

EVALUATING THE IMPACTS OF HUMAN-MEDIATED DISTURBANCES ON
SPECIES' BEHAVIOUR AND INTERACTIONS

by

Sandra Frey

B.Sc., University of Victoria, 2013

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ABSTRACT

Developing effective conservation strategies requires an empirical understanding of species' responses to human-mediated disturbances. Observable responses are typically limited to dramatic changes such as wildlife population declines or range shifts. However, preceding these obvious responses, more subtle responses may signal larger-scale future change, including changes in species' behaviours and interspecific interactions. Disturbance-induced shifts to species' diel activity patterns may disrupt mechanisms of niche partitioning along the 24-hour time axis, altering community structure via altered competitive interactions. I investigate the main questions and methods of analysis applicable to camera-trap data for furthering our understanding of temporal dynamics in animal communities. I apply these methods to evaluate the impacts of human-mediated disturbance on species' activity patterns and temporal niche partitioning in two separate studies, focusing on responses in the mammalian carnivore community. In the Canadian Rocky Mountain carnivore guild, species alter diel activities in relation to anthropogenic landscape development, although these shifts may be manifesting through indirect biotic effects instead of direct responses to human disturbance. Mesocarnivore species on a mixed-use landscape featuring anthropogenic land-use and introduced free-ranging dogs (*Canis familiaris*) shift activities in relation to spatiotemporal dog activity. Native carnivores partition diel activities differently on open landscapes of enhanced predation risk but abundant prey resources. Detecting shifts in species' temporal behaviours and competitive interactions may enable identification of potential precursors of population declines and shifting community assemblages, providing us with opportunities to pre-emptively manage against such biodiversity losses on human-modified landscapes.

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Chapter 1

Introduction

The human footprint extends into nearly every last corner of our planet (Sanderson et al. 2002). From densely populated settlements to remote road networks and natural resource industries, our impacts across landscapes and ecosystems are truly global (Hoekstra 2008). Today, we live in a geological epoch characterized by a human-dominated planet and profound anthropogenic landscape change (Steffen et al. 2007). In response to the cumulative impacts from human activities, global biodiversity is in rapid decline (Butchart et al. 2010; Dirzo et al. 2014). While human-driven climate change will have significant impacts on biodiversity in the twenty-first century, land-use remains the single most important projected driver of global biodiversity change (Sala et al. 2000). And with an ever-increasing human population extending anthropogenic disturbances further into wildlife habitats (Venter et al. 2016), effectively managing against current and future ecological losses is of critical global conservation concern.

Although anthropogenic landscape change is directly implicated with wildlife population declines and species' extirpations (Gibbon et al. 2000; McKinney 2006; Dirzo et al. 2014), mechanisms of biodiversity loss aren't always as simple as habitat loss. Beyond habitat conversion and the spatial exclusion of wildlife on developed landscapes, our presence and activities also impose subtle and non-lethal disturbances on ecological communities (Frid and Dill 2002). These sublethal effects may manifest through fear-based avoidance behaviours, short- and longer term stress, and negative fitness responses (Sheriff et al. 2009), reducing long-term population sustainability on human-modified landscapes. Furthermore, disturbance-induced changes to species' behaviours and resource-use may also impact competitive interactions between sympatric species (e.g. Wang et al. 2015; Smith et al. 2018), differentially conferring

competitive advantages to some species over others. Combined, these subtle processes may manifest as significant changes in species' assemblages and community structure over larger spatial and temporal scales.

Despite a vast literature documenting spatial shifts and range contractions in wildlife populations in response to anthropogenic disturbance (Karanth and Nichols 1998; Laliberte and Ripple 2004; Ceballos et al. 2017), significantly less research has evaluated sublethal responses to human-associated disturbances. Such responses may include altered species' diel behaviours and patterns of temporal niche partitioning over the 24-hour cycle. A species use of time as a resource is an important feature of its ecology (Schoener 1974), while segregation along the temporal niche axis is an important mechanism facilitating stable coexistence within diverse assemblages of ecologically similar species (Kronfeld-Schor and Dayan 2003; Di Bitetti et al. 2009; Monterroso et al. 2014). Understanding how human disturbances impact species' diel behaviours and patterns of temporal niche partitioning may provide a mechanistic understanding of the processes driving wildlife declines and community restructuring on human modified landscapes.

Remote camera-trap technology offers important opportunities for extending insight into species' behaviours and interactions, including the impacts of human-mediated disturbances. From the early days of trip-wire photography to modern infrared cameras, camera-trap technologies have been in use for over a century (Rovero and Zimmermann 2016). Most popularly used for inventorying biodiversity, studying species' distributions, and estimating population density, camera-trap data also lend themselves to behavioural studies (O'Connell et al. 2010; Burton et al. 2015; Steenweg et al. 2017). Griffiths and van Schaik (1993) were among the first to recognize their potential for studying animal activity patterns, and a growing body of literature now focuses on time-stamped camera-trap data to address unresolved questions regarding species' activities and interactions over the diel cycle (Frey et al. 2017). Recently, an increasing number of studies report on altered species activity patterns in relation to anthropogenic disturbance (Carter et al. 2012; Ohashi et al. 2013; Reilly et al. 2017; Ngoprasert et al. 2017), although the resultant impacts on species' spatiotemporal interactions largely remain untested (but see Wang et al. 2015).

In this thesis, I endeavor to further our understanding of sublethal anthropogenic disturbance impacts on wildlife communities by testing for altered species' activity patterns and interactions over the diel cycle. I discuss technological and analytical advances for studying species activity shifts and resultant changes to community-level

temporal niche partitioning using camera data. I apply these methods to test the effects of human disturbances on species' diel activity and interspecific temporal niche partitioning. Focusing on responses within the carnivore community, I investigate subtle and indirect species' responses to human-associated disturbances, including anthropogenic land-use and development, as well as domestic dog (*Canis familiaris*) activity.

Thesis Overview:

For the second chapter of this thesis, I review the applications and challenges of using camera trap technology to study temporal patterns in species' activities and niche partitioning. A large variety of analytical approaches have been applied to camera-trap data to ask questions about species activity patterns and temporal overlap among heterospecifics, including:

- (i) How do species structure their activity over the diel cycle?
- (ii) How do abiotic and biotic variables influence species' activity patterns?
- (iii) How do species partition their activities along the temporal niche axis?
- (iv) How do biotic and abiotic variables influence temporal niche partitioning?

Despite the many advances for describing and quantifying the temporal aspects of species activities and interactions, few existing studies explicitly test how multiple interacting biotic and abiotic variables may influence species' activity and capacity to segregate along the temporal niche dimension. I discuss how combined spatial and temporal analyses will improve our understanding of changes to species distributions and activities, and how anthropogenic activities and landscape changes may alter competitive interactions among species.

In the third chapter, I investigate the impacts of anthropogenic landscape disturbance on species' activity patterns and temporal niche partitioning in the Canadian Rocky Mountain carnivore guild. Applying kernel density estimation on species' detection histories from camera trap images collected across two regions encompassing a large gradient of human footprint, I test for carnivore species' activity shifts (1) between disturbed and undisturbed landscapes, and (2) in relation to site-scale disturbance, to determine species' behavioural responses to local and landscape-scale

disturbance. To evaluate the influence of human disturbance on species' interactions through altered temporal niche partitioning, I model activity overlap between co-occurring carnivore species in relation to carnivore community composition and landscape characteristics, including anthropogenic landscape development.

I observe multiple carnivore species shifting activity patterns between disturbed and undisturbed landscapes and camera sites. Detecting effects of landscape disturbance on activity overlap between spatially co-occurring species is highly sensitive to site-level detection sample sizes, and I therefore recommend future studies seek to maximize species' co-occurrence data across disturbed landscapes to unequivocally disentangle such effects. Results from this study indicate that mesocarnivores and apex predators respond differently to human landscape change, suggesting that anthropogenic disturbance may confer competitive advantages to some species over others.

For the fourth chapter, I apply similar methods of kernel density estimation of species' activity patterns and temporal overlap to test for wildlife responses to a different type of human-associated disturbance: domestic dogs (*Canis familiaris*). I test for altered behaviours and interactions in the native mesocarnivore community in response to the distribution and activity of free-ranging dogs on a mixed-use landscape featuring ex-urban developments, resource extraction, and pockets of protected forests. My findings indicate that coyote increase diurnal activity in response to nocturnal dog activity during summer. I also demonstrate that mesocarnivores partition activities differently on open landscapes with reduced vertical escape cover but abundant in prey resources. This highlights potential considerations for the impacts of land-use practices such as agricultural and logging on species' interactions and community structure.

The final chapter summarizes the conclusions drawn from these studies. I discuss potential improvements and next steps for refining our understanding of the impacts of human-mediated disturbances on species' ecology and competitive interactions.

Chapter 2

Investigating animal activity patterns and temporal niche partitioning using camera trap data: Challenges and Opportunities

Frey, S., Fisher, J. T., Burton, A. C. and Volpe, J. P. (2017), Investigating animal activity patterns and temporal niche partitioning using camera-trap data: challenges and opportunities. Remote Sens Ecol Conserv, 3: 123–132

2.1 Introduction

Global biodiversity declines are being driven by the direct and indirect effects of anthropogenic disturbances (Cardinale et al. 2012; Hooper et al. 2012). Though these direct effects manifest in obvious ways through habitat loss and wildlife population declines, more subtle are the myriad indirect and cascading effects of human-driven disturbances, including altered species behaviours and interspecific interactions. A better understanding of these indirect impacts is needed to inform effective conservation planning. Recent technological and statistical advances in the application of camera trapping suggest that this emerging methodology may help provide such

understanding.

Camera trapping is widely used in ecology and conservation for investigating species' distributions, estimating population densities, and inventorying biodiversity (O'Connell et al. 2010; Burton et al. 2015; Steenweg et al. 2017). While camera-trap studies have typically focused on the spatial and numerical aspects of species and population ecology, (e.g. Karanth and Nichols 1998; Linkie et al. 2007; Tobler et al. 2008), they have less often examined species' behaviours and interactions and their associated consequences for community structure. Only recently have researchers focused attention on the finer-scaled temporal data provided by time-stamped camera-trap images (e.g. Ridout and Linkie 2009; Rowcliffe et al. 2014), which detail the timing of wildlife occurrences across points in space. While such temporal data present analytical challenges, they are critical for developing a more complete understanding of population and community dynamics in the face of global change.

Temporal camera-trap data offer the opportunity to address unresolved questions regarding species ecology and community interactions, such as variation in activity patterns and partitioning along the temporal niche axis. These temporal insights are not only valuable from an ecological perspective. They also provide insight into human-driven changes to species' behaviours and interactions, and the resulting impacts on niche partitioning and community structure. The increase in camera-trap studies focused on temporal analyses is beginning to generate new ecological and applied insights, but a synthesis of recent approaches and trends is lacking. In this review, we pursue this synthesis through exploring several principal questions and analytical approaches for investigating temporal data collected by wildlife cameras. These questions reflect common themes we observed in the literature, and associated methods for analyzing temporal data in the context of species' behaviour and interactions. Based on an *ad hoc* review, we provide a synthetic overview of frequently cited and more recent papers, building on notable past reviews (Bridges and Noss 2011) by adding more recent advances in approaches and thought. We review the theoretical basis for activity patterns and temporal niche partitioning, summarize current approaches, assess current limitations to more complete analyses, and highlight significant advances in gaining a fuller understanding of species and community ecology. Ultimately, species' interactions and community dynamics can only be fully resolved by combining spatial and temporal data, therefore we also discuss new directions where combined spatiotemporal aspects of species niche partitioning and responses to environmental stimuli can be explored.

2.2 Exploring Time as a Niche Axis

Temporal dynamics are integral to niche theory (Hutchinson 1957; Hutchinson 1959; MacArthur and Levins 1967), including species autecology and community assembly, diel activity patterns, and temporal niche partitioning among sympatric heterospecifics. Animal activity – quantifying how species distribute their activity over the day – is an important dimension of animal behaviour; how species use time as a resource provides valuable information about their ecological niche (Schoener 1974). Extending to the community level, understanding how sympatric species partition time provides insight into the mechanisms facilitating stable coexistence (Carothers and Jaksić 1984; Kronfeld-Schor and Dayan 2003). Numerous studies employing camera-trap data have observed temporal niche partitioning as an important strategy for enabling the coexistence of ecologically similar species (e.g. Di Bitetti et al. 2010; Monterroso et al. 2014; Sunarto et al. 2015). As diel activities are adapted to local conditions (Halle 2000), the influence of abiotic and biotic variables on activity patterns and temporal niche partitioning is a primary question for both ecological research and biodiversity conservation. Already there is mounting evidence from camera-trap studies that human-driven landscape and community impacts - including land-use change (Ramesh and Downs 2013), human activity (Wang et al. 2015; Ngoprasert et al. 2017), hunting (Di Bitetti et al. 2008), predator control (Brook et al. 2012), and presence of invasive competitors or predators (Gerber et al. 2012; Zapata-Ríos and Branch 2016) - may alter species' activity patterns and competitive or predatory interactions through altered temporal niche partitioning. Therefore, effective conservation decisions must also consider how environmental stressors and shifts in community composition may impact sympatric species' ability to segregate not just spatially, but also temporally.

The circular distribution of temporal data comes with its own set of analytical challenges, and very large sample sizes are required to explore fine-scale temporal responses across spatial gradients. Recent statistical and software developments have made important strides in tackling the challenges of temporal camera-trap data analysis (e.g. Ridout and Linkie 2009; Oliveira-Santos et al. 2013), thereby facilitating characterization of activity patterns and temporal niche overlap. Nevertheless, modelling the degree to which external variables (habitat characteristics, community structure, disturbance variables, etc.) cumulatively influence species' activity patterns and temporal niche partitioning continues to present considerable challenges.

To date, few researchers have attempted such multivariate analyses with temporal data (e.g. Norris et al. 2010; Wang et al. 2015). Even more challenging is combining both spatial and temporal species' distributions to gain a fuller resolution of the underlying dynamics structuring interspecific interactions and community-level responses. Tackling this challenge starts with analyzing the activity patterns of single species, and builds iteratively towards more complex multispecies and multivariable models.

2.3 Current Approaches to the Analysis of Activity Patterns

Activity data reflect an important dimension of animal behaviour and ecology, as they provide relevant information on species' natural history and ecological niche. Temporal data extracted from time-stamped wildlife images have provided some of the first analyses of diel (or circadian) activity of populations and species (e.g. Gerber et al. 2012; Bu et al. 2016).

Early camera-trap studies derived descriptive inferences from tabulated records or graphical displays of activity over discrete time periods of the diel cycle (e.g. van Schaik and Griffiths 1996; Lizcano and Cavelier 2000; de Almeida Jacomo et al. 2004). This allowed assignment of taxa to general behavioural groups (e.g. diurnal, nocturnal) and better describe the temporal aspects of species' ecological niches. More recently, graphical displays of diel activity patterns use nonparametric kernel density estimates (e.g. Ridout and Linkie 2009; Linkie and Ridout 2011; Farris et al. 2015) to view species' activity as a continuous distribution over the wrapped 24-hour cycle, treating the estimates as a random sample from an underlying continuous distribution instead of grouping them into discrete time categories. Kernel density estimation wraps an assumed non-negative, symmetric probability distribution with a mean of zero and area of one (i.e. the kernel function) to each data point. For circular distributions, such as animal activity over the diel cycle, the von Mises kernel (a close approximation to the wrapped normal distribution; Fisher 1995) takes the role of the Gaussian kernel in linear statistics. Meredith and Ridout's (2014) R package *Overlap* produces kernel density curves of species activity patterns from camera-trap data, with a similar function offered by the R package *Circular* (Agostinelli and Lund 2013). Such graphical displays of activity patterns reflect aspects of temporal variability

in species activity over the diel cycle, including basic behavioural categorizations (e.g. diurnality versus nocturnality) and periods of peak activity. This approach dramatically improved the level of insight gained without any further investment in data acquisition, and thus represents significantly improved return on investment of camera-trap arrays.

Quantitatively investigating activity patterns comes with various challenges. Time is a wrapped distribution with an arbitrary zero point, thus classical statistical methods cannot be applied (Zar 2013). To solve this, circular statistics use trigonometric functions to derive descriptive statistics of temporal data, including mean time of activity (the mean vector), circular median, standard deviation and variance, as well as other dispersal estimates such as concentration (Batschelet 1981). Various software packages offer functions for deriving the statistical parameters on circular data, including ORIANA (Kovach 2011) and the R packages *CircStats* (Lund and Agostinelli 2011) and *Circular* (Agostinelli and Lund 2013). However, multimodal distributions indicating multiple peaks of activity (for example, a crepuscular species showing activity peaks at dawn and dusk) do not yield intuitive statistical estimates of centrality (Batschelet 1981). As bimodal activity patterns are widespread (Aschoff 1966), the derived mean vector may fall between the two activity modes. Although studies have reported the mean vector to quantify species' mean activity time (e.g. Di Bitetti et al. 2010; Norris et al. 2010; Ramesh et al. 2012), this should be done with great caution to ensure the derived mean vector reflects a biologically accurate and meaningful value.

