# Appendices for Algar Wildlife Monitoring Final Report

The following supplementary materials accompany the project report:

Burton, C., C. Beirne, C. Sun, E. Tattersall, J. Burgar and J. Fisher. 2020. Efficient monitoring of wildlife responses to seismic line restoration in the Algar Habitat Restoration Program. Final Project Report (revised October 2020). University of British Columbia and InnoTech Alberta.

# Appendix 1: Camera Trap Detection Summaries

## Supplementary Table 1

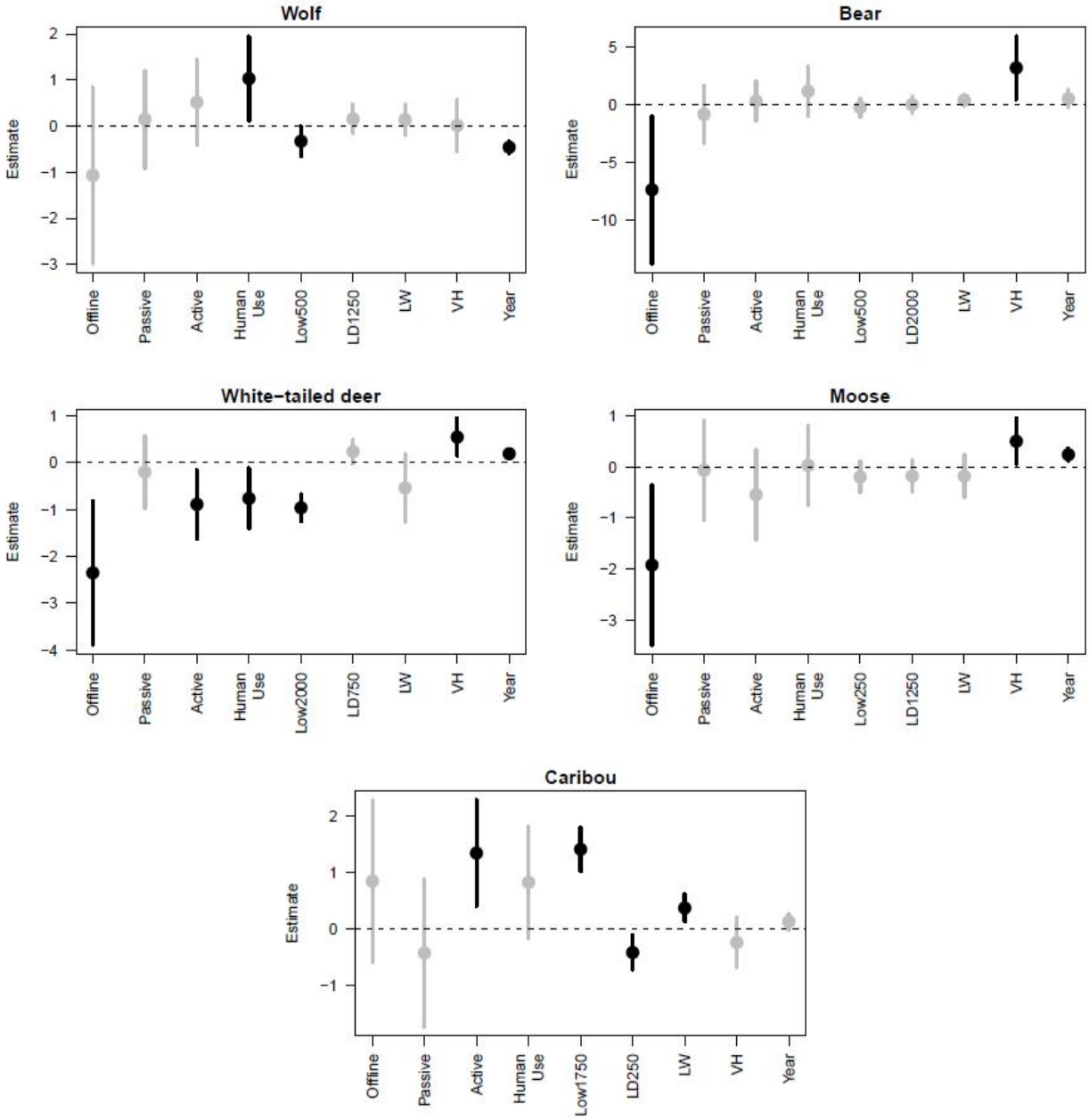
Summary detection table for the species detected during camera trap surveys in the Algar study area from November 2015 to November 2019. Where: 'number of detections' represents the number of independent detections (after removing events which occur within 30 minutes of the previous event); 'detection rate' is the number of independent events per 100 camera-trap days; and 'Proportion of sites' is the number of sites where the species was detected ('Sites detected') divided by the total number of sites (n = 73 camera trap stations).

| Species | Common name | Number of detections | Detection rate (per 100 days) | Sites detected | Proportion of sites |
|---|---|---|---|---|---|
| *Odocoileus virginianus* | White-tailed deer | 1844 | 2.489 | 59 | 0.81 |
| *Grus canadensis* | Sandhill crane | 1476 | 1.993 | 56 | 0.77 |
| *Ursus americanus* | Black bear | 855 | 1.154 | 66 | 0.90 |
| *Lepus americanus* | Snowshoe hare | 793 | 1.071 | 44 | 0.60 |
| *Alces alces* | Moose | 553 | 0.747 | 63 | 0.86 |
| *Canis lupus* | Wolf | 509 | 0.687 | 55 | 0.75 |
| *Rangifer tarandus* | Caribou | 470 | 0.634 | 42 | 0.58 |
| *Lynx canadensis* | Lynx | 185 | 0.250 | 48 | 0.66 |
| *Homo sapiens* | Human | 167 | 0.225 | 20 | 0.27 |
| *Canis latrans* | Coyote | 162 | 0.219 | 25 | 0.34 |
| *Tamiasciurus hudsonicus* | Red squirrel | 124 | 0.167 | 16 | 0.22 |
| *Martes americana* | Marten | 89 | 0.120 | 33 | 0.45 |
| *Canachites canadensis* | Spruce grouse | 29 | 0.039 | 18 | 0.25 |
| *Vulpes vulpes* | Red fox | 24 | 0.032 | 15 | 0.21 |
| *Corvus corax* | Common raven | 15 | 0.002 | 11 | 0.15 |
| *Marmota monax* | Groundhog | 13 | 0.018 | 2 | 0.03 |
| *Tympanuchus phasianellus* | Sharp-tailed grouse | 12 | 0.016 | 7 | 0.10 |
| *Martes pennanti* | Fisher | 9 | 0.012 | 7 | 0.10 |
| *Weasel spp.* | Weasel spp. | 5 | 0.007 | 5 | 0.07 |
| *Castor canadensis* | Beaver | 4 | 0.005 | 3 | 0.04 |

| Species | Common name | Number of detections | Detection rate (per 100 days) | Sites detected | Proportion of sites |
|---|---|---|---|---|---|
| *Lontra canadensis* | River otter | 4 | 0.005 | 3 | 0.04 |
| *Strix nebulosa* | Great grey owl | 4 | 0.005 | 4 | 0.05 |
| *Gulo gulo* | Wolverine | 3 | 0.004 | 2 | 0.03 |
| *Branta canadensis* | Canada goose | 2 | 0.003 | 1 | 0.01 |
| *Cervus canadensis* | Elk | 2 | 0.003 | 2 | 0.03 |
| *Puma concolor* | Cougar | 1 | 0.001 | 1 | 0.01 |

# Appendix 2: Single species models

## Supplementary Figure 1




**Appendix 2 Figure 1** 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); 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 Control strata 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 Control 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.

# Appendix 3: Community Modelling

## Supplementary Figure 1


**Appendix 3 Figure 1** Correlation coefficients between putative predictors of wildlife detection frequency in Algar. The numbers on the left hand side and the size of the symbols on the right hand side donate the correlation coefficient magnitude.

# Supplementary Table 1

**Appendix 3 Table 1** Convergence diagnostics for the HMSC models

| Species | Independent events | Minimum count | Naïve occupancy | Mean ESS | Mean PSRF | Max PSRF |
|---|---|---|---|---|---|---|
| *Alces alces* | 554 | 694 | 0.86 | 931.3 | 1.15 | 1.56 |
| *Canis latrans* | 162 | 176 | 0.34 | 512.7 | 1.04 | 1.09 |
| *Canis lupus* | 511 | 860 | 0.75 | 682.3 | 1.07 | 1.19 |
| *Castor canadensis* | 4 | 4 | 0.04 | - | - | - |
| *Cervus canadensis* | 2 | 2 | 0.03 | - | - | - |
| *Grus canadensis* | 1476 | 2541 | 0.77 | 858.7 | 1.04 | 1.1 |
| *Gulo gulo* | 3 | 3 | 0.03 | - | - | - |
| *Lepus americanus* | 793 | 802 | 0.6 | 853.1 | 1.04 | 1.14 |
| *Lontra canadensis* | 4 | 10 | 0.04 | - | - | - |
| *Lynx canadensis* | 185 | 189 | 0.66 | 709.6 | 1.03 | 1.14 |
| *Martes americana* | 89 | 93 | 0.45 | 467.1 | 1.02 | 1.06 |
| *Martes pennanti* | 9 | 10 | 0.1 | - | - | - |
| *Odocoileus virginianus* | 1845 | 2286 | 0.81 | 804.3 | 1.1 | 1.47 |
| *Puma concolor* | 1 | 1 | 0.01 | - | - | - |
| *Rangifer tarandus* | 470 | 658 | 0.58 | 766.9 | 1.05 | 1.4 |
| *Tamiasciurus hudsonicus* | 125 | 127 | 0.22 | 515.1 | 1.09 | 1.25 |
| *Ursus americanus* | 855 | 954 | 0.9 | 705.2 | 1.06 | 1.16 |
| *Vulpes vulpes* | 24 | 25 | 0.21 | 221.4 | 1.01 | 1.03 |

**Appendix 3 Table 1 Summary capture data and convergence diagnostics for the medium/large vertebrate species detected on the camera traps.** Species with fewer than 10 independent detections were excluded from the HMSC analysis due to lack of parameter convergence. Mean ESS = mean effective sample size - the average effective sample size across all parameters for each species; Mean PRSF = Mean Potential Scale Reduction Factor across all parameters estimated for a given species - assesses the distribution of samples from chains and as a general rule of thumb should be <1.1 for all parameters.

# Appendix 4: Density Estimation

## Supplementary Tables

**Appendix 4 Table 1.** Sigma estimates (km) for caribou in the Algar study area from the Aug. 1- Oct. 31 sampling period from 2016 - 2019, estimated with SC and SPIM models with either an informative gamma (24,8) or uniform (0,10) prior for sigma. For SPIM models, data used either detections from individuals across all group sizes or detections from singleton individuals not in groups. Mean and mode estimates with 95% HPDI in parentheses are provided.

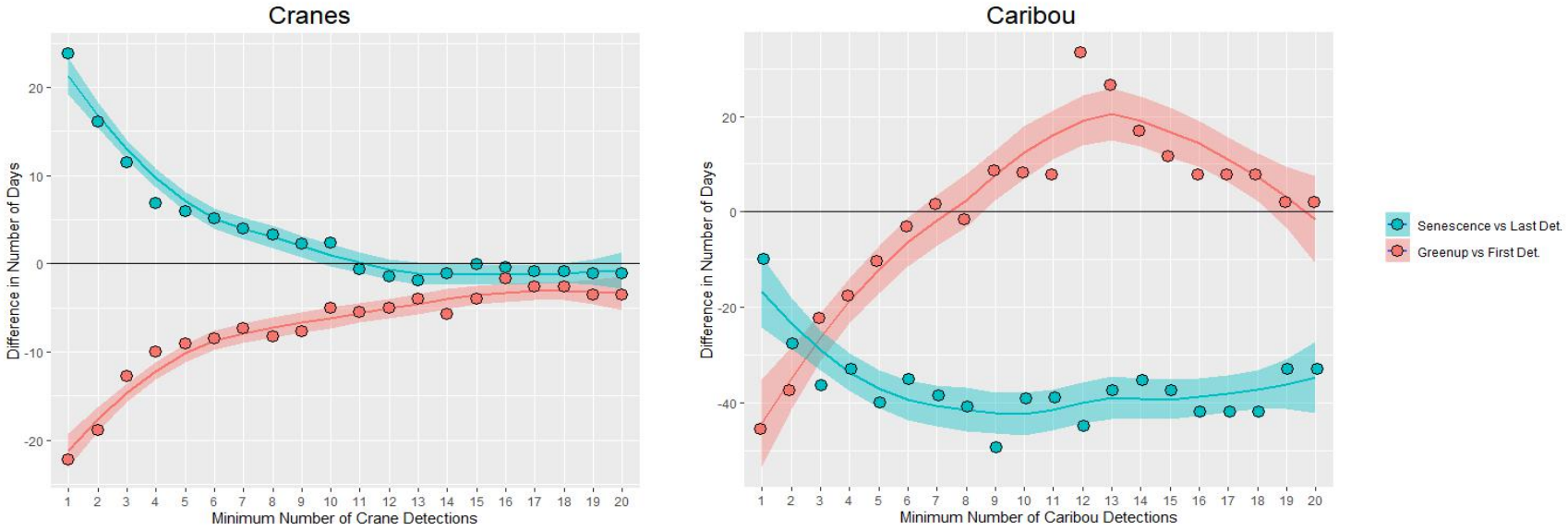
| Model | Data Subset | Sigma Prior | 2016 | 2017 | 2018 | 2019 |
|---|---|---|---|---|---|---|
| SC | All | Gamma | 2.9, 2.1 (1.7 - 4.1) | 2.2, 1.6 (1.6 - 2.9) | 0.6, 0.6 (0.5 - 0.8) | 1.4, 1.2 (1.0 - 1.9) |
| SC | All | Uniform | 1.0, 0.3 (0.1, 3.9) | 0.7, 0.4 (0.2 - 1.6) | 0.5, 0.5 (0.3 - 0.6) | 0.6, 0.5 (0.4 - 0.8) |
| SPIM | All | Gamma | 2.8, 2.7 (1.7 - 4.0) | 2.8, 2.3 (1.7 - 4.1) | 1.9, 1.5 (1.0 - 2.9) | 2.6, 1.2 (1.3 - 3.9) |
| SPIM | All | Uniform | 15, 0.2 (0.1 - 77) | 12, 0.3 (0.3 - 49) | 0.5, 0.4 (0.4 - 0.7) | 0.6, 0.5 (0.4 - 0.9) |
| SPIM | Singletons | Gamma | 2.8, 2.2 (1.7 - 4.0) | 2.8, 3.0 (1.7 - 4.0) | 2.8, 3.0 (1.7 - 3.9) | 2.5, 2.6 (1.4 - 3.7) |
| SPIM | Singletons | Uniform | 1.0, 0.4 (0.04 - 5.2) | 3.0, 0.3 (0.3 - 8.5) | 0.6, 0.5 (0.3 - 1.1) | 0.5, 0.3 (0.3 - 0.8) |

**Appendix 4 Table 2**. Detection probability estimates for caribou in the Algar study area from the Aug. 1- Oct. 31 sampling period from 2016 - 2019, estimated with SC and SPIM models with either an informative gamma (24,8) or uniform (0,10) prior for sigma. For SPIM models, data used either detections from individuals across all group sizes or detections from singleton individuals not in groups. Mean and mode estimates with 95% HPDI in parentheses are provided.

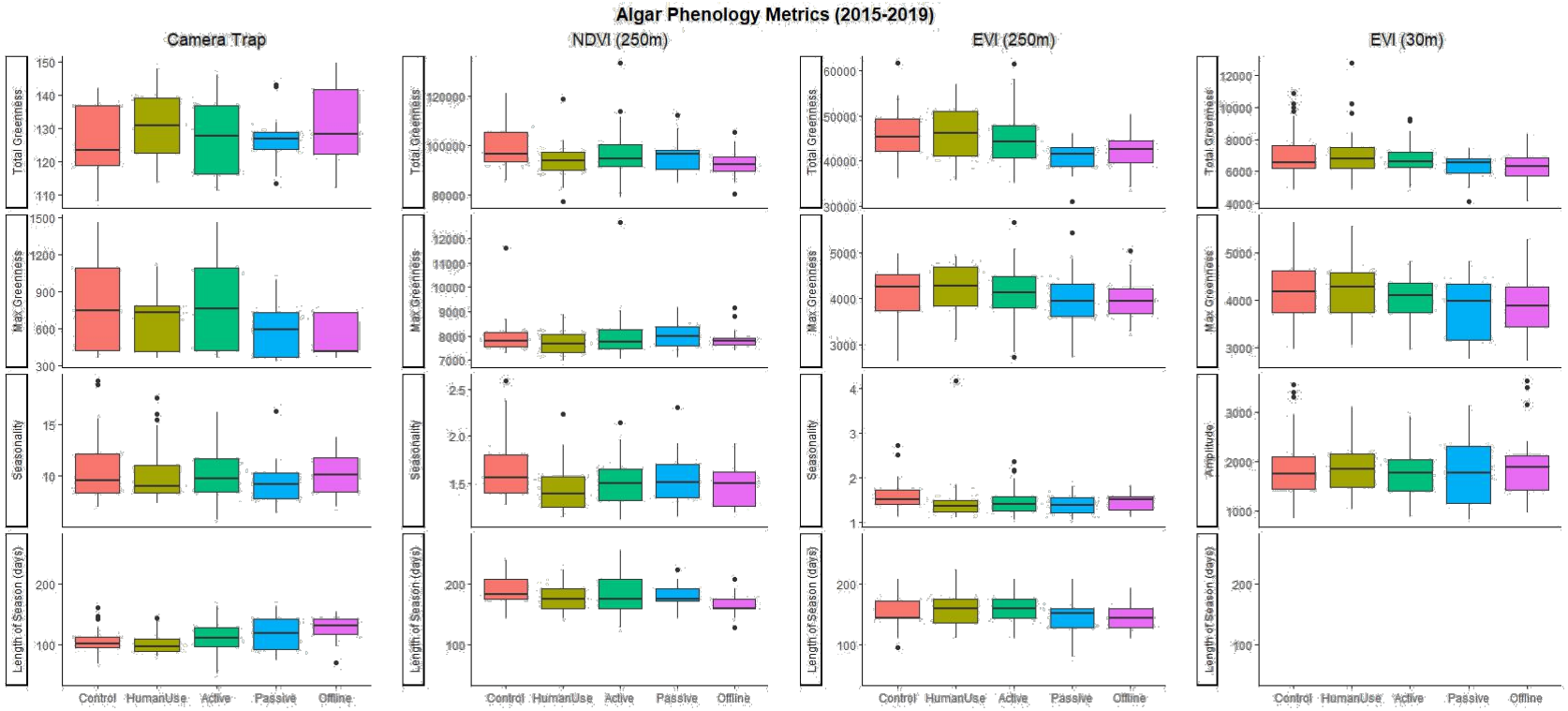
| Model | Data Subset | Sigma Prior | 2016 | 2017 | 2018 | 2019 |
|---|---|---|---|---|---|---|
| SC | All | Gamma | 0.14, 0.0005 (5.6e-5 - 0.32) | 0.05, 0.03 (0.01 - 0.08) | 0.13, 0.09 (0.07 - 0.20) | 0.07, 0.0.9 (0.03 - 0.11) |
| SC | All | Uniform | 0.57, 1.0e-4 (7.1e-5 – 3.8) | 0.24, 0.05 (0.01-0.57) | 0.17, 0.18 (0.08 – 0.30) | 0.11, 0.10 (0.05 – 0.18) |
| SPIM | All | Gamma | 0.012, 7.0e-5 (5.2e-5 - 0.005) | 0.003, 3.5e-4 (2.2e-4 - 0.004) | 0.005, 1.8e-3 (1.9e-3 - 0.01) | 0.003, 9.9e-4 (8.2e-4, 0.005) |
| SPIM | All | Uniform | 0.008, 3.6e-6 (3.2e-6 - 0.020) | 0.006, 9.7e-6 (7.0e-6, 0.010) | 0.019, 1.7e-3 (9.7e-3 - 0.031) | 0.015, 1.3e-3 (5.6e-3 - 0.024) |
| SPIM | Singletons | Gamma | 0.009, 6.6e-5 (1.0e-5 - 0.010) | 0.004, 2.2e-4 (1.4e-4 - 0.006) | 0.003, 7.8e-4 (1.1e-3 - 0.004) | 0.002, 3.6e-4 (2.8e-4 - 0.004) |
| SPIM | Singletons | Uniform | 1.4, 2.8e-5 (9.6e-6 – 7.6) | 0.004, 2.5e-5 (1.2e05 - 0.010) | 0.014, 9.4e-4 (3.7e-3 - 0.026) | 0.014, 1.1e-3 (3.9e-3 - 0.027) |

# Appendix 5: Phenology Monitoring

## Supplementary Figures




**Appendix 5 Figure 1**. For cranes and caribou detected in the Algar study area from 2016-2019, the average mismatch in days between dates of first detection at a site and date of vegetation greenup (red), and dates of last detection at a site and date of vegetation senescence (blue). A smoothed line with 95% confidence interval is included. Values above 0 indicate that the wildlife detection date occurred before the vegetation date; values below 0 indicate that the detection date occurred after the vegetation date.




