Efficient monitoring of wildlife responses to seismic line restoration in the Algar Habitat Restoration Program

Final Report

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Summary

Increasing rates of species endangerment and a growing human footprint necessitate ambitious efforts to protect and recover threatened species. This need is acute in working landscapes, where resource development must be compatible with the persistence of wildlife populations dependent on habitats that overlap resources of interest. An important example is the conservation of woodland caribou in western Canadian boreal forests, where declines of caribou populations have been linked to habitat disturbance from oil and gas extraction. In particular, seismic exploration lines cut extensively through these forests have been linked to altered predator-prey dynamics that result in unsustainable wolf predation on caribou. Accordingly, a key focus of caribou recovery efforts is the restoration of seismic lines in caribou habitats, with a goal of reducing line use by wolves and other predators, and thus restoring mammal community dynamics that are compatible with caribou conservation.

The Algar Caribou Habitat Restoration Program was a pioneering, industry-led initiative to restore legacy seismic lines in a portion of the Algar caribou herd range within the East Side Athabasca River population. Between 2012-2015, the Program treated 386 km of seismic lines, including 148 km receiving active restoration treatments (mounding, woody debris, tree planting) and 192 km designated for natural regeneration protection (i.e. passive restoration). We initiated the Algar Wildlife Monitoring Project in late 2015 to monitor wildlife responses to the restoration treatments (vegetation recovery was monitored by a separate program). We developed an experimental sampling design to assess the use of seismic lines by caribou, their predators, and other medium- and large-bodied mammals using noninvasive camera trap surveys. We deployed 73 camera trap stations across 5 sampling strata: actively restored lines, passively restored lines, unrestored lines left open as experimental controls or for human use, and off-line areas. Camera trap sampling concluded in November 2019, for a total sampling effort of 74,076 camera trap-days (averaging 1,015 days per station).

All motion-triggered images were processed to identify species and classify animal behaviours, while daily timelapse images were used to quantify snow cover and vegetation phenology. We developed a data management system to meet emerging camera trap metadata standards and facilitate efficient, repeatable analyses. We obtained 7,354 independent detections of medium- and large-bodied vertebrates, including 19 mammal species, as well as humans and several bird species. The most commonly detected mammals were white-tailed deer, black bear, and snowshoe hare, with an intermediate number of detections of wolf, moose, and caribou (see report section 4). Spatial patterns of detections showed some segregation of focal species according to major habitat preferences, e.g. caribou in lowlands and white-tailed deer in uplands. Temporal patterns suggested some trends in detections over the sampling period, most notably decreases in detections of wolves and coyotes, and increases in detections of caribou and white-tailed deer. We conducted a series of statistical analyses to rigorously evaluate species behavioural and population responses to restoration and other factors (sections 5-9).

We used generalized linear mixed models to estimate differences in habitat use by the focal species (caribou, wolf, black bear, white-tailed deer, and moose) across the 5 restoration treatment categories, while controlling for other covariates like habitat and seasonality. Models

using data from the first 3 years of monitoring (without off-line sites) indicated that the short-term responses to restoration were muted, with no avoidance of restored lines by wolves or bears, but an indication that white-tailed deer used actively restored lines less frequently (published in Tattersall et al. 2020b, https://doi.org/10.1016/j.biocon.2019.108295; Appendix 7). We updated these models using the full 4 years of camera trap data and incorporating off-line samples as undisturbed references. Results from the updated analysis were broadly similar but highlighted that among the five focal species, only caribou did not prefer seismic lines over off-line areas, regardless of whether the lines were restored or not (section 5.1). More encouragingly, the models showed some subtle albeit mixed signals of restoration effectiveness: wolves used restored lines (active and passive) less than human-use lines, bears used passively restored lines less than other lines, deer and moose used actively restored lines less, and caribou used actively restored sites more than unrestored controls.

To gain a more complete picture of responses to restoration across the sampled vertebrate community, we used joint species distribution models to simultaneously model multispecies responses (section 5.2). We also used continuous descriptors of the characteristics of sampled seismic lines (line of sight, line width, mounding height and line density), rather than the discrete restoration categories used in our previous models, and we incorporated annual trends. Across the sampled community, line characteristics explained relatively little variation in species detections, as compared to other factors like season, habitat, and unexplained site-level variation (captured through random effects). Nevertheless, line characteristics—particularly line of sight—explained some variation in detections for several species, notably white-tailed deer, wolf, moose, and sandhill crane (all > 5% variation explained). Residual co-occurrence patterns from these multispecies models confirmed that caribou were grouping separately from their predators and apparent competitors. Model-based predictions of shifts in community structure under fully restored conditions (i.e. line characteristics consistent with restored lines) suggested that caribou may experience less predation risk under restoration due to declines in habitat use by wolves and coyotes. Nevertheless, assessing changes in species interactions is challenging; we completed an initial evaluation of predator interactions in the Algar landscape (published in Tattersall et al. 2020a, https://doi.org/10.1002/ece3.6028; Appendix 6), but we recommend further work to more directly investigate shifts in species interactions following restoration.

To enable assessment of population-level responses, we evaluated models for estimating population density of focal species (section 7). Since these species do not have unique markings that allow identification of individuals, we developed unmarked spatial count (SC) and spatial partial identity (SPIM) models to estimate densities of caribou and black bear in Algar in different years, and in a different landscape within the Richardson caribou range. While additional research is needed to further evaluate and improve these models, our estimates are the first for these species and landscapes, and suggest a local increase in caribou density within the Algar survey area from 2016 to 2019. These estimates are consistent with the hypothesis that linear restoration and wolf population management are improving conditions for caribou in this landscape. We created a decision framework to guide further research and application in density estimation using models for unmarked and partially marked populations.

While our project was focused on monitoring wildlife responses to restoration, we also collected daily timelapse images that allowed us to characterize the local environment at camera trap stations. We developed an approach to measure vegetation phenology and productivity from camera trap images, demonstrating different patterns in the understory dynamics relative to overstory phenology captured by satellite remote sensing (section 8). Our phenology metrics indicated that plants on passively restored lines showed phenological patterns more similar to off-line undisturbed conditions. Phenology on actively restored lines was more variable, and, for some measures (e.g. length of growing season, date of senescence, productivity) was more similar to unrestored control and human-use lines than to off-line or naturally regenerating lines. We showed that wildlife activity was related to phenology at different scales, with a strong link between the occurrence of migratory sandhill cranes and the vegetative growing season. Weaker but significant links were documented between vegetation productivity (measured as greenness) and annual and weekly detections for both caribou and white-tailed deer, which we suggest is consistent with these herbivores tracking forage availability along seismic lines. Our phenology analyses established the ability of camera trapping to monitor the progress of habitat restoration by evaluating vegetation characteristics and its impacts on wildlife species.

In a final exploratory analysis, we compared wildlife community structure and behaviours of ungulate herbivores between the Algar study area and another camera trap survey area in the Richardson caribou range (section 9). We found marked differences in species detections and behavioural patterns between the landscapes, consistent with our hypotheses that the relatively more disturbed Algar landscape would have higher proportions of wolves and deer, and that ungulate prey would show more risk-averse behaviours where there were more wolves. We believe that such landscape-scale comparisons across standardized camera trap surveys represent an important tool for assessing the effectiveness of linear restoration programs and other caribou recovery actions.

This project has clearly demonstrated the utility of camera trap surveys for monitoring restoration effectiveness in boreal environments. The cameras facilitated the collection of longitudinal data on the effects of seismic line restoration on wildlife behaviour and community composition, plant phenology and productivity, and the links between them. We found some evidence for positive outcomes emerging from the Algar restoration program, including trends towards reductions in predator activity and abundance. However, our results highlight that predators and other species continue to heavily use restored and unrestored lines in this landscape, and that the short-term responses to restoration are likely insufficient to drive rapid recovery of caribou. We recommend that future efforts carefully consider these results and attempt more aggressive methods for linear restoration (e.g. line blocking), alongside other recovery measures (such as wolf control), and rigorously evaluate the outcomes within an adaptive management framework (see section 10 for detailed recommendations). The relatively weak short-term effects observed in Algar highlight the need for long-term monitoring of wildlife and vegetation responses to restoration efforts, and for landscape-scale comparisons between different restoration techniques and environmental contexts.

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The following appendices to this report are available in a separate document (*Appendices for Algar Wildlife Monitoring Final Report.pdf*), which contains the following supplementary materials:

Appendix 1: Camera Trap Detection Summaries

Appendix 2: Single Species Models

Appendix 3: Community Modelling

Appendix 4: Density Estimation

Appendix 5: Phenology Monitoring

Appendix 6: Publication (Tattersall et al. 2020a) - Boreal predator co-occurrences reveal shared use of seismic lines in a working landscape

Appendix 7: Publication (Tattersall et al. 2020b) - Mammal seismic line use varies with restoration: Applying habitat restoration to species at risk conservation in a working landscape

1. Introduction & Objectives

1.1 Wildlife management in working landscapes

Human activities have transformed global terrestrial land surfaces and altered the structure and function of natural ecosystems (Newbold et al. 2015; Venter et al. 2016). Land use activities such as farming, timber harvest, mining, and petroleum extraction are fundamental components of local, regional, and global economies, but have also driven loss and degradation of natural habitats that support a diversity of plant and animal life. Habitat loss is a key driver of global declines in biodiversity that have led to elevated species extinction rates and deterioration in ecosystem functions and services (Butchart et al. 2010; Díaz et al. 2019). Habitat loss is particularly important for large-bodied terrestrial mammals, whose wide-ranging movements, high energy requirements, and relatively slow life-histories make them vulnerable to the rapid fragmentation and diminishment of forests, grasslands and wetlands (Ripple et al. 2014, 2016).

At the global scale, one-quarter of all mammal species are considered to be threatened with extinction (Schipper et al. 2008), and many more are undergoing population declines (WWF 2018). A cornerstone of conservation responses to wildlife declines has been the creation of protected areas, which now cover over 15% of the global terrestrial land surface (www.protectedplanet.net). Despite the rapid growth in protected areas, their coverage is inadequate to prevent continued declines in many mammal species, as most parks and reserves are too small, poorly connected, or contain insufficient high-quality habitat (Joppa & Pfaff 2009; Crooks et al. 2017). Many high-quality wildlife habitats and critical corridors occur in “working landscapes”, that is, landscapes used for key economic endeavours like agriculture, forestry, and oil and gas development (Kremen & Merenlender 2018). There is thus a pressing need to ensure these landscapes can meet economic demands while safeguarding wildlife values.

The need to mitigate the effects of industrial land uses on wildlife is particularly important in Canada’s boreal forests, which provide critical habitats for many large mammals and other species, yet are facing increasing rates of development alongside other stressors such as climate change (Schindler & Lee, 2010; Venier et al., 2014). In western Canada’s boreal forests, such as within Alberta’s Oil Sands region, widespread resource extraction has disturbed landscapes beyond the natural range of variability (Pickell et al. 2015; Fisher & Burton 2018). Individual industrial projects undergo regulatory processes, such as environmental impact assessments, designed to safeguard wildlife and other valued ecosystem components, yet such processes have been critiqued for not always effectively reducing or mitigating impacts to wildlife (Campbell et al. 2019; Collard et al. 2020; Burton & Chetkiewicz 2020). In particular, the cumulative impacts of multiple interacting stressors, operating over multiple spatial and temporal scales, pose a critical challenge for wildlife management in working landscapes (Burton et al. 2014; Toews et al. 2017, 2018)

1.2 Caribou conservation

The impacts of industrial land use changes on mammal species and communities have been highlighted by the conundrum of caribou conservation in Canada. Woodland caribou (*Rangifer tarandus caribou*) is a widely distributed species dependent on forest habitats that overlap areas of economic importance to extractive industries. Populations of woodland caribou (hereafter caribou) are declining across most of their range, with the strongest declines in areas with the greatest degrees of habitat disturbance (Johnson et al. 2020). Caribou ranges in northern Alberta overlap bitumen deposits driving energy development in the oil sands region (Schneider et al. 2012; Hebblewhite 2017), and most of these populations are undergoing significant declines (Hervieux et al. 2013).

While land use changes associated with industrial development are an ultimate cause of caribou declines, the proximate drivers of decline underscore the importance of the indirect effects of altered dynamics in the boreal mammal community. Research in Alberta and elsewhere has identified increased wolf predation on caribou as a proximate cause of reduced caribou survival and recruitment (Boutin et al. 2012; Hebblewhite 2017). This increased predation is driven by both numerical and functional responses of wolves to the changing environment. The numerical response (i.e. increase in wolf abundance) follows population increases in other prey species of wolves, particularly white-tailed deer, which have benefited from greater early successional forage in harvested forests, as well as milder winters associated with climate change (Latham et al. 2011b; Dawe et al. 2014; Fisher et al. 2020). Wolves have also shown a functional response—that is, an increase in predation efficiency—through increased travel rates along the network of linear features associated with oil and gas development (e.g. roads, pipelines, seismic exploration lines; Latham et al. 2011a; Dickie et al. 2017a,b). The ability of wolves to move faster and farther into degraded caribou habitats is thought to increase their encounter rates with caribou (McKenzie et al. 2012; DeMars & Boutin 2018).

Seismic lines in particular have been implicated in caribou declines, as their extensive coverage and persistence in industrial boreal landscapes have resulted in broad impacts (Lee & Boutin 2006; van Rensen et al. 2015; Dabros et al. 2018). Seismic lines influence the structure of boreal ecosystems in many ways, including altered micro-site topography (e.g. Caners and Lieffers, 2014), hydrological flow (e.g. Braverman and Quinton, 2016), and vegetation species composition on seismic lines (e.g. van Rensen et al., 2015) and immediately surrounding them (e.g. Abib et al., 2019). Such changes in physical and hydrological structure have knock-on implications for the wildlife that use the habitat in and around seismic lines (Dabros et al., 2018; Finnegan et al., 2018b; Pattison et al., 2020). Not only have seismic lines influenced movement of wolves, there is evidence of impacts to many other wildlife species, including caribou (Dyer et al. 2002; DeMars & Boutin 2018), black bear and marten (Tigner et al. 2014, 2015) and other mammal, bird, and insect species (Bayne et al. 2005; Venier et al. 2014; Toews et al. 2017, 2018; Fisher & Burton 2018; Riva et al. 2018; Dickie et al. 2020). Natural recovery of vegetation on seismic lines is slow, particularly in wetland habitats preferred by caribou (Lee & Boutin 2006; van Rensen et al. 2015; Dabros et al. 2018). Given the strong association between seismic line density and caribou declines, and the fact that the primary industrial use of the lines is during oil and gas exploration (as opposed to during extraction or transport of identified resources), restoring seismic lines is a key part of caribou recovery strategies.

Recovery plans for boreal woodland caribou have been developed at the national and provincial levels (Environment Canada 2012; Government of Alberta 2017), and several recovery actions are being implemented. A major focus in many caribou ranges has been on wolf population management (i.e. lethal control to reduce wolf abundance), which can quickly reduce predation pressure and has been linked to reductions in rates of decline in some caribou populations (Hervieux et al. 2014; Serrouya et al. 2019). Other emergency recovery actions have included translocations, prey population management (e.g. increased moose harvest), and maternity pens to protect pregnant caribou cows and their calves (Serrouya et al. 2019). These are intensive measures with mixed success to date, and are at best short-term solutions to caribou conservation. Without protecting adequate amounts of caribou habitat, the prospects for long-term viability of caribou populations will remain grim. Federal and provincial recovery strategies have identified a minimum target threshold of 65% undisturbed habitat within caribou ranges for self-sustaining populations (Environment Canada 2012; Government of Alberta 2017). However, many caribou ranges in Alberta and British Columbia are already disturbed well above this threshold. For instance, the East Side Athabasca River range, containing the Algar sub-range, has only 10% undisturbed habitat, being heavily fragmented by anthropogenic disturbances, including nearly 20,000 km of seismic lines (Government of Alberta 2017). The restoration of existing disturbances is thus critical to achieving caribou recovery objectives.

1.3 Seismic line restoration for caribou recovery

Restoration of seismic lines has been identified as an important recovery action for caribou for some time (e.g. Bentham & Coupal 2015). Several recent studies have used simulation modelling to predict the potential role of linear restoration in reducing predator encounters with caribou, and thereby helping to recover caribou populations (Spangenberg et al. 2019; Serrouya et al. 2020). Other simulation studies have explored regional prioritization scenarios to try to maximize the ecological benefits of restoration relative to their costs (e.g. Yemshanov et al. 2019). However, on-the-ground attempts to implement and evaluate linear restoration have been limited until recently.

Seismic line restoration initiatives focus on modifying several key line characteristics that influence predators and prey. Firstly, the removal of vegetation during seismic line creation increases the line-of-sight for visual and highly mobile predators, such as wolves (McKenzie et al., 2012; Kansas et al., 2015; Dickie et al. 2017a). Reducing the line-of-sight through tree planting or physical structures (such as fences) is hypothesized to reduce predator hunting efficiency through the reduction of predator-prey contact rates, reducing pressure on vulnerable caribou populations (DeMars and Boutin 2018). Compaction of the earth beneath seismic lines during their creation and use (e.g. by all terrain vehicles), both inhibits natural regeneration (Filicetti et al., 2019) and facilitates the movement of “upland” species, such as white-tailed deer, into historically lowland habitat favored by woodland caribou (Latham et al., 2011b). Furthermore, the early seral vegetation prevalent on seismic lines may be a resource subsidy further promoting the incursion of white-tailed deer and moose into caribou habitat (Ray, 2014; Bentham and Coupal, 2015). Increasing white-tailed deer abundance in caribou habitat acts, in turn, as a food subsidy for wolves, subsequently increasing wolf density and caribou-wolf contact rates (Kinley and Apps 2001, Wittmer et al. 2007, Latham et al. 2011a,b). Thus, restoration projects use soil mounding and coarse woody debris to promote seedling survival, reduce soil compaction, and act as movement barriers to caribou predators and competitors. Ultimately, reductions in the density of linear features on the landscape through habitat restoration should support threatened caribou populations through the reduction of predator-prey contact rates (Newton et al. 2017).

Pyper et al. (2014) reviewed several linear restoration initiatives in Alberta's oil sands region, identifying promising efforts underway but highlighting the high costs of restoration (averaging $12,500 per km of treated line), the need for larger scale projects, and the general lack of effectiveness monitoring. Empirical evidence that seismic line restoration can achieve hypothesized changes in wildlife behaviours and population densities remains scarce. Few rigorous monitoring programs focused on wildlife responses to restoration have been conducted. Some emerging results have been gathered at small spatial scales that may not translate into the needed effects at the scale of caribou populations (e.g. Keim et al. 2019). Furthermore, the dynamic nature of boreal ecosystems, including natural disturbances and population fluctuations (e.g. Krebs et al. 2001), means that monitoring must consider responses over relatively long time scales, rather than only through the short snapshots typical of many wildlife studies (Williams et al., 2020).

One of the pioneering restoration projects reviewed by Pyper et al. (2014) was the Algar Caribou Habitat Restoration Program. Between 2012 and 2105, this program restored a total of 386 km of seismic lines, covering 246 ha within the East Side Athabasca Range, using both active and passive silvicultural restoration techniques (Silvacom & Nexen 2015). This effort has been lauded as an operational success, and it provided an important opportunity to assess the effectiveness of these techniques for caribou recovery, to guide future restoration efforts that will be needed to reach recovery targets across caribou ranges.

1.4 Camera trap monitoring to inform caribou conservation

Concurrent with the increasing focus on caribou recovery and seismic line restoration has been rapid development in the use of remote cameras (hereafter camera traps or CTs) as a tool for wildlife survey and monitoring (O'Connell et al. 2011; Burton et al. 2015). Camera traps are remotely triggered by animal movement and body temperature, and have proven to be a powerful method for detecting terrestrial vertebrate species, particularly rare or elusive larger-bodied mammals (Wearn & Glover-Kapfer 2019). CT images provide unambiguous evidence of the occurrence of a species at a particular time and place, and have been effectively used to make inferences on animal behaviour, habitat use, distribution, abundance, and community dynamics (Steenweg et al. 2017). The ability to standardize CT surveys and link detections and associated inferences across large spatial scales has led to calls for CTs to play a key role in global biodiversity monitoring efforts (Steenweg et al. 2017; Kissling et al. 2018). Several regional and global networks have recently formed to improve the coordination, standardization, and synthesis of CT surveys in support of wildlife management and conservation (e.g. eMammal, McShea et al. 2005; Wildlife Insights, Ahumada et al. 2011, 2019; WildCAM, wildcams.ca).

The use of camera traps to monitor caribou populations had been limited until recently. Similar to many large ungulate species, caribou populations have typically been monitored using aerial surveys and telemetry tracking. For instance, the Government of Alberta estimates caribou survival by monitoring the fate of VHS- or GPS-collared adult females, and estimates recruitment through aerial cow:calf counts (Hervieux et al. 2013). These survival and recruitment estimates are combined to estimate the rate of population change and determine if caribou populations are increasing, decreasing or stable. More recently, genetic mark-recapture methods have been used to estimate caribou population size, providing a means of monitoring trends in abundance (Wasser et al. 2011; Hettinga et al. 2012). Other monitoring methods used (or in development) for boreal caribou have recently been reviewed by the National Boreal Caribou Knowledge Consortium (forthcoming, https://www.cclmportal.ca/portal/boreal-caribou).

While the ultimate measure of success for caribou recovery efforts is population persistence, there are limitations to the current monitoring approaches. Estimates of population demography and abundance are critical, but may provide slow or indirect feedback on the success of recovery actions. For example, detectable changes in population growth rates may only occur as a delayed consequence of fitness costs related to underlying behavioural changes, such as changes in movement, energy expenditure, or habitat use. GPS collars are an important tool for monitoring animal movements and habitat selection, but results from GPS tracking can be harder to relate to specific management actions, such as seismic line restoration. Researchers do not know *a priori*, and cannot control, the features or areas with which collared animals will interact. This may necessitate large samples of collared animals, which can be prohibitively expensive. Longer time intervals between consecutive telemetry locations (i.e. fix intervals) are typically used to prolong battery life and reduce data costs, but they make it difficult to understand fine-scale animal interactions with linear features. Furthermore, most telemetry studies focus on a single-species, such as caribou, whereas caribou recovery is inherently a multispecies problem. Achieving and maintaining large samples of multiple interacting species can be logistically and financially prohibitive (Burgar et al. 2018, 2019a). Similarly, collecting robust multispecies data from methods such as aerial survey and genetic tagging can be expensive and challenging, particularly when considering differences in detectability (e.g. wolves and white-tailed deer are more difficult to detect in aerial surveys than caribou and moose).

The aforementioned advances in camera trap methodology provide an opportunity to evaluate the utility of this approach for monitoring the effectiveness of caribou recovery actions. CTs enable simultaneous monitoring of multiple interacting species—such as the predators and prey involved in the “caribou food web”—and of the relationships between these species and specific features on the landscape, such as restored and unrestored seismic lines. A well-designed CT survey can facilitate inferences across multiple spatial, temporal, and ecological scales, from short-term, site-level behaviours to longer term landscape-level abundances of focal populations and communities. CT surveys can be cost-effective (e.g. Burgar et al. 2018) and have great potential to be standardized to enable synthesis across multiple landscapes (such as different caribou ranges). Despite the promise of CTs surveys as a monitoring method to support caribou conservation, their effectiveness has yet to be rigorously evaluated.

1.5 Objectives of the Algar Wildlife Monitoring Project

The Algar Caribou Habitat Restoration Program provided an important opportunity to test the application of camera trap monitoring methods to the challenge of linear feature restoration in caribou habitat. With support from the proponents of the restoration program, we initiated this project in 2015 to evaluate the short-term effects of the restoration on medium- to large-bodied mammals within the Algar caribou range in northeastern Alberta. Our project is titled “Efficient monitoring of wildlife responses to seismic line restoration in the Algar Habitat Restoration Program”, with a short title of the Algar Wildlife Monitoring Project (hereafter “the project”).

Our primary objectives were to develop a standardized camera trap survey design and protocol to address two central questions:

1. To what extent do the restoration treatments implemented in the project area reduce the use of seismic lines by caribou predators?

2. How do the restoration treatments affect the broader mammal community, i.e. can they restore mammal community composition?

We had both short- and long-term objectives, including comparing mammal occurrences between restored lines and unrestored controls in the period immediately following restoration, as well as developing a foundation for temporal evaluation of longer term mammal responses to restoration. We focused primarily on the behavioural use of seismic lines by focal species, but also aimed to consider the larger spatial scale of population-level responses. The key focal species targeted by our monitoring were wolf and black bear, since they are the main predators of caribou in this system. We set out to test the hypothesis that linear feature restoration could reduce predation risk for caribou, and the associated prediction that wolf and black bear use of restored lines would be lower than their use of unrestored lines. Given that camera trapping provides data on multiple species, our additional focal species included caribou and their main apparent competitors (white-tailed deer and moose) as well as other members of the medium- and large-bodied terrestrial mammal community (e.g. lynx, coyote, mustelids, snowshoe hare). The community-level hypothesis we aimed to test is that linear restoration can restore community composition to expectations for undisturbed habitats, and thus our prediction was that there would be consistent and differentiated patterns of use of restored vs. unrestored lines across species, with more disturbance-sensitive species (e.g. caribou, lynx) preferentially using restored lines, and more disturbance-tolerant species (e.g. white-tailed deer, coyote) preferentially using unrestored lines.

During the course of addressing these overarching objectives and hypotheses, we aimed to develop and test new CT methodologies that could be applied to other projects in northern Alberta and elsewhere that are focused on evaluating the effectiveness of linear feature restoration, or of other caribou recovery actions or wildlife management more broadly. This report details our methods and summarizes our main results and interpretations. We start with general summaries of the camera trap detections over space and time and then describe our main analytical lines of inquiry. Specifically, we present single- and multi-species models of wildlife responses to restoration and other factors, consideration of species interactions, estimates of population density, analysis of vegetation phenology, and initial comparisons with wildlife dynamics in a different landscape outside the Algar range. We end by summarizing our main findings and recommendations.

We note that this project did not focus specifically on monitoring vegetation responses to restoration, as this theme was being addressed by a separate monitoring program led by Silvacom. We also note that additional details on our Algar Wildlife Monitoring Project can be found in previous annual reports (Burton et al. 2017, 2018), as well as the Tattersall et al. (2020a,b) publications (appendices 6 and 7). All are available by emailing the principal investigator at cole.burton@ubc.ca. Further publications based on the material in this report are being prepared for submission to peer-reviewed journals.

2. Study System & Sampling Design

2.1 Description of study system

Our wildlife surveys were conducted within the area covered by the Algar Caribou Habitat Restoration Program (Silvacom & Nexen, 2015). The study area encompassed 6 townships in northeastern Alberta (82-16-W4, 83-16-W4, 84-16-W4, 85-16-W4, 86-16-W4, 85-17-W4, 86-17-W4), approximately 70 km southwest of Fort McMurray (centred at ~ 56.2588 N, 112.6909 W; Fig. 2.1). It covered ca. 570 km^2 delineated in the north and west by the Athabasca River and in the south by Alberta Township 82. Wildlife using the study area are connected to the surrounding boreal landscape, although the steep and rugged Athabasca River valley could limit wildlife movement from the west and north. The study area is located in the Central Mixedwood subregion of the Boreal Forest Natural Region (Natural Regions Committee 2006), and is characterized by a) extensive lowland terrain (58% of landscape composition) consisting of wet and poorly drained fens and bogs; b) upland forests (31%), primarily along the river valleys and consisting of a mix of aspen (*Populus* spp.) dominated deciduous stands, aspen-white spruce (*Picea glauca*) mixed-wood stands, and white spruce and jack pine (*Pinus banksiana*) coniferous stands, and c) small lakes and rivers (10%). Further details on the study area can be found in Burton et al. (2017), OSLI (2012a,b) and Silvacom & Nexen (2015).

The majority of the study area contains woodland caribou habitat, encompassing the Algar caribou range (Fig. 2.1), a sub-herd of the East Side of the Athabasca River (ESAR) population (ASRD & ACA 2010). The ESAR population is declining and not currently considered self-sustaining (Hervieux et al. 2013). Environment Canada (2012) reported an estimated 90-150 individuals in the population; more recently, a minimum count of 227 caribou was reported for ESAR (Alberta Government 2017). Burgar et al. (2019a) estimated a density of 0.22 caribou per 100 km^2 (95% confidence interval = 0.08–0.65) within the Christina sub-range of ESAR. Using various government data sources from 1992 to 2017, the three-year mean annual population growth was estimated to be 0.93 (95% CI: 0.84-1.01), and the 10-year mean rate at 0.90 (95% CI: 0.77-1.00; Alberta Government 2017). It is presumed that the Algar sub-herd is experiencing similar declines to the greater ESAR population of which it is a part. A wolf control program began in ESAR in 2016/2017 (Alberta Government 2017).

The Algar study area falls within the Athabasca Oil Sands Region and the predominant anthropogenic land-use disturbance is from steam assisted gravity drainage (SAGD) operations, primarily through footprints created by spatially extensive seismic lines and well sites. Other common land-use footprints in the region include access roads, pipelines, power lines and utility corridors, processing plants, borrow pits, and forestry cut blocks. Compared to other northern boreal forest landscapes, the Algar study area is a medium intensity land-use landscape, with a seismic line density of ca. 1.1 km/km^2 and an average of 1.3 SAGD well-sites every 10 km^2 (Fig. 2.2; ABMI 2014). By comparison, the Christina caribou sub-range to the south-east (also within ESAR range) has a greater disturbance intensity of 3.4 km of seismic line per km^2 and 8.0 well-sites every 10 km^2, while the less disturbed Richardson caribou range (approx. 200 km north-east) has 0.5 km/km^2 seismic line density and 0.4 well-sites every 10 km^2 (J. Burgar, unpublished analysis).

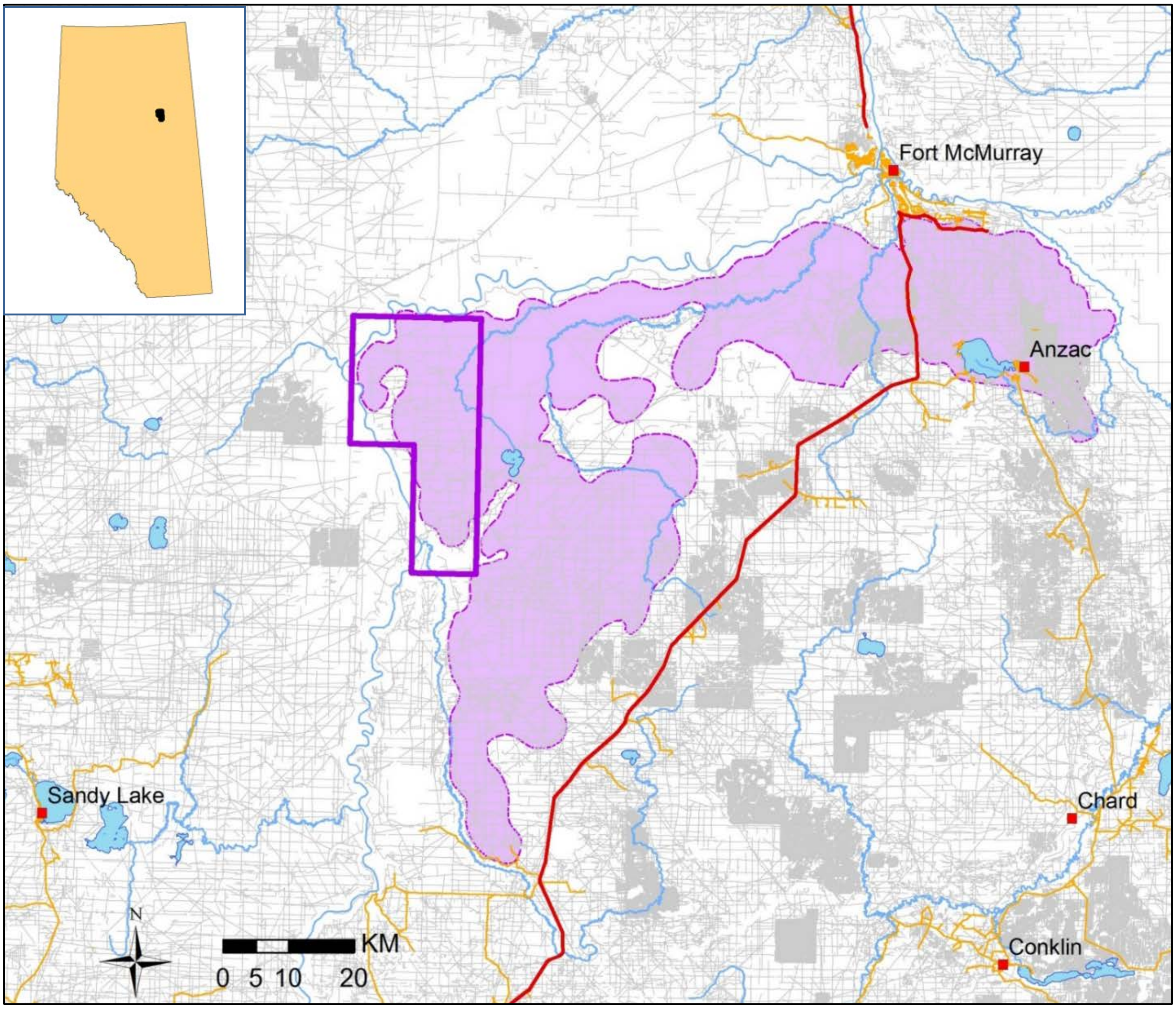

Figure 2.1 Location of study area for the Algar Wildlife Monitoring Project (dark purple rectangle). Also shown in purple is the range of the Algar caribou subpopulation (part of the East Side Athabasca River population). Nearby cities and towns are labelled, and highways are shown in red (major) or orange (minor). Rivers and lakes are shown in blue, and the grey shading displays linear disturbances (GIS layer from the Alberta Biodiversity Monitoring Institute, Caribou Monitoring Unit). The inset map show the project location (black) within Alberta (orange).

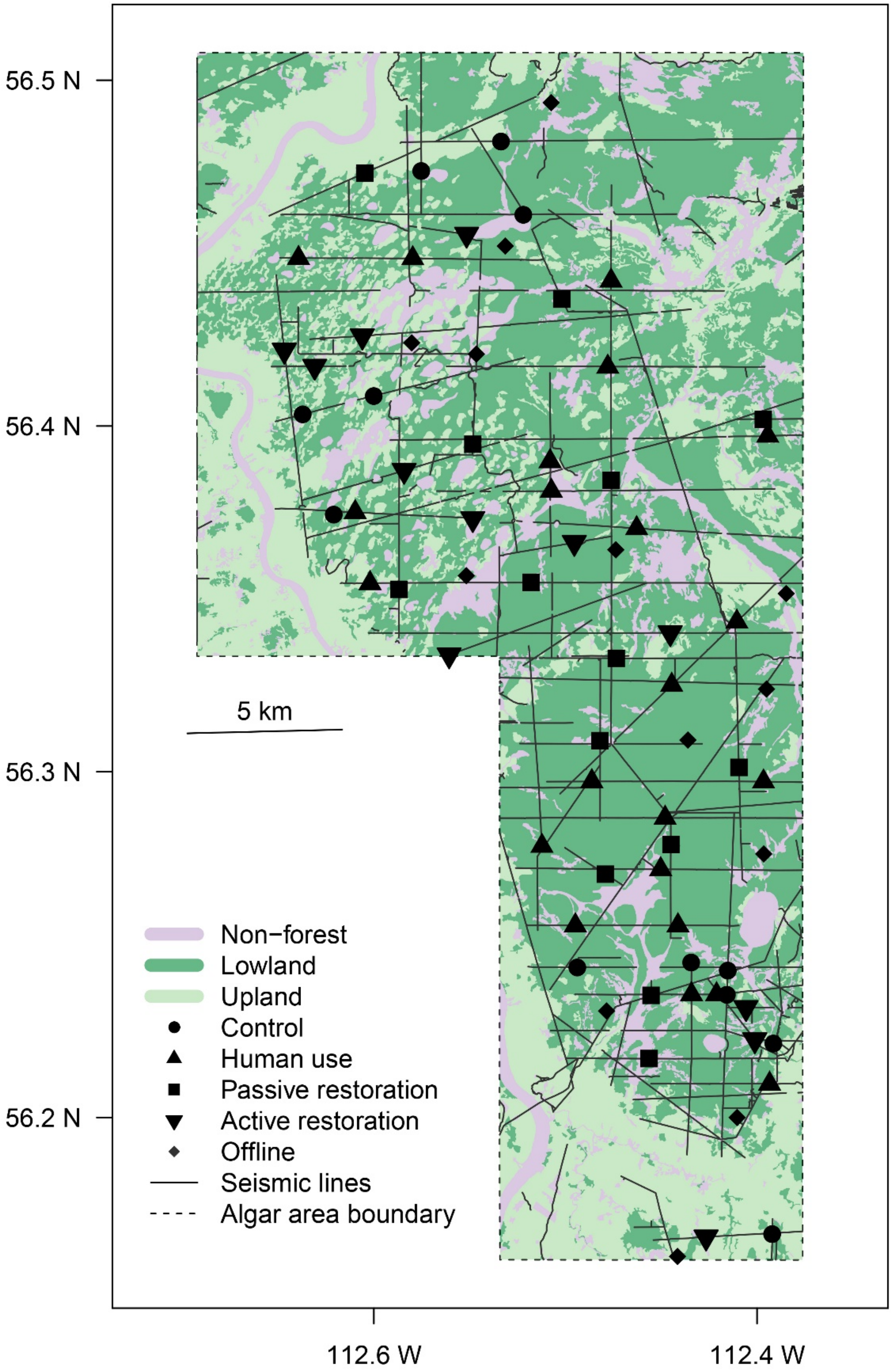

Figure 2.2 The Algar study area showing major habitat distinctions, seismic lines, and camera trap locations. Symbols indicate the restoration treatment categories (i.e. sampling strata) to which camera traps were assigned.

2.2 Description of restoration program

The Algar Caribou Habitat Restoration Program began in 2011, initiated by the Oil Sands Leadership Initiative group (OSLI) which became part of the Canadian Oil Sands Innovation Alliance (COSIA). The goal of the program was to restore 264 of the 830 ha of legacy seismic lines within the study area (OSLI, 2012a; Silvacom and Nexen, 2015), a target based on achieving a minimum threshold of 65% undisturbed habitat within boreal caribou range (following Environment Canada, 2012). The program aimed to address both structural and functional restoration (Dabros et al., 2018) by simultaneously promoting vegetative regeneration and providing movement barriers for caribou predators. In devising the wildlife monitoring study, we considered restoration to be any activity with the aim of achieving ecosystem recovery to the reference state, including (i) passive restoration as protection to allow natural vegetation regeneration, and (ii) active restoration as assisted regeneration and reconstruction.