Oliveira-Santos et al. (2013) proposed conditional circular kernel density functions to characterize “activity range” and “activity core” from time-of-detection camera data. Following an approach similar to telemetry-based home range contours, they created density functions yielding 95% isopleths representing the time interval in which 95% of the animal activity occurs – an ecologically relevant activity range that eliminates outlying periods of activity produced by the statistical smoothing process. More conservatively, the 50% isopleth can be used to determine during which time interval(s) core activity is focused. This approach allows for a more quantitative analysis of temporal data, delimiting hours of peak activity to characterize specific aspects of species' circadian activities. Rowcliffe et al. (2014) also applied kernel density functions to camera data in developing an analysis to quantify the overall proportion of time that an animal spends active (i.e. activity level). The R package *Activity* (Rowcliffe 2016) fits circular distributions to temporal camera-trap data

to create activity schedules and calculate species' activity level, thereby facilitating inquiry into animal energetics, predation risk, and foraging effort, although key assumptions for deriving this metric may not be met in certain populations (Rowcliffe et al. 2014).

Species' activity patterns may also be characterized according to selection for certain time periods by discretizing the 24-hour diel cycle into categories such as dawn, day, dusk, and night. Chi-square tests determine if species' activity patterns are non-random (e.g. Bu et al. 2016). Resource selection functions (Manly et al. 2007) have also been used to determine how species distribute activity over various time periods given their availability (e.g. Gerber et al. 2012; Bu et al. 2016), which provides an approach to ascribing behavioural categorizations to species' activity patterns (e.g. diurnal, nocturnal, or crepuscular). Species can also be assigned into such categorizations using niche selectivity indices, such as Ivlev's Electivity Index (Ivlev 1961) or its derived Jacobs Selectivity Index (Jacobs 1974). Using a novel approach to investigating how species selectively use different time periods, Farris et al. (2015) used hierarchical Bayesian Poisson analysis by modelling photographic rate (capture events/available hours) for each time category.

Camera-trap studies using such descriptive and quantitative approaches have produced considerable insight into the activity patterns of a wide range of species from diverse systems. These have included carnivore guilds (Di Bitetti et al. 2010; Monterroso et al. 2014), ungulates (Ferreguetti et al. 2015), rodents (Meek et al. 2012), primates (Gerber et al. 2012), birds (Srbek-Araujo et al. 2012) and various other mammals (Oliveira-Santos et al. 2008; Galetti et al. 2015). Interestingly, some conclusions from camera-trap research on species activity patterns have challenged previous conclusions regarding species-specific temporal activity (Bischof et al. 2014), which may arise from past sampling constraints that did not allow noninvasive, 24-hour sampling. It is possible that activity data collected by camera traps may contain biases related to temporal variability of detectability caused by temperature, humidity, or other factors suppressing detectability, but these remain untested to the best of our knowledge.

Despite the potential limitations of sampling species' activity patterns using camera-trap data, many emerging advances in documenting these patterns have been developed. The logical first step is comparing these activity patterns among sympatric species to ask how species divide the temporal niche axis.

2.4 Analyses of Temporal Niche Partitioning

Perhaps the ecologically most interesting questions asked of species activity data is how sympatric species partition their activities to promote stable coexistence. MacArthur and Levin's (1967) limiting similarity theory predicts that no two species can coexist in time and space; thus sympatry demands species divide their resources to avoid extinction by competition (Figure 2.1). Time can be considered as a resource as it is consumed analogous to other resources with limited availability (Halle 2000). Although not previously emphasized as an important mechanism for reducing competition, partitioning time of activity may be one of the most relevant strategies for the coexistence of species (Schoener 1974). Understanding how ecologically similar species coexist is not just a key question in ecology but also crucial for understanding community diversity.

Early investigations of temporal niche partitioning relied on qualitative analyses of histograms. Researchers later began using linear frequency statistical procedures with the 24-hour cycle categorized in contingency tables (de Almeida Jacomo et al. 2004; Lucherini et al. 2009; Gerber et al. 2012). Measures of niche similarity and overlap – such as Renkonen's similarity index and Pianka's measure of niche overlap (Krebs 1998) – evaluate differential use and partitioning of time as a resource (e.g. Lucherini et al. 2009; Hofmann et al. 2016), although these require discretization of data into arbitrary bin sizes.

Software packages which fit nonparametric circular density functions to camera-trap data allow researchers to analyze activity through a circular inferential statistical approach. A descriptive measure of the degree of similarity between two kernel density curves can be calculated following Meredith and Ridout's (2014) innovative coefficient of overlap, which fits camera-trap data to a kernel density function and then estimates a symmetrical overlapping coefficient between species using a total variation distance function (Figure 2.2). This coefficient of overlap (Δ), whose precision can be estimated via bootstrapping and ranges from 0 (no overlap) to 1 (complete overlap), has often been used to investigate potential competitive and interaction possibilities between species (e.g. Linkie and Ridout 2011; Farris et al. 2015; Cusack et al. 2017). As Δ is a relative measure, interspecific differences in activity patterns may also be tested for statistical significance. The nonparametric circular Mardia-Watson-Wheeler (MWW) statistical test (Batschelet 1981) and Watson U^2 -test (Zar 2013) have both been used to determine if two or more circular distributions vary sig-



Figure 2.1: Sympatric species must partition time or space to coexist. These four species (clockwise: grizzly bear *Ursus arctos*; wolverine *Gulo gulo*; mule deer *Odocoileus hemionus*; moose *Alces alces*) were detected at the same camera-trap location. Spatiotemporal partitioning reduces competition and the potential for agonistic encounters.

nificantly. Meredith and Ridout's (2014) *Overlap* package remains a popular tool for presenting the overlap of two activity curves visually and estimating Δ , despite the biases introduced by the smoothing process when applying kernel density functions to temporal data and deriving an estimation of Δ (as discussed by Ridout and Linkie 2009).

Exploring temporal niche partitioning with camera traps has highlighted the prevalence and importance of segregation along the temporal axis for enabling coexistence within diverse assemblages of sympatric species. For example, Bischof et al. (2014) concluded that the elusive Altai mountain weasel (*Mustela altaica*) compensates for spatial overlap with intraguild predators by adopting an inverse activity pattern to its sympatric dominant predators while still maintaining spatial access

to prey. Ferregueti et al. (2015) concluded that two sympatric deer species may mitigate competition for similar space and food resources through differences in their activity patterns. Di Bitetti et al.'s (2010) analysis of Neotropical felid species activity patterns observed diurnal, nocturnal, and cathemeral behaviours among species. Morphologically similar species had the most contrasting activity patterns, suggesting that the ability of species to segregate temporal activities may explain the lack of character displacement seen in certain assemblages (Di Bitetti et al. 2010). Similarly, Sunarto et al. (2015) observed that within a tropical community of felids, those species with the most similar body size or with similarly sized prey had the lowest temporal overlap. Monterroso et al. (2014) observed a negative correlation between mean pairwise temporal overlap and species richness (number of species with at least 10 detections) across a mesocarnivore community. They suggest that temporal niche partitioning may be influenced by community diversity and likely plays an important role in facilitating stable coexistence in mesocarnivore guilds showing high diversity.

With statistical techniques to quantify temporal niche partitioning using camera data quickly developing, it is increasingly possible to ask questions about the factors that affect partitioning, including anthropogenic pressures induced by landscape and climate change.

2.5 Investigating Changes to Species' Activity Patterns and Niche Partitioning

Animal activity patterns evolve via processes of natural selection (Kronfeld-Schor and Dayan 2003) such as historic coevolutionary competitive interactions (“the ghost of competition past” (Connell 1980), but behavioural plasticity may allow flexible changes to activity patterns in response to environmental stimuli (Halle 2000). Environmental cues such as predation risk, resource availability, and the potential for agonistic encounters with dominant competitors influence behavioural decisions that alter a species' activity (Halle 2000). Activity during suboptimal times of higher predation risk, increased energy demand, or lower prey availability may incur fitness costs. Comparing activity patterns in response to external stimuli provides insight into the degree of plasticity in species activity schedules and into the extent to which various environmental factors may alter an animal's activity pattern.

Changes to species' activity patterns may lead to altered temporal niche parti-

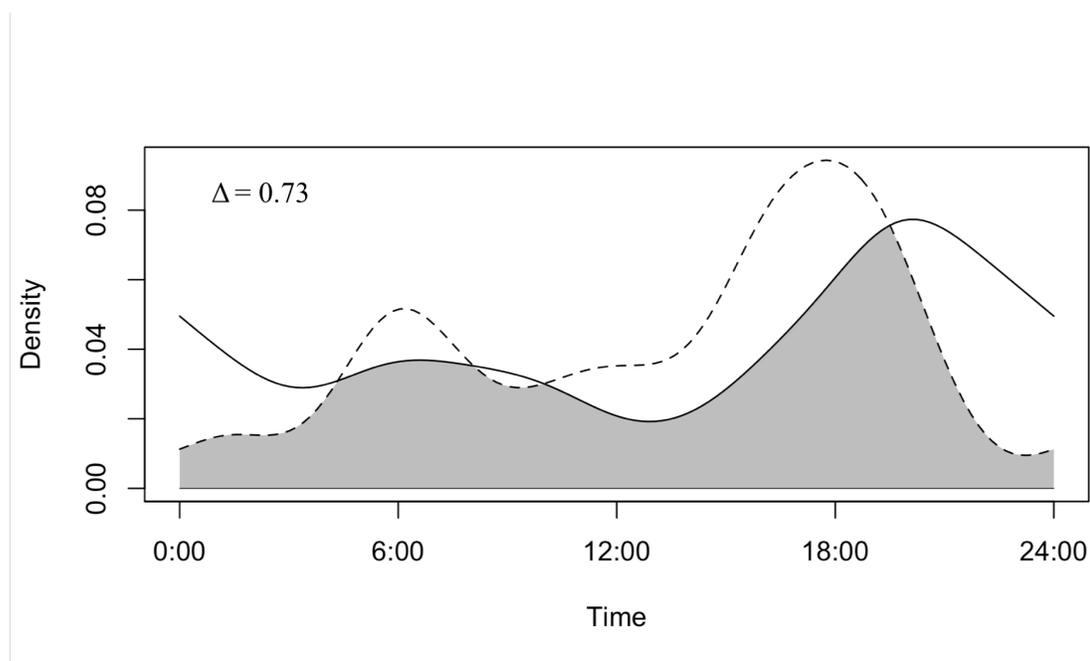


Figure 2.2: An example of the characterization of diel activity patterns from camera-trap data. Kernel density functions were used to depict grey wolf (*Canis lupus*; solid line) and coyote (*Canis latrans*; dashed line) activity sampled via camera trapping during October - March 2006 to 2008, in the Willmore Wilderness Area, Alberta, Canada. The overlap coefficient (Δ) is the area under the minimum of the two density estimates (denoted in grey).

tioning between species, with potential repercussions to species interactions such as intraguild competition and predator-prey dynamics. Indirect effects of anthropogenic stressors such as climate and landscape change could increase temporal overlap between species, augmenting interspecific conflict and exploitation of prey, or conversely, releasing species from predation or competitive pressure with reduced overlap. However, very few studies have empirically quantified how external factors may influence temporal niche partitioning (but see Wang et al. 2015).

Investigations of altered activity patterns, as with simpler investigations of animal activity, have typically involved descriptive comparisons of activity distributions from graphical displays but also paired with simple statistical tests to determine whether two or more circular distributions differ significantly. Largely, these data have come from time-stamped wildlife images collected via camera trapping (but see Suselbeek et al. 2014). Generally, authors have divided the camera-trap data into two or three treatment groups based on abiotic or biotic factors such as sea-

son, lunar phase, presence/absence of predators or competitors, human activity, or landscape change. Significant differences between activity times may be quantified statistically through a chi-squared contingency table of frequency of photographic records (e.g. de Almeida Jacomo et al. 2004), but again this requires categorization of the temporal data into discrete time bins. The aforementioned MWW and Watson U²-tests have also both been used to determine if activity distributions between populations vary significantly. For example, Di Bitetti et al. (2009) observed that pampas foxes (*Lycalopex gymnocercus*) showed significantly different activity patterns in areas where the competitively dominant crab-eating fox occurred. Likewise, statistical comparisons of activity records between two colour polymorphs of oncilla (*Leopardus tigrinus*) revealed significant intraspecific differences in diel activity patterns (Graipel et al. 2014).

Intraspecific comparisons between study systems or treatments groups have also been performed using Ridout and Linkie's Δ (e.g. Monterroso et al. 2014; Wang et al. 2015). For example, Monterroso et al. (2014) observed a considerable degree of plasticity in European mesocarnivore nocturnal activity times between seasons and sites based on mean Δ values. By overlaying intraspecific activity curves of predators experiencing high versus low levels of human disturbance, Wang et al. (2015) demonstrated the timing and direction of activity shifts between two treatment groups. Activity overlap may also be quantified at conditional isopleths to determine whether overlap is more concentrated in the activity cores of the species (Oliveira-Santos et al. 2013). Rheingantz et al. (2016) observed very low activity overlap at 95% and 50% conditional isopleths between the two studied otter populations (45.6% and 14.1%, respectively), suggesting a high level of plasticity in activity patterns; this was hypothesized to be a product of human activity or shifts in prey availability.

To date, the majority of studies evaluating the impact of external variables on species activity patterns have analyzed the effect of a single variable at a time. Comparative tests do not allow for modelling multiple explanatory variables, potentially missing cumulative effects of multiple stressors, and interaction terms. Moreover, differences arising between treatment groups may potentially manifest in response to confounding (or collinear) variables. Alternative options include angular-linear correlations, as done by Hofmann et al. (2016) in comparing peccary activity time in relation to air temperature. Using an information-theoretic analysis of species activity, Norris et al. (2010) used linear mixed effects models to evaluate how abiotic conditions and human disturbance influenced activity pattern of three Amazonian

terrestrial mammals. They observed that the time since isolation of forest patches had the strongest influence on agouti activity timing (2010). However, care should be taken to ensure that the linear (as opposed to circular) scale used to define activity patterns upholds biological relevance; as mentioned, there is little biological difference but marked statistical difference between 2355 hrs and 0005 hrs on the linear scale.

One noteworthy study by Wang et al. (2015) evaluated the influence of external variables on temporal niche partitioning in areas of ex-urban development near the Santa Cruz Mountains of California. Using an information-theoretic approach, these authors modelled Δ between mesocarnivore species-pairs as a response to landscape development, human activity, and forest cover. Wang et al.'s (2015) approach represents one of the few studies that simultaneously models the effect of multiple variables on species' activities and partitioning along the temporal axis. However, such fine-scale inferential analysis requires large amounts of data and a robust sampling design for capturing the effect of multiple explanatory variables across a spatial gradient. Many studies of species activity patterns and temporal niche partitioning are performed as secondary investigations, repurposing camera-trap data collected primarily for analyzing spatial patterns or other responses (e.g. Di Bitetti et al. 2006; Sunarto et al. 2015; Ikeda et al. 2016). For all the reasons detailed above, spatially-focused study designs with sample sizes only sufficient to confidently yield spatial and numerical responses may not be adequate to extend insight to complex and fine-scale investigation of species' activity patterns and temporal niche partitioning.

In summary, scientists have only begun to delve into discovering how animals spend their days, how species divide up time among them, and how our marked impacts on landscapes, climates, and biotic communities change these temporal processes. Moreover, although it is tacitly understood that space and time are inextricably linked, their integration in this context remains to be explored.

2.6 Future Directions: Analyzing Spatiotemporal Species Interactions

With an increasing number of statistical approaches, and emerging studies of species behaviours and partitioning along both the spatial and temporal niche dimensions, our understanding of species interactions across time and space is mounting. However, this subfield is still relatively young, and most studies use opportunistic, not purpose-

designed, data. There are many interacting ecological processes and cumulative effects of anthropogenic impacts yet to disentangle. This is a key future area of research, as the indirect effects of environmental stressors on species activity and interactions may be as important as the direct effects (Strauss 1991; Schoener et al. 1993; Abrams 1995).

The opportunity to parse the relative influences of space and time in species sympatric coexistence is an intriguing prospect. The competitive interactions shaping community structure likely manifest as both spatial and temporal patterns, but few studies to date have directly assessed such spatiotemporal interactions (but see Lewis et al. 2015; Swanson et al. 2016; Karanth et al. 2017). Based on a comparison of approaches, Cusack et al. (2017) suggested that approaches using the combined spatial and temporal data generated by camera traps yield better insight into the associative patterns between sympatric species.