**Appendix 5 Figure 2.** Comparison of phenology metrics calculated from camera traps and remote satellite products, at camera trap sites across restoration categories in the Algar study area from 2016-2019. 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; Amplitude was the difference between minimum and maximum values of each annual cycle. Length of Season was the number of days between estimated dates of greenup and senescence, and was not available for EVI data at the 30 m resolution.

# Supplementary Tables

**Appendix 5 Table 1**. Null model selection results for annual caribou and deer counts in the Algar study area from 2016-2019 at camera trap sites. Model sets identified the most supported null model structure under a negative binomial response distribution, for variance structure (linear or quadratic), zero inflation (zi), and hurdle model. K is the number of parameters, AICc is the AIC corrected for small sample sizes; ΔAICc is the difference in AICc compared to the top model; Weight is the model support weight; LogLik is the log likelihood.

| Species | Model | K | LogLik | AICc | ΔAICc | Weight |
|---|---|---|---|---|---|---|
| Caribou | linear_noZI | 4 | -298.8 | 605.8 | 0 | 0.84 |
| Caribou | quadratic_noZI | 4 | -300.63 | 609.5 | 3.7 | 0.13 |
| Caribou | linear_ZI | 5 | -301.11 | 612.6 | 6.7 | 0.03 |
| Caribou | Linear_hurdle_ZI | 5 | -332.23 | 674.8 | 69.0 | 0 |
| **Species** | **Model** | **K** | **LL** | **AICc** | **Delta_AICc** | **Weight** |
| Deer | quadratic_noZI | 4 | -481.46 | 971.1 | 0 | 0.69 |
| Deer | linear_noZI | 4 | -482.58 | 973.4 | 2.2 | 0.23 |
| Deer | linear_ZI | 5 | -482.58 | 975.5 | 4.4 | 0.08 |
| Deer | quadratic_hurdle_ZI | 5 | -506.24 | 1022.8 | 51.7 | 0 |
| Deer | linear_hurdle_ZI | 5 | -508.81 | 1028.0 | 56.8 | 0 |

**Appendix 5 Table 2.** Phenology model selection results for annual caribou and deer counts in the Algar study area from 2016-2019 at camera trap sites. Full model sets included all additive linear combinations of maximum annual greenness (MGI), total annual greenness (AUC), and length of season in days (LOS). The log number of camera operation days was considered as an offset, and site and year were included as random effects. K is the number of parameters, AICc is the AIC corrected for small sample sizes; ΔAICc is the difference in AICc compared to the top model; Weight is the model support weight; LogLik is the log likelihood.

| Species | MGI | AUC | LOS | SSN | nDays | K | LogLik | AICc | AICc | Weight |
|---|---|---|---|---|---|---|---|---|---|---|
| Caribou | X | | | | X | 5 | -295.9 | 602.2 | 0 | 0.21 |
| Caribou | X | | X | | X | 6 | -295.5 | 603.5 | 1.3 | 0.11 |
| Caribou | X | X | | | X | 6 | -295.7 | 603.8 | 1.6 | 0.1 |
| Caribou | X | | | X | X | 6 | -295.8 | 604.1 | 2 | 0.08 |
| Caribou | X | X | | | | 6 | -296 | 604.6 | 2.4 | 0.06 |
| Caribou | X | X | | X | X | 7 | -295.3 | 605.2 | 3 | 0.05 |
| Caribou | X | X | X | | X | 7 | -295.3 | 605.2 | 3.1 | 0.05 |
| Caribou | X | | X | X | X | 7 | -295.4 | 605.5 | 3.3 | 0.04 |
| Caribou | | | | | X | 4 | -298.8 | 605.8 | 3.7 | 0.03 |
| Caribou | X | X | | X | | 7 | -295.6 | 605.8 | 3.7 | 0.03 |
| Caribou | X | X | X | | | 7 | -295.7 | 606 | 3.8 | 0.03 |
| Caribou | X | | | | | 5 | -297.9 | 606.2 | 4 | 0.03 |
| Caribou | X | X | X | X | X | 8 | -294.9 | 606.7 | 4.5 | 0.02 |
| Caribou | | | X | | X | 5 | -298.3 | 607 | 4.8 | 0.02 |
| Caribou | X | | X | | | 6 | -297.4 | 607.2 | 5 | 0.02 |
| Caribou | X | X | X | X | | 8 | -295.2 | 607.3 | 5.1 | 0.02 |
| Caribou | | | | X | X | 5 | -298.6 | 607.5 | 5.3 | 0.02 |
| Caribou | | X | | | X | 5 | -298.7 | 607.8 | 5.6 | 0.01 |
| Caribou | X | | | X | | 6 | -297.9 | 608.3 | 6.1 | 0.01 |
| Caribou | | | X | X | X | 6 | -298.1 | 608.7 | 6.5 | 0.01 |
| Caribou | | | | | | 4 | -300.3 | 608.7 | 6.6 | 0.01 |
| Caribou | | X | | | | 5 | -299.2 | 608.8 | 6.6 | 0.01 |
| Caribou | | X | X | | X | 6 | -298.2 | 608.9 | 6.7 | 0.01 |
| Caribou | | X | | X | X | 6 | -298.3 | 609.1 | 6.9 | 0.01 |
| Caribou | X | | X | X | | 7 | -297.4 | 609.3 | 7.2 | 0.01 |
| Caribou | | | X | | | 5 | -299.7 | 609.8 | 7.7 | 0.01 |
| Caribou | | X | X | | | 6 | -298.7 | 609.9 | 7.7 | 0.01 |
| Caribou | | X | | X | | 6 | -298.8 | 610 | 7.8 | 0 |
| Caribou | | X | X | X | X | 7 | -297.7 | 610 | 7.9 | 0 |
| Caribou | | | | X | | 5 | -300.2 | 610.8 | 8.6 | 0 |
| Caribou | | X | X | X | | 7 | -298.1 | 610.8 | 8.7 | 0 |
| Caribou | | | X | X | | 6 | -299.7 | 611.9 | 9.7 | 0 |

| Species | MGI | AUC | LOS | SSN | nDays | K | LogLik | AICc | AICc | Weight |
|---|---|---|---|---|---|---|---|---|---|---|
| Deer | | | X | | | 5 | -479.6 | 969.4 | 0 | 0.1 |
| Deer | X | | X | | | 6 | -478.6 | 969.7 | 0.3 | 0.09 |
| Deer | X | | X | | X | 6 | -478.8 | 970 | 0.6 | 0.07 |
| Deer | | | X | | X | 5 | -479.9 | 970.1 | 0.7 | 0.07 |
| Deer | | | | | | 4 | -481.2 | 970.6 | 1.1 | 0.06 |
| Deer | X | | | | X | 5 | -480.2 | 970.8 | 1.4 | 0.05 |
| Deer | X | | | | | 5 | -480.3 | 970.9 | 1.5 | 0.05 |
| Deer | | | | | X | 4 | -481.5 | 971.1 | 1.7 | 0.04 |
| Deer | | X | X | | | 6 | -479.4 | 971.4 | 1.9 | 0.04 |
| Deer | | | X | X | | 6 | -479.5 | 971.4 | 2 | 0.04 |
| Deer | X | X | X | | | 7 | -478.4 | 971.5 | 2 | 0.04 |
| Deer | | X | X | | X | 6 | -479.5 | 971.6 | 2.1 | 0.03 |
| Deer | X | X | X | | X | 7 | -478.5 | 971.7 | 2.3 | 0.03 |
| Deer | X | | X | X | | 7 | -478.6 | 971.8 | 2.3 | 0.03 |
| Deer | X | | X | X | X | 7 | -478.8 | 972.1 | 2.7 | 0.03 |
| Deer | | | X | X | X | 6 | -479.9 | 972.3 | 2.8 | 0.02 |
| Deer | | X | | | | 5 | -481 | 972.4 | 2.9 | 0.02 |
| Deer | X | X | | | | 6 | -480 | 972.4 | 3 | 0.02 |
| Deer | | | | X | | 5 | -481.1 | 972.5 | 3.1 | 0.02 |
| Deer | | X | | | X | 5 | -481.1 | 972.6 | 3.1 | 0.02 |
| Deer | X | X | | | X | 6 | -480.1 | 972.6 | 3.2 | 0.02 |
| Deer | X | | | X | X | 6 | -480.2 | 972.9 | 3.5 | 0.02 |
| Deer | X | | | X | | 6 | -480.2 | 973 | 3.5 | 0.02 |
| Deer | | | | X | X | 5 | -481.5 | 973.2 | 3.8 | 0.02 |
| Deer | | X | X | X | | 7 | -479.4 | 973.5 | 4 | 0.01 |
| Deer | X | X | X | X | | 8 | -478.4 | 973.7 | 4.2 | 0.01 |
| Deer | | X | X | X | X | 7 | -479.5 | 973.7 | 4.2 | 0.01 |
| Deer | X | X | X | X | X | 8 | -478.5 | 973.9 | 4.4 | 0.01 |
| Deer | | X | | X | | 6 | -481 | 974.5 | 5 | 0.01 |
| Deer | X | X | | X | | 7 | -480 | 974.6 | 5.2 | 0.01 |
| Deer | | X | | X | X | 6 | -481.1 | 974.6 | 5.2 | 0.01 |
| Deer | X | X | | X | X | 7 | -480.1 | 974.8 | 5.3 | 0.01 |

**Appendix 5 Table 3.** Habitat model selection results for annual caribou and deer counts in the Algar study area from 2016-2019 at camera trap sites. Full model sets included either the percentage of lowland habitat at the 1 km scale or the dominant habitat type (lowland, upland, or non-forest) at the 30 m scale. The log number of camera operation days was considered as an offset, and site and year were included as random effects. K is the number of parameters, AICc is the AIC corrected for small sample sizes; ΔAICc is the difference in AICc compared to the top model; Weight is the model support weight; LogLik is the log likelihood.

| Species | % Lowland | Dom. Habitat | nDays | K | LogLik | AICc | AICc | Weight |
|---|---|---|---|---|---|---|---|---|
| Caribou | X | | X | 5 | -282.7 | 575.7 | 0 | 1 |
| Caribou | | | X | 4 | -298.8 | 605.8 | 30.1 | 0 |
| Caribou | | X | X | 6 | -297.7 | 608.0 | 32.2 | 0 |
| Deer | X | | X | 5 | -465.3 | 941 | 0 | 1 |
| Deer | | X | X | 6 | -476.8 | 966.1 | 25.1 | 0 |
| Deer | | | X | 4 | -482.6 | 973.4 | 32.4 | 0 |

**Appendix 5 Table 4.** Anthropogenic model selection results for annual caribou and deer counts in the Algar study area from 2016-2019 at camera trap sites. Full model sets included all additive linear combinations of seismic line density (LD) (km/km2) at 1 km, 250 m, and 30 m buffers, the width of the seismic line (LW) (m), and the restoration category (Rest.: Offline, Control, Human Use, Passive restoration, Active Restoration). The log number of camera operation days (nDays) was considered as an offset, and site and year were included as random effects. K is the number of parameters, AICc is the AIC corrected for small sample sizes; ΔAICc is the difference in AICc compared to the top model; Weight is the model support weight; LogLik is the log likelihood.

| Species | LD_1km | LD_250m | LD_30m | LW | Rest. | nDays | L | logLik | AICc | AICc | Weight |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Caribou | | | | | X | X | 8 | -291.6 | 600 | 0 | 0.16 |
| Caribou | | | X | | X | X | 9 | -290.7 | 600.5 | 0.5 | 0.13 |
| Caribou | X | | | | X | X | 9 | -291.3 | 601.7 | 1.69 | 0.07 |
| Caribou | | | | X | X | X | 9 | -291.6 | 602.2 | 2.2 | 0.05 |
| Caribou | | X | | | X | X | 9 | -291.6 | 602.2 | 2.2 | 0.05 |
| Caribou | X | | X | | X | X | 10 | -290.6 | 602.5 | 2.47 | 0.05 |
| Caribou | | | X | X | X | X | 10 | -290.6 | 602.5 | 2.49 | 0.05 |
| Caribou | | X | X | | X | X | 10 | -290.6 | 602.6 | 2.53 | 0.05 |
| Caribou | | | | | X | | 8 | -292.9 | 602.6 | 2.57 | 0.05 |
| Caribou | | | X | | X | | 9 | -291.9 | 602.8 | 2.83 | 0.04 |
| Caribou | X | X | | | X | X | 10 | -291.3 | 603.8 | 3.83 | 0.02 |
| Caribou | X | | | X | X | X | 10 | -291.3 | 603.9 | 3.93 | 0.02 |
| Caribou | X | X | X | | X | X | 11 | -290.3 | 604.1 | 4.11 | 0.02 |
| Caribou | X | | | | X | | 9 | -292.6 | 604.3 | 4.27 | 0.02 |
| Caribou | | X | | X | X | X | 10 | -291.6 | 604.5 | 4.43 | 0.02 |
| Caribou | | X | X | X | X | X | 11 | -290.5 | 604.5 | 4.5 | 0.02 |
| Caribou | X | | X | X | X | X | 11 | -290.5 | 604.6 | 4.56 | 0.02 |
| Caribou | | X | | | X | | 9 | -292.9 | 604.8 | 4.76 | 0.02 |
| Caribou | | | | X | X | | 9 | -292.9 | 604.8 | 4.78 | 0.02 |
| Caribou | X | | X | | X | | 10 | -291.8 | 604.8 | 4.82 | 0.02 |
| Caribou | | X | X | | X | | 10 | -291.8 | 604.9 | 4.89 | 0.01 |
| Caribou | | | X | X | X | | 10 | -291.8 | 604.9 | 4.89 | 0.01 |
| Caribou | | | | | | X | 4 | -298.8 | 605.8 | 5.8 | 0.01 |
| Caribou | X | X | | X | X | X | 11 | -291.3 | 606.1 | 6.09 | 0.01 |
| Caribou | X | X | X | X | X | X | 12 | -290.2 | 606.2 | 6.2 | 0.01 |
| Caribou | X | X | | | X | | 10 | -292.6 | 606.5 | 6.45 | 0.01 |
| Caribou | X | | | X | X | | 10 | -292.6 | 606.5 | 6.5 | 0.01 |
| Caribou | X | X | X | | X | | 11 | -291.5 | 606.5 | 6.53 | 0.01 |
| Caribou | | X | X | X | X | | 11 | -291.7 | 607 | 6.94 | 0.01 |
| Caribou | X | | X | X | X | | 11 | -291.7 | 607 | 6.96 | 0.01 |
| Caribou | | X | | X | X | | 10 | -292.9 | 607 | 7 | 0.01 |
| Caribou | | X | | | | X | 5 | -298.5 | 607.3 | 7.29 | 0 |

