

Spatial distribution of marten, lynx, and moose and power to detect trends in occupancy using snow-tracking data from the Tulita and Norman Wells region of the Northwest Territories

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Introduction

Occupancy surveys are a common method for efficiently tracking changes in the relative abundance and the spatial distribution of wildlife (MacKenzie et al. 2002). Rather than trying to count the number of individuals, occupancy surveys simply determine whether or not a species was present, and are thus well suited for species such as grizzly bears and lynx that are not identifiable by their colour or markings. Imperfect detection, where an animal is present but undetected, is a challenge faced by all occupancy and abundance surveys. When a species is detected ($y_i = 1$) at site i , it is known to occur (true state $z_i = 1$). However, if species is undetected ($y_i = 0$), the true state is unknown as the species could either be truly absent from the site ($z_i = 0$) or the species could be present but undetected ($z_i = 1$). Repeat surveys at a site are typically used to estimate probability of detection p given a species is present ($z_i = 1$). As the cumulative probability of detecting a species at least once across repeat surveys approaches 1, studies can have confidence that species are truly absent ($z_i = 0$) when undetected. The cumulative probability of detection p^* can be calculated as $p^* = 1 - (1 - p)^k$, where k is the number of repeat sampling occasions at a site (Figure 1). Power to detect changes in occupancy depends on p^* and the number of sites M . Previous studies recommend $p^* > 0.8$ (Long and Zielinski 2008) or near 0.9 (McKann et al. 2013) and at least 60 sites to estimate occupancy rates ψ (McKann et al. 2013, Whittington et al. 2015, Steenweg et al. 2016) and approximately 120 sites to estimate colonization and extinction (McKann et al. 2013).

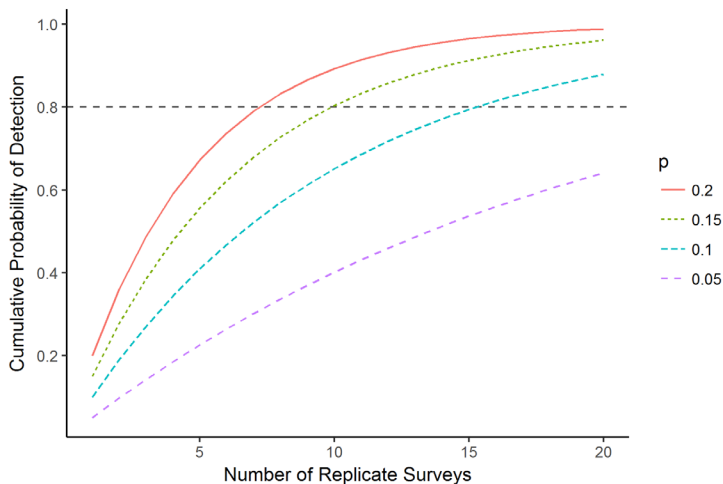


Figure 1. The cumulative probability of detecting a species at least once across replicate surveys depends on the probability of detection p and the number of replicate surveys.

Replicate surveys are commonly repeated in time, where surveyors visit a site multiple times with the caveat that occupancy within a site does not change from the first to last survey. Some occupancy surveys use multiple observers to estimate detection probability, although probability of detection for the two observers should be independent. Occupancy surveys can also use spatial replicates (Hines et al. 2010, Thorn et al. 2011) or a combination of spatial and temporal replicates (Charbonnel et al. 2014, Whittington et al. 2015). With spatial replicates, detection data (y_i) is collected along multiple linear transects or trail segments within a grid cell. Encounter histories along the spatial replicates are used to estimate whether or not each grid cell is occupied. The challenge with these surveys, is that species presence on a given trail segment may depend on whether the species was detected on the previous segment, especially for animals that travel long distances on trails. Successive correlation in detection probability must be appropriately modelled (Hines et al. 2010, Charbonnel et al. 2014, Hines et al. 2014, Whittington et al. 2015), otherwise occupancy models may overestimate detection probability and underestimate both occupancy and associated confidence intervals.

Snow tracking data was collected in the Norman Wells and Tulita regions of Northwest Territories (NWT), Canada (Figure 2). Explor collected snow tracking data during 2012 and 2013 southwest of Norman Wells along recently cut seismic lines (hereafter referred to as the Explor data). In 2015, the GNWT Department of Environment and Natural Resources, in collaboration with community members collected snow tracking data near Tulita (hereafter referred to as the Tulita data). The objectives of this study were to estimate occupancy rates for marten, lynx, and moose, assess the effects of temperature and sampling window on detection probability, determine the optimal study design in terms of grid size and segment length, and to assess power to detect changes in occupancy.

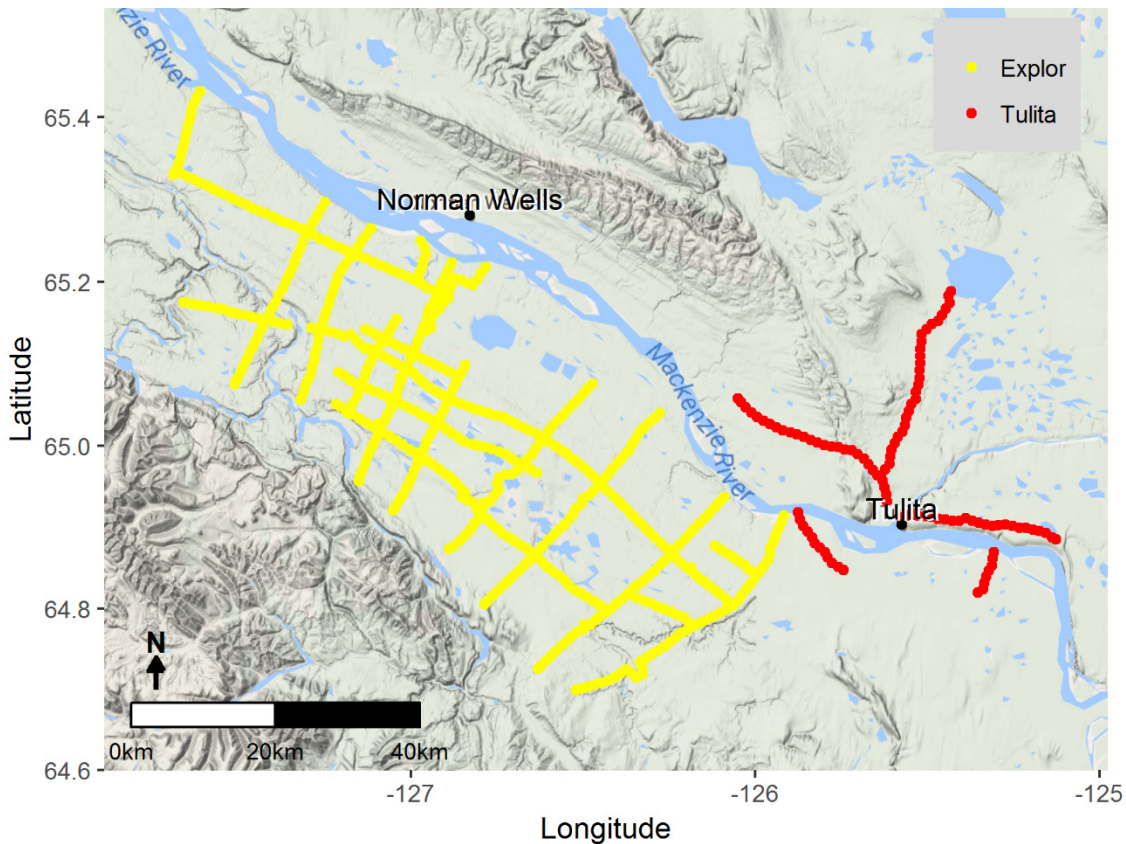


Figure 2. Map of snow-tracking transects in the Norman Wells and Tulita regions of the Northwest Territories.

Methods

Data Collection

Snow tracking data was collected in 2012 and 2013 by Explor southwest of Norman Wells and in 2015 by GNWT-ENR and community members within 40 km of Tulita (Figure 2). Surveyors recorded their travel route and wildlife tracks that they observed en route. Surveyors also recorded the date and the time since the last snow. Survey routes were discretized into 250, 500 and 1000 m segments and species detections ($y = 0$ or 1) were recorded for each segment. Marten data was entered for all three segment lengths; lynx data was entered for lengths of 500 and 1000m; and moose data was entered for the 1000 m segments. I omitted the 250 m marten data after a preliminary analysis found it produced similar results to the 500 m segment lengths. I created square grid cells of 3, 4, 5, 6, and 10 km widths. I created an occupancy model for each species, grid width, and segment length combination, which resulted in 22 data sets and models.

