test our hypothesis that human disturbance impacts species' temporal niche partitioning, we modelled activity overlap between co-occurring carnivore species in relation to natural and anthropogenic landscape features, as well as carnivore community composition. Multiple carnivore species altered activity patterns between the low versus high disturbance landscapes and camera sites, but these shifts varied considerably among species. While wolves appeared to increase nocturnal activity in relation to disturbance, coyote activity consistently trended towards cathemerality and marten increased diurnal activity. Detecting effects of landscape disturbance on activity overlap between co-occurring species was highly sensitive to site-level detection sample sizes, and our results suggest altered temporal niche partitioning between marten and wolverine in relation to forest cover. This study indicates that mesocarnivores may respond differently and perhaps indirectly to anthropogenic disturbance compared to apex predators. Apex predator shifts to nocturnality may

We investigated the impacts of human landscape disturbance on carnivore species' daily activity patterns and temporal niche partitioning using camera trap images collected across the Canadian Rocky Mountains. Multiple species altered activity patterns between low versus high disturbance landscapes and camera sites, but these shifts varied considerably among species. Mesocarnivores responded differently and perhaps indirectly to anthropogenic disturbance compared to apex predators, with the potential for apex predators shifts to nocturnality to facilitate a 'behavioural release' in mesocarnivores. This may be a likely component of mesocarnivore population release, with important management implications for ecological communities on disturbed landscapes.

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facilitate a 'behavioural release' in mesocarnivores. This may be a likely component of mesocarnivore population release, with important management implications for ecological communities on disturbed landscapes.

Keywords: activity overlap, activity patterns, human disturbance, niche partitioning, species coexistence

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Introduction

Developing effective conservation strategies requires a full and empirical understanding of species' responses to human-mediated disturbances (Dirzo et al. 2014, Maxwell et al. 2016). To date, extensive research has documented spatial and numerical responses of wildlife populations to anthropogenic disturbances, such as population declines and local extirpations (Karanth and Nichols 1998, Laliberte and Ripple 2004, Ceballos et al. 2017). In contrast, significantly less research has investigated more subtle and complex responses, such as changes to species' behaviours and interactions (Wang et al. 2015, Stewart et al. 2016, Mori et al. 2019). Understanding how anthropogenic disturbances impact species' behaviour and competitive interactions via altered activity patterns and niche partitioning over the 24-h cycle is an important component of designing appropriate management strategies to facilitate human–wildlife coexistence and support biodiversity on impacted landscapes (Carter et al. 2015). Furthermore, understanding human impacts on species' activity and interactions may also shed light on the underlying mechanisms driving changes to species' distributions and population size on human-modified landscapes. Detecting such subtle shifts may therefore enable us to identify potential precursors of species' extirpations and population declines, thereby providing us with important information and opportunities to pre-emptively manage against such losses.

Recent technological and analytical advances have opened novel avenues for quantifying behavioural shifts and resultant changes to interspecific interactions in wildlife (Frey et al. 2017). Remote camera trapping provides cost-effective opportunities to study population and community-level processes across large spatial and temporal scales (Burton et al. 2015), including shifts in species' behaviours and interactions (O'Connell et al. 2010, Stewart et al. 2016, Rovero and Zimmermann 2016). Increasingly, researchers are turning to time-stamped wildlife images collected via camera trapping to address questions of temporal dynamics of wildlife communities, including daily activity schedules and patterns of interspecific niche partitioning along the 24-h time axis (Ridout and Linkie 2009, Frey et al. 2017).

Time – in the context of the circadian period – is a resource consumed like other resources with limited availability (Halle 2000). Understanding how species use and partition this resource along the temporal niche axis (Schoener 1974, Carothers and Jaksić 1984) provides important insights into species' ecology, and the mechanisms facilitating stable coexistence within communities. A species' use of time over the diel period – its 'activity pattern' – can be characterized by its selectivity for certain photoperiods (e.g. daytime, nighttime, twilight). Although regulated by an endogenous clock

(Kronfeld-Schor and Dayan 2003), species also show plasticity in activity patterns in response to abiotic and biotic factors such as season (Monterroso et al. 2014, Farris et al. 2015), habitat loss and fragmentation (Norris et al. 2010), presence of apex predators (Shores et al. 2019), co-occurrence with native and nonnative competitors (Gerber et al. 2012, Zapata-Ríos and Branch 2016), and human disturbance (Ramesh and Downs 2013, Wang et al. 2015).

Increasing evidence suggests that partitioning along the temporal axis enables spatially sympatric species to reduce the negative effects of competition (Kronfeld-Schor et al. 2001, Di Bitetti et al. 2009). Indeed, temporal niche partitioning has been observed across many taxa (Adams and Thibault 2006, Valeix et al. 2007, Di Bitetti et al. 2010), but may be an especially important strategy within carnivore guilds where interference competition can incur lethal costs. Given the potentially lethal consequences of direct interaction with a dominant predator (Palomares and Caro 1999, Donadio and Buskirk 2006), subordinate carnivores may reduce the potential for aggressive encounters through proactive temporal avoidance over the diel cycle, i.e. being active at times when their predator is less likely to be active. As division of resources is a critical component of establishing stable coexistence between sympatric competitors (MacArthur and Levins 1967), segregation along the temporal niche dimension may allow subordinate competitors to maintain spatial access to shared resources and habitat (Bischof et al. 2014).

Despite growing recognition of temporal segregation as an important driver of community structure, few studies have directly evaluated to what degree human disturbance may alter the capacity for species to segregate their activities to facilitate coexistence within biodiverse communities (but see Wang et al. 2015, Shores et al. 2019). Disturbance-mediated activity shifts and resultant changes to temporal niche partitioning between competitors may impact important processes of top–down control, or introduce various lethal and sub-lethal effects due to increased interference competition. To gain a better understanding of the potential for process changes to important dynamics structuring ecological communities, studies evaluating disturbance-mediated activity shifts should also investigate changes to interspecific temporal niche partitioning (Wang et al. 2015, Frey et al. 2017). To address this research gap, we evaluated the effects of anthropogenic landscape disturbance on carnivore species' activity patterns and temporal niche partitioning using data collected via remote camera-trapping across two regions in the Rocky Mountains of Alberta encompassing a large spatial gradient of human footprint.