| Species | LD_1km | LD_250m | LD_30m | LW | Rest. | nDays | L | logLik | AICc | AICc | Weight |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Caribou | | | | X | | X | 5 | -298.7 | 607.7 | 7.69 | 0 |
| Caribou | | | X | | | X | 5 | -298.8 | 607.9 | 7.9 | 0 |
| Caribou | X | | | | | X | 5 | -298.8 | 607.9 | 7.91 | 0 |
| Caribou | X | X | X | X | X | | 12 | -291.4 | 608.7 | 8.68 | 0 |
| Caribou | X | X | | X | X | | 11 | -292.6 | 608.7 | 8.7 | 0 |
| Caribou | | | | | | | 4 | -300.3 | 608.7 | 8.71 | 0 |
| Caribou | | X | X | | | X | 6 | -298.2 | 608.8 | 8.83 | 0 |
| Caribou | | | X | X | | X | 6 | -298.3 | 609.1 | 9.08 | 0 |
| Caribou | X | X | | | | X | 6 | -298.4 | 609.3 | 9.24 | 0 |
| Caribou | | X | | X | | X | 6 | -298.5 | 609.4 | 9.41 | 0 |
| Caribou | X | | | X | | X | 6 | -298.7 | 609.8 | 9.82 | 0 |
| Caribou | | X | X | X | | X | 7 | -297.6 | 609.9 | 9.89 | 0 |
| Caribou | X | | X | | | X | 6 | -298.8 | 610 | 10.01 | 0 |
| Caribou | | X | | | | | 5 | -300 | 610.3 | 10.31 | 0 |
| Caribou | | | | X | | | 5 | -300.2 | 610.7 | 10.69 | 0 |
| Caribou | | | X | | | | 5 | -300.2 | 610.8 | 10.76 | 0 |
| Caribou | X | X | X | | | X | 7 | -298.1 | 610.8 | 10.79 | 0 |
| Caribou | X | | | | | | 5 | -300.2 | 610.8 | 10.82 | 0 |
| Caribou | X | | X | X | | X | 7 | -298.3 | 611.2 | 11.18 | 0 |
| Caribou | X | X | | X | | X | 7 | -298.4 | 611.4 | 11.39 | 0 |
| Caribou | | X | X | | | | 6 | -299.6 | 611.7 | 11.71 | 0 |
| Caribou | X | X | X | X | | X | 8 | -297.6 | 611.9 | 11.93 | 0 |
| Caribou | | | X | X | | | 6 | -299.8 | 612 | 12.02 | 0 |
| Caribou | X | X | | | | | 6 | -299.9 | 612.3 | 12.3 | 0 |
| Caribou | | X | | X | | | 6 | -300 | 612.5 | 12.44 | 0 |
| Caribou | X | | | X | | | 6 | -300.2 | 612.8 | 12.82 | 0 |
| Caribou | | X | X | X | | | 7 | -299.1 | 612.9 | 12.86 | 0 |
| Caribou | X | | X | | | | 6 | -300.2 | 612.9 | 12.87 | 0 |
| Caribou | X | X | X | | | | 7 | -299.5 | 613.7 | 13.71 | 0 |
| Caribou | X | | X | X | | | 7 | -299.7 | 614.1 | 14.11 | 0 |
| Caribou | X | X | | X | | | 7 | -299.9 | 614.5 | 14.46 | 0 |
| Caribou | X | X | X | X | | | 8 | -299.1 | 614.9 | 14.93 | 0 |
| Deer | | | | | X | | 8 | -475.1 | 967 | 0 | 0.12 |
| Deer | | | | | X | X | 8 | -475.3 | 967.5 | 0.54 | 0.09 |
| Deer | | | X | | X | | 9 | -474.6 | 968.3 | 1.37 | 0.06 |
| Deer | X | | | | X | | 9 | -474.9 | 968.8 | 1.84 | 0.05 |
| Deer | | | X | | X | X | 9 | -474.9 | 968.8 | 1.87 | 0.05 |
| Deer | | X | | | X | | 9 | -474.9 | 968.9 | 1.97 | 0.05 |
| Deer | | | | X | X | | 9 | -475.1 | 969.1 | 2.18 | 0.04 |
| Deer | X | | | | X | X | 9 | -475.2 | 969.4 | 2.45 | 0.04 |
| Deer | | X | | | X | X | 9 | -475.2 | 969.4 | 2.47 | 0.04 |

| Species | LD_1km | LD_250m | LD_30m | LW | Rest. | nDays | L | logLik | AICc | AICc | Weight |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Deer | | | | X | X | X | 9 | -475.3 | 969.7 | 2.71 | 0.03 |
| Deer | X | | X | | X | | 10 | -474.3 | 969.9 | 2.94 | 0.03 |
| Deer | X | X | | | X | | 10 | -474.5 | 970.2 | 3.23 | 0.02 |
| Deer | X | | X | | X | X | 10 | -474.6 | 970.5 | 3.55 | 0.02 |
| Deer | | X | X | | X | | 10 | -474.6 | 970.5 | 3.59 | 0.02 |
| Deer | | | X | X | X | | 10 | -474.6 | 970.5 | 3.6 | 0.02 |
| Deer | | | | | | | 4 | -481.2 | 970.6 | 3.63 | 0.02 |
| Deer | X | X | | | X | X | 10 | -474.8 | 970.8 | 3.83 | 0.02 |
| Deer | X | | | X | X | | 10 | -474.9 | 971 | 4.05 | 0.02 |
| Deer | | X | X | | X | X | 10 | -474.9 | 971 | 4.09 | 0.02 |
| Deer | | | X | X | X | X | 10 | -474.9 | 971.1 | 4.11 | 0.02 |
| Deer | | | | | | X | 4 | -481.5 | 971.1 | 4.18 | 0.02 |
| Deer | | X | | X | X | | 10 | -474.9 | 971.1 | 4.19 | 0.02 |
| Deer | X | | | X | X | X | 10 | -475.2 | 971.6 | 4.65 | 0.01 |
| Deer | | X | | X | X | X | 10 | -475.2 | 971.6 | 4.68 | 0.01 |
| Deer | | X | | | | | 5 | -480.7 | 971.6 | 4.69 | 0.01 |
| Deer | | | X | | | | 5 | -480.7 | 971.8 | 4.88 | 0.01 |
| Deer | X | X | X | | X | | 11 | -474.2 | 971.9 | 4.9 | 0.01 |
| Deer | X | | X | X | X | | 11 | -474.3 | 972.1 | 5.19 | 0.01 |
| Deer | | X | | | | X | 5 | -480.9 | 972.2 | 5.28 | 0.01 |
| Deer | X | X | | X | X | | 11 | -474.4 | 972.4 | 5.47 | 0.01 |
| Deer | | | | X | | | 5 | -481.1 | 972.4 | 5.49 | 0.01 |
| Deer | X | X | X | | X | X | 11 | -474.5 | 972.5 | 5.51 | 0.01 |
| Deer | | | X | | | X | 5 | -481.1 | 972.5 | 5.55 | 0.01 |
| Deer | X | | | | | | 5 | -481.2 | 972.7 | 5.73 | 0.01 |
| Deer | X | | X | X | X | X | 11 | -474.6 | 972.8 | 5.8 | 0.01 |
| Deer | | X | X | X | X | | 11 | -474.6 | 972.8 | 5.85 | 0.01 |
| Deer | X | X | | X | X | X | 11 | -474.7 | 973 | 6.07 | 0.01 |
| Deer | | | | X | | X | 5 | -481.4 | 973.1 | 6.11 | 0.01 |
| Deer | X | X | | | | | 6 | -480.3 | 973.1 | 6.17 | 0.01 |
| Deer | X | | | | | X | 5 | -481.5 | 973.2 | 6.29 | 0.01 |
| Deer | | X | X | X | X | X | 11 | -474.9 | 973.3 | 6.36 | 0.01 |
| Deer | | X | X | | | | 6 | -480.6 | 973.6 | 6.69 | 0 |
| Deer | | X | | X | | | 6 | -480.7 | 973.8 | 6.83 | 0 |
| Deer | X | X | | | | X | 6 | -480.7 | 973.8 | 6.85 | 0 |
| Deer | X | | X | | | | 6 | -480.7 | 973.8 | 6.86 | 0 |
| Deer | | | X | X | | | 6 | -480.7 | 973.8 | 6.9 | 0 |
| Deer | X | X | X | X | X | | 12 | -474.2 | 974.1 | 7.19 | 0 |
| Deer | | X | X | | | X | 6 | -480.9 | 974.3 | 7.33 | 0 |
| Deer | | X | | X | | X | 6 | -480.9 | 974.4 | 7.42 | 0 |
| Deer | | | X | X | | X | 6 | -481 | 974.5 | 7.55 | 0 |

| Species | LD_1km | LD_250m | LD_30m | LW | Rest. | nDays | L | logLik | AICc | AICc | Weight |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Deer | X | | X | | | X | 6 | -481 | 974.5 | 7.58 | 0 |
| Deer | X | | | X | | | 6 | -481 | 974.5 | 7.59 | 0 |
| Deer | X | X | X | X | X | X | 12 | -474.5 | 974.7 | 7.79 | 0 |
| Deer | X | | | X | | X | 6 | -481.3 | 975.2 | 8.22 | 0 |
| Deer | X | X | X | | | | 7 | -480.3 | 975.2 | 8.24 | 0 |
| Deer | X | X | | X | | | 7 | -480.3 | 975.3 | 8.32 | 0 |
| Deer | | X | X | X | | | 7 | -480.5 | 975.7 | 8.75 | 0 |
| Deer | X | | X | X | | | 7 | -480.6 | 975.8 | 8.88 | 0 |
| Deer | X | X | X | | | X | 7 | -480.6 | 975.9 | 8.96 | 0 |
| Deer | X | X | | X | | X | 7 | -480.7 | 976 | 9 | 0 |
| Deer | | X | X | X | | X | 7 | -480.8 | 976.3 | 9.36 | 0 |
| Deer | X | | X | X | | X | 7 | -480.9 | 976.5 | 9.58 | 0 |
| Deer | X | X | X | X | | | 8 | -480.2 | 977.2 | 10.28 | 0 |
| Deer | X | X | X | X | | X | 8 | -480.6 | 977.9 | 10.99 | 0 |

**Appendix 5 Table 5**. Final model set with top covariates from the phenology, habitat, and anthropognic model sets for annual caribou and deer counts in the Algar study area from 2016-2019 at camera trap sites. Full model sets included all additive linear combinations of maximum annual greenness (MGI), percentage of lowland habitat at 1 km, and restoration category (Offline, Control, Human Use, Passive restoration, Active Restoration). The log number of camera operation days (nDays) was considered as an offset, and site and year were included as random effects. K is the number of parameters, AICc is the AIC corrected for small sample sizes; ΔAICc is the difference in AICc compared to the top model; Weight is the model support weight; LogLik is the log likelihood.

| Species | MGI | % Lowland | Restoration | nDays | K | LogLik | AICc | ΔAICc | Weight |
|---|---|---|---|---|---|---|---|---|---|
| Caribou | X | X | X | X | 10 | -274.9 | 571.1 | 0 | 0.42 |
| Caribou | X | X | | X | 11 | -279.5 | 571.5 | 0.44 | 0.34 |
| Caribou | | X | X | X | 12 | -277.7 | 574.5 | 3.44 | 0.08 |
| Caribou | X | X | X | | 13 | -276.8 | 574.9 | 3.81 | 0.06 |
| Caribou | | X | | X | 14 | -282.7 | 575.7 | 4.65 | 0.04 |
| Caribou | X | X | | | 15 | -281.7 | 575.9 | 4.83 | 0.04 |
| Caribou | | X | X | | 16 | -279.1 | 577.3 | 6.23 | 0.02 |
| Caribou | | X | | | 17 | -284.3 | 578.9 | 7.86 | 0.01 |
| Caribou | X | | X | X | 18 | -289.2 | 597.4 | 26.31 | 0 |
| Caribou | | | X | X | 19 | -291.6 | 600 | 28.94 | 0 |
| Caribou | X | | X | | 20 | -290.9 | 600.8 | 29.77 | 0 |
| Caribou | X | | | X | 21 | -295.9 | 602.2 | 31.1 | 0 |
| Caribou | | | X | | 22 | -292.9 | 602.6 | 31.51 | 0 |
| Caribou | | | | X | 23 | -298.8 | 605.8 | 34.75 | 0 |
| Caribou | X | | | | 24 | -297.9 | 606.2 | 35.09 | 0 |
| Caribou | | | | | 25 | -300.3 | 608.7 | 37.66 | 0 |
| Deer | X | X | X | X | 10 | -459.1 | 939.5 | 0 | 0.21 |
| Deer | X | X | X | | 10 | -459.3 | 939.9 | 0.48 | 0.16 |
| Deer | X | X | | X | 6 | -463.9 | 940.3 | 0.86 | 0.13 |
| Deer | X | X | | | 6 | -463.9 | 940.4 | 0.98 | 0.13 |
| Deer | | X | | | 5 | -465.1 | 940.5 | 1.04 | 0.12 |
| Deer | | X | | X | 5 | -465.3 | 941 | 1.53 | 0.10 |
| Deer | | X | X | | 9 | -461.2 | 941.4 | 1.91 | 0.08 |
| Deer | | X | X | X | 9 | -461.3 | 941.6 | 2.16 | 0.07 |
| Deer | X | | X | X | 9 | -472.8 | 964.6 | 25.09 | 0 |
| Deer | X | | X | | 9 | -472.9 | 965 | 25.5 | 0 |
| Deer | | | X | | 8 | -475.1 | 967 | 27.48 | 0 |
| Deer | | | X | X | 8 | -475.3 | 967.5 | 28.02 | 0 |
| Deer | | | | | 4 | -481.2 | 970.6 | 31.12 | 0 |
| Deer | X | | | X | 5 | -480.2 | 970.8 | 31.35 | 0 |
| Deer | X | | | | 5 | -480.3 | 970.9 | 31.46 | 0 |
| Deer | | | | X | 4 | -481.5 | 971.1 | 31.67 | 0 |

**Appendix 5 Table 6.** Null model selection results for weekly caribou and deer counts in the Algar study area from 2016-2019 at camera trap sites. Model sets identified the most supported null model structure under a negative binomial response distribution, for variance structure (linear or quadratic), zero inflation (zi), and hurdle model. K is the number of parameters, AICc is the AIC corrected for small sample sizes; ΔAICc is the difference in AICc compared to the top model; Weight is the model support weight; LogLik is the log likelihood.

| Species | Model | K | LogLik | AICc | ΔAICc | Weight |
|---|---|---|---|---|---|---|
| Caribou | quadratic_noZI | 4 | -1348.38 | 2704.77 | 0 | 0.56 |
| Caribou | quadratic_ZI | 5 | -1347.91 | 2705.84 | 1.07 | 0.33 |
| Caribou | linear_ZI | 5 | -1349.05 | 2708.11 | 3.34 | 0.11 |
| Caribou | linear_noZI | 4 | -1355.38 | 2718.78 | 14.01 | 0 |
| Caribou | quadratic_hurdle_ZI | 5 | -1382.26 | 2774.53 | 69.76 | 0 |
| Deer | linear_ZI | 5 | -3222.33 | 6454.68 | 0 | 0.85 |
| Deer | quadratic_noZI | 4 | -3225.36 | 6458.74 | 4.06 | 0.11 |
| Deer | quadratic_ZI | 5 | -3225.36 | 6460.74 | 6.06 | 0.04 |
| Deer | linear_noZI | 4 | -3234.13 | 6476.26 | 21.58 | 0 |
| Deer | quadratic_hurdle_ZI | 5 | -3516.99 | 7043.98 | 589.30 | 0 |
| Deer | quadratic_linear_ZI | 5 | -3518.10 | 7046.20 | 591.52 | 0 |

**Appendix 5 Table 7**. Full model selection results for weekly caribou and deer counts in the Algar study area from 2016-2019 at camera trap sites. Full model sets included all additive linear combinations of weekly greenness and week of the year. Caribou models considered either percentage of lowland habitat at 1 km or dominant habitat type (lowland, upland, non-forest), while deer models considered only the percentage of lowland habitat at 1 km, The log number of camera operation days (nDays) was considered as an offset, and site and year were included as random effects. K is the number of parameters, AICc is the AIC corrected for small sample sizes; ΔAICc is the difference in AICc compared to the top model; Weight is the model support weight; LogLik is the log likelihood.

| Species | Greenness | % Lowland | Week | nDays | K | LogLik | AICc | ΔAICc | Weight |
|---|---|---|---|---|---|---|---|---|---|
| Caribou | X | X | X | | 7 | -1281.13 | 2576.3 | 0 | 0.50 |
| Caribou | X | X | X | X | 7 | -1281.57 | 2577.2 | 0.88 | 0.32 |
| Caribou | X | X | | | 6 | -1283.92 | 2579.9 | 3.58 | 0.08 |
| Caribou | X | X | | X | 6 | -1284.36 | 2580.7 | 4.47 | 0.05 |
| Caribou | X | | X | | 6 | -1285.36 | 2582.7 | 6.46 | 0.02 |
| Caribou | X | | X | X | 6 | -1285.82 | 2583.7 | 7.38 | 0.01 |
| Caribou | X | | | | 5 | -1288.18 | 2586.4 | 10.1 | 0 |
| Caribou | X | | | X | 5 | -1288.64 | 2587.3 | 11.02 | 0 |
| Caribou | | X | X | | 6 | -1334.91 | 2681.8 | 105.55 | 0 |
| Caribou | | X | X | X | 6 | -1335.77 | 2683.6 | 107.27 | 0 |
| Caribou | | | X | | 5 | -1339.33 | 2688.7 | 112.39 | 0 |
| Caribou | | | X | X | 5 | -1340.2 | 2690.4 | 114.14 | 0 |
| Caribou | | X | | | 5 | -1342.98 | 2696 | 119.68 | 0 |
| Caribou | | X | | X | 5 | -1343.83 | 2697.7 | 121.39 | 0 |
| Caribou | | | | | 4 | -1347.51 | 2703 | 126.76 | 0 |
| Caribou | | | | X | 4 | -1348.38 | 2704.8 | 128.49 | 0 |
| Caribou | X | | X | | 6 | -1285.36 | 2582.7 | 0 | 0.44 |
| Caribou | X | | X | X | 6 | -1285.82 | 2583.7 | 0.91 | 0.279 |
| Caribou | X | X | X | | 8 | -1284.99 | 2586 | 3.26 | 0.086 |
| Caribou | X | | | | 5 | -1288.18 | 2586.4 | 3.64 | 0.071 |
| Caribou | X | X | X | X | 8 | -1285.44 | 2586.9 | 4.17 | 0.055 |
| Caribou | X | | | X | 5 | -1288.64 | 2587.3 | 4.56 | 0.045 |
| Caribou | X | X | | | 7 | -1287.79 | 2589.6 | 6.87 | 0.014 |
| Caribou | X | X | | X | 7 | -1288.25 | 2590.5 | 7.78 | 0.009 |
| Caribou | | | X | | 5 | -1339.33 | 2688.7 | 105.92 | 0 |
| Caribou | | | X | X | 5 | -1340.2 | 2690.4 | 107.68 | 0 |
| Caribou | | X | X | | 7 | -1339.08 | 2692.2 | 109.44 | 0 |
| Caribou | | X | X | X | 7 | -1339.96 | 2693.9 | 111.19 | 0 |
| Caribou | | | | | 4 | -1347.51 | 2703 | 120.3 | 0 |
| Caribou | | | | X | 4 | -1348.38 | 2704.8 | 122.03 | 0 |
| Caribou | | X | | | 6 | -1347.25 | 2706.5 | 123.77 | 0 |
| Caribou | | X | | X | 6 | -1348.11 | 2708.2 | 125.5 | 0 |

| Species | Greenness | % Lowland | Week | nDays | K | LogLik | AICc | AICc | Weight |
|---|---|---|---|---|---|---|---|---|---|
| Deer | X | X | X | X | 8 | -3123.6 | 6263.2 | 0 | 0.705 |
| Deer | X | X | X | | 8 | -3124.58 | 6265.2 | 1.97 | 0.263 |
| Deer | X | | X | X | 7 | -3128 | 6270 | 6.79 | 0.024 |
| Deer | X | | X | | 7 | -3129.01 | 6272 | 8.81 | 0.009 |
| Deer | X | X | | X | 7 | -3147.62 | 6309.2 | 46.03 | 0 |
| Deer | X | X | | | 7 | -3148.03 | 6310.1 | 46.85 | 0 |
| Deer | X | | | X | 6 | -3152.15 | 6316.3 | 53.1 | 0 |
| Deer | X | | | | 6 | -3152.59 | 6317.2 | 53.97 | 0 |
| Deer | | X | X | X | 7 | -3180.7 | 6375.4 | 112.19 | 0 |
| Deer | | X | X | | 7 | -3181.62 | 6377.3 | 114.03 | 0 |
| Deer | | | X | X | 6 | -3184.69 | 6381.4 | 118.16 | 0 |
| Deer | | | X | | 6 | -3185.62 | 6383.2 | 120.03 | 0 |
| Deer | | X | | X | 6 | -3218.25 | 6448.5 | 185.29 | 0 |
| Deer | | X | | | 6 | -3218.42 | 6448.9 | 185.64 | 0 |
| Deer | | | | X | 5 | -3222.34 | 6454.7 | 191.46 | 0 |
| Deer | | | | | 5 | -3222.52 | 6455.1 | 191.83 | 0 |

# Appendix 6: Publication - Boreal predator co-occurrences reveal shared use of seismic lines in a working landscape

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ORIGINAL RESEARCH

# Boreal predator co-occurrences reveal shared use of seismic lines in a working landscape

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## Abstract

Interspecific interactions are an integral aspect of ecosystem functioning that may be disrupted in an increasingly anthropocentric world. Industrial landscape change creates a novel playing field on which these interactions take place, and a key question for wildlife managers is whether and how species are able to coexist in such working landscapes. Using camera traps deployed in northern Alberta, we surveyed boreal predators to determine whether interspecific interactions affected occurrences of black bears (*Ursus americanus*), coyotes (*Canis latrans*), and lynx (*Lynx canadensis*) within a landscape disturbed by networks of seismic lines (corridors cut for seismic exploration of oil and gas reserves). We tested hypotheses of species interactions across one spatial-only and two spatiotemporal (daily and weekly) scales. Specifically, we hypothesized that (1) predators avoid competition with the apex predator, gray wolf (*Canis lupus*), (2) they avoid competition with each other as intraguild competitors, and (3) they overlap with their prey. All three predators overlapped with wolves on at least one scale, although models at the daily and weekly scale had substantial unexplained variance. None of the predators showed avoidance of intraguild competitors or overlap with prey. These results show patterns in predator space use that are consistent with both facilitative interactions or shared responses to unmeasured ecological cues. Our study provides insight into how predator species use the working boreal landscape in relation to each other, and highlights that predator management may indirectly influence multiple species through their interactions.