A second key opportunity is in using environmental stressors as treatments in large-scale experiments designed specifically to understand the factors affecting species activity and interactions. Very little is known about how natural and anthropogenic changes to landscapes and biotic communities influence competitive interactions in animal populations. As it stands, it is difficult to predict how climate change, landscape change, and anthropogenic changes to community composition may impact the competitive interactions and behavioural adaptations integral to maintaining biodiversity and ecosystem stability. Altered spatiotemporal interactions between sympatric species in communities could have rippling effects throughout the entire ecosystem (Crooks and Soulé 1999). With anthropogenic landscape changes projected to continue globally (Theobald 2005; Seto et al. 2011; Maxwell et al. 2016), focusing research efforts on understanding species spatiotemporal responses to those impacts is vital to sound conservation and management decisions. However, these questions are exceedingly difficult to answer within a single landscape.

Camera-trap surveys are invaluable for tracking direct effects of anthropogenic change on species distributions and abundances. However, the indirect effects of human influence, mediated by interactions among species in shifting communities, reside at the frontier of our knowledge of wildlife responses in the Anthropocene. With the growth of camera-trap networks deployed across multiple landscapes (Ahumada et al. 2013; Burton et al. 2015; McShea et al. 2016), hopefully growing into a global biodiversity network (Steenweg et al. 2017), network nodes deployed as coordinated distributed experiments (*sensu* Fraser et al., 2013) may help tease apart the effects

of landscape and climate change on species interactions in complex environments. This research coordination and accompanying sampling designs remain the greatest opportunity for this emerging field of research. Fully capitalizing on the multi-scale spatial and temporal data produced by these networks may represent one of our best chances of advancing our ecological discoveries and meeting the pressing demands of biodiversity conservation.

Chapter 3

Please do not disturb: Carnivore activity patterns and temporal niche partitioning in relation to human-mediated disturbance

Chapter 2 of this thesis is in preparation to be submitted as a manuscript with co-authors Jason T. Fisher and John P. Volpe.

3.1 Introduction

Climate change and land use remain the most important projected drivers of global biodiversity change in the Anthropocene (Sala et al. 2000). However, mechanisms of biodiversity loss are not always simply construed, and developing effective conservation strategies requires a full and empirical understanding of species' responses to human-mediated disturbances. To date, extensive research has documented spatial and numerical responses of wildlife populations to anthropogenic disturbances, including population declines and local extirpations (e.g. 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, temporal activity, and interactions (e.g. Wang et al. 2015; Stewart et al. 2016; Swanson et al. 2016). These are important features of species' ecology, and

significant drivers of community structure and stability (Schoener 1974; Halle 2000; Kronfeld-Schor and Dayan 2003). Understanding how disturbances alter such features of species' and community-level ecology may shed light on the underlying mechanisms driving spatial and numerical responses of wildlife populations on human-modified landscapes. Detecting subtle shifts in species' behaviours and competitive interactions may also enable us to identify potential precursors of species' and population declines, thereby providing us with important information and opportunities to preemptively manage against such losses.

The paucity of field studies evaluating behavioural shifts and resultant changes to interspecific interactions in meso- and large mammals is largely due to the inherent challenges of quantifying these responses, but recent technological advances have opened novel avenues for exploring such complex responses (Frey et al. 2017). The advent of remote camera trapping has provided cost-effective opportunities to study population and community-level processes across large spatial and temporal scales (Rovero and Zimmermann 2016; Burton et al. 2015; Steenweg et al. 2017). Camera trap arrays deployed across impacted landscapes can provide novel insights into the more subtle and complex shifts occurring at the species and community level in response to human disturbance, including altered species' behaviours and interactions (O'Connell et al. 2010; Fisher et al. 2013; 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-hour time axis (Ridout and Linkie 2009; Frey et al. 2017).

Understanding how species use time and partition this resource along the temporal niche axis (Schoener 1974; Case and Gilpin 1974; Carothers and Jaksić 1984) provides important insights into species' ecology, and the mechanisms facilitating stable coexistence within communities – or destabilization of that coexistence, as a mechanism of decline and extirpation. A species' use of time over the 24-hour diel period – its “activity pattern” – can be characterized by its selectivity for or against activity during 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; Hofmann et al. 2016), habitat loss and fragmentation (Norris et al. 2010), co-occurrence with native and nonnative competitors (Di Bitetti et al. 2009; Gerber et al. 2012; Zapata-Ríos and Branch 2016), and human disturbance (Keuling

et al. 2008; Ramesh and Downs 2013; Wang et al. 2015). Understanding how landscape changes may disrupt important mechanisms underlying species interactions and community structure is a priority for better understanding spatiotemporal ecological processes, as well as developing informed conservation strategies and land-use policies. To address this research gap, we evaluated the effects of anthropogenic 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.

At the community level, species' differential use of the temporal niche is an important mechanism for minimizing competitive interactions, and may be particularly important in communities where interference competition dominates (Carothers and Jaksić 1984; Caro and Stoner 2003; Harrington et al. 2009). Previously regarded as the least important of the three main niche axes (space, time, and resources) along which species may segregate (Schoener 1974), evidence increasingly suggests that partitioning along the temporal axis enables spatially sympatric species to reduce the limiting effects of competition (Kronfeld-Schor et al. 2001; Di Bitetti et al. 2009; Sunarto et al. 2015). Indeed, temporal niche partitioning has been observed across many taxa (e.g. Adams and Thibault 2006; Castro-Arellano and Lacher 2009; Di Bitetti et al. 2010; Lucherini et al. 2009), but may be an especially important strategy within carnivore guilds where interference competition can incur lethal costs, as in the case of intraguild predation and interspecific killing (Polis et al. 1989). Given the potentially lethal consequences of direct interaction with a dominant predator, 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 while mitigating against direct interaction with dominant competitors (e.g. Bischof et al. 2014).

An increasing number of studies over the last decade have highlighted the prevalence of temporal niche partitioning across diverse assemblages of ecologically similar competitors (Frey et al. 2017). Yet 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. 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 species' activity shifts should also investigate changes to interspecific temporal niche partitioning when anthropogenic disturbance is suspected to have induced activity shifts in one or more species (e.g. Wang et al. 2015).

Evaluating whether human-mediated disturbances impact species' capacity to segregate along the 24-hour time axis requires an understanding of how sympatric species alter their activity schedules in relation to human activity or anthropogenic landscape change. In areas of high human density, temporal displacement from periods of high human activity has been observed for various species, often in the form of increased nocturnality (e.g. Ohashi et al. 2012; Carter et al. 2015; Ngoprasert et al. 2017). Some studies have also attributed species' activity shifts to landscape changes such as the conversion of natural habitat to farmland (Ramesh and Downs 2013). This suggests alterations to resource composition or configuration may induce behavioural shifts potentially attributed to exploiting novel resources, or compensating for altered predation risk on the impacted landscape. However, such responses may vary by species, landscape, and the nature of disturbance; activity shifts following human disturbance do not always manifest in clear or significant ways (Kolowski and Alonso 2010), but nonetheless provide insights into behavioural responses to human disturbance.

Disturbance is widespread in many ecosystems (Vitousek et al. 1997), and the east slopes of the Rocky Mountains have experienced uniquely intensive disturbance in the last decades (Global Forest Watch 2014). This region is home to a diverse suite of large and mid-sized mammalian carnivore (mesocarnivore) species, including wolves (*Canis lupus*), grizzly and black bear (*Ursus arctos* and *americanus*), coyote (*Canis latrans*), wolverine (*Gulo gulo*), lynx (*Lynx canadensis*), and American marten (*Martes americana*). Human impacts in the Kananaskis Country region include motorized (e.g. off-road vehicles, snowmobile, motorbike) and non-motorized (hiking, biking, skiing, equestrian) recreation, and various forms of resource extraction (e.g. timber harvest, mining, oil and gas exploration, and agriculture). We tested for carnivore activity shifts in relation to anthropogenic disturbance using two approaches, looking for con-

vergence to test our hypothesis that human disturbance alters species diel activity patterns. First, we compared carnivore activity patterns between a disturbed and undisturbed landscape and tested for shifts in activity. Second, we investigated carnivore activity shifts in relation to the site-scale landscape 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) anthropogenic landscape change. We predicted that disturbance-sensitive species such as wolves and wolverine would increase selectivity for the nocturnal period on the disturbed landscape, and at disturbed camera sites. We hypothesized mesocarnivores would alter activity patterns in response to landscape change, but we did not form *a priori* predictions about directionality in mesocarnivore activity shifts as they could respond either directly to human activity, or indirectly, by altering activity patterns to avoid potentially shifting activity times of dominant predators. Lastly, we hypothesized that human disturbance alters patterns of temporal niche partitioning within communities, and tested this by quantifying the influence of anthropogenic landscape change on interspecific activity overlap. We predicted that disturbance-induced activity shifts would increase activity overlap between disturbance-sensitive carnivore species due to increased nocturnal activity.

3.2 Methods

3.2.1 Study Area

Our study area encompassed two proximal areas within in the Rocky Mountains of Alberta, Canada: the Willmore Wilderness Area (WW) and the Kananaskis Country (KC) region (Figure 3.1). Both the WW and KC are characterized by rugged mountain topography with elevations ranging from 1200m to over 2400m, with steep-sloped ridges and valley bottoms, 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*). Small stands of deciduous (*Populus tremuloides*, *Populus balsamifera*) occur throughout, with trembling aspen, Labrador tea (*Ledum groenlandicum*), and mosses (*Sphagnum spp.*) dominating the forest floor. The KC 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 KC share many of their natural landscape characteristics across the alpine, subalpine, and montane sub-regions (Natural Regions Committee 2006), the two differ markedly in the extent of human footprint and anthropogenic activities on the landscape. The WW, a 4600m² conservation area, is largely protected from anthropogenic development, with low levels of deforested linear features (petroleum exploration or “seismic” lines; Fisher and Burton 2018) present within the front ranges to the east. Access is limited to foot and horse trails, precluding most forms of motorized recreation. In contrast, KC 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 recreational use encompasses both motorized (e.g. hiking, biking, skiing, equestrian) and non-motorized activities (e.g. off-road vehicles, snowmobile, and motorbike).

Despite the striking differences in human footprint across the two study areas, both the WW and KC support a common mammalian carnivore community including grizzly and black bear, wolf, cougar (*Puma concolor*), coyote, wolverine, lynx, red fox (*Vulpes vulpes*), American marten, and short-tailed weasel (*Mustela ermina*). Fisher (*Pekania pennanti*) are present only within the Willmore and surrounding area, while the northern range of bobcat (*Lynx rufus*) extends into KC and not the WW (Fisher et al. 2011; Heim 2015). In addition to supporting a diverse carnivore community, both regions also support large and diverse populations of ungulates and smaller prey species.

3.2.2 Sampling Design

We used photographic data collected in remote camera arrays deployed using identical sampling designs and sampling methods (Fisher et al. 2011; Fisher et al. 2013; 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 (e.g. Stewart et al. 2016). In both the WW (n=66) and KC (n=237), baited camera sites were deployed in a systematic study design in October–December, and monitored monthly until March. In the WW, camera sites were placed an average of 5727m apart (SD 1574) and sampled 2006–2008. In the KC, sites were

separated by a minimum of 6000m and sampled 2011–2014. For both the KC and WW studies, Reconyx™ infrared-triggered digital cameras (models RM30, PM30, and PC900; Reconyx, Holmen, WI, USA) were deployed paired with a frozen beaver carcass nailed to the tree facing the camera (see Fisher and Bradbury 2014 for full details on sampling design and examination of detection probabilities).

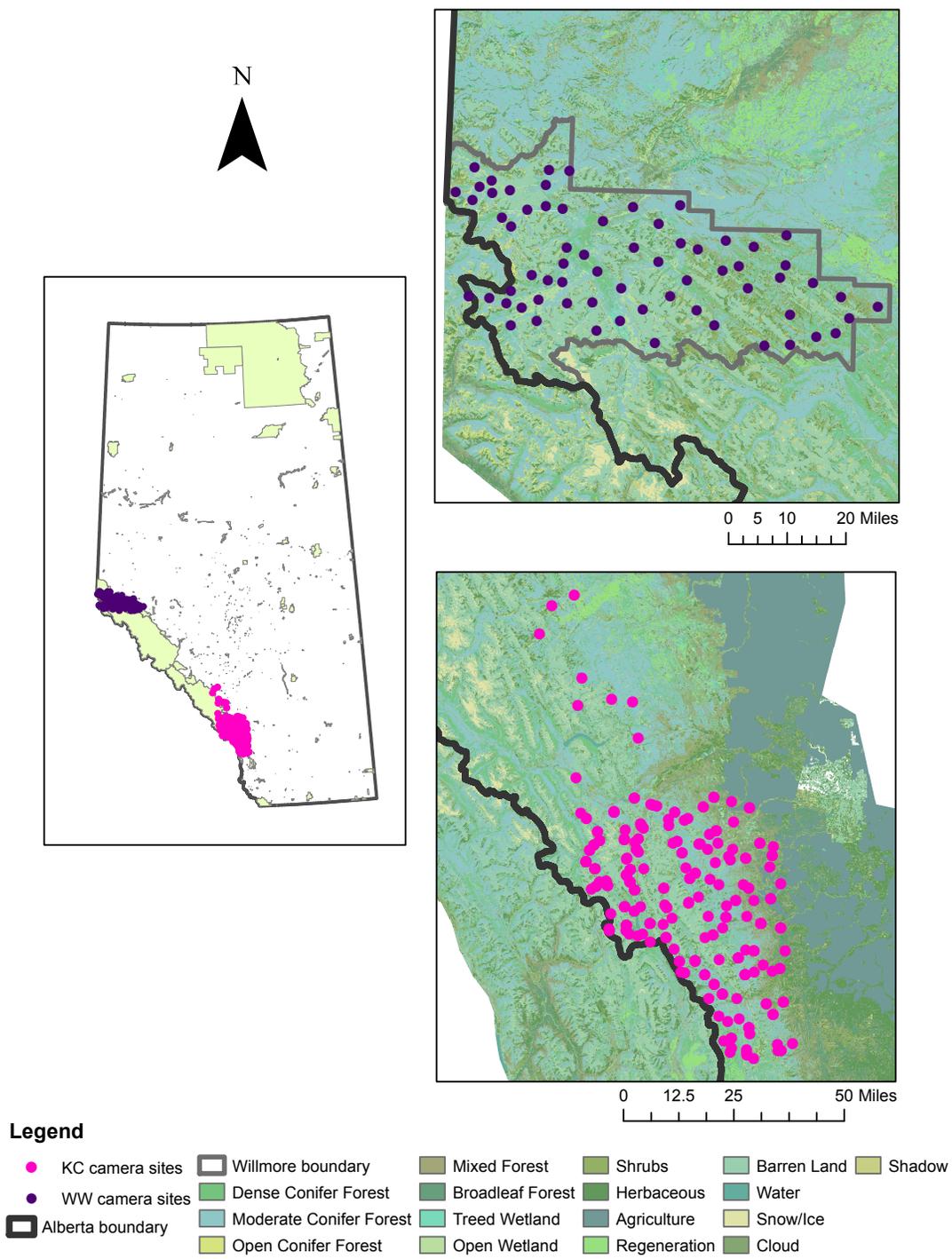


Figure 3.1: Camera trap locations in the Willmore Wilderness (WW) and Kananaskis Country (KC) study areas of Alberta, Canada.

3.2.3 Activity shifts in response to anthropogenic landscape change

To test our hypothesis that species shift diel activity patterns in response to human disturbance, we compared carnivore species' 24-hour activity curves between (1) the WW and KC study area, and (2) camera-sites in areas of high versus low levels of landscape development within each study area. For all wildlife images we recorded the date, time of detection, 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-minute time period (Di Bitetti et al. 2006; Farris et al. 2014; Wang et al. 2015). 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-hour day length with sunrise at 0600 h and sunset at 1800 h to facilitate ecological interpretation (Carver et al. 2011; 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) and Linkie and Ridout (2011) to generate activity curves using the package *Overlap* (Meredith and Ridout 2014) in R (R Core Development Team 2013). Density of activity (y-axis) uses a von Mises kernel and corresponds to the circular distribution of recorded capture times on the 24-hour 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 ES 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. Following the recommendations of Meredith and Ridout (2014), we used Δ_4 estimate if the smaller sample had more than 75 observations, otherwise we used Δ_1 estimate, which is recommended for smaller sample sizes. For all activity curves, we applied a standard smoothing parameter of 1 (Bu et al. 2016; Bogdan et al. 2016). We used 10,000 bootstrapped samples from each distribution to estimate 95% confidence intervals of Δ for each comparison. Lastly, to determine whether any

observed shifts in activity curves represented statistically significant differences in activity distributions over the 24-hour cycle, we applied the nonparametric Mardia-Watson-Wheeler (MWW) test (Batschelet 1981) using the *Circular* package in R-software (Agostinelli and Lund 2013).