Seismic lines within the study area were assessed and categorized by the program prior to restoration (OSLI 2012a). Line segments considered for active restoration had to meet the following criteria: not used for industrial or trapper/outfitter access, little or no natural regeneration, and accessible for restoration activities. Active restoration included site preparation with mounding and addition of coarse woody material (i.e. dead and damaged trees) where available, as well as planting of black and white spruce seedlings in densities ranging from 400 to 1200 stems per ha. Line segments designated for passive restoration (termed natural regeneration protection by the program) were defined as those with regeneration ≥1.5 m in height (roughly representing a caribou sightline) and crown cover > 50% (OSLI 2012a).

Restoration treatments were implemented during winters between 2012 and 2015. A total of 386 km of seismic lines (246 ha) were reported to have been treated, with over 160,000 trees planted or seeded (mostly black spruce), 148 km of line segments receiving physical treatment (site preparation and planting) and 192 km designated for natural regeneration (passive restoration). Other untreated line segments included those left open for human access (e.g. trapping and outfitting activities), which we designated as “human use” lines, and “research lines” left unrestored as controls for this wildlife monitoring program (i.e. line segments meeting the conditions for active restoration but set aside as untreated controls to represent a “business as usual” case of no restoration). Further details of the restoration program are summarized in Silvacom & Nexen (2015; see also Burton et al. 2017).

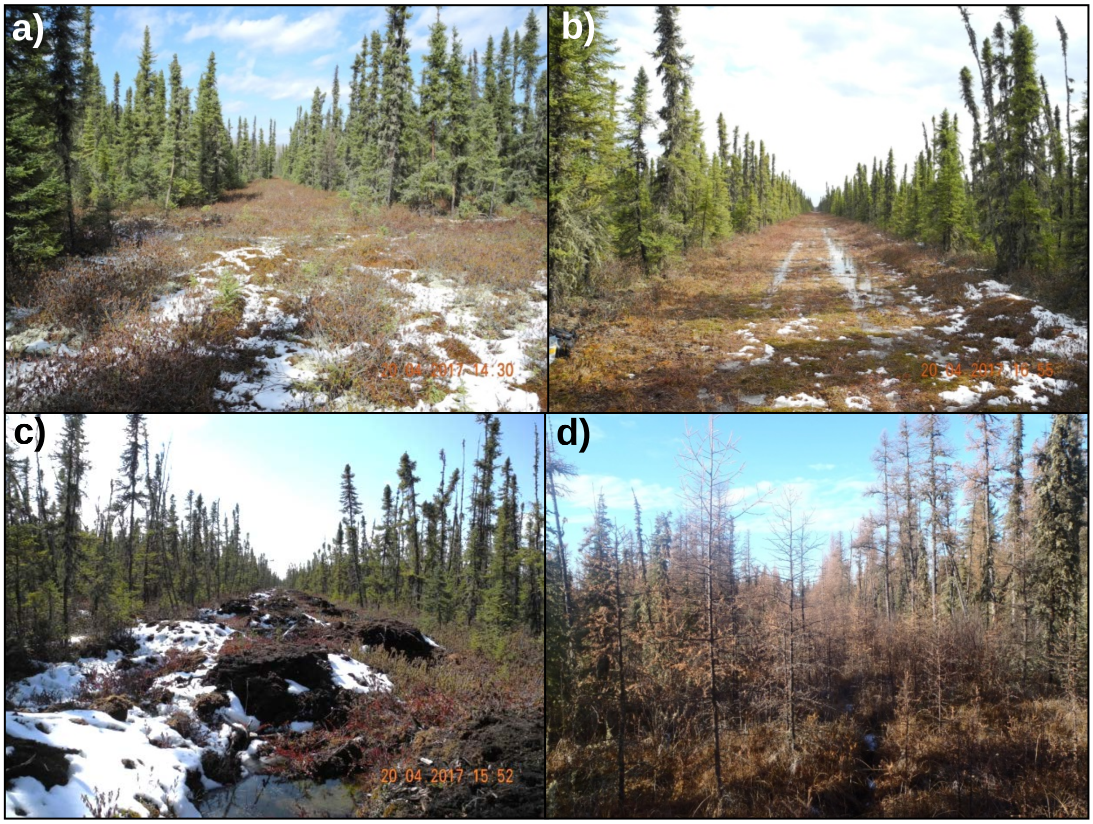

Figure 2.3 Examples of the four seismic line strata used to assess large mammal responses to seismic line restoration in northeastern Alberta, Canada. The top row displays unrestored lines: Control (**a**) and Human-Use lines (**b**). The bottom row shows restored lines: Active (**c**) and Passive (**d**) lines. (Off-line sites not pictured.)

2.3 Sampling Objectives & Design

Our wildlife sampling design was guided by the two primary monitoring objectives: 1) test the hypothesis that restoration treatments reduced the use of seismic lines by caribou predators (namely wolf and black bear); and 2) assess the effect of treatments on mammal community structure (i.e. richness and relative abundance of medium- and large-bodied species). To assess treatment effects, it is important to have experimental controls, or reference points, against which to compare the responses by mammal species to the treatments. During the initial stages of project planning, we recommended a Before-After-Control-Impact (BACI) monitoring design, which provides the strongest experimental inferences (Stewart-Oaten et al. 1986; Underwood 1992). However, due to operational logistics (i.e. existing budgets, contracts, expectations and/or momentum for operators implementing the restoration treatments), the restoration program prioritized completion of treatments prior to initiation of wildlife monitoring. We therefore focused on a Control-Impact design that consisted of a spatial contrast between restored line segments, unrestored “controls”, and undisturbed off-line areas. We also aimed to distribute sampling effort across the survey area to provide a representative sample at the population and community scales.

We chose camera trapping as a non-invasive sampling technique to measure mammal responses to seismic line restoration. Camera trapping is increasingly used to assess wildlife distribution, abundance and behavior across multiple spatial scales (e.g. Burton et al. 2015; Steenweg et al. 2017), and we had previously used it successfully to survey the boreal mammal community in northeastern Alberta (Fisher & Burton 2018). Camera traps had also previously been used to assess wildlife use of seismic lines (e.g. Tigner et al. 2014, 2015).

We measured mammal responses to restoration using seismic line segments as sampling units. We defined a segment as a continuous section of line at least 200 m long within similar ecological conditions (i.e. ecosite classification, Beckingham & Archibald, 1996). Line segments were the spatial unit used by the restoration program to develop treatment prescriptions (OSLI, 2012a; Silvacom & Nexen, 2015). We could not consider entire seismic lines as the sampling unit as these could be many kilometres long and cross more than one treatment and landcover type, therefore displaying different effects on wildlife along their length.

We randomly selected line segments from within each sampling stratum (also referred to as restoration category or treatment) for camera trap sampling locations. The five strata consisted of two categories of restoration (Active and Passive), two unrestored categories (Control and Human Use), and one undisturbed category (Off-line). We first deployed 24 camera stations in November 2015 (12 Active, 12 Control), followed by 36 more in November 2016 to include Passive and Human Use strata, and 13 Off-line stations in November 2017. Off-line camera locations were randomly selected from candidate areas of contiguous forest at least 200m from the nearest seismic line. The total number of camera trap stations deployed was 73, distributed across strata as follows: 22 Active, 12 Passive, 14 Human Use, 12 Control, and 13 Off-line. Camera stations were deployed until November 2019.

Camera stations were generally deployed on different seismic lines (except for off-line cameras). When stations were deployed on the same line in different restoration strata (i.e., different line segments), we set cameras at least 500 m apart to increase the probability of independent detections between stations (Tigner et al., 2014). In some cases, line segment proximity resulted in camera stations on different line treatments being less than 500 m apart (minimum distance 338 m).

We used camera trap sampling to test hypothesized differences in mammal species use of line segments across the restoration categories (Fig. 2.4). We considered both Active and Passive strata to represent forms of restoration treatment since both resulted from line segment-specific silvicultural assessments during the restoration program (i.e. regenerating lines were assessed and designated for protection to promote continued recovery). We considered both the Control and Human Use segments to represent forms of spatial controls for comparison of restoration effects. And we considered Off-line areas to represent an undisturbed reference (although we note that these areas could have been within the zone of influence of other linear disturbances in the study area; Fig. 2.2).

Following our primary hypothesis that vegetation recovery and movement impediment should reduce the use of restored seismic lines by caribou predators, we predicted that wolf and black bear detections would decrease along a gradient of restoration categories from least to most restored (i.e., detections on Human Use > Control > Active > Passive > Off-line; Fig. 2.4). More generally, we hypothesized that this pattern would hold for wildlife species that tend to use linear features for movement (e.g. predators), or that are attracted to disturbed lines for early seral forage (e.g. white-tailed deer, moose). We predicted that the pattern would be reversed for species expected to avoid linear disturbances, such as caribou, which are hypothesized to avoid areas of higher predation risk (i.e. highest detections expected on Off-line > Passive > Active > Control > Human Use).

We note that this project was designed to test the short-term responses of wildlife to linear restoration. While vegetation growth is slow in northern boreal environments, measurable reductions in predator use of restored lines is necessary in the short-term if ongoing declines of caribou are to be halted and reversed. But it will also be important to assess the longer-term effectiveness of linear restoration, over time scales for which substantial vegetation regrowth is expected (e.g. 10-40 years). Our project provides a baseline that can be used to assess long-term changes in restoration effectiveness. We also note that monitoring vegetation recovery on restored lines is a critical part of understanding restoration effectiveness; vegetation monitoring is being done separately from this project by Silvacom.

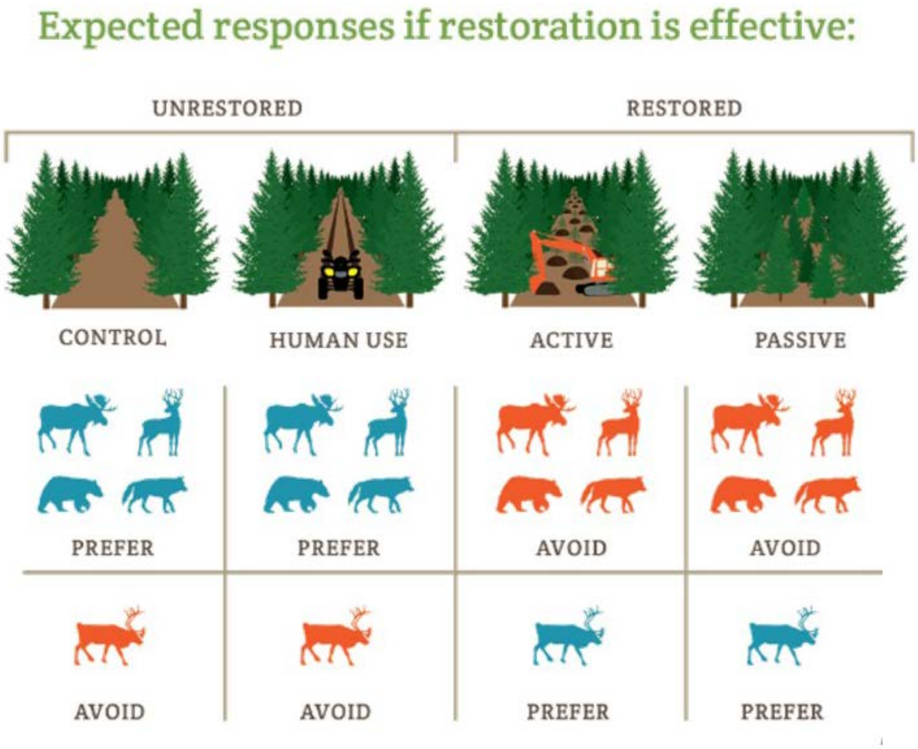

Figure 2.4 Predicted responses of focal mammal species to the four main restoration categories applied to seismic lines in our study area (i.e. sampling strata). We hypothesized that both Active and passive restoration should reduce line use by caribou predators (wolf, black bear) and apparent competitors (white-tailed deer, moose), and accordingly increase use by caribou. We expected the opposite patterns to be observed on unrestored lines left open for human use or as experimental controls. We also sampled off-line areas as undisturbed references. (Figure prepared by Fuse Consulting.)

3. Camera Trap Protocols

3.1 Camera Trap Deployment

As described in section 2.3, a total of 73 Reconyx PC 900 camera traps (Reconyx, Holmen WI, USA) were deployed in the Algar study area. We accessed the study area and camera locations by helicopter from Fort McMurray, with field trips timed for spring and fall periods when frozen ground facilitated helicopter landing and walking to survey sites, but without the deep snow or very cold conditions associated with mid-winter. One camera trap was deployed at each randomly selected site on a seismic line, or on a game trail for Off-line sites. We set each camera trap on a tree at the edge of a seismic line/game trail, facing across the line (i.e., perpendicular to expected direction of animal travel), at a height of approximately 0.8 m above the ground (range = 0.7 – 1.1 m). To minimize glare on cameras, they were deployed to face north whenever possible (depending on line direction and suitable attachment trees). Cameras were set to record temperature in ºC and time in 24-hour format, and to take one picture per motion trigger with no delay between subsequent triggers. Sensitivity was set to maximum with a fast shutter speed. Cameras were active continuously (24 hours per day, no quiet period), and one timelapse picture was taken each day at 12:00 (i.e., noon). This timelapse photo captured a consistent daily image of conditions (e.g. vegetation characteristics, snow cover) and allowed us to determine if there were any periods of camera malfunction. Cameras were positioned on the tree with the goal of capturing medium- and large-bodied animals moving along the seismic line/game trail at a target distance of approximately 2-5 m from the camera (using the PC900 walk test mode). No type of attractant was added to the site (i.e. no bait or lure). Cameras were not directed at any well-used game trails that crossed the line perpendicularly (i.e. from and to adjacent habitat) to minimize potential bias by maintaining focus on animals moving along the line. To maximize detections at off-line sites, cameras were directed at game trail intersections wherever available.

During the course of this project, we documented our standardized protocols for camera trap deployment and shared them with the emerging WildCAM camera trap network. One of the goals of WildCAM is to develop and share recommendations for best practices with the camera trap community. Further details are available at wildcams.ca.

3.2 Additional Field Data Collected at Camera Sites

We collected vegetation data during the field visits in April and November 2017, for potential use as covariates in statistical models to explain wildlife detections. (The vegetation monitoring program by Silvacom was not conducting monitoring at the camera trap locations.) Our field measurements included: broad categories of vegetation on the line (grasses, mosses, shrubs, and trees); average vegetation height; estimated vegetation cover on the line; and dominant tree and shrub species in the surrounding habitat. We also collected information on line condition, such as width, openness (i.e. whether the forest canopy closes over the line), and the presence of coarse woody debris or planted seedlings. In April 2018, we measured line of sight along seismic lines and game trails using a laser range finder.

3.3 Camera Trap Data Management

We used the program Camelot for camera trap data management and image identification (Hendry & Mann, 2017; https://gitlab.com/camelot-project/camelot). Camelot is a free and open-sourced platform designed for full project management, with multi-user capacity and compatibility with other camera trapping software. Following collection of image data in the field, we processed camera trap images using Camelot in conjunction with the R software package camtrapR (Niedballa et al. 2016) and custom R scripts developed for the project (R Core Team 2019; www.r-project.org). This workflow allowed for streamlined and organized data management that adhered to metadata standards outlined by Forrester et al. (2016). camtrapR included functions for basic image management and summary (e.g., image renaming, detection summaries), while Camelot provided a camtrapR-compatible, multi-user interface for recording deployment and image identification data. We processed images by identifying species, sex, age, and behaviour (when identifiable). In the case of uncertain species identification, we flagged images for review by a second observer. We then summarized detection events using our custom R script, considering detection events independent when occurring at least 30 minutes apart (Rovero & Zimmermann, 2016).

In efforts complementary to this project, we contributed to the development of the WildCAM network (wildcams.ca), including refinement of global camera trap metadata standards to the Canadian context (Forrester et al. 2016; RISC 2019). We also developed a more efficient cloud database system for managing camera trap data, and we note here the emergence of other data management systems that were not available at the outset of this project, such as WildTrax (www.wildtrax.ca) and Wildlife Insights (www.wildlifeinsights.org; Ahumada et al. 2019).

4. General Summary of Wildlife Detections

4.1 Sampling Effort

Over the course of the project, 73 camera stations were deployed across the 5 restoration treatment categories (22 Active, 12 Passive, 14 Human Use, 12 Control, and 13 Off-line; see section 2, Fig. 2.2). The total survey period lasted 4 years from November 2015 to November 2019. During this period, 1 Control and 1 Passive Restoration site were affected by ongoing industrial activities in the study area, with the line vegetation being removed and opened up for access. We therefore reclassified these sites in April 2018 as being in the Human Use category, so that wildlife detections would best reflect the status of the category of the line at the time of detections. As noted in section 2.3, camera traps were deployed in three phases (Fig. 4.1): phase one was implemented in November 2015 (n = 24); phase two implemented in November 2016 (n = 36) and phase 3 in November 2017 (n = 13). Cameras were run continuously at the same location from the date of deployment until November 2019, aside from malfunctions and breakages (Fig. 4.1). During 2017-18, we experienced higher than expected rates of malfunction due to SD memory card errors, which we suspect was due to a faulty batch of cards (we subsequently changed suppliers). Other causes of camera inactivity included battery failure, bear damage, snow occlusion, filled memory storage (due to false triggers by moving vegetation), two cases of camera theft, and a few unexplained sources of camera error. Given the remote location of the study area (necessitating helicopter access), we could only check camera traps a maximum of twice per year (more frequent checks could reduce periods of camera inactivity). After accounting for all periods of camera inactivity, our total sampling effort was 74,076 camera trap days, with an average of 1,015 days at each station (min = 539; max = 1,477).

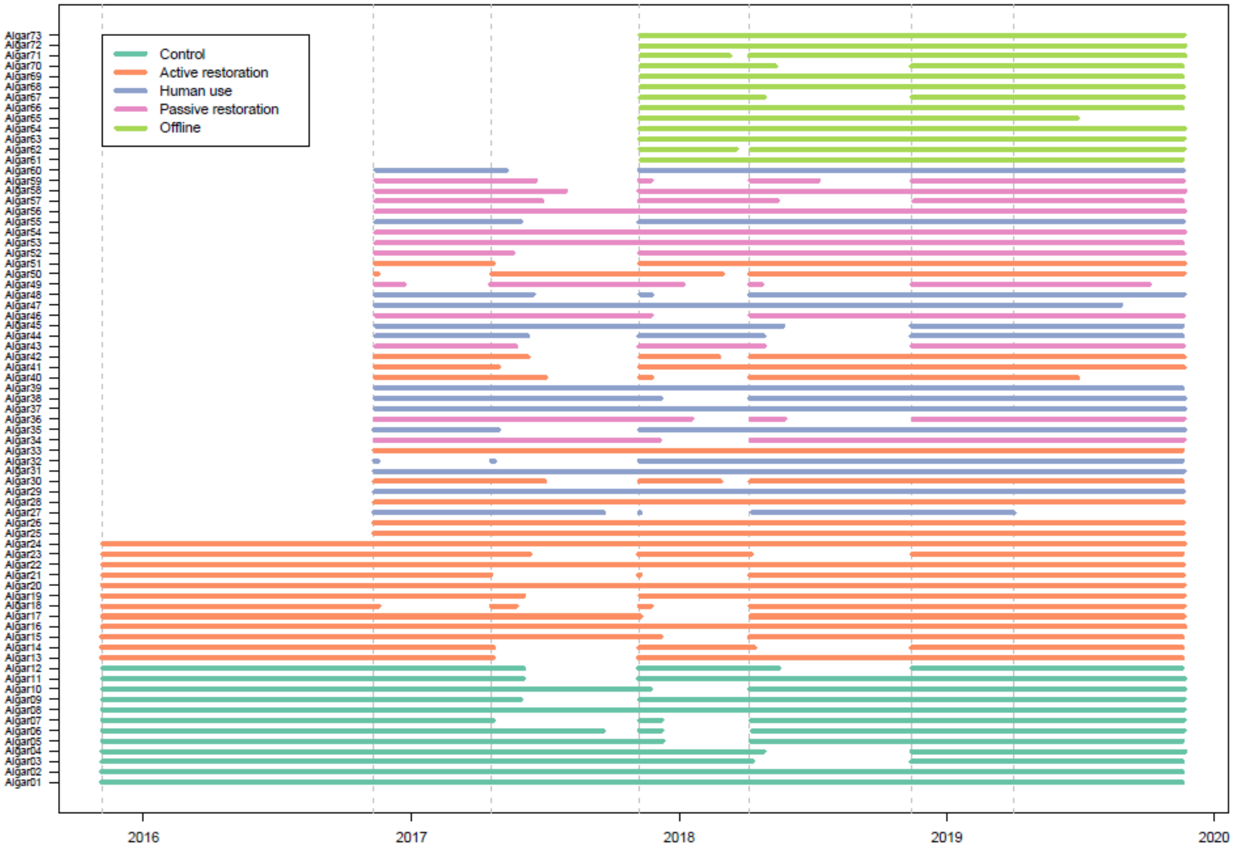

Figure 4.1 Summary of camera trap activity. The solid lines show the period when individual camera trap stations (listed on y-axis) were actively collecting data, with colours denoting the seismic line restoration category (i.e., experimental treatments, sampling strata). Gaps in the lines mark periods where a camera was inactive due to malfunctions, weather (e.g. snow covering the lens) or theft.

4.2 Species Detections

4.2.1 Summary statistics

In total we accrued 105,663 photographs from the 73 camera stations. Of these, 47,203 were of animals, 461 of humans, and 57,999 false triggers (i.e. cameras triggered by moving vegetation). Of the animal detections, 97% were identified to species or genus level. The 1,422 photographs of animals which it was not possible to identify belonged to either small birds or small mammals. Reducing the dataset to only independent detections of animals which occurred at least 30 minutes from a previous detection of the same species (to reduce the chance of repeatedly counting the same individual), resulted in a dataset comprising of 7,354 independent detections of 25 identifiable animal species and humans (Fig. 4.2).

The most frequently detected species was white-tailed deer with 1844 detections. However, the species detected at the most sites were the black bear (0.90) and moose (0.86). The least frequently detected species were cougars and Canada geese (n=1) and wolverine and elk (n=2; Fig. 4.2; Appendix 1).

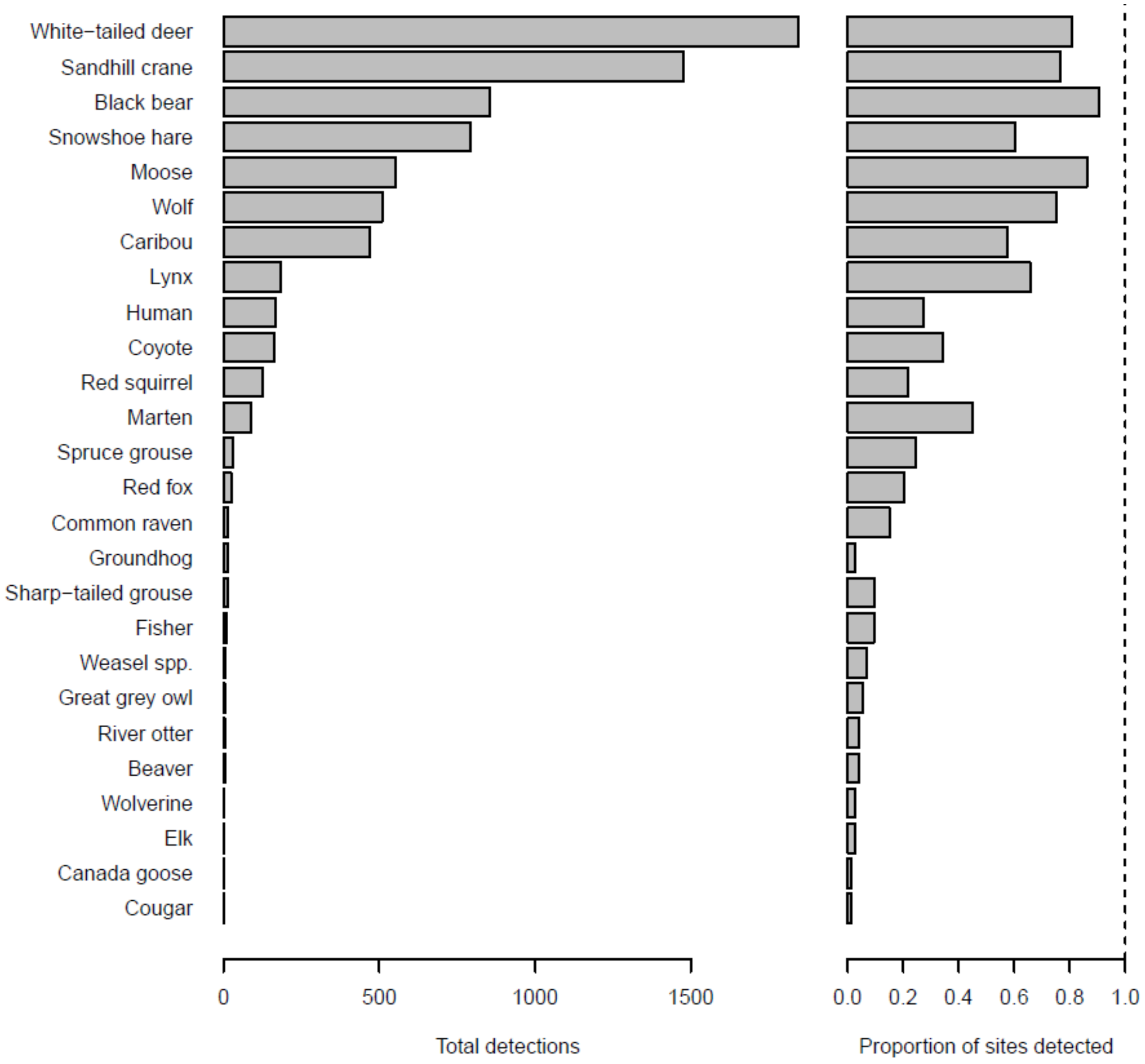

Figure 4.2 Summary of the total number of independent detections for each species (left panel) during the Algar camera trap survey, and the proportion of sites a given species was detected at (right panel). For raw detection numbers and scientific names, see Appendix 1 Table 1.

4.2.2 Area-wide temporal trends

Deploying camera traps continuously at the same survey locations allowed us to examine how patterns of wildlife detections changed through time. Summed across all species, wildlife detections peaked in the summer months and declined in winter, and this pattern was consistent across years (Fig. 4.3).

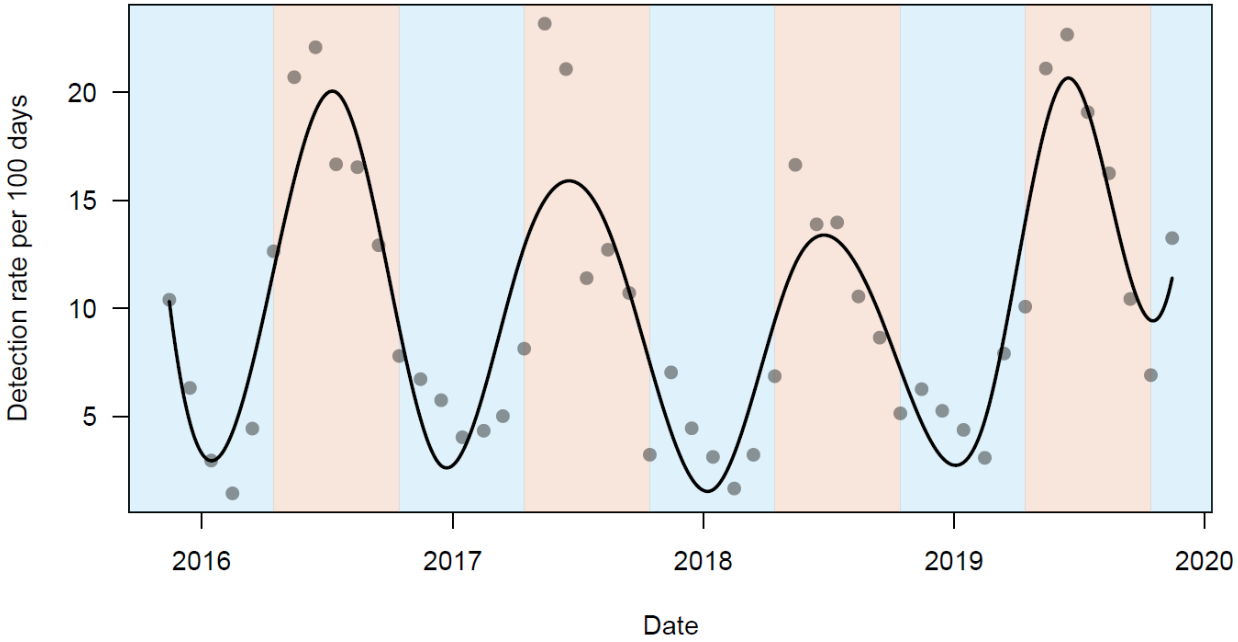

Figure 4.3 Summary of the total number of independent detections through time for all species. Where: dots = the monthly total detection rate (per 100 days of camera effort); blue sections = winter months (October-March); red sections = summer months (April-September); line = smoothed spline fitted to the monthly detection rate.

Whereas the overall detection rates appeared similar in amplitude and frequency across years (Fig. 4.3), there were several species that showed marked changes in detection rates through time. The wolf detection rate (Fig. 4.4 left panel) declined from ~2 detections per 100 camera days to ~0.5 detections per 100 camera days between 2016 and 2019. This is consistent with the timing of the Alberta government's wolf population management program delivery (as part of the caribou conservation program), which removed 23 wolves from in and around the Algar range between January 2017 and March 2019 (Government of Alberta unpublished data). The lynx detection rate (Fig. 4.4 centre panel) initially declined from the start of the monitoring to its lowest point in 2018, but subsequently rebounded to the highest detection rate at the end of 2020. The change in lynx detection rate is likely to be linked to the population dynamics of the snowshoe hare (Fig. 4.4 right panel), which typically undergo characteristic 10-year cycles in the boreal forest (Krebs et al. 2001), and in our study area appeared to be steadily recovering from a population crash which occurred pre-2016. We suggest that further evaluation of such temporal trends, and comparison with trends in other caribou ranges undergoing different management actions, is an important area for future research and monitoring (e.g. section 9).

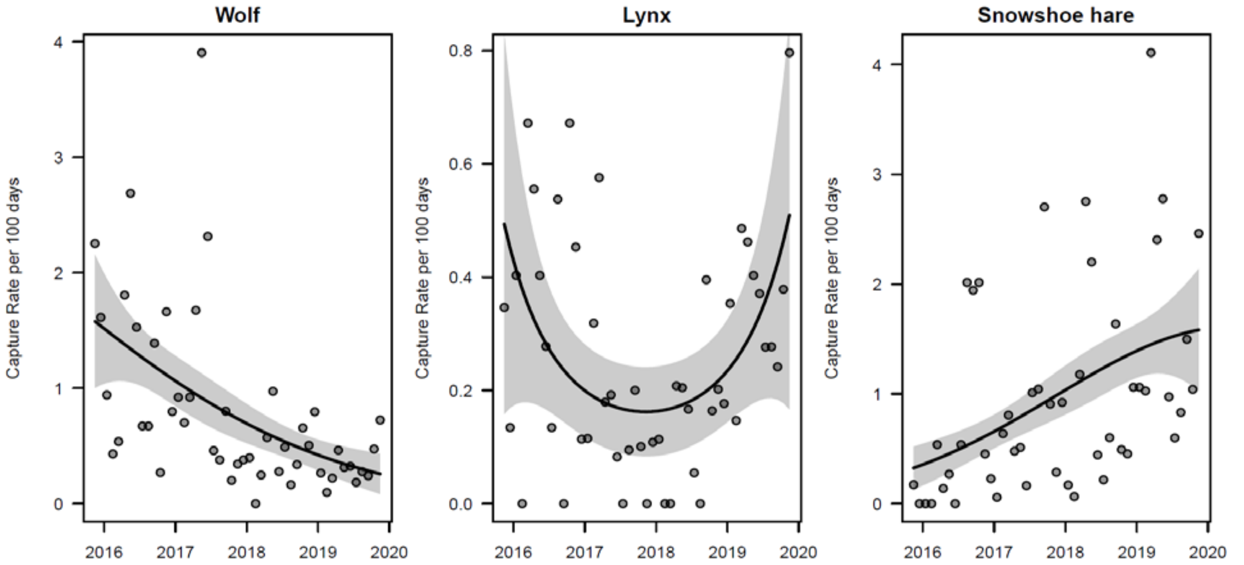

Figure 4.4 Temporal trends in monthly camera trap detection rates for three species: wolf (left), lynx (centre), and snowshoe hare (right). Points represent the observed detection rate for each month, lines show the predicted detection rate from a Poisson generalized linear model with date as the fixed effect, and the shaded area depicts the standard error of the prediction. For full statistical consideration of temporal trends accounting for other covariates see sections 5.1 and 5.2.

4.2.3 Spatial patterns

Camera trapping in a standardized fashion across a large area of interest also allows us to explore the spatial patterns of species detections (Fig. 4.5). Here we show the spatial structure of detections for five focal species detected in the Algar landscape: caribou, white-tailed deer, moose, wolf and black bear. Whereas caribou were largely detected in the eastern edge of the survey area and a large cluster of lowland habitat in the south, white-tailed deer showed the opposite pattern. Wolf detections peaked at stations in the central western side of the survey area, while moose were detected more on the eastern side. Relative to the other species, black bears appear more homogeneously distributed, albeit with an apparent preference for sites with upland habitat. For quantitative assessment of species-specific habitat preferences see sections *5.1 and 5.2.*

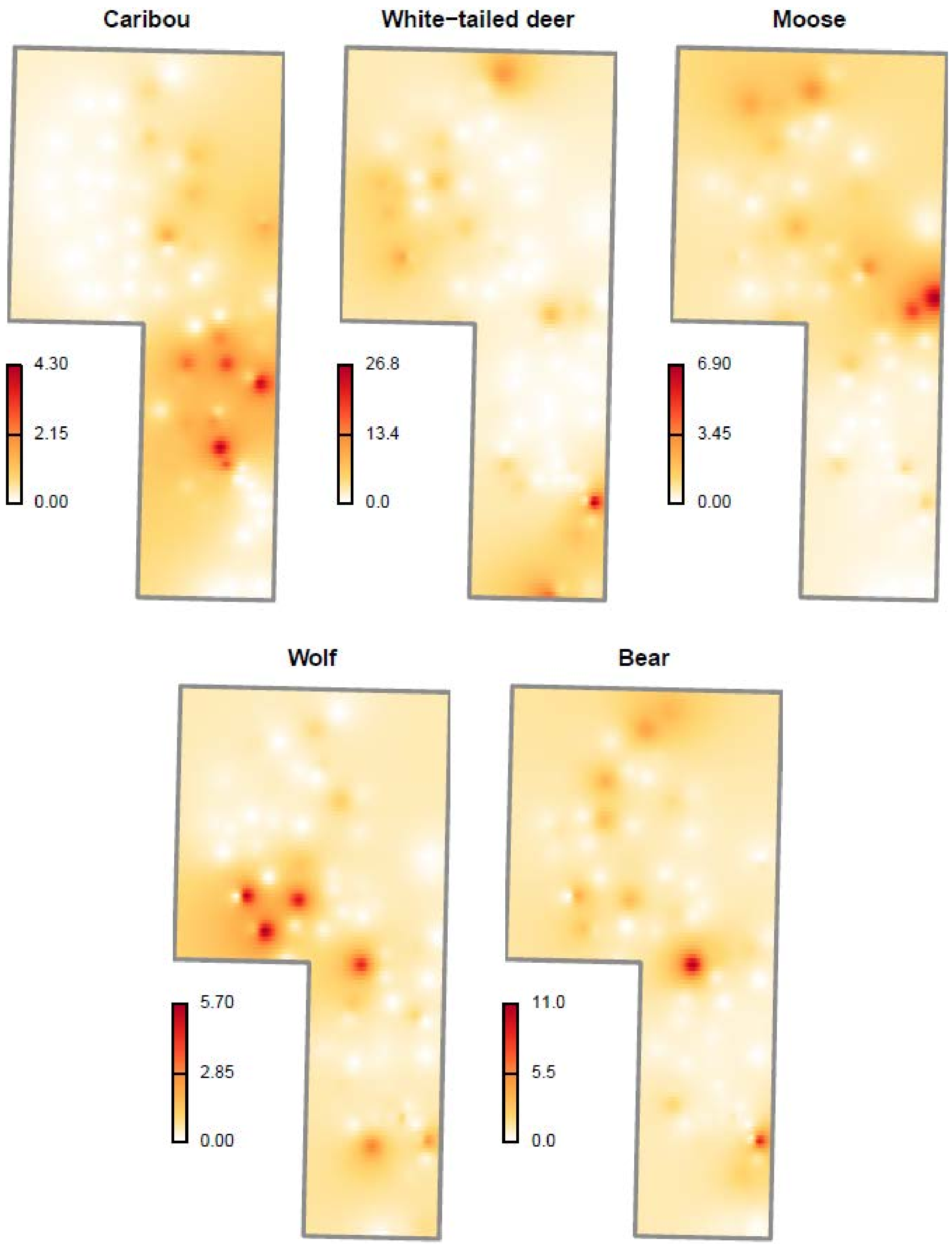

Figure 4.5 Interpolated spatial patterns of focal species detections by camera traps within the Algar landscape. Where: colours denote spatial variation in detection rate along a gradient from zero detections (white) to the maximum detection rate for each given species (red); numbers in the legends denote the detection rates for each species.