KEYWORDS

camera traps, community ecology, facilitation, large carnivores, predator interactions

## 1 | INTRODUCTION

Human resource consumption is driving dramatic changes to natural landscapes around the world (MacDougall, McCann, Gellner, & Turkington, 2013; World Wildlife Fund, 2018). These changes alter the suitability of landscapes in different ways for different species, which in turn is likely to alter the interactions among these species (e.g., Steinmetz, Seuaturien, & Chutipong, 2013). Interspecific interactions are an integral aspect of ecosystem function, as they influence both population dynamics of interacting species and community-level responses to environmental change (MacMahon, Phillips, Robinson, & Schimpf, 1978). Of the many types of interactions described in classic ecological theory, two important types are facilitation—in which one species benefits from another (Bertness & Callaway, 1994; Bruno,

Stachowicz, & Bertness, 2003)—and competition—in which one species dominates another (Alley, 1982; Schoener, 1974). Although consequences for interacting species vary, both facilitation and competition can influence resource availability (Bruno et al., 2003; Wiens, 1993) and thus ultimately species coexistence (MacMahon et al., 1978). Maintaining these interactions is therefore vital to maintaining resilient ecological communities in an increasingly anthropocentric world (Valiente-Banuet et al., 2015).

The Canadian boreal forest is one biome experiencing dramatic landscape change due to natural resource extraction, which is creating a heterogeneous "working" landscape shared between industry and wildlife (Pickell, Andison, Coops, Gergel, & Marshall, 2015). Logging alone has an area footprint of approximately 15 million hectares, while energy development has created over half a million kilometers of linear features across the region (Pasher, Seed, & Duffe, 2013). The cumulative effects of these extensive industrial footprints impact the distribution and abundance of a number of boreal mammals, though the strength and nature of influence vary by species (Fisher & Burton, 2018; Toews, Juanes, & Burton, 2018). Behavioral and population changes in individual species can in turn affect interactions among species (Ritchie & Johnson, 2009), leading to broader indirect effects of industrial development in boreal ecosystems.

In northeastern Alberta, where industrial development has the greatest footprint (Pickell et al., 2015), linear features directly affect animal behaviors and population dynamics. Networks of seismic lines—wide trails (5 m–10 m, Dabros, Pyper, & Castilla, 2018) cut for seismic exploration of oil and gas reserves—facilitate movement for gray wolves (*Canis lupus*) across challenging boreal wetland terrain (Dickie, Serrouya, McNay, & Boutin, 2016), improving their abilities to hunt in these habitats (McKenzie, Merrill, Spiteri, & Lewis, 2012). Like wolves, evidence suggests that black bears prefer linear features for ease of travel (Latham, Latham, & Boyce, 2011; Tigner, Bayne, & Boutin, 2014). Mesocarnivores such as coyotes (*Canis latrans*) and Canada lynx (*Lynx canadensis*) may also benefit from linear features. Human development, including linear corridors, is positively related to coyotes' northern expansion and persistence in the boreal forest (Hody & Kays, 2018) and lynx presence (Fisher & Burton, 2018; but see Bayne, Boutin, & Moses, 2008). With at least some members of the boreal predator community responding to extensive seismic line networks, we expect these networks to potentially influence the interactions among predators. More specifically, we predict that linear disturbances result in changes in the co-occurrence patterns of sympatric predator species. We hypothesize that these changes may be driven by three different types of intraguild interactions.

First, wolves may exert top-down influences on subordinate predators that influence how the latter use the landscape (Estes et al., 2011). Wolves are commonly regarded as dominant over black bears, coyotes and lynx in direct confrontation, suggesting that these subordinate predators would seek to avoid encounters with wolves (Fuller & Keith, 1981; Palomares & Caro, 1999). However, predators also benefit from scavenging subsidies proffered by wolf kills and may thus have a facilitative interaction with wolves (Allen, Elbroch, Wilmers, & Wittmer, 2014; Atwood & Gese, 2008, 2010; Paquet, 1992; Wilmers, Crabtree, Smith, Murphy, & Getz, 2003). In addition, some mesocarnivores may indirectly profit from wolves via suppression of competitors, as demonstrated for red foxes (*Vulpes vulpes*; Levi & Wilmers, 2012; Sivy, Pozzanghera, Colson, Mumma, & Prugh, 2018) and suggested for lynx (Ripple, Wirsing, Beschta, & Buskirk, 2011).

Second, subordinate predators may experience intraguild competition from one another. Although there is little evidence in the literature of intraguild competition between black bears and other subordinate predators, competition between coyotes and lynx has been insinuated in areas of human disturbance (Bayne et al., 2008) and may influence habitat selection (Murray, Boutin, & O'Donoghue, 1994). Third, all three subordinate predators should track availability of their prey. Black bears predate boreal ungulates (Linnell, Aanes, & Andersen, 1995; Pinard, Dussault, Ouellet, Fortin, & Courtois, 2012). Both coyotes and lynx predate small mammals such as red squirrels (*Tamiasciurus hudsonicus*) and snowshoe hare (*Lepus americanus*), and coyotes also predate white-tailed deer (Latham, Latham, Boyce, & Boutin, 2013; O'Donoghue et al., 2001). Interspecific interactions are not necessarily mutually exclusive and may happen simultaneously within the same systems, including across separate spatial or temporal scales (Karanth et al., 2017; Sivy, Pozzanghera, Grace, & Prugh, 2017).

In this study, we investigated how apex predators —wolves—and subordinate predators—black bears, coyotes, and lynx—interact on a disturbed landscape by assessing spatiotemporal co-occurrences within a network of linear anthropogenic features. We developed predictions of co-occurrence patterns consistent with hypothesized interactions. Specifically, we predicted that (1) if black bears, lynx, and coyotes experience top-down pressures from wolves, they should spatiotemporally segregate from wolves; (2) subordinate predators should segregate from their intraguild competitors with whom they share resources (O'Donoghue et al., 2001; Guillaumet, Bowman, Thornton, & Murray, 2015); and (3) subordinate predators should overlap with their prey (Keim, DeWitt, & Lele, 2011; Theuerkauf, 2009). We further hypothesized that higher densities of disturbance would result in lower occurrences of black bears, but higher occurrences of lynx and coyotes (Fisher & Burton, 2018), and that coyotes and lynx would occur less frequently in the winter (Pozzanghera, Sivy, Lindberg, & Prugh, 2016).

To test these hypotheses, we modeled black bear, coyote, and lynx spatiotemporal occurrences in relation to wolf and prey occurrences, and coyote and lynx spatiotemporal occurrences relative to one another (Table 1). We further compared the effects of interspecific interactions on predator occurrences with the effects of season and anthropogenic disturbance, allowing for interactions between the two (Table 1).

## 2 | METHODS

### 2.1 | Sampling design

Our study was located along the east side of the Athabasca River, approximately 70 km southwest of Fort McMurray, Alberta, Canada (56.2588 N, 112.6909 W; Figure 1). The 570-km$^2$ study area is

**TABLE 1** Candidate model sets to test the relative effect of interspecific interactions on predator occurrences

| Species | Hypothesis—Predator occurrence best explained by | Predictor variables |
|---|---|---|
| Mesocarnivore 1 | Habitat | Significant forest cover variables from step 1 |
| | Anthropogenic features | Linear density (LD) + Habitat |
| | Seasonality | Snow + Habitat |
| | Apex predator | Wolf + Habitat |
| | | Wolf + Snow + Habitat |
| | | Wolf × Snow + Habitat |
| | | Wolf + LD + Habitat |
| | | Wolf × LD + Habitat |
| | Intraguild competition | Mesocarnivore2 + Habitat |
| | | Mesocarnivore2 + Snow + Habitat |
| | | Mesocarnivore2 × Snow + Habitat |
| | | Mesocarnivore2 + LD + Habitat |
| | | Mesocarnivore2 × LD + Habitat |
| | Predation opportunities | Prey + Habitat |
| | | Prey + Snow + Habitat |
| | | Prey × Snow + Habitat |
| | | Prey + LD + Habitat |
| | | Prey × LD + Habitat |
| Black bear | Habitat | Significant forest cover variables from step 1 |
| | Anthropogenic features | LD + Habitat |
| | Apex predator | Wolf + Habitat |
| | | Wolf + LD + Habitat |
| | | Wolf × LD + Habitat |
| | Predation opportunities | Prey + Habitat |
| | | Prey + LD + Habitat |
| | | Prey × LD + Habitat |

*Note:* Models were negative binomial GLMs at the spatial-only scale, and binomial GLMMs at the two spatiotemporal scales. Each model set corresponds to a hypothesized interspecific interaction. We tested models with co-occurring species as a predictor variable against three base models describing environmental effects. Candidate model sets for mesocarnivores (coyote and lynx) are identical, with mesocarnivore 1 describing the responding predator and mesocarnivore 2 describing the co-occurring intraguild competitor (e.g., when mesocarnivore 1 is coyote, mesocarnivore 2 is lynx and vice versa). At the spatial-only scale of analysis, we excluded season models for all species because the response variable aggregated detections across the entire survey period.

bounded to the north and west by the Athabasca River and has linear feature density of 1.1 km/km$^2$, including 523.6 km of seismic lines (Figure 1; Alberta Biodiversity Monitoring Institute, abmi.ca). We deployed Reconyx PC900 HyperFire camera traps (Reconyx, Holman, WI) between November 2015 and 2016 as part of an ongoing monitoring project assessing wildlife responses to seismic line restoration. One of the objectives of this restoration was to deter predator movements, but the effect on predator line use was minimal (Tattersall, Burgar, Fisher, & Burton, 2019). We selected 60 camera sites (Figure 1) based on a stratified random design to sample along seismic lines that spanned a gradient of restoration strata. We installed one camera at each site at a height of approximately 1 m and facing across a seismic line. Cameras were set up at least 500 m apart to increase the probability of independent detections (Tigner et al., 2014). We set all cameras to take one image per trigger, with a one-second lag between triggers and no quiet periods.

We considered a survey period as 30 continuous months between November 2015 and April 2018 for coyotes and lynx, and the two eight-month periods between April and October 2016 and 2017 for black bears. We treated detection events of the same species as independent when occurring at least 30 min apart (Rovero & Zimmermann, 2016). All methods for wildlife monitoring were approved by the Canadian Council of Animal Care administered by the University of British Columbia (protocol A17-0035).

## 2.2 | Analytical framework

For large mammal species ranging across entire landscapes, interspecific interactions can be inferred using spatiotemporal relationships of species occurrences (Cusack et al., 2016; Karanth et al., 2017; Swanson, Arnold, Kosmala, Forester, & Packer, 2016).

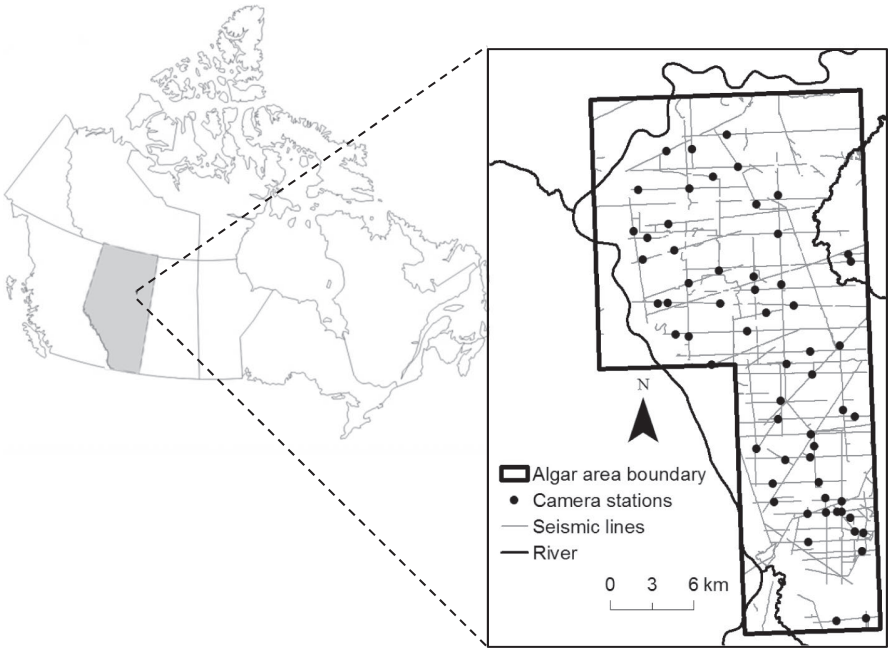


**FIGURE 1** The study area, camera trap locations, and linear disturbances along the east side of the Athabasca River (56.2588 N, 112.6909 W). The inset map shows the location of the study area in Alberta, Canada

Correlation is not equivalent to causality, but examining these associations reveals whether patterns in predator co-occurrences are consistent with those predicted from interspecific interactions.

For interactions between predators, we assumed segregation of occurrences in space or time was suggestive of competition, while overlap in space and time was suggestive of facilitation (Cusack et al., 2016; Fahrig, 1992; Frey, Fisher, Burton, & Volpe, 2017; Karanth et al., 2017). To address multiple potential scales of interactions, we examined predator co-occurrences at the spatial-only scale (i.e., entire survey period) and at two finer spatiotemporal scales (weekly and daily). We predicted that spatial segregation was indicative of competition (Fuller & Keith, 1981), whereas spatial overlap alone indicated weak or indirect interactions. We assumed that overlap at finer spatiotemporal scales—where species co-occur at a given location within a given occasion length—suggested intentional proximity between two species, and thus was evidence of a facilitative interaction (Cusack et al., 2016; Swanson et al., 2016).

### 2.2.1 | Spatial relationships in species' occurrences

To examine spatial relationships between predators, we tested the degree to which spatial variation in species detections across the entire survey (i.e., relative abundance or frequency of use) was explained by the detections of potentially interacting species, using number of independent detections per camera trap site as the response variable. We included each camera's survey effort (number of days active) as a predictor variable, thus accounting for the effect of periods of camera inactivity on detections. This predictor variable was the only fixed effect in the null model and excluded from comparisons of effect size. We modeled detections in a generalized linear model (GLM) framework using a negative binomial distribution for overdispersed count variables (Bolker, 2009). We conducted all statistical analyses using the R package *glmmTMB* (Brooks, Kristensen, & Benthem, 2017).

### 2.2.2 | Fine and coarse spatiotemporal scales of occurrence

To test whether species co-occurring in space were also co-occurring in time, we examined co-occurrences at two temporal scales. At the finest temporal scale, we recorded the presence (1) or absence (0) of a species' at a given site within each day, producing a binary occurrence metric for each camera trap day. Although methods exist for assessing finer scale temporal niche partitioning, they require large amounts of detection data (Frey et al., 2017; Swanson et al., 2016; Wang, Allen, & Wilmers, 2015). Given our observed detection rates, a daily occasion length was the finest temporal scale we could reliably model. However, a single day occasion length results in low detection rates, leading to zero-inflated occurrence data (Rovero & Zimmermann, 2016). We therefore also discretized occurrence data into week-long periods to assess whether results were consistent across temporal scales. For both spatiotemporal scales, we modeled occurrences using binomial generalized linear mixed effects models (GLMMs; Cusack et al., 2016). We included a random effect of camera trap site to account for repeated (nonindependent) sampling within sites. We omitted inactive days from the daily occurrence analysis and included the predictor variable *proportion of active days per week* in the weekly occurrence analysis.

## 2.3 | Modeling approach

### 2.3.1 | Habitat modeling and scale analysis

We analyzed data using a two-step process: species-habitat modeling followed by co-occurrence modeling (Chow-Fraser, 2018; Cusack et al., 2016). In the first step, we modeled species response to habitat at multiple spatial scales (Fisher, Anholt, & Volpe, 2011; Levin, 1992). We ranked species-habitat models at multiple spatial scales using model selection with Akaike's information criterion (AIC, Burnham & Anderson, 2002) to determine the characteristic scale of selection (i.e., scale of best ranked model; Fisher, Anholt, & Volpe, 2011). Each habitat model consisted of six variables describing forest cover types predicted to have an effect on predator occurrence (Latham et al., 2013; Poole, Wakelyn, & Nicklen, 1996; Tigner et al., 2014). We used Alberta Vegetation Inventory digital forest data (AVI; Alberta Vegetation Interpretation Standards 2005) and reclassified by dominant tree species and moisture regime, to create five habitat variables describing forest types (Table 2; Fisher & Burton, 2018). Additionally, we included a predictor variable for the proportion of open forest as a measure of forest density (Murray et al., 1994). We quantified the proportion of each variable around cameras within buffers of 250- to 2000-m radius (spatial scales), at intervals of 250 m. This resulted in eight habitat models, consisting of six habitat variables, one for each spatial scale (and each consisting of the six habitat variables). We used AIC model selection to compare among models and retained the characteristic scale of selection and significant habitat variables of the best supported (lowest AIC) model in the subsequent stage of modeling co-occurrences (described below; Figure 3a and Figure 4). We extracted all spatial variables using the R packages *rgeos* and *rgdal* (Bivand & Rundel, 2019; Bivand, Keitt, & Rowlingson, 2019).