The east slopes of the Rocky Mountains have experienced uniquely intensive disturbance over the last decades. This region is home to a diverse suite of large and mid-sized mammalian

carnivore (mesocarnivore) species. Human impacts include motorized (e.g. off-road vehicles, snowmobile) and non-motorized (hiking, skiing, equestrian) recreation, and various forms of resource extraction (e.g. timber harvest, mining, oil and gas exploration). We tested for carnivore activity shifts in relation to human landscape disturbance using two approaches, looking for convergence to test our hypothesis that disturbance alters species diel activity patterns. First, we compared carnivore activity patterns between a high disturbance and low disturbance landscape and tested for activity shifts. Second, we investigated carnivore activity shifts in relation to the camera site-scale disturbance within the two landscapes. We hypothesized that carnivore species would alter activity patterns in response to both local (camera-site) and landscape-scale (study area) human landscape disturbance.

We predicted that disturbance-sensitive species including wolf, wolverine and fisher would decrease diurnal activity on disturbed landscapes or camera sites. We hypothesized that other mesocarnivores, such as coyote, lynx and marten, would alter activity patterns in response to landscape disturbance, but we did not form a priori predictions about directionality in activity shifts as they could respond either directly to human activity, or indirectly to shifting activity times of dominant predators and competitors. Lastly, we hypothesized that human disturbance alters patterns of temporal niche partitioning within communities, and tested this by quantifying the influence of anthropogenic landscape disturbance on interspecific activity overlap. We predicted that disturbance-induced activity shifts would increase activity overlap between carnivore species due to increased nocturnal activity in one or both species.

Methods

Study area

Our study area encompassed two proximal areas in the Rocky Mountains of Alberta, Canada: the Willmore Wilderness Area (WW) and the Kananaskis Region (KR) region (Fig. 1). Both the WW and KR are characterized by steep and rugged mountain topography grading into adjacent foothills to the east. The WW region is predominantly characterized by coniferous forest 80–120 years old (*Pinus contorta*, *Picea glauca*, *Picea mariana* and *Abies balsamea*). The KR region features Engelmann spruce *Picea englemannii* and sub-alpine fir *Abies lasiocarpa* in the higher elevation, with Douglas fir *Pseudotsuga menziesii*, trembling aspen *Populus tremuloides* and lodgepole pine *Pinus contorta* dominating the lower elevations.

Although the WW and KR share many of their natural landscape characteristics (Natural Regions Committee 2006), the two differ markedly in the extent of human footprint and anthropogenic activity on the landscape. The WW, a 4600 km² conservation area, is largely protected from anthropogenic development. Human landscape disturbance in the WW consists almost exclusively of deforested linear features (petroleum exploration or 'seismic' lines, Fisher and Burton 2018), covering 2.37 km² (0.05%) of the total landscape and largely

restricted to the east (Fig. 1). Access is limited to foot and horse trails, precluding most forms of motorized recreation. In contrast, the KR experiences variable land-use practices within and adjacent to protected area boundaries and is managed by various land-use directives including recreation, tourism and natural resource extraction. Industrial developments include petroleum extraction, roads, timber harvest, trapping and agriculture, while considerable recreational use encompasses both non-motorized (e.g. hiking, biking, skiing, equestrian) and motorized activities (e.g. off-road vehicles, snowmobile). Kananaskis County, within which the vast majority of our KR sites were located, features a linear feature footprint of 57.5 km² (1.35%; including roads, rail, trails, seismic lines, transmission lines and pipelines) with a total human footprint of all linear and polygonal (e.g. harvest cut-blocks, residential land, well-sites) features of 256.1 km² (6.0%).

Despite the striking differences in landscape development across the two study areas, both the WW and KR support a common mammalian carnivore community including grizzly and black bear (*Ursus arctos* and *americanus*), wolf *Canis lupus*, cougar *Puma concolor*, coyote *Canis latrans*, wolverine *Gulo gulo*, lynx *Lynx canadensis*, red fox *Vulpes vulpes*, American marten *Martes americana* and short-tailed weasel, or stoat *Mustela erminea*. Fisher *Pekania pennanti* are present only within the WW and surrounding area, while bobcat *Lynx rufus* extend only into KR (Heim 2015). Both regions also support large and diverse populations of ungulates and smaller prey species.

Sampling design

We used photographic data collected in remote camera arrays deployed using identical sampling designs and sampling methods (Heim et al. 2017) explicitly designed to be networked (sensu Steenweg et al. 2017) to examine predator distribution across gradients of disturbance the Canadian Rocky Mountains. Species were surveyed in a systematic grid-based sampling design, with individual 12 × 12 km grid cells as our sampling unit, the size of a wolverine's home range which is the most wide-ranging species we sought to sample. Within grid cells cameras were placed on landscape features to maximize probability of detection. We deployed baited camera sites in both the WW (n = 66) and KR (n = 157) in October–December, monitoring monthly until March. Our sampling period is therefore representative of species' activity over the prolonged winter season in the Canadian Rockies. Sites were accessed by ground (ski, snowmobile, all-terrain vehicles) or helicopter. While sampling years and duration differed between the two study areas (WW = 2006–2008; KR = 2011–2014), we have no evidence to indicate this affects any observed differences in species' behaviour.

