Multi-Species Occupancy Monitoring using Snow Surveys in Banff National Park

Photo by K. Heuer

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Abstract

We piloted a snow tracking survey to monitor changes in the spatial distribution and relative abundance of multiple species in Banff National Park. We used an occupancy modelling approach to account for imperfect species detection and estimated detection probabilities using both spatial and temporal replication of 419 one km survey segments within thirty-seven 100 km^2 hexagons (3700 km^2 were surveyed). Including repeated sampling of some survey routes we completed 630 km of sampling. Because some species travel long distances on trails, we compared three types of occupancy models (Hines et al. 2010): 1) Independent: assumed spatial independence among adjacent trail segments, 2) Detection process: modeled correlation in detection rates among adjacent segments, 3) Spatial process: modeled correlation in occupancy rates among adjacent segments. The spatial process models performed best for wolverine, cougar, fox, and coyote. The independent models performed best for lynx, deer, and moose. The number of cells occupied (and associated area) for each species was: wolverine (n = 31.7, 95% CI = 26 – 37), lynx (n = 12.6, 95% CI = 11 – 16), cougar (n = 7.3, 95% CI = 2 - 29), fox (n = 9.6, 95% CI = 4 - 24), coyote (n = 16, 95% = 10 - 26), deer(n = 12.4, 95% CI = 8 - 24), moose (n – 12.3, 95% CI = 13 – 21). Detection probabilities from the independent models were highest (approximately 0.25) for wolverine, lynx, and moose. The 2012 survey design had greater than 80% power to detect a 20% decline in occupancy for species with detection probabilities greater than 0.10. This snow tracking technique shows promise as an inexpensive, efficient, and powerful tool to monitor the spatial distribution and relative abundance of multiple species, including wary, low density carnivores such as wolverine and lynx.

Introduction

Wary and elusive carnivores such as wolverine (*Gulo gula*) and lynx (*Lynx canadensis*) occur in rugged and remote landscapes and are rarely observed and difficult to monitor. Consequently, little is known about their population trends along the Rocky Mountains and in Banff National Park. Wolverine are classified as *Special Concern* in Canada (COSEWIC 2003) and *May Be at Risk* (*Data Deficient)* in Alberta. Populations are declining in the United States and have been designated as W*arranted for Protection* under the Endangered Species legislation (Inman et al. 2012).   Lynx are classified as *Not at Risk* in Canada (COSEWIC 2001) and as *Secure* in Alberta, but populations are thought to have declined in the southern part of their range and are now listed as *Threatened* in the United States (U.S. Fish and Wildlife Service 2000). Given the lack of information about these species and their threatened status elsewhere, inexpensive and non-invasive techniques are required to monitor them across large geographic areas like Banff National Park.

Reasons for the decline of wolverine and lynx along the southern extent of their range are varied. Wolverine populations are thought to be threatened by trapping (Krebs et al. 2004), declining snow packs (Brodie and Post 2010, Copeland et al. 2010, McKelvey et al. 2011), backcountry recreation (Krebs et al. 2007), industrial development (Krebs et al. 2007, Fisher et al. 2012 *in prep*.), and potentially competition with other mammals (Inman et al. 2012, Fisher et al. 2012 *in prep*.).   Lynx populations trends and distribution are strongly dependent upon snowshoe hare (*Lepus americanus*) densities

(Boutin et al. 1995, O'Donoghue et al. 1997, Krebs et al. 2001). Snowshoe hare and lynx populations exhibit large 9 to 11 year oscillations in northern Canada. However, snowshoe hare oscillations and densities are much lower in the southern portion of their range and this likely results in lower lynx densities (Murray et al. 2008). Lynx in Banff National Park exhibited highly variable survival and low recruitment rates (Apps 2003), which were likely influenced by prey availability. It is unclear how recreational activities might affect lynx populations (Murray et al. 2008). Fragmented landscapes and snowshoe hare densities strongly affected lynx population densities and distribution along the southern extent of their range (Koehler et al. 2008, Murray et al. 2008). Lynx and wolverine both exhibit low population densities and low reproductive rates, which makes them both susceptible to habitat fragmentation, population declines, and range contraction.

In the past, Banff, Kootenay, and Yoho National Parks used snow track surveys (called "Sensitive Species Surveys") to monitorwildlife distributions (1995 to 2008). These surveys were conducted during mid-February and recorded a point location for carnivore and moose tracks. Within these data there appeared to be large changes in the relative abundance of wolverine that matched anecdotal observations (Figure 1). However, these surveys did not quantify survey effort or total areas sampled, which strongly affects the number of tracks observed each year. We built upon the Sensitive Species Survey approach by explicitly recording survey effort, areas sampled, and adopting rapidly emerging analytical techniques to estimate occupancy rates and the spatial distribution of multiple species within Banff National Park.
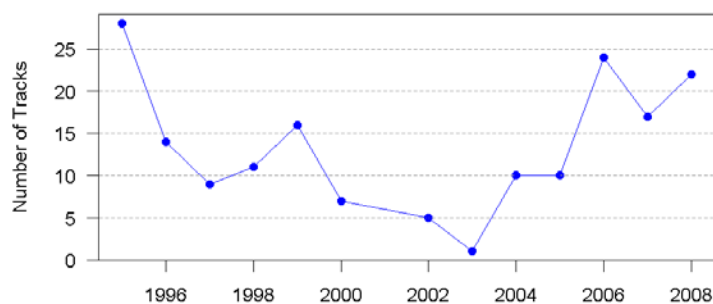
Figure 1. Number of wolverine tracks observed on winter snow track surveys in Banff National Park from 1995 through 2008.

One challenge facing monitoring surveys is that species are not always detected even when they are present. Repeating surveys is a way of addressing this deficiency. Such temporal replication allows for estimates of detection probabilities (proportion of time a species is detected given that is detected at least once) and those detection probabilities are used to estimate occupancy rates for sites where the species was not detected. Failing to account for detection probability can lead to underestimation of species relative abundance and distribution (MacKenzie et al. 2006, Royle and Dorazio 2008). It can also mask trends in abundance and distribution. Standard approaches for estimating detection probabilities include repeated surveys of sites, distance sampling, and using multiple observers. Repeated surveys (temporal replication) of snow track surveys were done opportunistically this past winter in Banff National Park but performing them across the entire survey area would be difficult and labour intensive. Recently, other studies have used spatial replicates to estimate detection probabilities for track surveys

covering large geographic areas (Hines et al. 2010, Thorn et al. 2011). In these studies, track surveys were conducted for tigers on trails in India and brown hyenas on roads in Africa. Both of these studies laid a grid across their study area and used 1 km trail/road segments within each grid cell as spatial replicates. These spatial replicates were used to estimate detection probabilities, occupancy estimates, and number of animals. We piloted this promising approach with snow surveys in Banff National Park using both spatial replication and temporal replication for more accessible trails.

Our primary objective was to:
- Estimate occupancy rates and the distribution of wolverine, lynx, cougar (*Felis concolor*), fox (*Vulpes vulpes*), coyote (*Canis latrans*), deer (*Odocoelius* species), and moose (*Alces alces*). This analysis is the focus of this paper.

Field work for this project served multiple other objectives including:
- Determine late winter wolf (*Canis lupus*) pack sizes and wolf density because wolf density can strongly influence demographic rates of ungulates such as elk (*Cervus canadensis*) and caribou (*Rangifer tarandus caribou*). These results, though important, are not included in this analysis.
- Estimate relative abundance of snowshoe hares (a strong driver of lynx trends) and marten (*Martes americana*).
- Service remote cameras being used for concurrent multi-species monitoring.
- Results from these secondary objectives are not included in this report.

Methods

We established 36 survey routes throughout all major valleys within Banff National Park south of the David Thompson Highway (Figure 2). We then divided each ski route into 497 one km segments. We surveyed routes in late March and early April instead of mid-February (when Sensitive Species Survey were conducted) for two reasons: 1) late winter snow packs are stronger which results in easier travel conditions and safer skiing conditions through avalanche terrain; b) ski tracks earlier in the winter can provide wolves with easier access to moose and caribou and thereby alter normal predator-prey relationships. Each survey team included at least one person with extensive snow-tracking experience and, depending on the terrain, appropriate avalanche training (as per Parks Canada Avalanche Safety Plan). When avalanche danger was high, trips through challenging and complex avalanche terrain were either postponed or not completed.

For each 1 km segment, surveyors identified all large mammal tracks and classified to species (Table 1). Common species included wolverine, lynx, cougar, fox, coyote, wolves, deer, and moose. We counted the number of snowshoe hare and marten tracks. Surveyors estimated the number of days that carnivore tracks could be observed given previous snowfall, wind, and sun events. We expected that this sampling window would strongly influence detection rates.   We recorded the same metric for ungulates that have deeper snow penetration. We also recorded percent snow cover, which we also expected would influence detection rates.