### 2.3.2 | Co-occurrence modeling

In the second step of our two-step approach, we added heterospecific occurrences as variables to the best supported habitat model and weighed evidence for their ability to explain additional variation in predator occurrences (Table 1; Fisher et al., 2013). We created a model set for each of the interactions hypothesized to influence black bears, coyotes, and lynx, namely top-down influences from wolves, bottom-up influences from prey species, or competitive influences of lynx and coyotes on each other. We excluded models assessing interspecific interactions between black bears and coyotes or lynx because we found no supporting evidence for these interactions in the literature (Table 1). To assess influences of prey, we included a variable aggregating detections of all prey species for each of the target predators (Table 2). As we further predicted that the strength of interspecific interactions could be influenced by season and level of anthropogenic disturbances, we also included additive and interaction models with variables for snow presence and linear density (Table 1). Linear features are the most prevalent anthropogenic disturbance within the study area (Tattersall et al., 2019); therefore, we considered the effects of other anthropogenic features to be negligible. We tested all co-occurrence models against three base models (i.e., models without species interactions): one with only habitat variables, one with snow presence and habitat, and one with linear density and habitat. Because black bears are inactive in the winter, we only included snow presence in model sets for lynx and coyotes. At the spatial-only scale, we excluded season from the analysis for all species because the response variable aggregated detections across the entire survey period.

We assessed snow presence from daily "time-lapse" images, using the camera trapping software Timelapse 2.0 Image Analyzer (Greenberg & Godin, 2015; http://saul.cpsc.ucalgary.ca/timelapse). Snow was measured as a binary variable at the daily scale and a proportion at the weekly scale (i.e., mean number of days on which snow was present; Table 1). We considered snow to be present if it covered over 50% of the line surface within the camera's field of view. As with forest cover variables, we conducted a scale analysis to obtain appropriate scales of measurement for linear density for each species (Figure 3b). We used data exploration techniques prior to modeling to assess all predictor variables for outliers, collinearities, and heterogeneity of variance (Zuur, Ieno, & Elphick, 2010). We also scaled all nonbinary variables by subtracting the mean and dividing by two standard deviations, thus improving model convergence and interpretation (Gelman, 2008).

## 2.4 | Model interpretation and model validation

Following co-occurrence modeling, we compared candidate models using AIC model selection to determine whether interspecific interactions influenced predator occurrences at each of the three spatiotemporal scales. We considered all models within 2ΔAIC of the top-ranked model as having similar explanatory power over the data (Burnham & Anderson, 2002). We consequently examined variables in these models for their influence on predator occurrence, with mean parameter estimates as measures of effect size and direction and 95% confidence intervals as measures of statistical significance (i.e., not overlapping zero). We used pseudo-$R^2$ to assess the proportion of variance explained by the top models for each species relative to the proportion of variance explained by a null model (McFadden, 1974). We considered $R^2$ values between 0.2 and 0.4 to be indicative of good model fit (McFadden, 1977).

In both top-ranked models for coyotes and lynx at the daily scale, standard errors around the estimates for interacting species were over three orders of magnitude larger than the estimates (−15.730 [−7943, 7912] for the top coyote model and −15.763 [−8613, 8582] for the top lynx model), and patterns in the model residuals indicated model misspecification. We therefore removed these models from all subsequent analyses.

**TABLE 2** Full list of predictor variables used to model occurrence patterns of black bears, lynx, and coyotes

| Predictor variables | Step of modeling process | Description |
|---|---|---|
| pOpen | 1 | Proportion of forest with <50% density surrounding camera stations |
| UpCon | 1 | Proportion of forest with black spruce (*Picea mariana*), white spruce (*Picea glauca*), balsam fir (*Abies balsamea*), or jack pine (*Pinus banksiana*) as a dominant tree species and a dry or mesic moisture regime |
| LowCon | 1 | Proportion of forest with black spruce (*Picea mariana*), white spruce (*Picea glauca*), balsam fir (*Abies balsamea*), or jack pine (*Pinus banksiana*) as a dominant tree species and a wet or aquatic moisture regime |
| UpDecid | 1 | Proportion of forest with trembling aspen (*Populus tremuloides*), balsam poplar (*Populus balsamifera*), or paper birch (*Betula papyrifera*) as a dominant tree species and a dry or mesic moisture regime |
| LowDecid | 1 | Proportion of forest with trembling aspen (*Populus tremuloides*), balsam poplar (*Populus balsamifera*), or paper birch (*Betula papyrifera*) as a dominant tree species and a wet or aquatic moisture regime |
| Tamarack | 1 | Proportion of forest with Tamarack (*Larix laricina*) as a dominant tree species |
| Wolf | 2 | Binary presence (1)/ absence (0) of wolves per site per day or week; number of detections of wolves per site |
| Lynx | 2 | Binary presence (1)/ absence (0) of lynx per site per day or week; number of detections of lynx per site |
| Coyote | 2 | Binary presence (1)/ absence (0) of coyotes per site per day or week; number of detections of coyotes per site |
| Prey | 2 | Binary presence (1)/ absence (0) of prey species[1] per site per day or week; number of detections of prey per site. |
| LD | 2 | Linear density measured as total length of linear features divided by a given area surrounding camera stations |
| Snow | 2 | Binary presence (1)/ absence (0) of snow per site per day, or number of snow days/ total days in a weekly sampling period. We marked snow as 'present' in daily time-lapse images if it covered 50% of the seismic line surface within the camera's field of view |

*Note:* [1]Prey species consisted of snowshoe hare (*Lepus americanus*) and red squirrel (*Tamiasciurus hudsonicus*) for lynx; hare, squirrel, and white-tailed deer (*Odocoileus virginianus*) for coyotes; and deer, moose (*Alces alces*), and caribou (*Rangifer tarandus*) for black bears (Latham et al., 2013; Zager & Beecham, 2006; Linnell et al., 1995; O'Donoghue et al., 2001)

For each species, we included all habitat variables in the first step of the modeling process, and retained habitat variables with confidence intervals that did not overlap zero to create a null model for the second step. We measured forest cover variables from the Alberta Vegetation Inventory (Alberta Vegetation Interpretation Standards, 2005) and linear feature data from the Alberta Biodiversity Monitoring Institute (ABMI, abmi.ca). We used camera trap data to extract all species occurrence and snow variables. Species' variables differed with modeling scale, as spatiotemporal scale affected occasion length and thus occurrence aggregation.

## 3 | RESULTS

From November 2015 to April 2018, total sampling effort was 14,054 camera-days for black bears (during their active season) and 32,436 camera-days for all other species (year-round). Of the four focal boreal predator species, black bears and wolves were detected most frequently, followed by coyotes and lynx (Table 3). At the daily spatiotemporal scale, both coyotes and lynx infrequently co-occurred with interacting species, and lynx infrequently co-occurred with their prey at the weekly scale (Table 3). For all species, models at the daily and weekly scales explained relatively little variance in occurrence data (pseudo-$R^2$ = 0.008–0.074), while models at the spatial-only scale performed much better (pseudo-$R^2$ = 0.166–0.283; Table 4).

Heterospecific occurrences were significant predictors of all three predators' occurrences, explaining variance in addition to that explained by habitat and anthropogenic features. Wolves had a positive association with all three other predators on at least one spatiotemporal scale. This effect was most consistently seen for black bears, which significantly co-occurred with wolves at the spatial-only, weekly, and daily scale ($\beta$ = 1.11 [0.503, 1.722], 0.774 [0.277, 1.271], and 0.807 [0.226, 1.389], respectively; Figure 2). At the spatial-only scale, when wolves occurred more frequently at higher linear densities, black bears also occurred more frequently ($\beta$ = 1.850 [0.374, 3.326]). Coyotes co-occurred with wolves at the weekly scale ($\beta$ = 0.857 [0.175, 1.538]), but not at the spatial-only or daily scales (Figure 2). Lynx, on the other hand, only co-occurred with wolves at the spatial-only scale ($\beta$ = 0.499 [0.081, 0.918]), not on spatiotemporal scales (Figure 2).

Prey models were included in the top-ranked models for lynx at the both the spatial-only and weekly occurrence scales (Table 4). Lynx were less likely to occur at high linear density sites where prey were present ($\beta$ = −1.074 [−1.934, −0.214] at the spatial-only scale; Figure 2). Black bears and coyotes were not affected by prey occurrences at any scale (Table 4).

The occurrence of other mesocarnivores was not a strong predictor for either coyotes or lynx. For coyotes, models with lynx were included among top-ranked models at the daily and weekly scales, but neither main effects nor season and linear density interactions were significant predictors. The same was true for lynx, although coyote occurrences only helped explain lynx occurrences at the daily scale (Table 4).

All three predators responded to linear density on at least two scales, but the direction and scale of influence differed across species. Black bear occurrences decreased with linear density at both the weekly and the daily scales ($\beta$ = −0.729 [−1.326, −0.131] and −0.715 [−1.347, −0.075], respectively; Figure 2). Conversely, both coyote and lynx occurrences increased with linear density at the spatial-only and weekly scales ($\beta$ = 2.651 [1.794, 3.507] and 2.214 [1.322, 3.106] for coyotes; 0.878 [0.229, 1.528] and 0.995 [0.283, 1.707] for lynx; Figure 2). The characteristic scale of selection for linear density was comparable for all three species (1500 m for black bears and coyotes, 1750 m for lynx) and remained constant at all three spatiotemporal scales of analysis (Figure 3b). Season was included in the top-ranked model for both coyote and lynx at the daily scale, but did not affect occurrences for either species (Table 4).

All three predators occurred less frequently as the proportion of open forest increased on all three spatiotemporal scales of analysis (Figure 4). This significant habitat relationship was retained at all spatiotemporal scales with the inclusion of species' interactions for black bears and lynx, and at the weekly and daily scales for coyotes (Figure 2). Additionally, lynx occurrences increased with proportions of lowland and upland coniferous forest at all three scales prior to adding interspecific interactions (Figure 4). After the inclusion of occurrence variables, lynx retained the positive relationship with lowland coniferous forest at all scales and the relationship with upland coniferous forest at the spatial-only scale (Figure 2). Black bear occurrences also increased with proportions of tamarack and lowland and upland coniferous forest at the spatial-only scale and retained the positive relationship with upland coniferous forest with the inclusion of species' interactions (Figure 2). The characteristic scales of selection for natural habitat variables were smallest for black bears (250 m) and highest for coyotes and lynx (1750 m and 1500 m, respectively; Figure 3a). As with spatial-only scales for linear density, the characteristic scales for each species remained constant across all spatiotemporal scales of analysis.

## 4 | DISCUSSION

### 4.1 | Inferring interspecific interactions from predator co-occurrences

Black bears, coyotes, and lynx all co-occurred with wolves on at least one of the spatial and temporal scales observed in our study (Figure 2). This suggests either that wolf spatial ecology is a determinant of space use by subordinate predators in working landscapes or that all predator species are cueing into the same resources in time and space in this complex environment (DeMars & Boutin, 2018). The poor fit of all models at the weekly and daily scales suggests that either our models do not account for other sources of variation at these finer temporal scales or our detection rates are too low to meaningfully interpret species co-occurrences. Nevertheless, our results point toward patterns in predator use of the boreal working landscape, particularly their use of linear features. Spatiotemporal correlations among predators have potential implications for managing multipredator communities and their prey, making it crucial to understand factors underlying these relationships.

Relative to other species, wolves and black bears occur at high densities in the boreal forest (Burgar, Burton, & Fisher, 2018), and both select industrial linear features for easy travel, making them likely candidates for strong interspecific interactions in industrializing landscapes (Latham, Latham, & Boyce, 2011; Latham, Latham, Boyce, & Boutin, 2011). Although anecdotal evidence describes aggressive interactions between individual wolves and bears (Palomares & Caro, 1999; Rogers & Mech, 1981), we propose that spatiotemporal overlap at the daily scale may be consistent with facilitative interaction between the two. Black bears were more likely to occur at a site even within a day of wolf occurrences, mirroring spatiotemporal patterns in lion-kill scavengers in Africa (Cusack et al., 2016; Swanson et al., 2016). Further, we found that black bears occurred more frequently at high linear density sites when wolves frequently occurred at those sites. Black bears are adept scavengers and may benefit considerably from carrion subsidies left by wolves (Allen et al., 2014; Wilmers et al., 2003). However, our results indicate that there are additional factors influencing black bear occurrences that were not included in our study (i.e., much unexplained variance in occurrences). Further research should investigate these sources of variance, as well as explore time elapsed between predator occurrences or analyze patterns in occurrences (i.e., which species occurs first) to observe these relationships at a finer temporal resolution (Schliep, Gelfand, Clark, & Kays, 2018; Swanson et al., 2016).

The positive association between coyotes and wolves at coarse spatiotemporal scales may also be a result of facilitation (Figure 2). Positive coyote–wolf interactions have been observed elsewhere (Atwood & Gese, 2008, 2010; Paquet, 1991, 1992; Sivy et al., 2017). However, as sympatric canid species with considerable niche overlap, coyotes and wolves are also likely to experience strong competition in which wolves frequently kill coyotes (Palomares & Caro, 1999; Paquet, 1991). We hypothesize this paradox could reflect density-dependent interactions: Where coyotes exist in low densities, they segregate themselves from wolves to reduce competition. When coyotes exist in high densities, they may be able to reduce competition through behavioral mitigations such as increased group size or fine-scale temporal partitioning, thus increasing the benefits of scavenging (Atwood & Gese, 2008, 2010). Coyote density (2.64/100 km$^2$) eclipsed wolf density (0.77) by threefold south of our study area (Burgar et al., 2018). Densities have not yet been estimated in our study area, but wolf detections exceeded coyote

**TABLE 3** Total co-occurrences of predator species across three spatiotemporal scales of analysis

| Spatiotemporal scale | | Wolf | Prey | Black bear | Lynx | Coyote |
|---|---|---|---|---|---|---|
| Day | Black bear | 15 | 16 | | – | – |
| | Lynx | 2 | 1 | – | | 2 |
| | Coyote | 2 | 8 | – | 2 | |
| | Total | 179/295 | – | 315 | 71 | 131 |
| Week | Black bear | 33 | 55 | | – | – |
| | Lynx | 5 | 2 | – | | 6 |
| | Coyote | 15 | 22 | – | 6 | |
| | Total | 124/224 | – | 226 | 67 | 106 |
| Spatial-only | Black bear | 38 | 43 | | – | – |
| | Lynx | 23 | 18 | – | | 17 |
| | Coyote | 21 | 18 | – | 17 | |
| | Total occupied sites | 46 | – | 44 | 27 | 23 |
| | Total detections (across sites) | 334 | – | 360 | 73 | 154 |

*Note:* Each value represents the total number of times both species were present at the same site and—for weekly and daily scales—within the same occasion. Rows represent response variables, and columns represent predictor variables. The total occurrences of wolves are given both within the summer-only sampling period for black bears (14,054 site-days) and the full sampling period for coyotes and lynx (32,436 site-days). Cells are marked with a dash where no interactions were hypothesized or tested.

**TABLE 4** Model selection tables of models of top-ranked models for black bears, coyotes, and lynx

| Species | Scale | Predictor variables | *k* | ΔAIC | AICwt | $R^2$ |
|---|---|---|---|---|---|---|
| Black bear | Day | Wolf + LD +pOpen | 5 | 0.00 | 0.510 | 0.00818 |
| | | Wolf × LD + pOpen | 6 | 1.66 | 0.223 | 0.00805 |
| | Week | Wolf + LD +pOpen | 6 | 0.00 | 0.533 | 0.0196 |
| | | Wolf × LD + pOpen | 7 | 1.23 | 0.289 | 0.0201 |
| | Spatial-only | Wolf × LD + pOpen +UpCon + LowCon +Tamarack | 10 | 0.00 | 0.752 | 0.166 |
| Coyote | Day | Lynx × season + pOpen | 6 | 0.00 | 0.373 | 0.0513 |
| | | Season + pOpen | 4 | 1.16 | 0.209 | 0.0475 |
| | | Lynx + season +pOpen | 5 | 1.28 | 0.196 | 0.0489 |
| | Week | Wolf + LD +pOpen | 6 | 0.00 | 0.420 | 0.0561 |
| | | Wolf × LD + pOpen | 7 | 1.25 | 0.225 | 0.0571 |
| | | Lynx × LD + pOpen | 7 | 1.53 | 0.195 | 0.0567 |
| | Spatial-only | Wolf + LD +pOpen | 6 | 0.00 | 0.270 | 0.241 |
| | | LD + pOpen | 5 | 0.47 | 0.214 | 0.228 |
| | | Wolf × LD + pOpen | 7 | 0.78 | 0.183 | 0.247 |
| Lynx | Day | Coyote × season + pOpen +LowCon + UpCon | 8 | 0.00 | 0.220 | 0.0554 |
| | | Season + pOpen +LowCon + UpCon | 6 | 0.26 | 0.193 | 0.0510 |
| | | Coyote + season +pOpen + LowCon +UpCon | 7 | 0.34 | 0.186 | 0.0530 |
| | | Wolf + season +pOpen + LowCon +UpCon | 7 | 1.21 | 0.121 | 0.0521 |
| | | Wolf × season + pOpen +LowCon + UpCon | 8 | 1.36 | 0.112 | 0.0540 |
| | Week | Prey × LD + pOpen +LowCon + UpCon | 9 | 0.00 | 0.597 | 0.0744 |
| | Spatial-only | Wolf + LD+pOpen + LowCon +UpCon | 8 | 0.00 | 0.360 | 0.279 |
| | | Prey × LD + pOpen +LowCon + UpCon | 9 | 1.24 | 0.194 | 0.283 |
| | | Wolf × LD + pOpen +LowCon + UpCon | 9 | 1.48 | 0.172 | 0.282 |

*Note:* For each species, top-ranked models are shown for each of the three spatiotemporal scales of analysis. Top-ranked models were those within 2ΔAIC of the highest weighted model. The column *k* is the number of parameters in the model, ΔAIC indicates the difference in AIC scores from the top model, and $R^2$ is a pseudo-$R^2$ measure describing the proportion of variance explained by each model relative to the variance explained in the null model. The top models for coyote and lynx at the daily scale were not included in subsequent analyses due to large confidence intervals.

detections, suggesting lower coyote relative abundance. Coyotes in this area may therefore be avoiding direct competition but benefitting indirectly via scavenging. This would be consistent with the observed co-occurrence at the weekly scale and lack thereof at the daily scale. However, as we did not observe segregation at the daily scale and these models had substantial unexplained variance, this hypothesis requires further inquiry.