In both areas Reconyx infrared-triggered digital cameras (models RM30, PM30 and PC900) were deployed paired with a frozen beaver carcass nailed to the tree facing the camera ca 6-m away. Cameras were placed ca 1.5 m off the ground oriented north to prevent false triggers and set to high sensitivity with no trigger delay. Data were collected and bait replenished monthly (see Fisher and Bradbury 2014 for further details).
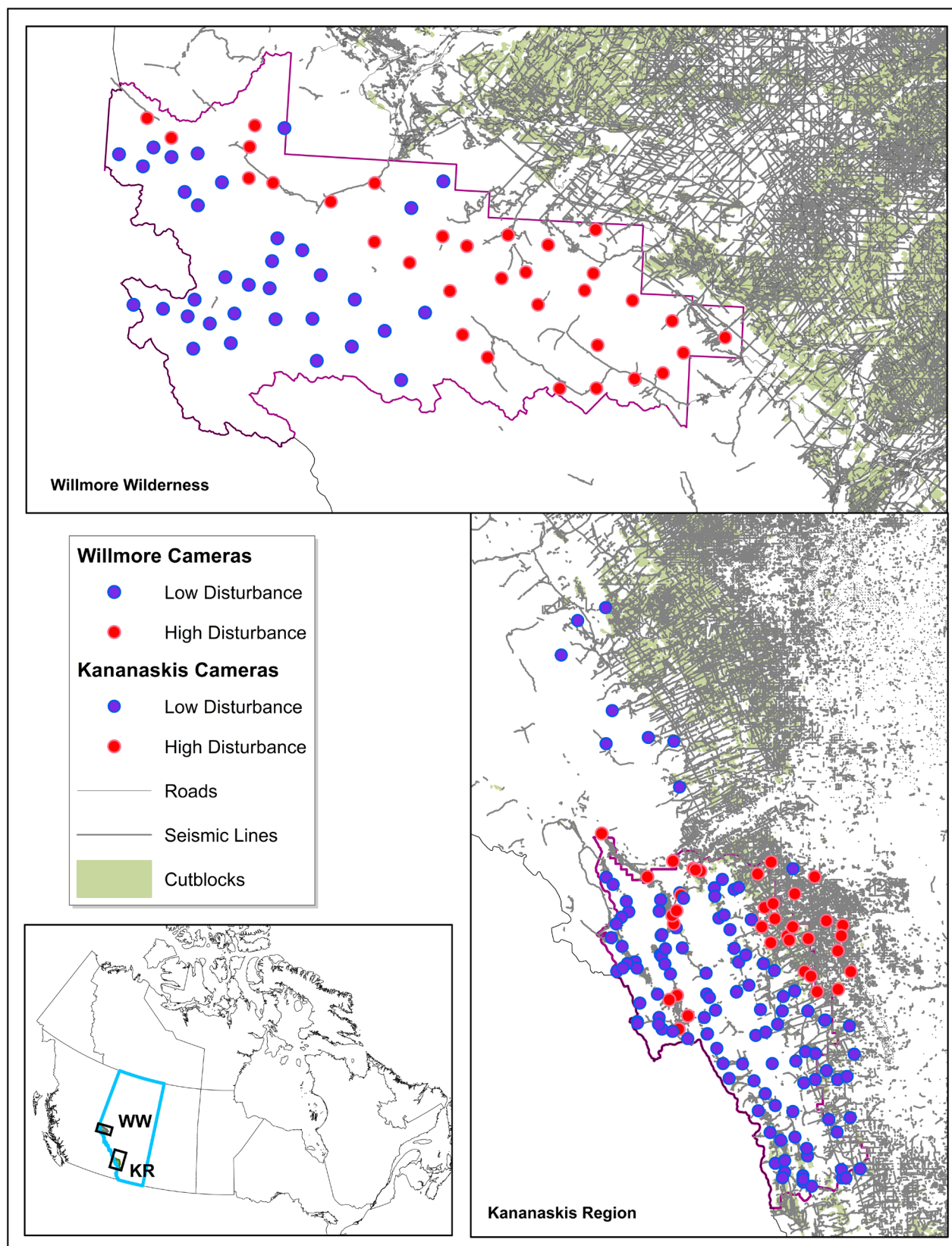
Figure 1. Camera trap locations in the Willmore Wilderness (WW) and Kananaskis Country (KR) study areas of Alberta, Canada. Camera sites were classed as 'high' (red) versus 'low' (blue) disturbance sites relative to the degree of disturbance within each study region. In the WW, 'high' disturbance sites are those with a linear feature footprint of 0.1-5% within a 5000 m radius buffer, while 'low' disturbance sites contain no linear features. Given the prevalence of linear features across the KR, 'high' disturbance sites are those with >2% area covered by linear features, and 'low' disturbance sites as those with <2%..

Activity shifts in response to anthropogenic landscape change

To test our hypothesis that species shift diel activity patterns in response to human landscape disturbance, we compared carnivore species' activity curves between 1) the low disturbance WW and high disturbance KR study area, and 2) camera-sites in areas of low versus high levels of landscape disturbance within each study area. For all wildlife images we recorded the date, detection time, camera site ID and species. To remove any temporal autocorrelation between consecutive photographs we defined a single and independent capture event as all photographs of a particular species within a 30-min time period (Rovero and Zimmermann 2016). If two or more individuals of the same species were captured within a single image, we treated the event as a single data point. We transformed the raw observations of clock-time for each detection to a relative solar time corresponding to the position of the sun in the sky (sensu Nouvellet et al. 2012) to remove the influence of day-length variation over the sampling period. We standardized image timestamps to a 12-h day length with sunrise at 06:00h and sunset at 18:00h to facilitate ecological interpretation (Rheingantz et al. 2016).

Pooling all observations for each species within each study area, we applied non-parametric kernel density estimation methods described by Ridout and Linkie (2009) to generate activity curves using the package *overlap* (Meredith and Ridout 2014) in R (ver. 3.6.1; <www.r-project.org>). Density of activity (y-axis) uses a von Mises kernel and corresponds to the circular distribution of recorded capture times on the 24-h x-axis. Using the same kernel density approach, we calculated an overlap term between each species' activity curves for the two study areas to test for activity shifts between the high disturbance KR and low disturbance WW. This overlap coefficient (Δ) represents the shared area under the two density functions and ranges from 0 (no overlap) to 1 (complete overlap). We expected a low Δ value if species altered their activity patterns in relation to regional-scale human footprint. On the basis of Ridout and Linkie's (2009) overlap coefficient simulation study, we used the Δ_4 estimator if the smaller sample had more than 75 observations and applied a smoothing parameter of 1, otherwise we used the Δ_1 estimator and a 0.8 smoothing parameter recommended for smaller sample sizes (Ridout and Linkie 2009, Meredith and Ridout 2014). We used 10 000 bootstrapped samples from each distribution to estimate 95% confidence intervals of Δ for each comparison. Lastly, to determine whether observed activity shifts represented statistically significant differences, we applied the nonparametric Mardia–Watson–Wheeler (MWW) test (Batschelet 1981) using the R package *circular* (Agostinelli and Lund 2013). This test compares the mean and variance of the two activity distributions, and requires a minimum of ten elements in each sample (Batschelet 1981). We therefore limited our analyses of activity shifts to species for which at least ten independent detections were observed.