One cause for concern in caribou recovery efforts is the gradual encroachment of white-tailed deer into caribou habitat (Dawe et al. 2014; Fisher et al. 2020). The spatial distribution of camera traps allows us to explore potential locations where white-tail deer and caribou activity are overlapping (Fig. 4.6). The southern and western portions of the Algar study area support the lowest ratios of caribou to white-tailed deer detections (i.e., more white-tailed deer relative to caribou), which is also where the majority of upland habitat is present. In lowland habitat, the ratio of caribou to white-tailed deer detections is at its largest (i.e., more caribou relative to white-tailed deer). The areas of greater overlap appear to fall within the buffer between core lowland habitat and upland areas. This is consistent with our understanding of caribou and white-tailed deer habitat preferences. We suggest that repeating this type of camera trap survey in the future (e.g. in 5-10 years) could be useful for evaluating whether the "interaction" zone between white-tailed deer and caribou (and/or other species) has shifted through time. In other words, testing the hypothesis that linear restoration should reduce overlap between caribou and their apparent competitors and predators as vegetation recovery progresses.

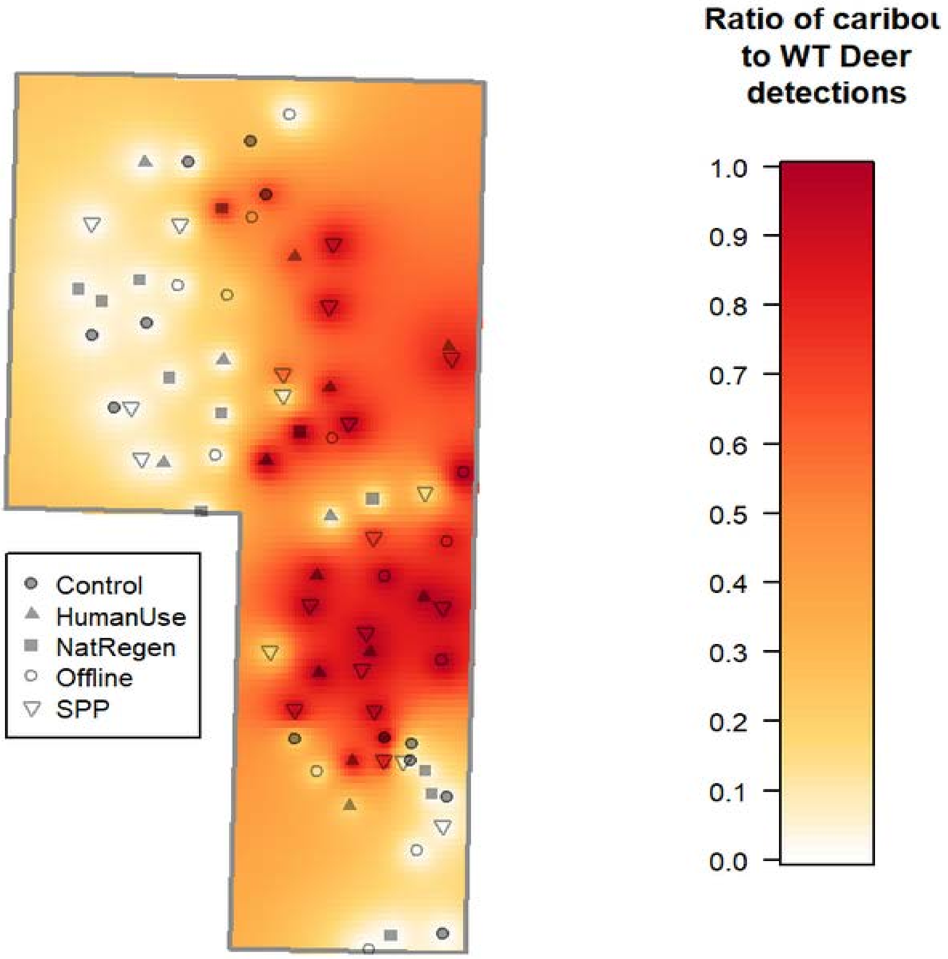

Figure 4.6 Interpolated plots of the ratio of caribou to white-tailed deer detections across the Algar study area. Where: white = stations at which white-tailed deer were the dominant species, red = stations at which caribou were the dominant species.

5. Wildlife responses to restoration and other landscape factors

5.1 Single-species models of focal species responses

Quantifying how individual species respond to seismic line restoration is essential to determine if target species are responding as expected after completion of restoration projects. Our team previously published a paper assessing the responses for five focal species (caribou, white-tailed deer, moose, bear and wolves) to seismic line restoration in the Algar region, using the first 3 years of camera trap data from this project (Tattersall et al. 2020b). In short, we found that white-tailed deer preferred unrestored seismic lines over actively restored lines, while wolves preferred human-use lines but did not avoid restored lines. Caribou preferred lines in lowland habitat and lines surrounded by low linear density regardless of restoration. In general, species-specific responses to restoration were weak, indicating that restoration alone may not be effective in stabilizing threatened caribou populations in the short term (Fig. 5.1).

Here we repeat the analysis conducted in Tattersall et al. (2020b) for two reasons: *i)* to include an additional year of data not included in the original manuscript (November 2018 to November 2019) and *ii)* to include the 13 Off-line stations not considered in the original analysis. Inclusion of the final year of data will allow us to determine if the conclusions of the original manuscript are consistent with those reached with all available data and will allow more robust characterization of temporal trends. Assessment of the Off-line stations will give an idea of the impacts of seismic line treatments relative to reference conditions that can serve as a target for animal activity in restored lines.

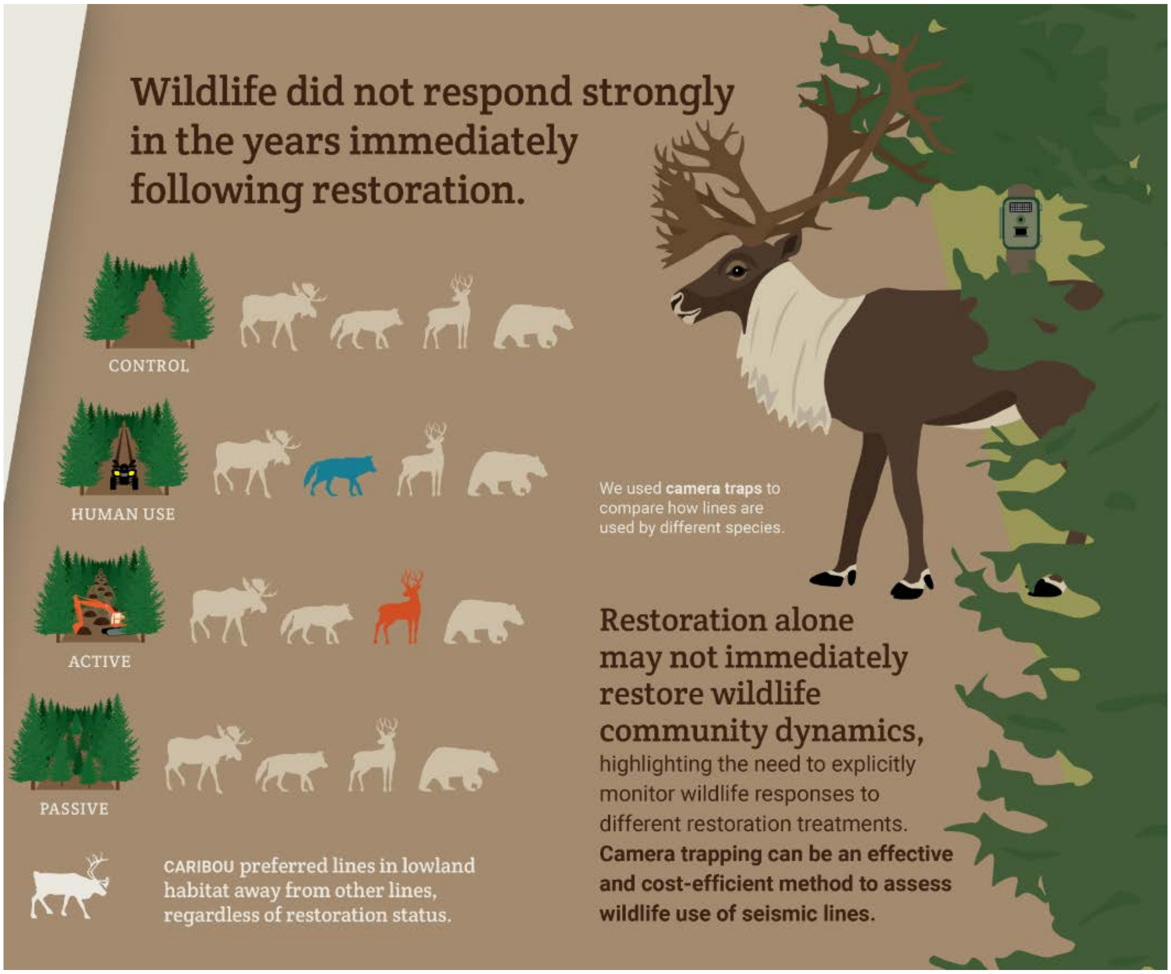

Figure 5.1 Infographic summarizing the key results presented in our publication using the first 3 years of camera trap monitoring data from this project (Tattersall et al. 2020b; Appendix 7. Infographic prepared by Fuse Consulting).

5.1.1 Methods

We repeated the analyses as described in Tattersall et al. (2020b) with three key differences. First, the reference level in the original analysis were Control (unrestored) seismic lines, whereas here we use Off-line stations as the reference level, which is consistent with the goal of restoring lines back to the conditions of undisturbed habitat. Second, we included a continuous fixed effect of Year to capture linear temporal trends in focal species detection frequencies. Third, we did not include Snow as a binary variable as it was not available at all temporal scales, rather we used a categorical variable for season distinguishing summer (Oct-Mar) and winter (Apr-Sep) to capture seasonal differences in habitat use and movement behaviour which might influence detection frequencies. As in Tattersall *et al.* (2020b), the statistical sampling unit was Site-Month, with repeated, non-independent monthly samples at individual camera stations. We therefore modeled monthly detections within a zero-inflated generalized linear mixed modelling (GLMM) framework, modelling monthly species' detections as a function of restoration treatment strata, as well as predictors capturing additional variation hypothesized to affect species' line use, specifically: seismic line characteristics (Line Density, Line Width), habitat (Proportion of Lowland Habitat, Vegetation Height) and time (Year). We included Site as a random intercept term to account for non-independence of monthly detections at the same site and a random intercept of month to account for multiple month-level observations across years. Finally, we included an offset of the number of sampling days in a given sampling interval to control for instances where sampling effort was not equal between different months. We deemed coefficients where the 95% confidence intervals do not include zero to be 'statistically significant', and we discuss the covariate importance in terms of their estimated effect sizes (given that they are statistically significant).

5.1.2 Results

The results from analysis of the full dataset were broadly consistent with those detailed in Tattersall et al. (2020b), however there were some notable differences. We break down these findings by species below and discuss the additional information provided by the Off-line control where appropriate.

Wolves

We confirmed that wolves were more frequently detected on Human-Use lines than on other seismic lines (Fig. 5.2). Wolves were also detected more frequently on all seismic line treatments relative to the Off-line control, however the differences were not statistically significant. We confirmed that wolves were detected less frequently in lowland habitat than upland habitat. There was also statistical support a decline in the frequency of wolf detections through the four-year survey period.

Black Bear

In the original analysis, there was no statistical support that seismic line treatment category influenced black bear detection frequency. However, addition of the Off-line treatment revealed statistical support for bears being detected more frequently on Active, Control and Human-Use lines relative to the Off-line controls (Fig. 5.2). We confirmed a statistically significant positive relationship between bear detections and vegetation height, but found no statistical support for the previously reported negative relationship between bear detections and proportion of lowland habitat.

White-tailed deer

All seismic line treatments increased the detection rates of white-tailed deer relative to the Off-line control, and this effect was statistically significant for natural regeneration, unrestored Controls and Human-Use lines (Fig. 5.2). We confirmed the previously reported reduction in use of Active strata relative to Control (Appendix 2), negative relationship between white-tailed deer and proportion of lowland habitat (deer preferred upland habitat) and a positive relationship with vegetation height. There was no statistical support for the previously reported positive relationship with line density. There was also a significant positive relationship between deer detections and survey year, suggesting an increase in deer activity over time.

Moose

All seismic line treatments showed increased detection rates of moose relative to the Off-line control, however this effect was only significant for Passive lines (natural regeneration), Control and Human-Use lines (Fig. 5.2). We found no statistical support for the previously reported negative effect of proportion of lowland habitat and line width on moose detections, however we did find statistical support for the positive relationship with vegetation height. We also found a positive effect of survey year on moose detection frequency, indicated an increase in moose over time.

Caribou

There was no significant statistical support for caribou detections either increasing or decreasing on the seismic line treatments relative to the Off-line controls. We confirmed the previously reported large positive effect of proportion of surrounding lowland habitat on caribou detection frequency, as well as the smaller positive effect of line width and the negative effect of line density (Fig. 5.2).

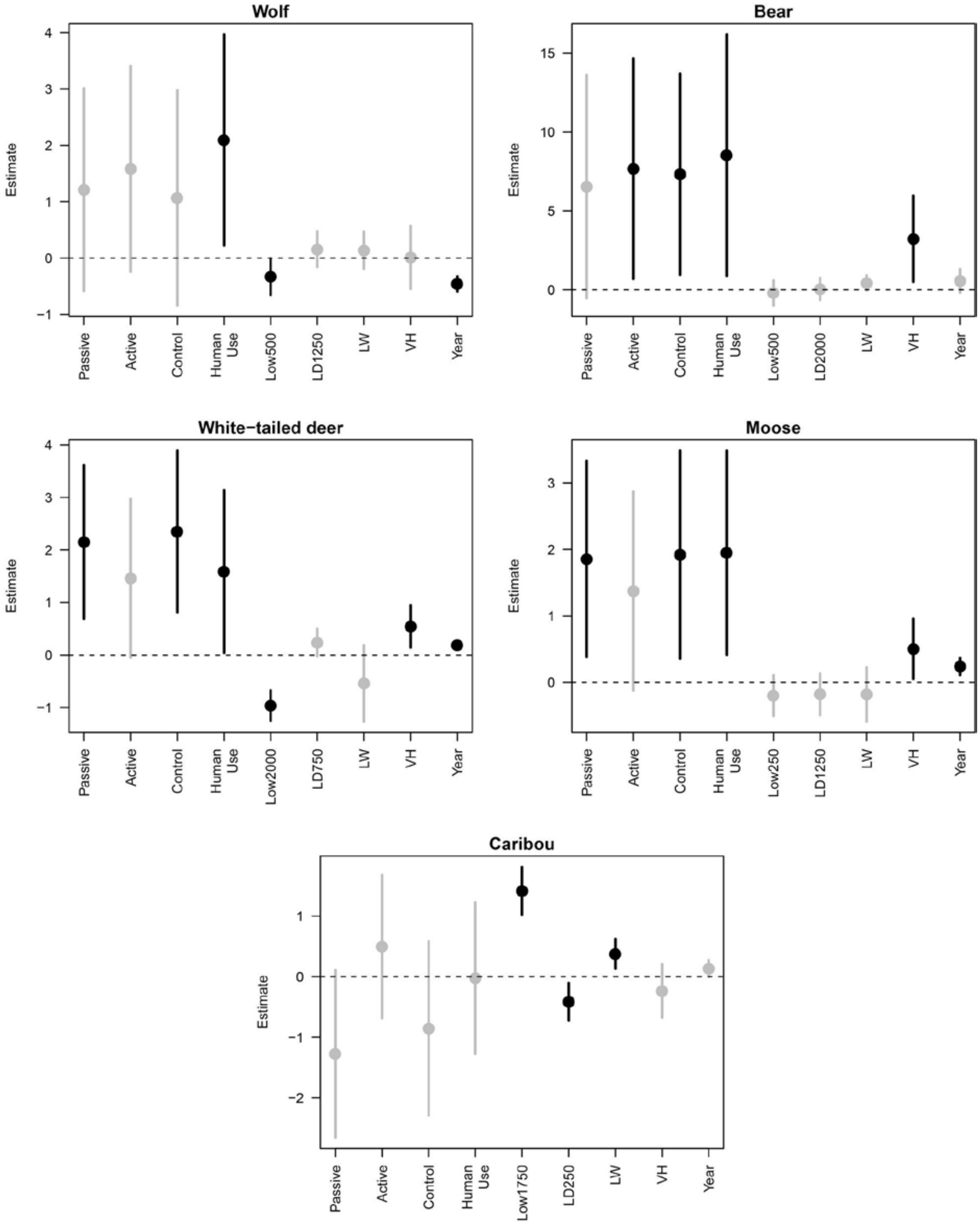

Figure 5.2 Estimated effects of seismic line strata and other factors on line use by boreal mammals in northeastern Alberta. Where: points = mean effect ± 95% confidence interval (lines); black = estimates whose confidence intervals do not span zero (statistically significant); grey = estimates whose confidence intervals do include zero (statistically non-significant);

[*figure caption continued on next page …*]

[*figure caption continued …*] Low### = proportion of surrounding lowland within buffer, LD### = line density in buffer; LW = line width; VH = vegetation height on line; ### = buffer radius (m). We used Off-line camera trap stations as our reference stratum in the models to assess the relative effect of seismic line treatments (dashed line). We centred and standardized predictor variables to indicate effect sizes relative to the Off-line strata for categorical variables, with all other variables held constant at their mean value. Further details on variables in section 5.2 or Tattersall et al. 2020b. See Appendix 2 Figure 1 for the results of models with the Control strata as the reference level (as in Tattersall et al. 2020b).

5.1.3 Discussion

Addition of the final year of camera data did not significantly change the conclusions of Tattersall et al. (2020b): white-tailed deer preferred Passive, Control and Human Use seismic lines over Active lines; wolves preferred Human-Use lines but did not avoid Active restoration lines; and caribou preferred lines in lowland habitat and lines surrounded by low linear density regardless of restoration. Thus, in the short-term, the forestry prescriptions used to restore seismic lines in the Algar region did not fully achieve their objective of reducing use by caribou predators and apparent competitors. This may be due to a time lag in effect, in which the returns on restoration will be seen in later years; long-term monitoring is needed to test this hypothesis. Alternatively, it is possible that different restoration prescriptions are needed to achieve restoration and caribou conservation goals.

Our extended analysis, to include an additional year of monitoring data and the Off-line category, did provide additional perspectives on wildlife use of seismic lines within the Algar study area. Four of the five focal species were detected more frequently on seismic lines (regardless of treatment type) than in Off-line habitats (white-tailed deer, bear, wolf and moose). Even where the differences between line treatments and Off-line sites were not significant for these species, the effect size was positive and large (relative to the other predictors). Thus seismic lines are used more by most of the large mammal community - not just wolves - which will have large implications for predator-prey dynamics. Only caribou showed no statistical difference in detection rates between seismic line treatments and Off-line cameras. This suggests that the greatest effects in seismic line restoration may not occur directly on species most threatened by their existence (i.e. caribou), but rather they will be mediated by indirect effects on their predators and apparent competitors.

Our extended analysis showed that certain effects detected using the first three years of monitoring data (in Tattersall et al. 2020b) were not supported with the additional year of data and Off-line stratum. This highlights the value of longer-term monitoring and larger sample sizes of camera trap detections, particularly in the relative low productivity environments of northern boreal forests. With the additional year of data, and the incorporation of time directly into our models, we began to see some interesting temporal trends in species detections (see also section 4.2.2). The observed decline in wolf detections through time would be a desired outcome of linear restoration, however it is also consistent with Alberta's delivery of wolf population management, which we consider to be a more direct impact to wolves and thus more likely mechanism underlying the decline. Furthermore, we detected significantly positive trends in detections of deer and moose, which is not a desired outcome for caribou. If populations of apparent competitors increase in the region—whether due to wolf control, climate change, land-use change, or other factors—it is likely to undermine caribou recovery over the long-term. We suggest that camera trap monitoring of longer-term population trends is an important direction for further research and monitoring in support of caribou recovery.

5.2 Multi-species modelling of community-level responses

Assessing the impact of seismic line restoration is complicated by the fact that the effects of altering line characteristics are unlikely to be limited to only a few focal species (e.g. caribou, wolves and white-tailed deer); rather they have the potential to influence other parts of the vertebrate community (e.g. Fisher and Burton, 2018). Different species are expected to respond in different ways to restoration prescriptions, due to their differing niche requirements and life-history traits, including differing forage preferences (e.g. early vs. late seral vegetation), movement behaviour (e.g. Finnegan et al 2018b) and habitat selection (e.g. Dickie et al. 2020). These interact with divergent vegetation profiles and physical characteristics between areas on and off of seismic lines (Finnegan et al., 2018a) and between restored and unrestored lines, to create considerable interspecific variation to seismic line restoration.

Given this expected variation in species responses, focusing on only a few focal species (as in section 5.1 and Tattersall et al. 2020b) may restrict our ability to elucidate the broader mechanisms underlying responses to anthropogenic disturbance and habitat restoration (Seibold et al., 2018). Examining multiple species allows us to compare responses to test hypothesized mechanisms, and one way to gain a multispecies perspective is through the use of joint species distribution models (Warton et al. 2015). Such approaches jointly model detections across multiple taxonomic groups whilst accounting for environmental predictors, allowing the quantification of residual correlations (co-occurrences) between species. Understanding how the vertebrate community responds to habitat restoration, and the potential interactions between species within the community (Aslan et al., 2016), is of key importance if we want to make informed and effective conservation decisions which maximize the benefits and minimize the negative consequences of habitat restoration (Burgar et al., 2019a; Fraser et al. 2015; Shackelford et al. 2013).

In this section, we applied joint species distribution modelling framework to the camera trap detections in order to characterize the sensitivity of the medium- and large-bodied vertebrate community to seismic line characteristics in the Algar study area. We pursued the following three main objectives:

i) Quantify effects of seismic line characteristics on species occurrences across the community.

ii) Identify groups of species with similar vs. divergent responses to line characteristics.

iii) Predict changes in community structure in response to restoration.

5.2.1 Methods

Modelling framework

We used a joint species distribution modelling approach implemented in the Bayesian Hierarchical Modelling of Species Communities (HMSC) package v3.0 (Tikhonov et al., 2020) within the R statistical environment (R Core Team, 2019). Joint species distribution models allow multivariate response terms (here species counts in a given time interval) to be related to hypothesized predictors through a regression framework whilst quantifying species co-occurrences through random effects. It facilitates the modelling of multiple members of a given community simultaneously in what is essentially a multispecies generalized linear mixed effects model. Here, we do not interpret the estimated species-level co-occurrences as species interactions (see Blanchet et al., 2020), rather we consider them to represent systematic covariance in station-level counts between species that is not explained by the predictors included in the model (Ovaskainen et al., 2017). Species interactions are one such process contributing to this variation, but it could also reflect between-species correlations in responses to unmeasured covariates.

Multispecies response term

The response term in our models was a site-time-by-species matrix, where each row specified the number of independent detection events within a given six-month (seasonal) time period for a given site. Any site-time period with less than 30 camera-days of sampling effort was excluded from the modelling. The fixed effects were composed of five linear predictor terms describing line characteristics (see below), a linear effect of year (allowing temporal trends in detections), a linear effect of water table depth (to capture habitat variation), a binary factor capturing seasonal variation (winter/summer), and a linear offset reflecting sampling effort (active camera-days within each given time period). We also assessed multispecies responses in monthly time periods and predictor effect sizes and directions were consistent with results from models using the six-month blocks, however the variance explained (R^2) and effective sample sizes were smaller for all species assessed at the monthly scale (results not shown), so we focused on the six-month responses. We assume that our response variable—the number of independent detection events—is an index of ‘habitat use’ by species (following Tattersall et al. 2020b). Although this response term contains information on local population density, the degree to which detection rates correlate with density vs. movement is likely to be species and context specific (Broadley et al. 2019).

Predictor variables

In our previous analyses of the first three years of camera trap data collected during this project, we modelled seismic line restoration treatment as a categorical fixed effect (Tattersall et al., 2020b). Here we take a different approach, decomposing restoration treatment categories into continuous measures of line characteristics. This change should better capture within-treatment, between-site variation in line characteristics, allow assessment of species-specific responses to individual line characteristics, and facilitate predictive modelling. We quantified five seismic line characteristics (four from field measurements, one remotely) which reflected the structure, regeneration status and spatial configuration of the seismic lines within the study area (Table 5.1). The characteristics measured in the field were: i) ‘line of sight’ representing mean observable distance in meters along the line (for seismic treatments) or game trail (for off-line sites) in both directions quantified using a laser range finder (distances are right truncated at 500m - the maximum distance quantifiable with the rangefinder used); ii) vegetation height (m), the average of three representative woody shrubs/trees measured haphazardly within 10m of the camera in November 2017, iii) line width in meters measured at the time of camera installation; and iv) mounding height in cm measured at three haphazard locations within 10 meters of the camera station in November 2017. Line density was calculated using the Alberta linear feature GIS data layer (Alberta Biodiversity Monitoring Institute, Caribou Monitoring Unit, unpublished data). A principal components analysis showed that these continuous predictors adequately discriminated the original restoration treatment categories in multivariate space (Fig. 5.3). However, we chose to use the individual predictors in models of wildlife detection frequencies to ensure clear, unambiguous interpretation of the effects of line characteristics. Line characteristics showed low pairwise correlations (correlation coefficients <0.5), except vegetation height was negatively correlated with line of site and line width and was thus excluded from the model (Appendix 3 Figure 1).

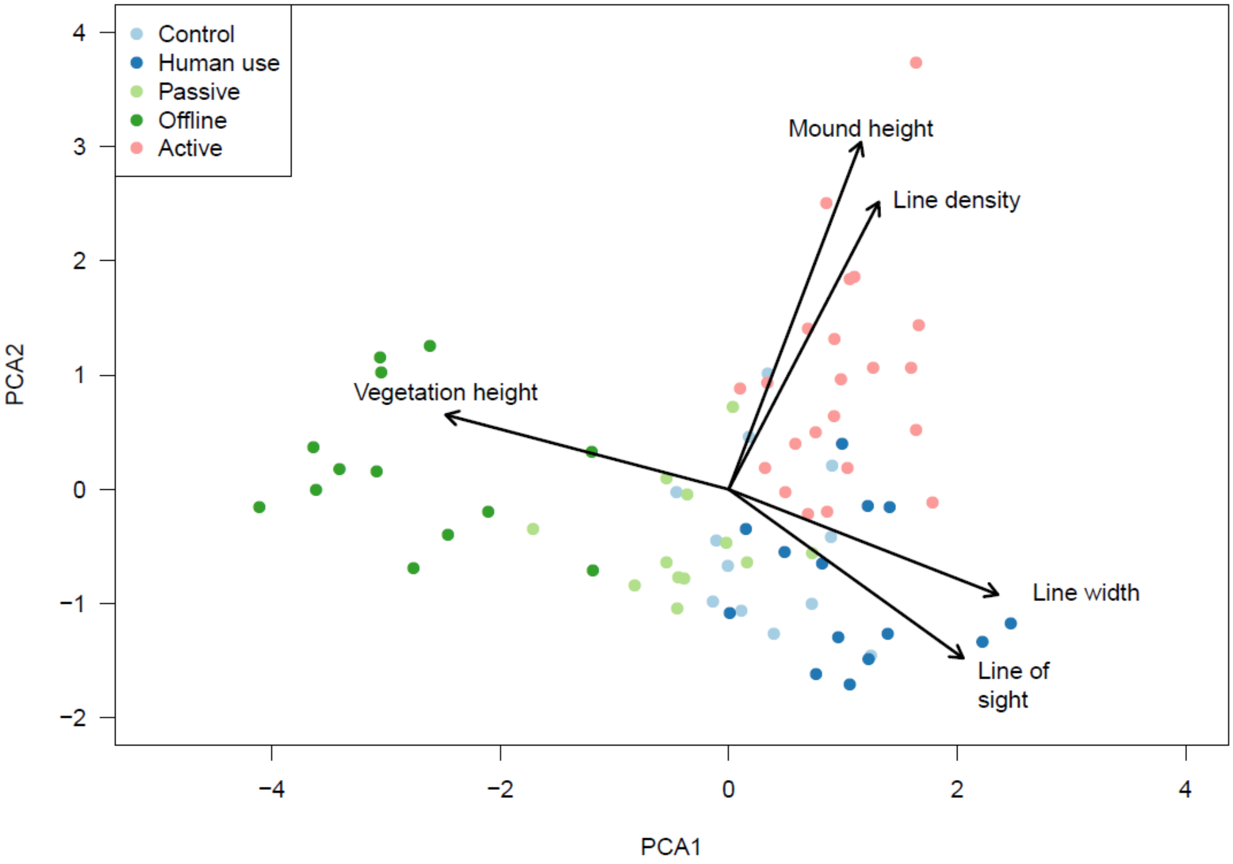

Figure 5.3 Major axes of variation from a principal components analysis for the five seismic line characteristics considered in our analysis of multispecies responses to restoration. Where: points = sites (i.e. camera trap stations); arrows = direction and magnitude of covariate loading; colours = seismic line restoration treatment categories.

In addition to the seismic line characteristics, we also accounted for a suite of other covariates expected to influence wildlife detection frequencies, including habitat, seasonality and temporal trends (Table 5.1). To account for between-site variation in habitat type, we included average distance to water table in the 500m surrounding each camera location using the 1m Wet Area Mapping (WAM) layer provided by Alberta Environment and Sustainable Resource Development (White et al. 2012). Water regime is a major determinant of habitat type and has been linked to the capacity of seismic lines to regenerate (Revel et al., 1984): lowland habitat will have close proximity to the water table, whereas drier, mesic, upland sites have a greater distance to the water table. To control for seasonality in activity patterns, movement behaviour or habitat use, we included a categorical two-level factor distinguishing the two primary seasons: summer (April – September, mostly snow-free) and winter (October-March, mostly snow-covered. We used summer as the reference level). We accounted for between-station variation in habitat quality through the inclusion of site-specific NDVI (Normalized Difference Vegetation Index). Mean NDVI within each six-month time period was calculated by extracting 16-day NDVI values for the 250m pixel within which each camera was situated for the duration of the project using the MODIStools package (Tuck et al., 2014). The average NDVI for each station within each given 6-month time period was calculated. We reduced the covariance between season and average NDVI by standardizing NDVI scores within each season (summer/winter), thus the NDVI covariate used in our models represented the within-season heterogeneity in vegetation productivity at each site. To account for species-specific temporal trends in the count data, we included a linear effect of survey year (2015-2019). To control for variation in survey effort due to periods of camera trap malfunction, we included the number of days a given camera trap was active in a given time period as an offset. Finally, we included station as a random intercept term to account for the non-independence of six-month wildlife detection frequencies arising from repeated observations from the same station.

Table 5.1 Predictor variables used in the HMSC models and their corresponding hypothesized relationships with use of seismic lines by species in the mammal community.

Covariate Group	**Name**	**Predictions**
Line characteristics	Line density	Predator use is higher and prey use lower with increasing density of seismic lines around a sampling site
Line characteristics	Line of sight	Predator use is higher and prey use is lower with increasing line of sight
Line characteristics	Line width	White-tailed deer and moose use is higher with wider lines (due to increased availability of early seral vegetation)
Line characteristics	Mounding height	Use by predators and white-tailed deer is lower where mound height is higher, due to movement restrictions
Habitat	Water table distance	Caribou use will increase and white-tailed deer use will decrease as distance to the water table decreases (habitat preferences)
Habitat	NDVI (seasonally normalized)	Herbivore use will increase with increasing NDVI values (more forage availability)
Seasonality	Season	Use of all species will decrease in winter relative to summer (due mainly to more restricted movement/activity in snow)
Temporal trend	Year	Concurrent wolf population management will decrease wolf use through time, which could lead to increases in use by their prey. Restoration could also reduce use over time by predators and apparent competitors.

Statistical analysis

We used a Bayesian framework with Markov chain Monte Carlo (MCMC) to estimate the model parameters. Species counts were assumed to follow a Poisson distribution, and species responses to the predictors were assumed to follow a multivariate Gaussian distribution. We used the default, non-informative priors described in (Tikhonov et al., 2020). Species with 10 or fewer independent detections (beaver, elk, wolverine, otter, fisher, and cougar) were excluded from the HMSC analysis as their parameter estimates failed to adequately converge (results not shown). The final model was fit with four MCMC chains, each composed of 200,000 iterations with a thinning interval of 1,000 and a burn in length of 100,000. Parameters were confirmed to be converged and well mixed through visual inspection of trace plots, examination of effective sample size and potential scale reduction factor. We used pseudo-R^2 as a measure of model fit, calculated as the squared Spearman correlation between observed and predicted values, times the sign of the correlation (Tikhonov et al., 2020). We also examine the proportion of the psuedo-R^2 explained by each of the predictors of wildlife habitat–use as a measure of their relative importance.

Predicting community compositional change

To examine the compositional shift of the community in response to variation in seismic line characteristics, we used model-estimated parameters to predict species-specific habitat use (i.e. relative abundance) under ‘non-restored’ characteristics (i.e., high line of sight, high line density, large line width, and no mounding) and compared it to habitat use predicted under ‘restored’ characteristics (i.e., low line of sight, low line density, zero line width and mounding). We standardized the predictions using estimates for summer and with all other continuous predictors held at their average value (year, water table depth, and NDVI). Species were ranked in terms of their predicted level of habitat use, and we interpreted any predicted change in rank-order of species from unrestored to restored characteristics as a predicted change in the relative abundance of that given species in a restored landscape.

5.2.2 Results

Across the medium- and large-bodied vertebrate community, species responses to seismic line characteristics and other modelled factors were highly variable. The degree to which our multispecies, joint distribution model explained variation in wildlife habitat use (i.e. camera trap detection frequency) was highly species-specific: comparison of pseudo-R^2 values showed that the model explained over 60% of the variation in camera trap detection frequency for three species (sandhill crane, white-tailed deer and black bear), between 30-45% of variation for four species (caribou, snowshoe hare, wolf and moose); and less than 20% of the variation for five species (coyote, lynx, squirrel fox and marten) (Fig. 5.4).

Variance in species occurrences explained by seismic line characteristics

Taken together, variation in line characteristics (line of sight, line width, mounding height and line density) did not explain the majority of variation in habitat use relative to the other predictors (season, habitat type/quality, temporal trend or the station-level random effect) for any species, suggesting that line characteristics are relatively weak predictors of line use at the site scale (i.e. individual camera trap stations; Fig. 5.4).

At the species level, season explained the majority of variation in habitat use for hibernating and migratory species (black bear = 78% of variance explained by the model, sandhill crane = 72% of variance explained by the model), with relatively low explanatory power in other species (Fig. 5.4). Habitat variables explained the majority of variation in use explained by the model for caribou (61%), and also a relatively large proportion for white-tailed deer (21%) and coyote (21%). The station-level random effect accounted for the majority of variation explained by the model in seven species (white-tailed deer, snowshoe hare, wolf, moose, coyote, lynx and squirrel; Fig. 5.4), suggesting that other unmodelled factors associated with individual camera stations may have been important (e.g. unmodelled habitat attributes or line characteristics).

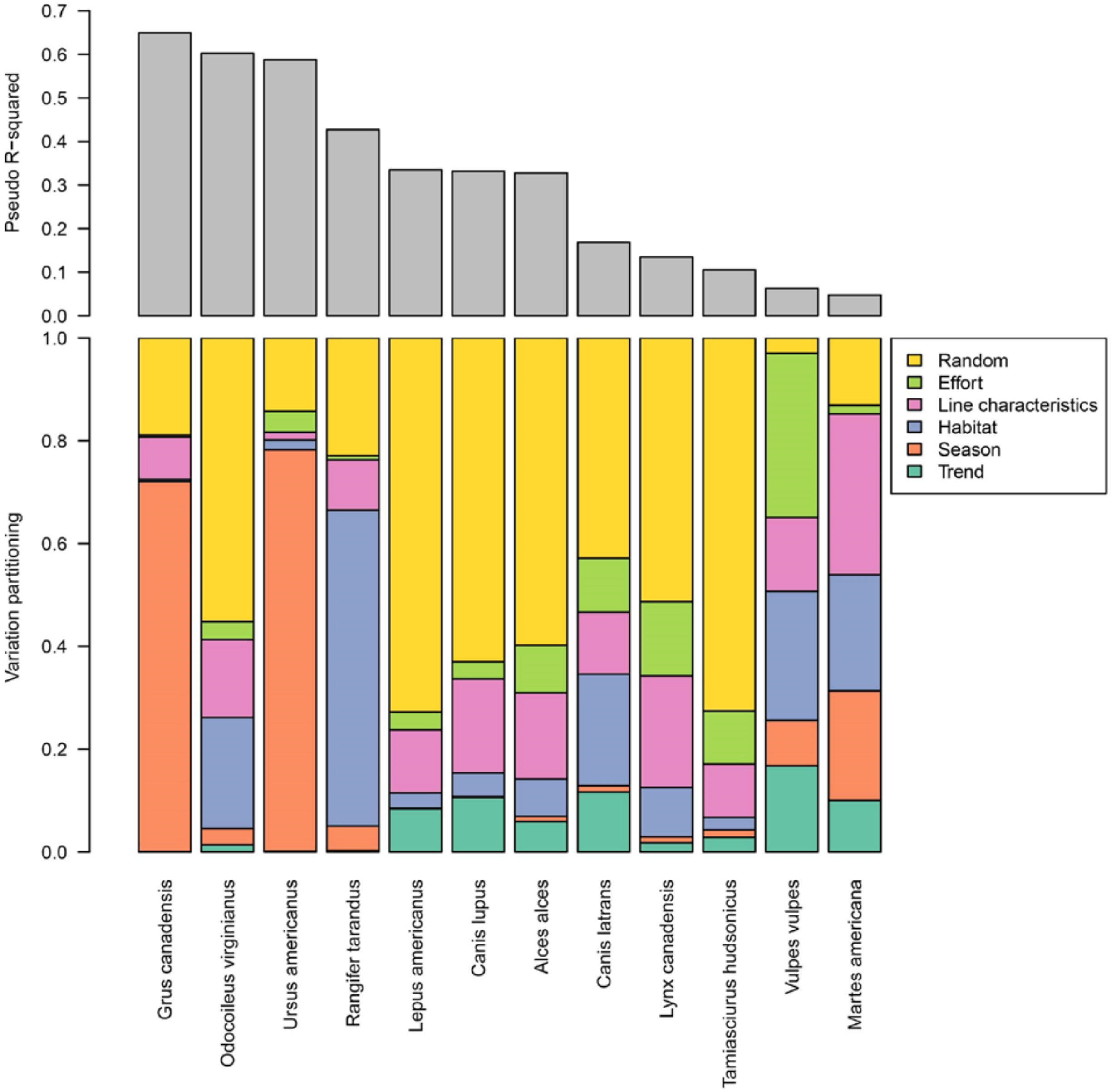

Figure 5.4 The amount of variance explained (pseudo-R^2, top graph) and partitioning of that variance among classes of predictor variables (proportion of explained variance, bottom graph) for each of the species included in the HMSC model (see Table 5.1 for details on predictor variables).