Lynx and wolves spatially co-occurred, but did not temporally co-occur with wolves at the weekly or daily scale (Figure 2). This suggests that although lynx share a landscape with wolves, they may not interact at finer temporal scales. We also found an unexpected negative interaction between lynx prey and linear density at the weekly scale, where lynx were less likely to occur at high linear density sites where their prey were present. This result may be a spurious result arising from low co-occurrences between lynx and their prey ($n$ = 2; Table 3). Given the poor fit of this model, we suggest that further research is needed on additional factors influencing lynx occurrences at fine temporal scales to elucidate this finding.

The negative effect of linear density on black bears, as well as the positive effect on coyotes and lynx, agrees with previous research conducted in northern Alberta (Fisher & Burton, 2018; Toews et al., 2018). We only found evidence of black bear and wolf co-occurrences changing as a function of anthropogenic disturbance at the spatial-only scale, indicating increasing overlap between these predators with increasing anthropogenic disturbance. This was also seen by other studies in tropical, semiurban, and mountain ecosystems (Chow-Fraser, 2018; Karanth et al., 2017; Wang et al., 2015). This system has less of a disturbance gradient than other landscapes in Alberta's boreal forest (Government of Alberta, 2017), which might explain the lack of response from other species or at finer temporal scales. Further, humans are largely absent from the study area, so direct human influence on interspecific interactions would be minimal. To better assess the influence of anthropogenic disturbance on interspecific interactions, a similar study could be conducted across a number of landscapes with varying levels and types of landscape change (Chow-Fraser, 2018).

An alternative interpretation of our results is that the overlapping occurrences we observed could be a result of predators responding to similar resource cues rather than responding to each other. Bears and wolves select linear features and linear feature density in similar ways (DeMars & Boutin, 2018; Finnegan et al., 2018), while coyotes and wolves may also sometimes select the same habitat (Latham et al., 2013). Like black bears and wolves, coyotes and lynx may also be using linear features as movement corridors, which may mean that all four predators prefer similar linear feature characteristics. This interpretation has important consequences for predator–prey dynamics in working landscapes, indicating high predation risk areas for prey species, particularly species at risk such as the woodland caribou (*Rangifer tarandus caribou*; DeMars & Boutin, 2018, Dickie, McNay, Sutherland, & Avgar, 2019). It would also indicate a change in functional habitat for predators, as their space use behaviors shift in

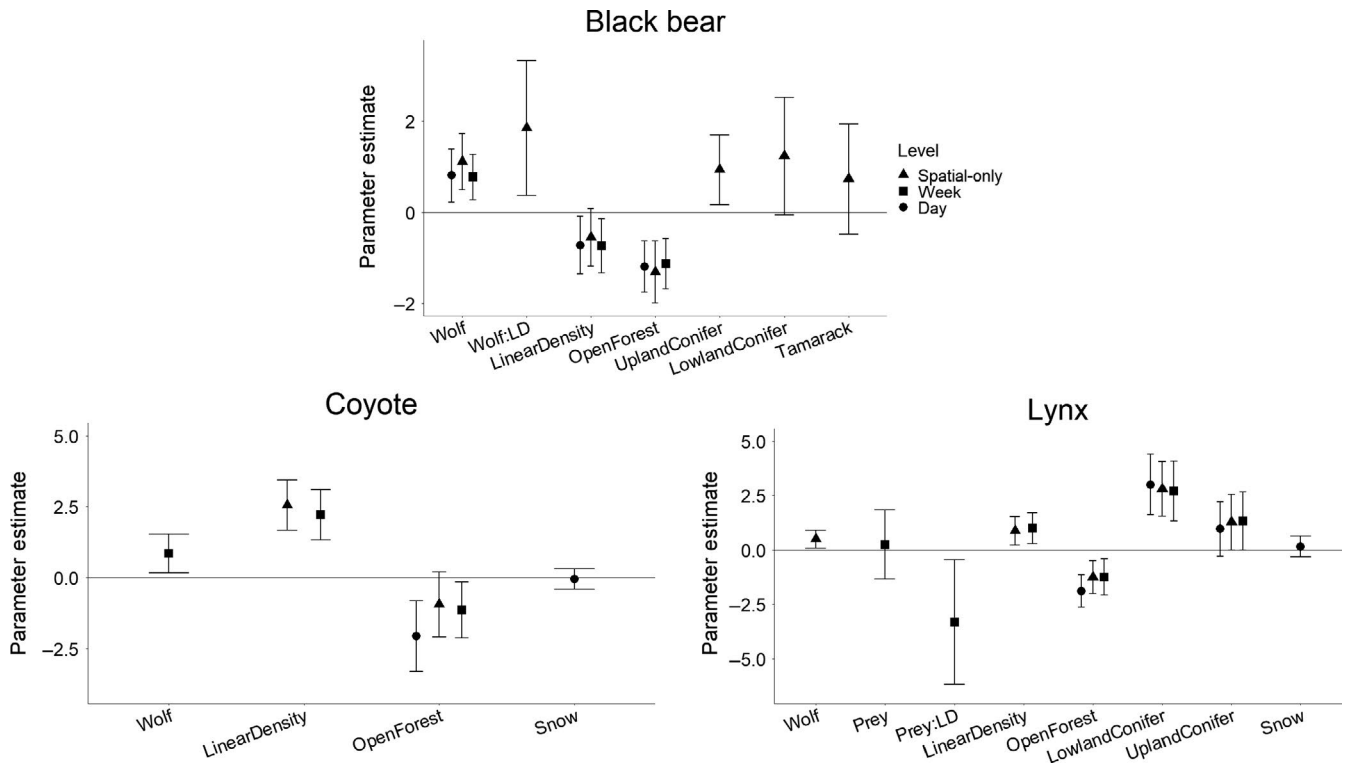


**FIGURE 2** Effects of interspecific interactions and environmental features on predator occurrences. Effect sizes are shown as parameter estimates (mean ± 95% confidence intervals) from negative binomial GLMs (spatial level) and binomial GLMMs (weekly and daily levels) of black bear, coyote, and lynx occurrences at three levels of analysis. Estimates are shown for the most parsimonious model within the top-ranked models. Estimates have not been back-transformed, and therefore, values are not directly interpretable in terms of predator occurrences

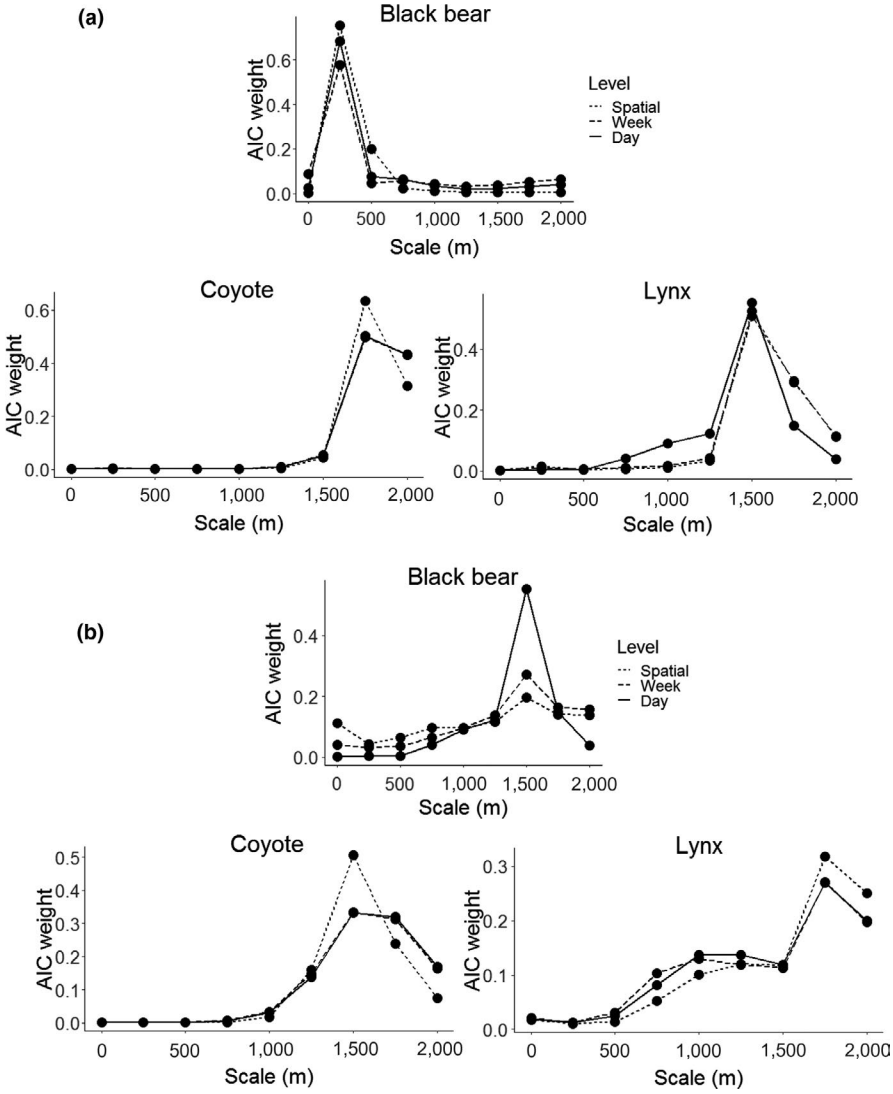


**FIGURE 3** AIC model weights indicating scale of influence for habitat features (a) and linear density (b). The scale with the most model weight indicated the scale that best explains occurrences of each predator species, as determined by using AIC model selection to compare identical models measured at different spatial scales

response to industrial land use (Fisher & Burton, 2018). We suggest that further research into characteristics influencing linear feature use by predators would provide insight into species co-occurrences in a working landscape.

## 4.2 | Limitations

Fine-scale temporal analyses of interspecific interactions often require large sample sizes of detections to reveal patterns in activity and co-occurrence (Frey et al., 2017). In our study, low numbers of occurrences—and consequently, co-occurrences—may have limited our ability to reliably model effects of interacting species (Table 3). Indeed, this is likely the cause of unexplained variance in our models at finer spatiotemporal scales. We urge caution when modeling co-occurrences from rare or elusive species at fine spatiotemporal scales. More robust methods to assess interactions for these species could use baited camera traps to increase detection probabilities (Stewart et al., 2016), include cameras in undisturbed habitat, or increase either spatial or temporal extent of the camera trap survey to increase sampling effort. Further, telemetry studies of interacting species could account for interspecific effects on movement patterns, thereby assessing how individual animals respond to space use by other species on a shared landscape (James, Boutin, & Hebert, 2004).

Caution is obviously necessary when inferring interactions and their mechanisms from co-occurrence data. Although techniques exist to derive interaction strength and predict mechanisms, such approaches are either nontemporal (Dorresteijn et al., 2015) or require large amounts of data (Schliep et al., 2018; Swanson et al., 2016) or even direct observation (Atwood & Gese, 2008; Cusack et al., 2016). Whereas we assume that species co-occurrences indicate intentional proximity and thus suggest facilitative interactions, co-occurrences of predators with similar niches may be equally indicative of species competing for a shared resource (Chow-Fraser, 2018). To make the distinction between interaction mechanisms, spatiotemporal patterns must be related to the underlying ecological process. Camera traps offer a unique opportunity to do so by enabling direct observation of interactions while simultaneously relating this information to spatiotemporal relationships on a landscape scale (Caravaggi et al., 2017).

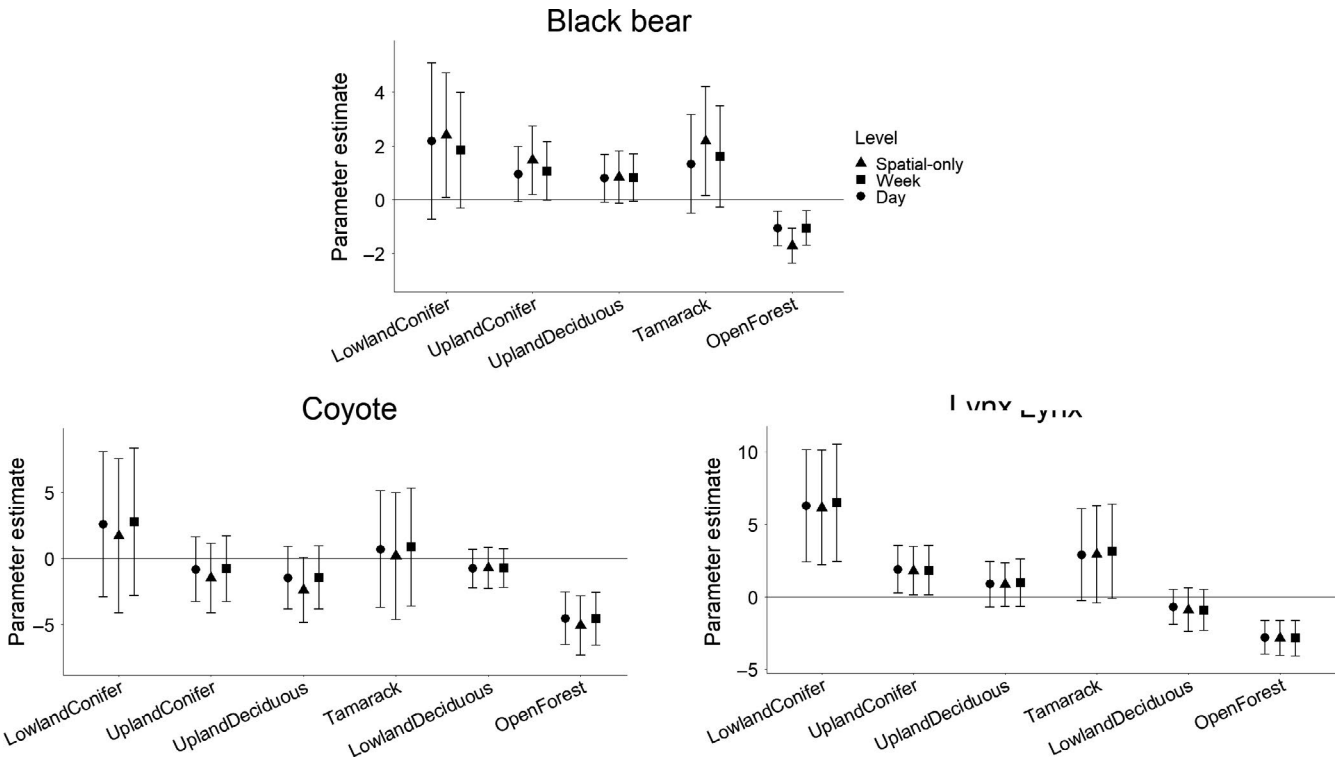


**FIGURE 4** Effects of habitat features on predator occurrences in the habitat modeling step of analysis. Effect sizes are shown as parameter estimates (mean ± 95% confidence intervals) from negative binomial GLMs (spatial level) and binomial GLMMs (weekly and daily levels) of black bear, coyote, and lynx occurrences at three levels of analysis. Results are shown from habitat variables measured at the optimal spatial scale of influence: 250 m for black bears, 1750 m for coyotes, and 1500 m for lynx. Note that LowDecid is absent for black bears because lowland deciduous forest did not occur with 250 m of any camera stations. Significant habitat variables (with confidence intervals that did not overlap zero) were then included in the second step of the analysis to model effects of interspecific interactions on predators

### 4.3 | Management implications

In response to growing wolf populations, and out of concern of high predation rates on woodland caribou, the government of Alberta implements annual wolf reduction programs within some caribou herds at high risk of extirpation (Government of Alberta, 2017; Hervieux, Hebblewhite, Stepnisky, Bacon, & Boutin, 2014). Although effective in boosting caribou numbers in the short term, wolf removal is controversial and has direct consequences for the interactions structuring the boreal mammal community (Darimont, Paquet, Treves, Artelle, & Chapron, 2018; Sivy et al., 2017). As wolf reduction programs continue in caribou ranges in western Canada, we suggest that research should focus not only on caribou response, but also on responses of other species in the boreal mammal community.

Interspecific interactions arise from coexisting species partitioning space, time, and life-sustaining resources on a shared landscape where such resources are limited (Schoener, 1974). Understanding those interactions enables us to predict how they will respond when perturbed, empowering us to make informed and proactive management decisions. Here, we showed that nonapex predators exhibit spatiotemporal overlap with an apex predator on a working landscape. This overlap identifies patterns in how these four boreal predators use this landscape, which may indicate facilitative interactions or responses to the same ecological signals. These species additionally show individual responses to anthropogenic disturbances, though responses vary and further investigation is necessary to evaluate consequences for interactions. Results from this study highlight important considerations of the impact of predator management decisions, which may unintentionally alter the behavior of coexisting species (Burgar et al., 2018). The relationships observed in this study occur in the context of a landscape experiencing ongoing industrial development, offering insight into species coexistence patterns in the face of continuing anthropogenic landscape change. To keep wildlife communities on such landscapes, we must commit to understanding the underlying relationships that allow them to thrive.

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## CONFLICT OF INTEREST

The authors have no competing interests to declare.

## AUTHOR CONTRIBUTIONS

ERT developed the research question and analytical framework, processed and analyzed data, and wrote the manuscript. ACB wrote the original funding proposals and developed the camera trap sampling design. JMB and ACB managed field operations, with input from JTF. ERT, JMB, JTF, and ACB acquired data, and JMB, ACB, and JTF assisted in data interpretation and provided conceptual feedback. All authors provided feedback on drafts of the manuscript.

## DATA AVAILABILITY STATEMENT

Model input data: Dryad https://doi.org/10.5061/dryad.hx3ffbg9x.

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# Appendix 7: Publication - Mammal seismic line use varies with restoration: Applying habitat restoration to species at risk conservation in a working landscape

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# Mammal seismic line use varies with restoration: Applying habitat restoration to species at risk conservation in a working landscape

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ABSTRACT

Restoration of degraded habitats is increasingly used to mitigate the effects of anthropogenic landscape change on wildlife populations, but wildlife responses to habitat restoration are often assumed rather than verified. In the western Canadian boreal forest, restoration of seismic lines-linear corridors cut for oil exploration-has been proposed to mitigate declines in woodland caribou (*Rangifer tarandus caribou*) driven by altered predator-prey dynamics in industrialized landscapes. Seismic lines fragment caribou habitat, facilitate predator (wolves *Canis lupus* and black bears *Ursus americanus*) movements, and may enhance apparent competition from white-tailed deer (*Odocoileus virginianus)* and moose (*Alces alces)*. Here, we tested the assumption that restoration provides immediate wildlife conservation benefits, using a caribou-boreal forest case study. We used camera traps to monitor seismic line use by caribou, their competitors, and predators following restoration in northeastern Alberta. We assessed species responses to four line strata: two restored (active and passive) and two unrestored (human-use and control). Three-to-six years after restoration, 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. Species responses to restoration were muted, indicating that restoration alone may not be immediately effective in stabilizing threatened caribou populations. Our results highlight that wildlife responses to restoration must be tested. We recommend rigorous wildlife monitoring following restoration, particularly when the indirect, interspecific effects of habitat change drive species endangerment or recovery.