Data Analysis

Occupancy data is frequently modelled as zero-inflated binomial models (MacKenzie et al. 2002). These models contain two hierarchical components: a logistic regression model for whether or not a site is occupied. The state of z_i is unknown when the species is not detected and is thus a latent variable. The second component of the model is another logistic regression for whether or not a species is detected conditional on the site being occupied ($z_i = 1$). Within this hierarchical framework, covariates can be included on a logit scale. Standard occupancy models can be easily fit using a maximum likelihood framework using either the unmarked package (Fiske and Chandler 2011) in R (R Development Core Team 2016) or in the program Presence (Hines 2006). I used a Bayesian approach for the analysis because occupancy models can easily be expanded to model more complicated process such as serial correlation among segments or colonization and extinction. The books Bayesian population analysis using WinBugs (Kéry and Schaub 2012) and Applied hierarchical modelling in ecology (Kéry and Royle 2016) offer excellent introductions to Bayesian analyses and occupancy models. I used the R interface to JAGS 4.2 (Plummer 2003) using the jagsUI 1.4.4 (Kellner 2016) package. Using JAGS/WinBugs notation, the observation component for a standard occupancy model with independent temporal replicates can be coded as:

Standard Occupancy Model: $\psi(\cdot)p(\cdot)$

```
for (i in 1:n.sites){ # Loop through each site.
  logit(psi[i]) <- B0 + B1*X1[i] # Probability of site occupancy with covariates
  z[i] ~ dbern(psi[i]) # Likelihood for occupancy. z[i] is a latent variable 0/1
  for (j in 1:n.temporal){ # Independent Temporal and Spatial replicates within site i
    logit(p[i, j]) <- A1 + A2*X2[i, j] # Probability of detection with covariates
    # calculate likelihood for detection probability using observed data y[i, j]
    y[i, j] ~ dbern(p[i, j] * z[i]) # Likelihood for p. Note p equals 0 when z[i] = 0
  }
}
```

Data from snow tracking surveys with spatial replication can have high serial correlation in detection probability either because animals travel along the survey route or because of spatial correlation in habitat quality. Two approaches can be used to model this serial correlation in detection probability: Markovian detection and Markovian occupancy models. The two methods produce similar estimates, but model slightly different ecological processes. The simplest method is to use Markovian detection models to model serial correlation in detection probability, which is ideal for situations where animals travel large distances and especially for when they travel along survey routes. The observation model for detection probability includes a covariate for whether the species was detected on the previous segment on the same survey (i.e. same temporal replicate). However, for the first segment of a survey we do not know if a species was detected on the previous survey and therefore must use the equilibrium probability of detection, which can be calculated as $p_{mean} = p / p + (1 - p')$ where p is detection probability when the species was not detected on the previous segment and p' is detection probability when the species was detected on the previous segment. Using JAGS/WinBugs, the observation component of the Markovian detection model can be written as:

Markovian Detection Model: $\psi(\cdot)p(\cdot)p'(\cdot)$

```
for (i in 1:n.sites){ # Loop through each site.
  logit(psi[i]) <- B0 + B1*X1[i] # Probability of site occupancy with covariates
  z[i] ~ dbern(psi[i]) # Likelihood for occupancy
  for (j in 1:n.temporal){ # Temporal replicates within site i
    # Detection probability for first segment is p.mean because no previous detection.
    # A1ag is the coefficient for serial correlation when detected on previous.
    # A2 and X2 are beta coefficients and data for covariates on detection probability
    logit(p0[i, j, 1]) <- A1 + A2*X2[i, j, 1] # Not on previous.
  }
}
```

```

logit(p1[i,j,1]) <- A1 + A1ag + A2*X2[i,j,1] # On previous.
p[i,j,1] <- p0[i,j,1] / (p0[i,j,1] + (1 - p1[i,j,1])) # Mean p.
y[i,j,1] ~ dbern(p[i,j,1] * z[i]) # Likelihood for p. Note p equals 0 when z[i] = 0
for (k in 2:n.spatial){ # Spatial replicates within site i and temporal replicate j
  logit(p[i,j,k]) <- A1 + A1ag*Y[i,j,k-1] + A2*X2[i,j,k] # Probability of detection
  y[i,j,k] ~ dbern(p[i,j,k] * z[i]) # Likelihood for p. Note p equals 0 when z[i] = 0
}
}

```

The Markovian detection models are ideal for serial correlation in tracks because animal tracks and movements are observed for short period of time (within a temporal replicate) and then they are covered by new snow or wind. Conversely, Markovian occupancy models, also referred to as Markovian segment models (Whittington et al. 2015), are ideally suited for spatial correlation in animal use associated with habitat related features. They add a third level to the hierarchical occupancy model such that the model includes likelihoods for probability of site occupancy ψ , probability of segment use θ at any point in time conditional on site occupancy, probability of segment use θ' given the previous segment was used, and probability detection p conditional on site occupancy and segment use. Because of imperfect detection, θ is also considered a latent variable (i.e. a species could be present but unobserved on a segment). Note that p is conditional on θ and therefore detection probabilities from Markovian detection and Markovian occupancy models cannot be directly compared. JAGS/WinBugs code for the observation component of a Markovian occupancy model with covariates for ψ and p , but not θ can be written as:

Markovian Occupancy Model: $\psi(\cdot)\theta(\cdot)\theta'(\cdot)p(\cdot)$

```

logit(theta0) <- T1 # Previous segment not used
logit(theta1) <- T1 + T1ag # Previous segment used
theta.mean <- theta0 / (theta0 + (1 - theta1)) # Mean probability of use
for (i in 1:n.sites){ # Loop through each site.
  logit(psi[i]) <- B0 + B1*X1[i] # Probability of site occupancy with covariates
  z[i] ~ dbern(psi[i]) # Likelihood for occupancy
  # For first segment, do not know if it was ever previously used. Thus, use mean.
  # z.seg[i, j] is a latent variable for segment use.
  theta[i,1] <- theta.mean
  z.seg[i,1] ~ dbern(theta[i,1] * z[i]) # Likelihood for segment use.
  for (j in 2:n.spatial){ # Spatial replicates within site i
    # Probability of use depends on whether the animal used the previous segment
    theta[i,j] <- theta0*(1 - z.seg[i, j-1]) + theta1*z.seg[i,j-1]
    z.seg[i,j] ~ dbern(theta[i,j] * z[i]) # Likelihood for segment use.
    for (k in 1:n.temporal){ # Temporal replicates within site i
      logit(p[i,j,k]) <- A1 + A3*X3[i,j,k] # Probability of detection
      y[i,j,k] ~ dbern(p[i,j,k] * z.seg[i,j]) # Likelihood for p.
    }
  }
}
}

```

Markovian detection and Markovian occupancy models generally produce similar estimates of ψ (Hines et al. 2010, Charbonnel et al. 2014, Whittington et al. 2015). Markovian occupancy models are increasingly used in multi-season occupancy surveys for large mammals (Hines et al. 2014, Thapa and Kelly 2016) and in breeding bird surveys (Clement et al. 2016). Markovian occupancy models marginally outperform Markovian detection models in some situations (Hines et al. 2010, Charbonnel et al. 2014), but they require more data, are more likely to encounter convergence failure (Hines et al. 2010), sometimes produce larger confidence intervals (Charbonnel et al. 2014, Whittington et al. 2015), and take a lot longer to run (e.g. 5 days vs a few hours to run the 22 models). More importantly, interpretation can be more complicated with the inclusion of covariates. For the analysis of the NWT data, I ran both Markovian detection and Markovian occupancy models.

I combined the Explor and Tulita data into a single analysis to improve estimates of covariates on occupancy and detection probability. However, I included separate intercepts for occupancy and detection probability for the two studies given that they occurred in different regions and in different years. However, I combined the two years of Explor data into a single occupancy estimate and thus assumed that occupancy did not change from 2012 to 2013.

I considered the following covariates in the Markovian detection models. First, I included a dynamic habitat index (Coops et al. 2008) calculated as the cumulative normalized difference vegetation index (NDVI) from 2003 to 2014 with a resolution of 1 km² (<http://silvis.forest.wisc.edu/dhi>). I included cumulative NDVI as a covariate on occupancy (range 0 to 8.8, mean 6.3). I calculated the average cumulative NDVI across the each grid cell. Second, I included the effects of the average previous week's temperature (range -37 to -12, mean = -24) on detection probability because it has influenced detection rates in other snow tracking surveys (Kawaguchi et al. 2015). I downloaded Environment Canada daily weather data from the Norman Wells weather station and used the mean daily temperature averaged across the week prior to the survey date. Finally, I included days snow (range 0 to 8, mean = 2.0) as it can influence probability of detection (Whittington et al. 2015). I scaled all covariates by their mean and standard deviation prior to modelling to improve convergence. I used Gibbs variable selection (GVS) for the covariates cumulative NDVI, serial correlation in detection, temperature, and days snow (Hooten and Hobbs 2015, Linden and Roloff 2015). I first fit a global model with all covariates and then used parameter estimates and standard deviation of posterior estimates as hyper-parameters for variable selection. Resulting posterior estimates from covariates subject to GVS were not model averaged, whereas covariates included in all models were averaged across all models. I used vague priors $N(0, 100)$ on a logit scale for all parameters and ran all models with 3 chains, 1000 iterations for adapting the tuning parameters, 500 iterations of burnin, and then ran the model for 10 000 iterations. I thinned the posterior samples by saving every 5th iteration. I assessed model convergence by examining trace plots and assessing Gelman-Rubin diagnostics with values greater than 1.1 indicating lack of convergence. I assessed model fit using Bayesian goodness of fit tests where values close to 0.5 indicate good model fit and values less than 0.05 and greater than 0.95 indicate poor model fit (Kéry and Royle 2016).