At the community level (i.e. across all modelled species), the cumulative effect of our measured line characteristics explained no more than 9 % of the total variation in detection frequency (Fig. 5.5). Decomposing the variation into individual characteristics revealed that, on average, line of sight explained the highest proportion of variation at the community level (1.8 %), followed by line width (0.6 %), mound height (0.6 %), and line density (0.5 %). Line of sight explained the greatest proportion of variation in the habitat use of white-tailed deer (5.7 %), followed by wolves (4.2 %), sandhill cranes (4.2 %) and caribou (2.4 %) (Fig. 5.4). Relative to other line characteristics, line density explained the most variation for lynx (1.8 %), coyotes (1.2 %) and American marten (1.0 %). Line characteristics had negligible effects on habitat use for black bear, marten, red squirrel and red fox.

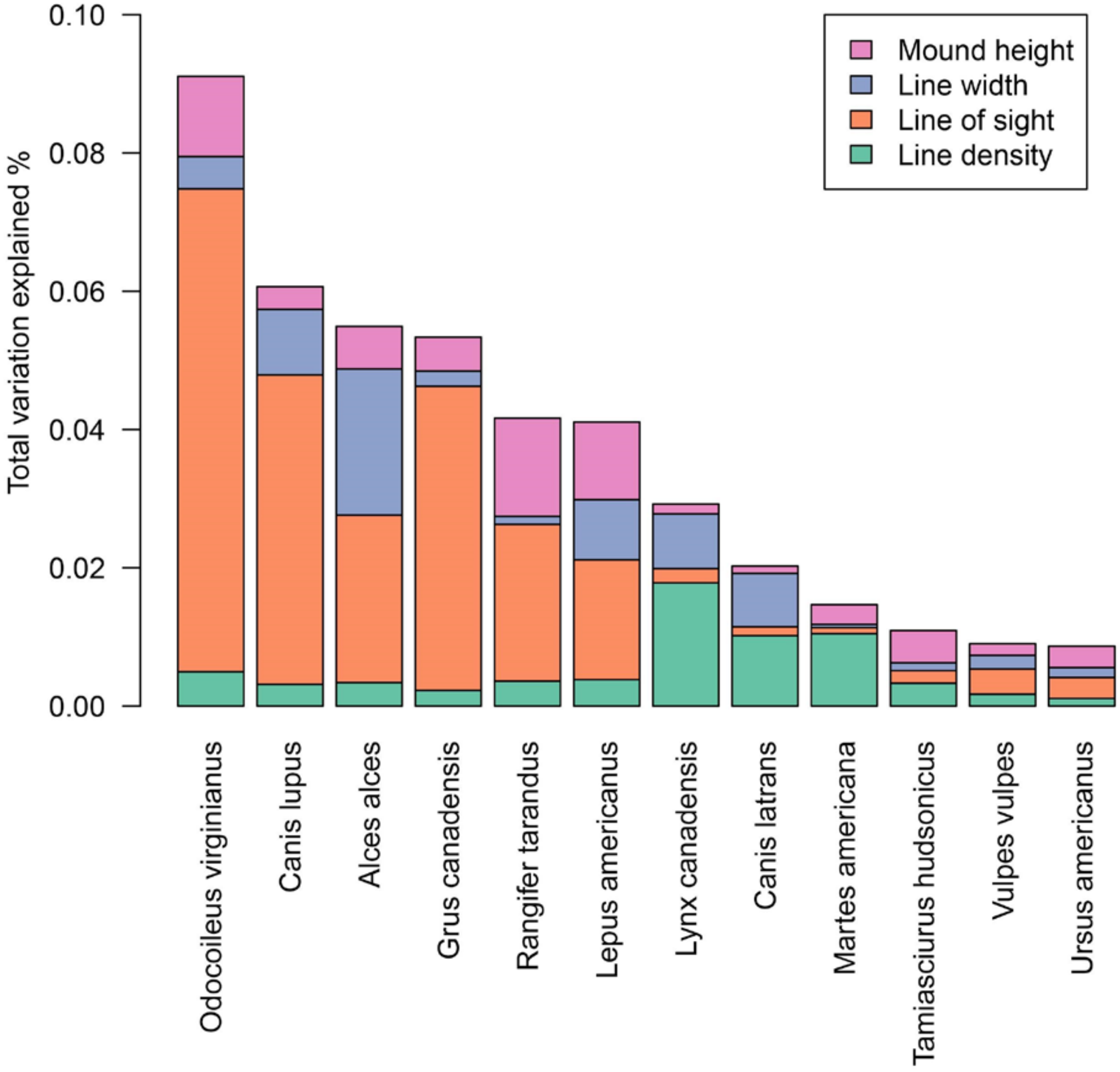

Figure 5.5 The scaled proportion of variation explained in our joint distribution models by variation in seismic line characteristics with the Algar study area.

Characterizing the size and direction of responses to seismic line characteristics

Residuals of species co-occurrences from the HMSC models suggested that the vertebrate community sorted into three distinct groups of co-occurring species within the Algar landscape (Fig. 5.6). Group 1 was defined by high co-occurrences among caribou, sandhill crane and marten. Group 2 had only moose, which showed no clear co-occurrence pattern with other species. And Group 3 is comprised of the remaining species which co-occurred with one another, with the strongest co-occurrences between the medium- and large-bodied predator species (wolf, coyote, lynx and black bear) as reported in Tattersall et al. 2020a and section 6.

There were no clear, general patterns whether habitat use responded positively or negatively to seismic line characteristics, both within co-occurring groups and across the community as a whole (Fig. 5.6). Statistically significant effects of line of sight were detected for six species; habitat use increased with increasing line of sight for three species (sandhill crane, caribou and wolf), and decreased for three other species (white-tailed deer, snowshoe hare and moose). There was statistical support for a positive correlation between line density and habitat use for three species: marten, coyote and lynx. Three species were significantly influenced by mounding height: habitat use by caribou and red squirrel increased with higher mounds, whereas use by marten decreased. Finally, there was support for increasing habitat use on wider lines for four species: coyote, lynx, wolf and moose (Fig. 5.6).

Significant linear temporal trends were detected in eleven species, suggesting changes in habitat use or relative abundance over the study period. Six of these species showed significant increases in detections through time (caribou, moose, deer, sandhill crane, marten and hare), while five species were found to decrease through time (wolf, coyote, fox, bear and squirrel). The largest decrease was detected for wolves.

Consistent with the variance partitioning presented above, factors other than line characteristics and temporal trend had, on average, larger effect sizes across the community. As expected, the detection frequencies of black bear and sandhill crane decreased dramatically in winter, as they hibernated or migrated, respectively (Fig. 5.6). Habitat use also declined in winter for the majority of species, likely reflecting the increased cost of moving in snow or seasonal habitat selection patterns. Only marten and red squirrel were detected more frequently in winter months, potentially reflecting an increase in detection probability due to snow cover (increasing their proximity to the camera detection zone or reducing vegetation obstruction).

Caribou habitat use was greatest at camera stations in closer proximity to the water table, as expected given the affinity of caribou for wetter, lowland habitat, (Fig. 5.6). Habitat use by coyote and marten were also higher in wet areas. White-tailed deer, red fox, and black bear were detected less frequently in wet areas. Habitat use was influenced by NDVI for ten species, although the average effect size was small relative to other predictors. The habitat use of seven species increased with increasing NDVI score, while use by three species decreased (Fig. 5.6).

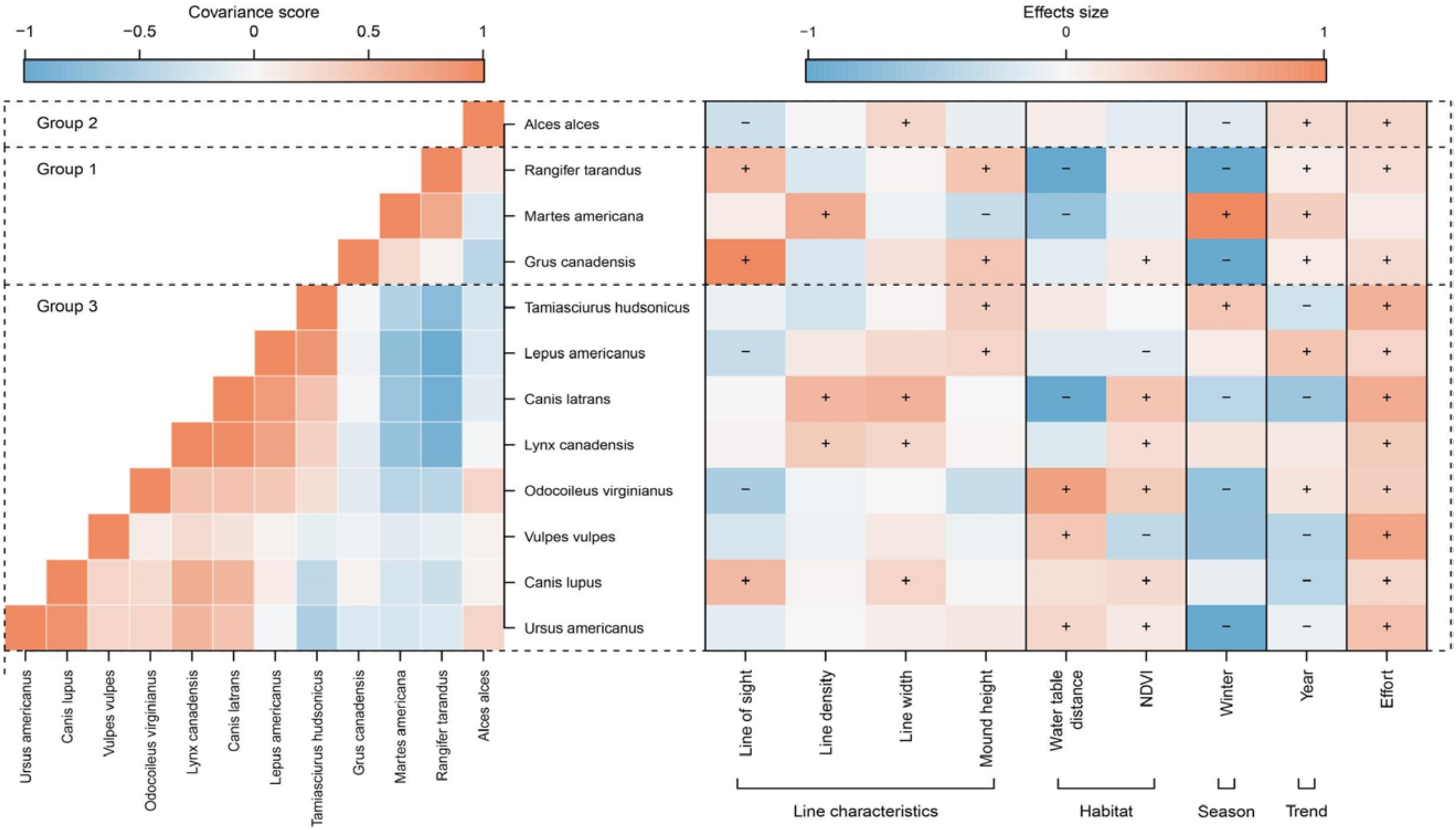

Figure 5.6 Residual co-occurrences between species (left) and estimated effect sizes for the predictors hypothesized to influence habitat use (right) for mammals in the sampled community. Values are estimated from the HMSC model. Colours denote the estimate covariance between species (left) or standardized effect size (right) and direction; '+' symbols denote positive credibility intervals which do not span zero; '-' symbols denote negative credibility intervals which do not span zero.

Predicted changes in community structure in response to restoration

The cumulative amount of variation explained by seismic line characteristics appeared to be sufficient to affect habitat use by multiple mammal species (Fig. 5.5), even though line characteristics explained only a small amount of variation relative to other factors (Fig. 5.4). Model-predicted changes in species habitat use (i.e. relative abundances) from unrestored to restored line conditions suggested potential for a shift in community composition. Relative abundance of wolves and coyotes had the most profound predicted declines under restored conditions, with changes in rank order of six and seven places, representing declines in predicted habitat use of 98.4 and 98.7% respectively. Restoration of degraded lines was predicted to be most beneficial for red squirrel, which dramatically increased its rank order, representing a 1200% increase in relative abundance (driven by a positive association with mound height). Other species predicted to benefit from line restoration, according to our model results, were white-tailed deer (+99%), snowshoe hare (+88%) and black bear (+111%).

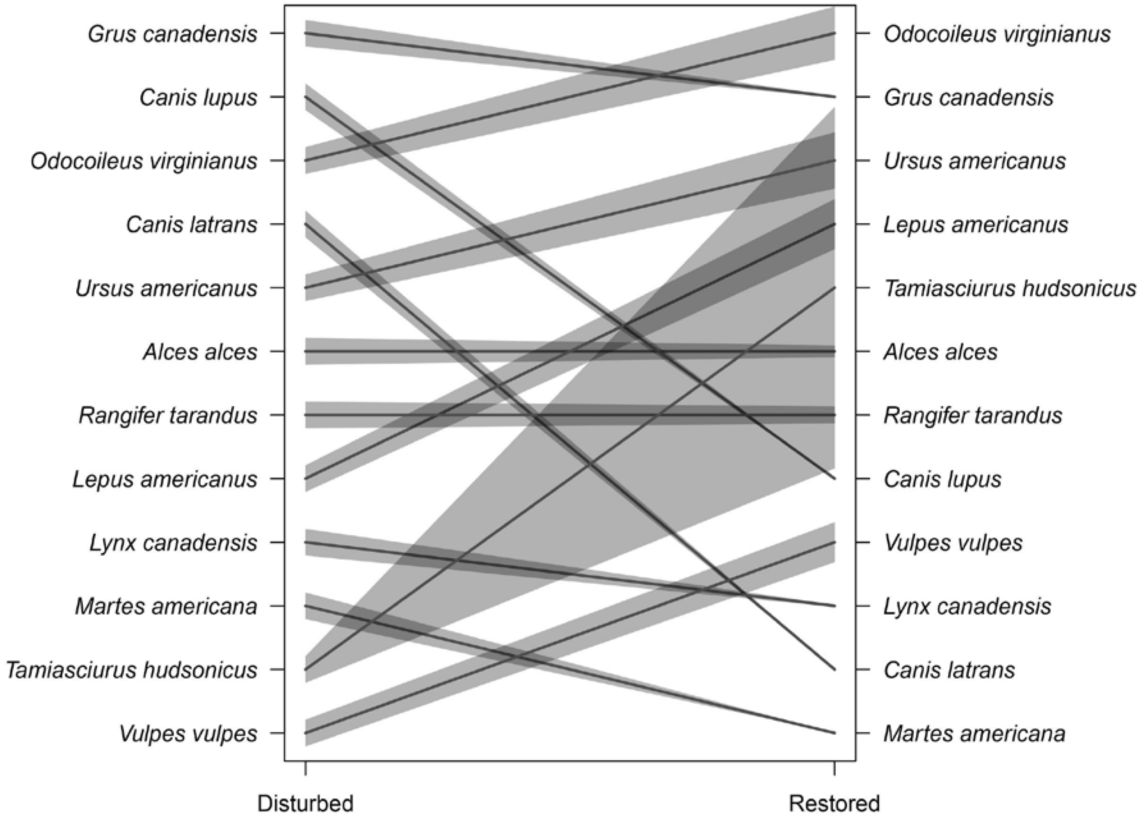

Figure 5.7 Predicted changes in rank-order of habitat use (i.e. relative abundance) among species due to variation in seismic line characteristics, with all other model predictors held at their mean values. The order of the species on the y-axis denotes the model-predicted habitat use for a given species, with the most frequently detected species at the top to the least frequently detected species at the bottom. The width of the shaded area denotes the predicted % change in habitat use from unrestored to restored line characteristics.

5.2.3 Discussion

Our results highlight that the medium- and large-bodied mammal community was influenced by variation in seismic line characteristics within the Algar study area, but that the direction and magnitude of individual species' responses to seismic line restoration were highly variable. This mirrors the marked variability previously observed in these species responses to anthropogenic disturbances more generally (Fisher and Burton 2018; Toews et al. 2018; Heim et al. 2019). The effects of seismic line characteristics on vertebrate occurrence were generally small relative to the effects of seasonality and natural habitat type (i.e. lowland vs. upland habitats). Nevertheless, our models suggested shifts in community structure in relation to seismic line characteristics, and predicted that restoring seismic lines (i.e., decreasing line of sight and line density) has the potential to change the relative abundances of species within the landscape - most notably through reducing the frequency of wolves and coyotes in restored areas.

Across all species, line characteristics explained less than 10% of the variation in camera trap detection rates across sites, and the community-averaged effect size of seasonality and habitat type were substantially larger than that of the best-supported line characteristic (line of sight). This is largely consistent with our previously documented weak short-term responses of focal mammal species to seismic line restoration treatments (section 5.1; Tattersall et al., 2020b). Reassuringly however, four of the five species showing the greatest response to seismic line characteristics were species targeted by the restoration program: white-tailed deer, wolves, caribou and moose. Furthermore, despite the relatively small effect size of each individual line characteristic, cumulatively they did appear sufficient to drive a shift in the rank-order of species within the community, with wolves and coyotes in particular showing the greatest declines in occurrence. If this pattern holds or strengthens as vegetation continues to recover on restored lines, it suggests that restoration could meet the objective of reducing predation risk for caribou over time. However, this remains a hypothesis to be tested by future monitoring.

Of the line characteristics that we assessed in our models, line of sight was a significant predictor of detection rates for 50% of species and had the largest average effect size. This suggests that restoration initiatives which rapidly and effectively block line of sight may have the greatest potential to influence habitat use in boreal environments, however its effects were not evenly distributed across the whole community. Caribou, wolves, and sandhill cranes all showed reduced occurrence in areas with low line of sight. Reductions in the detection frequency of wolves through seismic line restoration should reduce caribou-predator contact rates (McKenzie et al. 2012). However, caribou detections were also positively correlated with line of sight, potentially reflecting their affinity for more open lowland habitats. This finding suggests that complete reduction of line of sight may not be optimum in all scenarios, especially given that the detection frequency of deer (the main apparent competitor for caribou in this system) was negatively correlated with line of sight. Consequently, it is important that restoration efforts aim to restore to conditions reflecting natural habitat variation, rather than 'over restoring' lowland habitat to higher vegetation densities and lower line of sight than those naturally found in preferred caribou habitat, which may risk increasing deer abundance at the expense of caribou.

The community-level co-occurrence patterns we observed are also consistent with previously documented spatial segregation between caribou, their apparent competitors (deer and moose) and their predators (Keim et al., 2019; Wasser et al., 2011; Latham et al. 2011a,b). Caribou less frequently co-occurred with both their predators and apparent competitors, suggesting spatial segregation. The key predators of caribou– wolves and bears – co-occurred frequently with each other and with white-tailed deer and lynx. Previous work has suggested that such co-occurrence patterns may be driven by direct species interactions (e.g. Tattersall et al. 2020a); however, recent work has emphasized that co-occurrence patterns can also result from other mechanisms, including common responses to unmeasured habitat variables (e.g. Blanchet et al. 2020). Therefore, we do not infer direct interactions between co-occurring species in our models, particularly given that the detection frequencies were calculated at the six-month scale (too coarse for discerning interactions in time), but we suggest that the patterns reflect community composition after controlling for effects of habitat, seasonality, and seismic line characteristics.

The fact that seasonality was the strongest predictor of wildlife detection rates at the community-level was not surprising given the large intra-annual fluctuations in temperature and precipitation in the boreal ecosystem (e.g. Fisher et al. 2020). The majority of species had detection frequencies significantly lower in winter than in summer, particularly those of hibernating (bear) and migrating (sandhill crane) species. All of the ungulate species (caribou, white-tailed deer and moose) were detected less frequently in winter, likely due to seasonal shifts in home range (Henderson et al. 2018) or through reductions in movement (and thus detection rates) due to snow and cold (Richard et al. 2014; Singh et al. 2012; Broadley et al. 2019). Habitat was also a key predictor of wildlife detection frequency at the community-level, particularly for caribou and white-tailed deer that showed opposite patterns in relation to water table distance. The species-specific habitat affinities are likely a key driver of the spatial segregation between these species. The affinity of caribou to wetter, lowland habitat (which accounted for >60% of the variance in caribou habitat use explained by the model) further highlights that restoration initiatives should be focused on wet sites where natural regeneration occurs slowly or not at all (Van Rensen et al., 2015). However, these sites are among the most difficult to restore given the high water table (Filicetti et al. 2019).

Longitudinal camera trap survey designs, such as the one employed here, are relatively rare in the literature: studies typically move cameras after short 30-60 day samples (e.g. Kays et al. 2020). However, the deployment of camera traps at the same survey locations for extended periods (up to four years) facilitated robust longitudinal assessment of temporal trends in wildlife detection frequencies, and mitigated the danger of flawed inference on environmental drivers of changes in detection probability (e.g. Urbanek et al., 2019). Eleven of the twelve species assessed here showed evidence of linear trends in detection frequencies across the 2015-2019 survey period, with six species increasing through time and five decreasing through time. Four of the species showing declines were predators (coyote, wolf, fox and bear – in order of effect size large to small). The declines in wolf detections are consistent with active wolf population management in northeastern Alberta, including in and around the Algar caribou range. While other predators can be hunted or trapped in the region, they are not targeted by similar government population management. The observed declines in predator detections may be reducing predation risk in the study area. Corresponding increases over time in detections of prey species (caribou, moose, deer, hare and sandhill crane), and of a mesocarnivore (marten), are consistent with population or behavioral changes that could be related to a reduction in top-down control due to decreased predator abundance or activity (Crooks & Soule 2010; Terborgh et al. 1999). However, we suggest that continued monitoring is needed to more thoroughly assess multispecies responses to wolf population management and other caribou conservation efforts.

Future work and caveats

Although we assessed several of the key structural (e.g. line of sight) and spatial (e.g. line density) characteristics of seismic lines expected to affect their use by wildlife, one of the most important predictors of habitat use may be the vegetation characteristics of the survey site (Finnegan et al., 2018a). Our index of vegetation quality was both spatially coarse (250m NDVI) and largely based on canopy reflectance unavailable to terrestrial wildlife. Thus a greater proportion of variance in habitat use may be explained using finer scale, camera viewshed metrics currently under development (see section 7). We also recommend a more thorough *in situ* assessment of the vegetation composition, quality and quantity on seismic lines, to better understand the factors underpinning repeatable inter-station variation in habitat use.

There has been some small scale success in limiting predator movements on seismic lines via movement barriers (e.g. Keim et al., 2019). However, the low productivity landscape in the Algar region did not provide sufficient woody material to perform debris piling for movement blockage. Such an approach, if feasible, could enhance the short term effects of restoration activities on caribou predators.

The total variation in species detections explained by our community-level model was low, and the proportion of the total variation explained by site-level random effects was high, particularly for small-bodied consumers (such as snowshoe hare and red squirrel) relative to large bodied, focal species (e.g. white-tailed deer). The low explanatory power in the smaller members of the boreal community could be due to several reasons. Firstly, multispecies camera data are not trivial to analyze, as small differences in camera microsites (camera angle, height, microsite topography) could cascade into marked site-to-site variation in the detectability of smaller species (Hofmeester et al., 2019). Secondly, as small species have small home ranges, the potential for between-camera heterogeneity in detection frequency is much larger (i.e. sites within an individual’s home range will record a lot of detections, sites outside of a home range will record none). Greater consideration of microsite characteristics may make community-level comparisons more robust (Hofmeester et al., 2019).

Although we discuss our results in terms of “community-level” changes, there are still several species which we omitted due to low sample size (with resultant poor model fit), leaving our assessment of the impacts of seismic line characteristics incomplete. There are both methodological (e.g. use of lure; Holinda et al. 2020) and analytical (e.g. low sample size modelling) innovations which will be required to effectively fill in the gaps of missing species. It is unlikely that one method alone will be sufficient to cover all species, thus integration of multiple survey methods could be assessed in the future.

Finally, in this analysis we interpreted camera trap detection frequency as unambiguously signaling habitat use by the species of interest. We note that observed changes in detections could also reflect changes in behaviour (see sections 6, 9) or density (see section 7), or a combination of the two.

6. Characterizing species interactions

Our previous models (in section 5) focused on interpreting the frequency of camera trap detections as an indicator of habitat use by species at sites differing in seismic line characteristics (including off-line). In our multispecies joint distribution models, we investigated species co-occurrences as indicators of community structure in relation to seismic line restoration. In this section we briefly summarize our publication (Tattersall et al. 2020a; Appendix 6) in which we further evaluated patterns of co-occurrences among predator species to determine if the patterns were consistent with hypothesized interspecific interactions.

6.1 Estimating spatial and temporal interactions among predators

A key advantage of camera trap surveys is the ability to survey multiple species simultaneously. This facilitates inferences on community-level dynamics, as explored in our multispecies models (section 5.2). Species co-occurrences in space and time are also often used to explore potential interactions between species (Frey et al. 2017; Niedballa et al. 2019), as well as between people and wildlife (e.g. Naidoo & Burton 2020). It is important to note that co-occurrence patterns do not necessarily imply direct interactions, and Blanchet et al (2020) have recently shown how different mechanisms may drive the patterns, such as common responses to unmeasured habitat variables. Nevertheless, the generation of spatio-temporal co-occurrences from camera traps provides a tool for testing whether observed patterns are consistent with those predicted from hypotheses of species interactions.

We used the first 3 years of monitoring data from this project (November 2015 to November 2018) to explore spatio-temporal co-occurrence patterns among predator species in the Algar landscape (wolf, black bear, coyote, and lynx). Specifically, we hypothesized that (1) subordinate predators would avoid competition with the apex predator, wolf; (2) they would avoid competition with each other as intraguild competitors, and (3) they would overlap with their prey. We used a generalized linear model (GLM) framework to test whether co-occurrence patterns were consistent with these hypotheses across camera trap sites for the entire survey period, as well as at daily and weekly time scales. Details of this work are published in Tattersall et al. (2020a; available at https://doi.org/10.1002/ece3.6028).

In brief, we found that subordinate predators spatially overlapped with the apex predator (wolves) at different temporal scales, and we did not detect any strong avoidance of intra-guild predators or overlap with prey (Fig. 6.1). The observed patterns in predator space use were consistent with facilitative interactions or shared responses to unmeasured ecological cues. We did find some interactions in our models between co-occurrence patterns and anthropogenic landscape features (e.g. interactions between line density and wolf occurrence or prey abundance; Fig. 6.1), suggesting that different management actions, such as linear restoration and wolf control, could have synergistic and indirect effects on multispecies interactions. We recommend further work to more directly test the consequences of management actions for species interactions, including using these actions as experimental manipulations in an adaptive management framework (e.g. Nichols et al. 2015).

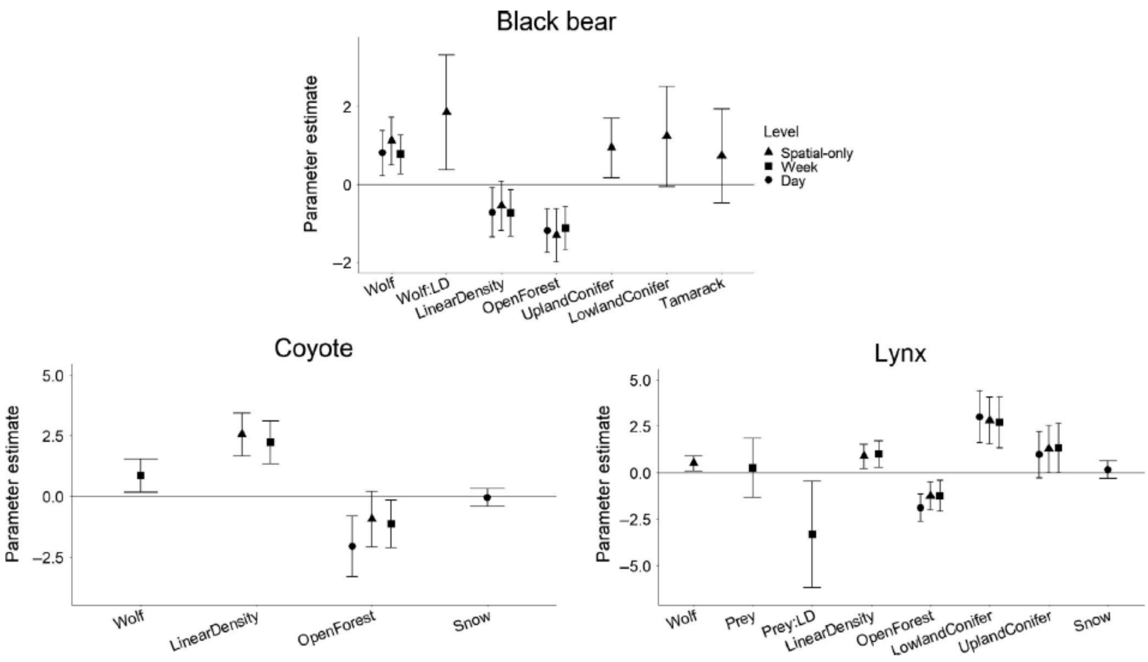

Figure 6.1 Effects of interspecific interactions and environmental features on predator occurrences in the Algar landscape. Effect sizes are shown as parameter estimates (mean ± 95% confidence intervals) from negative binomial GLMs (spatial level) and binomial GLMMs (weekly and daily levels) of black bear, coyote, and lynx occurrences at three levels of analysis. Estimates are shown for the most parsimonious model within the top-ranked models. Positive values indicate a positive association between occurrences of the modelled species and the given predictor variable at the indicated scale (and vice versa for negative values). Figure is reproduced from Tattersall et al. 2020a, to which we refer readers for more details.

7. Estimating Population Density

The ultimate goal of a wildlife habitat restoration program is to stabilize or increase declining populations. In the context of caribou recovery in western boreal forests, seismic line restoration efforts are intended to reduce predation on caribou and ultimately ensure their populations are viable over the long term. In the previous sections of this report, we have focused primarily on assessing wildlife responses to restoration through differences in their use of restored vs. unrestored seismic lines. However, it is also important to measure population responses to restoration at the landscape scale. Currently, the dynamics of caribou populations in Alberta are monitored through population growth rates estimated from cow:calf recruitment surveys and survival of a sample of collared females (Hervieux et al 2013, 2014). Direct estimates of caribou population densities have been limited, largely due to methodological challenges (Wasser et al. 2011; Boutin et al. 2012), and there have been very few estimates of the density of other species important to caribou conservation (e.g. black bear, moose, white-tailed deer). Camera traps and new statistical models have provided increased capability to simultaneously estimate densities of multiple interacting species (Burgar et al. 2019a), but these methods require further refinement and testing. In this section, we develop and apply new models for estimating population densities (and abundances) in the context of assessing the efficacy of seismic line restoration and other caribou recovery actions.

Estimating density and abundance with camera trap data presents unique challenges when individuals are unmarked, i.e., lack visible features about unique individual identity. This is because robust methods of spatial-capture-recapture (SCR) require tracking individuals over space and time in order to model them as a spatial point process on a landscape (Royle and Young 2008). Missing identities in camera trap data have motivated the development of numerous approaches to estimate abundance of unmarked populations (Gilbert et al. 2020).

Three broad, alternative approaches to abundance estimation use additional data about animal movement or make assumptions about detection probability in order to estimate abundance and density without individual identity. First, the random encounter model (REM) and its extension, the random-encounter-and-staying-time model (REST), use rates of encounter along with movement speed or the amount of time that individuals are visible in front of a camera trap, assuming that individuals move like gas particles diffusing in space (Rowcliffe et al. 2008, Nakashima et al. 2017). A second class includes the time-to-event (TTE) model and its extensions, the space-to-event (ST) and instantaneous sampling (IS) models, which use the times to first detections of the species and assume perfect detection within the camera frame of view (Moeller et al. 2018). Finally, distance sampling methods require measuring the distance between cameras and detected individuals to model detection probability to estimate the number of undetected individuals (Buckland et al. 2001, Howe et al. 2017). While a primary advantage of these models is that individual identities are not required, it is often difficult to collect ancillary data on animal movement and camera fields of view, or meet stringent assumptions about detection probability.

Even without complete information on individual identities, a suite of models based on SCR approaches have recently been developed to estimate population abundance and density. In spatial mark-resight (SMR) models and its extension, the generalized spatial mark-resight (gSMR) model, identities for a portion of the population are known so that parameters estimated from them are used as the parameters for the unidentified individuals (Chandler and Royle 2013, Whittington et al. 2018). When no individuals are known, spatial count (SC) models use the spatial correlation in counts to estimate abundance (Chandler and Royle 2013). Finally, spatial partial identity models (SPIM) use partial information about identity of individuals in addition to the spatial correlation in detections, such as sex, coat color, or partial genetic profiles to probabilistically assign detections to individuals (Augustine et al. 2018, Augustine et al. 2019). Spatial and partial identity information alone may be insufficient to tell apart all individuals, but can still help distinguish between individuals detected at adjacent camera traps. SMR, SC, and SPIM models have the same assumptions as SCR models, notably that individuals and their detection histories are independent of each other. SMR, SC, and SPIM models represent the most recent developments in estimating density for unmarked populations using individuals as the unit of inference.

SMR and in particular SC models have been applied with varying success, while SPIM models have seen minimal implementation so far due to the recency of their development. gSMR and SPIM approaches have produced estimates more precise than SMR and even SCR models (Whittington et al. 2017, Murphy et al. 2019, Ruprecht et al. 2020). Some studies also have found SC models to perform comparably to SCR models (Burgar et al. 2018, Evans and Rittenhouse 2018), but still others found that SC models yielded estimates that were sensitive to the choice of priors for parameters (Chandler and Royle 2013, Burgar et al. 2018, Augustine et al. 2019), addition of supplemental telemetry data (Ruprecht et al. 2020), and trap spacing (Ramsey et al. 2015). Posterior probability distributions of abundance estimates can be highly skewed with a long right tail, and data sparseness can lead to underestimated abundance or model convergence failures (Chandler and Royle 2013, Burgar et al. 2019a). Furthermore, model assumptions may be violated by aspects of the ecology of sampled species, such as movement and social behaviour (Chandler and Royle 2014, Augustine 2019, Bischof et al. 2020). Therefore, careful interpretation and application of models for partially or wholly unmarked populations to empirical data are necessary, and can advance our understanding of model performance as well as inform conservation efforts.

In the Algar study area, SC and SPIM modeling approaches are the most viable SCR-based modeling approaches because few individuals of any species have natural markings or GPS/telemetry collars that enable unique identification for SCR and SMR approaches. We considered application of the non-SCR based approaches to be less feasible due to the lack of ancillary data on movement speeds, distances between camera traps to individuals in the camera trap images, or information about the regions of camera fields of view with perfect detection probability. We applied SC and SPIM models to camera trap data to estimate population density and distribution for two focal species in the Algar study area: caribou and black bear. The threatened status of caribou and the role of black bear as both caribou predator (Latham et al 2011c) and harvested species motivate the need for accurate and precise density estimates of their populations. However, ecological and biological features of the species could impact the robustness and performance of SC and SPIM models. Caribou exhibit sociality (i.e. herding behaviour) that could violate the model assumption of independence of detections among individuals. Bears have few individually distinguishing features for estimating abundance with SPIM models. Therefore, in addition to improved understanding of boreal wildlife ecology in an area impacted by natural resource extraction and subsequent habitat restoration, these efforts also contribute to the development of a decision framework for the application of SCR-based models to populations of partially or wholly unmarked individuals.

In this study, we aimed to

1. Estimate caribou and bear density in two landscapes, the Algar and Richardson study areas, in order to explore population trends over a four year period (2016 – 2019);
2. Compare the performance of SC and SPIM models, especially when
    a. herding behavior may violate the model assumption of independence between detections of different individuals, and
    b. data and individual identity covariates are sparse;
3. Develop a working decision framework for choosing between SC, SPIM, and other modeling approaches for estimating density of unmarked populations.

7.1 Methods

7.1.1 Model Descriptions

SC models estimate population abundance from counts of individuals detected at sampling locations (Chandler & Royle 2013). With its origins in SCR, a sub-model first describes the detection process of individuals according to a baseline detection rate that decreases monotonically over space as a function of sigma, a scale parameter. Here, we use the half normal detection function (Buckland et al. 2001). The parameter σ can be interpreted as the range of individual movement, and in SC models, also the degree of spatial correlation among the observed counts. The number of detections at a location for any individual is assumed to follow a Poisson distribution, although it is not observed because individual identities are not observed. The count data at a location, i.e., the sum of detections across all individuals, are observed and are also assumed to follow a Poisson distribution. The count data are conditional on an underlying spatial point process that describes the number and location of individuals. The spatial region of this point process, termed the state-space, should be large enough so even individuals near the edge of the sampling extent are detectable. Estimating the number of individuals uses a data augmentation approach where the population size N is a subset of an oversized population M (Royle and Dorazio 2012). The existence, ω, of each individual i in M follows a Bernoulli distribution with parameter ψ. Each individual contributes to the population N even if it was completely undetected if $\omega_i = 1$, and not if $\omega_i = 0$. Then N is then derived by summing over ω. Density, D, is calculated by dividing N by the state-space.

SPIM models estimate population abundance from the detections of individuals that are only partially distinguishable from each other (Augustine et al. 2019). Each individual observed at a location on an occasion is not associated with detections at any other location or occasion because the identities of individuals are uncertain. However, each detection is associated with independent categorical covariates that provide partial information about the identity of the individual. The individual-level detection process and estimation of abundance and density through data augmentation are similar to the SC approach. However, there is additional model structure to estimate the latent identities of the observed individuals, by assessing different configurations of identity assignments across the observed detections that are consistent with the identity covariates (Augustine et al. 2018). Thus, in addition to estimating detection probability, sigma, and the number and location of individuals in the population across the state-space, SPIM models also estimate the latent identities of the observed individuals and population-level probabilities of each observed value of the identity covariates.

7.1.2 Data Collection

We used SC and SPIM models to estimate patterns in density and distribution of caribou and black bear from 2016 - 2019 in the Algar study area. A total of 24, 60, 73, and 73 cameras were active in each year, respectively. For caribou, we used camera trap detections from August 1 to October 31 of each year, as we assumed that this period met the model assumption of demographic closure, falling between spring calving and winter movement. During this period, both sexes have antlers that are in the final stages of growth, such that sex and number of antler points could be used as information about partial identity. For bear, we used camera trap detections from May 1 to August 31 of each year, when the consistent majority of detections occurred in each year and before movements patterns changed in the fall (Alt et al. 1980).