## 1. Introduction

More than 75% of the Earth's terrestrial surface has now been modified by humanity's efforts to acquire resources (Venter et al., 2016). Such drastic landscape transformations trigger widespread responses in wildlife, altering their habitat use, activity patterns, and movement rates (Fisher and Burton, 2018; Wang et al., 2015; Tucker et al., 2018). Ultimately, anthropogenic disturbance is a primary contributor to global biodiversity loss (Maxwell et al., 2016), prompting calls to scale up habitat restoration efforts worldwide (Suding, 2011). However, proposed restoration solutions can be very costly (e.g. Hebblewhite, 2017) and are rarely evaluated for their conservation efficacy (Cooke et al., 2018).

Habitat restoration is the process of assisting the recovery of a disturbed ecosystem; it focuses on returning a disturbed landscape to a reference state by re-introducing or recovering native plant and animal species (McDonald et al., 2016; Shackelford et al., 2013). In doing so, restoration aims to re-establish complex processes that maintain biodiversity, improve ecosystem services, and make the landscape resilient to environmental stress (Brudvig, 2011; Suding et al., 2015). Restoration ecology – which applies the scientific method to restoration – is a relatively recent field that is only beginning to embrace theoretical and evidence-based guidance (Cooke et al., 2018; Shackelford et al., 2013). Outcomes of restoration can be unpredictable and, in the case of wild animals, often go unmeasured entirely (Fraser et al., 2015). All too frequently, site-level restoration is implemented under the assumption that vegetative regeneration will re-establish complex landscape processes, but the assumption is rarely challenged. Crucially, if restoration is aimed at re-building landscapes capable of sustaining wildlife, restoration planning must consider the wildlife community dynamics that the landscape originally supported (Fraser et al., 2015). Without a clear understanding of how restoration efforts impact species-landscape

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relationships, there is little hope of restoration reliably reinstating original landscape functionality.

Western Canadian boreal forests have been transformed into working landscapes where biodiversity competes for space with large-scale industrial development. Oil and gas extraction is a primary driver of boreal landscape change, generating a novel landscape unlike any produced through natural processes (Pickell et al., 2015). Exploration and in situ drilling create a vast network of linear corridors, of which seismic lines are the most common (Lee and Boutin, 2006; Pickell et al., 2015). Seismic lines fragment habitats by increasing the number and decreasing the size of forest patches, while increasing the amount of forest edge (Pattison et al., 2016). They also slow forest succession in this primarily lowland landscape (i.e. dominated by wetland areas, such as bogs and fens), altering abiotic processes at the microsite level that change vegetation successional trajectories (Dabros et al., 2018; Lee and Boutin, 2006). The result of decades of petroleum exploration is an extensive network of "legacy", or conventional, seismic lines, which are 10–40 years old, 5 − 10 m wide (Dabros et al., 2018) and predicted to remain on the landscape for over 50 years (van Rensen et al., 2015).

Such widespread and persistent networks of linear disturbances affect relationships between species and their landscape, which can in turn have cascading influences on community structure (Fisher and Burton, 2018). Perhaps the most dramatic of these consequences is ongoing and precipitous declines of populations of the woodland caribou (*Rangifer tarandus caribou,*hereafter caribou). Federally listed as threatened in 2002 (COSEWIC, 2002), caribou have declined in part due to changes in predator-prey encounter rates caused by seismic lines, as well as human-mediated apparent competition (McLoughlin et al., 2003; Hervieux et al., 2013). In addition to effects of a warming climate, widespread replacement of mature forest with early seral vegetation has facilitated the northward expansion of white-tailed deer (*Odocoileus virginianus*, hereafter deer; Dawe et al., 2014), which has in turn driven increases in grey wolf (*Canis lupus)*, and subsequently amplified predation pressures on caribou (Latham et al., 2011a). Linear corridors also influence wolf movement by increasing their travel distance and speed across challenging lowland terrain (McKenzie et al., 2012; Dickie et al., 2016) and increasing wolf encounters with caribou (Mumma et al., 2017). Within the boreal forest, caribou have historically mitigated predation risks from wolves by avoiding moose (*Alces alces*) habitat (James et al., 2004). However, the increasingly fragmented landscape has enhanced spatial overlap between moose and caribou and improved wolf access to caribou habitat (Peters et al., 2013; Dyer et al., 2002). Facilitation of wolf movement by seismic lines thus likely increases wolf predation on caribou (Dickie et al., 2016). In addition, black bear (*Ursus americanus)* use of seismic lines could contribute to caribou calf mortality by increasing caribou encounter rates with this opportunistic predator (Latham et al., 2011a,b; Tigner et al., 2014). As caribou prefer lowland bog and fen habitats (James and Stuart-Smith, 2000; Stuart-Smith et al., 1997) where natural regeneration of seismic lines is negligible, these altered predator-prey dynamics are predicted to persist, posing a lasting threat to boreal caribou populations (van Rensen et al., 2015).

Given their widespread footprint and lack of natural regeneration, seismic lines are a high priority target for habitat restoration in western Canada's boreal forests. To return the landscape to its previous functionality (i.e. the ecological processes occurring in the absence of anthropogenic disturbance), restoration should recreate the natural vegetation structure and species on lines (Shackelford et al., 2013; Dabros et al., 2018). At the very least, it should provide resistance to predator movement and facilitate caribou habitat regeneration by reducing early seral vegetation preferred by alternate prey species (Ray, 2014; Bentham and Coupal, 2015). Thus, habitat restoration is considered a promising tool for caribou conservation, but one that has rarely been tested (Bentham and Coupal, 2015).

In this study, we evaluated the assumption that habitat restoration restores the dynamics of animal communities impacted by habitat disturbance. Specifically, we used a large-scale restoration program to test predictions about short-term (i.e. in the years immediately following restoration) responses of mammal species implicated in caribou recovery. We used camera traps (Burton et al., 2015) to monitor seismic line use by caribou, wolves, black bears, white-tailed deer, and moose across four restoration strata: actively restored lines ("active"), passively restored lines ("passive"), human-use lines ("human-use"), and unrestored control lines ("control") (Fig. 1, Fig. A1, and Appendix A1). We hypothesized that if seismic line restoration is to be effective for caribou conservation, it should re-establish boreal landscape functionality by spatially segregating caribou from their predators and apparent competitors. That is, relative to control lines, we predicted that restored

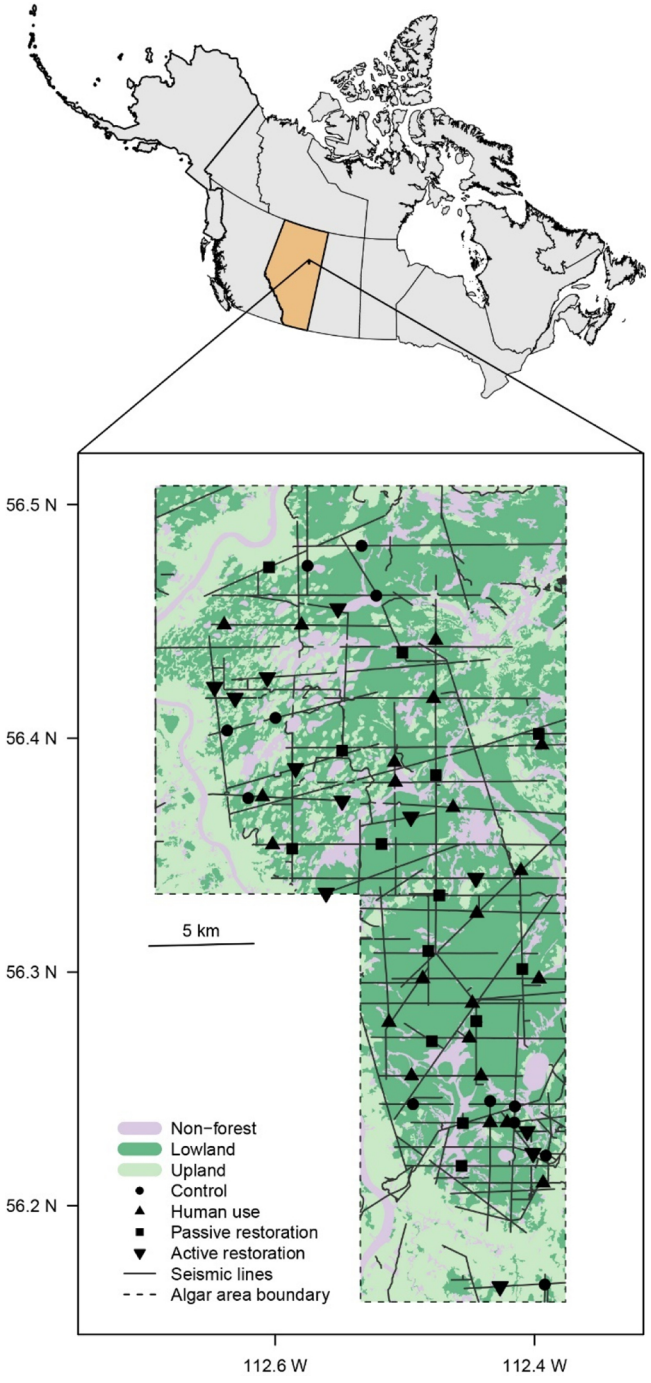


**Fig. 1.** The Algar study area, camera trap locations, and seismic line strata for the Algar Caribou Habitat Restoration Program located along the east side of the Athabasca River in northeastern Alberta, Canada (56.2588 N, 112.6909 W).

seismic lines would be used less frequently by wolves, black bears, deer, and moose, and used more frequently by caribou. Additionally, we predicted that snow, natural landcover, landscape-scale linear density, line width, and vegetation height would also affect line use by the focal species (Dickie et al., 2017; Fisher and Burton, 2018; Tigner et al., 2014). This study is one of the first to evaluate the efficacy of boreal habitat restoration as a strategy for wildlife conservation (Fraser et al., 2015), and our results may inform restoration practice for re-establishing landscape functionality in support of species at risk conservation across forest ecosystems.

## 2. Methods

### 2.1. Study area

Our study took place in the Algar sub-range of the East Side Athabasca River (ESAR) caribou range, approximately 70 km southwest of Fort McMurray, Alberta (56.2588 N, 112.6909 W; Fig. 1). The 570 $km^2$ area is within the western sedimentary basin of the Canadian boreal forest, and contains vegetation cover broadly typical of this region: lowland habitat of mature black spruce (*Picea mariana)* and tamarack (*Larix laricina)* wetlands, with upland habitat of aspen (*Populus tremuloides)*, white spruce (*Picea glauca)*, and jack pine (*Pinus banksiana)*. We considered this area to have low-intensity disturbance relative to other landscapes in the oil sands region (e.g. Fisher and Burton, 2018): anthropogenic features were almost exclusively legacy seismic, with a total of 524 km of seismic lines and a linear feature density of 1.1 $km/km^2$ (Fig. 1; Alberta Biodiversity Monitoring Institute, www.abmi.ca). In comparison, Lee and Boutin (2006) reported linear densities as high as 10 $km/km^2$ in other townships of the oil sands region. Due to the relative lack of other disturbances, we considered additional anthropogenic effects to be negligible compared to seismic lines and did not include them in our analyses.

### 2.2. Restoration and camera trapping

The Algar Caribou Habitat Restoration Program began in 2011, with a goal of restoring 264 of the 830 ha of legacy seismic lines within the study area (OSLI (Oil Sands Leadership Initiative), 2012; Silvacom and Nexen, 2015). This goal was based on achieving a minimum target of 65% undisturbed habitat within boreal caribou range (Environment Canada, 2012). The program's objectives aimed to address both structural and functional restoration (Dabros et al., 2018) by simultaneously promoting vegetative regeneration and providing movement barriers for caribou predators. We followed internationally accepted terms to define the program's restoration activities (McDonald et al., 2016); specifically, 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 (spontaneous) 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 (Oil Sands Leadership Initiative), 2012). 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 $\geq$1.5 m in height (roughly representing a caribou sightline) and crown cover > 50% (OSLI (Oil Sands Leadership Initiative), 2012). For the remaining seismic lines in the study area, we categorized two unrestored strata as "human-use" – line segments left open for industrial or trapper access – and "control" – line segments meeting the conditions for active restoration but set aside as untreated controls for this wildlife assessment (representing a "business as usual" case of no restoration; Fig. A1).

We randomly selected line segments from within each stratum for camera trap sampling locations, deploying a total of 60 Reconyx HyperFire PC900 camera traps (Reconyx, Holman, WI) distributed across strata as follows: 22 active, 12 passive, 14 human-use, and 12 control camera stations (Appendix A1). Camera trap data used in this study were collected between November 2015 and November 2018. During the April and November 2017 site visits we measured site-level characteristics for inclusion as predictor variables (Table A1, described in Appendix A3). Species identifications were made from camera images by two observers (ET, JB) using *Camelot* software (Hendry and Mann, 2017; https://gitlab.com/camelot-project/camelot); any uncertain identifications were referred to a third observer (ACB) and excluded from analysis if they could not be identified with certainty. We used *camtrapR* (Niedballa et al., 2016) within R statistical software (R Core Team 2018; www.r-project.org) to organize image data for statistical analysis. All methods for wildlife monitoring were approved by the Canadian Council of Animal Care administered by the University of British Columbia (protocol A17-0035).

### 2.3. Data analysis

#### 2.3.1. Model variables

We assessed mammal responses to seismic lines in terms of the number of detection events for each focal species at each camera station in each month (i.e. station-month was our spatiotemporal unit of sampling, Appendix A2). We summarized detection events for each species in *camtrapR* record tables, treating events as independent when occurring at least 30 min apart (Rovero and Zimmermann, 2016). We discretized continuous camera data into month-long period's *sensu* Fisher and Burton (2018). As our statistical sampling unit was "month" and months sample a seismic line multiple times, our sampling units were not independent from one another. We therefore modeled monthly detections within a zero-inflated generalized linear mixed modelling (GLMM) framework, modelling monthly species' detections as a function of seismic line strata, as well as site- and landscape-scale variables hypothesized to affect species' line use (Table A1, Appendix A3). We included a random intercept for station to account for non-independence of monthly detections at the same site. We also included a random intercept of month because we sampled the same calendar month up to three times across the multi-year survey (Appendix A2). For example, observations in January of each year may be similar due to their occurrence in mid-winter. We included the full 36-month sampling period for caribou, deer, moose, and wolves. We only used months between April and October for black bear detections to account for the bears' winter denning period. During the 36-month survey period, camera failures resulted in some inactive camera periods (Table B1), which we accounted for by including the number of active days per month per camera as a model variable.

Our hypothesis testing focused on the role of seismic line strata in explaining variation in the detections of focal species during each station-month. We used the control lines as the reference stratum to represent a "business as usual" case of no restoration. We sought to model additional heterogeneity in mammal line use by including predictor variables for proportion of lowland habitat, snow presence, seismic line density, vegetation height on-line, and line width at each station (Table A1, Appendix A3). For spatial variables – lowland habitat and line density – we performed a multi-scale analysis to determine scales at which habitat best described occurrence for each species (Fig. A2, Appendix A4; Fisher et al., 2011).

#### 2.3.2. Model building

We constructed sets of candidate models with different combinations of predictor variables. We used model selection based on Akaike

Information Criterion (AIC) to assess the relative degree of support among candidate models (Burnham and Anderson, 2002). The null model included only active days − the measure of sampling effort that was included in all models (Table A1). We included restoration stratum in all other candidate models. Our fully parameterized model included all five additional predictor variables (Table A1). As very little is known about species-habitat associations from this region of the boreal forest, we did not have *a priori* reasons to test only specific candidate models. We therefore constructed multiple permutations of candidate models using the "dredge" function from the R package *MuMin* (Bartoń, 2009). This function generated candidate models using combinations of five predictor variables while keeping the strata and active days variables fixed in all candidate models, then performed AIC model selection on the model set (Bartoń, 2009). We considered predictors contained in all models that ranked within 2 ΔAIC of the top model to be influential variables for that species (Burnham and Anderson, 2002). We then compared effect sizes of predictor variables using parameter estimates from a fully parameterized model. We report results as regression coefficients (β) and standard error (SE) for each model variable.

## 3. Results

Total sampling effort over the 36-month study period was 43 361 camera-days, with a median of 735 active days per camera (range = 326–1108). There were 3 058 independent detection events of mammals recorded (Table B1), from which we identified 16 mammal species (Table B2). Of the 2 309 detections of the five target species, deer were most frequently detected (n = 835) and caribou were least frequently detected (n = 271; Table B2). Seismic line strata was the best-supported predictor variable only for wolves, whereas line use by all other species was more strongly influenced by habitat variables (Fig. 2).

Deer use of actively restored lines was lower than their use of control lines (-1.07 ± 0.418, $p = 0.011$; Fig. 2c), but caribou, predators and moose showed no response to active restoration. Wolf use of human-use lines was higher than of control lines (1.15 ± 0.530, $p = 0.030$; Fig. 2a), but this effect was not seen for black bears, caribou, or caribou competitors. Passive restoration did not have an effect on line use by any of the five target species (Fig. 2).

Lowland habitat had the strongest effect for caribou and deer, with more frequent caribou use (3.47 ± 0.583, $p < 0.001$; Fig. 2e) and less frequent deer use of lowland sites (-1.85 ± 0.354, $p < 0.001$; Fig. 2c). Higher seismic line density resulted in less frequent line use for caribou (-1.32 ± 0.394, $p < 0.001$) but more frequent line use for deer (0.748 ± 0.306, $p = 0.015$). The presence of snow on lines resulted in less frequent line use for caribou and wolves (-1.59 ± 0.291, $p < 0.001$ and -0.608 ± 0.243, $p = 0.012$, respectively). Black bears, deer, and moose line use was higher on lines with taller vegetation (0.677 ± 0.321, $p = 0.035$; 1.11 ± 0.300, $p < 0.001$; and 0.835 ± 0.352, $p = 0.018$; Fig. 2b, c, and d respectively).

For all species except black bear, the model with the highest AIC weight included predictor variables with significant effects on line use (Table 1). The null model had the most support for black bear, indicating that predictor effects were weak. All predictor variables appeared in the top model set for wolves, though line density, vegetation height and line width only occurred in one model each. The top model for deer included lowland habitat, linear density, vegetation height and snow, though line width was also included twice in the three next-best models. Moose line use was best explained by a model containing vegetation height. Finally, the best-supported model for caribou included snow presence, lowland habitat and linear density. In the subsequent two ranked models for caribou, vegetation height and line width each appeared once.

## 4. Discussion

Seismic line restoration, or lack thereof, influenced line use for only two of the five large mammal species that play a central role in caribou dynamics in northern boreal forests. If linear restoration is to support recovery of threatened caribou populations, it should "remove" the ecological effects of seismic lines by re-establishing spatial segregation between caribou, their predators, and their apparent competitors. However, in the short-term (three-to-six year) period post-restoration covered by this study, we found that only white-tailed deer showed the predicted lower use of restored seismic lines. Contrary to our prediction, caribou predators did not show lower use of lines actively restored via mounding and re-planting, indicating that these treatments did not create movement barriers. However, wolves did show higher use of lines left open for human access (relative to control lines). Caribou used seismic lines in lowland habitat, regardless of the seismic line type. Our results suggest that, at least in the short term, seismic line restoration alone may not re-establish landscape functionality enough to support caribou conservation on the working landscape. Our study challenges the common, yet rarely tested, assumption that habitat restoration aimed at vegetation regeneration supports wildlife conservation on disturbed landscapes, thus emphasizing the need to monitor the outcomes of restoration for wildlife communities.