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 development in the surrounding environment. We quantified human footprint using digital map inventories (Alberta Biodiversity Monitoring Institute, Human Footprint Map 2012). Linear features were the most widespread anthropogenic feature in the region so we used these as proxies of overall landscape change. In the WW, seismic lines were the only linear feature whereas in the more disturbed KC, this included a variety of anthropogenic linear disturbance features such as roads, recreational trails, and industrial cutlines (e.g. seismic and power lines). 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 classified “high” disturbance sites in the WW (n=11) as those encompassing linear features (0.1-5% area), and “low” disturbance sites as those with no linear features. As all camera sites within the KC exhibited some level of linear footprint within a 5000-m radius, we classified sites into 184 “high” disturbance (>2% area) sites and 54 “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.

3.2.4 Influence of anthropogenic landscape change on carnivore temporal niche partitioning

To test our hypothesis that human-mediated landscape change alters temporal niche partitioning, we modelled interspecific activity overlap against multiple biotic variables hypothesized to influence temporal overlap, including human footprint (Table 3.1), following a similar approach to Wang et al. (2015). We calculated Δ between spatially co-occurring species-pairs at camera sites where we observed a minimum of ten independent detections of both species. This restricted our analysis to wolver-

ine and marten overlap within the WW. Fortunately, this is a model species pair to study as their diets and niches overlap and commonly co-occur across wolverine ranges (Fisher et al. 2011; Fisher and Bradbury 2014).

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 potential predators or competitors may also influence species' activity patterns, we also included the presence and frequency of fishers (*Pekania pennanti*) within candidate models. Fishers are an ecologically similar competitor of marten (Fisher and Bradbury 2014), and co-occur with wolverine in the WW. Finally, to account for induced variability on Δ from low sample sizes via under-smoothed activity curves (Ridout and Linkie 2009), we included sample size of detections of wolverine and marten detections within candidate models outlining our null hypotheses.

We modelled overlap coefficients against natural land cover, anthropogenic features, 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 (w_i) and ranked resulting candidate models using AICc and w_i (Burnham & 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.

As our initial candidate model selection ranked wolverine sample size as the top model predicting marten and wolverine overlap, we conducted a *post-hoc* model selection on the previously established models but included wolverine count as an additional covariate to account for any bias introduced by low sample sizes and to isolate the influence of ecological variables on marten–wolverine overlap.

Table 3.1: 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
	Marten + Wolverine	Number of marten and wolverine events
<i>Null hypotheses</i> (Sample size sensitivity)	Marten	Number of marten events
	Wolverine	Number of wolverine events
<i>Natural Land Cover</i> (Perceived riskiness of forested versus open landscapes)	Forest	Forest cover (coniferous, deciduous and mixed combined)
	NatOpen	Natural open cover (shrub and herbaceous combined)
<i>Competitor Co-occurrence</i> (Prevalence of fisher, presence vs absence of fisher)	Fisher	Number of fisher events
	FisherPA	Presence / absence of fisher
<i>Anthropogenic Landscape Disturbance</i>	Seismic	Anthropogenic linear features (seismic lines)
<i>Landscape Development + Competitor Co-occurrence</i>	Seismic + Fisher	Anthropogenic linear features and prevalence of fisher
	Seismic + FisherPA	Anthropogenic linear features and fisher presence/absence
<i>Risky Landscapes + Competitor Co-occurrence</i>	NatOpen + Fisher	Natural open land cover and prevalence of fisher
	NatOpen + FisherPA	Natural open land cover and fisher presence/absence

3.3 Results

3.3.1 Carnivore activity shifts among disturbed and undisturbed landscapes

Multiple carnivore species shifted their activity patterns between protected and disturbed landscapes (Figure 3.2). Of the eight carnivore species compared between the WW and KC (see Appendix A, Table A.1 for species' detection summaries), we observed significant differences in activity distributions for coyote (MWW test, $\chi^2 = 6.90$, d.f. = 2, $p < 0.05$), marten ($\chi^2 = 58.63$, d.f. = 2, $p < 0.001$), and short-tailed weasel ($\chi^2 = 9.08$, d.f. = 2, p-value < 0.05). Coyotes in the undeveloped WW peaked activity around the crepuscular period but were indiscriminately active at all hours on the disturbed KC landscape. Marten in the undeveloped WW selected strongly for the nocturnal period, with a sharp activity decline during the diurnal hours. In contrast, the KC marten population selected for the diurnal period. Short-tailed weasel were largely nocturnal across both the WW and KC, but the WW population had higher proportion of diurnal activity compared to the KC. Wolves in the disturbed KC reduced diurnal activities and compensated with increased activity during the nocturnal hours, though this failed the test for significance ($\chi^2 = 4.0877$, d.f. = 2, p-value = 0.13).

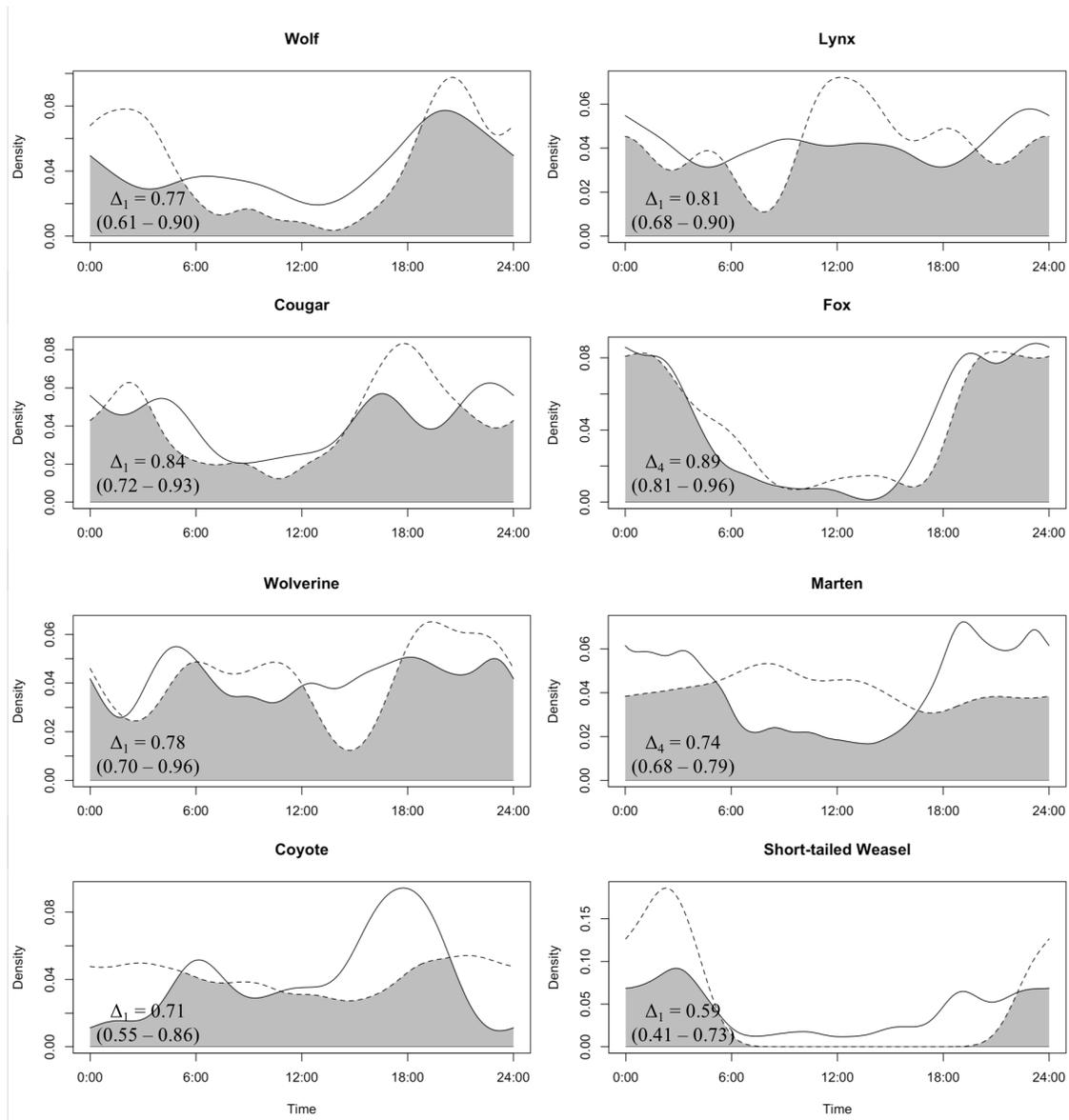


Figure 3.2: Kernel density estimates representing diel activity curves and temporal overlap of eight carnivore species between the WW (solid line) and KC (dashed line) study area. Periods of activity overlap is represented by the coefficient of overlap (Δ ; denoted in grey) accompanied by the 95 % confidence intervals in parentheses; $\Delta = 1$ represents no activity shift between the WW and KC while $\Delta=0$ represents complete activity shift.

3.3.2 Carnivore activity shifts in response to site-specific landscape disturbance

Within the WW landscape, with its much lower proportion of disturbance, carnivore species nonetheless shifted activities in relation to site-scale disturbance (Figure 3.3). We captured sufficient detections ($n \geq 10$) to apply the MWW test for five carnivore species (see Appendix A, Table A.2 for species' detection summaries). Significant activity shifts between low versus high disturbance camera sites occurred for marten ($\chi^2 = 13.39$, d.f. = 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; Appendix A, Table A.2) precluded application of statistical tests of significance.

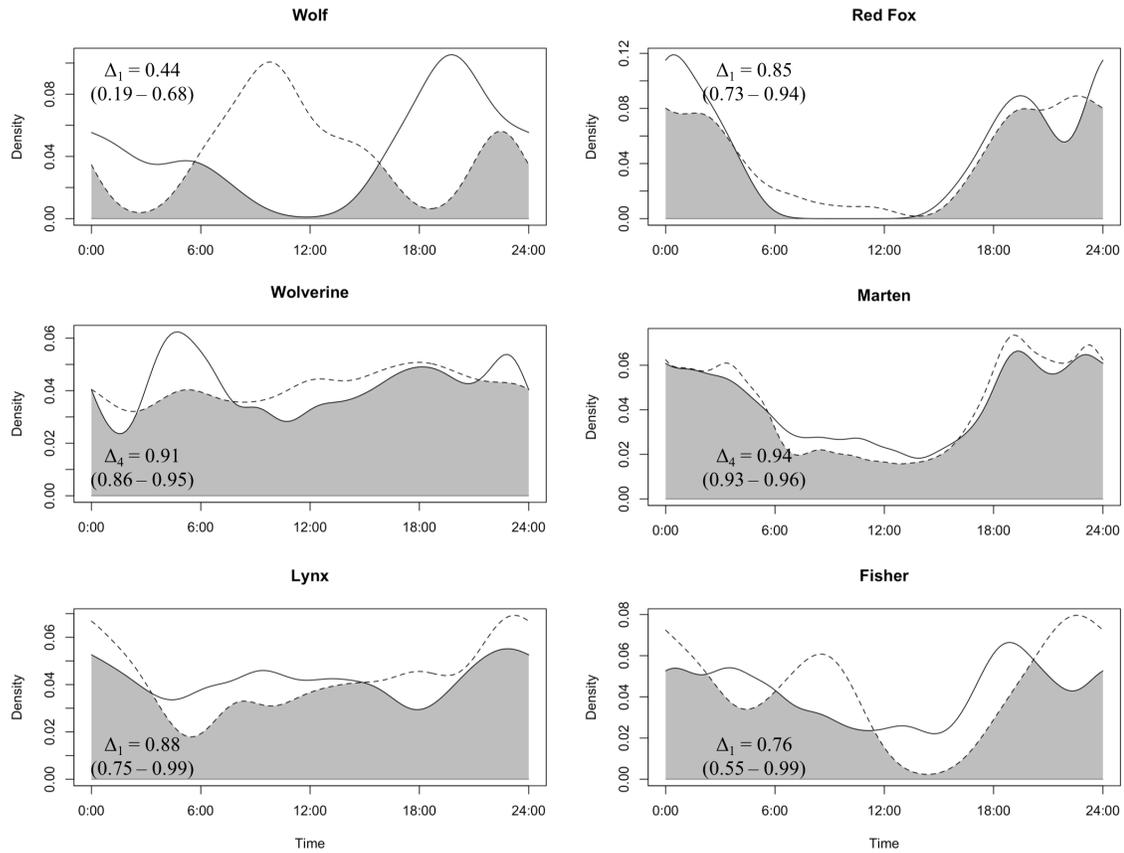


Figure 3.3: Diel activity curves and temporal overlap of carnivore species between high (solid line) versus low (dashed line) levels of linear disturbance features at the camera-site level in the Willmore Wilderness. Activity overlap (i.e. periods of no change in activity) is represented by the coefficient of overlap (Δ ; denoted in grey) accompanied by the 95 % confidence intervals in parentheses.

Within the more disturbed KC landscape, carnivore species also shifted activity patterns in relation to degree of linear disturbance (Figure 3.4). We captured a minimum of ten detections for five carnivore species, including cougar, marten, coyote, bobcat, and fisher (Appendix A, Table A.3). Similar to the WW, marten significantly shifted activities between camera sites of low versus high levels of linear disturbance ($\chi^2 = 6.61$, d.f. = 2, p-value < 0.05), increasing diurnal activities at low disturbance camera sites. Bobcat activity also shifted significantly in response to site-scale linear disturbance ($\chi^2 = 10.61$, d.f. = 2, p-value < 0.01), sharply increasing nocturnal and pre-dawn activities at high disturbance sites. Coyote increased diurnal activity at low disturbance sites ($\chi^2 = 5.64$, d.f. = 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.

Activity shifts at the camera-site level were

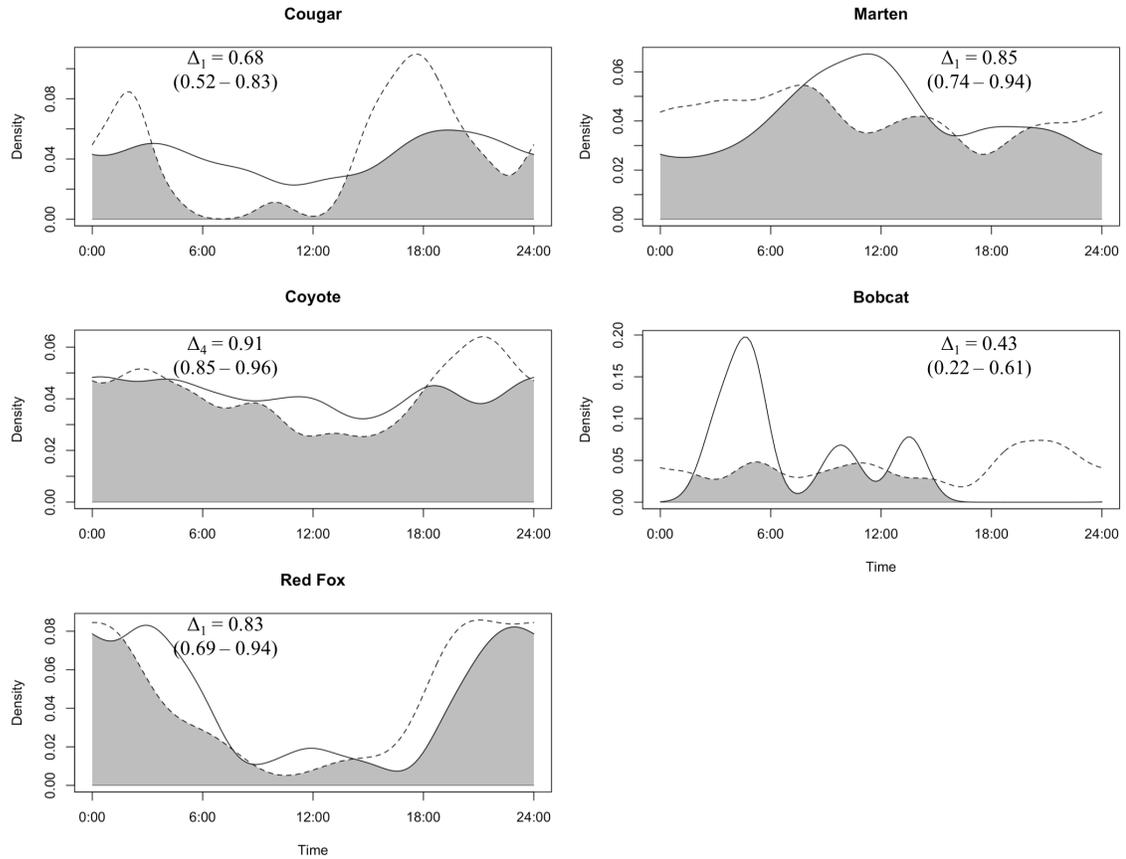


Figure 3.4: Diel activity curves and temporal overlap of carnivore species between high (solid line) versus low (dashed line) levels of linear disturbance features at the camera-site level in Kananaskis Country. Activity overlap (i.e. periods of no change in activity) is represented by the coefficient of overlap (Δ ; denoted in grey) accompanied by the 95 % confidence intervals in parentheses.