Camera trap images were grouped into detection events based on a 30-minute threshold, beyond which detections of the same species at a site were considered separate events. For each detection event, we recorded the maximum group size observed rather than summing group sizes in order to avoid overestimating count due to indistinguishable individuals appearing in multiple groups. We calculated a daily count for the SC models by then summing group sizes across all events within each day.

For SPIM models, we generated daily individual-level data by distinguishing between individuals across groups within each detection event. For partial identity information on caribou, we recorded sex (Male, Female), the total number of antler points if the camera angle afforded a view of both antlers, and whether the individual was wearing a GPS collar (from the Government of Alberta’s caribou monitoring program). We considered two versions of the caribou SPIM data, with the first including only data from detections of single individuals, and the second version including data from detections across all group sizes. This was done to isolate potential effects of non-independence between individuals that would violate model assumptions. For partial identity information on bear, we recorded size with 3 categories (small, medium, large) and coat color with 4 categories (black, brown, cinnamon, blond). We did not include sex because males were indistinguishable from females without cubs. Missing covariate values were included as NAs.

7.1.3 Model Implementation

Caribou and bear data were analyzed in a Bayesian framework in program R, using custom SC models in the 'nimble' package (de Valpine et al. 2017) and SPIM models in the 'SPIM' package (Augustine et al. 2019). We accounted for variable effort per camera trap, due to camera malfunctions. For caribou, we ran SC and SPIM models for all years with two different priors on sigma based on home range sizes from GPS telemetry data in a nearby landscape (Burgar et al. 2019b). We first considered a flat prior on sigma [Uniform(0,10)] to accommodate a maximum home range size of 1194 km^2 and then with an informative prior distribution on sigma [gamma(24,8)] that results in a mean of 3 km with a standard deviation of 0.6 km to accommodate more typical home range sizes between 38 – 619 km^2. Flat priors were used for all other parameters. For bears, we ran SC models for all years using an informative prior on sigma [gamma(24,8)], and ran a SPIM model for data in 2016 (the year for which individual covariates were scored). We defined the state-space (i.e., landscape within which sampled individuals occurred) as the rectangular region around the minimum and maximum extents of camera trap sites with a buffer of 7 km for caribou and 15 km for bear. This resulted in a state-space of 1,505 km^2 for caribou and 3,092 km^2 for bear. We determined buffer sizes as three times the median values of sigma, used to specify the informative sigma prior distribution (Burgar et al. 2019b). We used the 'coda' package (Plummer et al. 2006) to monitor parameters until Gelman-Rubin statistics indicated convergence (Rhat <1.1) across 3 Markov Chain Monte Carle (MCMC) chains and effective sizes for abundance reached 400. We reported mode estimates with 95 highest posterior density (HPD) intervals. We also created maps of realized density, derived from tabulating the proposed locations of individuals across all MCMC chains (Chandler and Royle 2013, Royle et al. 2014).

7.1.4 Comparison between caribou ranges

Our goal in developing these models is to be able to estimate, monitor and compare population densities in different landscapes, such as between different caribou ranges or restoration projects. To initiate such a comparison, we compared density estimates in the Algar study area with those from another study area undertaken by our team in the Richardson caribou range. In the Richardson study area, camera trapping occurred at 30 sites in 2018 and 58 sites in 2019 (see Fig. 9.1; J. Burgar & A.C. Burton, unpublished report). For each year, we estimated abundance and distribution using SC and SPIM models for caribou, and only SC models for bear. Furthermore, for SPIM analyses we used individual detections from all group sizes and did not consider detections from only groups of 1 individual. We subsetted data to the same time frames as in the Algar analyses described above, and only considered an informed gamma prior on sigma [gamma(24,8)]. We used a 1,999 km^2 state-space for caribou and a 3,698 km^2 state-space for bear.

7.2 Results

7.2.1 Algar Landscape

Woodland Caribou

The number of independent caribou detections varied in each year during the Aug. 1 - Oct. 31 sampling period used for density estimation, from a low of 5 detections in 2016 to a maximum of 61 in 2018 (Table 7.1). The number of detections per site showed a similar increase over the years, suggesting that the pattern of increasing detections may have been due to increasing population sizes and not merely to increased camera trapping effort over time. Most caribou were detected as singletons and not in groups, so mean group sizes remained relatively low and constant over the 4 years, ranging from 1.2 to 1.5. However, group size reached a maximum of 4 individuals in 2018 and 2019. We detected one female caribou with a GPS collar detected twice at a single camera trap in 2019.

Table 7.1. Summary statistics on detections of caribou at camera trap sites in the Algar study area during the Aug. 1 - Oct. 31 sampling period of each year (2016 - 2019).

Year	**2016**	**2017**	**2018**	**2019**
# Active Camera Trap Sites	24	34	59	70
Mean Distance between Neighboring Sites (km)	1.9	2.2	1.6	1.4
# Sites with Detections (%)	4 (0.17)	9 (0.26)	18 (0.31)	21 (0.30)
Total Detection Events	5	18	61	56
Maximum Daily Count	2	3	5	8
Mean Detections per Site (max, SD)	0.3 (2, 0.6)	0.6 (7, 1.6)	1.0 (11, 2.3)	1.1 (13, 2.5)
Mean Group Size (max, SD)	1.2 (2, 0.4)	1.2 (3, 0.6)	1.5 (4, 0.9)	1.3 (4, 0.7)
% Detections of Singletons	0.8	0.89	0.72	0.77

Posterior distributions of caribou density were skewed, with 95 HPD intervals that were particularly wide for SPIM estimates. Still, estimates of caribou density (i.e., number and location of individual activity centres) varied over the landscape and over time (Figs. 7.1, 7.2). Importantly, results varied by modeling approach (Fig. 7.2). Posterior mode estimates of abundance from SPIM models were larger than SC estimates, except for in 2017. With a gamma prior distribution on sigma, estimates of density from SC models increased from 0.1 per 100 km^2 in 2016 to a maximum of 4.3 per 100 km^2 in 2018 and then decreased to 1.3 in 2019. In contrast, estimates from SPIM models increased from a minimum of 0.4 caribou per 100 km^2 to a maximum of 9.4 caribou per 100 km^2 in 2019. For both SC and SPIM modeling approaches, the uniform prior distribution on sigma resulted in greater posterior skewness and lower precision (i.e., wider 95% HPD intervals).

In SPIM models, density estimates increased with the inclusion of individuals observed in groups, which represented 11 - 28% of the entire annual detection datasets. Only in 2019 did the additional data from groups also increase precision, with the 95% HPD interval narrowing by 3.3 caribou per 100 km^2. The additional data in 2019 included detections of a collared female. No detections of collared individuals occurred in previous years, so the third identity covariate (presence of collar) was used only in 2019.

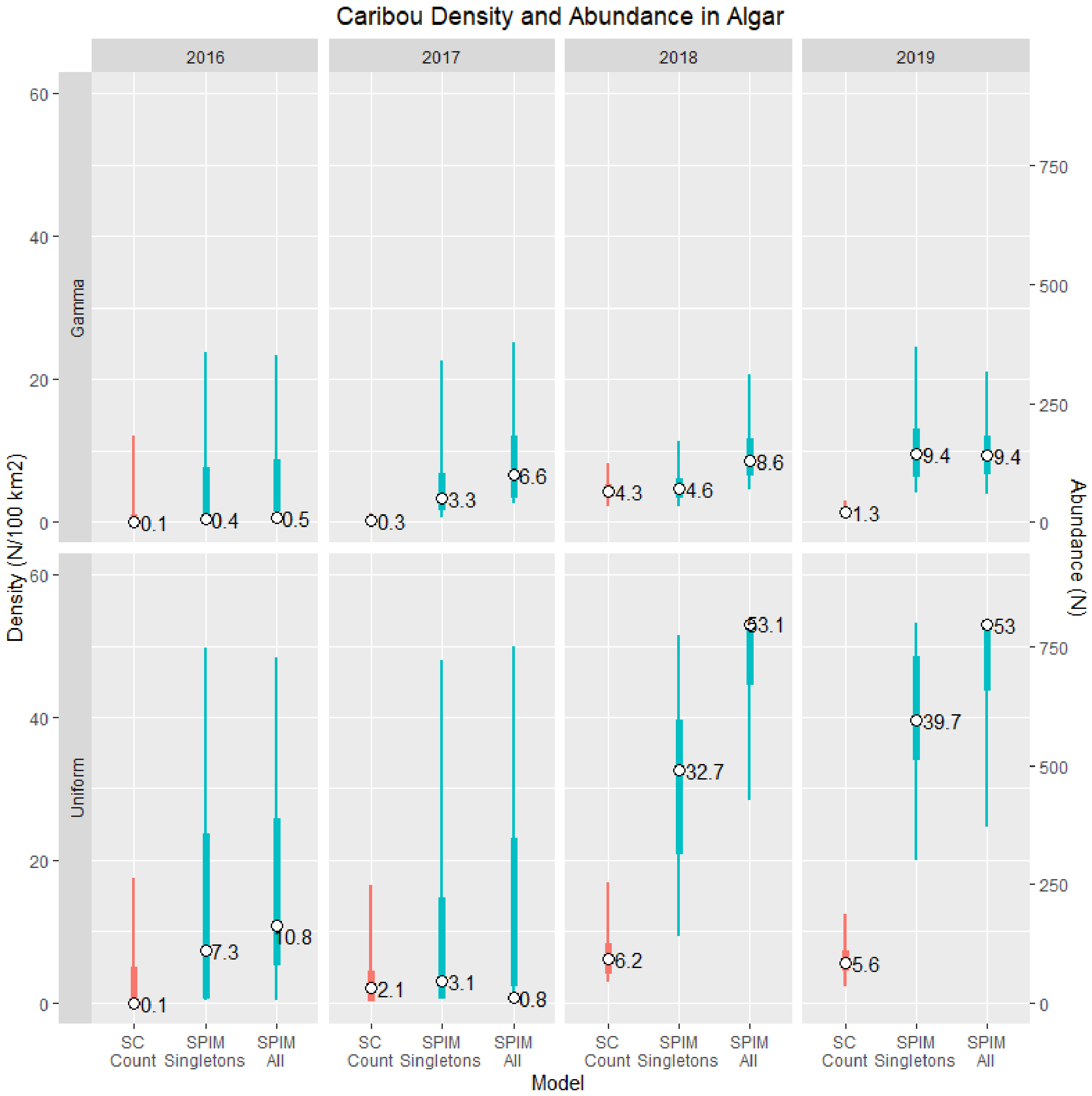

Figure 7.1 Estimates of annual caribou density (per 100 km^2) and abundance in the Algar study area during the Aug. 1 - Oct. 31 sampling period of each year (2016 - 2019) from camera trap data. Both SC and SPIM models considered two different prior distributions for sigma [gamma(24,8) in top plots and uniform(0,10) in bottom plots], and SPIM evaluated two versions of the data: detections of singleton individuals and detections of individuals across all group sizes. Numbers highlight the mode density estimate. Whiskers indicate 50 and 95 HPD intervals.

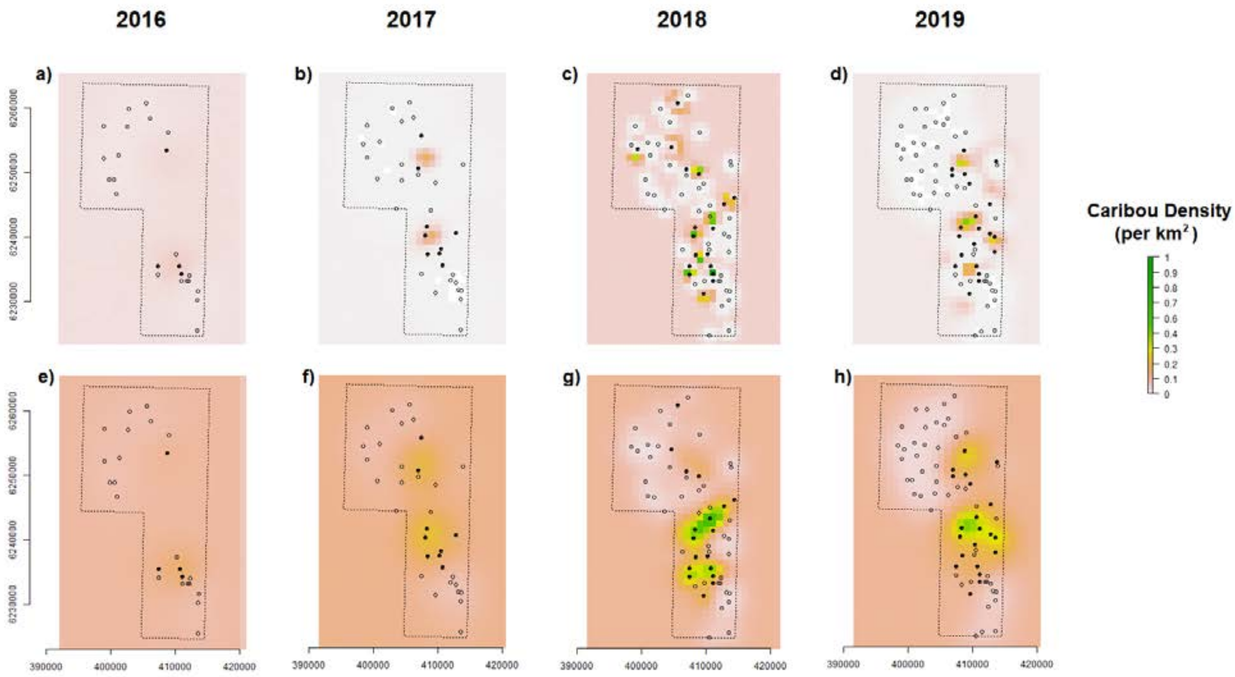

Figure 7.2 Estimated distribution of caribou activity centers for the Aug. 1 - Oct. 31 period for each year in 2016 - 2019 for the Algar study area from camera trap data, according to SC (a-d) and SPIM (e-h) models using a gamma prior for sigma. Dotted line shows the polygon of the Algar study area while the larger region shows the entire state space. Open circles indicate camera trap sites that operated at least some time during the period but did not detect caribou, while closed circles indicate sites that did detect caribou.

Due to the hierarchical nature of SC and SPIM models, estimates of abundance are related to estimates of sigma and detection probability. Estimates differed by modeling approach and choice of prior on sigma. Mode estimates of sigma ranged from 1.5 - 3.1 km across years for SPIM models using the informative gamma prior, and were smaller with the SC model, with estimates that ranged 0.6 - 2.1 km (Appendix 4 Table 1). A flat prior on sigma resulted in estimates that were smaller and generally more imprecise. For detection probability, estimates differed drastically by modeling approach and less by choice of prior (Appendix 4 Table 2). Mode estimates of detection probability reached only 0.004 in SPIM models, but ranged up to 0.18 with SC models.

Black bears

Detections of bears occurred at more sites and more frequently than caribou (Table 7.2). The overwhelming majority of bears were detected as singletons and not in groups. Posterior estimates of bear abundance were right-skewed and had wide HPD intervals. Mode estimates were centered around 100 in 2016 and 2018 (Fig. 7.4), with activity centers distributed across the study area (Fig. 7.5). Estimates of bear abundance were not reliable in 2017 and 2019, with SC models failing to converge to realistic posterior distributions. Furthermore, estimates of abundance in 2016 with the SPIM model also failed to produce realistic results, with the posterior distribution of abundance truncated by the upper bound of 900 individuals.

Table 7.2. Summary statistics on detections of bears at camera trap sites in the Algar study area during the May 1 - Aug. 31 sampling period of each year (2016 - 2019). Camera malfunctions resulted in differences between the number of active versus deployed camera trap sites (n=58).

Year	**2016**	**2017**	**2018**	**2019**
# Active Camera Trap Sites	24	52	65	72
Mean Distance between Neighboring Sites (km)	1.9	1.7	1.4	1.4
# Sites with Detections (%)	19 (79%)	33 (63%)	41 (63%)	53 (74%)
Total Detection events	122	173	162	234
Maximum Daily Count	4	6	4	6
Mean Detections per Site (max, SD)	5.9 (25, 6.8)	3.8 (41,7.8)	2.6 (26,4.2)	3.8 (54, 7.7)
Mean Group Size (max, SD)	1.1 (3, 0.5)	1.1 (4, 0.5)	1.1 (4, 0.3)	1.2 (3, 0.5)
% Detections of Singletons	0.93	0.94	0.94	0.90

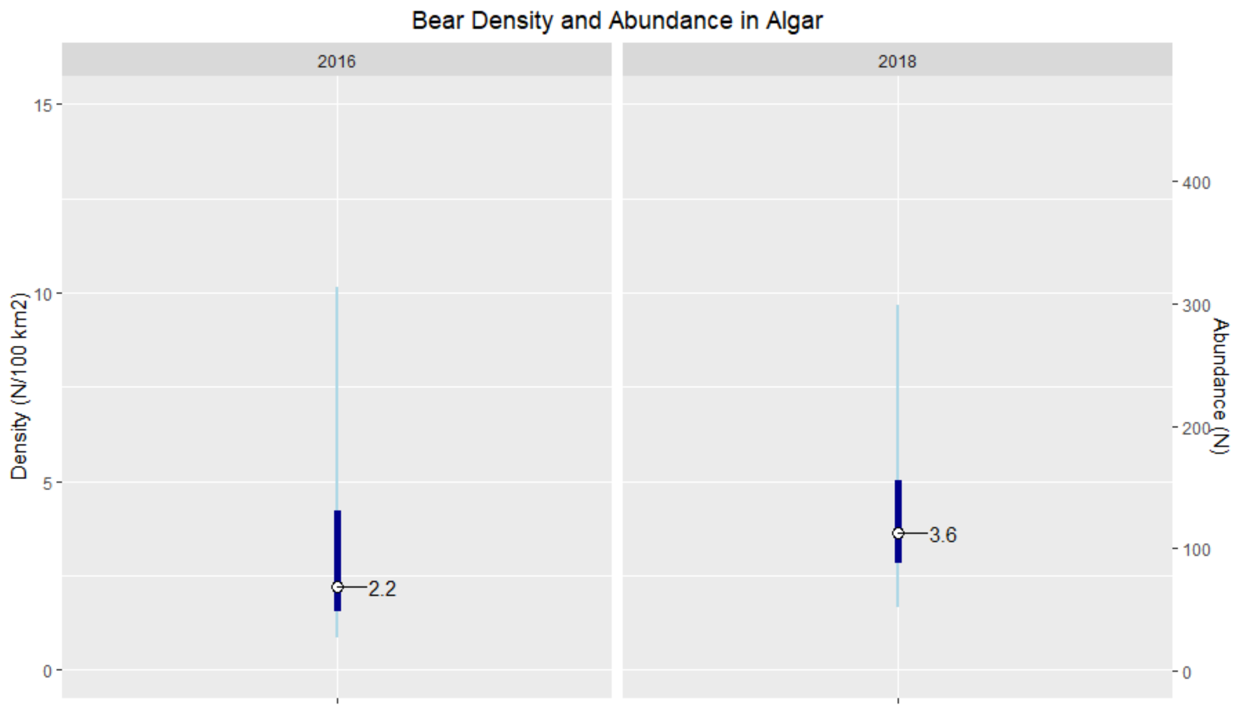

Figure 7.4 Estimates of bear density (per 100 km^2) and abundance in the Algar study area during the May 1 - Aug. 31 sampling periods in 2016 and 2018 from camera trap data. SC models used a gamma prior distribution on sigma. Numbers highlight the mode density estimate. Whiskers indicated 50 and 95 HPD intervals. Results are not shown for 2017 and 2019, when models did not converge to realistic posterior distributions.

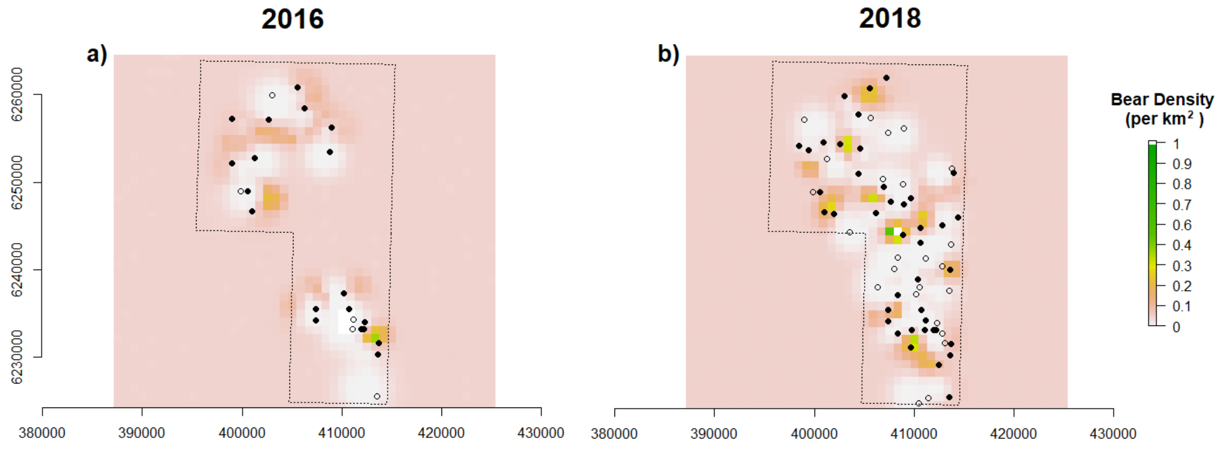

Figure 7.5 Estimated distribution of bear activity centers from May 1 - Aug. 31 in 2016 and 2018 for the Algar study area from camera trap data, according to SC models using a gamma prior distribution for sigma. Dotted line shows the polygon of the Algar study area while the larger region shows the entire state space. Open circles indicate camera trap sites that operated at least some time during the period but did not detect bear, while closed circles indicate sites that did detect bear.

7.2.2 Landscape Comparisons

The Richardson study area had more caribou detections at more camera trap sites than the Algar study area (Table 7.3). Results of the comparison of caribou densities between Algar and Richardson study areas in 2018 and 2019 depended on the modeling approach. Whereas the SC results suggested that densities in the two study areas were similar, SPIM results suggested an approximately twofold higher caribou density in the Richardson than the Algar study area (Fig. 7.6). Furthermore, while estimates from SC models suggested that the two study areas had opposing trends over the two years, with Algar density decreasing and Richardson density increasing, estimates from SPIM suggested populations were stable over time. Richardson density estimates were higher using the SPIM approach compared to the SC approach, with the difference between methods greater than for Algar densities.

Table 7.3. Summary statistics on detections of caribou and bear at camera trap sites in the Richardson study area during the species-specific sampling periods of each year (2018, 2019). Camera malfunctions in 2019 resulted in differences between the number of active versus deployed camera trap sites (n=58).

Species (Sampling Period)	**Caribou (Aug. 1 - Oct. 31)**		**Bear (May 1 - Aug. 31)**	
Year	2018	2019	2018	2019
# Active Camera Trap Sites	30	45	30	55
Mean Distance between Neighboring Sites (km)	2.7	2.7	2.7	2.5
# Sites with Detections (%)	7 (23%)	21 (47%)	22 (73%)	39 (71%)
Total Detection Events	65	187	137	203
Maximum Daily Count	9	6	5	4
Mean Detections per Site (max, SD)	2.1 (17, 5.1)	5.2 (34, 8.1)	4.9 (38, 8.9)	3.6 (27, 5.5)
Mean Group Size (max, SD)	1.2 (2, 0.36)	1.3 (4, 0.60)	1.1 (3, 0.3)	1.1 (3, 0.3)
% Detections of Singletons	0.85	0.77	0.95	0.96

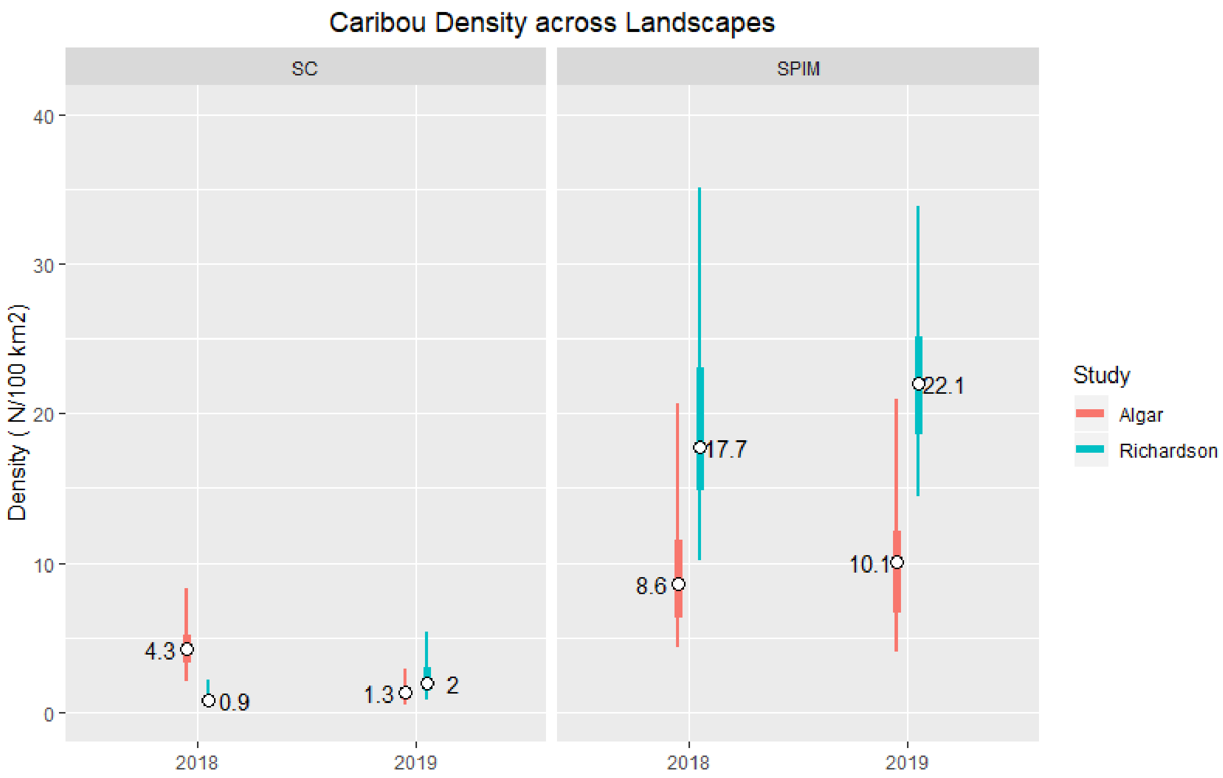

Figure 7.6 Comparison of caribou density estimates in the Algar and Richardson landscapes during the Aug. 1 - Oct. 31 sampling periods in 2018 and 2019 from camera trap data. SC and SPIM models used a gamma(24,8) prior distribution on sigma. Numbers highlight the mode density estimate. Whiskers indicated 50 and 95 HPD intervals.

For bears, the Richardson study area had fewer detections at fewer camera trap sites compared to the Algar study area (Table 7.3). According to SC models, bear densities in the Algar and Richardson study areas were similar (Fig. 7.7). However, estimates were more precise for the Richardson study area.

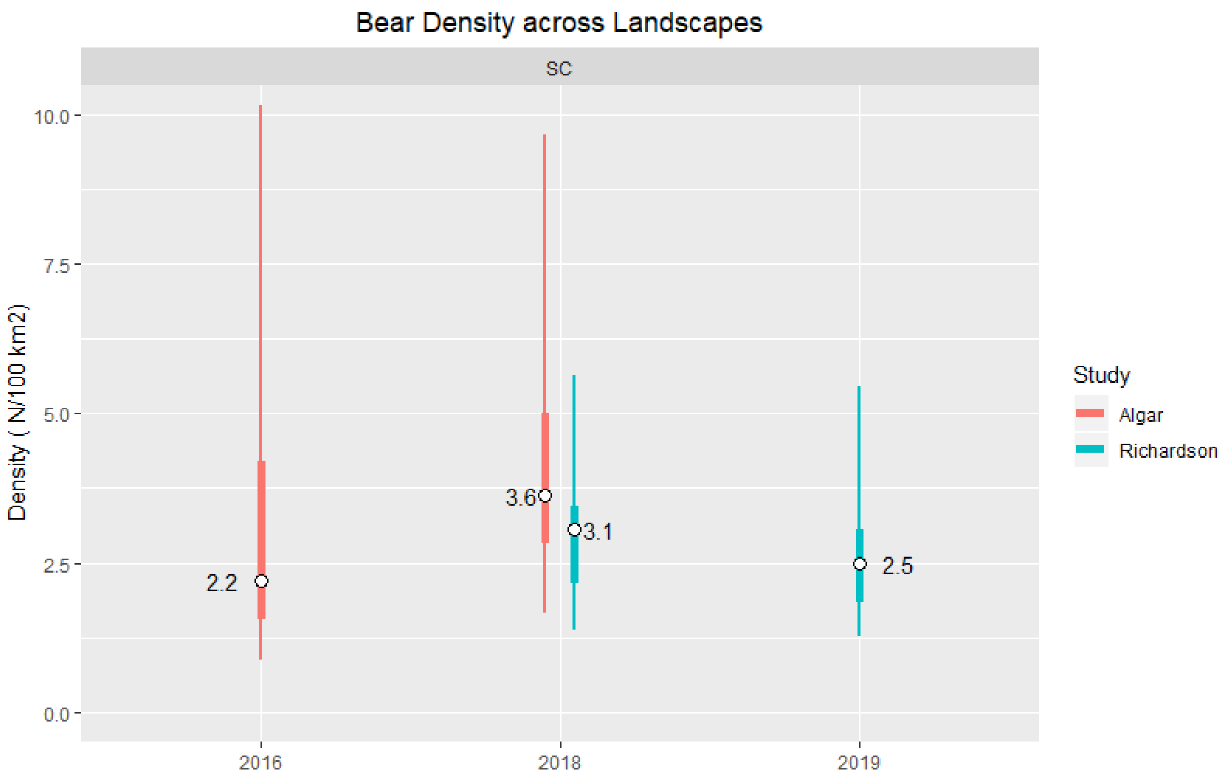

Figure 7.7 Comparison of bear density estimates in the Algar and Richardson landscapes during the May 1 - Aug. 31 sampling periods across years with available data and converged estimates. SC models used a gamma(24,8) prior distribution on sigma. Numbers highlight the mode density estimate. Whiskers indicated 50 and 95 HPD intervals. No estimates shown for Algar in 2017 and 2019 due to lack of model convergence, or for Richardson in 2016 and 2017 as sampling had not yet started.

7.3 Discussion

Caribou management at the population scale has been based on estimation of population growth rates (from estimates of survival and recruitment), which are key parameters for understanding population change but require intensive information to be collected over long time frames (Hervieux et al. 2013). Until now, our ability to take snapshots of the population density of caribou and their predators and apparent competitors has been very limited. The latest spatial capture-recapture model variants evaluated here allow us to make these density estimates across landscapes and through short time periods with precision comparable to more expensive, single-species, data-hungry methods (such as aerial surveys). The preliminary results from our research suggest the possibility of an increase in caribou population density over the last few years, concomitant with the timing of seismic line restoration. Their remains considerable uncertainty in these estimates, which require more refinement, and we recommend further research to confirm the estimates and investigate whether the (potential) population increase persists and is related to the linear restoration, concurrent government wolf cull, natural fluctuations, or a combination of these factors.

Although offering marked improvement over past methods, our density estimates of caribou and black bear differed by modeling approach and had relatively low precision, making conclusive inferences about spatial and temporal trends difficult. As we expect that density estimation will become a key component of future monitoring of the effectiveness of seismic line restoration (and other caribou recovery actions), we explored the sources of the imprecision and offer advice for future analyses.

7.3.1 Model performance

Bias from Social Herding Behavior and High Densities

Caribou SC density estimates were more precise but lower than SPIM estimates. Some underestimation with SC models was expected because group sizes within detection events were not summed and therefore sometimes true group sizes and detections were likely undercounted. However, we suspect also that high local caribou densities and social herding behaviors rendered SC models unable to distinguish between spatially proximate unmarked individuals, combining their detections into recaptures of single individuals. High local densities of activity centers, due to patchy resource distribution for example, may have reduced the spatial variation in counts that is informative about individual identity (Chandler and Royle 2013), especially as camera traps were spaced within the range of individual movement in accordance with recommendations (Ramsay et al. 2015). For bears, high local densities may have contributed to SC model failure in 2017 and 2019 rather than underestimation, as the total number of detections and maximum daily counts were highest in those years. Considering custom MCMC samplers may have helped performance and convergence of the SC models for bears by better exploring the parameter space (Ponisio et al. 2020). Thus, even large numbers of detections, if due to high densities, may be problematic for density estimation by SC approaches.

Furthermore, social herding behavior in caribou would have caused correlated movements across individuals, leading to non-independent detections that would further inflate detection probability and precision and negatively bias abundance estimates (Clare et al. 2017, Bischof et al. 2020). If movement patterns of individuals in groups were completely correlated and individuals were always detected together, SC abundance and density estimates would reflect herds instead of individuals. However, such high correlation may not be the case for caribou (i.e., fission/fusion dynamics; Body et al. 2015). Thus, even low levels of grouping behavior may have contributed to SC models underestimating density with inflated precision. In contrast, results from SPIM models suggest that they may be less sensitive to violations of independence. SPIM estimates of caribou density did not increase in precision when data from group sizes >1 were added in 2016 – 2018, only increasing the mode abundance estimate. This suggests that the additional data contributed relatively more information about density and abundance than the influence of non-independence. Nonetheless, the impact of violating the assumption of independence in SC and SPIM models, and more generally models estimating unmarked populations, has not yet been assessed and requires additional investigation.

Data Sparseness

Caribou detections were relatively sparse in the first two years, due likely to low detection probability and population density rather than limited sampling occasions. Data sparseness and lack of information about parameter values can cause poor estimation. Thus, density estimates in both SC and SPIM models improved when an informative prior on sigma was used to constrain estimates within reasonable values, by stating that the range of individual movement is mostly likely around 3 km. This is in comparison to when the uniform prior was used that stated any value between 0 - 10 km was equally likely. The direction of improvement, however, showed patterns opposite to those commonly observed elsewhere (Chandler and Royle 2013, Ramsey et al. 2015). When models used the informative prior on sigma instead of the uniform prior, we observed a decrease in the number of estimated individuals each with larger ranges of movement (i.e., decreased density and increased sigma estimates), rather than an increase in the number of individuals each with smaller ranges of movement (i.e., increased density and decreased sigma estimates). This effect was particularly notable in the last two years with SPIM models, when density estimates were originally unrealistically high with a uniform sigma prior. Evidently, the direction in which estimates change (i.e., bias) and improve is sensitive to how the prior distribution is specified, the pattern and reason for sparse data, as well as other factors such as local density and movement relative to trap spacing (as described above). Indeed, SC results for fisher (*Pekania penannti*) in a landscape broadly similar to the Algar and Richardson study areas showed the same direction of change as ours when an informative prior distribution for sigma was used (Burgar et al. 2018).

Here we used a gamma distribution to provide models with additional information about the value of sigma, but stronger priors and other distributions such as the half-cauchy are also possible. The degree to which the prior should restrain possible parameter values will depend on the confidence in the available prior knowledge about the true parameter values. Furthermore, prior information and distributions that are strong but also incorrect can bias estimates. We therefore echo the recommendation of Burgar et al. (2018) to consider a range of slightly informative priors to balance the need to address data sparseness with the danger of being overly prescriptive. Use of prior information has also been shown to improve model convergence with sparse datasets, although model failures in our analyses were likely due to MCMC sampling issues. Thus, while incorporating available prior knowledge about individual range of movement can improve precision, further investigation into model behavior, data sparseness, and influence of informed priors is warranted.

SPIM results showed that having few identity covariates or different values per covariate to inform SPIM models will decrease precision of density estimates (Augustine et al. 2019). The amount of information in an identity covariate to distinguish between individuals depends on the number and proportion of its different values within the population and detected individuals: an individual with a rare attribute, such as a very high antler point count, is more distinguishable than an individual with multiple common attributes, such as gender or size. For example, the detection of only one caribou with a GPS collar in 2019 allowed for the inclusion of the third collar-identifying covariate in 2019, resulting in a precision increase not observed with previous years. (This also highlights the contribution of collared individuals to unmarked population estimation, even without telemetry data). In contrast, bears had only 2 identity covariates, coat color and body size, with only 4 and 3 values respectively. More covariates and more values per covariate are needed to tell individuals apart when density is high and more individuals are detected at the same locations. Otherwise precision decreases and models may not converge (Augustine et al. 2019). The scarcity of bear identity covariates and few categories likely contributed to the poor performance of the SPIM model with 2016 data.

In SPIM models, we minimized errors when assigning partial identity covariates by allowing for missing values. While this reduced the amount of data and decreased power to distinguish between individuals, it also helped avoid false re-detections from incorrect assignment of multiple individuals to images of a single individual, i.e., the *ghost effect* that is common in camera trap studies and leads to overestimated abundance (Johannson et al. 2020). Instead, we were more likely to miss re-detections by assigning the same identity to multiple individuals, analogous to allelic dropout in genotypes, leading to shadow effects and thus underestimating abundance (Mills et al. 2000). Still, errors in the caribou data could have arisen from miscounting antler points and misclassifying sex because of too few or blurry images. Errors in antler point counts were more likely to occur for individuals with fewer points, because individuals with many points - even if undercounted - were more likely to remain distinct and discernable from others. Finally, the SPIM approach used the partial identity covariates to probabilistically rather than deterministically assign identities. Thus, any errors that remained after conservative assignment of identity covariates were less likely to cause biased estimation.

7.3.2 Ecological Inferences

Despite differences in the magnitude of SC and SPIM estimates of caribou density, both modeling approaches showed a general increase in caribou density in the Algar study area from 2016 to 2019. Changes in mode estimates over the 4 year period mirrored patterns in total detections and mean detections per site, suggesting that SC and SPIM results could serve as relative abundance indices for tracking spatial and temporal trends and patterns, even if absolute values of density estimates may not be reliable. However, caution is necessary when making inferences about spatiotemporal trends in density. Differences in estimated density may also reflect variation in movement patterns and site fidelity (Hazell and Taylor 2008). Furthermore, density estimates from our analyses should not be extrapolated to other regions because they represent realized density for the particular data set under a null model, while inference about expected density in unsampled areas would have required that we included habitat covariates in our SC and SPIM models; this added model complexity is currently under development and evaluation for SC models (Evans and Rittenhouse 2018) and requires custom MCMC samplers for SPIM models.