Occupancy Rates. We estimated occupancy rates for a grid of 100 km^2 hexagons spread across the study area. We used the 1 km segments as spatial replicates within grid cells to estimate detection probabilities. We surveyed some grid cells multiple times and we used these repeated surveys as temporal replicates for estimating detection probabilities. We chose 100 km^2 as our grid cell size based on the number of 1 km spatial replicates within each cell (mean = 11.3), home range size of target species, and resolution to detect change within Banff National Park. Other studies using spatial replicates matched grid cell size with the home range size of their target species (Hines et al. 2010) so that their occupancy estimates would reflect the number of individuals within the study. Most of our carnivore species have home ranges greater than 100 km^2 and we felt that using larger grid cells would result in decreased resolution of occupancy throughout the park and results would be more strongly influenced by how hexagons aligned with home ranges. We used hexagons rather than square grids because hexagons increased the minimum and mean number of replicates per cell and reduced effects associated with sharp corners. The layout of hexagons originated from a randomly located anchor.

We estimated the number of grid cells for each species present using an occupancy modelling approach (MacKenzie et al. 2006, Royle and Dorazio 2008, Kery and Schaub 2011). We estimated the number of occupied cells based on the observed number of cells occupied and detection probabilities where

$N_{predicted} = \frac{N_{oberved}}{Probability\ of\ Occupancy}$. Given that animals often travel along trails for multiple segments, we expected that if a species was detected on one segment it would also be detected on the adjacent segment. Therefore, we compared a model assuming independence among adjacent trail segments to two models that estimated the wildlife movement processes used to generate spatially correlated trail segments (Table 1). Failing to account for spatial correlation can lead to underestimates of species occupancy. We compared models with and without the spatial dependence using Deviance Information Criterion (DIC) and selected the model with the lowest DIC as the best supported model (Spiegelhalter et al. 2002). When multiple models had similarly low DIC values, we selected the model that made the most biological sense based on model coefficients. We included DaysSnow as a predictor for detection probability in all models (Table 1). We excluded PercentSnowCover as a covariate because 99% of the segments had 100% snow cover. Inclusion of PercentSnowCover resulted in positive coeffients with wide credibility intervals that encompassed 0. Lynx models included average number hare tracks per days snow for each grid cell as a predictor of occupancy because lynx populations are known to depend on snowshoe hare abundance. We centred all explanatory variables prior to analysis to improve convergence ($x_{centred} = \frac{x - x_{mean}}{st.dev(x)}$). We used a Bayesian Monte Carlo Markov Chain (MCMC) hierarchical approach to estimate these more complicated models that cannot be readily estimated using classical maximum likelihood approaches. For each MCMC model we ran 3 chains with 20,000 iterations for each chain. We removed the first 10,000 iterations (burn in) and then selected every 5th iteration for analysis. We monitored traceplots and the Gelman–Rubin statistic to determine whether or not the MCMC algorithm converged. We wrote and ran the models in R 2.15 (R Development Core Team 2012) and OpenBugs (Lunn et al. 2009).

Power Analysis. We explored the effects of detection probability ranging from 0.05 to 0.40 on power to detect 20, 30, 40, and 50% decline in occupancy. We simulated data and declines using a starting

occupancy rate of 0.631 (2012 wolverine occupancy rate), our current number of grid cells (n = 37), and the 2012 suite of spatial and temporal replicates for each cell. For each iteration we simulated two years of occupancy data, created a simple occupancy model for each year, and then compared the occupancy estimates and standard errors following Guillera-Arroita and Lahoz-Monfort (2012). We ran 1000 simulations for each scenario and calculated the percentage of simulations whose test statistic exceeded 1.64 (the critical Wald value for α = 0.10). Power analyses were conducted using the R package unmarked package (Fiske and Chandler 2011).

We used the following R packages for data preparation and analysis: sp, maptools, rgdal, plyr, reshape, lubridate, ggplot2, R2WinBugs, BRugs, mcmcplot, and unmarked (Bivand et al. 2008, Fiske and Chandler 2011, Keitt et al. 2012). We used freely available, open source software QGIS (www.qgis.org) for mapping survey routes.

Table 1. List of attributes recorded for each 1 km segment on the snow surveys.

Variable	Description	Range
Species	Mammal Species marten and larger	Occupancy Modelling: Wolverine, Lynx, Cougar, Fox, Coyote, Moose Deer
Number	Minimum number of individuals. Number of tracks for marten and snowshoe hare.	
Days snow meso-carnivores	Estimated number of sampling days for wolverine and lynx based on timing of snowfall, wind, and sun.	Mean = 4.1 Median = 3.0 Range = 0.2 – 13.
Days snow ungulates	Estimated number of sampling days for large ungulates based on timing of snowfall, wind, and sun.	Mean = 8.1 Median = 7.0 Range = 0.3 – 20.
Percent Snow Cover	Percentage snow cover for 1 km intervals	Mean= 99.8 Median = 100 Range = 50 - 100

Table 2. Description of three models used to estimate species occupancy from snow track surveys. Models were adapted from Hines et al. (2010). All detection probabilities were modelled as a function of days since snow. All models predicted the number of occupied cells.

| Model	Description	Parameters
Independent	Assumes spatial independence among adjacent trail segments.	• Cell Occupancy (Ψ) • Detection probability (p).
Detection Process	Assumes the probability of detection is influenced by detection on the previous trail segment	• Cell Occupancy (Ψ) • Detection probability (p). • Detection probability when species was detected on previous segment (p')
Spatial Process	Assumes that within a survey, segment occupancy is influenced by segment occupancy on the previous trail segment given that the cell is occupied. Occupancy rates of segments change for each temporal replicate and reflect animal movement along a trail.	• Cell Occupancy (Ψ) • Segment Occupancy given Cell is Occupied on Current Survey ($\Psi_{segment}$) • Segment occupancy given Cell is Occupied and Previous Segment is Occupied on Current Survey ($\Psi_{segment'}$) • Detection probability given that segment is occupied (p).
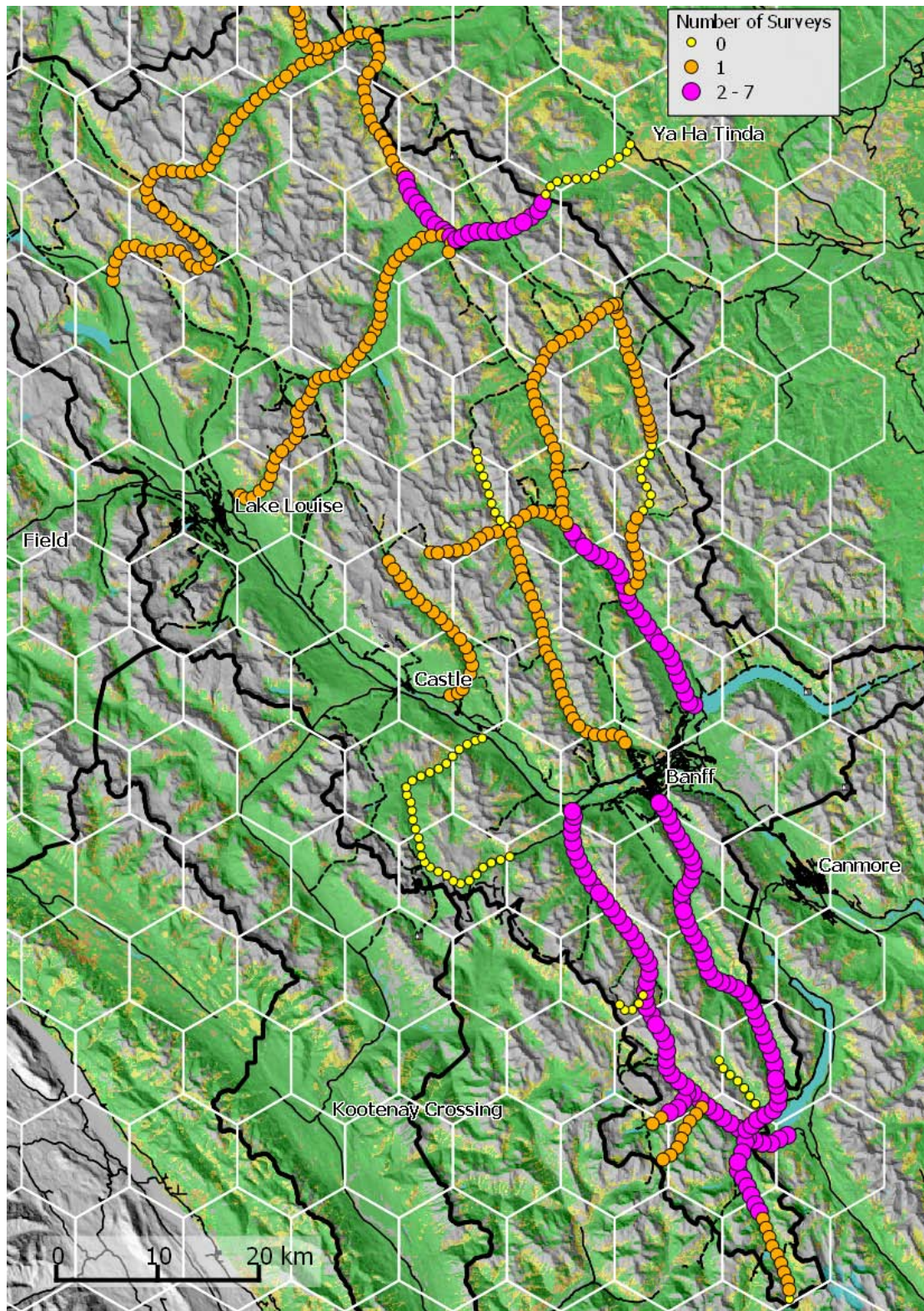
Figure 2. Map showing number of times each 1 km segment was surveyed for wildlife tracks during March and April 2012 in Banff National Park. The 100 km^2 white hexagons were used for estimating occupancy rates of large mammal species. Spatial and temporal replicates within the hexagons were used to estimate detection probabilities.