Power Analysis

I used simulations to assess the effects of survey effort on power to detect an absolute decline in occupancy of 0.2 collected over five years of sampling. For each simulation, I simulated five independent years of data with occupancy rates declining linearly on a logit scale from $\psi = 0.7$ to 0.5 over the five years. I estimated occupancy rates for each year using the Markovian detection models. I used the resulting β coefficients and standard errors for occupancy on a logit scale to test for a significant decline using the metafor package (Viechtbauer 2010). The meta-analysis models thus included both point estimates and measures of uncertainty. I tested for a linear decline in occupancy by comparing meta-analysis models with and without a linear covariate for year and classified the simulation as successfully detecting a decline if the p-value was less than 0.10 (i.e. I used a Type I error of $\alpha = 0.10$). I ran over 500 simulations per scenario and calculated power as the proportion simulations that detected the decline in occupancy. Monitoring programs usually strive for statistical power of 0.8 (Type II error rates $\beta = 0.2$).

I assessed statistical power for 360 scenarios using the following parameters. Values of parameters used to simulate data were based on observed NWT data and Markovian detection model parameter estimates with NDVI, DaysSnow, and Temperature set to their mean value.

- Number of grid cells: 50, 60, 70, 80, 90, 100
- Number of temporal replicates: 1, 2, 3
- Number of spatial replicates: 10, 20, 40
- Segment length: 500, 1000 m
- Detection probability, species not detected on previous segment: 0.05, 0.10, 0.15, 0.20, 0.25

- Increase in detection probability if species detected on previous segment on logit scale: 1.5

Results

Snow Tracking

The Explor and Tulita studies tallied over 2567 km of snow tracking surveys (Figure 3). Lynx, marten, and moose were detected at least once in most regions of the study area. I varied grid cell sizes from 3 km wide to 10 km wide, which influenced the number of grid cells surveyed (range 50 to 243, Figure 4). Similarly, the choice of grid cell size and segment length influenced the number of spatial replicates per grid cell and the cumulative probability of detection (Figure 5). Half of the segments were surveyed two or more times (Figure 5).

Naïve occupancy estimates that simply tallied the number of grid cells where a species was detected, substantially underestimated true occupancy rates (Figure 6). As expected, occupancy rates increased with grid cell size. The Markovian occupancy models generally produced slightly higher realized occupancy estimates compared to the Markovian detection models. Lynx occupancy rates ranged between 0.5 and 1.0 in the Explor region but were near 1.0 in the Tulita region. Marten occupancy rates were near 0.8 in Explor and 1.0 in Tulita. Moose occupancy rates were near 1.0 in both regions.

There was strong serial correlation in segment use (Figure 7) and detection probability (Figure 8) for the Markovian occupancy and Markovian detection models respectively. The β coefficient for serial correlation in detection probability in the Markovian detection models was near 1.5 for all species. The serial correlation in detection probability should decrease as segment length is increased because segments should become more independent (Hines et al. 2010). When moving from 500 m to 1000 km segments, the lag term decreased for marten but surprisingly increased for lynx, perhaps because of habitat related effects. The median observed cumulative probability of detection exceeded 0.8 for marten in all study designs (Figure 9). The median cumulative probability of detection for lynx exceeded 0.8 for the 10 km grid cells and was near 0.8 for the 5 and 6 km grid cells. The cumulative probability of detection for moose exceeded 0.8 in all Tulita surveys but none of the Explor surveys.

The Markovian occupancy models generally had a higher number of plausible candidate models and thus higher model uncertainty compared to Markovian detection models (Appendix Table 1). The cumulative NDVI averaged within each grid cell had a marginally positive effect on lynx, marten, and moose occupancy rates, but only for the Markovian occupancy models (Figure 10). Days snow had a strong positive effect on marten detection rates but not on lynx or moose detection rates (Figure 11). The average weekly temperature had a negative effect on moose detection rates, but not on lynx or marten detection rates (Figure 12). All models had excellent fit with Bayesian p-values near 0.5 (Figure 13).

Snow Tracking Detections
1 km Segments

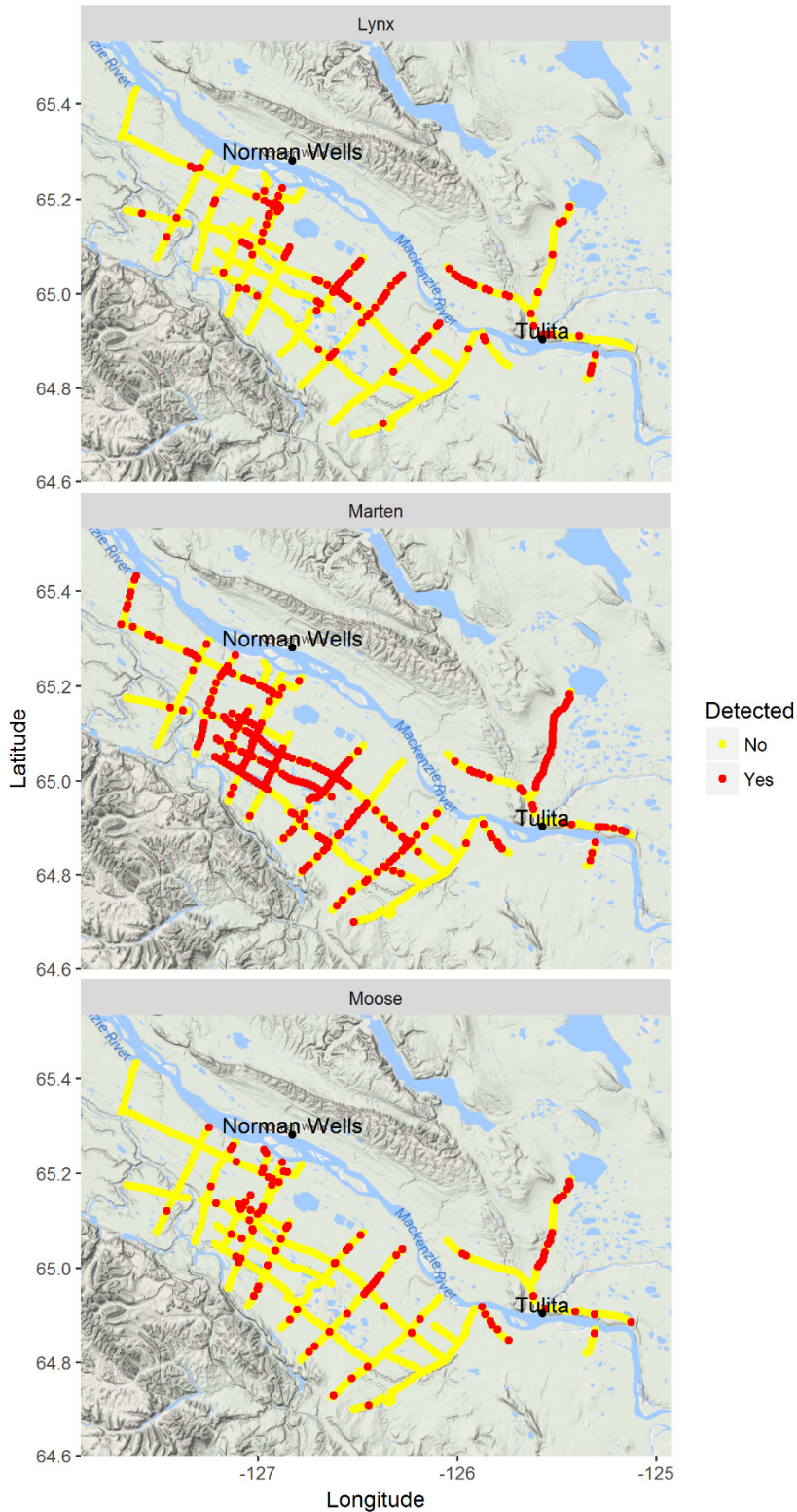


Figure 3. Detections of marten, lynx, and moose from snow tracking surveys, NWT.

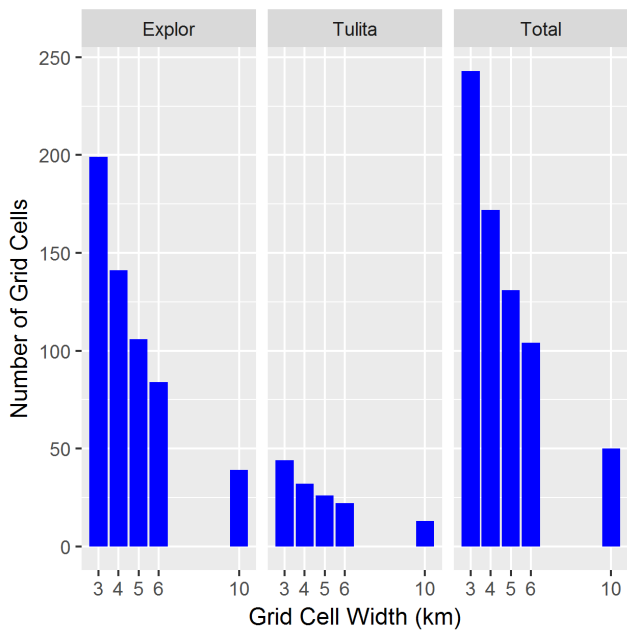


Figure 4. Number of grid cells surveyed by Explor, Tulita, and the two studies together.