Given the potential bias in SC models, we cautiously place greater confidence in SPIM models, which we estimated a density of 8.6 – 10.1 caribou per 100 km^2 in the Algar study area in 2018-2019. These estimates are approximately half of the density estimated in the neighboring Cold Lake caribou range by Burgar et al. (2019a). Still, our results for a region of the Algar subrange would suggest that the population status could be improving, given that the larger ESAR caribou herd is considered declining with a minimum of 227 individuals reported in 2017 (Government of Alberta, 2017). According to SPIM models, caribou density in the Richardson study area seem to be approximately double that of Algar, contributing new information to conservation of the Richardson caribou range, as the population size was previously unknown but believed to be stable with a minimum population size of 125 individuals (Government of Alberta, 2017).

SC models estimated similar bear densities in the Algar and Richardson study areas, with mode estimates ranging from 2.2 – 3.6 bears per 100 km^2. Underestimation due to high local densities is possible, even though bears do not exhibit social herding behaviors that could violate the model assumption of independence. However, as a relative measure of density, these results are consistent density estimates from SC models in the neighboring Cold Lake landscape (Burgar et al. 2019a).

7.3.3 Future Work

Robust estimates of absolute density and abundance are necessary for estimating baselines and monitoring population trends. We set out to further explore the possibility of estimating density of unmarked populations from camera traps, particularly by incorporating partial identity information. Our results reinforce that this is a promising possibility but a task requiring further development, as consistent and precise estimates remain elusive. Nevertheless, we maintain that our results represent an improvement over expensive and equally (or more) imprecise single-species estimates currently being used, and are certainly better than no information on density at all, which is the case for most mammals in the western boreal forest.

One appeal of SCR-based models is the mechanistic framework that allows for extension to model the trends underlying population dynamics. However, SC models were potentially sensitive to high densities, social herding behaviors, and small trap spacings that biased estimates. SPIM approaches formalized the process of partially distinguishing individuals used to determine group sizes for SC models, but precision was still low due to sparse identifying features. Importantly, our results reveal that questions remain around the data requirements, model specifications, and ecological conditions that are best suited for the various unmarked population modeling approaches (Fig. 7.8). Further work is required to assess the performance of SCR-based models. We recommend that simulations and empirical analyses evaluate the number of marked/collared individuals necessary to improve estimates for varying population densities (Chandler and Royle 2013, Augustine et al. 2019), the potential for telemetry data to improve estimates (Ruprecht et al. 2020), how informative priors are specified and choice of MCMC sampler (Burgar et al. 2018, Ponisio et al. 2020), and the impact of social herding behavior (Bischof et al. 2020). Finally, SCR based approaches should be compared to alternative, non-SCR-based approaches, including the REST, TTE, and distance-sampling models and their variants, that do not require individual identities but instead ancillary information on animal movement or properties of detection probability related to the camera trap field of view (Buckland et al. 2001, Rowcliffe et al. 2008, Howe et al. 2017, Nakashima et al. 2017, Moeller et al. 2018).

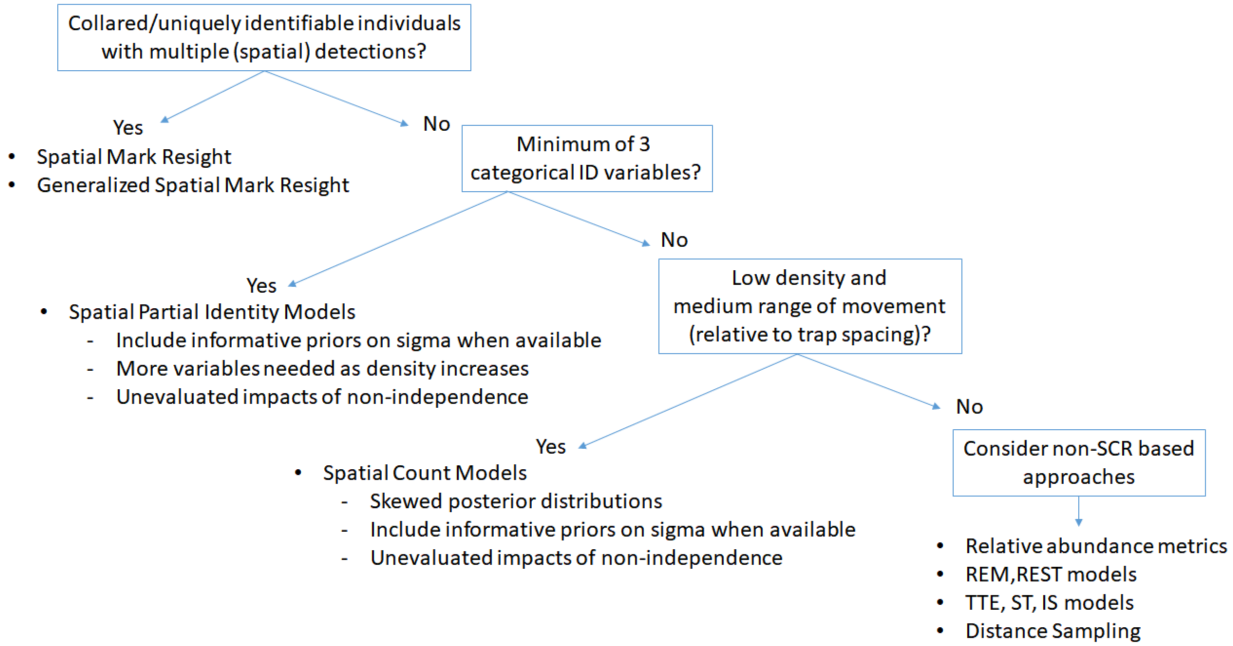

Figure 7.8 A decision framework for choosing methods for estimating abundance of partially marked or unmarked populations. Decision points are based on insights from the analyses described here, and require validation through simulations and field-based comparisons. Where: SCR = Spatial Capture Recapture model; REM = Random Encounter Model; REST = Random-Encounter-and-Staying-Time model; TTE = Time-To-Event model; ST = Space-To-event model; IS = Instantaneous Sampling model.

8. Assessing phenological changes

The timing of recurring events of abiotic conditions and vegetation growth patterns (i.e., phenology) can impact the distribution, activity, and behavior of wildlife species. Abiotic cues, such as changes in temperature and precipitation, can trigger physiological and behavioural changes in animals. For example, colour molting in species like snowshoe hare helps maintain camouflage from predators through seasonal changes in the environment (Zimova et al. 2018). Similarly, vegetation is the source of primary productivity that drives energy through the trophic web and therefore resource availability across the landscape. As a result, seasonal changes in resource availability can cause wildlife populations to track the moving front of maturing vegetation (i.e., 'surfing the green wave'; Merkle et al. 2016). When such phenological patterns in habitat conditions change, for reasons including ecological disturbance and succession (Navas et al. 2010), climate change (Visser and Both 2005), and anthropogenic alteration of habitat (Felton et al. 2006), wildlife must move, adapt, or risk reductions in fitness and survival (Johannson et al. 2015, Zimova et al. 2016).

In the Canadian boreal forest landscape, including the Algar study area, the creation of seismic lines has removed overstory vegetation and altered the understory vegetation that terrestrial wildlife depend on for shelter and forage (Johnson et al. 2003, Denryter et al. 2017). Efforts to restore wildlife habitats have had variable success due to spatial heterogeneity in moisture regimes and slow tree growth (Rossi et al. 2009, van Rensen et al. 2015, Finnegan et al. 2019), as well as variation in restoration practices that range from soil manipulation to tree planting (Pinno and Hawkes 2015, Chen et al. 2018, Filicetti et al. 2019). Habitat recovery in the boreal landscape has been documented to be slow at best, on the timescale of decades, and nonexistent or halted at worst (Finnegan et al. 2019, Lupardus et al. 2019). While studies evaluating the impact of anthropogenic disturbance or habitat restoration on wildlife have typically focused on changes in habitat type (e.g. from natural to anthropogenic, or restored to unrestored; Fisher and Burton 2018, Tattersall et al. 2020b), we are not aware of any that considered indirect impacts on wildlife through changes in vegetation phenology. In fact, changes in habitat phenology due to seismic lines have only been hypothesized (Dabros et al. 2018). Furthermore, focusing on understory vegetation and phenology may actually be more effective at distinguishing changes during early stages of habitat restoration than other commonly used volume-related metrics like live tree basal area (Gilman et al. 2016, Lupardus et al. 2019), stem count/density (Filicetti et al. 2019) or line of sight (Pyper et al. 2014). Before establishment of trees on seismic lines, the early seral vegetation that appears is composed of diverse deciduous shrubs, forbs and graminoids (Dabros et al. 2018, Finnegan et al. 2018a). Monitoring understory plant phenology in boreal landscapes can therefore help evaluate the progression of habitat disturbance, restoration, and related impacts on the wildlife community (Buisson et al. 2017, Walker and Soulard 2019).

Camera trapping is increasingly used to measure environmental and wildlife phenology (Bater et al. 2011, Ide and Oguma 2010, Siren et al. 2018, Zimova et al. 2020). Important abiotic and vegetation phenological processes at the ground and understory levels directly impact wildlife distribution and activity (Gentry and Emmons 1987, Sheriff et al 2011). However, above-ground and satellite imagery [e.g., Phenocam (Seyednasrollah et al. 2019), MODIS, Sentinel (Zhang et al. 2003, Klosterman et al. 2014, Bolton et al. 2020)] are not ideal for characterizing understory phenology due to physical obstruction by the forest canopy, which has different phenological patterns and processes (Richardson and O'Keefe 2009, Tuanmu et al. 2010). Additionally, direct human observations of phenology may not be possible over broad scales or remote areas unless there is additional coordination for citizen science approaches (Denny et al. 2014). Therefore, ground-level camera trapping to monitor wildlife has promise for also monitoring the phenology of understory vegetation, with potential to achieve greater spatiotemporal coverage with minimal additional effort (Vartanian et al. 2014, McClelland et al. 2019, Hofmeester et al. 2020). The red, green, and blue color values in each camera image can be used to estimate phenologically relevant dates and derive metrics such as lengths of growing seasons, metrics of greenness, and habitat indices (Filippa et al. 2016, Radeloff et al. 2019). Extracted phenology patterns can then be related to wildlife data collected by the same camera traps (Hofmeester et al. 2020).

We posit that ground-based camera trapping can contribute novel information about site-level environmental phenology to inform inferences about spatial and temporal patterns of wildlife distribution and resource use. Here, we used our camera trap monitoring in the Algar study area to characterize vegetation phenology, assess the degree to which phenology was influenced by habitat restoration, and evaluate its impact on wildlife use of seismic lines. Past research suggests some bias in habitat quantification between oblique camera images and satellite imagery (Liu et al. 2017, Siren et al. 2018, Fortin et al. 2019). We examined the performance of automated methods for extracting vegetation greenness and phenology from camera trap data, and compared outputs with those of satellite-derived Normalized Difference Vegetation Index (NDVI) and Enhanced Vegetation Index (EVI) products. We expected camera traps to capture additional phenological information about understory vegetation when compared to the satellite-derived phenology products. Next, we hypothesized that plant phenology measured by camera traps would vary across our categories of seismic line restoration treatments (see section 2). We assumed that initial success in habitat restoration should lead to increased understory plant growth, so we expected phenology metrics to reflect more primary productivity and greenness on seismic lines with active restoration than on unrestored lines. We further predicted that sites with active restoration would have less greenness (as a measure of productivity) than sites with passive restoration, which have had more time for plant growth. We expected all sites on seismic lines to show different phenologies from off-line sites, which represented undisturbed vegetation phenology.

Finally, we predicted that plant phenology patterns measured by our camera traps would be associated in varying degrees with patterns in wildlife activity. We assumed that measures of greenness in camera trap images from understory seral vegetation should reflect availability of forage for herbivores. We therefore hypothesized that the timing and intensity of habitat use by species that depend on early seral vegetation as a forage resource should track plant phenology. We focused on three species for these analyses: sandhill crane, woodland caribou, and white-tailed deer. We expected the timing of sandhill crane activity to correlate most strongly with the vegetation growing season, especially at sites with habitat restoration and relatively more greenness because cranes seasonally migrate to use boreal habitat to raise young in areas of high plant productivity (Hobson et al. 2006). In contrast, caribou and deer boreal caribou are non-migratory and thus use the boreal landscape for more than just summer forage, including calving, rutting, and seasonal movement (Rettie and Messier 2001). We therefore expected the spatial and temporal patterns of caribou and deer activity to track vegetation phenology and greenness less than cranes. Specifically, we predicted that the timing of caribou activity would not closely match the vegetation growing season, although with less mismatch at sites on seismic lines than off lines because caribou need to balance foraging opportunities with increased predation vulnerability (Spangenberg et al. 2019) in order to maximize relative forage benefits on seismic lines. Finally, we hypothesized that finer scale spatial and temporal patterns of caribou detections would be less correlated with phenology patterns than deer detections. Deer should show stronger patterns of habitat use related to vegetation greenness given their dependence on the early seral vegetation (Schneider and Wasel 2000) that has facilitated their range expansion (Latham et al. 2011b) as it becomes increasingly available in the boreal habitat due to anthropogenic landscape disturbance and climate change (Dawe et al. 2014, Fisher et al. 2020).

8.1 Methods

All camera traps were programmed to take a daily timelapse image at noon. This was originally set up to ensure camera functionality, but also provided a consistent daily record of the local environment at the camera site. We used the set of available timelapse images collected from January 1, 2016 to the retrieval of cameras in November 2019. We did not include images from 2015 as they were taken only after the end of the vegetation growing season.

8.1.1 Extracting and modelling phenology patterns

We defined the entire visible foreground in camera trap images, where wildlife are directly interacting with understory vegetation, as regions of interest (ROIs) for characterizing vegetation phenology. We used the ‘phenopix’ package (Filippa et al. 2016) in program R (R Core Team 2019) to automate extraction of phenology data from daily timelapse images. For each site (i.e., camera station), we delineated the ROI with a bounding polygon (quadrilateral) for each deployment period, as the camera fields of view changed slightly when cameras were handled for data collection (Fig. 8.1). An index of greenness for each timelapse image was calculated from the red, green, and blue color values extracted across pixels within the ROI of each image (Filippa et al. 2016) (Fig. 8.2). Greenness index values were filtered to remove noise and outliers using default phenopix parameter values (Filippa et al., 2016). If timelapse images were available for at least 60% of a year (≥220 days), we fit a smoothing spline to the trend in daily greenness indices (using with package default parameters).

From fitted splines, we estimated a set of annual phenological dates and metrics. Date of the onset of vegetation greenup was identified as the earliest date that greenness was 15% of the maximum value, while date of the onset of vegetation senescence was the latest date when greenness was 90% of the maximum value (McClelland et al. 2019). Dates are for the onset of phenological patterns, but for succinctness we hereafter omit mention of “onset”. We defined first dates of 50% greenness before peak and 15% of greenness after peak as dates of the onset of vegetation maturity and dormancy, respectively. We calculated the length of the growing season as the number of days between the mean dates of greenup and senescence. Finally, we extracted the maximum value of greenness (i.e., peak value) and derived the total amount of greenness and seasonality, calculated as the area under the curve and the coefficient of variation, respectively. These metrics are similar to the components of dynamic habitat indices developed to characterize the environmental conditions and primary productivity of a habitat (Coops et al. 2008, Radeloff et al. 2019), although we substituted minimum values for maximum values due to lack of variation.

To compare with the camera trap data, we also estimated phenological patterns with remote satellite data at two spatiotemporal scales (Table 8.1). First, we used normalized difference vegetation index (NDVI) and enhanced vegetation index (EVI) data at 250m spatial resolution and 16-day frequency from the MOD13Q1 v6 product (Didan 2015). These data were available for the entire 4 year period (2016-2019). We extracted these data using the ‘MODISTools’ package (Tuck et al. 2014) in program R. As with the greenness values extracted from camera traps, splines were fit to NDVI and EVI values at each site and the same phenological dates and metrics were calculated (i.e., dates of greenup and senescence, length of growing season, maximum greenness values, total greenness, and seasonality). We also used EVI metrics derived from 30 m spatial resolution, 1-4 day frequency harmonized Landsat 8 and Sentinel 2 (HLS2) data (Bolton et al. 2020). These data were available for the first 3 years of the study (2016-2018). Metrics at this finer spatiotemporal resolution included the annual maximum value, amplitude, and total area of the EVI vegetation cycles.

Table 8.1. Annual phenological metrics extracted or derived from camera trap timelapse images and satellite-based phenology products for camera trap sites in the Algar study area from 2016-2019. Dates refer to the onset of events, with length of growing season calculated as the difference in days. Maximum greenness is the peak value during each annual cycle; total greenness is the area under each annual greenness curve; seasonality is the coefficient of variation at the daily scale; amplitude is the difference in maximum and minimum values in each annual cycle.

Dataset	**Camera Trap**	**NDVI (250 m)**	**EVI (250 m)**	**EVI (30 m)**
Source	Ground	Satellite (MODIS)	Satellite (MODIS)	Satellite (Landsat + Sentinel 2)
Date of Greenup	X	X	X	
Date of Senescence	X	X	X	
Length of Growing Season	X	X	X	
Maximum greenness	X	X	X	X
Total Greenness	X	X	X	X
Seasonality	X	X	X	
Amplitude				X

We evaluated vegetation phenology differences across the seismic line restoration categories (Active, Passive, Control, Human Use and Off-line, as described in section 2). With camera trap data, we first used generalized linear mixed models (GLMMs) to evaluate differences in dates of greenup and senescence as a function of the restoration category, including camera site and year as random intercept terms. We also used linear models to compare the inter-annual ranges in greenup and senescence dates at a site as a function of the restoration category (i.e., no random effects). For the three components of the dynamic habitat index (annual total, maximum, and seasonality of greenness), we compared the mean values across restoration strata using pairwise t-tests with a Bonferroni adjustment for multiple tests. Additionally, we used GLMMs to evaluate if length of season and seasonality in annual greenness were measured differently across the camera trap and remote satellite NDVI (250 m) and EVI (250 m) datasets as well as to identify differences due to restoration category. We included the camera site and year as random intercept terms. We did not evaluate the consistency of other phenology metrics across datasets due to changes in the units used in each dataset. Still, to compare all metrics derived from camera imagery and satellite imagery, we calculated pairwise

Pearson's correlation coefficients for each year (2016-2019) as well as averaged over the 3-4 year periods.

Figure 8.1 Example of a camera trap timelapse image in the Algar study area. The polygon outlined in black shows the understory region of interest for the deployment period, from which red, green, and blue color values were extracted to estimate dates of (the onset of) greenup, maturity, senescence, and dormancy and derive phenology metrics.

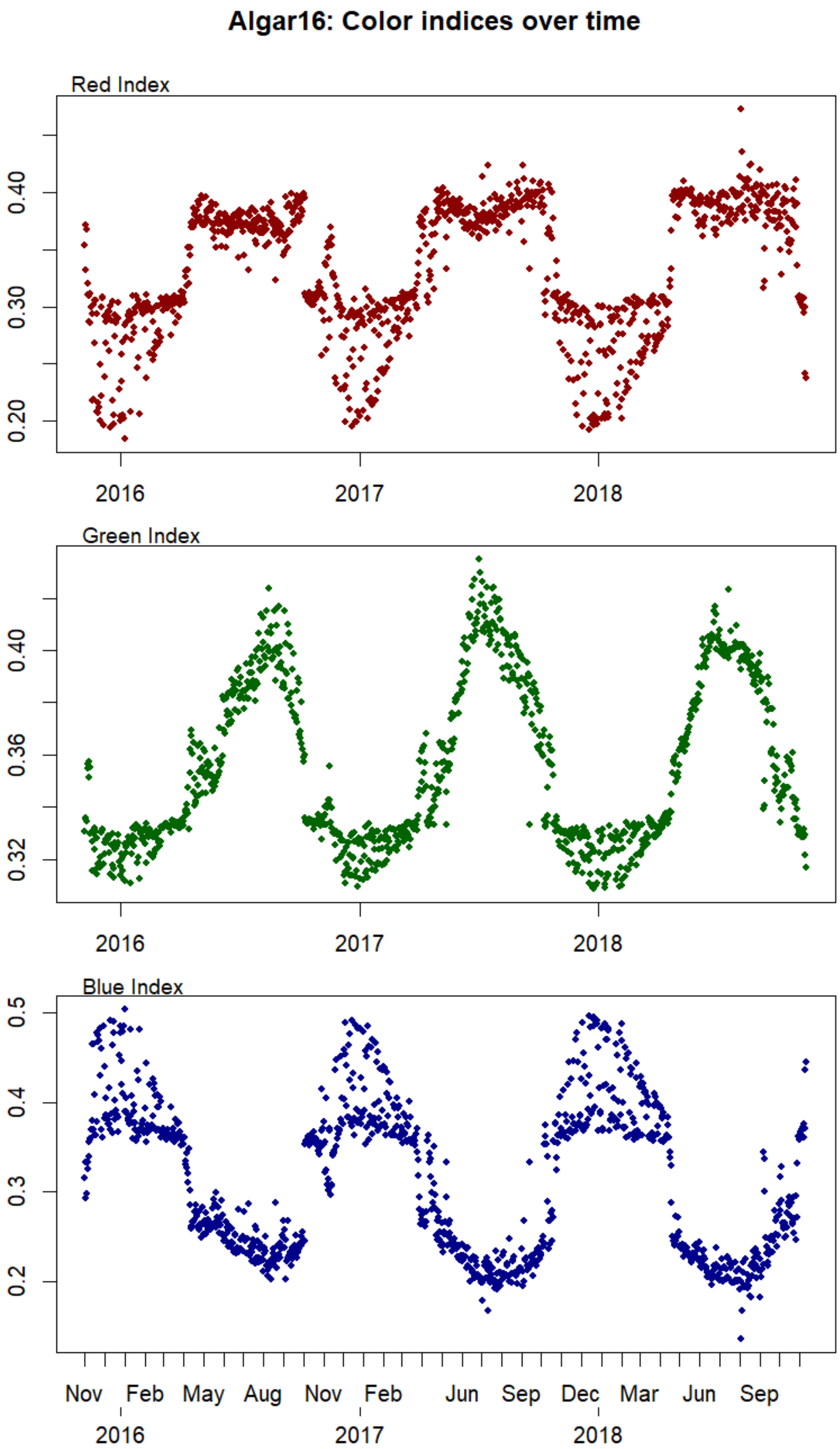

Figure 8.2 Example of the time series of the relative red, green and blue values extracted from camera traps in the Algar study area from Nov. 2015 - Nov. 2019 (for camera station ‘Algar 16’). Each point represents one day. Splines were fit to each annual subset to estimate phenological dates and derive metrics.

8.1.2 Linking wildlife patterns to habitat phenology

We used generalized linear mixed models (GLMMs) to compare the timing of first and last detections in each year of sandhill cranes and caribou to dates of greenup and senescence. Response variables were the difference in days between first detection and greenup and between last detection and senescence. We controlled for the effect of restoration strata on seismic lines by including restoration category as a fixed effect, and we used random effects to account for additional variation due to site and year. To avoid inflated mismatches with phenological dates due to outlier detections, we limited analyses to sites with a threshold minimum number of detections determined as the number of detections beyond which average differences between phenological and detection dates stabilized (Appendix 5 Figure 1). The threshold minimum was 5 detections for cranes. There was no conclusive threshold for caribou, so we set the threshold to 2 detections for caribou.

For finer-scaled spatial and temporal analyses of ungulate activity and habitat use related to vegetation greenness and primary productivity, we also related annual and weekly counts of caribou and deer detections to the phenology metrics extracted from camera traps. First, to compare spatial patterns of caribou and deer detections to site-level phenology, we used GLMMs to model annual counts (i.e. total number of independent detections in a calendar year) as a function of cumulative vegetation greenness, maximum greenness reached, seasonality of greenness, and length of season (in days). We did not include dates of green up or senescence in models because of significant correlation with length of season (Kendall’s rank correlation $p<2.2e^{-16}$). We expected that sites with larger counts would have measures of higher annual greenness and productivity.

We included covariates to control for effects of habitat and anthropogenic disturbance on the spatial pattern of counts. For habitat covariates, we considered the percentage of lowland habitat at the 1 km scale around cameras and the dominant habitat type at 30 m scale. We defined lowland habitat as forest where the moisture regime was categorized as “wet” in the Alberta Vegetation Inventory (Alberta Vegetation Interpretation Standards 2005). Based on Tattersall et al. 2020b and section 5.1, we expected counts of caribou and deer detections to respectively increase and decrease with lowland habitat. To account for anthropogenic disturbances, we included the restoration strata as a categorical covariate (as in Tattersall et al. 2020b), the width of the seismic line in meters, and the density of seismic lines (km / km^2) within 30 m, 250 m, or 1000 m buffers of the sites. Buffer sizes were chosen across a range of distances within home range movement for caribou and deer (Dalerum et al. 2007, Lesage et al. 2000). Based on findings in section 5.2, we expected limited effects of anthropogenic disturbances on counts of ungulate detections. All continuous covariates had non-significant pair-wise collinearity less than 0.5, and were scaled to the mean and standardized. We included year and site as random intercepts, and also considered the (log) number of days that the camera operated (176 – 366 days) at each site as an offset to control for variation in sampling effort.

We used a multi-stage AICc approach to identify the best supported model structure (Morin et al. 2020). First, we identified the appropriate variance formulation of the negative binomial distribution (quadratic or linear) and considered zero inflation or a hurdle model due to potential overdispersion in the count data. Then, for each set of covariates (phenology, habitat, and anthropogenic) we identified the most supported model structure among all possible additive combinations of covariates. We then evaluated all of the top covariates across covariate sets together in a final full model set, which was possible because Kendall's correlations across sets of covariates were <0.50. The stepwise approach reduced the number of possible models to evaluate and allowed for easier assessment of the relative impacts of covariates. It also addressed uncertainty within each covariate set rather than only identifying the overall best supported model across all covariates. Models were evaluated with the 'glmmTMB' package (Brooks et al. 2017), with the aid of the 'MuMIn' (Barton 2009) and 'AICmodavg' (Mazerolle 2019) packages in program R.

Finally, we used GLMMs to identify fine-scale temporal patterns and differences between caribou and deer habitat-use relative to weekly vegetation phenology. We modeled weekly counts of each ungulate species at each site where they occurred as a function of the average weekly greenness and annual maximum greenness at the site measured by the camera trap. If counts increased with only weekly greenness, then any significant annual patterns related to phenology in previous models were likely only a result of the finer-scale weekly greenness; however if weekly counts increased with both weekly and maximum greenness, then individuals were likely tracking both available and expected greenness. We expected deer counts to be greater and increase more with weekly greenness than caribou counts. We also included the week of the year as a covariate to investigate a linear within-year trend in detections distinct from seasonal greenness phenology. To control for habitat effects on deer detections, we included the percentage of lowland habitat at 1km scale but not the dominant habitat type at the 30m scale as the latter was significantly correlated with greenness covariates. For caribou detections, we considered habitat covariates at 1 km and 30 m in different models (i.e., not considered simultaneously) due to high correlation described above. Continuous covariates were scaled to the mean and standardized. We did not consider restoration category as a fixed covariate because we were primarily interested in temporal patterns where the species occurred. However, impacts of restoration strata on weekly detections was captured in considering each site as a random intercept. We also used year as random intercept and the (log) number of days per weekly camera operation at each location as an offset. We used AICc model selection to identify the most supported negative binomial variance formulation, and assessed the need for zero inflation or a hurdle model. Covariates were then evaluated with full model sets that included all possible linear covariate combinations.

For all final annual and weekly models, we report the overdispersion parameter and the Ω^2 statistic, a measure of goodness of fit that compares the residual variances of the full and null models (Xu 2003). Overdispersion occurs when the variance in data is greater than expected based on the model with random effects. Significant overdispersion values greater than 1 require adjustments to the model likelihood before model selection and inference. The Ω^2

statistic is interpreted similarly to the traditional R^2 measure of variance explained, with a maximum value of 1.

8.2 Results

8.2.1 Extracting phenological patterns

We extracted phenology patterns from camera trap timelapse images, and identified variation across the restoration categories (Fig. 8.3).

Dates of greenup across all camera stations and years ranged from March 8 to June 4, with a mean date of April 24 (Fig. 8.3). Dates of senescence ranged from June 13 to September 13, with a mean date of August 13. However, off-line sites had the earliest greenup (April 13) and latest senescence (August 19) on average. This resulted in off-line sites having statistically longer growing seasons than Active, Human Use and Control sites. Indeed, Control and Human Use sites had significantly later dates of greenup by 16 days (standard error, SE = 5) and 20 days (SE = 5) respectively, while Control and Active Restoration sites had significantly earlier dates of senescence by 10 days (SE = 5) and 8 days (SE = 5), respectively. Off-line sites had the greatest variation across years in the date of greenup (range = 15 days, SE = 4), but the least amount of variation in date of senescence (range = 5, SE = 4). Human Use sites had less variable greenup dates. Sites with restoration (i.e., both Active and Passive) had significantly greater variation in senescence dates, averaging an additional 20 (SE = 6) and 13 (SE = 5) days respectively.

Restoration categories did not differ significantly in any of the three components of the dynamic habitat index, i.e., annual total, maximum, or seasonality of greenness (Fig. 8.4). However, mean values of maximum greenness was significantly lower at Off-line sites (542 +/- 162) than at Control (787 +/- 354 ; adjusted p value = 0.008) and Active sites (753 +/- 326 ; adjusted p value = 0.003).

There were significant differences between the indices of vegetation phenology measured by camera traps and those measured by satellite. Growing seasons measured by satellite-derived NDVI and EVI (at the 250 m and 16-day resolution) were significantly longer than when measured from camera trap images, by 72 days and 42 days (SE = 2.4) respectively (Fig. 8.5, Appendix 5 Figure 2). The seasonality of greenness was also less in the satellite measures than in the camera trap measures. Correlations between camera and satellite metrics varied annually and across spatiotemporal resolutions (Fig. 8.5). Seasonality estimated from camera traps was significantly correlated every year with at least some satellite-based metrics, with the strongest correlation being in 2016 with NDVI seasonality ($r^2 = 0.64$, $p = 0.001$) and EVI total greenness at 30m resolution ($r^2 = 0.72$, $p < 0.001$). Maximum greenness estimated by camera traps was correlated the least frequently, and on average the most weakly, with satellite-based metrics (Fig. 8.6).

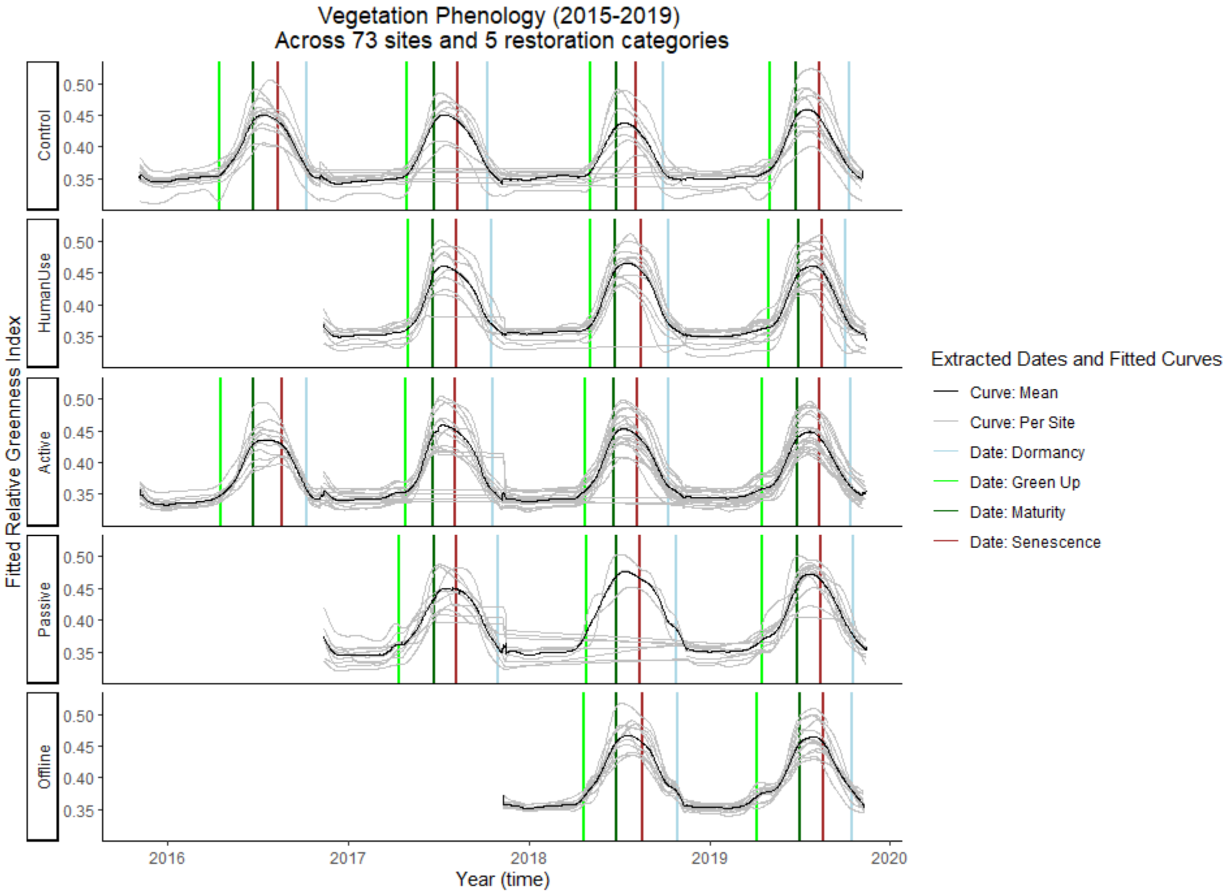

Figure 8.3 Spline curves fit to the relative greenness values extracted from understory vegetation at n = 73 camera traps in the Algar study area, from 2016 - 2019 across 5 different site restoration categories. Gray lines represent spline curves per camera trap in available years, with missing timelapse images due to camera malfunctions shown as linear segments. The black spline curves represent the means across sites. Vertical lines represent estimated annual phenological dates of the onset of plant greenup, maturity, senescence, and dormancy.

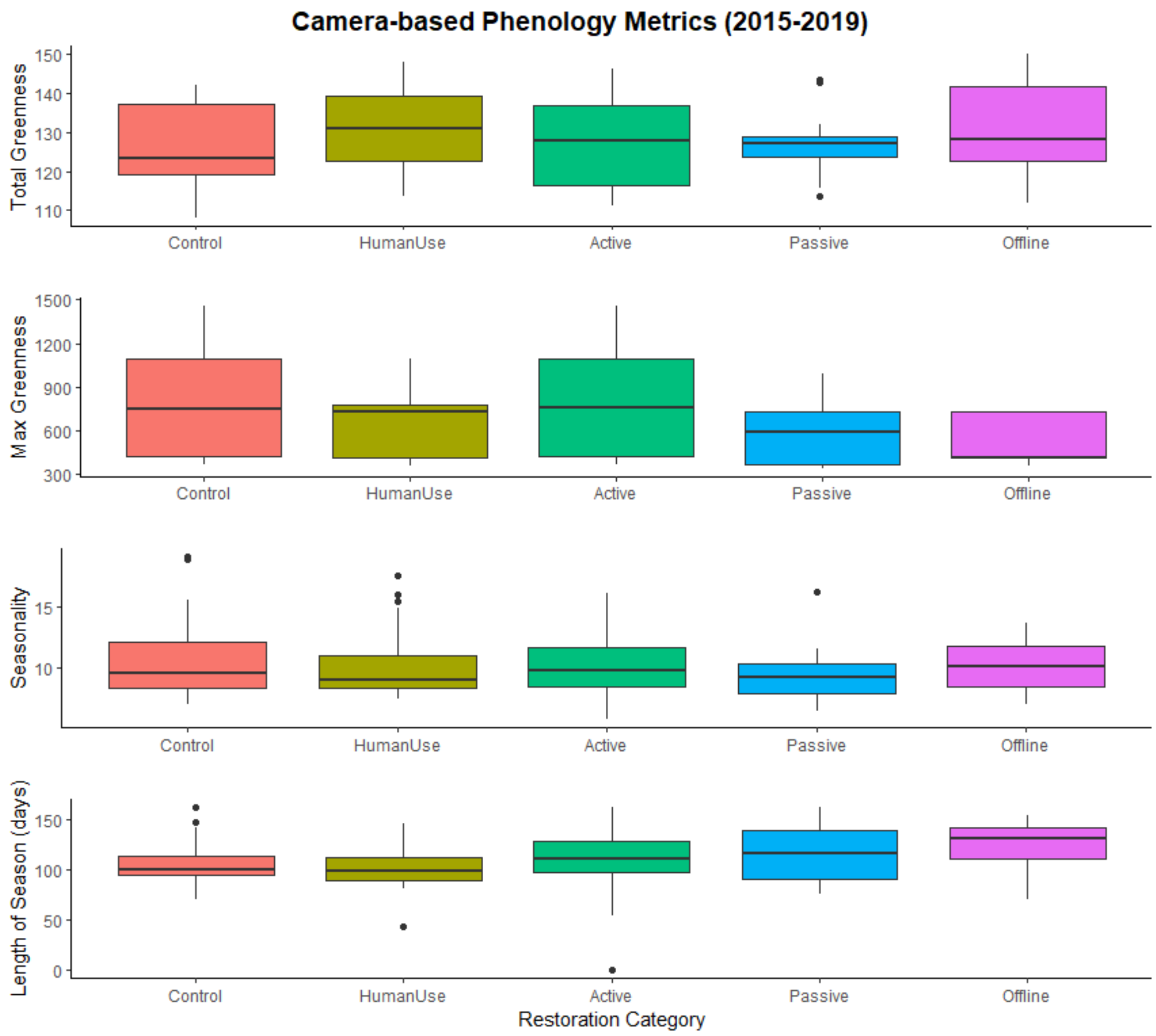

Figure 8.4 Comparison of camera-based phenology metrics across restoration categories in the Algar study area from 2016 - 2019. Metrics were derived from spline curves, as illustrated in Fig. 8.3. Total greenness was calculated as the area under annual curves; max greenness was the peak value in annual curves; seasonality was the intra-annual variation in greenness calculated as the coefficient of variation; length of season was the number of days between estimated dates of greenup and senescence.