Results

We sampled 419 of the 497 one-km-long intervals in 2012. These surveys sampled thirty-seven 100 km^2 hexagons within Banff National Park (Figure 2). Each grid cell encompassed an average of 11.32 segments, which provided spatial replicates (Figure 3). We surveyed 36% (n = 153) of the segments multiple times. With these temporal replicates, we accumulated 630 km of sampling.
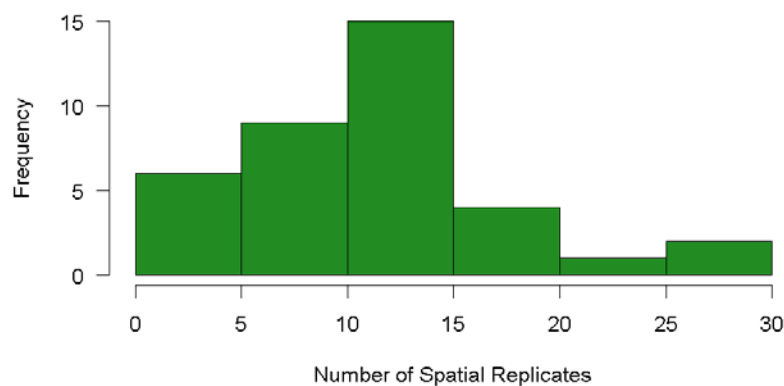

Figure 3. Histogram showing number of spatial replicates (1 km segments) per 100 km^2 hexagon in Banff National Park (n = 37 hexagons).

Wolverine tracks were detected in all higher elevation regions of the study area (Figure 9). Lynx had concentrated distribution in the Bryant, Brewster, Cascade, and Red Deer Valleys. Cougar were only detected along the lower Cascade and Clearwater Valleys. Fox were detected in both the Cascade and Panther Valleys. Wolves and coyotes were detected in all lower elevation areas sampled. Deer were detected in low elevation areas near the Bow Valley and sparsely detected in the lower Red Deer and Clearwater Valleys. Moose were concentrated in the Spray, Bryant, Brewster, and Clearwater Valleys.

The spatial process model predicted wolverine, cougar, fox, and coyote occurrence better than the non-spatial model (Table 3). These spatial models also predicted higher occupancy estimates for those species than the independent model (see Table 4 in Appendix I for all parameter estimates). The independent models performed best for lynx, deer, and moose. While there was some support for the detection process models, these models showed a negative effect of previous detections on detection probability for these species (but not wolverine). Given that negative correlation in detection probabilities is an unlikely biological process, we selected the simpler independent model for lynx, deer, and moose. All models appeared to converge based on traceplots and the Gelman–Rubin statistic.

Occupancy estimates were highest for wolverine and lowest for cougar (Figure 4, Figure 5). An estimated 31 of the 37 cells (95% CI = 26 -37) were occupied by wolverine and approximately 13 (95% CI

= 11 - 16) of the cells were occupied by lynx. The number of cells occupied (and associated area) for other species were: cougar (n = 7.3, 95% CI = 2 - 29), fox (n = 9.6, 95% CI = 4 - 24), coyote (n = 16, 95% = 10 - 26), deer(n = 12.4, 95% CI = 8 - 24), moose (n – 12.3, 95% CI = 13 – 21).   Confidence intervals were reasonably tight for wolverine, lynx, deer, and moose.

Monitoring programs work best for species with high detection probabilities because fewer spatial and temporal replicates are required to achieve precise occupancy estimates. Detection probabilities from the independent models ranged near 0.07 for cougar, 0.15 for fox and coyote, 0.20 for deer, and 0.25 for wolverine, lynx, and moose (Appendix I Table 4). The cumulative probability of detecting an animal in a cell was greater than 95% after two surveys for all species except cougar (Figure 6).   The sampling window (DaysSnow) was positively correlated with detection probabilities for wolverine, deer, and moose. It was not a strong predictor of detection probability for lynx, cougar, fox, and coyote. The number of snowshoe hare tracks per day was a strong predictor for lynx occupancy ($B_{HareDays}$ = 4.918, 95% CI = 1.350 - 10.174).

Power analysis based on 2012 survey effort showed that we have at least 80% power to detect a 30% decline in occupancy for species with detection probabilities greater than 0.15 (Figure 8). All species except cougar had detection probabilities greater than 13%. The power analysis suggests we had low power to detect a 20% decrease in occupancy. The analysis likely underestimated power for wolverine, cougar, fox, and coyotes because it did not account for spatial correlation among adjacent segments.

Table 3. Comparison of DIC values for models assuming independence between adjacent segments, models where detection of a species in one segment increases the detection probability in the next segment, and models where occupancy of one segment increases the probability of occupancy in the next segment. Lower DIC values indicate better model performance. The best model for each species is highlighted in gray. We selected the Independent rather than Detection Process model for Lynx because the Detection Process model showed an inverse correlation between adjacent segments.

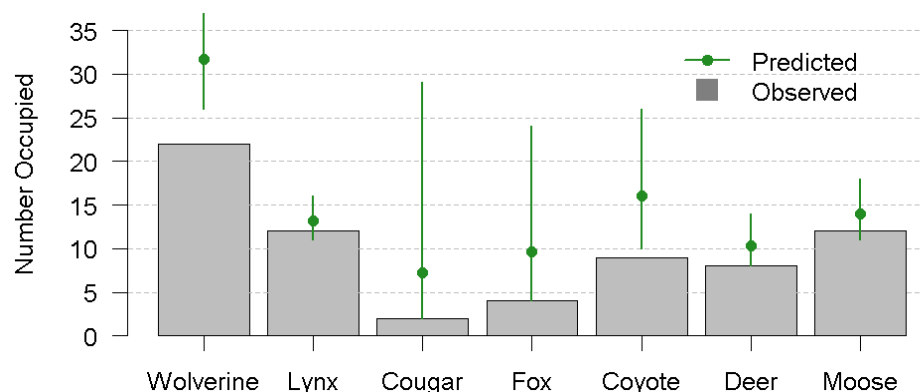| Model	Wolverine	Lynx	Cougar	Fox	Coyote	Deer	Moose
Independent	422.2	361.6	44.3	85.3	191.6	193.9	330.3
Detection Process	359.8	317.6	45.8	77.4	194.8	192.6	325.4
Spatial Process	261.1	465.1	42.4	63.4	135.3	444.6	896.6

Figure 4. Observed (shaded bars) and predicted (green points with 95% confidence intervals) number of grid cells occupied by each species. 37 grid cells were sampled in 2012. Predicted values were based on the best model identified in Table 2.
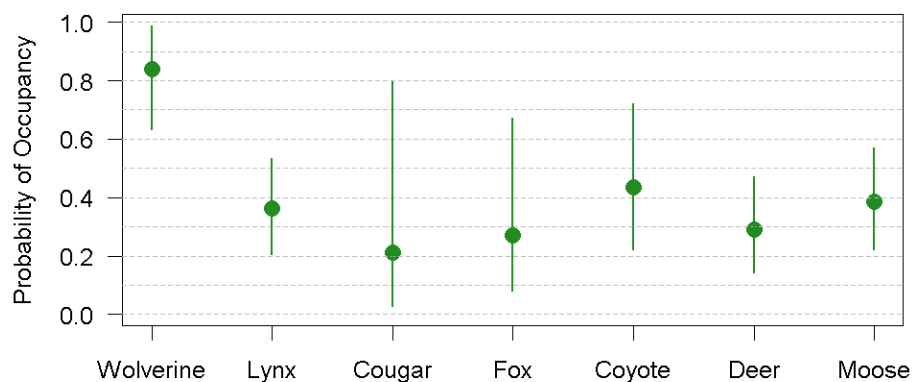