3.3.3 Influence of anthropogenic landscape change on carnivore temporal niche partitioning

Our *post-hoc* candidate model selection supported our hypothesis that anthropogenic landscape change and occurrence of competitor species were the most important factors predicting wolverine–marten activity overlap in the WW. Specifically, a combination of seismic line density, frequency of fisher occurrences, and wolverine sample size were retained in the best-supported model (Table 3.2). Activity overlap between these species significantly decreased with increasing site-scale disturbance, while the presence of competitors increased overlap between wolverine and marten (Table 3.3). Wolverine sample size was an important predictor across all top models ($\Delta\text{AIC} < 2$; Table 3.2), demonstrating that data density is a vital consideration in activity overlap analyses.

Table 3.2: Wolverine and marten temporal overlap in response to natural landscape features, anthropogenic disturbance, and community characteristics. Model 8 is the best-supported.

Model Set	Model No.	Model Variables	AICc score	ΔAICc	AICc weight
<i>Landscape Development + Competitor Co-occurrence</i>	8	Seismic + Fisher + Wolverine	-44.91	0	0.35
<i>Null Hypotheses (Sample size sensitivity)</i>	2	Wolverine	-43.07	1.84	0.14
<i>Null Hypotheses (Sample size sensitivity)</i>	1	Marten + Wolverine	- 42.87	2.04	0.13
<i>Anthropogenic Landscape Development</i>	7	Seismic + Wolverine	- 42.20	2.51	0.10
<i>Natural Land Cover</i>	3	Forest + Wolverine	-41.55	3.36	0.07
<i>Competitor Co-occurrence</i>	5	Fisher + Wolverine	-41.24	3.67	0.06
<i>Landscape Development + Competitor Co-occurrence</i>	9	Seismic + FisherPA + Wolverine	-41.10	3.81	0.05
<i>Natural Land Cover</i>	4	NatOpen + Wolverine	-41.01	3.90	0.05
<i>Competitor Co-occurrence</i>	6	FisherPA + Wolverine	-40.48	4.43	0.04
<i>Risky Landscapes + Competitor Co-occurrence</i>	10	NatOpen + Fisher + Wolverine	-38.54	6.37	0.01
<i>Risky Landscapes + Competitor Co-occurrence</i>	11	NatOpen + FisherPA + Wolverine	- 38.11	6.80	0.01

Estimation of Δ was highly sensitive to sample sizes, and measures of activity overlap between marten and wolverine increased with an increasing number of wolverine detections (Table 3.3). For example, the exclusion of a single camera site with a high number of fisher detections (Appendix A, Table A.4) shifted results of our candidate model selection to weakly favour the combination of site-scale marten and wolverine detections as the best predictors of activity overlap (Model 1), with seismic disturbance recognized as an important predictor in the second-best model (Model 8; Appendix A, Table A.5).

Table 3.3: Parameter estimates of top model predicting activity overlap between marten and wolverine.

	Estimate	Standard Error	p-value
(Intercept)	0.93298	0.08846	< 2e-16
Seismic	-0.30670	0.10980	0.00522
Fisher Count	0.27366	0.12444	0.02787
Wolverine Count	0.35575	0.10122	0.00044

3.4 Discussion

Anthropogenic landscape change alters carnivore species' diel activity patterns, and how competitor species partition time as a resource. Multiple carnivore species shifted activity patterns between the disturbed and undisturbed landscapes, with consistent shifts in response to site-level landscape change. Wolves decreased diurnal activities and compensated with increased nocturnal activity peaks. In contrast, coyote broadened their activity distribution across the diel cycle, and marten increased diurnal activity in relation to anthropogenic landscape change. These varied responses within the carnivore guild suggest that behavioural shifts may manifest as both direct and indirect responses to human disturbance, with apex and mesocarnivores responding differently. For mesocarnivore species, indirect biotic drivers better explain behavioural changes over the diel cycle than direct measures of anthropogenic landscape disturbance.

3.4.1 Apex- and meso-carnivore responses to anthropogenic landscape change

Apex predators and mesocarnivore species respond differently to human-mediated disturbance. As predicted, wolves decreased diurnal activities in relation to anthropogenic landscape change, although low sample sizes could not provide a definitive significance test. Large carnivores are subject to a “landscape of fear” (Laundré et al. 2001) associated with mortality from humans. And wolves, which endure persecution in the KC and are culled in the Rockies to reduce mortality in endangered woodland caribou (Hervieux et al. 2014), are no exception. The reduced diurnal activity of wolves in the KC is likely a direct response to the 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 our results. 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 processes.

Activity shifts in the mesocarnivore guild manifested as bi-directional and complex responses, likely due to the indirect and cascading effects of disturbance. In contrast to other studies reporting increased nocturnality in coyote in relation to human disturbance (Wang 2015; Reilly et al. 2017), coyote in the KC 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 observed increased nocturnality in wolves, a main competitor and predator of coyotes (Berger and Gese 2007; Levi and Wilmers 2012), or to broader population declines and range contraction of apex predators on disturbed landscapes. Both wolves and cougars have been reported to avoid habitats with high levels of human activity (Heim 2015). 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 other findings reporting positive responses in

coyotes to human disturbance (Toews et al. 2018) providing further evidence that human-tolerant species likely benefit from disturbance-mediated behaviours in apex predators.

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 KC. Subdominant mesocarnivore species such as marten may be forced to shift activities into the diurnal period due to increased nocturnal activity of apex carnivores on disturbed landscapes, or 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 may incur potential fitness costs on subdominant carnivores, including ecological (e.g. decoupling from preferred prey species, increased competitive interactions) and physiological costs (coping with suboptimal light and temperature conditions). Over time, such negative fitness consequences may manifest as sublethal effects leading to population declines and species’ range contractions on human modified landscapes.

3.4.2 Caveats

A variety of caveats may have limited our ecological inference from the observations for species’ activity shifts in relation to human footprint. Firstly, recent studies (Lashley et al. 2018) have identified 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 KC, 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, this provides strong evidence that the observed activity shifts most likely manifested as a response to human disturbance.

3.4.3 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 sympatric carnivores. Models testing hypotheses of activity overlap between wolverine and marten were very sensitive to the number of site-scale detections (Appendix A, Table A.5). 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 we focused on our two most frequently observed species in the WW, marten ($n = 9939$) and wolverine ($n=993$), an average of 25 (SD 14) wolverines were observed per individual site and less than half of our camera sites had ≥ 10 detections of both species. Recent studies have suggested that a minimum of 100 detections are necessary to accurately estimate 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. This observed bias and error arising from the low sample sizes used in our study 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 KC landscape, which encompasses a much more significant human footprint gradient. 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. We therefore 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.

3.4.4 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; Fisher and Burton 2018). Such processes are likely at play in the KC 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 KC 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.

3.5 Conclusions

We demonstrate that carnivore species behave differently on human disturbed landscapes. Furthermore, this study highlights that the effect of human disturbance on species' activity patterns may manifest through indirect biotic effects instead of direct habitat effects, as we observed for mesocarnivore species. Detecting such shifts in species' activities and patterns of temporal niche partitioning provides us with direct insight into potential drivers of wildlife losses on disturbed landscapes. Although spatial and numerical responses to human-mediated disturbances are well documented, we know very little about the mechanisms effectuating them. Preceding obvious responses such as species' range contractions and population declines, more subtle responses may signal larger-scale future change, including changes in species' behaviours and altered species interactions. Further research focused on detecting changes to species' behaviour with an integrated understanding of species' spatiotemporal interactions may provide us with new information for pre-emptively managing against biodiversity losses as humans continue to expand into and develop natural areas across the planet.

Chapter 4

But seriously, who let the dogs out? Impacts of free-ranging dogs (*Canis familiaris*) on mesocarnivore ecology on a disturbed landscape

With Frances E.C. Stewart, Jason T. Fisher, and John P. Volpe

4.1 Introduction

As humans have spread across the world, thousands of introduced species have settled into various novel habitats (Vitousek et al. 1997). Although the negative impacts of wild invasive alien species on native species and wildlife communities are widely recognized (Diamond 1989; Simberloff and Stiling 1996), domestic animals closely associated with humans also pose a major conservation concern (Young et al. 2011; Loss et al. 2013). As a “seemingly welcome commensal” of humans (Gompper 2013), domestic dogs (*Canis familiaris*) have been introduced into a variety of habitats and ecosystems across the globe (Wandeler et al. 1993). With an estimated global population of 700 million–1 billion (Hughes and Macdonald 2013; Silva-Rodríguez and Sieving 2012), feral and domestic dogs are the most widespread carnivore (Vanak and

Gompper 2009). Given their close association with humans and human settlements (Gompper 2013), domestic dogs may represent an extension of anthropogenic disturbance into natural environments. However, despite their vast distribution across many different ecosystems, we are only beginning to understand the extent of impacts of domestic dogs on wildlife communities (Lenth et al. 2008; Vanak and Gompper 2010).

Understanding dog-wildlife interactions in ex-urban environments is an important component of managing human-associated disturbances on wildlife. Ex-urban development is a fast-growing form of land-use in many parts of the world (Hansen et al. 2005; Recio et al. 2015) and dogs are a strongly associated component of rural-residential developments (Butler et al. 2004; Krauze-Gryz et al. 2012). Rural areas bordering natural protected areas are also the most likely to experience dog-wildlife interactions (Gompper 2013). And as most dogs engage in free-roaming behaviour (WSPA 1990), this enables direct and unregulated interaction with native wildlife. Increasingly, such interactions are recognized as contributors to biodiversity decline in association with ex-urban development (Hughes and Macdonald 2013), extending human-mediated disturbances into previously undisturbed wildlife areas.

Free-ranging dogs are defined as those that are owned or peripherally associated with human habitations but are not confined to a prescribed outdoor area (Ritchie et al. 2014), and interact with native species in a variety of ways. Like their feral counterparts, free-ranging dogs may interact with wildlife as prey (Butler et al. 2004), predators (Young et al. 2011; Ritchie et al. 2014), and disease reservoirs (Laurenson et al. 1998; de Almeida Curi et al. 2010). Dogs also interact with native carnivore species as competitors (Butler et al. 2004; Vanak and Gompper 2010). Interference competition in the form of harassment, aggressive encounters, or in extreme cases, intraguild predation (Holt and Polis 1997) introduce both lethal and sublethal effects, exerting significant pressures on native carnivore communities.

Interference competition elicits a variety of responses in native carnivores which may contribute to population declines through both lethal and sublethal effects. Descended from the grey wolf (*Canis lupus*; Savolainen et al. 2002), dogs may impose top-down control on smaller carnivores (mesocarnivores). Beyond suppressing mesocarnivore populations through direct killing and intraguild predation (Glen et al. 2007), non-consumptive effects of dog presence and interaction may also incur demographic costs to native carnivore populations through sublethal effects associated with fear-induced changes in physiology, habitat-use, and behaviour (Doherty et al. 2017). Increased energy output and elevated stress levels from harassment may im-

pact species' growth, reproductive fitness, and survival. Likewise, increased vigilance and decreased food uptake due to predation risk from dogs also incur negative fitness costs on sympatric carnivores (Vanak et al. 2009). Numerous studies also report on spatial shifts as carnivores respond to a 'landscape of fear' (Laundré et al. 2001) imposed by dogs, including maned wolf (Lacerda et al. 2009); Indian fox (Vanak and Gompper 2010), Chilla fox (Silva-Rodriguez et al 2010); red fox (Mitchell and Banks 2005), fosa (Barcala 2009), and raccoons (Suraci et al. 2016).

Sub-lethal effects from interference competition with domestic dogs may also manifest through behavioural responses. In areas with domestic or feral dogs, native carnivores shift daily activity patterns away from dog activity periods, presumably to reduce the likelihood of direct interaction (Gerber et al. 2012; Farris et al. 2015; Zapata-Ríos and Branch 2016). Such temporal displacement can incur fitness costs as species shift activities into suboptimal foraging or thermoregulatory conditions, or decouple from prey activities (Brook et al. 2012). Furthermore, temporal partitioning from dog activity could increase competitive interactions between native carnivores as species increase activity overlap into periods when dogs are less active. Despite the growing recognition of domestic dog disturbance on wildlife communities, little is known to what extent native carnivores alter their behaviours and interactions in response to the presence of dogs. In this study, we seek to characterize the sub-lethal effects of free-ranging domestic dogs on native carnivores through altered species' behaviour and interactions.

We hypothesized that domestic dogs – as a competitor of native carnivores and a component of human disturbance on developed landscapes – drive behavioural responses in native mesocarnivore competitors that manifest as shifts in diel activity patterns. We tested for responses within the mesocarnivore community to dog activity and distribution on a mixed-use landscape of ex-urban developments, agriculture, and resource extraction amid a matrix of native protected forests. To understand the impacts of domestic dogs on native carnivore behaviour and competitive interactions on developed landscapes, we 1) tested for mesocarnivore species' activity shifts in relation to dog activity and 2) evaluated the influence of site-level anthropogenic landscape change and co-occurrence with dogs on activity overlap between native mesocarnivores. Given the documented lethal, competitive, and sublethal effects of domestic dogs on wildlife, we hypothesized that carnivores would shift diel activities away from dog activity at sites where dogs were detected. We predicted that species with a similar activity patterns as domestic dogs would exhibit the largest activity

shifts at sites where dogs were detected due to increased potential for direct interaction. We hypothesized that co-occurrence with domestic dogs and human-mediated landscape disturbance would predict patterns of temporal niche partitioning between native mesocarnivores, increasing activity overlap between species due to fear-based activity shifts.

4.2 Methods

4.2.1 Study Area

The Beaver Hills Biosphere (BHB) is a 1596 km² ‘knob and kettle’ landscape of steeply rolling hills and abundant water (Figure 4.1). Located in east-central Alberta east of Edmonton, this glacial moraine captures a diversity of landcover types including aspen parkland, wetlands, open meadows, and scattered pockets of spruce. The BHB is a mixed-use landscape featuring a patchwork of exurban development and agriculture with protected forest areas owned privately and by non-governmental organization (i.e. Ducks Unlimited, the Nature Conservancy of Canada, and the Edmonton Area Land Trust). This close integration of natural features and privately-owned land yields a high potential for human- and dog- wildlife interactions on this landscape. The edge effect between the Aspen Parkland and Dry Mixedwood Boreal natural sub-regions (Natural Regions Committee 2006) on this landscape contributes to a high biodiversity of species within the BHB. This includes a diverse mesocarnivore community of fisher (*Pekania pennanti*), red fox (*Vulpes vulpes*), coyote (*Canis latrans*), least weasel (*Mustela nivalis*), and short- and long-tailed weasel (*Mustela ermina* and *frenata*).