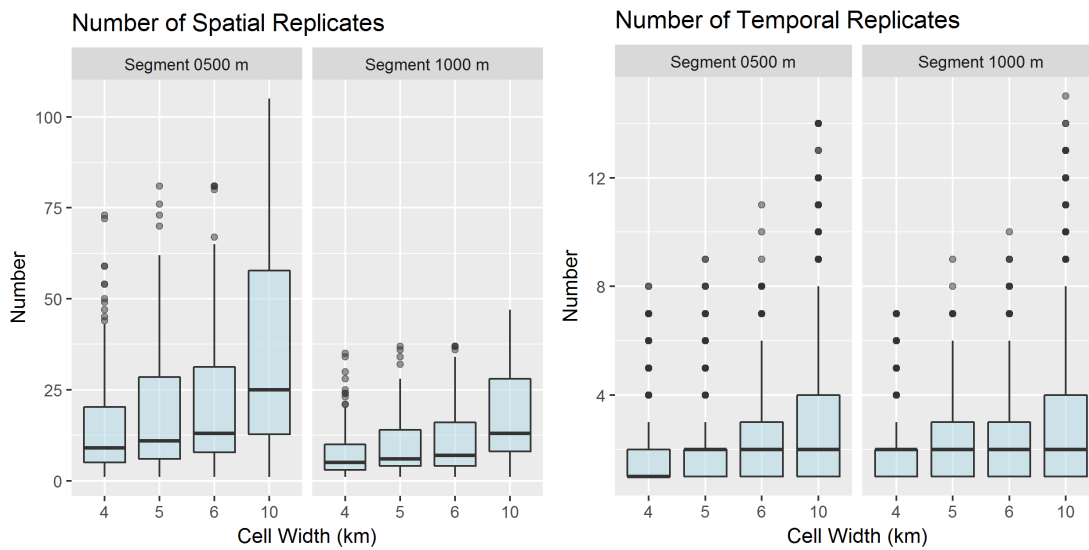


Figure 5. Boxplots for the number of spatial (segments per grid cell) and temporal (repeat surveys) versus grid cell width and segment length.

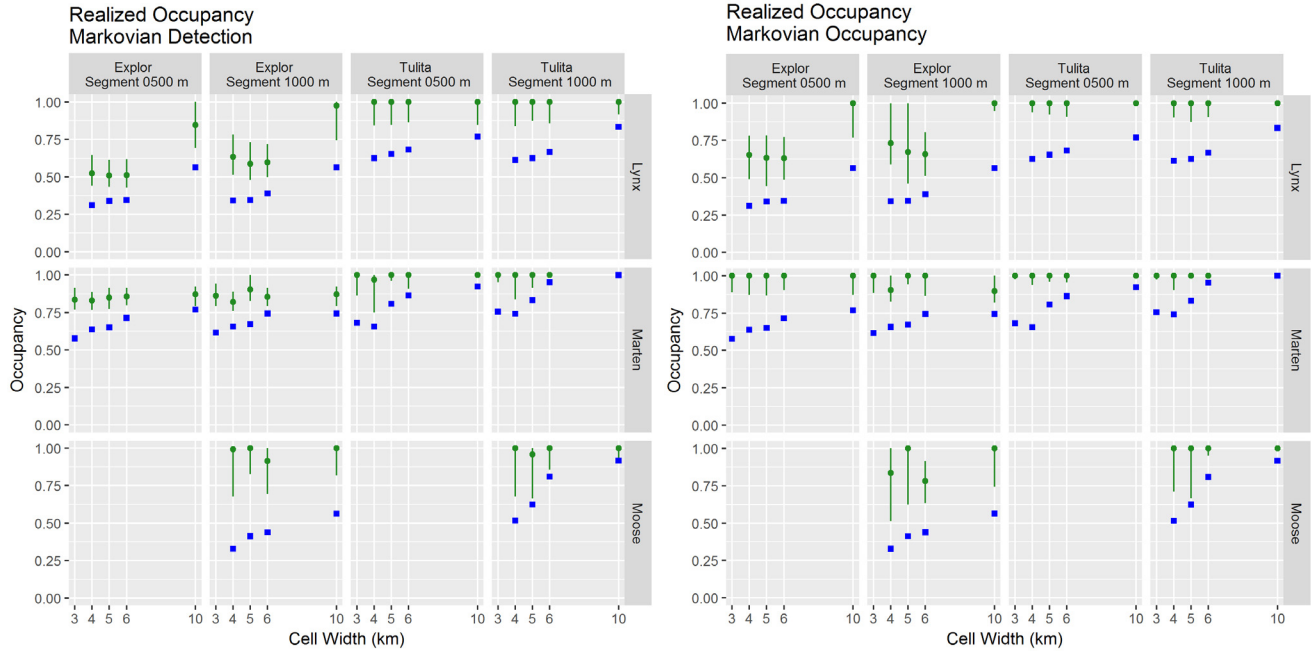


Figure 6. Naïve occupancy from observed detections (blue squares) and predicted occupancy and 95% CI from Markovian detection and Markovian occupancy models. Occupancy estimates are shown for the Explor and Tulita studies and for varying cell widths and segment lengths.

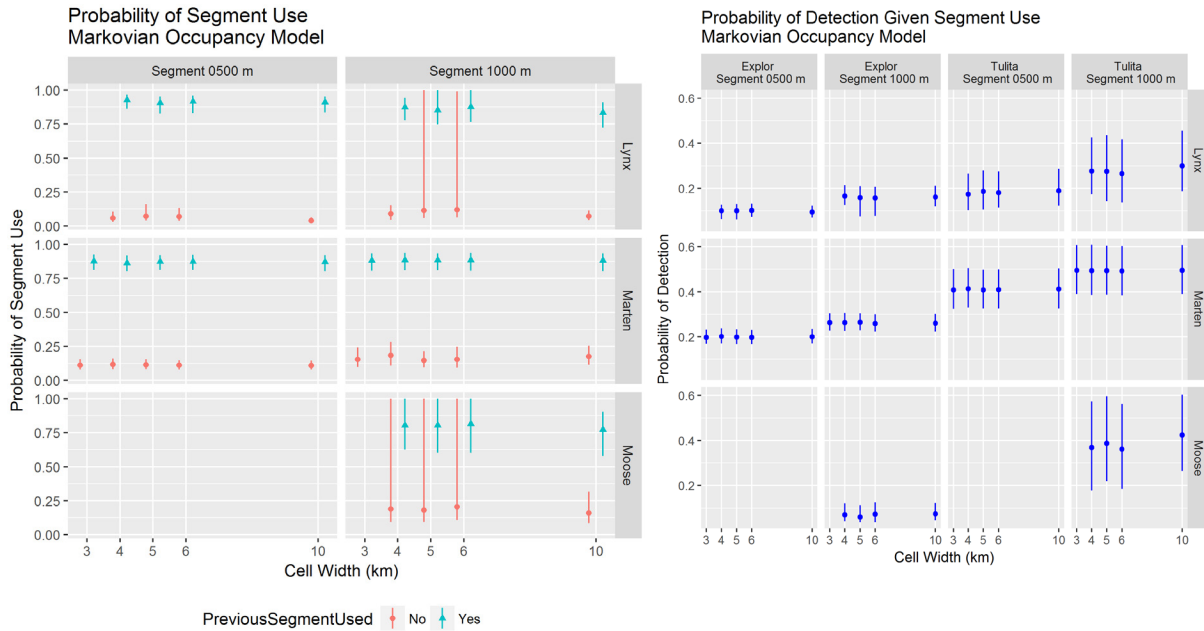


Figure 7. Probability of segment use given cell occupancy in the left graph depended on whether the previous segment was used. The right graph shows probability of detection with 95% CI given cell occupancy and segment use.