Figure 5. Occupancy estimates (proportion of grid cells occupied) and 95% confidence intervals for each species.
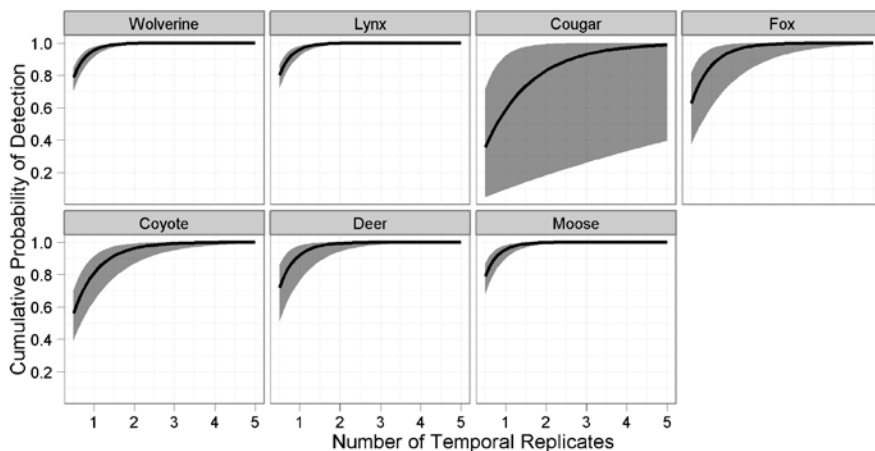
Figure 6. Cumulative probability of species detection versus the number of surveys (temporal replicates). Shaded areas represent 95% confidence intervals. Cumulative probabilities were calculated with 11 spatial replicates per cell (2012 mean), and an average number of days since snow (4.1 for carnivores, 8.1 for ungulates). Predictions were based on the Independent model, which under-predicted occupancy for wolverine, cougar, fox, and coyote.
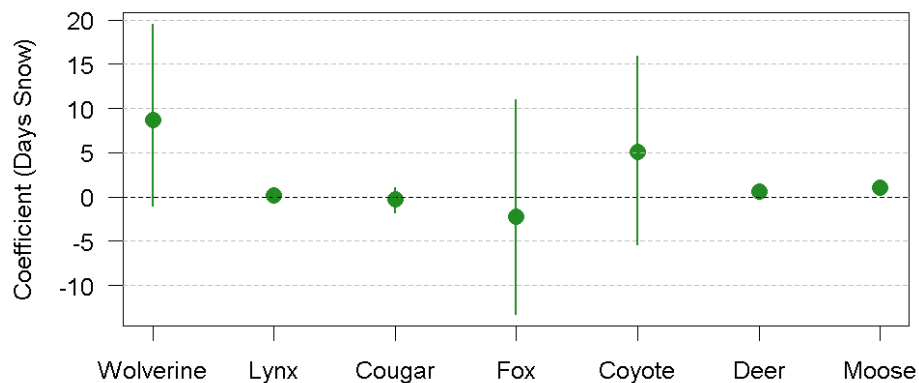
Figure 7. Estimated coefficients and 95% confidence intervals for the effect of Days Snow (the sampling time) on detection probabilities. Positive coefficients indicate that the probability of detecting a species increases with time.
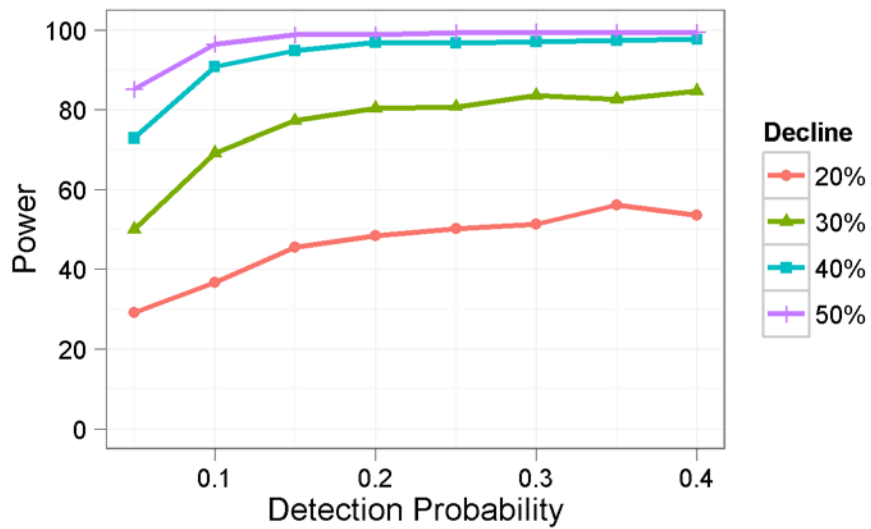
Figure 8. Power to detect 20, 30, 40, and 50% declines in occupancy versus detection probability. Power was calculated with 1000 simulations a starting occupancy of 0.631, 37 grid cells, and the 2012 suite of cell specific spatial and temporal replicates.

Figure 9. Maps showing where wolverine, lynx, cougar, fox, coyote, wolves, deer, and moose were detected on the 2012 snow tracking surveys.