To test our hypothesis that carnivore species shift activity patterns in response to disturbance at the scale of camera-sites,

we repeated the above-mentioned analyses on species data separated within each study area into photographs that were captured at camera sites with high versus low levels of landscape disturbance in the surrounding area. We quantified human landscape disturbance using digital map inventories (Alberta Biodiversity Monitoring Institute, Human Footprint Map 2012, <https://abmi.ca/home/old-data/gis-data/human-footprint-download.html>). Linear features were the predominant landscape development feature present in the WW and the most widespread anthropogenic feature in the KR, so we used these as proxies of overall landscape disturbance. In the WW, seismic lines from petroleum exploration were the only linear feature (Fisher and Burton 2018) whereas in the more disturbed KR, this included a variety of anthropogenic linear disturbance features such as roads, recreational trails and industrial cutlines (e.g. seismic and power lines). Based on the available human footprint data, we calculated the percent cover (% area) of linear features at a 5000-m buffer around each camera site (Fisher et al. 2011) by merging all anthropogenic linear features into a single 'linear disturbance' variable. We pooled camera sites within each landscape into 'high' and 'low' disturbance categories specifically in relation to the degree of disturbance within the study landscape. For the WW, we therefore classified 'high' disturbance sites (n = 32) as those encompassing linear features (0.1–5% area), and 'low' disturbance sites (n = 34) as those with no linear features. As all camera sites within the KR exhibited some level of linear footprint within a 5000-m radius, we classified sites into 37 'high' disturbance (>2% area) sites and 120 'low' disturbance sites (0.1–2% of area). We visually identified this threshold by examining the distribution of all linear disturbance data across our camera sites, identifying a natural break at about 2% for total percent of human linear footprint within a 5000-m circular buffer (Supplementary material Appendix 1 Fig. A1). Given the low levels of landscape disturbance across the WW, 'high' disturbance sites in this landscape would be considered 'low' in the KR. However, our intent in these site-scale analyses was not to compare pooled 'high' versus 'low' disturbance camera sites between the WW and KC. Instead, we sought to test the relative degree of species' activity shifts within each study region, in response to an increasing human footprint. We selected a 5000-m radius buffer based on the species with the largest home range size – wolverine – the spatial scale at which habitat best explains variability in wolverine distribution (Fisher et al. 2011).

Influence of anthropogenic landscape change on carnivore temporal niche partitioning

To test our hypothesis that human-mediated landscape disturbance alters temporal niche partitioning among carnivore species, we modelled interspecific activity overlap against multiple variables hypothesized to influence temporal overlap, including linear feature density (Table 1) following a similar approach to Wang et al. (2015). We calculated Δ between spatially co-occurring species-pairs at camera sites. Δ is sensitive to sample sizes used to generate activity curves (Meredith

Table 1. List and description of anthropogenic, natural land cover and community variables hypothesized to explain temporal niche partitioning between marten and wolverine in the Rocky Mountains of Alberta.

Model set	Model variables	Hypothesis: marten and wolverine temporal overlap (Δ) is predicted by
Null hypotheses	Wolverine	Number of wolverine events
(Sample size sensitivity)	Marten + Wolverine	Number of marten and wolverine events
Natural land cover	Forest + Wolverine	Forest cover (coniferous, deciduous and mixed combined) and wolverine events
(Perceived riskiness of forested versus open landscapes)	Shrub + Wolverine	Shrub cover and wolverine events
	Open + Wolverine	Natural open cover (herbaceous and barren ground combined) and wolverine events
Anthropogenic landscape disturbance	Seismic + Wolverine	Anthropogenic linear features (seismic lines) and wolverine events
Apex predator co-occurrence	Wolf + Wolverine	Presence/absence of wolf and number of wolverine events
Competitor co-occurrence	Fisher + Wolverine	Presence/absence of fisher and number of wolverine events

and Ridout 2014), with increasing error and decreasing mean Δ with decreasing species' detections (Lashley et al. 2018). To balance mitigating Δ bias introduced by low sample sizes (Lashley et al. 2018) while maintaining a sufficient number of camera sites to model sympatric species' activity overlap in relation to multiple landscape and community parameters, we restricted activity overlap estimation to sites where we observed a minimum of 15 independent detections of both species, a balance between number of sites and the number of observations at each site. This limited our analysis to wolverine and marten overlap within the WW only (Supplementary material Appendix 1 Table A4). Fortunately, this is a model species pair to study as their diets and niches overlap and commonly co-occur across wolverine ranges (Heim et al. 2017).

We included candidate models of natural land cover characteristics specifying open versus forested landscapes, which we hypothesized might influence perceived predation risk and may be particularly relevant to smaller mesocarnivores such as marten. As spatial co-occurrence with predators or competitors may also influence species' activity patterns, we included the presence of wolf and fisher within candidate models. Fisher are an ecologically similar competitor of marten (Fisher et al. 2011), and co-occur with wolverine in the WW.

Wolverine detections were the most limiting in our analysis, with a mean of 29 wolverine (SD 14) across selected sites (Supplementary material Appendix 1 Table A4). To account for bias in Δ introduced by smaller sample sizes (Lashley et al. 2018) and isolate the influence of ecological variables on wolverine–marten overlap, we included number of wolverine detections in each candidate model as an additional covariate. Our null hypothesis models were represented by the number of wolverine and marten detections, indicating activity overlap is influenced in part by sample sizes used to generate activity curves.

We modelled overlap coefficients against natural land cover, linear feature density and heterospecific occurrence using a beta regression model appropriate for response variables bounded by the standard unit interval, i.e. $0 < y < 1$ (Ferrari and Cribari-Neto 2004). We used Akaike's information criterion corrected for small sample size (AICc) to assess

model weights (wi) and ranked resulting candidate models using AICc and wi (Burnham and Anderson 2002). The models with the highest AICc weights were interpreted as the best-supported models describing marten–wolverine temporal overlap, and support for their corresponding hypotheses.

Results

Carnivore species' activity shifts observed between a low versus high disturbance landscape

Multiple carnivore species shifted their activity patterns between the low versus high disturbance landscapes (Fig. 2). Of the eight carnivore species compared between the WW and KR (see Supplementary material Appendix 1 Table A1 for species' detection summaries), we observed significant differences in activity distributions for coyote (MWW test, $\chi^2 = 6.90$, df = 2, $p < 0.05$), marten ($\chi^2 = 58.63$, df = 2, $p < 0.001$) and stoat ($\chi^2 = 9.08$, df = 2, p-value < 0.05). Coyotes in the low-disturbance WW peaked activity around the crepuscular period, but were indiscriminately active at all hours on the KR landscape. Marten in the low-disturbance WW selected strongly for the nocturnal period, with a sharp activity decline during the diurnal hours. In contrast, marten in the high-disturbance KR selected for the diurnal period. Stoat were largely nocturnal across both the WW and KR, but the WW population had higher diurnal activity compared to the KR. The KR wolf population reduced diurnal activities and compensated with increased activity during the nocturnal hours, though this failed the test for significance ($\chi^2 = 4.0877$, df = 2, p-value = 0.13).