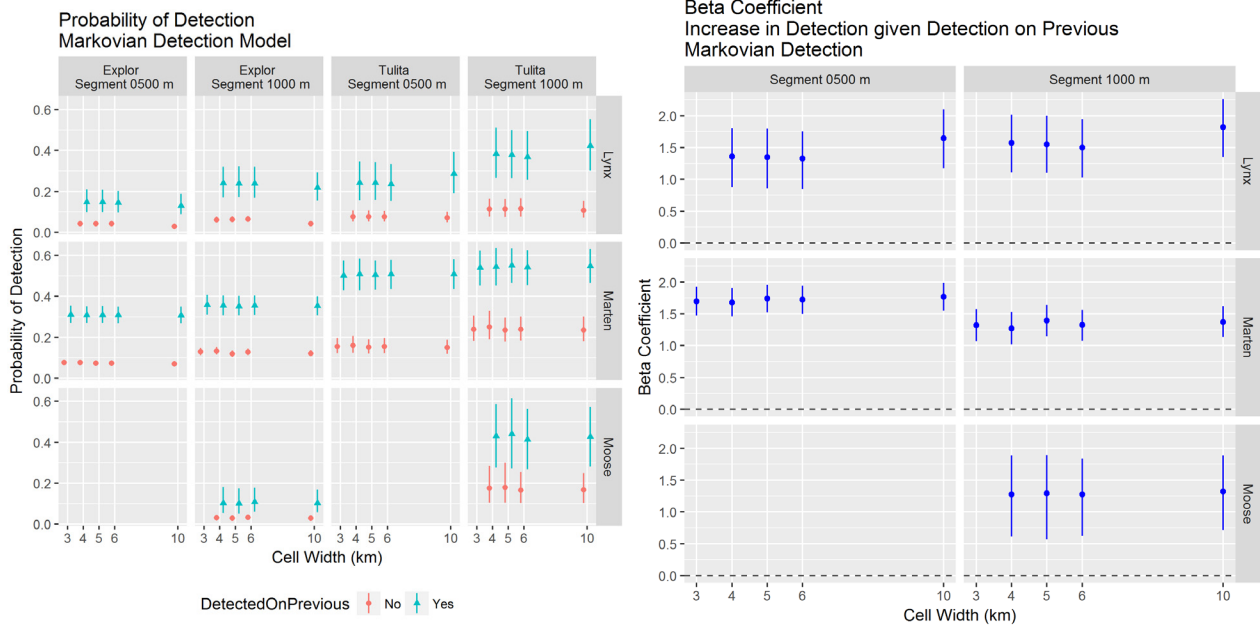


Figure 8. Probability of detection and 95% CI given cell occupancy for Markovian detection models. The left graph shows probability of detection when the species was and was not detected on the previous segment. The right graph shows how detecting a species on the previous segment increases probability of detection on the logit scale.

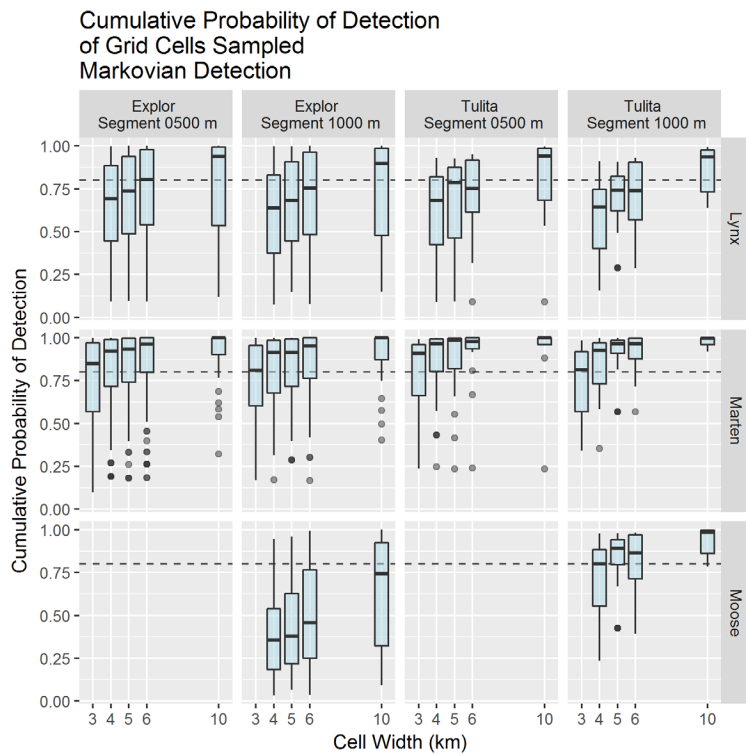


Figure 9. Cumulative probability of detection from sampled grid cells. Cumulative probability of detection was calculated $1 - (1 - p_{mean})^k$, where k was the number of spatial and temporal replicates and p_{mean} was the equilibrium probability of detection from when the species was and was not detected on the previous segment. Studies should aim to have a cumulative probability of detection > 0.8 or 0.9 .

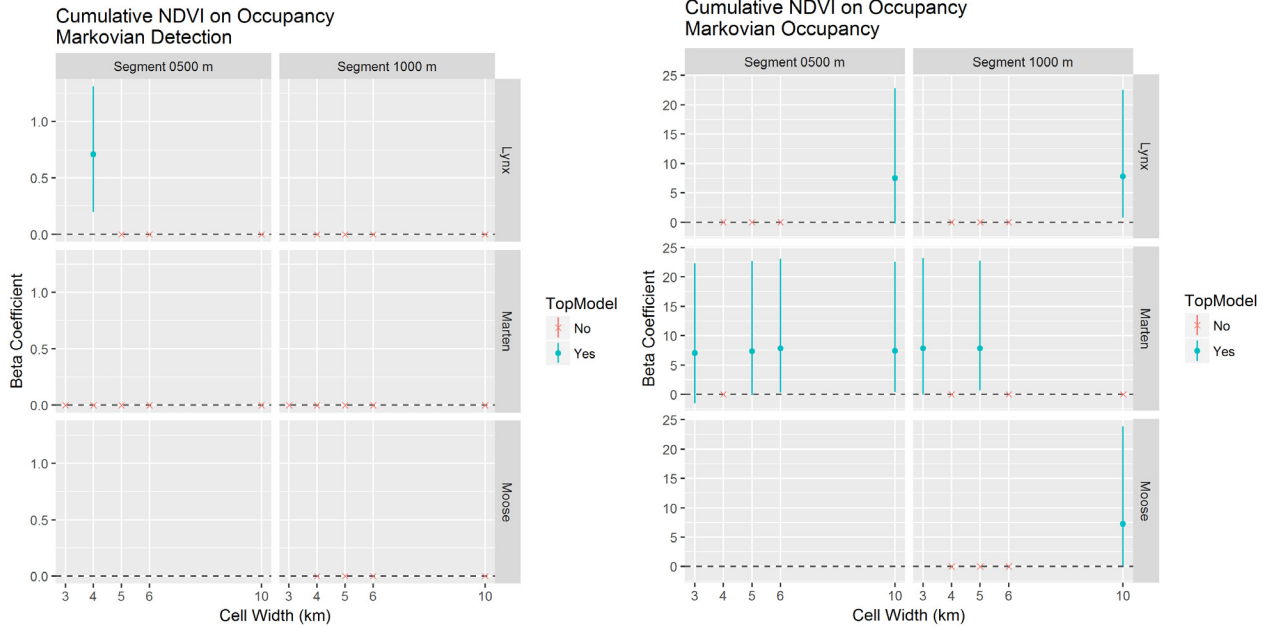


Figure 10. Effect of cumulative NDVI and 95% CI on cell occupancy when included in the top Markovian detection or Markovian occupancy model.

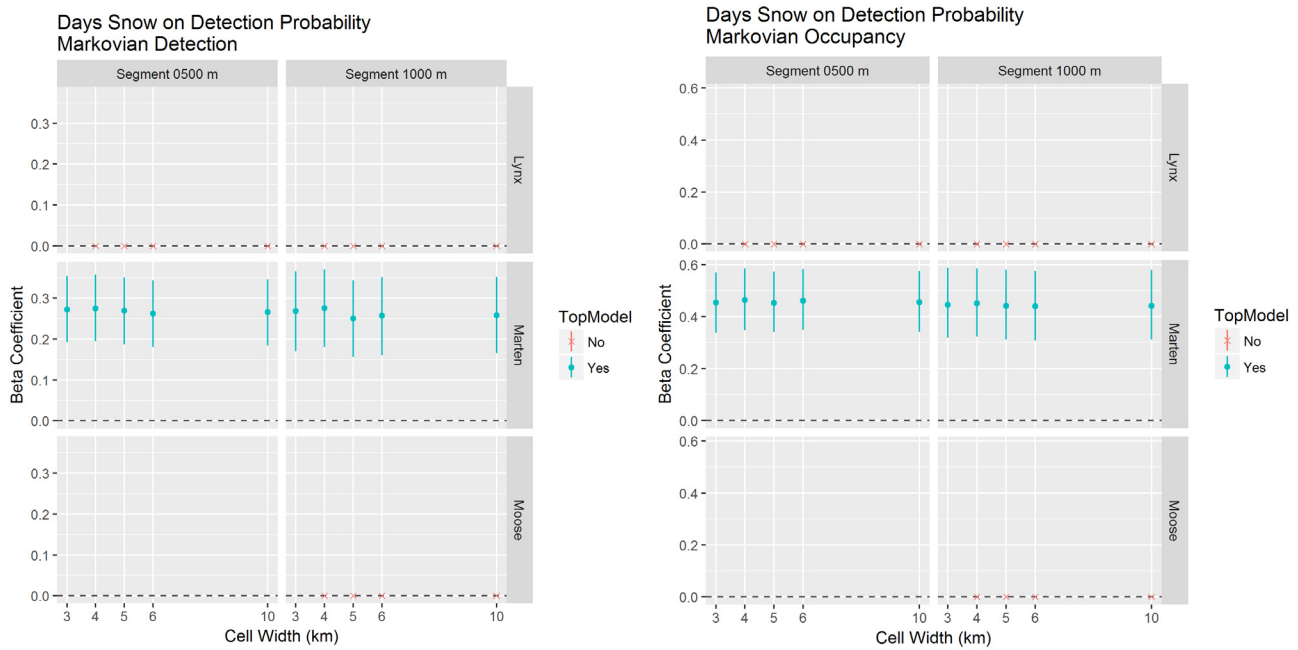


Figure 11. Effect of days since last snow on detection probability when included in the top Markovian detection or Markovian occupancy model.