Discussion

The snow track occupancy surveys appear to be an efficient, inexpensive, and powerful technique to monitor the winter distribution of multiple species, especially for wolverine, lynx, and moose (all had detection probabilities near 0.25). Accounting for spatial correlation between adjacent trail segments improved occupancy estimates for species that travel long distances along trails. Wolverine exhibited this mechanism most strongly; failing to accou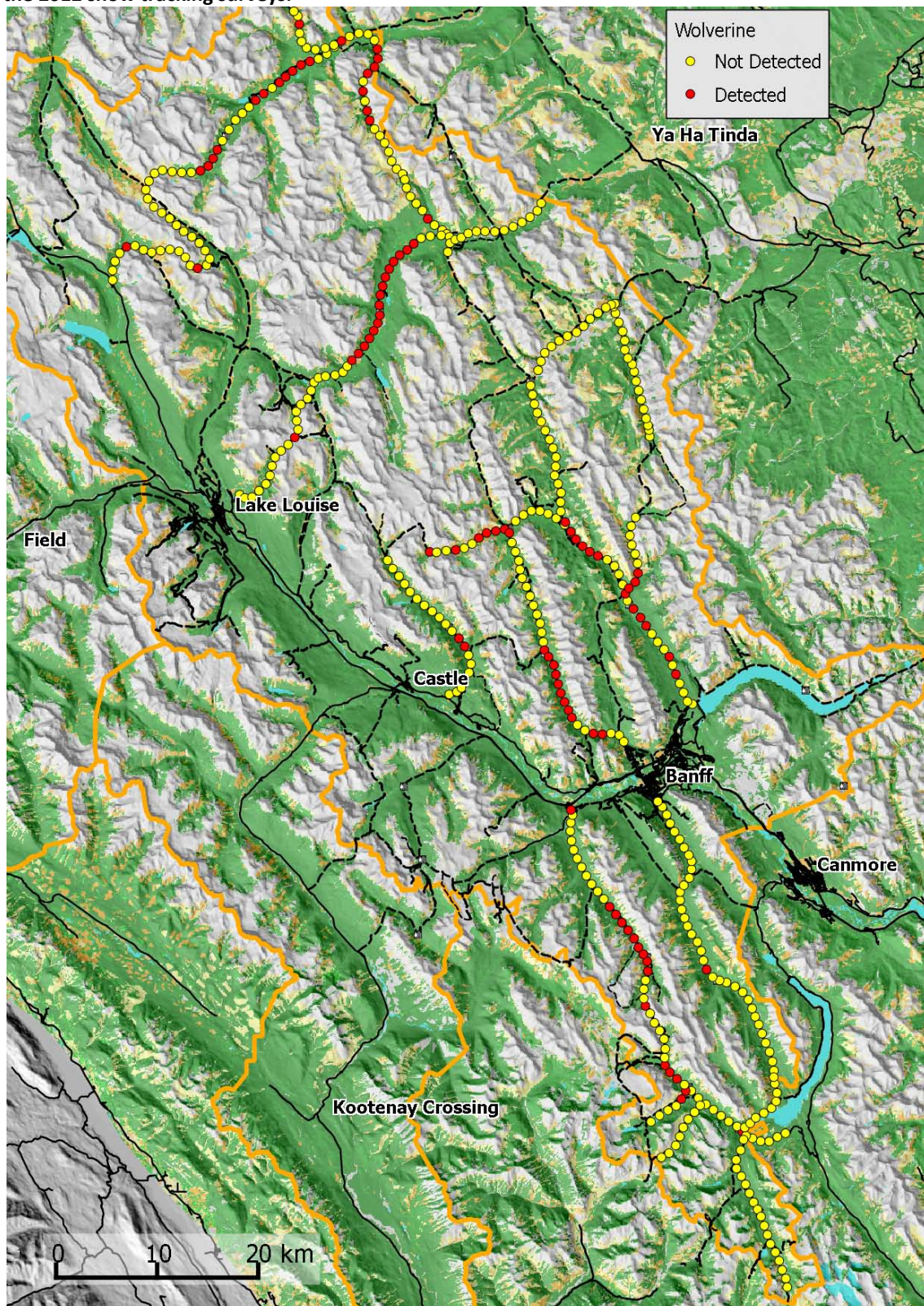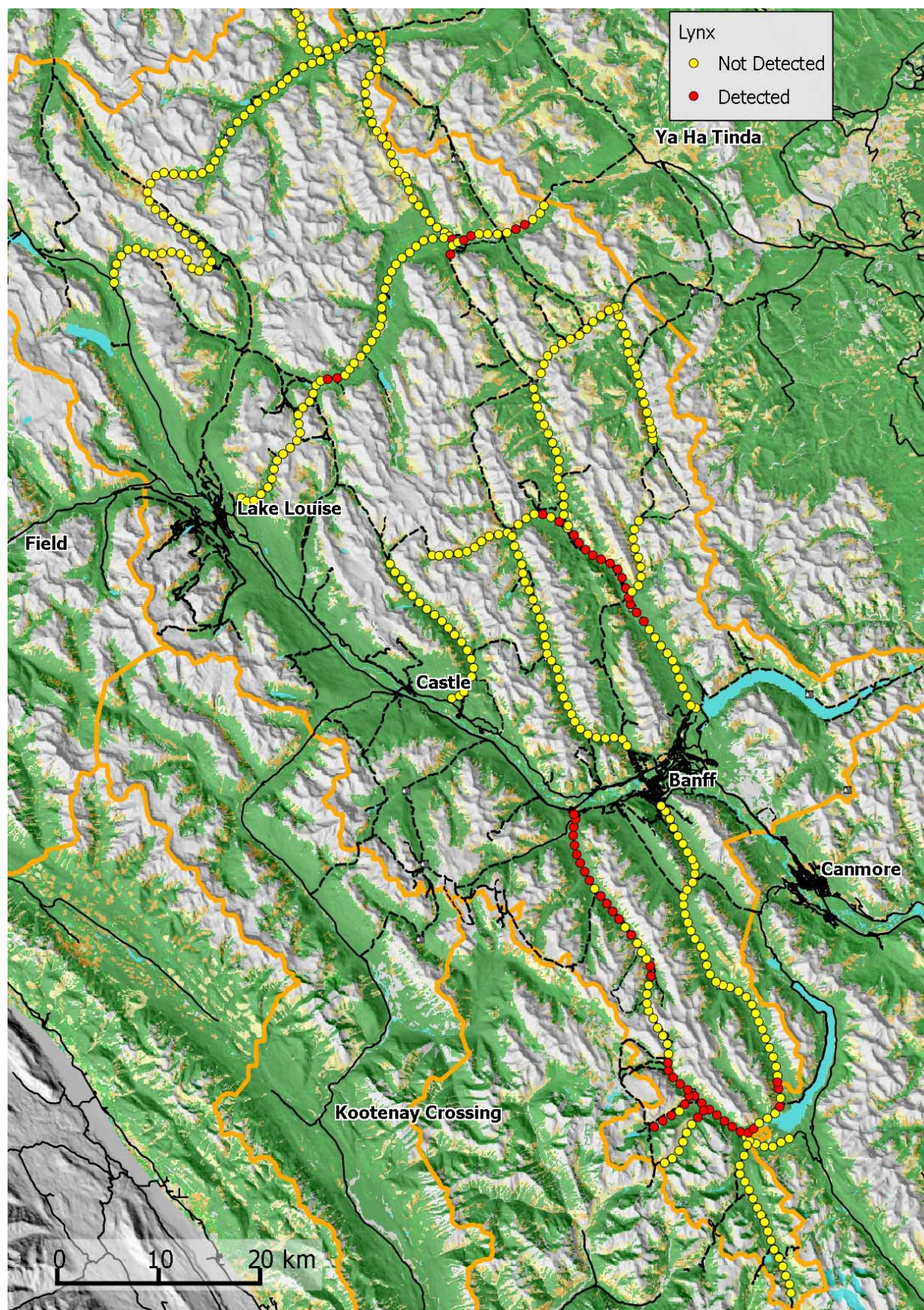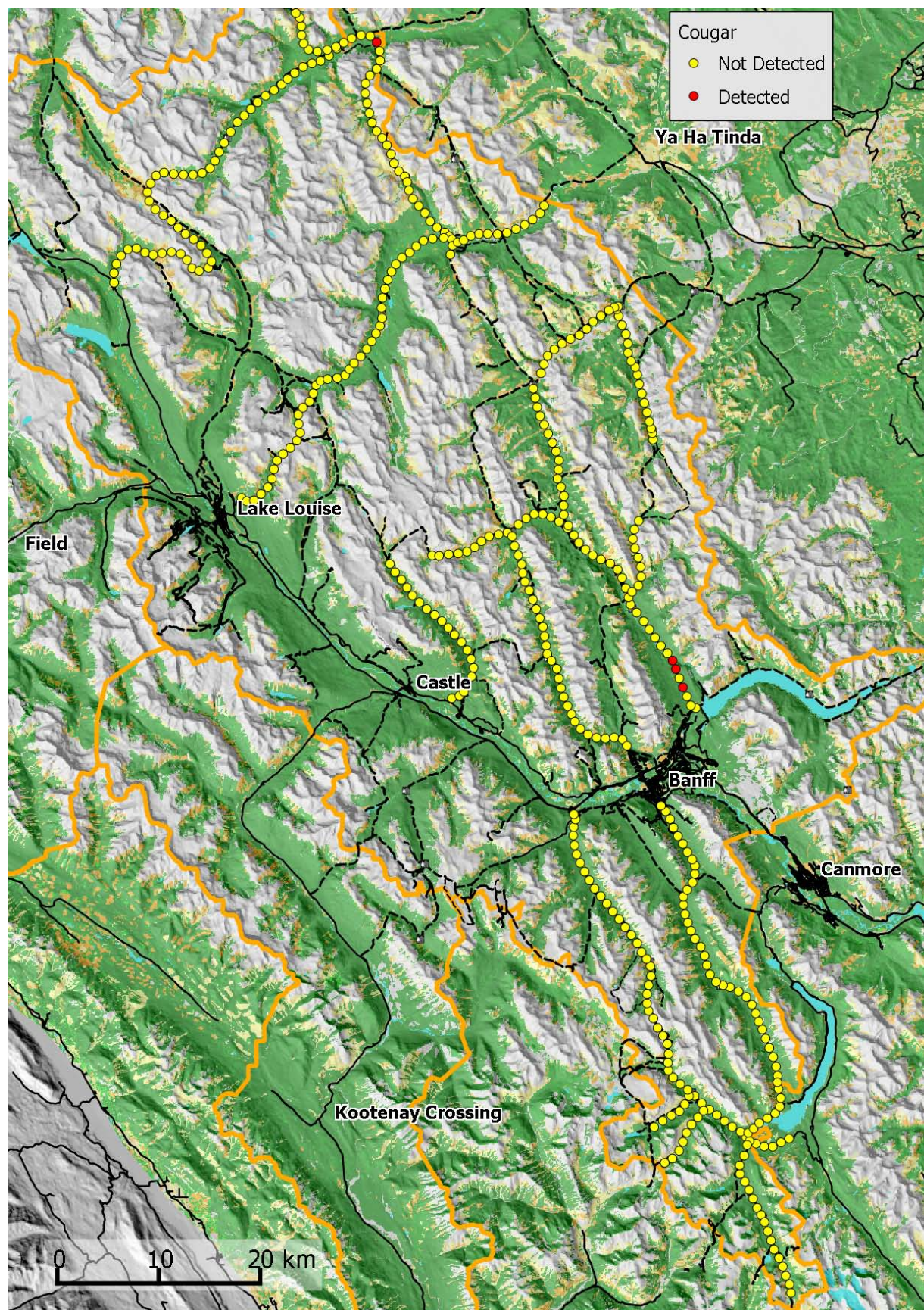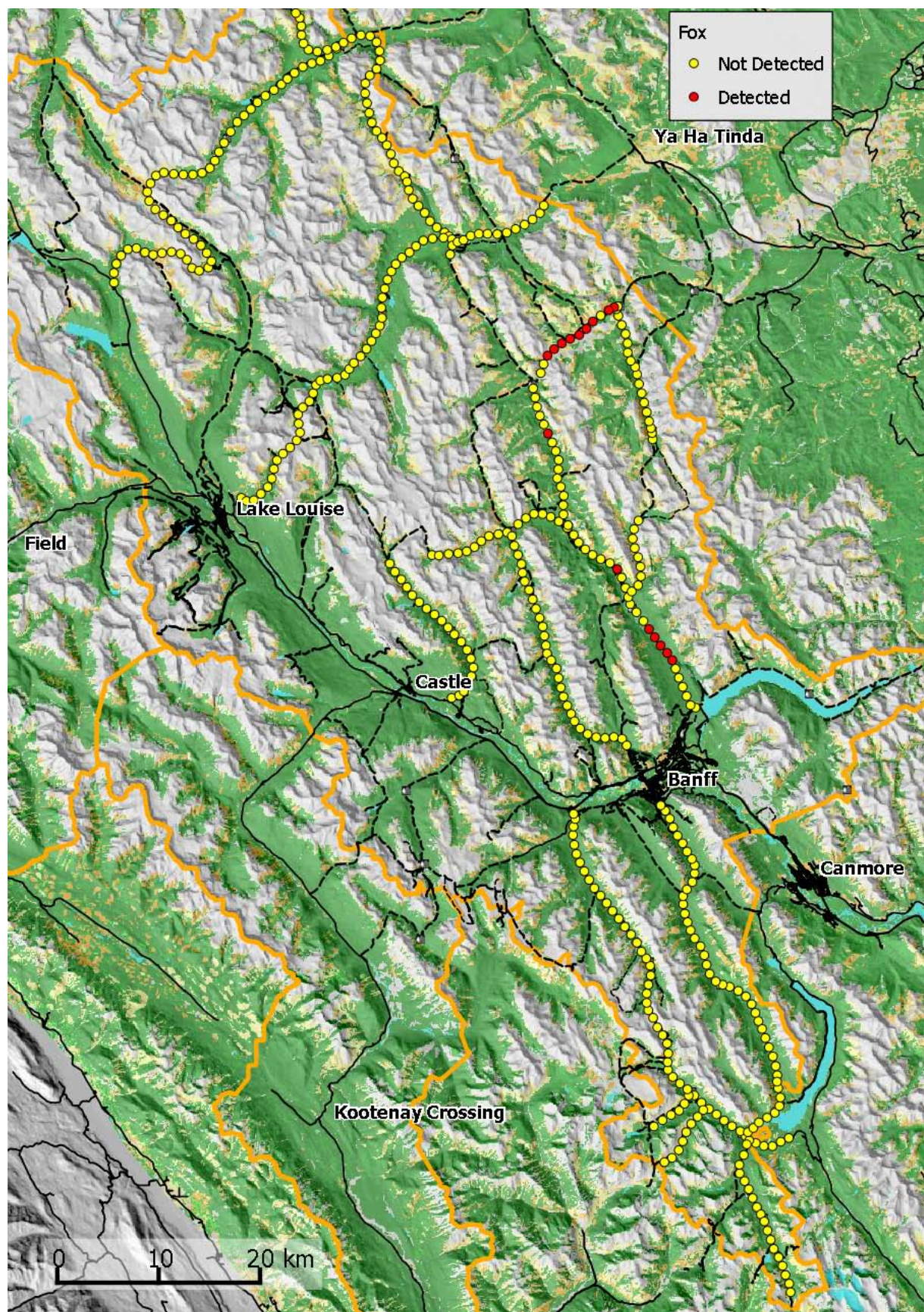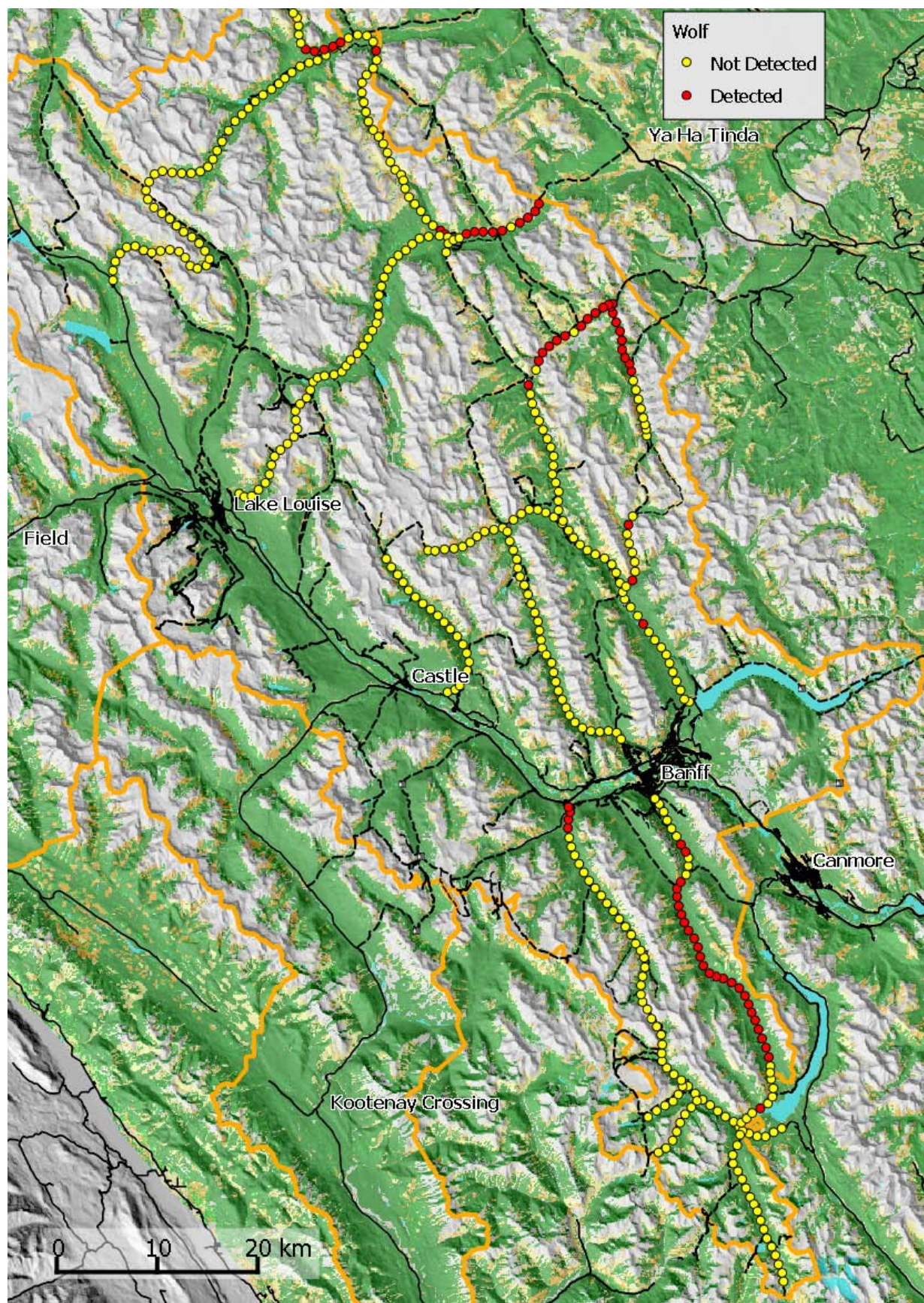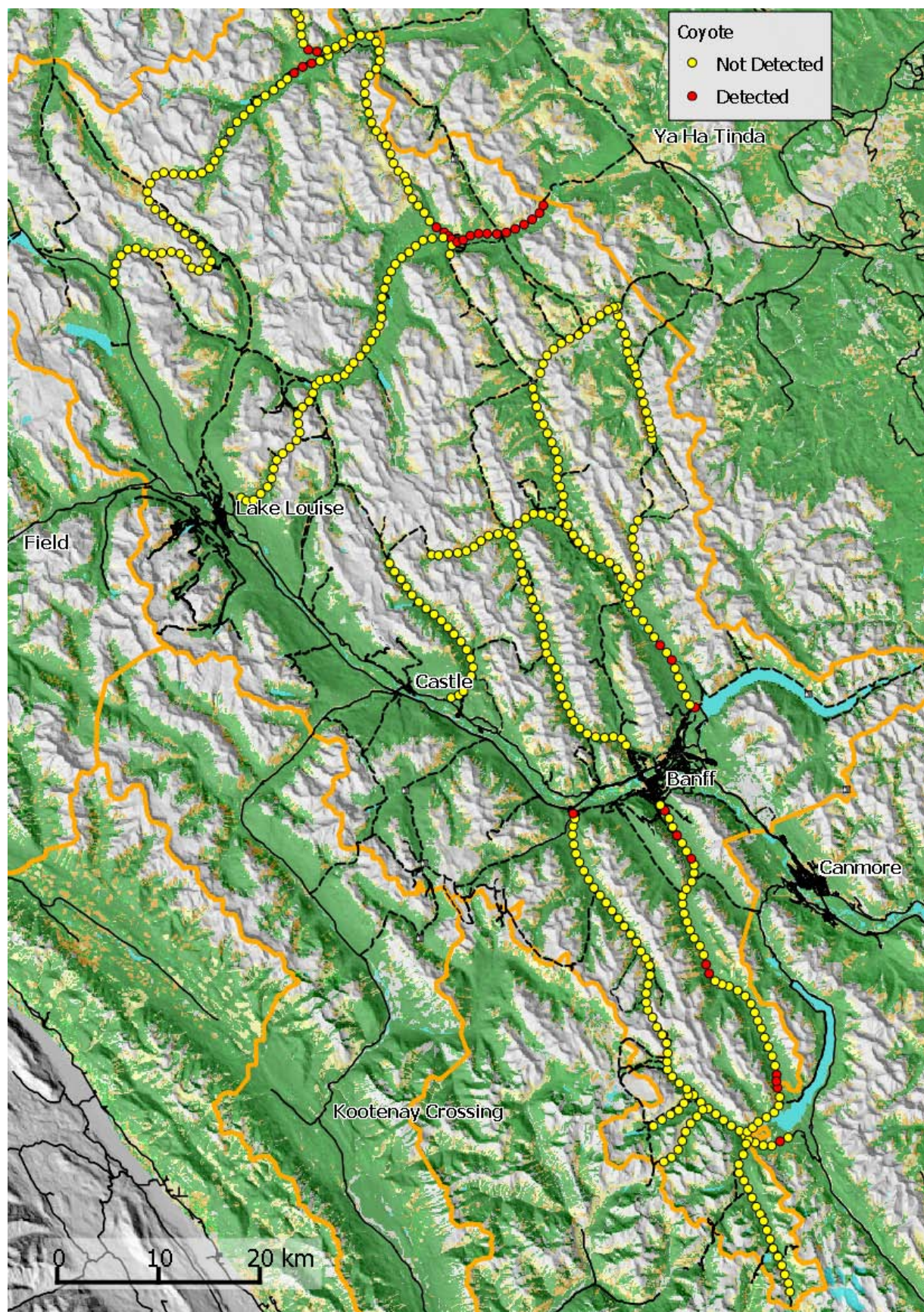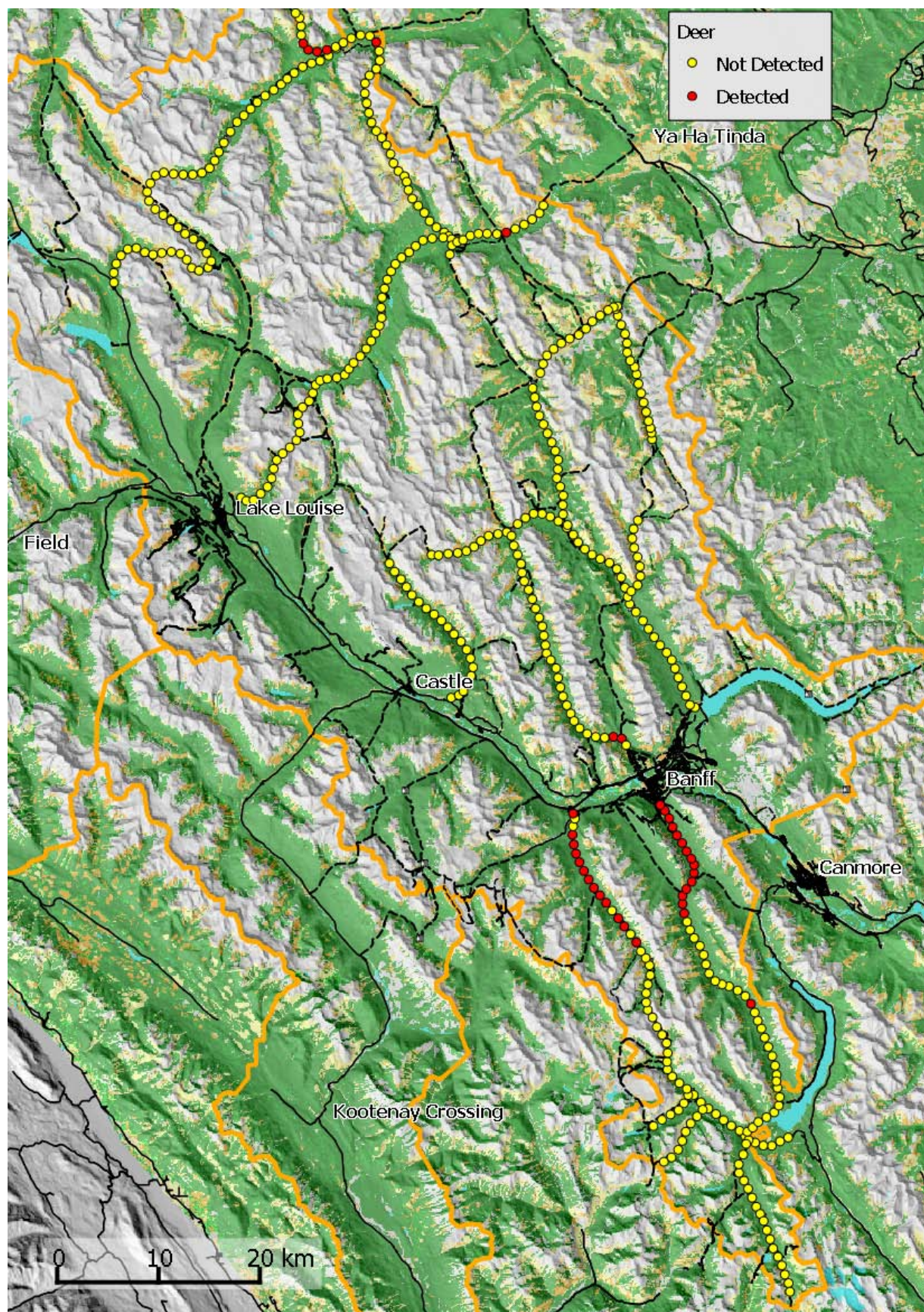