Carnivore species' activity shifts observed in response to site-specific landscape disturbance

Within the WW landscape, with its much lower proportion of landscape disturbance, carnivore species nonetheless shifted activities in relation to site-scale disturbance (Fig. 3). We captured sufficient detections (n > 10) to apply the MWW test for five carnivore species (see Supplementary
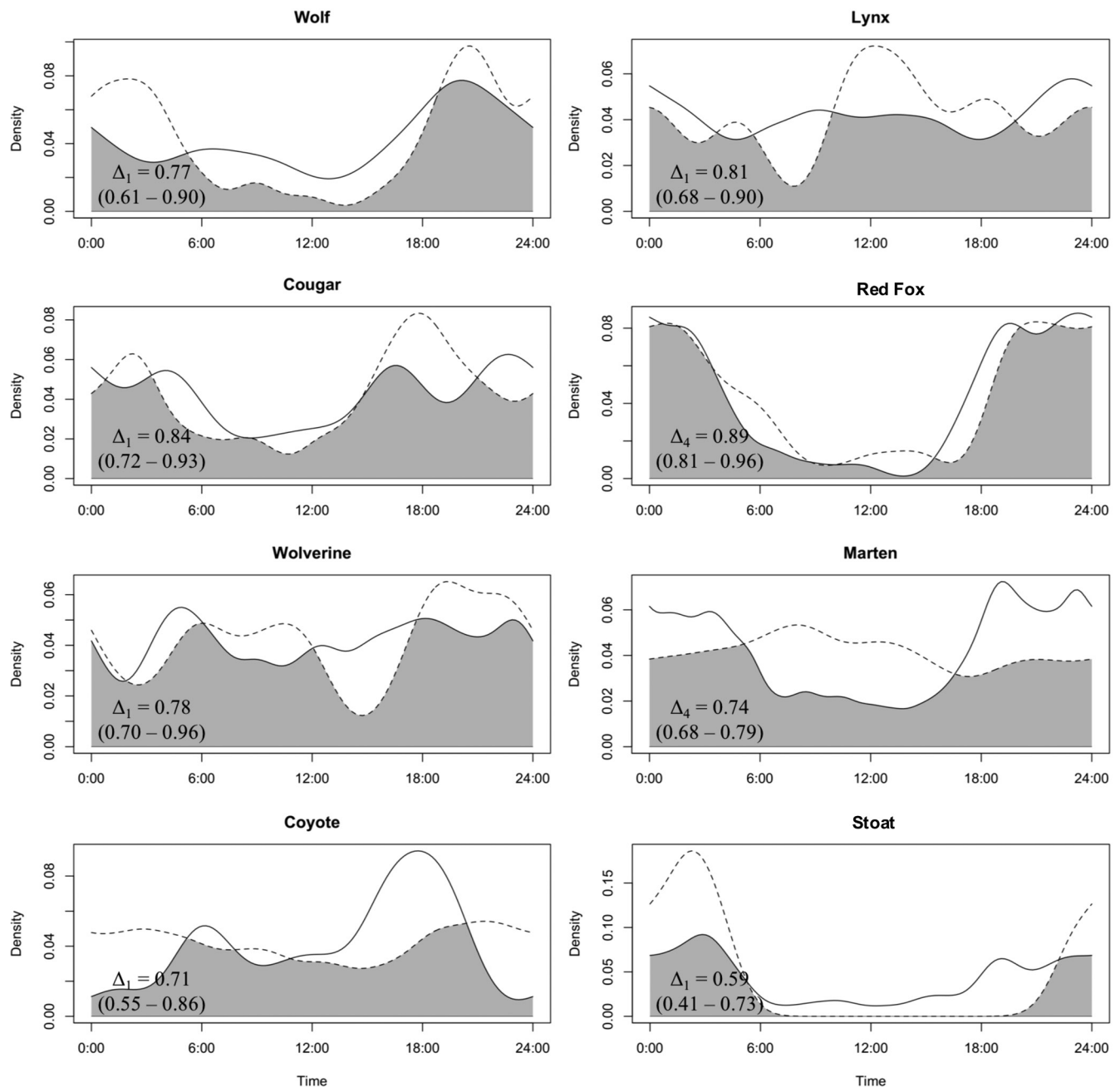
Figure 2. Kernel density estimates representing diel activity curves and temporal overlap of eight carnivore species between the Willmore Wilderness (WW; solid line) and Kananaskis Region (KR; dashed line) study area. Periods of activity overlap is represented by the coefficient of overlap (Δ; denoted in grey) accompanied by the 95 % confidence intervals in parentheses; Δ = 1 represents no activity shift between the WW and KR while Δ = 0 represents complete activity shift.

material Appendix 1 Table A2 for species' detection summaries). Significant activity shifts between low versus high disturbance camera sites occurred for marten ($\chi^2 = 13.39$, df = 2, p-value <0.01), which increased diurnal activities at camera sites with high levels of linear disturbance. Wolves selected strongly for the diurnal period at camera sites with