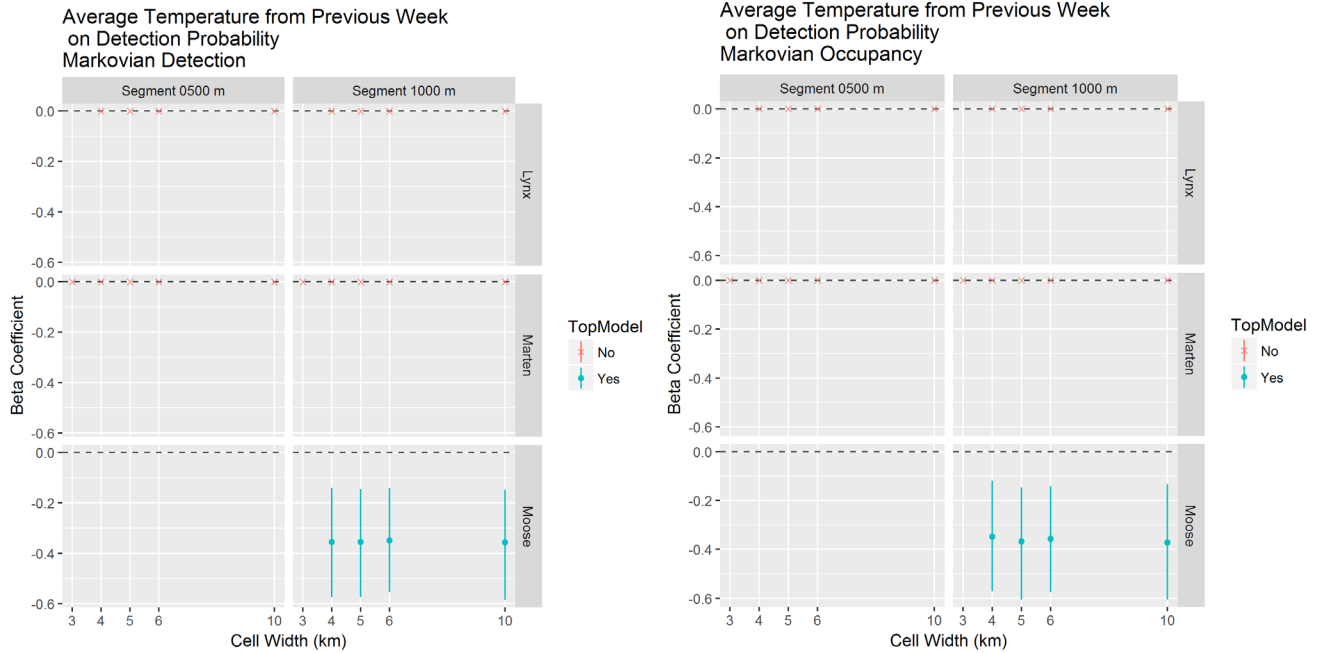


Figure 12. Effect of average temperature on detection probability when included in the top Markovian detection or Markovian occupancy model.

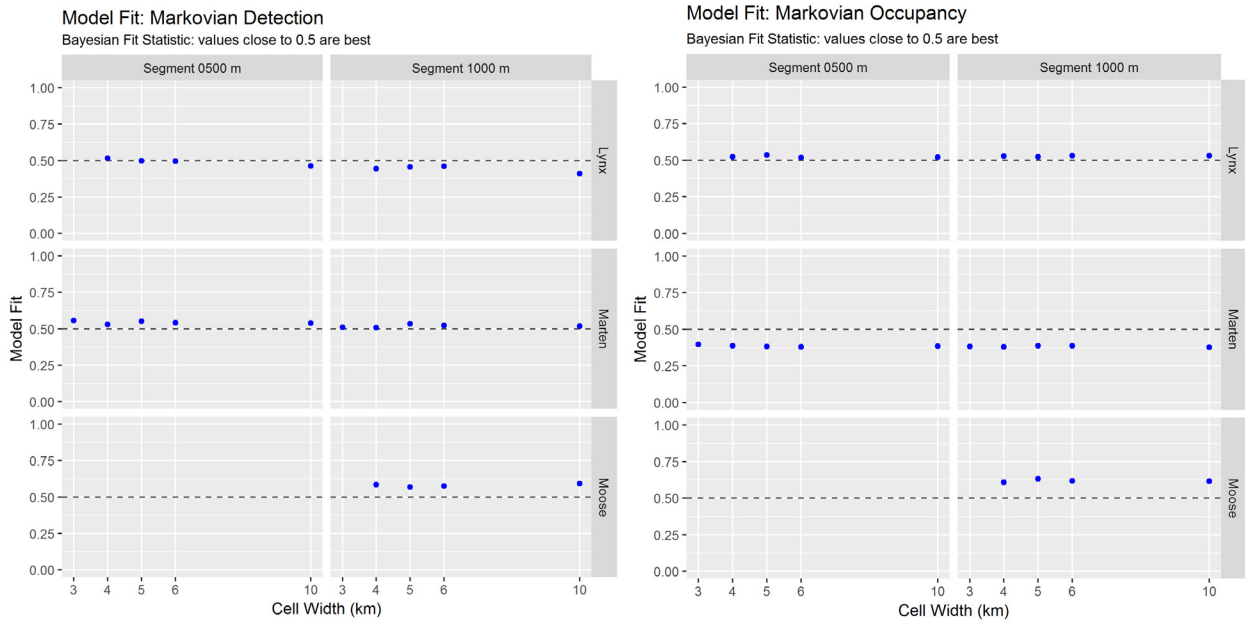


Figure 13. Model fit assessed by Bayesian p-values for Markovian detection and Markovian occupancy models. Values close to 0.5 indicate excellent fit and values less than 0.05 or greater than 0.95 indicate poor fit.