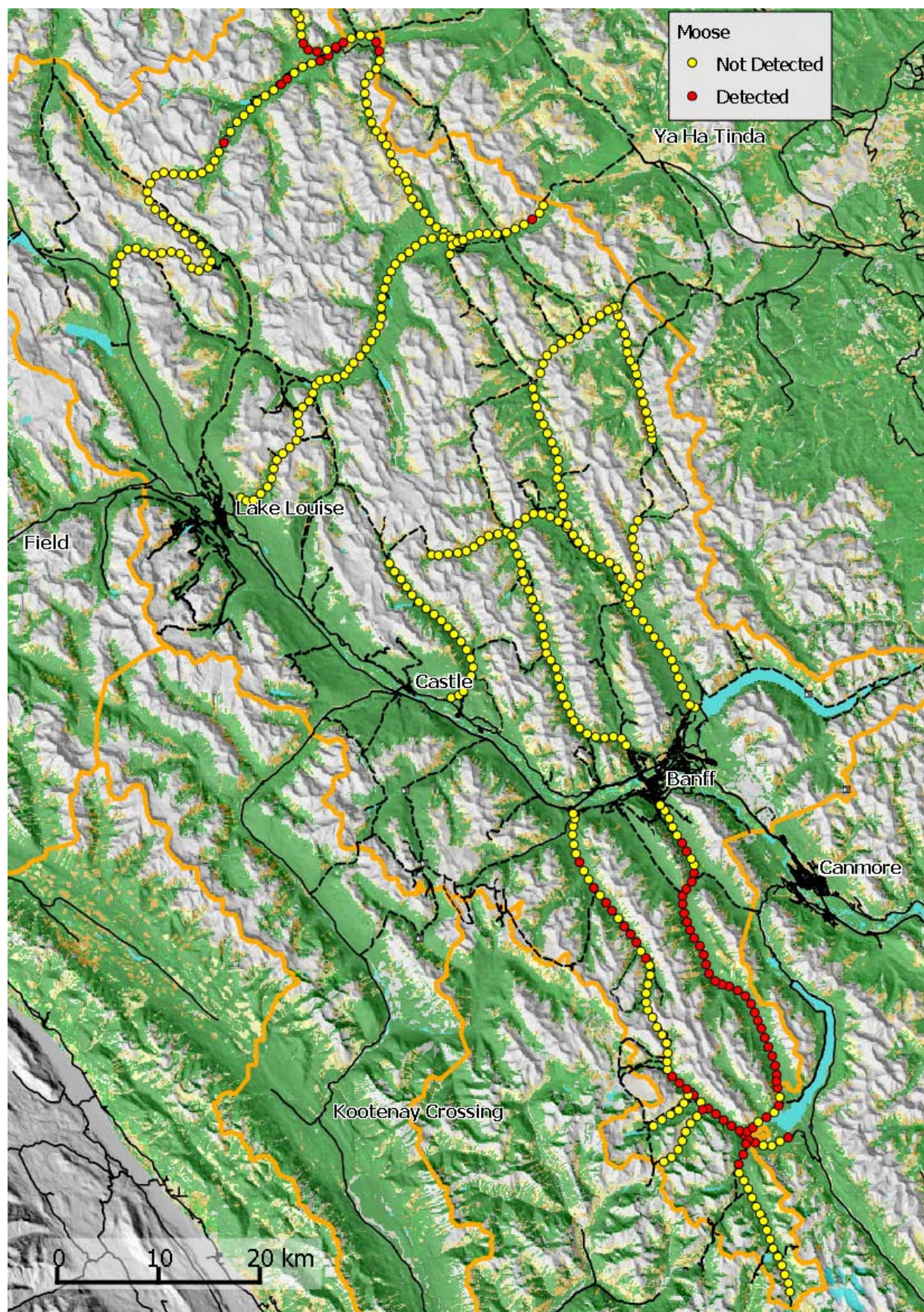nt for the spatial correlation would result in biased occupancy estimates. Recent advances in occupancy modelling techniques have made track surveys an increasingly promising approach for monitoring wide-ranging species over large geographic areas (Hines et al. 2010, Aing et al. 2011, Thorn et al. 2011).