### 4.1. Active restoration does not impede predator movement

Contrary to a key hypothesis motivating linear restoration in caribou habitats, wolves and black bears did not use seismic lines less often following restoration by site preparation and planting. Although mounding and application of coarse woody material has been proposed as a barrier to predator movement, providing functional restoration in addition to structural restoration (Bentham and Coupal, 2015; Dabros et al., 2018), our results do not support this assertion. Nevertheless, it is possible that this result is specific to our study area. In the Algar restoration program, coarse woody material could only be applied to lines where it was readily available in the surrounding forest. At many lowland sites, the restoration program reported that there was insufficient material to reach target application for movement barriers. One portion of the study area designated for restoration received 40% of targeted coarse woody material volume, while two other portions received only 16% (OSLI (Oil Sands Leadership Initiative), 2012; Silvacom and Nexen, 2015). In previous studies, line-blocking via tree-felling (where trees were felled every 10 − 15 m along a seismic line) did not impede wolf line use (Neufeld, 2006), but intense application of log debris (approximately 200 $m^3$/ha over a 200 m line segment) decreased wolf detections relative to open seismic lines (Keim et al., 2019). Taken together, these results suggest that without adequate woody material, mounding alone may not be an effective inhibitor of predator movement.

Consistent with previous studies, we observed higher use of human-use lines by wolves (Dickie et al., 2017). As accessible travel routes, human-use lines in our study experienced more vehicle traffic than other lines (e.g. snowmobile, all-terrain vehicle), causing soil compaction, altered vegetation structure, and decreased likelihood of natural regeneration (Bentham and Coupal, 2015; Dabros et al., 2018; Pigeon et al., 2016). These characteristics of human-use lines, relative to those of the other line types, likely ease movement barriers and permit faster, more efficient travel for wolves (Dickie et al., 2017; Finnegan et al., 2018a). During winter, vehicle traffic compacts snow on lines to provide firmer trails, decreasing energetic travel costs for wolves when snow presence on lines otherwise acts as a deterrent (Droghini and Boutin, 2017).

### 4.2. Small effects of restoration on caribou line use

Although one of the strategic goals of seismic line restoration is

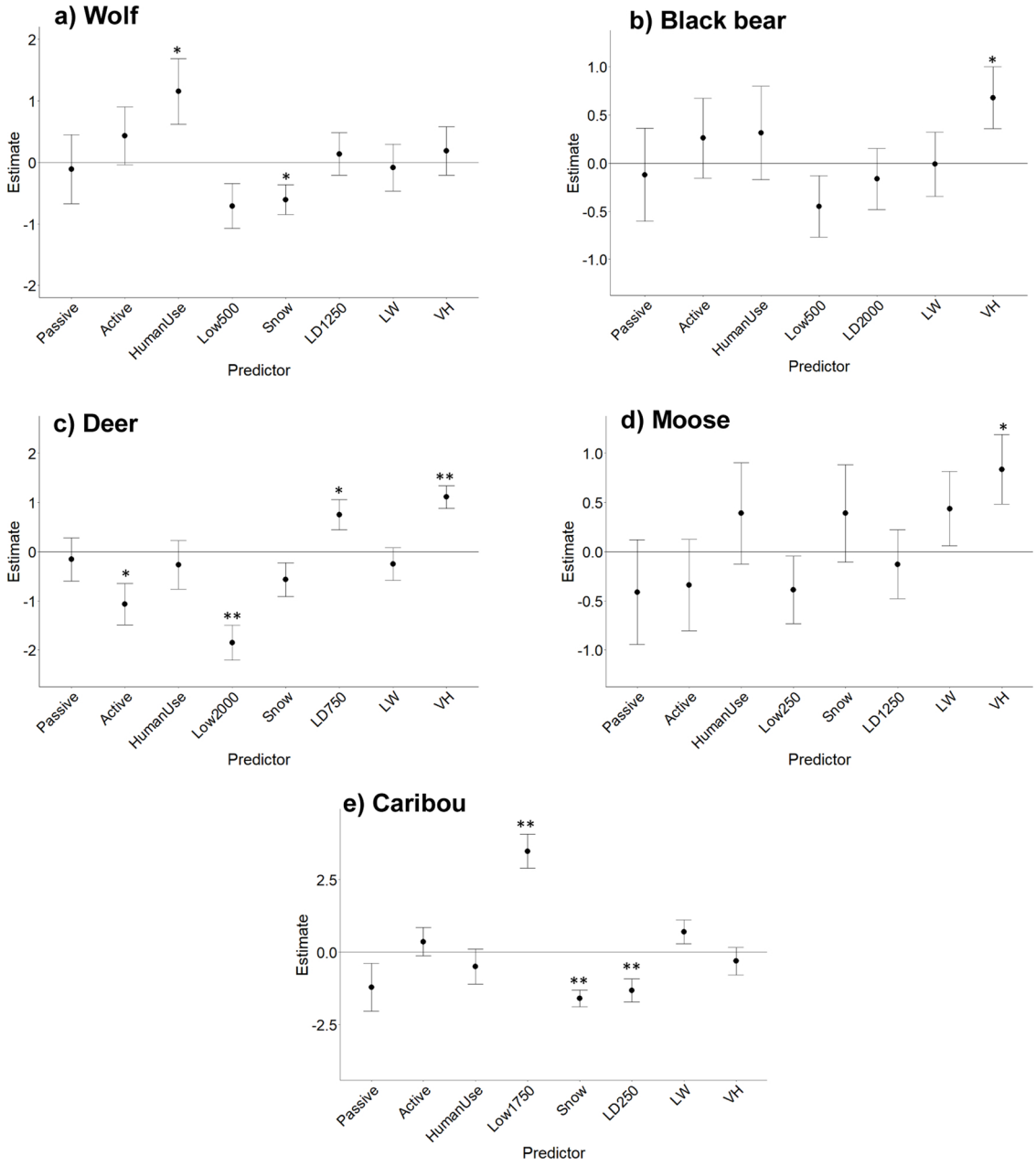


**Fig. 2. Estimated effects of seismic line strata and other factors on line use by boreal mammals in northeastern Alberta.** Parameter estimates from fully-parameterized zero-inflated GLMMs of monthly detections from 60 camera traps sampled Nov. 2015 – Nov. 2018 are displayed as mean ± standard error. We used control seismic lines as our reference strata to assess the relative effect of other seismic line strata. We centred and standardized predictor variables to indicate effect sizes relative to the control strata, with all other variables held constant at a mean value. We have included additional predictor variable details in Table A1. ** denotes estimates with $p < 0.01$, * denotes estimates with $p < 0.05$.

habitat regeneration that facilitates caribou use and hence conservation, in our study caribou did not use actively restored lines significantly more than controls. This is perhaps not surprising, given the slow regeneration time of native vegetation in this boreal landscape (van Rensen et al., 2015). Instead, caribou use of seismic lines was more strongly influenced by surrounding habitat, season, and landscape-scale linear density than by restoration. Caribou preference for lowlands has been well documented and is a primary motivation for restoration in this habitat (e.g. James and Stuart-Smith, 2000; Latham et al., 2011b). The negative effect of snow on caribou line use indicates decreased line use in winter, likely due to the higher energetic cost of moving through snow accumulated on lines (Fancy and White, 1987).

### 4.3. Apparent competitor line use

Our prediction that caribou apparent competitors would use restored lines less than controls was supported for deer, but not for moose. Deer used actively restored lines less than control lines, suggesting that active restoration via site preparation and planting is an effective tool for reducing line use for this range-expanding species (Dawe et al., 2014; Latham et al., 2011a). Although we did not observe a strong effect of restoration on moose, their positive responses to vegetation height and line width are consistent with studies reporting moose selection for woody shrubs and open-canopied habitat patches (Latombe et al., 2014; Wasser et al., 2011). These results highlight that functional restoration without structural restoration – that is, creating movement barriers without restoring vegetation composition – is

**Table 1**
**Model selection results for zero-inflated generalized linear mixed models describing effects of seismic line restoration and line characteristicsfor five target mammal species.** Top models (those within 2 ΔAIC) indicate which predictor variables (in addition to seismic line strata and active days) best explained seismic line use for each species. Strata = seismic line type, AD = proportion of active days, snow = proportion of snow days, low = lowland habitat, LD = line density, VH = vegetation height, and LW = line width. Values following lowland and line density indicate the buffer radius used to measure these variables. Distribution represents the underlying distribution of the response variable (Appendix A2), df is the degrees of freedom in the model, ΔAIC indicates the difference in AIC scores from the top model, AICwt is the AIC weight attributed to that model, Cum.Wt is the cumulative model weight, and ER is the evidence ratio (AIC weight of top model/AIC weight of model). We have included additional details on predictor variables and modelling approach in Table A1 and Appendices A2 and A3.

| Species | Predictor Variables | Distribution | Df | ΔAIC | AICwt | Cum.Wt | ER |
|---|---|---|---|---|---|---|---|
| Wolf | Strata + AD + Snow + Low500 | Nbinom2 | 11 | 0.00 | 0.188 | 0.188 | |
| | Strata + AD + Snow + Low500 + LD1250 | | 12 | 1.17 | 0.104 | 0.292 | 1.80 |
| | Strata + AD + Snow | | 10 | 1.34 | 0.096 | 0.389 | 1.95 |
| | Strata + AD + Snow + Low500 + VH | | 12 | 1.63 | 0.083 | 0.472 | 2.26 |
| | Strata + AD + Snow + Low500 + LW | | 12 | 1.81 | 0.076 | 0.548 | 2.48 |
| Black bear | AD | Nbinom2 | 6 | 0.00 | 0.354 | 0.354 | |
| | Strata + AD + Low500 + VH | | 11 | 1.66 | 0.154 | 0.508 | 2.29 |
| White-tailed deer | Strata + AD + Low2000 + LD750 + VH + Snow | Nbinom1 | 13 | 0.00 | 0.324 | 0.324 | |
| | Strata + AD + Low2000 + LD750 + VH | | 12 | 0.53 | 0.249 | 0.574 | 1.30 |
| | Strata + AD + Low2000 + LD750 + VH + Snow + LW | | 14 | 1.41 | 0.160 | 0.734 | 2.02 |
| | Strata + AD + Low2000 + LD750 + VH + LW | | 13 | 1.97 | 0.121 | 0.856 | 2.68 |
| Moose | Strata + AD + VH | Nbinom2 | 10 | 0.00 | 0.145 | 0.145 | |
| | Strata + AD + VH + Low250 | | 11 | 0.490 | 0.114 | 0.259 | 1.28 |
| | Strata + AD + VH + LW | | 11 | 0.528 | 0.112 | 0.371 | 1.30 |
| | Strata + AD + VH + LW + Low250 | | 12 | 1.315 | 0.075 | 0.446 | 1.93 |
| | Strata + AD + VH + Snow | | 11 | 1.360 | 0.074 | 0.519 | 1.97 |
| | Strata + AD + VH + Low250 + Snow | | 12 | 1.851 | 0.058 | 0.577 | 2.52 |
| | Strata + AD + VH + LW + Snow | | 12 | 1.867 | 0.057 | 0.634 | 2.54 |
| | Strata + AD + VH + LD1250 | | 11 | 1.984 | 0.054 | 0.688 | 2.70 |
| Caribou | Strata + AD + Low1750 + Snow + LD250 | Nbinom1 | 12 | 0.00 | 0.326 | 0.326 | |
| | Strata + AD + Low1750 + Snow + LD250 + LW | | 13 | 0.71 | 0.229 | 0.554 | 1.42 |
| | Strata + AD + Low1750 + Snow + LD250 + VH | | 13 | 2.00 | 0.120 | 0.674 | 2.71 |

insufficient as it does not deter apparent competitors from using seismic lines (Ray, 2014; Finnegan et al., 2018a,b).

White-tailed deer expansion into the boreal forest is in part attributed to industrial development (Dawe et al., 2014), as anthropogenic land conversion alters habitat in favour of deer. Deer selection for linear features and cut blocks has been previously documented (Fisher and Burton, 2018), and this relationship is further supported by the positive association observed in our study between deer, line density, and vegetation height. Lee and Boutin (2006) found that unrestored lines retained early seral vegetation long after the initial disturbance, and Finnegan et al. (2018b) documented more important forage species for deer and moose on seismic lines relative to interior forest plots. Decreased early seral forage on restored lines, combined with movement barriers from mounding, could explain the negative responses of deer to actively restored lines observed in our study. Active restoration may therefore provide structural restoration by returning disturbances to natural vegetation faster (Bentham and Coupal, 2015) as well as provide some functional restoration of habitat by deterring a key caribou competitor. Both responses could decrease competitive pressures on caribou over time.

### 4.4. Directions for future research

We suggest that there are several important implications of our study, as well as several key directions for future research. One such direction would be to expand on our study through inclusion of an additional sampling stratum in undisturbed habitat ("off-line"). Off-line sites could be used to sample species' space use away from local anthropogenic disturbances, thus providing a potential reference target with which to assess the effectiveness of restoration at achieving ecosystem recovery. However, we were limited in our ability to deploy camera traps in interior forest patches within our study area. The largest areas without seismic lines were open fens in lowland habitat (Fig. 1), which were not only difficult to access but would have confounded comparisons with our other sampling strata due to the strong habitat differences. Potential zones of influence around anthropogenic features – considered as a 500 m buffer by Environment Canada (2012) – also made it difficult to set off-line cameras in higher linear density areas within our sampled landscape, as off-line areas would have been close to other lines and thus may not have reliably represented species' presence in undisturbed habitat. Nevertheless, incorporating an "undisturbed" stratum would build on our comparison across line types, and would also help in characterizing population-level responses across the landscape (e.g. Burgar et al., 2019). The ultimate measure of restoration effectiveness for caribou recovery is the stabilization or growth of caribou populations. While the behavioural responses we documented in this study can be linked to population consequences, we recommend complementary monitoring at both behavioural and population scales. Camera traps are a promising tool for monitoring across multiple ecological scales, particularly if landscape-level interventions can be replicated (and monitored) across multiple landscapes and the populations they contain.

We suggest that active restoration in our study system provided few direct benefits to caribou over the short term. However, we caution that ours was a preliminary study conducted shortly after implementation of restoration, and restoration of landscape functionality is a goal usually realized over the longer term (Shackelford et al., 2013). Still, less frequent use of actively restored lines by deer may indicate the beginning of the restoration process. By deterring seismic line use by deer, active restoration may re-establish spatial segregation between caribou and a key apparent competitor, thus reducing predation risk for caribou on restored lines over time. Although caribou predators still used restored lines in our study, use of these lines may decrease as fewer of their prey species are found at those sites. We recommend that future studies should continue to monitor mammal responses over longer periods to allow for greater vegetation regeneration. Further research should seek to relate seismic line restoration to animal movement rates and behaviour in order to assess specific mechanisms behind line use (e.g. Dickie et al., 2017; Finnegan et al., 2018a). We also recommend comparisons of our results with studies in other areas to observe restoration effects across landscapes. Ultimately, responses to restoration at the behavioural level must also translate into population-scale responses in

caribou and their interacting species, thereby inducing changes in community-wide landscape use and re-establishing landscape function.

In its latest caribou range plan, the Government of Alberta advocated for an integrated land management approach to conservation, which may include prioritizing restoration in preferred caribou habitat while consolidating industry access routes to reduce human influence on the landscape (Government of Alberta, 2017; Yemshanov et al., 2019). We suggest that our results provide some support for a strategy in which linear restoration is implemented in areas where caribou and deer occurrences overlap to re-establish spatial segregation between caribou and their competitors. However, we call for further research to explore which scale of application would best balance human access, caribou habitat needs and predator movement. Integrated land management may allow for wildlife coexistence alongside industry, but only if sufficient functional habitat is available. Finding a balance between industry access and habitat protection should be a priority in future studies. In addition, a more comprehensive view should account for the cumulative impact of all anthropogenic disturbances on the landscape (Fisher and Burton, 2018; Neilson and Boutin, 2017), and how strategic habitat restoration might mitigate effects on the boreal mammal community.

The United Nations recently declared 2021–2030 the Decade on Ecosystem Restoration, increasing the global emphasis on restoration of impacted landscapes (United Nations Environment, 2019). This focus will require an associated emphasis on monitoring systems to ensure effectiveness of restoration efforts. While restoration monitoring is often focused on vegetation and soils, achieving successful restoration of broader ecosystem functions will require monitoring of vertebrate community responses (Fraser et al., 2015), as we have done here using camera traps. This tool provides the unique opportunity to assess community-wide influences of anthropogenic disturbance and associated mitigations (Fisher and Burton, 2018), which should ultimately improve conservation efficacy. Rather than studying single species, or a single predator-prey interaction in isolation, monitoring multiple species considers the broader ecological context within which focal species fit (Burgar et al., 2019). Multi-species studies are useful for identifying patterns and assessing general effects of landscape change, exposing both direct and indirect relationships between community members (Caravaggi et al., 2017). Not only is this approach valuable for taking a bigger picture approach to species conservation, but it also sheds light on interspecific relationships that have thus far been overlooked.

## 5. Conclusion

Habitat restoration is a key component of wildlife conservation, but animal responses need to be monitored to ensure the efficacy of restoration (Fraser et al., 2015; Dabros et al., 2018). At the early stage of vegetation recovery in our study, large boreal mammals are showing weak evidence of response to successful habitat restoration. However, continued monitoring is necessary to determine if current trends prevail and ultimately lead to positive change for caribou populations. Boreal habitat regeneration is a long-term goal; therefore, coordinated conservation strategies may need to be applied to sustain herds in the interim (Serrouya et al., 2019). By monitoring such efforts, management actions can be adapted to optimize their effectiveness. Our study is an example of how restoration projects can be monitored for their effects on specific focal species as well as the broader community in which they are embedded. Continued assessment of mammal responses to land management informs how wildlife and industry might best coexist, thereby helping to balance conscientious human development with healthy and sustainable ecosystems.

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## Declaration of Competing Interest

We confirm that the manuscript was written by E. R. Tattersall, J. M. Burgar, J. T. Fisher, and A.C. Burton and represents all original research that we conducted. None of the authors have conflicts of interest – financial, personal, or otherwise – to declare. All authors agree with the contents of the manuscript and its submission to the journal. No part of this research has been published elsewhere, nor is the manuscript being considered for publication elsewhere while it is being considered by Biological Conservation. All sources of funding are acknowledged in the manuscript, and all appropriate ethics and research permits were obtained for this research.

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## Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.biocon.2019.108295.

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