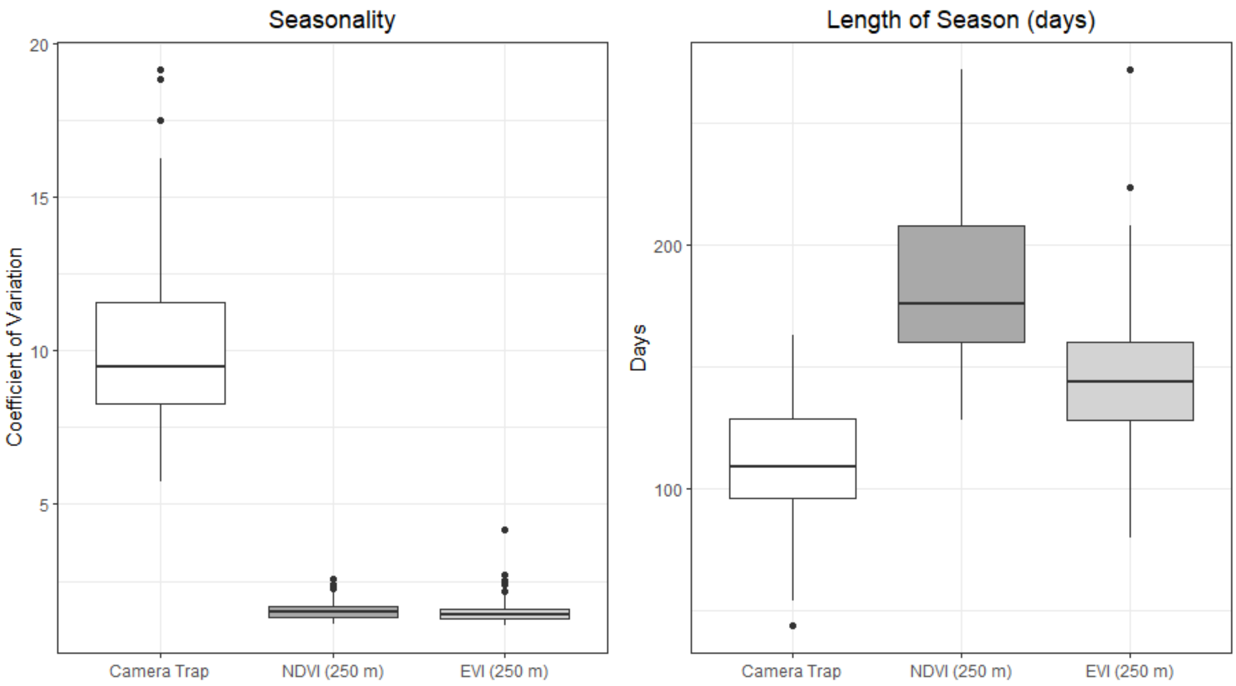

Figure 8.5 Comparison of seasonality in greenness and length of season calculated by camera traps and NDVI (250 m) and EVI (250 m) across restoration categories in the Algar study area from 2016 - 2019. Seasonality was the intra-annual variation in greenness calculated as the coefficient of variation. Length of season was the number of days between estimated dates of greenup and senescence. Seasonality and length of season were not available from the EVI dataset at 30 m resolution.

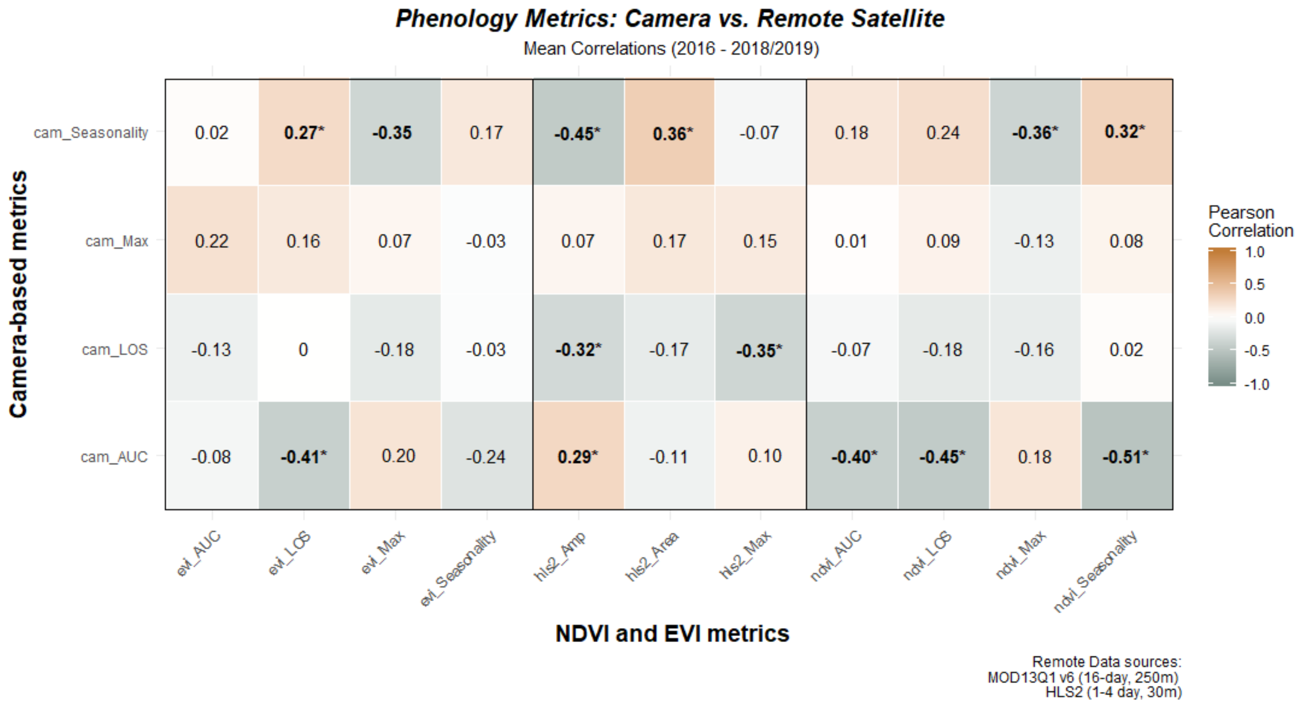

Figure 8.6 Correlation coefficients between camera-based and remote-sensed phenology metrics, averaged across restoration strata and years at the n=73 camera trap locations in Algar from 2016-2019. Bolded and asterisked coefficients represent statistical significance at the alpha=0.05 level.

8.2.2 Linking wildlife patterns to habitat phenology

Timing of wildlife detections in relation to vegetation growing seasons

Consistent with expectations, sandhill crane use of the study area was closely tied to vegetation phenology. Specifically, crane detections occurred mainly during the vegetation growing season measured by camera traps (Fig. 8.7). At sites where cranes were detected at least 5 times, the average growing season lasted from April 21 to August 5 while cranes were only detected on average from May 11 to July 24. However, we found no significant differences across seismic line restoration categories in the degree to which the period of crane detections matched the growing season. While we expected detection periods and growing seasons to be most aligned at Active and Passive, they did not match any better than at Human Use, Control, or Off-line sites. In fact, the mean difference in mismatch between dates of last detection and senescence was greatest between Active and Passive sites, with last crane detections at Active sites occurring 28 days (SE = 17) closer to the date of senescence compared to Passive sites.

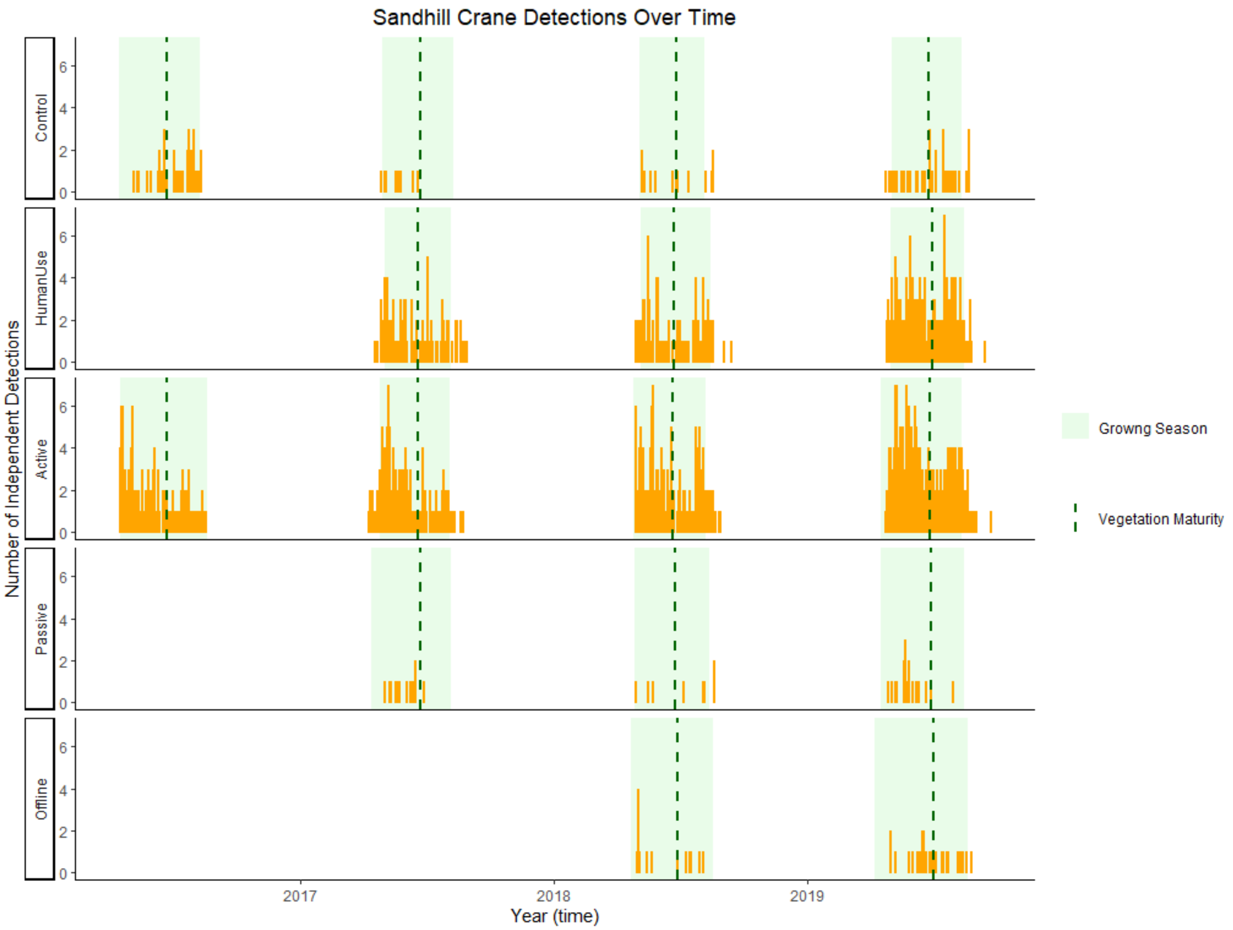

Figure 8.7 Number of independent sandhill crane detections at n=73 camera trap locations across seismic line restoration categories in the Algar study area from 2016 - 2019. Independent detections were identified based on a 30 minute maximum threshold for images to be considered part of the same detection event. Green rectangles show the growing season estimated from the extracted dates of plant greenup to senescence using camera trap timelapse images. The dotted green vertical line indicates the extracted date of plant maturity.

As expected, caribou site use was not closely related to vegetation phenology. The timing of caribou detections on average across years did not match the growing season measured by camera traps (Fig. 8.8). At sites where caribou were detected at least twice, they were first detected 5 - 81 days after greenup, but last detected anywhere from 60 days before to 55 days after senescence. At Passive restoration sites, detections occurred only within the growing season, while sites for all other restoration categories also had caribou detections outside the growing season. In particular, the period of caribou detections at Control, Human Use, and Active sites were extended past the growing season, with caribou detections at the latter two categories occurring significantly past the onset of senescence, by 55 days (SE = 16) and 41 days (SE = 12).

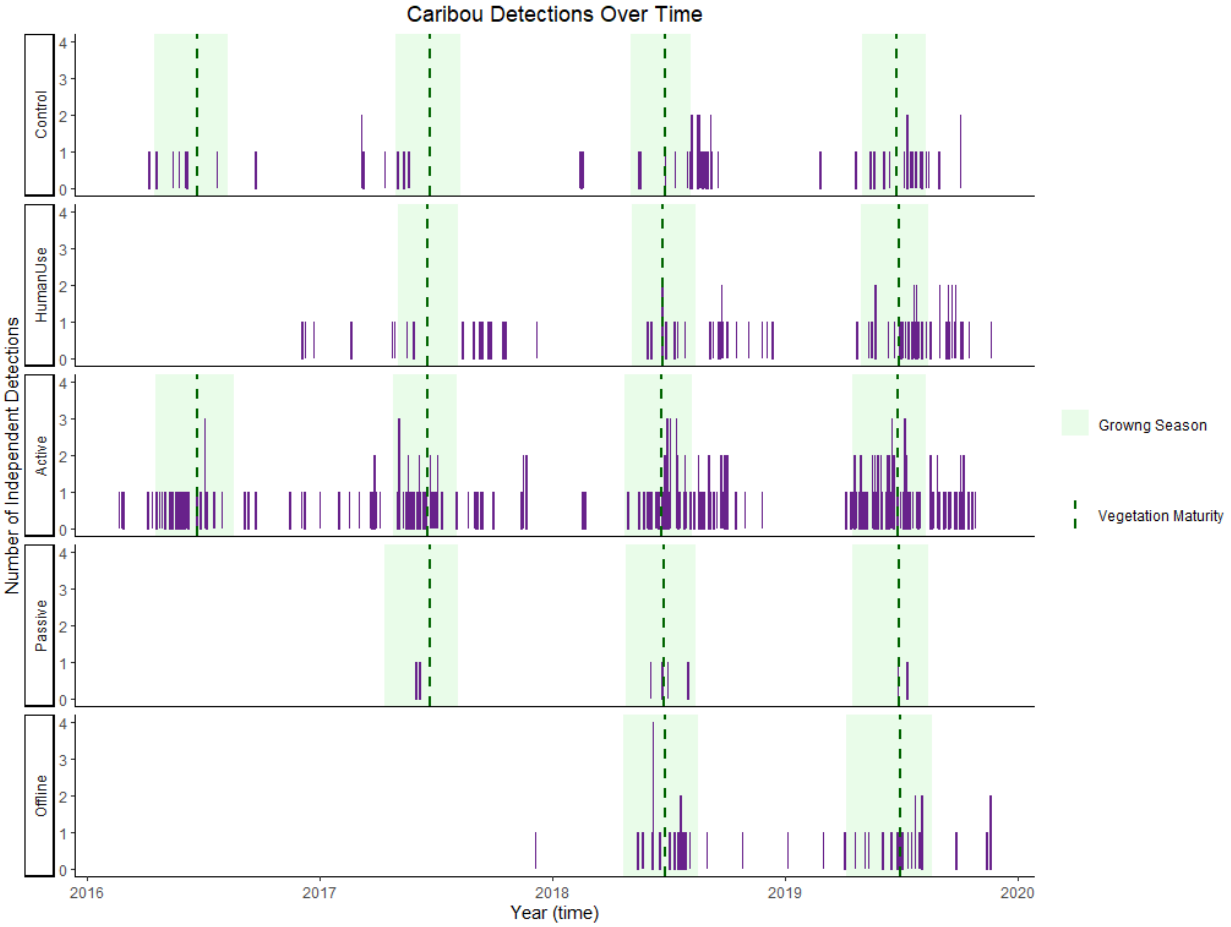

Figure 8.8 Number of independent caribou detections at n=73 camera trap locations across seismic line restoration categories in the Algar study area from 2016 - 2019. Independent detections were identified based on a 30 minute maximum threshold for images to be considered part of the same detection event. Green rectangles show the growing season estimated from the extracted dates of plant greenup to senescence using camera trap timelapse images. The dotted green vertical line indicates the extracted date of plant maturity.

Relating phenology to annual counts of ungulate detections

In models of annual detections of caribou and white tailed deer, the most supported model form for both species was the negative binomial distribution with a quadratic variance parameterization (Appendix 5 Table 1). Greater annual maximum greenness increased with the number of detections for both species, with a stronger effect as expected for deer (0.29 +/- 0.11, p=0.01) compared to caribou (0.20 +/- 0.07, p <0.01; Fig. 8.9). The maximum greenness covariate appeared in the top 8 phenology models for caribou (cumulative model weight 70%) and the top 4 models for deer (cumulative model weight 63%) (Appendix 5 Table 2). However, ungulate detections did not vary according to other site-level phenology covariates, i.e., total annual greenness, seasonality of greenness, and length of season, which were therefore excluded from the final model set for both species.

Among the habitat and anthropogenic covariates that we controlled for, only the percentage of lowland habitat at 1 km had a significant effect for both species. Consistent with our modelling results in section 5, the number of annual caribou detections increased (1.16 +/- 0.22, p<0.01) with increasing lowland habitat, while the number of annual deer detections decreased (-1.09 +/- 0.21, p<0.01) (Fig. 8.9, Appendix 5 Table 3). Among the anthropogenic covariates, restoration category had a significant effect on caribou in the top model, with annual detections lower at Passive Restoration sites (-1.63 +/- 0.79, p=0.04, Fig. 8.9). However, a more parsimonious model without the covariate was ranked 2nd and was within 1 ΔAICc of the top ranking model (Appendix 5 Table 4). Restoration strata was not a supported covariate for annual deer counts. We found no significant effects of line width or densities on the annual counts of detections of either species. Null models for both species carried 0% of the model weight.

The final top model for annual caribou detections, including the effects of maximum greenness, percentage of lowland habitat at 1 km, and restoration strata covariates, had a Ω^2 statistic of 0.83 and an overdispersion parameter of 0.82 (Pearson Chi squared 98.3, p=0.99). The final top model for annual deer detections, including the effects of maximum greenness and percentage of lowland habitat at 1 km, had an Ω^2 statistic of 0.77 with an overdispersion parameter of 2.91 (Pearson Chi squared 96.3 p=0.99). Null models for both species carried 0 of the model weight (Appendix 5 Table 5).

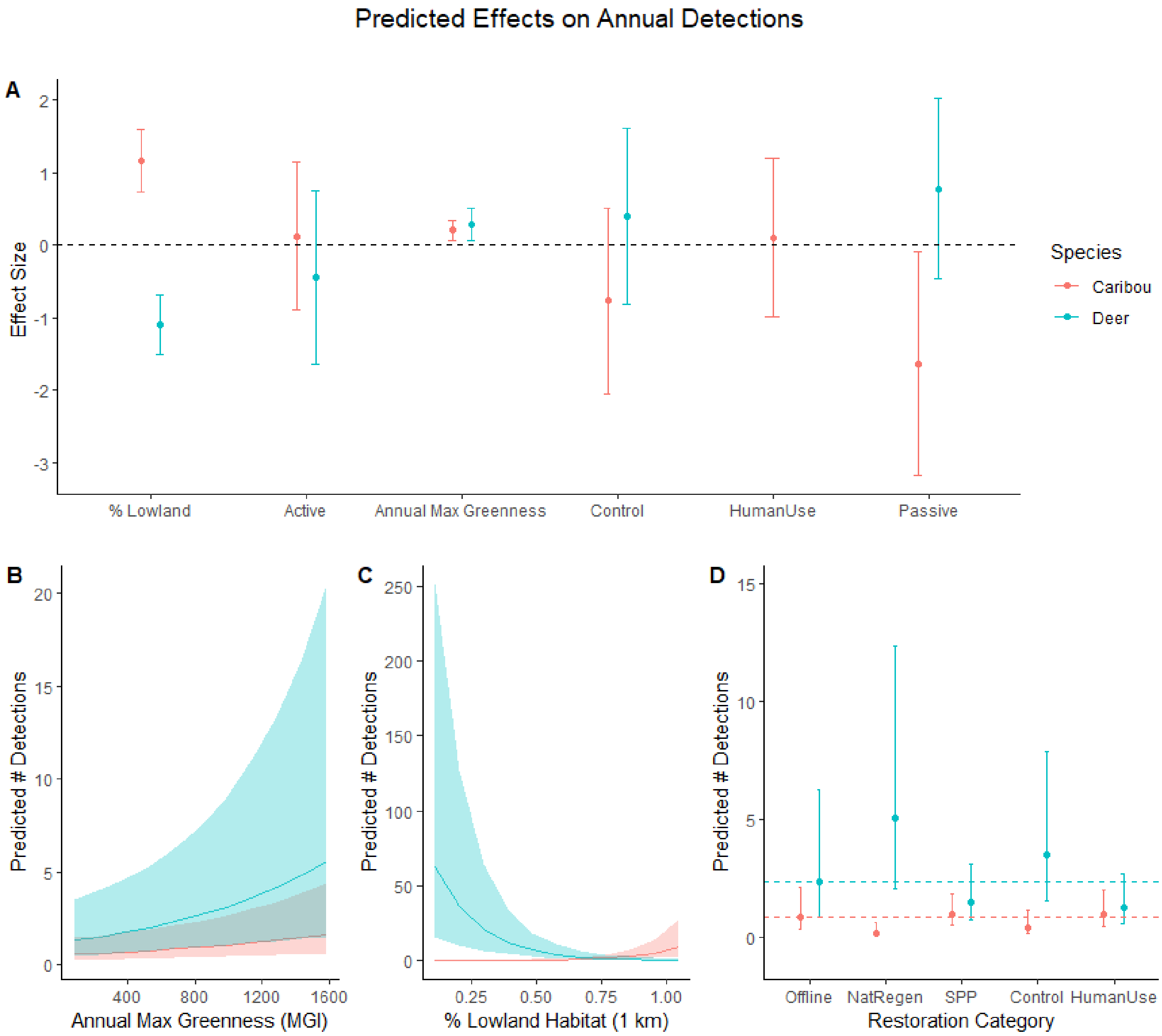

Figure 8.9 Predicted patterns of top covariates on annual number of caribou and deer detections in the Algar study area from 2016 - 2019. Restoration category was not a top covariate for deer, but is included here to illustrate differences compared to caribou. Estimated effect sizes with 95% confidence for covariate are shown in (A), and (B-D) show the predicted number of detections for each covariate with 95% confidence bands while other covariates were held constant at their mean value. Dashed lines in D at the values at off-line sites facilitate comparison across restoration categories. Results are from generalized linear mixed models, with year and camera trap as random effects and number of days of camera operation as an offset.

Relating phenology to weekly counts of ungulate detections

In models of weekly detections of caribou, the most supported model form was the negative binomial distribution with a quadratic variance parameterization (Appendix 5 Table 6). In contrast, for weekly detections of deer, a linear parameterization of the variance was most supported (Appendix 5 Table 6).

Weekly caribou detections responded more to phenology metrics than weekly deer detections, contrary to expectations. While detections of both species increased with weekly greenness, the effect was almost twice as great for caribou (0.61 +/- 0.06, $p < 2e-16$) than for deer (0.33 +/- 0.03, $p<2e-16$; Fig. 7.10). Weekly caribou detections increased significantly with greater annual maximum greenness in the top model (0.19 +/- 0.06, Fig. 7.10), whereas weekly deer detections did not. Weekly detections of both species increased slightly over time within each year (caribou: 0.01 +/- 0.005, $p = 0.02$; deer: 0.02 +/-0.003, $p < 0.001$; Fig. 8.10), but weekly greenness had a stronger effect. As with annual counts of detections, more lowland habitat at 1km had differing impacts on weekly detections: increasing detections for caribou (0.39 +/- 0.13, $p = 0.003$) while decreasing detections for deer (-0.40 +/- 0.13, $p=0.002$; Fig. 7.10).

The top model for weekly caribou detections included all covariates, weekly greenness, percent lowland habitat at 1 km, and time, with an Ω^2 statistic of 0.09 with an overdispersion parameter of 0.46 (Pearson Chi squared 3985.2, $p=0.99$). The top model for weekly deer detections did not include annual maximum greenness covariates, and had an Ω^2 statistic of 0.25 and overdispersion parameter of 0.65.

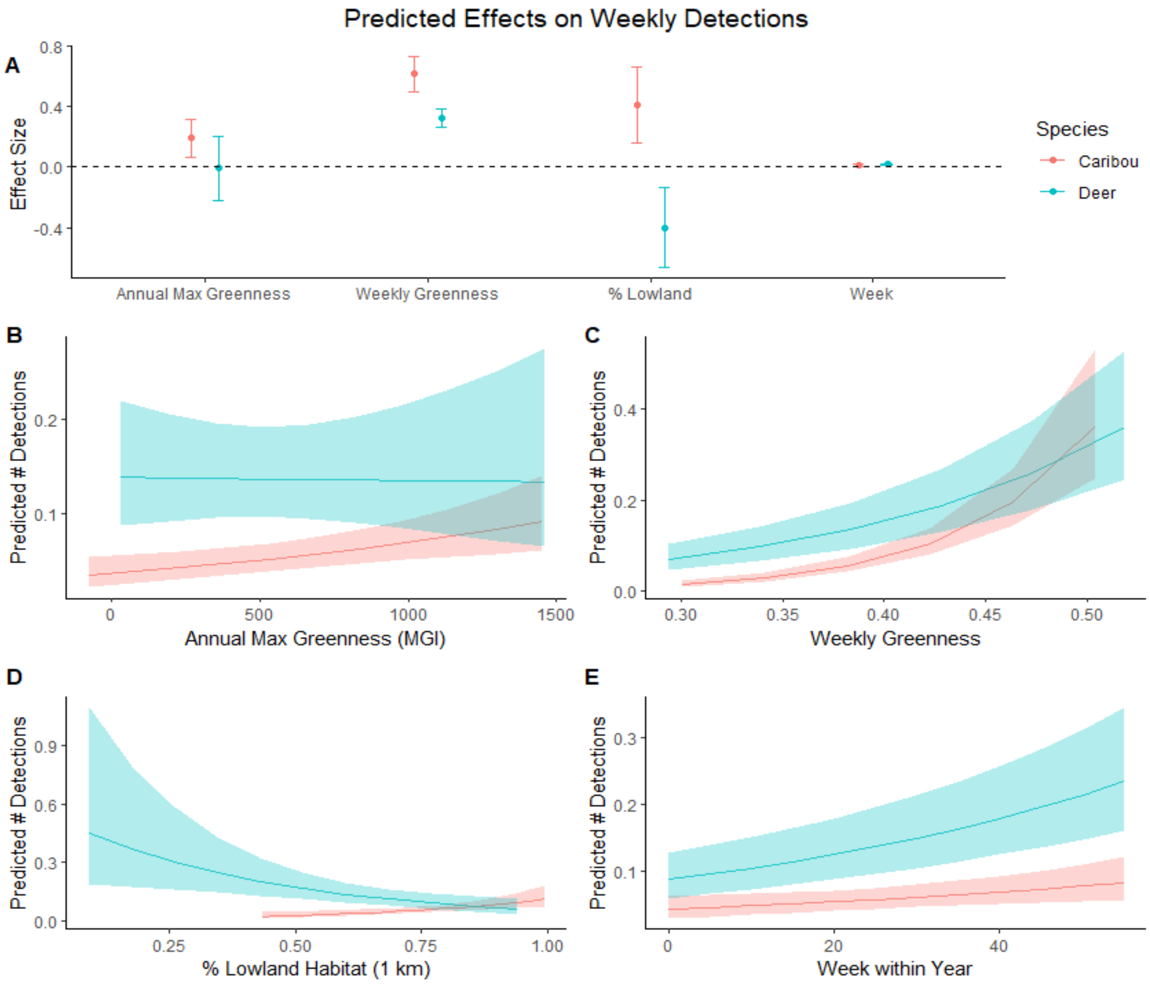

Figure 8.10 Predicted patterns of top covariates on weekly number of caribou and deer detections in the Algar study area from 2016 - 2019. Estimated effect sizes with 95% confidence for covariates are shown in (A), while (B-E) show the predicted number of detections for each covariate with 95% confidence bands. Annual maximum greenness was not a significant covariate for deer, but is included here to facilitate comparison with caribou patterns. Results are from generalized linear mixed models, with year and camera trap as random effects and number of days of camera operation as an offset.

8.3 Discussion

We demonstrated that camera trap timelapse images contain information about vegetation phenology to characterize seasonal, annual, and spatial variation in vegetation dynamics at sampled sites. Habitat restoration on seismic lines is ultimately focused on recovery of tree canopy (Pyper et al. 2014), but early vegetation growth on seismic lines is generally dominated by deciduous forbs, graminoids, and shrubs (Finnegan et al. 2018a). Our camera traps successfully detected the phenology of these understory plants. Furthermore, differences with satellite-based phenology metrics supported the hypothesis that phenology patterns from camera traps provide novel information about local vegetation. For example, greater seasonality and shorter growing seasons measured by camera traps are consistent with an understory composed of deciduous plants, while the canopy and overstory measured by satellite-based products contain more evergreen species. Importantly, the site-level information about vegetation and phenology from camera traps could be useful for monitoring changes in vegetation condition following habitat alteration and restoration.

8.3.1 Measuring restoration efforts through plant phenology

Vegetation phenology from camera traps showed differences across seismic line restoration categories that are consistent with ongoing but slow habitat restoration. Based on our phenology metrics, we suggest that natural plant growth and succession was returning plant phenology on seismic lines towards undisturbed conditions, as sites with passive restoration were equivalent to off-line sites for all but one phenology metric (variation in date of senescence). There was also some evidence for the progress of active habitat restoration. Sites with active restoration were similar to sites with passive restoration and off-line sites in dates of greenup, and to sites with passive restoration in the variation of dates of senescence. Interestingly, the significant variation in dates of senescence at sites with restoration could be attributed to plant succession through higher species turnover with annual species. However, unsurprisingly the phenology metrics indicated that impacts of habitat disturbance from seismic lines remained. Sites with active restoration were still more similar to unrestored control and human-use sites in length of season (shorter than off-line), date of senescence (earlier than off-line) and to a lesser degree, maximum greenness (more than off-line). Therefore, to date, phenological evidence of the effectiveness of active habitat restoration is limited in Algar, and continued plant growth is necessary to achieve complete habitat restoration. These findings are consistent with previous work identifying minimal short-term effects of linear habitat restoration on wildlife relative abundance in the Algar study area (Tattersall et al. 2020b).

8.3.2 Wildlife activity and distribution track greenness and primary productivity

Phenology patterns of understory vegetation estimated from camera traps influenced activity patterns of wildlife. Because greenness is a measure of primary productivity from vegetation (Radeloff et al. 2019), phenology metrics calculated from the greenness in camera trap images should reflect or correlate with understory forage availability. Across restoration categories, ungulate activity was greater at sites with higher annual maximum greenness, and also increased when greenness increased at a finer weekly resolution. Thus, ungulates were likely tracking summer food resources that included deciduous shrubs, soft mast, and other seral vegetation (Denryter et al. 2017, Dawe et al 2017). For deer, maximum annual greenness was a significant covariate for annual but not weekly detections, suggesting that its positive impact on annual detections was likely a result of the strong effect of weekly counts increasing with weekly greenness (Fig. 8.10). In contrast, caribou seemed to track both available forage as well as the expected forage, because weekly caribou detections increased with both weekly greenness as well as the time-invariant annual maximum greenness, which is a component of the dynamic habitat index that characterized site conditions. The mechanism underlying tracking of expected resource availability by caribou warrants further investigation, such as by using telemetry and phenology (Rickbeil et al. 2019). Also, there are likely additional factors contributing to patterns of weekly ungulate detections, including inter-species competition and predator-prey interactions, given the low explanatory power (i.e. low Ω^2 values) for the weekly models and mismatches between the period of caribou activity and timing of the growing season.

Mismatches between dates of last caribou detections and plant senescence are consistent with previous suggestions that attractive forage subsidies may turn seismic lines into ecological traps for caribou (Serrouya et al. 2020). Notably, detections of caribou continued significantly after senescence at unrestored and actively restored sites (Fig. 8.8). These sites also had shorter growing seasons with higher mean maximum greenness values (Fig. 8.4). These findings suggest that caribou may have been on seismic lines to forage on the larger amounts of vegetation and then remained after the growing season, potentially to continue foraging or for traveling purposes. Future evaluating this hypothesis could involve analyses of the behavior of caribou in camera trap images (e.g., foraging vs. traveling) before and after dates of senescence. Regardless of why caribou stayed on lines later than they otherwise would have, caribou might have then risked greater spatial and temporal overlap with wolves and bears that use seismic lines for hunting and travelling (McKenzie et al. 2012, Dickie et al. 2017b, 2020). This hypothesis could be assessed by analyzing the duration of caribou events from camera traps on seismic lines before and after senescence dates, with shorter events and more travelling behavior suggestive of greater perceived predation risk. Irrespective of mechanism, mismatch between caribou detections and vegetation phenology supports the importance of habitat restoration to return not only habitat conditions but also wildlife activity and interactions on and around seismic lines back to undisturbed conditions (Finnegan et al. 2018b).

The timing of sandhill crane detections in Algar closely matched that of the growing season, demonstrating strong seasonal dependence on boreal habitat related to their migratory behaviour (Krapu et al. 2011). While we found no significant differences in the timing or length of crane activity relative to the growing season across restoration categories, it is possible that crane activity and behavior at finer temporal resolutions were still affected by restoration (Toland 1999). Cranes detected in the Algar study area are part of the largest migratory sandhill crane population in the world (Mid-Continent Population; Case and Sanders 2009). They are also a gamebird species with low recruitment rates (Stephen et al. 1966, Sharp and Cornely 1997), so ensuring that habitat restoration truly preserves the function of their boreal breeding grounds is critical to conservation efforts that consider their entire annual migratory cycle (Runge et al. 2015).

Climate change is expected to impact northern boreal forests in numerous ways (Price et al. 2013), including changes in habitat phenology that will have prevailingly negative implications for caribou conservation. Increases in temperature (Gauthier et al. 2015), wildfire frequency (Barber et al. 2018, Stralberg et al. 2018) and insect outbreaks (Pureswaran et al. 2015) will likely reduce lichen-cover on which caribou forage (Gustine et al. 2014, Lewis et al. 2019, Nobert et al. 2020) and fragment forest habitat that caribou depend on for refugia from predators. While climate change may promote early successional habitat and related forage species (Pureswaran et al. 2015), increased variability in plant phenology (Montgomery et al. 2020) may hinder the ability of caribou to track forage availability. Increased unpredictability in the timing and composition of plant succession also casts into doubt the efficacy and trajectory of current habitat restoration efforts, given slow rates of restoration and climate changes that are already occurring (Gauthier et al. 2015). Successful caribou conservation will therefore require long-term consideration and monitoring of vegetation phenology and restoration effectiveness.

8.3.3 Future steps

Monitoring vegetation is a critical part of monitoring the effectiveness of habitat restoration, as sustainable population viability ultimately requires quality habitat and resources. This work demonstrates the ability of camera trapping to monitor vegetation as well as wildlife responses to landscape disturbance and restoration. We encourage continued monitoring of vegetation phenology with camera traps to evaluate the progress of habitat restoration, in conjunction with complementary vegetation monitoring. Long-term monitoring may reveal changes for which phenology metrics are informative; those that make up dynamic habitat indices may become more discriminating of habitat restoration as the understory transitions from shade-insensitive plants to shade-tolerant overstory tree species. Importantly, camera trapping provides multiple concurrent datasets about wildlife and the environment that can be used together to improve ecological inferences. To that end, we have identified several directions for further analysis. We recommend modeling patterns of wildlife distribution and habitat use with both camera trap and remote satellite-derived phenology metrics, such as annual maximum greenness, to evaluate the relative influence of understory and overstory vegetation. Analyses could also consider time lags between vegetation phenology and wildlife activity to identify the time scale and mechanism by which ungulates ‘surf the green wave’ to track expected and realized forage resources (Merkle et al. 2016). Finally, the red, blue, and brightness values in camera trap images that we did not use in our analysis could potentially be informative about wildfire and winter snowfall (Serbin et al. 2009, Frazier et al. 2018, Fisher et al. 2020), both of which are expected to influence wildlife activity.

Lastly, we offer recommendations in camera trapping methodology to support both wildlife and habitat restoration monitoring. Field protocols for setting up camera traps should generally suffice for phenology monitoring. Securing cameras with hardware such as C-brackets to minimize changes in the field of view will also reduce the need to later redraw the regions of interest in camera trap images. Minimizing periods of camera malfunction with regular camera maintenance and data retrieval will also be critical for obtaining temporally complete datasets on phenology. Finally, adhering to protocol recommendations for cameras to angle slightly downward with focus on a region 3-5 m away (e.g. https://wildcams.ca/protocols) will maintain a sufficient view of the understory vegetation with minimal hindrance from vegetation growth and debris.

9. Landscape-level comparison of community structure and animal behaviour

A key challenge in understanding the dynamics of large mammals and other wide-ranging species is that it is logistically challenging and prohibitively expensive to conduct controlled experiments at large spatial scales. However, using standardized camera trap surveys we can strategically exploit variation in management actions, anthropogenic impacts, and natural conditions thought to be important to structuring wildlife communities at the landscape scale. For example, we can use known regional gradients in anthropogenic disturbances, such as seismic line density, as a form of landscape experiment to tease apart the processes governing wildlife population and community dynamics. The use of camera traps facilitates synchronized sampling across all sites, which is often impossible when using human observer methods such as aerial transects. In this way, strategically distributed arrays of camera traps can function as “coordinated distributed experiments” (cf. Fraser et al. 2013; Steenweg et al. 2017) within an adaptive management framework.

One way to determine the implications of landscape scale variation in factors which influence wildlife communities is to explore changes in community structure. Given that previous work has identified there are species-specific responses to anthropogenic disturbance (generalist browsers and predators respond positively, whereas specialists respond negatively: Fisher and Burton 2018), the structure of communities captured by camera traps should also very in predictable ways to landscape scale gradients in disturbance. For example, white-tailed deer are thought to respond positively to anthropogenic disturbance given their preference for early seral vegetation, whereas caribou have undergone marked declines in disturbed landscapes.