Statistical Power

Power to Detect 0.2 Decrease in Occupancy

Markovian Detection $B.ylag = 1.5$
 $\alpha = 0.10$

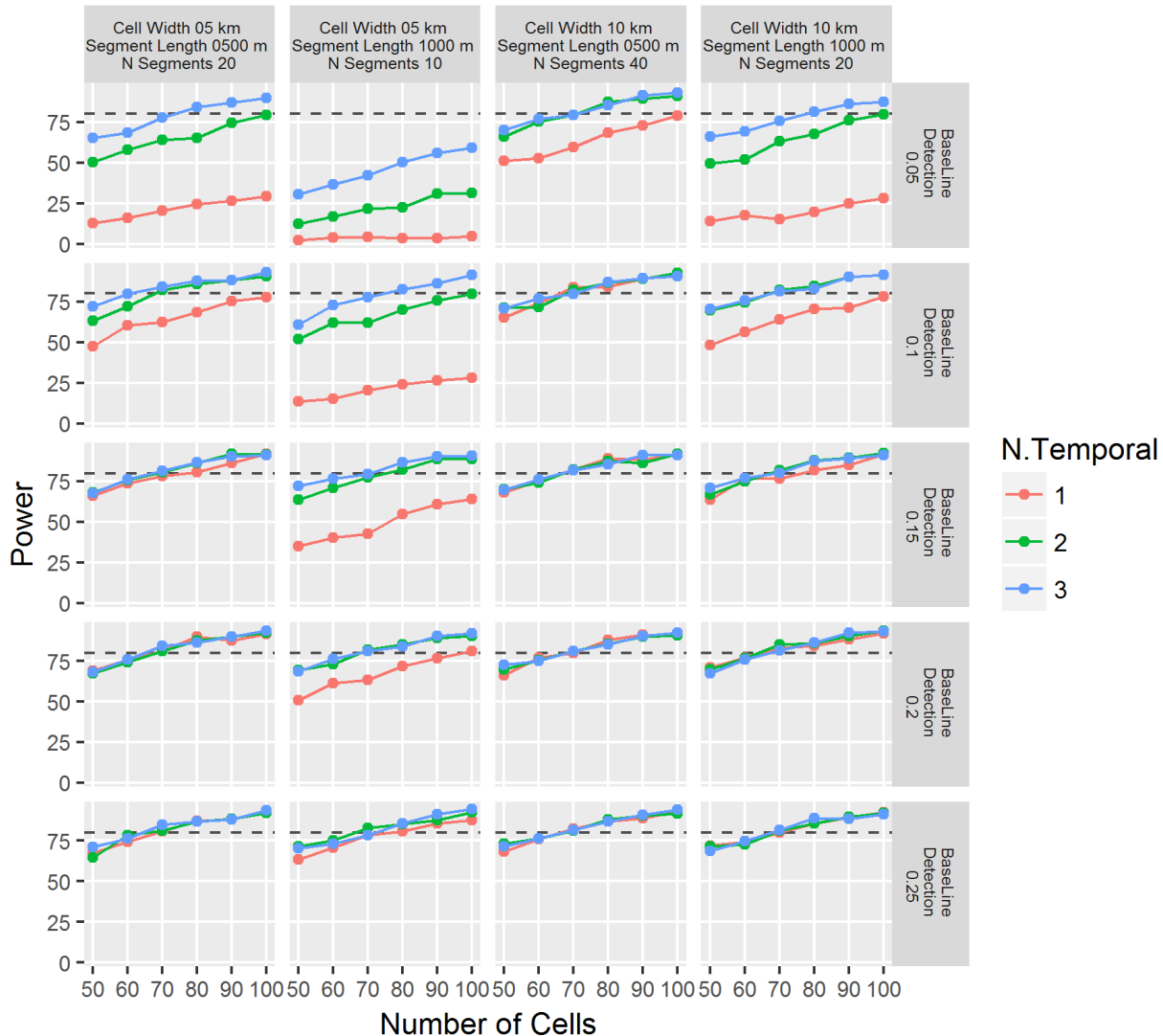


Figure 14. Effect of detection probability, cell width, segment length, and number of spatial (segments) and temporal replicates on statistical power to detect a 0.2 decline in occupancy across five years of sampling. Statistical power was assessed using Markovian detection models with the beta coefficient for an increase in detection probability given the species was detected on the previous segment.

Statistical power to detect a 0.2 decrease in occupancy over five years of sampling increased with detection probability, the number of grid cells and number of temporal and spatial replicates. At least 60 sites were required to achieve 80% power in all simulations. In simulations with low detection probability and one temporal replicate, 500 m segments appeared to have more power than 1000 m segments even when the total number of km tracked was the same. However, the 500 and 1000 m segments had similar power at higher rates of detection probability and with additional temporal replicates. The 5 km wide grid cells had higher power than

10 km grid cells, given that for a given area there would be four times as many 5 km wide grid cells as 10 km wide grid cells.

Discussion

Occupancy rates for marten, lynx, and moose were high throughout the Explor and Tulita study areas. There was strong serial autocorrelation in detection probability and segment use. Failure to account for this spatial correlation would lead to overestimates of detection probability and underestimates of occupancy with poor confidence interval coverage. Cumulative NDVI was a weak predictor of occupancy for all species and especially lynx. The probability of marten, lynx, and moose occurrence increased with NDVI and thus productivity for some but not all the grid cell widths and models. The reason why NDVI was a stronger predictor in the Markovian occupancy models likely stemmed from higher realized occupancy rates in areas with high NDVI. Probability of marten, but not lynx or moose, detection increased with DaysSnow. DaysSnow was used as a sampling window but the true sampling window can be difficult to estimate because the tracks of heavier animals such as moose persist longer and require more snow or wind to wipe clean. One reason moose detection probability was much lower for Explor data compared to Tulita data could be that Explor surveyors only recorded moose tracks if they occurred since the last snowfall, whereas Tulita surveys recorded tracks even if they occurred prior to the snow fall. Another, albeit imperfect, method for future surveys is to estimate the sampling window for carnivores and ungulates separately based on animal weights and cumulative snowfall (Whittington et al. 2015). However, when using this method confidence intervals overlapped zero for all species except lynx and moose. Moose detection rates were negatively associated with temperature for both classes of model and all grid cell sizes. Thus, moose detection rates decreased with increasing temperature and moose either moved more at lower temperatures or were more likely to occur near survey routes during low temperatures. While we found covariates that influenced occupancy and detection probability, future analyses could examine the effects of finer scale habitat characteristics such as landcover class, fire history, and forest cover. Understanding factors affecting occupancy and detection probability would lead to more precise occupancy estimates, increased statistical power, and links to how human activities and interspecific competition influences the ecology of the Northwest Territories.

Previous researchers recommended at least 60 sites for single year estimates of occupancy (McKann et al. 2013, Whittington et al. 2015, Steenweg et al. 2016), 120 sites for multi-year models with colonization and extinction (McKann et al. 2013), and a cumulative probability of detection > 0.8 (Long and Zielinski 2008) or 0.9 (McKann et al. 2013). Sixty sites were required in simulations that included perfect detection (Whittington et al. 2015). Thus, the number of sites is influenced by the characteristics of logistic regression and the absolute change in occupancy. One feature of the binomial proportions is that variation can be calculated as $p * (1 - p)/S$ where p is detection probability and S is the number of sites. Thus variation is highest for values of $p = 0.5$ and lowest near 0 and 1 (Guillera-Aroita and Lahoz-Monfort 2012, Steenweg 2017). I examined the change in occupancy from $\psi = 0.7$ to 0.5, which is near the centre of the Bernoulli distribution. Thus, statistical power could be slightly higher for changes in occupancy with ψ near 0 and 1.

I examined the influence of using segment lengths of 500 m vs 1000 m. I expected the two lengths to have similar power because detection probability should increase with segment length and serial correlation should decrease with segment length (Hines et al. 2010). However, because baseline detection probability and serial correlation in detection probability were similar for the two segment lengths, the power analysis suggested that using 500 m segment lengths will provide more power because of the increased number of spatial replicates. Other studies using spatial replication used segment lengths of 1 km (Hines et al. 2010, Thorn et al. 2011, Whittington et al. 2015), 5 km (Wibisono et al. 2011), or 0.6 km (Thapa 2014, Thapa and Kelly 2016).

The choice of grid cell width depends on animal home range sizes but is also influenced by the number of cells required to detect changes in occupancy using logistic regression, survey effort required to achieve a

cumulative probability of detection greater than 0.8 and preferably 0.9 (McKann et al. 2013). Grid cell size can vary among species because it can be defined after data collection. A grid cell width of 3 or 4 km could be used for marten because they have small home ranges, high baseline detection probability (p ranged from 0.08 to 0.25), and high cumulative probability of detection. Moose could use grid cell widths of 5 km or 10 km. Moose had a high baseline probability of detection (p approximately 0.17) and thus statistical power in Tulita, but not Explor (p approximately 0.03). Explor data would likely have had much higher probability of detection had they recorded tracks made prior to the most recent snow fall and thus would have similar power to Tulita. Lynx had lower detection probabilities (p ranged between 0.03 and 0.12), lower cumulative probability of detection, and lower power and could use either 5 or 10 km cell widths. Widths of 5 km had higher power to detect changes in occupancy but had marginal cumulative probability of detection.

Originally, the choice of grid cell size and the density of sampling sites was thought to influence how occupancy models track changes in abundance (He and Gaston 2000). However, simulations and analysis of remote camera data shows that the number of sites within a study area (i.e. density of sites and grid cell size) influences precision but not the occupancy-abundance relationship (Steenweg et al. 2017 *In Review*). Thus, with point sampling, decisions about grid cell size revolve around precision not occupancy-abundance relationships. However, grid cell size does influence occupancy abundance-relationships when sampling an entire grid cell rather than points in space. It is unclear how choice of grid cell size would affect occupancy-abundance relationships for snow-tracking surveys because they sample a portion of the grid cell rather than points in space. If they sample a relatively small proportion of the grid cell, then grid cell size should not influence occupancy-abundance curves. Most other studies using spatial replication for mammals used grid cell sizes that were approximately equal to or larger than the home range size of the focal species: cell widths of 13.7 or 17 km were used to estimate occupancy rates of tigers (Hines et al. 2010, Wibisono et al. 2011), 20 km for brown hyenas (Thorn et al. 2011), and 1.8 km for tigers and multiple other species in Nepal (Thapa 2014, Thapa and Kelly 2016). However, cell widths of 10 km were used for large mammals in the Canadian Rockies (Whittington et al. 2015) because that width had been used for wolverine surveys in Alaska (Magoun et al. 2007) and power to detect changes in wolverine occupancy were similar at 10 and 15 km cell widths and then decreased with 30 km cell widths (Ellis et al. 2014). The decision about what grid cell size to select is also influenced by levels of home range overlap for the focal species (Ellis et al. 2014) and the scale at which management decisions are made. In summary, grid cell widths of 3 km are likely appropriate for marten, 5 km for moose, and either 5 or 10 km for lynx even though lynx home ranges are often around 200 km².

Snow tracking surveys conducted in the Norman Wells and Tulita regions of the Northwest Territories show promise for monitoring large scale changes in the distribution of multiple large mammal species. A minimum of 60 grid cells are required to have sufficient statistical power to detect changes over time. Standardized survey routes and set survey intervals would increase sampling efficiency, be clearer for technicians when animals repeated travel on and off the survey route, and would simplify data preparation for analysis. Conversely, if points are recorded along survey routes other techniques such as distance to detection could be used to estimate occupancy (Guillera-Arroita 2011). Most importantly, standardizing data collection methods would provide a foundation for monitoring how changing climatic conditions, interspecific competition, and changes to the landscape affect the large scale distribution of large mammals.