low levels of disturbance, while at high disturbance camera sites, wolves were highly selective for the nocturnal hours. However, the low number of wolf detections in the WW (<10 wolf detections at low disturbance sites; Supplementary material Appendix 1 Table A2) precluded application of statistical tests of significance.
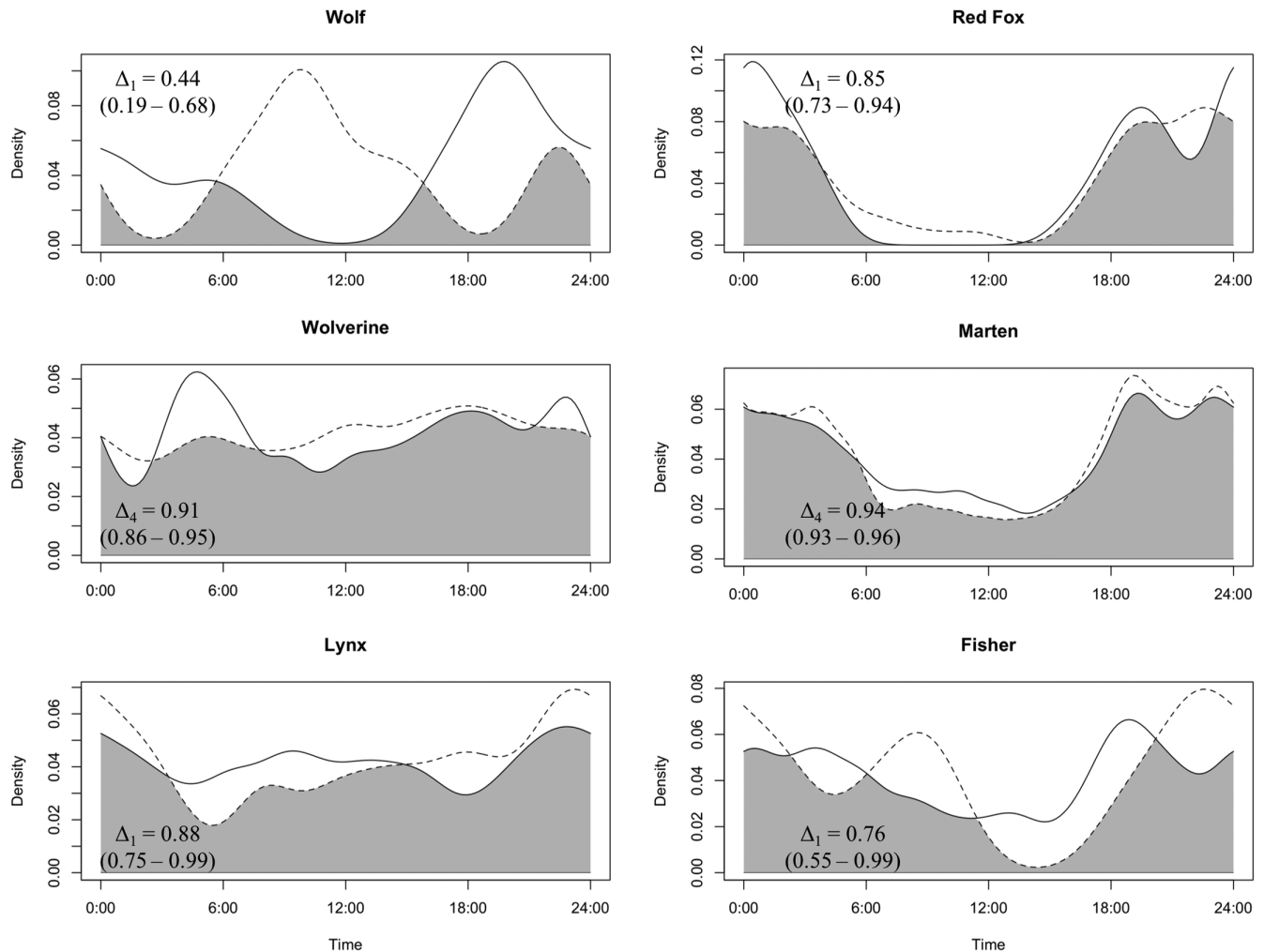
Figure 3. Diel activity curves and temporal overlap of carnivore species between high (solid line) versus low (dashed line) levels of linear disturbance features at the camera-site level in the Willmore Wilderness. Activity overlap (i.e. periods of no change in activity) is represented by the coefficient of overlap (Δ; denoted in grey) accompanied by the 95% confidence intervals in parentheses.

Within the more disturbed KR landscape, carnivore species also shifted activity patterns in relation to degree of linear disturbance (Fig. 4). We captured a minimum of ten detections for five carnivore species, including cougar, marten, coyote, bobcat and fisher (Supplementary material Appendix 1 Table A3). Similar to the WW, marten significantly shifted activities between camera sites of low versus high levels of linear disturbance ($\chi^2 = 6.61$, df = 2, p-value < 0.05), increasing diurnal activities at high disturbance camera sites. Bobcat activity also shifted significantly in response to site-scale linear disturbance ($\chi^2 = 10.61$, df = 2, p-value < 0.01), sharply increasing nocturnal and pre-dawn activities at high disturbance sites. Coyote increased diurnal activity at low disturbance sites ($\chi^2 = 15.64$, df = 2, p-value = 0.06) compared to high disturbance sites. Although the MWW-test revealed no statistically significant shifts in cougar activity, cougars at low disturbance sites revealed a strong bimodal pattern peaking at

dusk and shortly after midnight, which was absent at camera sites in high disturbance areas.

Influence of anthropogenic landscape change on carnivore temporal niche partitioning

Our candidate model selection did not support our hypothesis that anthropogenic landscape change influences wolverine–marten activity overlap in the WW. Instead, total forest cover and wolverine sample size were retained in the best-supported model (Table 2).

Activity overlap between wolverine and marten decreased significantly with increasing forest cover (Table 3; Supplementary material Appendix 1 Fig. A2). While wolverine sample size significantly increases ΔAIC, the addition of land cover features improved our ability to predict wolverine–marten activity overlap.
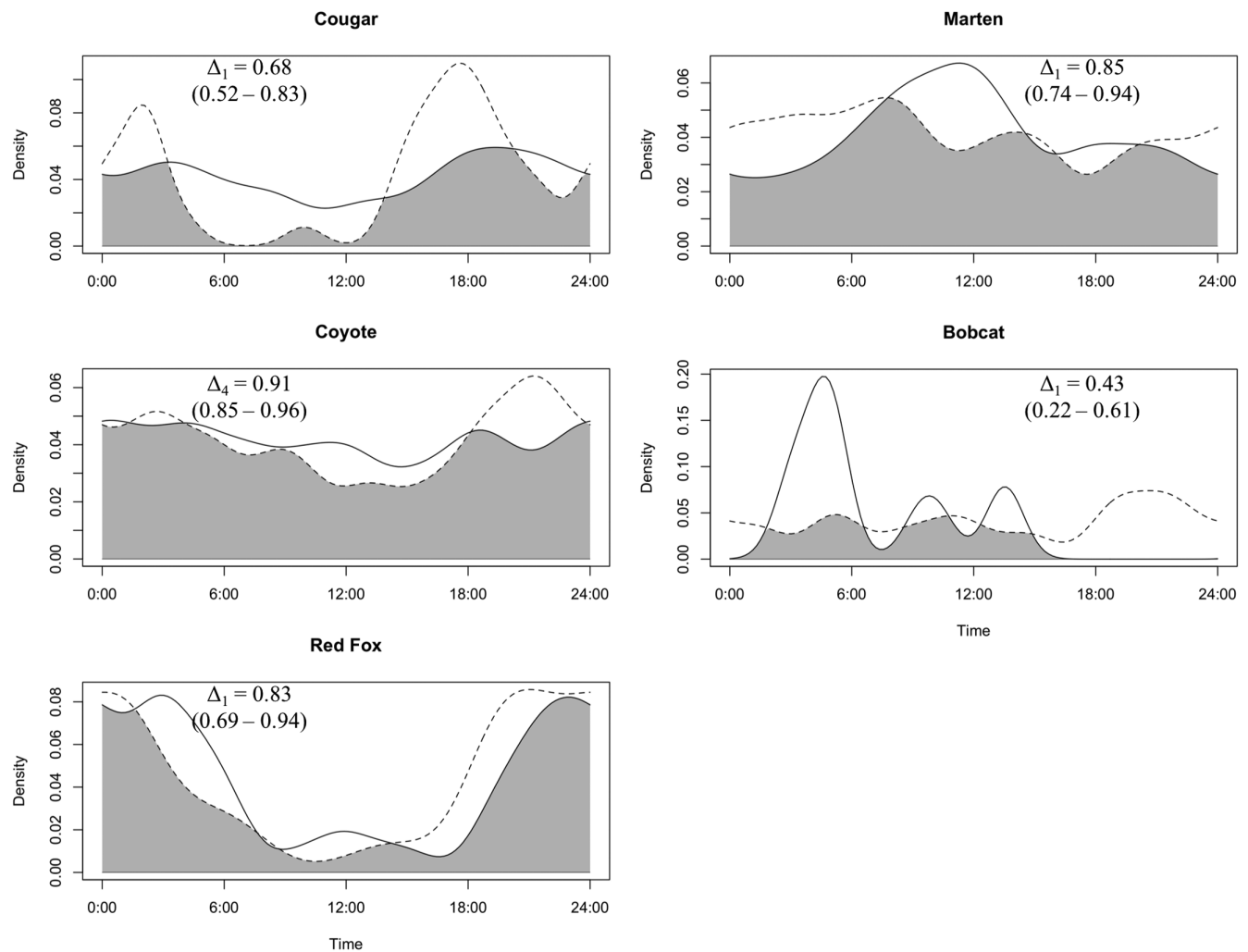
Figure 4. Diel activity curves and temporal overlap of carnivore species between high (solid line) versus low (dashed line) levels of linear disturbance features at the camera-site level in Kananaskis Region. Activity overlap (i.e. periods of no change in activity) is represented by the coefficient of overlap (Δ; denoted in grey) accompanied by the 95% confidence intervals in parentheses.