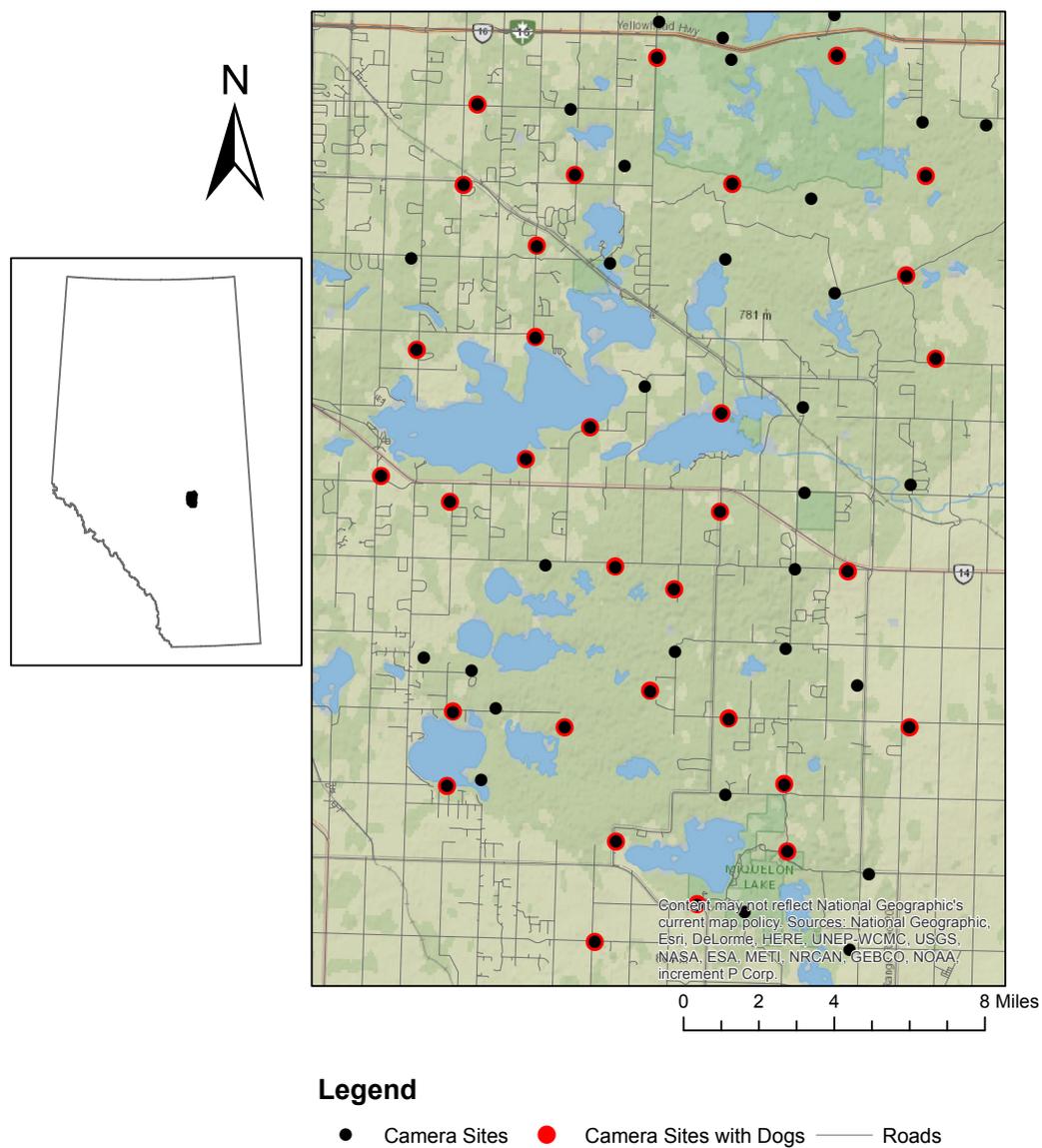


Figure 4.1: Sixty-four cameras traps were deployed across the Beaver Hills Biosphere in east-central Alberta, Canada. Red circles indicate camera sites where domestic dogs were detected.

4.2.2 Statistical Analyses

4.2.3 Sampling Design

We used remote camera trapping (Burton et al. 2015) to quantify species' activity patterns by capitalizing on previous studies monitoring mammal occurrence (Stewart et al. 2017; Stewart 2018; Burgar et al. in review) and diversity (Stewart et al. in review) in relation to landscape structure and connectivity. We collected photographic data 64 Reconyx infrared-triggered cameras (models PC900 and PC85; sensu Fisher and Bradbury 2014) deployed in a 4 x 4 km² systematic grid cell array across the BHB. Cameras were deployed and checked monthly from November 2013 to June 2014 and December 2015–April 2016. Camera sites were baited with commercial scent lure (O’Gorman’s Long Distance Call). Between December and April, and 5 kg beaver meat in view of the camera. During May–June, 0.5 kg of dog biscuits (Milk-Bone®Large) replaced the beaver bait due to complications with using raw bait in warmer temperatures. Each camera image represented the spatial, and temporal, location of species occurrence, as collected from the spatial location of the camera and time stamp on the camera image.

4.2.4 Statistical Analyses

We tested the hypothesis that mesocarnivores shift their diel activity in relation to domestic dog activity using kernel density estimation techniques (Ridout and Linkie 2009). First, we compared mesocarnivore species' activity patterns between camera sites where dogs were detected (“Present”) and sites where dogs were not detected and assumed to be absent (“Absent”). We tested for significant shifts in mesocarnivore activity in relation to site-level dog presence/absence by quantifying temporal overlap between dog activity averaged across the BHB, with mesocarnivore activity at camera sites with and without dogs. We also tested the influence of domestic dog activity and anthropogenic landscape disturbance on temporal niche partitioning between mesocarnivore species. We modelled site-scale activity overlap between co-occurring mesocarnivore species in relation to dog presence, landscape development features, and other landscape variables hypothesized to influence mesocarnivore temporal overlap.

For every wildlife detection captured by cameras, we recorded camera trap ID, date, time, species, and number of individuals recorded. We treated any dog and

mesocarnivore photographs containing more than one individual as a single observation (i.e. time data point) and excluded wildlife photographs captured within 30 minutes of a prior detection of the same species from all temporal analyses to maintain independence of detections. We adopted a standardized circadian scale to a 0600h sunrise and 1800h sunset to facilitate ecological interpretation of species’ activity patterns (Carver et al. 2011; Rheingantz et al. 2016). We rescaled raw observations of time of each detection record to this standardized scale through interpolation of the observed sunrise and sunset times at that location on that date determined through Nouvellet et al.’s (2014) *SunTime* code. As seasonal changes to temperature and photoperiod may drive behavioural shifts in seasonal activity, we separated our data into “winter” (November–April) and “summer” (May–June) sampling seasons. This division also reflects the methodological switch from raw beaver bait to dog biscuits. We determined whether mesocarnivores shifted activities in relation to presence and activity of domestic dogs by separating our data into photographs that were captured at sites where dogs were present and sites where dogs were absent.

4.2.5 Mesocarnivore activity patterns in relation to dog activity

We applied non-parametric kernel density estimation techniques described in Ridout and Linkie (2009) to the temporal data from camera traps. This approach treats detection times as a random variable from a continuous distribution, generating a probability density function representing the 24-hour activity pattern of a given species. We limited analyses of species’ activity patterns to those samples with a minimum of ten detections. All statistics were analyzed using the *Overlap* package (Meredith and Ridout 2017) in R (R Core Development Team, 2017).

To test our hypothesis that mesocarnivores shift activity patterns in response to dog co-occurrence, we compared mesocarnivore species’ diel activity curves between camera sites where dogs were present versus absent. We evaluated mesocarnivore activity shifts in relation to dog presence using a similar approach as Reilly et al.’s (2017) study investigating species’ activity shifts in response to recreation, focusing instead on dog activity. First, we estimated a mean activity pattern for dogs throughout the BHB for each season. Second, we calculated the overlap between mean activity patterns of dogs and mesocarnivores at sites (1) with dogs present, and (2) with dogs absent. We calculated activity using kernel density estimation techniques that

calculate a coefficient of overlap (Δ) as an integrated difference between two kernel density functions (Ridout and Linkie 2009). This coefficient of overlap (Δ) ranges between 0 and 1, with 1 indicating complete overlap. Following the recommendations of Meredith and Linkie (2017), we used Δ_4 for large sample sizes ($n > 75$) and Δ_1 for smaller sample sizes ($n < 75$). If mesocarnivores alter behaviour in relation to dog activities, we predicted they would temporally segregate from periods of overall dog activity where they co-occurred, but not at sites where dogs were absent. We calculated 95% confidence intervals for each Δ through 1000 bootstrap samples. For each mesocarnivore species, we compared the 95% confidence intervals for Δ at sites with dog detections to the corresponding 95% confidence intervals for Δ at sites where dogs were not detected and assumed to be absent. If the 95% confidence intervals did not overlap, we considered the mesocarnivore activity patterns to be significantly different, supporting our hypothesis of activity shift in relation to dog presence.

4.2.6 Influence of domestic dogs on mesocarnivore temporal niche partitioning

To test our hypothesis that human-mediated disturbances – including domestic dogs and landscape development – influence temporal niche partitioning between sympatric carnivores, we determined Δ between spatially co-occurring mesocarnivore species-pairs across camera sites. We limited this analysis to the winter sampling season (the period with suitable data density) and focused on the two most commonly detected mesocarnivores: fisher and coyote. We selected camera sites where a minimum of ten detections were observed for both native mesocarnivores. We formed multiple competing hypotheses about the effects of natural landscape features, human disturbance, and presence of domestic dogs on activity overlap. We ranked support for these hypotheses using multiple regression analyses in a model selection framework based on Akaike Information Criterion (AIC) scores (Burnham and Anderson 2002). We applied beta regression (appropriate for response variables bounded by the standard unit interval, i.e. $0 < y < 1$; Ferrari and Cribari-Neto 2004), to model coyote-fisher overlap against multiple landscape and disturbance variables hypothesized to influence temporal niche partitioning between these mesocarnivores (Table 4.1). Landscape features and human footprint were measured as the proportion area within a 2000-m circular buffer at each camera site using ArcGIS v10.3 (ESRI, Redlands, CA, USA) Geographic Information Systems. Landsat digital map inventories

from the Alberta Biodiversity Monitoring Institute (ABMI) were used to quantify the primary natural land cover features (Landsat Map 2014) and human footprint including linear features and anthropogenic block features (Human Footprint Map 2014; Appendix B, Table B.1).

We created candidate models of natural land cover characteristics specifying forested versus open landscapes, which we hypothesized influence perceived predation risk; open landscapes of grassland and shrub cover could be perceived as highly risky for fisher due to the absence of important vertical escape (tall tree) cover, leading to decreased activity overlap as fishers temporally avoid coyote. Open grassland areas support high densities of small mammalian prey (Brown 1995; Delattre et al. 1992), thereby also representing landscapes of abundant resources for mesocarnivores. Cultivated areas, though also risky landscapes with increased prey resources (Jeffrey 1977; Delattre et al. 1992), may be associated with enhanced human or dog activity. We therefore analyzed the effects of cultivation fields used for agriculture separately from natural open landscapes. To test for the effects of human-associated disturbance features including domestic dogs, we included various candidate models specifying linear features (hard roads, vegetated roads, trails, seismic lines, pipelines, and transmission lines), block features (rural residential homes, oil well sites, and development areas), and domestic dog presence. These we hypothesized would increase activity overlap between fisher and coyote due to temporal segregation from human and dog activity periods. Lastly, we tested for bias in Δ introduced by low sample sizes by including sample size of detections for coyote and fisher within candidate models: our null hypotheses. We used the R package *betareg* to perform beta regression (Cribari-Neto and Zeileis 2009), and *AICcmodavg* (Mazerolle and Mazerolle 2017) for our candidate model selection. We ranked models corresponding to each hypothesis using an information-theoretic approach (AIC) which uses maximum likelihood estimation and the principle of parsimony to evaluate the relative support for alternative hypotheses by estimating the model that best explains coyote-fisher activity overlap (Burnham and Anderson 2002). We used Akaike's Information Criterion adjusted for smaller sample sizes (AICc; Burnham and Anderson 2002). Lower AICc scores indicate increased parsimony and improved fit relative to other candidate models tested, and candidate models were ranked using AICc weights (AICw). We also calculated the evidence ratio (ER) to weigh support for the top model relative to the second-best model (Burnham and Anderson 2002).

Table 4.1: List and description of land cover, human footprint, and dog disturbance variables hypothesized to explain temporal niche partitioning between coyote and marten in the Beaver Hills Biosphere.

Model Set	Model No.	Model Variables	Hypothesis: Coyote and Fisher Temporal Overlap (Δ) is predicted by
Null hypotheses (Sample size sensitivity)	1	Coyote + Fisher	Number of coyote and fisher events
	2	Coyote	Number of coyote events
	3	Fisher	Number of fisher events
Land Cover (Perceived riskiness of forested versus open landscapes)	4	Forest	Forest cover (coniferous, deciduous, and mixed combined)
	5	NatOpen	Natural open cover (shrub and grassland combined)
	6	Cultivation	Agricultural open cover
	7	NatOpen + Cultivation	Natural and agricultural open cover
Domestic dogs	8	Dog	Presence / absence of domestic dogs
Human footprint	9	Linear	Anthropogenic linear features
	10	Block	Anthropogenic block features
	11	Linear + Block	Anthropogenic linear and block features combined
Human and dog disturbance (Combined effects of human footprint and dog presence)	12	Linear + Dog	Anthropogenic linear features and dog presence
	13	Block + Dog	Anthropogenic block features and dog presence
	14	Linear + Block + Dog	Anthropogenic linear features, block features, and dog presence
Land cover and dog disturbance (Combined effects of risky landscapes and dog presence)	15	NatOpen + Dog	Natural open cover and dog presence
	16	NatOpen + Cultivation + Dog	Natural and agricultural open land cover and dog presence

4.3 Results

Repeat observations of six native mesocarnivore species were detected across the 64 cameras, including coyotes, red fox, fisher, least weasel, and long- and short-tailed weasel. During the winter and summer sampling periods, dogs were detected across 29 (45%) and 16 (25%) sites, respectively (Table 4.2). Dogs were largely observed to be free-ranging (i.e. without an accompanying human present).

Table 4.2: Number of temporally independent dog and native mesocarnivore species' detections (number of camera sites at which species was detected) between the winter and summer sampling seasons.

Species	Winter	Summer
Domestic Dog	419 (29)	63 (16)
Coyote	1274 (61)	603 (57)
Fisher	723 (45)	184 (25)
Red fox	110 (23)	37 (11)
Short-tailed Weasel	135 (12)	13 (5)
Long-tailed Weasel	65 (10)	1 (1)
Least Weasel	0	3 (3)

4.3.1 Mesocarnivore activity patterns between camera sites with and without domestic dogs:

Mesocarnivores altered activity patterns at sites where they co-occurred with dogs, responding more strongly to dog disturbance during the summer when dogs were active at night. Activity shifts for coyote and possibly fisher suggested temporal avoidance from time-periods when dogs were most active, although these did not reach statistical significance. Dogs shifted activity patterns between the winter and summer sampling seasons, resulting in increased activity overlap with mesocarnivores during summer. During winter, dogs were primarily active during the diurnal hours (Figure 4.2). In contrast, dogs shifted towards increased nocturnality during the summer (Figure 4.3), with increased activity during the middle of the night. With the exception of long-tailed weasel, mesocarnivore species largely selected for the nocturnal period and overlapped minimally with domestic dog activity during winter (Figure 4.2, Table 4.3). However, increased nocturnal dog activity during summer greatly increased activity overlap with coyote and fisher (Table 4.3). Coyote and fisher activity patterns were largely consistent across camera sites with and without dog detections during the winter (Figure 4.2). Red fox remained largely nocturnal across all camera sites, but broadened nocturnal activities at camera sites where dogs were present (Figure 4.2). Short-tailed weasel were more active after midnight at camera sites without dogs than sites with dogs, while long-tailed weasel slightly increased their nocturnal activities where dogs were present (Figure 4.2). During the summer,

fisher slightly increased diurnal activities across camera sites with dogs compared to sites without dogs. Coinciding with peak dog activity, fisher decreased activity near midnight at sites where they co-occurred with dogs (Figure 4.3). Coyote increased diurnal activities across sites where dogs were present, with a midday activity peak that was absent across sites without dog detections. However, these activity shifts did not reach statistical significance, as 95% confidence intervals overlapped for dog-mesocarnivore Δ across sites with and without dogs (Table 4.3) .