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Appendix

Table 1. Model rank for covariates selected with Gibbs variable selection for both Markovian detection and Markovian occupancy models. Models were ranked by the proportion of MCMC iterations each combination of variables was selected (prob). I selected top models with a cumulative probability less than 0.95. Values of 0 and 1 represent covariates being excluded and included in their respective model.

Data Set	Species	Cell Width km	Segment Length (m)	prob	rank	NDVI	p' or θ'	DaysSnow	Temperature
Markovian Detection									
1	Lynx	4	500	0.52	1	1	1	0	0
	Lynx	4	500	0.46	2	0	1	0	0
2	Lynx	5	500	0.62	1	0	1	0	0
	Lynx	5	500	0.36	2	1	1	0	0
3	Lynx	6	500	0.90	1	0	1	0	0
	Lynx	6	500	0.08	2	1	1	0	0
4	Lynx	10	500	0.84	1	0	1	0	0
	Lynx	10	500	0.14	2	1	1	0	0
5	Lynx	4	1000	0.89	1	0	1	0	0
	Lynx	4	1000	0.09	2	1	1	0	0
6	Lynx	5	1000	0.66	1	0	1	0	0
	Lynx	5	1000	0.32	2	1	1	0	0
7	Lynx	6	1000	0.94	1	0	1	0	0
	Lynx	6	1000	0.03	2	1	1	0	0
8	Lynx	10	1000	0.75	1	0	1	0	0
	Lynx	10	1000	0.24	2	1	1	0	0
9	Marten	3	500	0.81	1	0	1	1	0
	Marten	3	500	0.18	2	1	1	1	0
10	Marten	4	500	0.96	1	0	1	1	0
11	Marten	5	500	0.95	1	0	1	1	0
12	Marten	6	500	0.96	1	0	1	1	0
13	Marten	10	500	0.89	1	0	1	1	0
	Marten	10	500	0.10	2	1	1	1	0
14	Marten	3	1000	0.66	1	0	1	1	0
	Marten	3	1000	0.33	2	1	1	1	0
15	Marten	4	1000	0.93	1	0	1	1	0
	Marten	4	1000	0.07	2	1	1	1	0
16	Marten	5	1000	0.93	1	0	1	1	0
	Marten	5	1000	0.07	2	1	1	1	0
17	Marten	6	1000	0.94	1	0	1	1	0
	Marten	6	1000	0.05	2	1	1	1	0
18	Marten	10	1000	0.90	1	0	1	1	0
	Marten	10	1000	0.10	2	1	1	1	0
19	Moose	4	1000	0.54	1	0	1	0	1
	Moose	4	1000	0.17	2	0	1	0	0

Data Set	Species	Cell Width km	Segment Length (m)	prob	rank	NDVI	p' or θ'	DaysSnow	Temperature
	Moose	4	1000	0.12	3	1	1	0	1
	Moose	4	1000	0.05	4	0	1	1	1
	Moose	4	1000	0.05	5	0	1	1	0
	Moose	4	1000	0.03	6	1	1	0	0
20	Moose	5	1000	0.48	1	0	1	0	1
	Moose	5	1000	0.19	2	0	1	0	0
	Moose	5	1000	0.12	3	1	1	0	1
	Moose	5	1000	0.07	4	0	1	1	0
	Moose	5	1000	0.05	5	0	1	1	1
	Moose	5	1000	0.05	6	1	1	0	0
21	Moose	6	1000	0.53	1	0	1	0	1
	Moose	6	1000	0.20	2	0	1	0	0
	Moose	6	1000	0.12	3	1	1	0	1
	Moose	6	1000	0.06	4	0	1	1	0
	Moose	6	1000	0.04	5	1	1	0	0
	Moose	6	1000	0.03	6	0	1	1	1
22	Moose	10	1000	0.53	1	0	1	0	1
	Moose	10	1000	0.19	2	1	1	0	1
	Moose	10	1000	0.12	3	0	1	0	0
	Moose	10	1000	0.05	4	0	1	1	1
	Moose	10	1000	0.04	5	0	1	1	0
	Moose	10	1000	0.04	6	1	1	0	0
Markovian Occupancy									
1	Lynx	4	500	0.85	1	0	1	0	0
	Lynx	4	500	0.09	2	1	1	0	0
	Lynx	4	500	0.03	3	0	0	0	0
2	Lynx	5	500	0.86	1	0	1	0	0
	Lynx	5	500	0.10	2	1	1	0	0
3	Lynx	6	500	0.83	1	0	1	0	0
	Lynx	6	500	0.13	2	1	1	0	0
4	Lynx	10	500	0.65	1	1	1	0	0
	Lynx	10	500	0.28	2	0	1	0	0
	Lynx	10	500	0.03	3	0	0	0	0
5	Lynx	4	1000	0.77	1	0	1	0	0
	Lynx	4	1000	0.17	2	1	1	0	0
	Lynx	4	1000	0.03	3	0	1	1	0
6	Lynx	5	1000	0.46	1	0	1	0	0
	Lynx	5	1000	0.39	2	1	1	0	0
	Lynx	5	1000	0.10	3	1	0	0	0
	Lynx	5	1000	0.02	4	0	1	1	0

Data Set	Species	Cell Width km	Segment Length (m)	prob	rank	NDVI	p' or θ'	DaysSnow	Temperature
7	Lynx	6	1000	0.82	1	0	1	0	0
	Lynx	6	1000	0.09	2	1	1	0	0
	Lynx	6	1000	0.06	3	0	0	0	0
8	Lynx	10	1000	0.68	1	1	1	0	0
	Lynx	10	1000	0.26	2	0	1	0	0
	Lynx	10	1000	0.04	3	1	1	1	0
9	Marten	3	500	0.54	1	1	1	1	0
	Marten	3	500	0.45	2	0	1	1	0
10	Marten	4	500	0.53	1	0	1	1	0
	Marten	4	500	0.46	2	1	1	1	0
11	Marten	5	500	0.52	1	1	1	1	0
	Marten	5	500	0.47	2	0	1	1	0
12	Marten	6	500	0.67	1	1	1	1	0
	Marten	6	500	0.33	2	0	1	1	0
13	Marten	10	500	0.65	1	1	1	1	0
	Marten	10	500	0.35	2	0	1	1	0
14	Marten	3	1000	0.56	1	1	1	1	0
	Marten	3	1000	0.43	2	0	1	1	0
15	Marten	4	1000	0.88	1	0	1	1	0
	Marten	4	1000	0.11	2	1	1	1	0
16	Marten	5	1000	0.70	1	1	1	1	0
	Marten	5	1000	0.29	2	0	1	1	0
17	Marten	6	1000	0.52	1	0	1	1	0
	Marten	6	1000	0.47	2	1	1	1	0
18	Marten	10	1000	0.73	1	0	1	1	0
	Marten	10	1000	0.26	2	1	1	1	0
19	Moose	4	1000	0.34	1	0	1	0	1
	Moose	4	1000	0.19	2	0	1	1	0
	Moose	4	1000	0.15	3	0	1	0	0
	Moose	4	1000	0.07	4	0	0	0	1
	Moose	4	1000	0.06	5	1	1	0	1
	Moose	4	1000	0.06	6	0	1	1	1
	Moose	4	1000	0.03	7	1	1	1	0
	Moose	4	1000	0.03	8	0	0	1	0
	Moose	4	1000	0.02	9	0	0	0	0
	Moose	4	1000	0.02	10	1	1	0	0
20	Moose	5	1000	0.29	1	0	1	0	1
	Moose	5	1000	0.22	2	1	1	0	1
	Moose	5	1000	0.11	3	0	0	0	1
	Moose	5	1000	0.07	4	0	1	1	0
	Moose	5	1000	0.06	5	1	1	1	0

Data Set	Species	Cell Width km	Segment Length (m)	prob	rank	NDVI	p' or θ'	DaysSnow	Temperature
	Moose	5	1000	0.06	6	0	1	0	0
	Moose	5	1000	0.05	7	0	1	1	1
	Moose	5	1000	0.05	8	1	1	1	1
	Moose	5	1000	0.03	9	1	1	0	0
	Moose	5	1000	0.03	10	0	0	0	0
21	Moose	6	1000	0.48	1	0	1	0	1
	Moose	6	1000	0.14	2	0	1	0	0
	Moose	6	1000	0.14	3	0	1	1	0
	Moose	6	1000	0.09	4	0	0	0	1
	Moose	6	1000	0.05	5	0	1	1	1
	Moose	6	1000	0.04	6	1	1	0	1
	Moose	6	1000	0.02	7	1	0	0	1
22	Moose	10	1000	0.28	1	1	1	0	1
	Moose	10	1000	0.19	2	0	1	0	1
	Moose	10	1000	0.14	3	0	1	1	0
	Moose	10	1000	0.12	4	1	1	1	0
	Moose	10	1000	0.07	5	1	1	0	0
	Moose	10	1000	0.06	6	1	1	1	1
	Moose	10	1000	0.05	7	0	1	0	0
	Moose	10	1000	0.05	8	0	1	1	1