Discussion

Anthropogenic landscape change alters carnivore species' diel activity patterns but not always with a shift toward nocturnality as might be predicted. Instead, varied responses within the carnivore guild suggest that behavioural shifts may manifest as both direct and indirect responses to human disturbance,

with apex predators and mesocarnivores responding differently. Mesocarnivore species shifted activity patterns in relation to landscape-level anthropogenic disturbance, with consistent shifts in response to site-level disturbance. Coyote broadened their activity distribution across the diel cycle, and marten increased diurnal activity in relation to anthropogenic landscape change. Wolf, as apex predators in our study

Table 2. Wolverine and marten temporal overlap in response to natural landscape features, anthropogenic disturbance and community characteristics. Model 3 is the best-supported.

Model set	Model no.	Model variables	AICc score	ΔAICc	AICc weight
Natural land cover	3	Forest+Wolverine	−41.82	0	0.53
Top predator co-occurrence	8	Wolf+Wolverine	−39.71	2.11	0.19
Natural land cover	5	Open+Wolverine	−38.85	2.97	0.12
Natural land cover	4	Shrubs+Wolverine	−42.20	2.51	0.10
Null hypothesis	1	Wolverine	−36.90	4.92	0.05
Competitor co-occurrence	7	Fisher+Wolverine	−35.75	6.07	0.03
Null hypothesis	2	Marten+Wolverine	−34.59	7.22	0.01
Landscape disturbance	6	Seismic+Wolverine	−33.96	7.86	0.01

Table 3. Parameter estimates of top model predicting activity overlap between marten and wolverine.

	Estimate	SE	p-value
(Intercept)	1.48	0.44	< 0.001
Forest	−1.74	0.60	0.004
Wolverine	0.019	0.007	0.008

region, appeared to decrease diurnal activities and compensated with increased nocturnal activity peaks. For mesocarnivore species, indirect drivers – such as the cascading effects of disturbance on apex predators – better explain behavioural changes over the diel cycle than direct measures of anthropogenic landscape disturbance.

Apex- and meso-carnivore responses to anthropogenic landscape change

Apex predators and mesocarnivore species appear to respond differently to human-mediated disturbance. Wolf activity may suggest a shift towards nocturnality in relation to landscape disturbance, and although this relationship was not significant, low sample sizes could not provide a definitive significance test and so we cannot state whether this hypothesis was supported or not. Logically, a shift should be expected; large carnivores are subject to a 'landscape of fear' (Darimont et al. 2015, Oriol-Cotterill et al. 2015) associated with mortality from humans. Wolves, which are culled throughout Alberta to reduce mortality in endangered woodland caribou (Hervieux et al. 2014), are no exception. Reduced diurnal activity of wolves in the KR might be expected as a response to increased likelihood of human encounters during the diurnal period, as has been observed by others in this region (Hebblewhite and Merrill 2008). Furthermore, Theuerkauf's (2009) meta-analysis of wolf behaviour throughout the Holarctic identified public road density as one of the best covariates explaining increased nocturnal activity in wolves. This is consistent with our observations of increased wolf nocturnality at camera sites containing high levels of linear disturbances in the WW, lending further confidence to this observation despite the low sample sizes and lack of significance.

Although disturbance-induced activity shifts towards nocturnality in large carnivores appears to be a global phenomenon (Gaynor et al. 2018), our results indicate that behavioural responses of mesocarnivores on disturbed landscapes differ substantially from those seen in apex carnivores and may be driven by more complex and indirect processes. Activity shifts in the mesocarnivore guild manifested as bidirectional and complex responses, probably due to the indirect and cascading effects of disturbance on apex predators. In contrast to other studies reporting increased nocturnality in coyote in relation to human disturbance (Wang et al. 2015, Reilly et al. 2017), coyote in the KR region broadened their temporal niche space into both the diurnal and nocturnal periods. Such shifts towards cathemerality in coyote may be a response to the increased nocturnality in wolves, a

main competitor and predator of coyotes (Berger and Gese 2007). Shores et al. (2019) observed increased coyote activity during dawn, day and dusk in areas where they overlapped with wolf. Coyote activity expansion may therefore be a response to a combination of interplaying processes involving both behavioural and numerical release from wolf predation, as well as anthropogenic resources. Observed expansion of coyote realized niche space on disturbed landscapes corroborates positive correlation between coyotes and human disturbance (Toews et al. 2018) providing evidence that human-tolerant species benefit from disturbance-mediated behaviours in apex predators. This 'behavioural mesocarnivore release' cascades down trophic links from apex predators to subdominants, and we contend this may be a component mechanism of widely observed mesocarnivore population releases: more time to forage translates into more resources required and greater fitness (Brown et al. 1999, Clinchy et al. 2013, Allen et al. 2014).