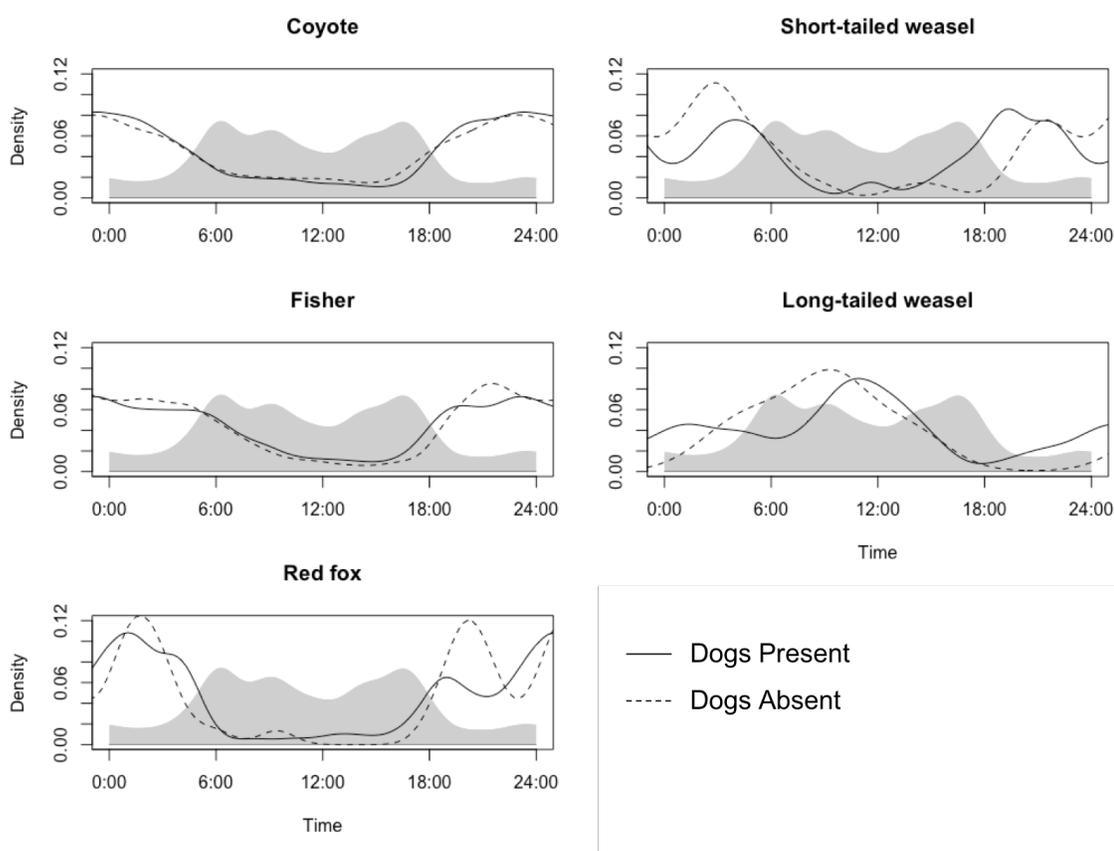


Figure 4.2: Winter activity patterns of five mesocarnivore species at camera sites where domestic dogs were present (solid line) versus absent (dotted line). Activity patterns of dogs across the BHB (grey shading) were largely diurnal. Mesocarnivore activity at sites with dogs did not differ significantly from the activity patterns at sites where dogs were absent.

Table 4.3: Seasonal overlap (Δ) between the overall activity pattern of domestic dogs in the BHB and mesocarnivore species across sites where dogs were detected (“present”) or not (“absent”). Overlapping 95% confidence intervals indicate that the difference in overlap was not statistically different for any mesocarnivore species. Insufficient detections of red fox, short- and long-tailed weasels precluded comparisons during the summer sampling period.

	Species	Dogs Present Δ(95%CI)	Dogs Present Δ(95%CI)	Difference (Presence- Absence)
Winter	Coyote	0.455 (0.407 - 0.503)	0.503 (0.455 - 0.557)	-0.048
	Fisher	0.526 (0.467 - 0.586)	0.460 (0.405 - 0.517)	0.066
	Red Fox	0.432 (0.290 - 0.474)	0.306 (0.215 - 0.407)	0.126
	Short-tailed weasel	0.511 (0.415 - 0.609)	0.426 (0.327 - 0.527)	0.085
	Long-tailed weasel	0.705 (0.604 - 0.800)	0.721 (0.551 - 0.872)	-0.016
Summer	Coyote	0.913 (0.831 - 0.985)	0.894 (0.804 - 0.972)	0.019
	Fisher	0.828 (0.712 - 0.917)	0.831 (0.734 - 0.924)	-0.003

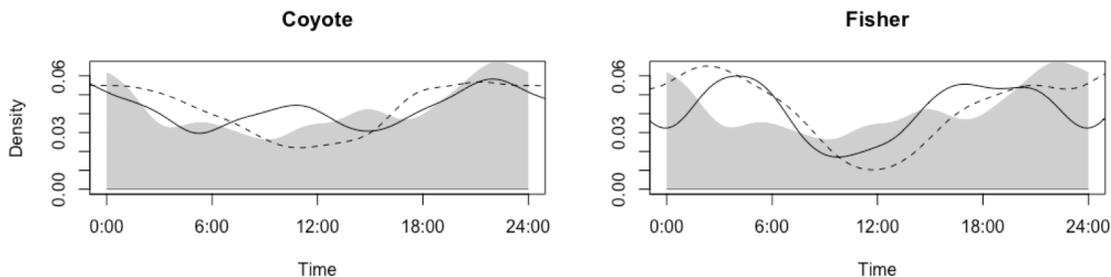


Figure 4.3: Summer activity patterns of fisher and coyote at camera sites where domestic dogs were “present” (solid line) versus “absent” (dotted line). Domestic dog activity (grey shading) increased during the nocturnal period. Activity patterns of mesocarnivores at sites where dogs were detected did not differ significantly from the activity patterns at sites where dogs were not detected. Due to small sample sizes, fox, short-tailed, and long-tailed weasel activity patterns are not shown.

4.3.2 Influence of domestic dogs on mesocarnivore temporal niche partitioning

Twenty-six (41%) camera sites captured a minimum of ten detections of both fisher and coyote during the winter sampling period, for which ten sites also detected dogs (Appendix B, Table B.2).

Natural open land cover strongly influenced coyote-fisher activity overlap (Model 5; Table 4.4). Coyote and fisher activity overlapped less in areas of increasing proportion of grassland and shrub cover (Appendix B, Figure B.1 ; parameter estimate -0.215 ± 0.066 standard error). This supports our hypothesis of temporal avoidance by fisher from coyote activity on open landscapes where encounters with a dominant competitor would be especially risky due to lack of vertical escape cover. Open land cover was 2.7 times better at explaining patterns of activity overlap between fisher and coyote than the combination of cultivation and open land cover, the second-best candidate model. After accounting for variability in activity due to land cover, dogs did affect coyote-fisher overlap. However, adding dog presence to the top model did not appreciably increase our explanatory power for predicting coyote-fisher overlap (Arnold 2010). Our hypothesis that competition with dogs influences winter activity overlap between sympatric mesocarnivores was therefore unsupported, with evidence instead indicating a strong influence of natural land cover on temporal niche partitioning and mesocarnivore interactions.

Table 4.4: Coyote and fisher temporal overlap in response to natural landscape features, anthropogenic disturbance, and domestic dog presence. Model 5 (in bold) is the best-supported.

Model Set	Model No.	Model Variables	AICc score	Δ AICc	AICc weight
Land Cover	5	NatOpen	-61.85	0	0.52
Land Cover	7	NatOpen + Cultivation	-59.85	2	0.19
Land Cover and Dog Disturbance	15	NatOpen + Dog	-59.26	2.59	0.14
Land Cover and Dog Disturbance	16	NatOpen + Cultivation + Dog	-56.77	5.08	0.04
Land Cover	6	Cultivation	-56.76	5.09	0.04
Dog Disturbance	8	Dog	-54.52	7.33	0.01
Human Footprint	9	Linear	-54.07	7.78	0.01
Land Cover	4	Forest	-53.49	8.36	0.01
Null Hypothesis	2	Coyote	-53.45	8.40	0.01
Null Hypothesis	3	Fisher	-53.43	8.42	0.01
Human Footprint	10	Block	-53.40	8.45	0.01
Human Footprint and Dog	12	Linear + Dog	-52.76	9.09	0.01
Human Footprint and Dog	13	Block + Dog	-51.72	10.13	0
Human Footprint	13	Block + Linear	-51.36	10.49	0
Null Hypothesis	1	Coyote + Fisher	-50.69	11.15	0
Human Footprint and Dog	1	Block + Linear + Dog	-49.73	12.12	0

4.4 Discussion

Domestic dog disturbance and landscape characteristics alter mesocarnivore diel activities and patterns of temporal niche partitioning. High levels of activity overlap with fisher and coyote during summer augments dog-mediated competitive pressures on the native mesocarnivore community. As a likely direct response to increased interference competition with dogs during nighttime, native mesocarnivores shifted activity patterns at sites where they co-occurred with dogs. In winter when dogs were primarily diurnal, co-occurrence with dogs did not shift mesocarnivore activity patterns nor did it appear to affect temporal niche partitioning within the mesocarnivore community. Instead, fisher and coyote partitioned activities differently in relation to landscape characteristics of perceived risk and resource abundance. Fisher and coyote segregated activities on open landscapes lacking vertical escape cover but abundant in prey resources.

Resultant activity shifts in mesocarnivores in relation to dog disturbance may not only impact species' fitness (Vanak et al. 2009) but also alter patterns of temporal niche partitioning within wildlife communities, with potential repercussions to community structure. Although dogs did not drive patterns of temporal niche partitioning between mesocarnivores beyond landscape effects during winter, dogs exert a strong influence during summer due to increased activity overlap with native mesocarnivores during the nighttime. While further research may confirm the effects of dog presence on niche partitioning between mesocarnivores, we provide evidence that mesocarnivore competitors partition their time differently on open landscapes.

4.4.1 Mesocarnivore activity shifts in relation to dog activity

Domestic dogs dramatically shifted activity patterns from diurnality in winter to nocturnality in summer. Of the few studies on free-ranging and feral dog activity patterns, most report diurnal or crepuscular activity (e.g. Gerber et al. 2012; Farris et al. 2015; Zapata-Ríos and Branch 2016). However, Krauze-Gryz et al.'s (2012) study on free-ranging farmland dogs in central Poland did report a slight increase in detection probability during the nocturnal period. Corroborating our observations for seasonal activity shifts, they also observed an increase in nocturnal detections during the warmer months (Krauze-Gryz et al. 2012). Observed diurnality in dogs during the winter in the BHB may be due to extreme temperature conditions during the night at higher latitudes (our cameras recorded a low of -37°C), or direct human

intervention constraining dogs to the diurnal period. However, the unexpected dramatic shift towards nocturnality in the summer indicates that dogs on this landscape retain a large degree of autonomy from people, enhancing the potential for direct interactions with native mesocarnivore species, and exacerbating the consumptive and non-consumptive effects of dogs on rural landscapes.

Consequently, increased levels of nocturnal activity during summer resulted in high levels of temporal overlap with nocturnal mesocarnivores. For both coyote and fisher, activity overlap with dogs was significantly higher in summer than in winter (Table 4.3). As a likely response to increased overlap and potential for direct interaction with dogs during summer, coyote increased diurnal activity at sites where dogs were detected (Figure 4.3). The diurnal activity peak for coyotes was present only at sites where dogs were detected, and we did not observe it during the winter season when dogs were primarily diurnal, lending confidence to this conclusion. Likewise, we did not observe any significant activity shifts across mesocarnivore species in response to dog presence during winter. This indicates that winter diurnality in dogs results in minimal interference with native species' behaviour due to intrinsic temporal partitioning on this landscape, but that summer nocturnality increases potential for direct dog-wildlife interactions, thereby influencing mesocarnivore activity.

4.4.2 Temporal Niche partitioning between co-occurring mesocarnivores

Landscape characteristics best predicted winter activity partitioning between spatially sympatric fisher and coyotes. Fisher temporally segregate from co-occurring coyote on open landscapes of shrub and grassland lacking vertical escape cover but with abundant prey. Interestingly, proportion of forest cover (where escape cover is abundant) was not an important predictor of coyote-fisher activity overlap. Characteristics other than tree cover - which we suggest is prey availability - influences how mesocarnivores segregate activities on open landscapes.

Early seral stage communities and cultivation fields support high densities of small mammalian prey species (Delattre et al. 1992) exploited by both fishers (Weir et al. 2005) and coyotes (MacCracken and Uresk 1984; Dumond et al. 2001). Although fisher have been observed to avoid open landscape features (Badry 1995; Stewart 2018), coyote select for agricultural land (Toews et al. 2018), likely given the high prey abundance. If coyote presence increases on open landscapes due to enhanced

resource availability, then fisher may respond to this increased associated predation risk by shifting their activity period away from that of coyote. Such processes on cultivated fields may have been confounded by their association with anthropogenic activities and disturbance. Interestingly, many native grass- and shrubland areas in the BHB are used for livestock grazing, or are regenerating areas from prior agricultural development and grazing (Stewart, *pers.comm.*). Altered patterns of temporal niche partitioning between native mesocarnivore species may therefore represent responses linked with past human activities and modifications to the landscape. This suggests potential lasting impacts of human disturbance to resource distribution, with resultant changes to species' behaviours and interactions even after these disturbance pressures have been removed.

4.4.3 Caveats

Various factors may have prevented our ability to detect significant mesocarnivore activity shifts in relation to domestic dog activity, if extant. As we did not account for missed detections (as there is no current way to integrate activity pattern estimation with occupancy models; MacKenzie et al. 2002), dog disturbance may therefore have been more widespread across the BHB than we accounted for, distorting signals of mesocarnivore activity shifts in relation to site-scale dog presence. Furthermore, we cannot confirm whether or not foxes and mustelid mesocarnivores (fisher, short- and long-tailed weasel) distinguish predation threat of free-ranging dogs from coyote. As coyote were detected almost ubiquitously across all camera sites in each sampling season, smaller mesocarnivores may be responding more strongly to competitive and predation pressures associated with coyote than to domestic dogs.

Finally, the scarcity of species' detections during the summer period hampered our ability to evaluate the effects of dog disturbance across mesocarnivore species. Nocturnal dog activities would have been more likely to induce activity shifts in the summer. However, a short sampling period and lower detection frequencies during this season precluded comparisons of foxes, short- and long-tailed weasel activities, and likely impeded our ability to confirm significant activity shifts in coyote and fisher. Future research evaluating the impacts of free-ranging dogs in northern latitudes where seasonal extremes in temperature may induce activity shifts towards nocturnality during summer should therefore focus on the summer period when dogs are more likely to overlap with nocturnal native wildlife and thereby alter species'

behaviours and interactions.

4.4.4 Ecological Implications

Dogs are the most abundant carnivore world-wide (Vanak and Gompper 2009) and populations continue to expand alongside an ever-increasing human footprint (Hughes and Macdonald 2013; Silva-Rodríguez and Sieving 2012). With landscape development remaining one of the biggest threats to wildlife populations and communities (Sala et al. 2000), understanding how dogs and human landscape impact species' ecology and interactions in an era of human-driven biodiversity loss is a global conservation issue.

Our results indicate a greater potential for direct interaction between dogs and native carnivore species than previously recognized, with seasonal shifts towards nocturnality in free-ranging dogs increasing temporal overlap with mesocarnivores. This increase in dog-mesocarnivore overlap could enhance lethal and sub-lethal effects from predation and interference competition by dogs. Resultant activity shifts in mesocarnivores to temporally avoid such costly antagonistic interactions may also incur negative fitness consequences as species decouple from prey activity or optimal foraging periods, or through increased temporal overlap with other carnivore competitors (Wang et al. 2015).

Changes to activity overlap between spatially sympatric competitors may disrupt important competitive interactions structuring the community (Linnell and Strand 2000), and our results indicate that landscape characteristics directly influence inter-specific patterns of niche partitioning. Mechanisms of coexistence between fisher and coyote appear to be linked to the perceived riskiness and resource abundance of the natural landscape, and human activities such as logging, agriculture, and livestock grazing may influence spatiotemporal interactions between mesocarnivores. Anthropogenic land change may therefore not only impact wildlife habitat-use, as is the focus of many conservation studies (e.g. Riley et al. 2003; Crooks 2002; Newbold et al. 2015). Activities altering resource abundance and predation risk may also drive behavioural changes and altered species interactions, potentially contributing to altered carnivore assemblages and cascading effects on lower trophic levels.

Given their close association with human settlements, the addition of dogs on disturbed landscapes likely exacerbates the impacts of anthropogenic activities and habitat modification on wildlife communities. Free-ranging dogs may encroach into

the last vestiges of undisturbed habitat on which species may eke out their existence on human-modified landscapes, pushing species' closer to the edge of local extirpation. Likewise, extension of human-associated disturbances into the nighttime due to nocturnal dog activity may compromise behavioural adaptations required for co-existence alongside humans, such as temporal partitioning away from human diurnal activities.

We demonstrate that free-ranging dogs overlap considerably with mesocarnivore activity throughout parts of the year, resulting in behavioural shifts in native competitors and an increased potential for negative dog-wildlife interactions. In addition to such behavioural responses to dog activity, native mesocarnivores also segregate activities differently on open landscapes. Anthropogenic activities which create open habitat may therefore impact competitive interactions within ecological communities in previously unrecognized ways. As dogs, alongside humans, expand into natural landscapes, recognizing such broader effects of human-associated disturbances on species' and community ecology will be necessary for developing more conservation-effective land-use practices.

Chapter 5

Conclusions

Mounting evidence indicates that our presence and activities on the landscape alter temporal dynamics in wildlife communities, shifting animal diel activities (Gaynor et al. 2018) and changing patterns of niche partitioning between sympatric species (Schuette et al. 2013; Smith et al. 2018). Disturbance-induced changes to species' diel activities are liable to influence competitive interactions between sympatric species through altered patterns of temporal niche partitioning (Wang et al. 2015; Thorsen 2016). This may compromise important mechanisms facilitating coexistence within diverse assemblages of species (Lucherini et al. 2009; Di Bitetti et al. 2010; Monterroso et al. 2014), leading to biodiversity loss on human disturbed landscapes. In this thesis, I investigate diel activity shifts and resultant changes to species' temporal interactions in carnivore communities. My research helps further the growing body of literature linking anthropogenic disturbance to community-level responses by directly testing the impacts of disturbance-induced activity shifts on interspecific niche partitioning over the diel cycle.