A second way to explore how landscape scale variation in anthropogenic disturbance can affect wildlife, is to use camera traps to quantify wildlife behavioural parameters. Conservation and management are typically focused on population-level responses, i.e. ascertaining whether populations are increasing, decreasing, or being maintained at desired levels. However, these population responses are influenced by responses at finer scales, such as changes in animal behaviour, and thus monitoring behaviours may allow faster detection of impacts (Caravaggi et al. 2017). In this monitoring program, our primary focus has been on evaluating behavioural responses in terms of changes in habitat use at restored vs. unrestored lines (section 5), and we have used camera traps to estimate population density for population-level monitoring (section 7). As an extension of our assessment, in this section we used the camera trap data to further characterize variation in animal behaviours where they were detected, and to test the evidence for landscape scale variation within them. More specifically, we focused on prey species and hypothesized that they would change their behaviours as a function of factors such as predation risk and group composition (e.g. Dickie et al. 2020). We tested whether camera trap-derived measures of behaviour were consistent with our prediction that prey species would show more risk-averse behaviour in areas of higher inferred predation risk, and more “secure” behaviours in areas of lower predation. We note this is a preliminary analysis with the intent of exploring the utility of this approach.

In an effort to move research towards landscape comparisons, and capitalize more broadly on the extensive sampling conducted as part of the Algar Wildlife Monitoring Project, we conducted an initial comparison of wildlife community structure and behaviour between Algar and a concurrent camera trap sampling project within the Richardson caribou range (Fig. 9.1). Specifically, we compared species-specific detection rates, co-occurrence patterns and behavioural patterns between the two landscapes (see also a density comparison in section 7).

Richardson survey area

Our project team is collaborating on another camera trap survey within the Richardson caribou range, approximately 200 km northeast of the Algar study area (Fig. 9.1). Camera traps were deployed at 30 sites in 2018 and at an additional 28 sites in 2019 (58 total camera stations deployed but 2 damaged/malfunction, so sample size of 56 cameras; J. Burgar & A.C. Burton, unpublished report). The habitat in Richardson is fire-dominated, consisting of stands of burned and unburned patches of upland jack pine (*Pinus banksiana*) and black spruce (*Picea mariana*) bog. Richardson was subjected to a huge burn event in 2011, the second largest documented fire in the history of western Canada (Pinno et al. 2013). From May to August 2011, the Richardson fire burned ~576 000 ha of forest with mixed-severity, leaving some residual unburned patches while other patches burned so severely that all overstory trees died. Although fire is prevalent, seismic line density is lower in Richardson (~0.5 km/km^2) than in Algar (~2.0 per km^2, section 2.1). Density estimates for the Richardson caribou herd are unknown (but see section 7) and it is considered to be in decline; between 1994 and 2012 the herd experienced a cumulative change of -5% and an average population growth rate of 0.903 (Hervieux et al. 2013).

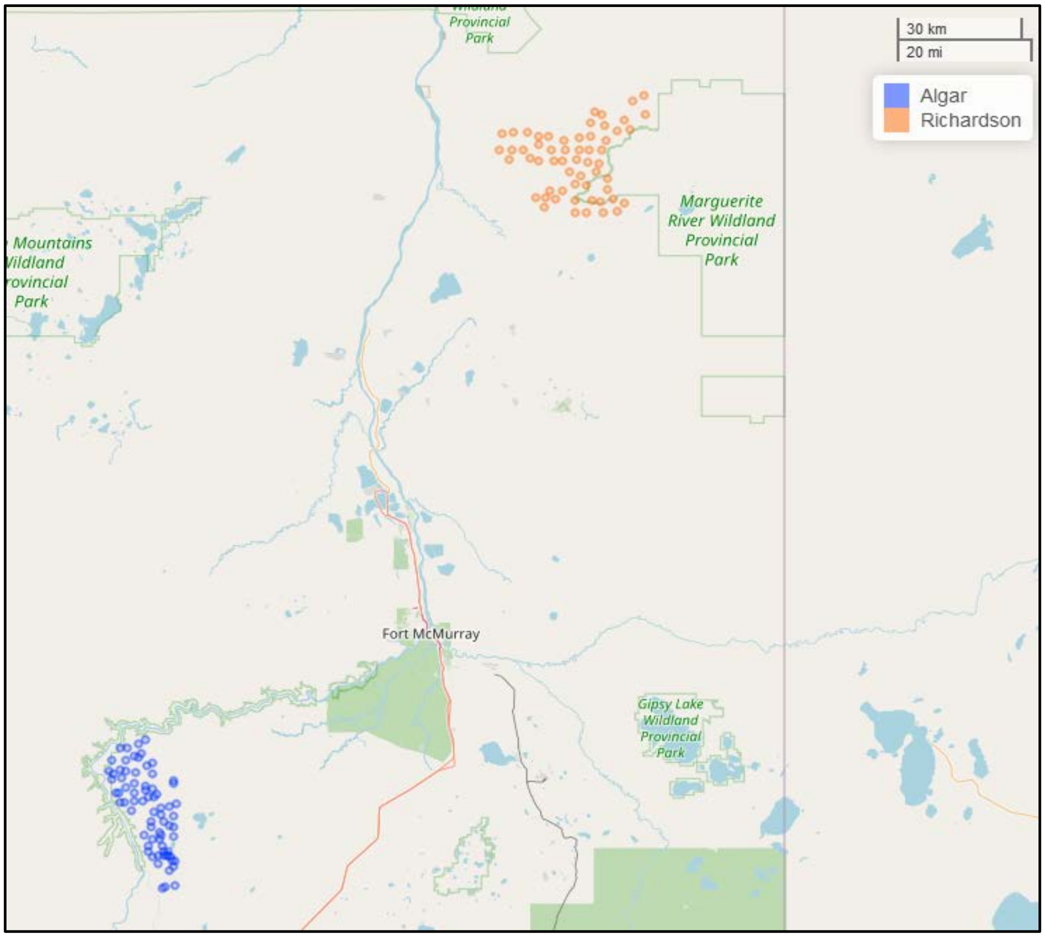

Figure 9.1 Map of the camera trap survey locations in the Algar (blue points; n = 73) and Richardson (orange points; n = 56) study areas.

Community structure

There were 12.5 independent wildlife detections for every 100 camera-trap days in Algar, compared to 9.6 detections per 100 days in Richardson (~23% less), with the change in detection rates varying by species (Fig. 9.2). Detection rates of white-tailed deer, wolf, and sandhill crane were lower in Richardson compared to Algar (Fig. 9.3), and coyotes were not detected in Richardson. In contrast, detection rates of caribou, and to a lesser extent red fox, were higher in Richardson. The changes in community structure are consistent with our understanding of anthropogenic disturbance between the two sites: seismic line density is lower and the proportion of lowland habitat is higher in Richardson than in Algar. These factors together, along with the more northerly location of Richardson, have likely limited the invasion of white-tailed deer into caribou habitat and thus limited the potential for deer to drive a numerical response in wolves. And the lower seismic line density likes limits the travel opportunities for wolves into caribou habitat.

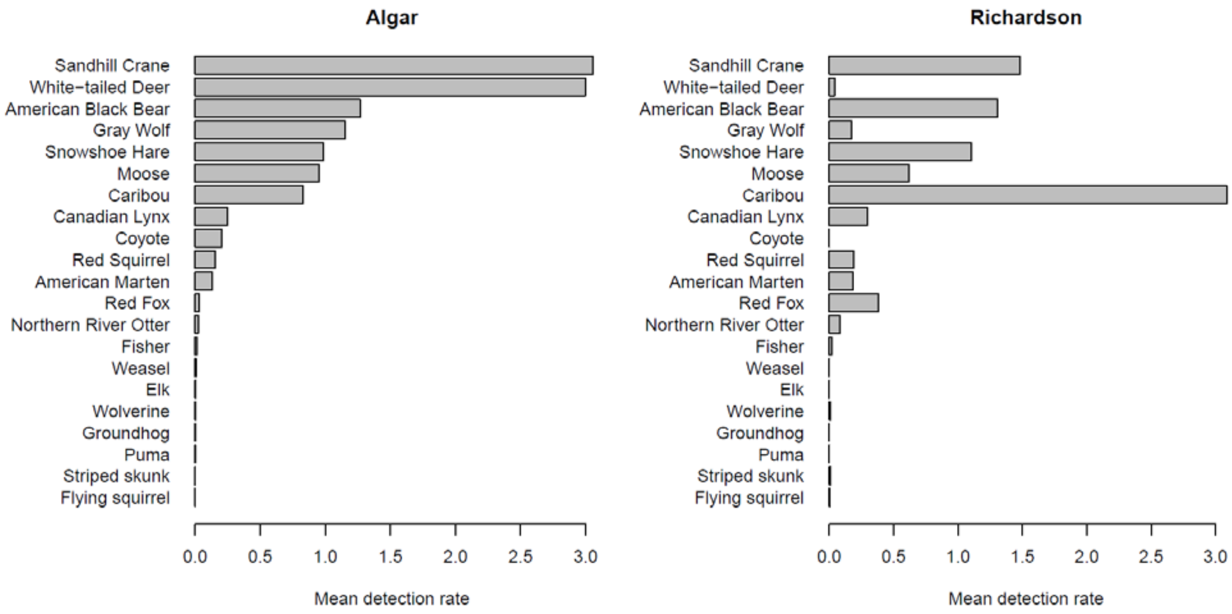

Figure 9.2 Species-specific detection rates from camera trap surveys conducted in Algar (left) and Richardson (right). Species are ordered the same way for both study areas to facilitate comparison.

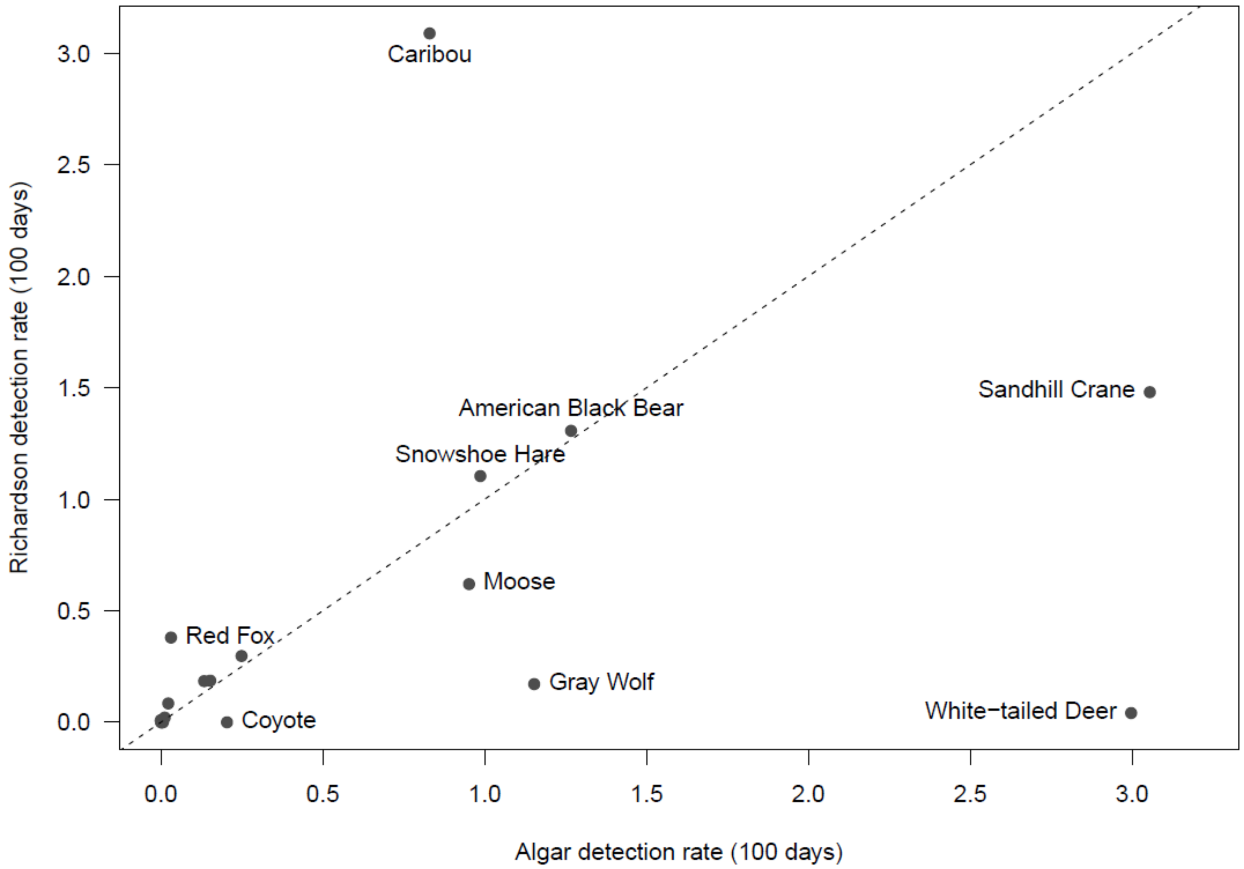

Figure 9.3 Comparison of species specific detection rates between Algar and Richardson. Species which occur below the dotted line are detected more frequently per unit effort in the Algar, whereas species above the line are detected more frequently per unit effort in Richardson.

Co-occurrence patterns

Co-occurrence plots quantify the raw station-level correlations between different species in the community. Positive correlations occur between pairs of species that are often detected at the same sites; negative correlations occur where species pairs are infrequently detected at the same sites. Despite large differences in species-specific detection rates between the two landscapes, the camera-level co-occurrence patterns have a very similar structure (Fig. 9.4). Marten, caribou and sandhill crane generally co-occurred with one another, whereas they rarely co-occurred with the other species. Lynx, snowshoe hare, wolf, black bear and red squirrel often co-occurred with one another across both landscapes. The consistency in co-occurrence patterns between the two landscapes suggests that despite the different levels of disturbance the sites are subjected to, similar processes are influencing co-occurrence patterns within them. This is perhaps not surprising given the similarity in habitat and the fact that they are separated by less than 200 km.

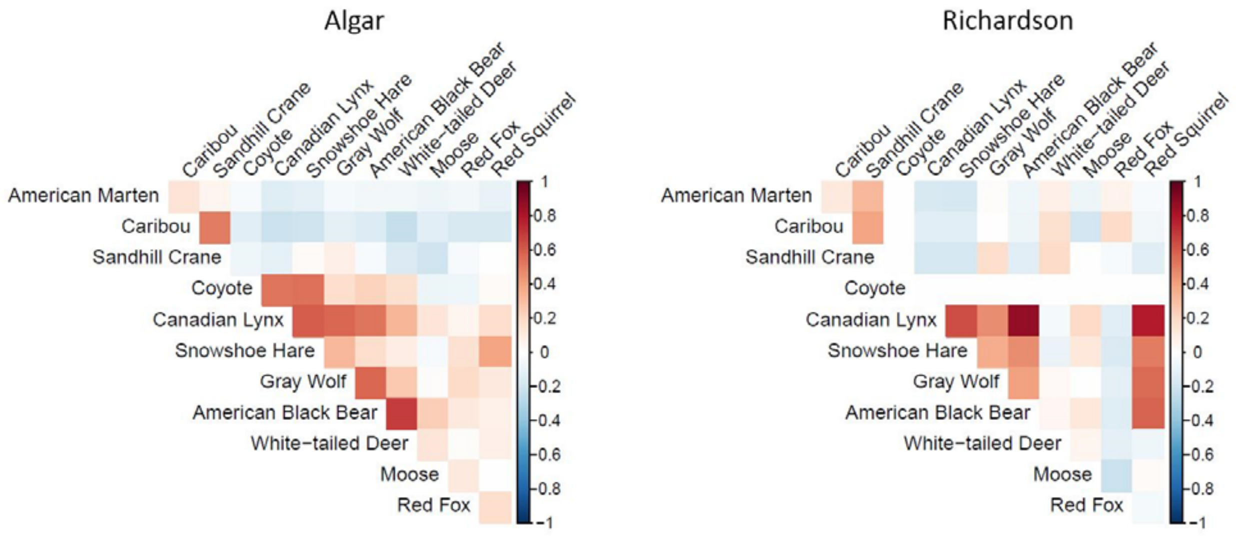

Figure 9.4 Camera trap level co-occurrence patterns in the Algar (left) and Richardson (right) landscapes. Red colours denote species often found together, blue colours denote species often found apart; white = neutral/random co-occurrence.

Behavioural differences

Given the community-level differences in predator detection rates in Richardson relative to Algar described above (i.e. fewer wolves and coyotes), we hypothesized that prey species (focusing on caribou and moose) should modify their movement and foraging behaviour to reflect the decrease in predation risk. Recent studies have highlighted the potential for assessing behaviour from camera-traps (Caravaggi et al. 2017), as they remain in-situ for long periods of time and can simultaneously collect data on multiple species (Wearn & Glover-Kapfer 2017). Species behaviours at camera traps can be inferred as measures of perceived risk (Stewart et al. 2016). We therefore explored whether camera trap-derived measures of behaviour were consistent with predictions of risk-averse behaviour in an area of higher inferred predation risk (Algar), and of more “secure” behaviours in an area of lower predation risk (Richardson). Specifically, we evaluated whether:

i. Average group sizes of prey species were larger in the lower predation risk landscape than the higher risk landscape; and

ii. Secure behaviours (i.e., foraging, inspecting the camera) were more prevalent than travelling behaviour in the lower risk landscape relative to the higher risk landscapes.

We defined events as a sequence of consecutive images of a species at a given site, with a maximum threshold of elapsed time between detections of 15 minutes (i.e. if more than 15 minutes passed without a new image of that species, the next image was considered the first of a new event). All unique moose and caribou detection events were given a minimum group size using the methods described in section 7. We also calculated the duration of each behavioural event, defined as the time in seconds between the first detection and last detections in a given event. We assumed that risk-averse behaviours would result in short event durations (i.e. animals moving quickly past the camera), while more secure behaviours would result in longer events (e.g. foraging, resting).

Contrary to our prediction, we found little variation in group size for moose between the Algar and Richardson landscapes, with each site showing an average of ~1.2 unique individuals per detection (Fig. 9.5). In contrast, caribou group sizes were on average 42% larger in Richardson (2.0 individuals per group) than in Algar (1.4 individuals per group).

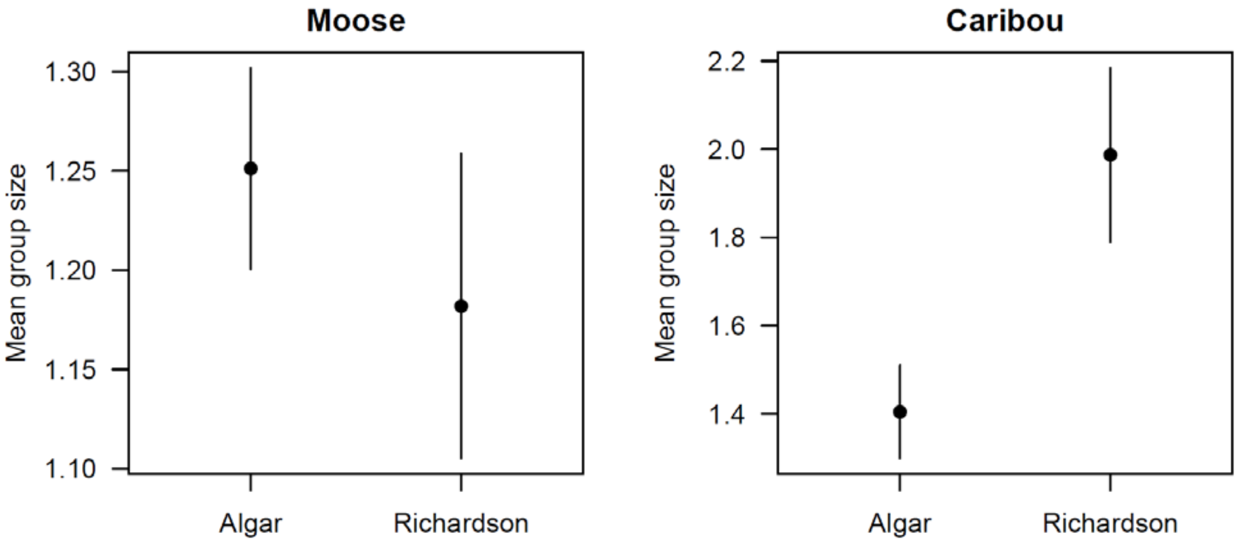

Figure 9.5 The average group size per camera trap detection event for moose (left) and caribou (right) between the Algar and Richardson survey areas. Points denote the mean ‘minimum group size’ (the number of unique individuals passing in front of the camera during a given event) and lines are 2 x the standard error of the mean.

We used event duration as a proxy for secure behaviour, as travelling results in shorter event durations than both foraging and inspecting the camera. The mean event duration of moose was similar between the two landscapes (Fig. 9.6; Algar = 75 seconds; Richardson = 105 seconds), whereas for caribou event durations we significantly longer in the Richardson landscape compared to Algar (Fig. 9.6; Algar = 70 seconds; Richardson 190 seconds). This is consistent with our prediction that these prey species would exhibit more secure behaviour (longer detection event durations) in the Richardson landscape, given an assumed lower perception of risk due to the relative lack of wolves. However, it could also reflect a higher quality of forage at the camera stations in Richardson relative to Algar, or other factors we have not considered here.

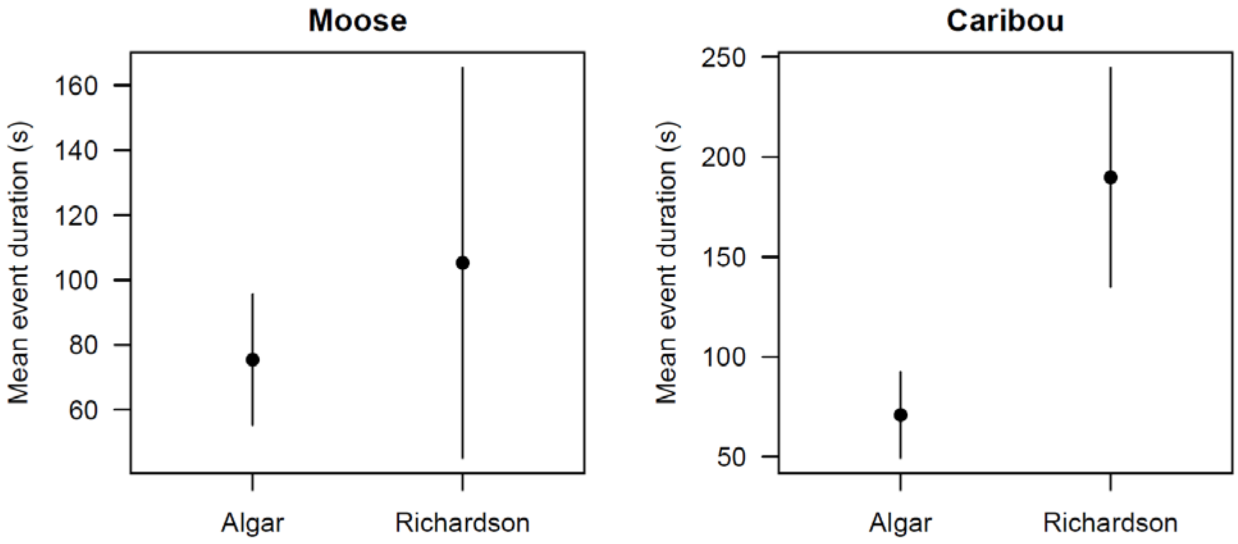

Figure 9.6 The average duration of camera trap detection events for moose (left) and caribou (right) between the Algar and Richardson survey areas. Points denote the mean event duration and lines show 2 x the standard error of the mean. Our assumption is that longer event durations reflect more secure behaviours at camera stations (e.g. foraging), while short durations reflect more risk-averse behaviours (e.g. travelling).

Conclusions

In this preliminary analysis, we have demonstrated that camera trap detections can be used to distinguish variation in behaviours among photographed animals. This general approach opens the door for using camera trap surveys to test hypotheses of behavioural responses to anthropogenic impacts and other environmental changes (e.g. Caravaggi et al. 2017). For instance, Dickie et al. (2020) outlined several hypotheses for different wildlife responses to linear features, and tested the hypotheses using telemetry data. We suggest that camera trap surveys can provide a complementary approach for further evaluating such hypotheses. However, we note that additional work is needed to refine the initial methods presented here, including consideration of the effects of camera traps themselves on animal behaviour (Caravaggi et al. 2020).

The comparisons between camera trap survey results in the Richardson and Algar landscapes presented here only scratch the surface of the potential use of camera trap data to test hypotheses about landscape-level differences in relative abundance, community composition and behaviour. Despite the two survey landscapes being relatively close in space (within 200 km), we found evidence for marked differences in species-specific detection frequencies and behavioural traits (group size and event duration). These differences are consistent with our hypotheses that more disturbed landscapes (i.e. Algar relative to Richardson) have higher proportions of wolves and deer relative to caribou, and that ungulate prey show more risk-averse behaviours in disturbed landscapes with more wolves. We believe that such comparisons of standardized camera trap survey data provide an important tool for adaptive management, with strong potential to robustly assess the effects of habitat restoration at the landscape scale (particularly where pre- and post-assessments are not feasible).

We recommend further research to build on our preliminary assessments here to more rigorously evaluate the mechanisms underlying observed differences, including seismic line density (or restoration), fire history, and potential interactions between them. Expansion of camera trap surveying to other landscapes which vary in restoration age, restoration methods and background disturbance level will further broaden the generalizability of the conclusions derived. Conducting such landscape-scale comparisons will add important value to studies within individual study sites, such as the Algar Wildlife Monitoring Project.

10. Conclusions & Recommendations

We conducted a unique, large-scale and long-term camera trap monitoring program to evaluate the effectiveness of seismic line restoration within the range of the declining Algar caribou subpopulation. Seismic line restoration is a critical component of recovery efforts for threatened boreal caribou — within Alberta and elsewhere — and robust monitoring programs are required to ensure restoration is having the intended benefit for caribou, and to direct improvements in future efforts. The Algar Caribou Habitat Restoration Program was a pioneering effort that actively and passively treated 386 km of seismic lines, with a goal of reaching the federal government's target of 65% undisturbed critical caribou habitat. We investigated whether the program resulted in desired outcomes over the short timeframe of the first 4-8 years after restoration. While forest regeneration is a slow process in northern boreal environments like the Algar region, short-term benefits are required if rapidly declining caribou populations are to be stabilized and recovered.

We achieved a sampling effort of 74,076 camera-days across 73 camera stations deployed between November 2015 and November 2019. This effort resulted in 7,354 detections of 25 species, including a large sample of detections of focal species in the caribou "food web" (wolf, black bear, white-tailed deer, moose). This demonstrates that camera traps are a reliable method of collecting multi-species data in boreal habitats. We used these data to test the priority hypotheses that restoration would result in reduced line use by caribou predators (section 5.1), and community structure reflecting undisturbed conditions (section 5.2). We developed and implemented analyses at different spatio-temporal scales and levels of ecological organization, from site-level measures of habitat use and behaviour to landscape-level estimates of population density (section 7) and community structure (section 5.2 & 9).

A key result from our monitoring was that caribou predators, along with a wide range of other species, continued to use seismic lines in the 4-8 years following active restoration (site preparation and planting) and passive restoration (protection of natural regeneration; section 5.1). Wolves and black bears did not show reduced use of restored lines relative to unrestored control lines, and they showed greater use of restored lines relative to undisturbed off-line areas. White-tailed deer, the key apparent competitor in this system, used all lines (regardless of treatment strata) more frequently than off-line sites; however, they used restored lines less than unrestored controls, suggesting a potential positive indirect effect of restoration for caribou.

More broadly, variation in seismic line characteristics across the sampled lines (e.g. line of sight, mound height, vegetation height) was a poor predictor of wildlife use at the community-level, relative to other ecological factors such as seasonality and habitat type (e.g. wetland vs. upland) (section 5.2). Responses to line characteristics were variable between species, even within groups of co-occurring species (e.g. species preferring upland vs. lowland habitats). Some species showed positive associations to line characteristics indicative of forest recovery, like reduced line of sight, while other species showed negative associations with the same characteristics. Encouragingly for caribou, wolves and coyotes were among the species negatively associated with characteristics of regenerating lines. Over time, the weak responses to seismic line characteristics that we observed could amplify and lead to greater segregation between species groups as the vegetation further recovers. Most importantly, this could result in more segregation between caribou and wolves, and thus reduced predation risk for caribou. Repeating the camera trap monitoring in the future (e.g. in 5-10 years) would allow us to confirm if this is the case.

Camera traps provide a useful tool for testing hypotheses about species interactions (section 6), and changes in these interactions ultimately motivate linear restoration (i.e., does restoration alter predator-prey relationships, and what are the implications of such changes?). While direct testing of mechanisms of interactions is difficult without experimental manipulations, we showed how co-occurrence patterns can be used to test for consistency with hypothesized interactions. In our example, we did not find evidence to support hypothesized avoidance among intraguild competitors, but rather documented co-occurrence between wolves and other subordinate predators (coyote, lynx and bear) along the seismic line network in the Algar landscape. As efforts to restore lines and manage wolves continue, these interactions among predators may be altered, with potential consequences for caribou and other prey species. We recommend further research to refine the use of camera traps (and complementary methods) for understanding changes in species interactions following caribou recovery actions.

Ultimately, for restoration to be successful, changes in habitat use need to lead to changes in population densities within restored landscapes, i.e., decreased densities of predators and increased densities of caribou. At the population scale, we found evidence suggestive of declining trends in detections of wolves and coyotes across the study area during the four years of surveys, with corresponding increases in trends for several prey species (e.g. caribou, moose, and white-tailed deer; section 5.2). While these trends are consistent with the expected trajectory for successful linear restoration (i.e. less predator use and more caribou use in the restored landscape), we suggest that the wolf trend is more likely due to the concurrent wolf population management undertaken by the Government of Alberta. In order to obtain more robust estimates of population densities for continued trend monitoring, we advanced development and testing of spatial count (SC) and spatial partial identity (SPIM) models (section 7). Based on our results, we developed a decision framework to guide selection among these and other emerging approaches for estimating density of unmarked populations. Further work is needed to continue evaluation of these models, including their sensitivity to differences in sampling designs (e.g. trap spacing) and animal behaviour (e.g. social grouping). Nevertheless, we were able to produce the first density estimates for caribou and black bear in the Algar sub-range. Our estimates were imprecise but suggested that the temporal changes in habitat-use detailed in section 5.2 were, at least in part, underpinned by a local increase in caribou density from 2016 to 2019 (section 7). This result should be considered cautiously, in light of the model uncertainty, but is consistent with the hypothesis that linear restoration and wolf population management are leading to more caribou within this landscape.

The fact that environmental variables, such as seasonality and habitat, had stronger effects on wildlife distribution and activity than line characteristics (section 5.2) is a reminder of the importance of environmental context. While the Algar restoration treatments were based on site-specific silvicultural prescriptions, the effectiveness of treatments may vary depending on local ecological and environmental characteristics. To address this, we demonstrated that camera traps are not only a useful tool for monitoring wildlife dynamics, but also for monitoring the vegetation phenology and productivity underpinning them (section 8). Using daily camera trap timelapse images we successfully extracted data which characterized seasonal, annual, and spatial variation in vegetation dynamics at sampled sites. Our analysis showed evidence consistent with expected progress of habitat recovery after restoration. The natural plant growth and succession on passively restored (regenerating) lines showed phenological patterns more similar to off-line controls than unrestored seismic lines. Vegetation patterns on actively restored lines were more variable, and, for some measures (e.g. productivity, length of growing season, date of senescence) were more similar to unrestored control and human use lines than to off-line or naturally regenerating lines.

We also showed that plant phenology and productivity can predict patterns of wildlife occurrences at different temporal scales (section 8), from the strong association between migratory sandhill cranes and the vegetation growing season, to weaker associations of caribou with plant greenness (as an indicator of site productivity) at annual and weekly scales. Furthermore, in an earlier analysis we showed the value of snow cover measured by camera traps as an additional predictor of wildlife use of seismic lines (Tattersall et al. 2020b). Given that the success of linear habitat restoration is ultimately dependent on vegetation recovery, and that patterns of animal habitat use are linked to phenological patterns in vegetation structure, forage availability, and snow cover—which in turn are affected by anthropogenic and natural disturbances, including climate change—we recommend that simultaneous monitoring of animals and plants with camera traps be an important part of monitoring restoration effectiveness.

Finally, we highlight the potential of coordinated networks of camera traps for monitoring wildlife population responses to gradients of natural and anthropogenic changes (such as wildfire, human disturbance, and habitat restoration) at the landscape scale (sections 7 and 9). Our estimates of caribou and bear densities in the Algar and nearby Richardson study areas provided the first density comparisons between these landscapes (caribou density in the Algar study area was approximately half of that estimated for the Richardson study area, while bear densities were similar) and hinted at potential mechanisms that could underlie such differences (e.g. more anthropogenic disturbance in Algar). We also explored a novel approach to quantifying variation in ungulate behaviour between landscapes, with behavioural changes potentially representing a more sensitive indicator of impacts. Consistent with our expectations, caribou in the Richardson landscape with lower wolf density showed more secure behavioral patterns. These preliminary comparisons of density and behaviour in two landscapes demonstrate the potential for using such coordinated camera trap arrays to drive the evidence base needed for adaptive management across boreal caribou ranges.

Overall, our study showed that the effects of seismic line restoration on caribou and their interacting species in the Algar restoration area were small in the 4-8 years following restoration. This in itself may not be that surprising, given the slow rates of recovery in these low productivity boreal ecosystems, and the focus of the Algar restoration program on tree planting rather than line blocking. Nevertheless, it is important to acknowledge that caribou do not have the luxury of time, given the rapid rates of decline documented in the East Side Athabasca River population (of which the Algar is a part) and other populations. This suggests that other restoration techniques and recovery actions must be attempted to stabilize and recover caribou.

Ultimately, we hope that the methods used in this project provide guidance for other caribou restoration and recovery projects in Alberta and elsewhere. We have demonstrated that an experimental sampling design consisting of a large array of camera traps deployed for multiple years can provide a wealth of information to assess restoration effectiveness and the dynamics of interacting species in a restored landscape. We suggest that further research is warranted to build on this study and continue to improve camera trap methodologies, including estimating density of unmarked populations, modelling species interactions, and linking animal habitat use to vegetation structure and phenology (from both the understory and overstory). Perhaps the greatest value for understanding the effectiveness of seismic line restoration will come from comparing results of this study with those from other landscapes and restoration methods. Such comparisons will help build a stronger evidence base with which to identify the management actions that can most effectively stabilize and recover threatened caribou populations, and ultimately better balance economic and environmental objectives in working landscapes.

In closing, we provide the following set of recommendations, based on our experiences and results in this study:

1. To gain stronger inferences on the effects of restoration treatments, we recommend prioritizing a **Before-After-Control-Impact (BACI) experimental design**. If the monitoring plan is incorporated into the overall restoration planning at early stages, the benefit gained from the monitoring effort can more effectively be maximized.

2. To maximize the utility of individual projects, we recommend **standardizing and comparing camera trap surveys across landscapes**, using landscapes as replicate sampling units (containing nested camera-level replicates) within an adaptive management and monitoring framework. Steps should be taken to identify and prioritize other restoration projects that can provide informative landscape-scale comparisons.

3. We recommend **visiting camera stations at shorter time intervals** if possible (i.e. more frequent than the 6-12 months used in this project), to avoid potential periods of data loss due to camera malfunction, although we recognize that in remote landscapes like Algar, the costs of frequent access can be prohibitively high.

4. Given that vegetation growth rates are slow in boreal forests, a **plan for long-term wildlife monitoring** is paramount for determining the success of habitat restoration. Assessing short-term responses is important, particularly for adjusting the course of ineffective treatments, but there is also a need to understand the long-term effects as species dynamics slowly change. We recommend **repeating the standardized camera**

trap survey in the Algar landscape within 5-10 years to assess whether the effects of restoration on wildlife are increasing through time. This is particularly important to further evaluate the early indications from our project that the Algar caribou population is stable (and perhaps increasing), potentially influenced by both wolf population management and linear restoration. Long-term monitoring can test hypotheses generated from our initial surveys, such as that continued vegetation recovery should further reduce overlap between caribou, their competitors, and their predators. The design of a long-term monitoring plan can be aided by making explicit predictions about when vegetation recovery is expected to be sufficient to achieve the desired effects on wildlife (e.g. when spruce saplings will be tall and dense enough to effectively block predator movement and line of sight). The design can also capitalize on data from this project to assess sampling requirements (e.g. precision analysis to optimize camera trap sample size and temporal sampling frequency).

5. While it is critical to monitor wildlife responses to habitat restoration, **wildlife monitoring should be more directly linked to complementary vegetation monitoring**. If there is no vegetation recovery, we should not expect wildlife recovery. Vegetation monitoring should follow rigorous sampling design and protocols and can include direct field measurements to establish plant growth rates, species composition, and structure (including mounds and debris). These measurements can be complemented by remote sensing of vegetation phenology, productivity, and structure in the understory (using ground-based sensors such as camera traps) and overstory (using aerial and/or satellite imagery). Integrated monitoring and analysis of wildlife and vegetation facilitates important connections and more direct inferences about how plant growth and habitat structure influences wildlife responses.

6. The use of **multiple wildlife survey methodologies** could improve the robustness of the conclusions drawn here. For example, deploying high resolution satellite collars on caribou and their predators within the Algar landscape would help parameterize camera trap density models and shed light on fine-scale, individual-level behavioural interactions with restored lines. Complementary data from camera traps and collars could also be combined in integrated population models.

7. Linear restoration programs for caribou recovery should **consider more aggressive line blocking strategies** (e.g. more mounding and coarse woody debris) to aim to achieve stronger short-term effects on caribou predators and competitors than those observed in this study.

8. Linear restoration programs should also **consider restoring all seismic lines within a targeted landscape** (notwithstanding experimental controls required to assess restoration outcomes). Our observation that wolves preferred lines left open for human access (e.g. trappers, oil field workers) suggests that leaving such lines unrestored may undermine restoration effectiveness in the broader landscape.

9. To the extent possible, we recommend **greater coordination between the different stakeholders working on caribou recovery actions** (e.g. linear restoration projects, wolf population management). There is a strong need to learn quickly about which actions are effective and under what conditions, in order to direct future actions and maximize return on conservation investments, as well as to scale up effective actions. As both wolf control and habitat restoration occurred in and around the Algar study area during our survey period, it proved difficult to tease apart the effects of each. Strong communication among groups is important, and ideally different recovery actions could be coordinated within an experimental adaptive management framework to maximize the strength of inferences gained from monitoring, and ultimately increase the effectiveness of caribou conservation.

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