Disturbance-mediated responses within dominant carnivores may also alter the 'landscape of fear' for the broader mesocarnivore community due to changes in competitive pressures and predation risk. Generally observed as selecting for the nocturnal period (Drew and Bissonette 1997), marten shifted towards increased diurnal activity in the disturbed KR. Subdominant mesocarnivore species such as marten may be forced to shift activities into the diurnal period due to cascading activity shifts within both apex carnivores and dominant mesocarnivore competitors which enhance predation and competitive pressures during the nighttime. Imposed activity shifts into 'safe' time periods could incur ecological and physiological fitness costs on subdominant carnivores, such as decoupling from preferred prey species or activity during suboptimal light and temperature conditions (Azlan and Sharma 2006, Brook et al. 2012). Over time, such negative fitness consequences may manifest as sublethal effects leading to population declines and species' range contractions on human modified landscapes.

Caveats

A variety of caveats are attached to our ecological inference from the observations for species' activity shifts in relation to human landscape disturbance. Firstly, recent studies (Rowcliffe et al. 2014, Lashley et al. 2018) identify considerable error arising from activity curve estimation using low sample sizes. This is reflected in the large 95% confidence intervals for some of our comparisons of Δ of species' activity curves between high versus low disturbance landscapes and camera sites. However, this may also be the product of interindividual variation in diel activity patterns. Secondly, Δ is a purely descriptive metric that does not provide a threshold value delimiting whether two activity curves might be significantly different. For those species' whose activity shifts did not reach statistical significance according to the MWW-test, we cannot conclude whether the observed differences in activity curves in relation to disturbed landscapes or camera sites represents both a statistical and ecologically relevant

response. Lastly, it is possible that some of the observed activity shifts between the disturbed and protected landscapes may be epiphenomena manifesting from regional differences between the WW and KR, as opposed to differing levels of human footprint. However, as these two regions share very similar landscape features and that the observed activity shifts for multiple species (e.g. wolf, coyote and marten) occurring at the landscape level were replicated at the camera-site level, we contend this provides evidence that the observed activity shifts most likely manifested as a response to human disturbance.

Challenges and opportunities for quantifying shifts to temporal niche partitioning

Sample size limited our ability to test hypotheses about disturbance-mediated disruption of temporal niche partitioning between the full suite of sympatric carnivores extant in the Canadian Rocky Mountains. Models testing hypotheses of activity overlap between wolverine and marten were very sensitive to the number of site-scale detections (Table 3). This indication of sample size bias highlights that while Ridout and Linkie's (2009) coefficient of overlap provides a useful metric quantifying similarity of activity curves, it remains highly sensitive to the sample sizes used to generate activity distributions. Although ours is one of the most spatially extensive sampling efforts in mountain Canada, with continuous sampling for several months or even years; and although we focused on our two most frequently observed species in the WW, marten (n = 9939) and wolverine (n = 993), where detection probabilities via camera are very high (Fisher and Bradbury 2014); only 23 out of the 66 camera sites yielded 15 detections for each species. Recent studies recommend 100 detections for accurately estimating species' activity curves and overlap (Rowcliffe et al. 2014, Lashley et al. 2018), with mean overlap increasing and overlap error decreasing rapidly with an increasing number of detections, until an asymptote near 100 detections. While we included detection sample size of in our models to account for this effect, observed bias and error arising from the low sample sizes likely hampered our ability to disentangle biological drivers of interspecific activity overlap.

Furthermore, the comparatively low levels of disturbance across the WW landscape and the small increase in diurnality in marten at 'high' disturbance sites possibly did not yield strong enough disturbance signals and resultant effect sizes to detect a statistically significant influence of landscape disturbance on activity overlap. Such an effect may have also been more easily detected on the KR landscape, which encompasses a much more significant gradient of disturbance. However, limitations imposed by site-level spatial sympatry of carnivore species precluded comparison of temporal overlap between co-occurring species across a sufficient number of camera sites to model against multiple environmental covariates. Limited site-scale sympatry may also indicate that spatial dynamics are at play whose effects exceed the temporal

responses we sought to test in this study. We recommend that future studies attempting to evaluate drivers of activity overlap and temporal niche partitioning develop study designs explicitly focused on maximizing site-level sympatry between species of interest and over timespans sufficiently long enough to gather large species' detections datasets robust against the implicit biases in kernel density estimation techniques.

Implications of altered carnivore activity patters on disturbed landscapes

Ultimately, human-mediated landscape change creates winners and losers in ecological systems by conferring competitive advantages to some species over others, leading to altered community assemblages on disturbed landscapes (McKinney and Lockwood 1999, Heim et al. 2019). Such processes are likely at play in the KR region, which experiences broad and varied human activity and landscape change. Our results indicate coyotes are benefitting from a broadened realized temporal niche space on disturbed landscapes, and this may translate into numerical and spatial expansion of coyote populations. Indeed, previous studies have observed a wide distribution of coyotes across the KR and Alberta (Heim et al. 2017, Toews et al. 2018). Human-tolerant species may benefit from disturbance-mediated avoidance behaviour and suppression of apex predators, with resultant spatial expansion and numerical increase reflecting exploitation of a novel temporal niche territory and release from top–down control.

Niche and population expansion of a dominant mesocarnivore may have significant implications on the carnivore guild structure and responses in the broader ecological community. Increased activity overlap with both diurnal and nocturnal prey in coyote may augment predation pressures on the small mammal community and also result in increased exploitative competition between mesocarnivore species. For example, Smith et al. (2018) observed an increase in dietary overlap between foxes and coyotes in areas of high human disturbance, where coyote were also observed to shift into the nocturnal niche space of foxes (Wang et al. 2015). Coyote activity expansion may also enhance interference competition with other mesocarnivores due to increased temporal overlap and potential for direct interactions. Although we could not directly test for the impacts of anthropogenic landscape change on activity overlap between coyotes and other mesocarnivores, coyote activity expansion across the diel cycle would be expected to also potentially compromise mechanisms of temporal niche partitioning within the mesocarnivore community. Enhanced competitive pressures arising from interference and exploitation of shared prey items may result in the spatial displacement and population declines of subdominant mesocarnivores on disturbed landscapes where dominant and disturbance-tolerant carnivores, such as coyotes, benefit from a larger realized temporal niche.

Over time, this may lead to major shifts in the carnivore community assemblage and resultant responses in the prey community as well.

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Supplementary material (available online as Appendix oik-07251 at <www.oikosjournal.org/appendix/oik-07251>). Appendix 1.