My second chapter investigates the principal questions and analyses for studying temporal dynamics in animal communities using camera traps. I highlight the potential for evaluating the effects of human disturbance on species' behaviours and spatiotemporal interactions. My investigation of the recent advances and growing literature in this developing subfield highlights the need for robust sampling designs focused on extending insight into species' interactions over both space and time.

The third and fourth chapters directly evaluate the impact of human-mediated disturbances on carnivore activity patterns, and resultant changes to species' temporal niche partitioning. In the Canadian Rocky Mountain carnivore guild, multiple species shift activity in response to landscape and site-level anthropogenic distur-

bance. My findings indicate that apex- and meso-carnivores respond differently to anthropogenic disturbance, suggesting that human activities may impact carnivore behaviours through indirect and biotic pathways. Anthropogenic landscape change appears to influence activity overlap between co-occurring marten and wolverine, indicating altered competitive interactions between carnivores on human-modified landscapes. However, this analysis is highly sensitive to sample sizes, emphasizing the need for explicit study designs focused on maximizing site-level detections of sympatric species.

My study of mesocarnivore behaviours on a mixed-use landscape indicates that species' shift diel activities in relation to interference with domestic dogs. Seasonal nocturnality in free-ranging dogs increases activity overlap with a primarily nocturnal mesocarnivore community, driving activity shifts in coyote and enhancing the potential for negative dog-wildlife interactions. My findings also demonstrate that landscape characteristics influence temporal dynamics in mesocarnivore communities, with species partitioning activities differently in open habitat. This highlights potential implications of anthropogenic land-use practices on the competitive interactions structuring mesocarnivore communities.

Future Research:

Camera traps are invaluable for tracking the direct and indirect effects of anthropogenic disturbance on species' behaviours and interactions. However, teasing apart the interacting ecological processes and anthropogenic impacts on species' competitive interactions over both space and time requires purpose-designed data. Future studies seeking to evaluate the influence of human disturbance on spatiotemporal niche partitioning will need to employ explicit study designs focused on maximizing species co-occurrence data. This will likely be best achieved through long-term monitoring studies featuring coordinated camera-trap networks (*sensu* Fraser et al. 2016) across a large gradient of human footprint.

While my results demonstrate that species structure and segregate activities differently on human-modified landscapes, the sublethal costs or competitive advantages of such altered temporal dynamics still need to be directly evaluated. Future studies should seek to explicitly test for negative fitness responses in relation to disturbance-induced activity shifts and altered temporal niche partitioning between competitors, predators, and prey. Furthermore, as increasing evidence indicates that human dis-

turbance redefines the realized temporal niche space for many species (George and Crooks 2006; Díaz-Ruiz et al. 2016; Ngoprasert et al. 2017), additional research should also evaluate how this impacts intraspecific competition in wildlife populations, and the resultant demographic responses. For example, does cathemerality in coyote on disturbed landscapes facilitate population expansion through novel foraging opportunities across the diel cycle? Further investigation of such processes could yield a more mechanistic understanding of shifting community assemblages in relation to anthropogenic disturbance.

Future studies should also give special focus to the indirect impacts of disturbance-induced activity shifts in apex predators on the broader ecological community. Altered spatiotemporal activities in top predators may drive behavioural and demographic responses in mesocarnivore and prey communities through disruption of predator-prey dynamics and top-down control (Brook et al. 2012; Wang and Fisher 2012). Observed activity shifts in prey and mesocarnivore species on disturbed landscapes may manifest as direct responses to human disturbance, or indirect responses to altered predation risk or interference competition with top predators. Disentangling such interacting effects is a challenging task. However, purpose-designed data collection of mesocarnivore and prey species' distributions across both time and space on landscapes experiencing varied disturbance and predation pressures may help parse the differential influence of ecological processes and human impacts driving behavioural change.

Extending the current knowledge of sublethal disturbance impacts on the subtle and interacting processes underlying species' and community ecology will be an important step towards improving current conservation practices. As argued by Frid and Dill (2002), there is a danger in interpreting a lack of spatial responses in wildlife populations as a lack of disturbance impacts. If we wish to conserve wildlife communities alongside our ever-increasing human footprint, then we must also consider how our presence and activities impact species' behavioural coexistence strategies.

The future of many wildlife populations across the globe is a precarious one (Sala et al. 2000; Bellard et al. 2012; Dirzo et al. 2014). Understanding how we impact fundamental processes underlying species' and community ecology – and implementing management practices to mitigate against those impacts – may ensure a more promising future of human-wildlife coexistence.

Appendix A

A.1 Appendix A

Supplementary Information from Chapter 3

Table A.1: Number of temporally independent carnivore species' detections (number of camera sites with detections) between the WW and KC study areas. All sampling occurred during October-March during 2007-2008 for the WW and 2011-2014 for the KC.

Species	Willmore Wilderness	Kananaskis Country
	64 cameras	237 cameras
Wolf	32 (11)	43 (27)
Cougar	68 (8)	68 (43)
Wolverine	993 (57)	20 (12)
Coyote	18 (6)	658 (141)
Lynx	197 (16)	33 (15)
Red fox	226 (21)	93 (42)
Marten	9939 (61)	243 (60)
Short-tailed weasel	410 (16)	10 (4)
Fisher	199 (14)	0
Bobcat	0	49(22)

Table A.2: Number of temporally independent carnivore species' detections (number of camera sites with detections) between low disturbance ($n = 54$) versus high disturbance ($n = 183$) camera sites within the KC. Species for which we captured sufficient detections ($n \geq 10$) to apply the MWW-test differences and for which we included kernel density estimation of diel activity patterns are shown in bold.

Species	Low Disturbance	High Disturbance
Wolf*	9 (4)	23 (7)
Cougar	2 (2)	66 (6)
Wolverine	395 (30)	598 (27)
Coyote	2 (2)	16 (4)
Lynx	25 (5)	172 (11)
Red fox	191 (7)	35 (14)
Marten	6857 (33)	3082 (28)
Short-tailed weasel	4 (1)	406 (15)
Fisher	11 (4)	188 (10)

*Kernel density estimate of activity pattern included in analysis despite low sample sizes ($n < 10$).

Table A.3: Number of temporally independent carnivore species' detections (number of camera sites with detections) between low disturbance ($n = 54$) versus high disturbance ($n = 183$) camera sites within the KC. Species for which we captured sufficient detections ($n \geq 10$) to apply the MWW-test differences and for which we included kernel density estimation of diel activity patterns are shown in bold.

Species	Low Disturbance	High Disturbance
Wolf	36 (21)	7 (6)
Cougar	37 (26)	29 (17)
Wolverine	19 (11)	1 (1)
Coyote	422 (99)	236 (42)
Lynx	27 (11)	6 (4)
Red fox	48 (25)	43 (17)
Marten	175 (51)	66 (9)
Bobcat	38 (16)	11 (6)
Short-tailed weasel	10 (4)	0

Table A.4: Site-level detections and activity overlap for wolverine and marten. Activity overlap modelled against fisher occurrences, proportion of anthropogenic features (seismic lines), and natural landscape features (forest and natural open land cover) within a 5000m-radius at each site.

Site	Overlap	Marten	Wolverine	Fisher	Seismic	Forest	NatOpen
W01	0.69	360	14	0	0.00	0.56	0.29
W02	0.62	149	15	0	0.00	0.70	0.17
W04	0.85	380	11	0	0.00	0.68	0.09
W08	0.59	181	24	0	0.03	0.56	0.14
W09	0.61	161	12	0	0.12	0.66	0.08
W11	0.80	322	10	0	0.00	0.61	0.09
W16	0.65	379	19	0	0.00	0.76	0.10
W17	0.75	223	28	0	0.00	0.69	0.14
W18	0.58	173	24	0	0.00	0.71	0.11
W19	0.71	290	31	0	0.00	0.67	0.06
W27	0.54	245	15	0	0.00	0.72	0.04
W28	0.70	34	29	0	0.00	0.67	0.07
W34	0.88	58	60	0	0.05	0.38	0.16
W35	0.77	110	17	1	0.00	0.57	0.12
W36	0.43	55	29	7	0.21	0.60	0.15
W39	0.81	174	45	17	0.44	0.77	0.18
W41	0.86	76	28	10	0.04	0.45	0.42
W42	0.79	217	17	10	0.13	0.66	0.26
W45	0.74	198	21	0	0.00	0.59	0.23
W46	0.68	100	21	0	0.03	0.64	0.15
W52	0.84	62	20	47*	0.22	0.34	0.26
W55	0.89	70	60	7	0.22	0.54	0.09
W56	0.83	56	55	19	0.08	0.58	0.13
W57	0.76	96	19	0	0.08	0.33	0.22
W58	0.40	11	15	11	0.39	0.49	0.25
W59	0.60	135	12	0	0.00	0.18	0.17
W60	0.72	171	18	4	0.00	0.67	0.04
W62	0.55	99	11	0	0.00	0.41	0.06
W63	0.84	243	44	1	0.00	0.20	0.08
W65	0.85	117	22	0	0.00	0.26	0.07

*Outlying number of fisher detections

Table A.5: Wolverine and marten temporal overlap in response to natural landscape features, anthropogenic disturbance, and community characteristics, excluding site with outlying number of fisher detections. Model 1 is the best-supported.

Model Set	Model No.	Model Variables	AICc score	Δ AICc	AICc weight
<i>Null Hypotheses (Sample size sensitivity)</i>	1	Marten + Wolverine	-43.21	0	0.25
<i>Anthropogenic Landscape Development)</i>	7	Seismic + Wolverine	-43.11	0.11	0.24
<i>Null Hypotheses (Sample size sensitivity)</i>	2	Wolverine	-41.85	1.37	0.13
<i>Landscape Development + Competitor Co-occurrence</i>	8	Seismic + Fisher + Wolverine	-41.77	1.44	0.12
<i>Landscape Development + Competitor Co-occurrence</i>	9	Seismic + FisherPA + Wolverine	-41.06	2.16	0.09
<i>Natural Land Cover</i>	3	Forest + Wolverine	-39.69	3.52	0.04
<i>Competitor Co-occurrence</i>	5	Fisher + Wolverine	-39.42	3.79	0.04
<i>Natural Land Cover</i>	4	NatOpen + Wolverine	-39.37	3.85	0.04
<i>Competitor Co-occurrence</i>	6	FisherPA + Wolverine	-40.48	4.43	0.04
<i>Risky Landscapes + Competitor Co-occurrence</i>	10	NatOpen + Fisher + Wolverine	-37.13	6.09	0.01
<i>Risky Landscapes + Competitor Co-occurrence</i>	11	NatOpen + FisherPA + Wolverine	-36.50	6.71	0.01

Appendix B

B.1 Appendix B

Supplementary Information from Chapter 4

Table B.1: Landscape, dog, and anthropogenic disturbance variables hypothesized to explain coyote-fisher activity overlap in the Cooking Lake Moraine.

Category	Habitat Features	Description
Natural Features	Forested land cover	Combined proportion of deciduous forest, coniferous forest, and mixed wood forest
	Natural open land cover	Combined proportion of native natural grass and shrub cover
Anthropogenic Features	Linear Features	Proportion of lines of urban footprint (e.g. hard roads, vegetated roads, trails, seismic lines, pipelines, and transmission lines)
	Block features	Proportion of blocks of urban footprint (e.g. well pads and rural residential) and country-residential and industrial developments.
	Cultivation	Proportion of agricultural lands used for cultivation
Non-native predators	Domestic dog presence	Presence versus absence of domestic dogs

Table B.2: Site-level detections and activity overlap for coyote and fisher. Activity overlap (Δ) was modelled against proportion of natural and anthropogenic features within a 2000m-radius at each site, as well as presence versus absence of domestic dogs.

Site	Coyote	Fisher	Overlap	Forest	NatOPen	Cult	DogPA	Linear	Block
12	41	10	0.83	0.24	0.12	0.18	0	0.03	0.10
13	22	35	0.84	0.51	0.11	0.09	0	0.03	0.05
14	31	13	0.65	0.36	0.12	0.21	0	0.03	0.06
15	42	12	0.81	0.34	0.07	0.30	0	0.03	0.06
20	11	26	0.73	0.46	0.06	0.26	0	0.05	0.11
24	24	44	0.72	0.66	0.04	0.00	1	0.00	0.03
26	41	51	0.79	0.62	0.04	0.10	1	0.02	0.05
30	19	19	0.87	0.47	0.12	0.25	0	0.04	0.09
31	18	11	0.59	0.43	0.40	0.03	1	0.06	0.10
32	64	28	0.60	0.60	0.19	0.08	0	0.05	0.09
34	33	32	0.82	0.53	0.19	0.05	0	0.03	0.09
35	30	20	0.70	0.55	0.21	0.12	1	0.04	0.11
36	16	24	0.80	0.64	0.11	0.13	0	0.02	0.04
37	34	58	0.80	0.79	0.05	0.01	1	0.02	0.05
40	29	13	0.65	0.49	0.24	0.01	0	0.00	0.11
41	12	62	0.76	0.53	0.30	0.00	1	0.00	0.09
43	56	47	0.59	0.64	0.18	0.00	0	0.03	0.05
44	49	45	0.80	0.67	0.06	0.04	0	0.03	0.10
45	71	27	0.77	0.69	0.06	0.03	1	0.02	0.08
46	72	12	0.78	0.57	0.17	0.04	1	0.03	0.10
51	25	27	0.70	0.58	0.26	0.00	0	0.01	0.05
52	14	36	0.80	0.69	0.17	0.00	0	0.00	0.07
55	96	11	0.79	0.30	0.10	0.40	0	0.03	0.09
62	16	55	0.68	0.52	0.36	0.00	1	0.02	0.07
63	31	29	0.69	0.64	0.16	0.00	1	0.00	0.06
64	69	37	0.81	0.59	0.07	0.15	0	0.01	0.11

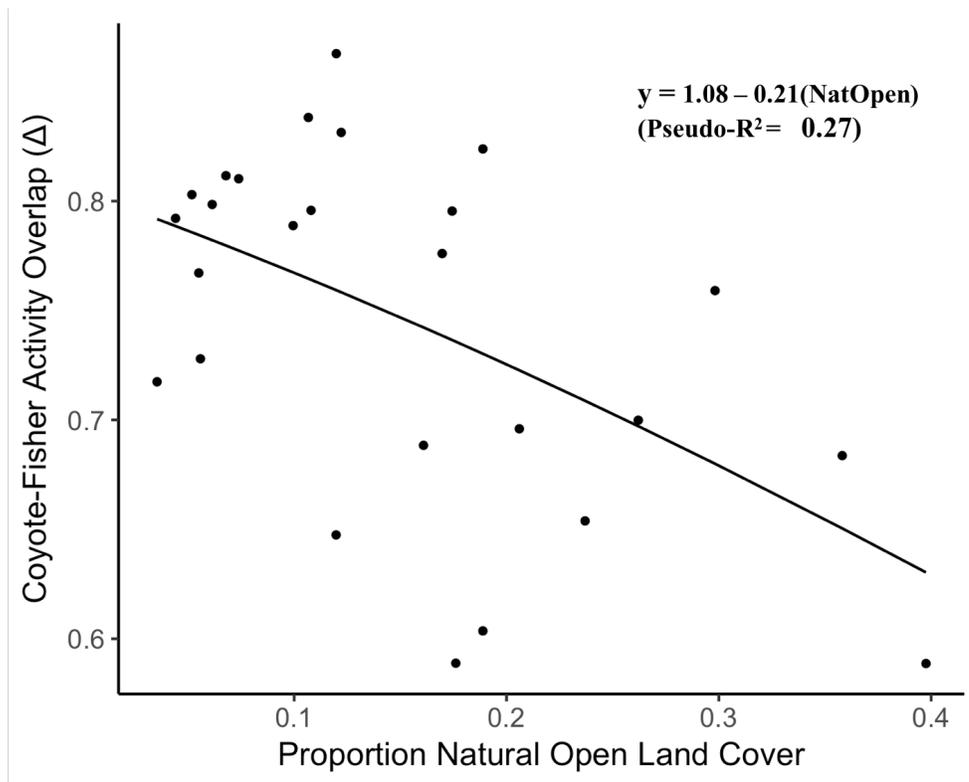


Figure B.1: Relationship between site-level coyote-fisher activity overlap and proportion of natural open land cover.

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