Adult female wolverine home ranges along the Rocky Mountains range from an average of 139 km^2 in Glacier National Park Ecosystem (Copeland et al. 2010) to 303 km^2 in the Yellowstone Ecoystem (Inman et al. 2012). Wolverine occupied approximately 3170 km^2 of our study area. Given these home range sizes, between 10 and 22 adult female wolverines likely used our study area. The ongoing wolverine DNA project currently occurring in Banff National Park will provide approximate wolverine home range sizes for Banff and a more accurate estimate of wolverine densities. Completion of this wolverine study will provide context for our occupancy estimates. Adult female lynx in the Southern Canadian Rockies Lynx Project including Banff National Park had average 100% minimum convex polygon home ranges of 211 km^2 (Apps 2003). Given that lynx occupied approximately 1260 km^2 of our study area, our study area likely contained a minimum of 6 adult females assuming non-overlapping home ranges. These population estimates are approximate and have inherent biases. For example, if wolverine and lynx only use a portion of the 100 km^2 grid cells, then we would overestimate the area occupied and the minimum number of animals. Conversely, if these species have overlapping home ranges, then we would underestimate the true number individuals.

Our analysis did not include explanatory variables that could affect cell occupancy for any species surveyed other than number of hare tracks for lynx. Variables such as elevation or spring snow cover could be important predictors of wolverine occupancy (Copeland et al. 2010, McKelvey et al. 2011) and inclusion of such variables in future analyses would provide more accurate occupancy estimates with tighter confidence intervals. Our analysis examined simple presence-absence of each species within hexagons, which works well for solitary and territorial species that occur in low densities. We could expand upon our analysis for species such as moose and deer that live in groups with overlapping home ranges. We recorded the minimum number of animals within each 1 km segment and could thus use binomial mixture occupancy models to predict the number of individuals within each 1 km segment (Kéry et al. 2005, Royle and Dorazio 2008). This would be useful for providing predictions for both spatial distribution and relative abundance.

Occupancy estimates could be biased because we focussed sampling along trails which usually occur in the valley bottoms. However, many of the valleys we sampled are narrow and rugged and most species in this analysis travel throughout the valley bottoms which contain the most productive habitat. Our analysis did not include bighorn sheep and mountain goats because although they were detected they

favour more rugged terrain. Similarly, we excluded elk from the analysis because they are more efficiently and accurately monitored using aerial elk surveys.

This study was unique in that it combined both spatial and temporal replication in occupancy estimates. Future occupancy estimates could be improved by increasing the number of surveys (temporal replicates) from February through April. These replicates could be conducted by staff travelling along the routes for other purposes. The surveys could also be improved by sampling hexagons that were missed or undersampled in the 2012 survey. Accessible hexagons that were not sampled included the Fairholme Bench, the Bow Valley Parkway from 5-mile to Hillsdale, Healy Creek, Redearth Creek, Castle Junction, Baker Creek, and the Pipestone Valley (Figure 2).

Remote cameras offer another promising non-invasive and inexpensive method for monitoring multiple species. Remote cameras sample a narrow spatial area over a long period of time including summer, whereas snow track surveys sample a large spatial area over a short temporal window in winter. In 2012, remote cameras will sample almost every 10x10 km cell within Banff National Park. Simultaneous collection of both snow track and remote camera data will allow a comparison of the two techniques. Moreover, the two complimentary techniques could be combined into a joint occupancy analysis.

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Appendix I

Table 4. Parameter estimates and 95% confidence intervals for the Independent, Detection Process, and Spatial Process occupancy models. The 95% credibility

Species	Parameter	Independent	Detection Process	Spatial Process
Wolverine	Deviance	402.334 (393.316, 417.293)	333.755 (321.783, 349.721)	33.760 (0.001, 79.980)
	Number of Occupied cells	23.613 (21.000, 27.000)	28.081 (23.000, 34.000)	31.699 (26.000, 37.000)
	Occupancy - Cell	0.631 (0.451, 0.801)	0.747 (0.541, 0.925)	0.838 (0.631, 0.986)
	Occupancy segment $_{Previous\ segment\ not\ occupied}$			0.106 (0.072, 0.151)
	Occupancy segment $_{Previous\ segment\ occupied}$			0.619 (0.517, 0.719)
	Detection prob. $_{Average}$	0.245 (0.199, 0.293)	0.108 (0.072, 0.152)	0.995 (0.954, 1.000)
	Detection prob. $_{Detection\ on\ Previous\ Segment}$		0.618 (0.511, 0.718)	
	$B\ detection\ _{Intercept}$	-1.130 (-1.392, -0.881)	-2.125 (-2.553, -1.722)	8.939 (3.036, 19.950)
	$B\ detection\ _{DaysSnow}$	0.163 (-0.095, 0.423)	0.139 (-0.168, 0.438)	8.681 (-2.722, 20.101)
	$B\ detection\ _{DetectionPreviousSegment}$		2.613 (2.025, 3.216)	
Lynx	Deviance	349.836 (344.193, 362.071)	293.535 (282.888, 309.308)	36.594 (0.000, 107.651)
	Number of Occupied cells	12.572 (11.000, 16.000)	15.774 (11.000, 23.000)	16.731 (12.000, 24.000)
	Occupancy - Cell	0.512 (0.265, 0.801)	0.653 (0.324, 0.972)	
	Occupancy segment $_{Previous\ segment\ not\ occupied}$			0.119 (0.076, 0.168)
	Occupancy segment $_{Previous\ segment\ occupied}$			0.673 (0.543, 0.804)
	Detection prob. $_{Average}$	0.255 (0.206, 0.308)	0.124 (0.082, 0.172)	0.976 (0.804, 1.000)
	Detection prob. $_{Detection\ on\ Previous\ Segment}$		0.631 (0.518, 0.738)	
	$B\ detection\ _{Intercept}$	-1.074 (-1.350, -0.811)	-1.976 (-2.419, -1.574)	8.309 (1.411, 21.095)
	$B\ detection\ _{DaysSnow}$	0.145 (-0.130, 0.424)	0.151 (-0.183, 0.482)	4.813 (-4.481, 17.205)
	$B\ detection\ _{DetectionPreviousSegment}$		2.520 (1.895, 3.179)	
	$B\ occupancy\ _{Intercept}$	0.058 (-1.020, 1.395)	0.819 (-0.734, 3.535)	1.055 (-0.538, 4.149)
	$B\ occupancy\ _{SnowShoeHares/dayt}$	4.918 (1.350, 10.174)	6.117 (1.339, 14.948)	6.457 (1.401, 15.980)
Cougar	Deviance	30.548 (24.118, 44.139)	31.239 (24.216, 45.071)	7.546 (0.000, 30.176)
	Number of Occupied cells	5.323 (2.000, 19.000)	5.210 (2.000, 18.000)	7.301 (2.000, 29.025)
	Occupancy - Cell	0.161 (0.028, 0.528)	0.159 (0.029, 0.493)	0.213 (0.028, 0.798)
	Occupancy segment $_{Previous\ segment\ not\ occupied}$			0.130 (0.005, 0.832)
	Occupancy segment $_{Previous\ segment\ occupied}$			0.472 (0.071, 0.924)
	Detection prob. $_{Average}$	0.077 (0.009, 0.207)	0.068 (0.007, 0.205)	0.807 (0.056, 1.000)
	Detection prob. $_{Detection\ on\ Previous\ Segment}$		0.152 (0.002, 0.578)	
	$B\ detection\ _{Intercept}$	-2.751 (-4.687, -1.344)	-2.943 (-5.023, -1.356)	6.622 (-2.817, 22.259)
	$B\ detection\ _{DaysSnow}$	-0.240 (-1.829, 1.022)	-0.380 (-2.054, 0.989)	2.944 (-7.195, 16.915)
	$B\ detection\ _{DetectionPreviousSegment}$		0.552 (-3.030, 3.647)	
Fox	Deviance	76.735 (71.937, 87.575)	70.016 (65.348, 79.992)	13.502 (0.000, 32.298)
	Number of Occupied cells	5.512 (4.000, 9.000)	5.644 (4.000, 9.000)	9.596 (4.000, 24.025)
	Occupancy - Cell	0.167 (0.058, 0.327)	0.169 (0.058, 0.329)	0.273 (0.079, 0.671)
	Occupancy segment $_{Previous\ segment\ not\ occupied}$			0.073 (0.015, 0.170)

Species	Parameter	Independent	Detection Process	Spatial Process
Fox (cont)	Occupancy segment *Previous segment occupied*			0.728 (0.443, 0.934)
	Detection prob. *Average*	0.164 (0.082, 0.267)	0.203 (0.103, 0.319)	0.871 (0.516, 1.000)
	Detection prob. *Detection on Previous Segment*		0.005 (0.000, 0.052)	
	B detection Intercept	-1.667 (-2.421, -1.012)	-1.404 (-2.160, -0.759)	4.622 (0.063, 18.283)
	B detection DaysSnow	-0.262 (-1.453, 0.899)	-0.343 (-1.601, 0.823)	-2.558 (-13.678, 11.023)
	B detection DetectionPreviousSegment		-9.277 (-23.714, -1.455)	
Coyote	Deviance	173.596 (165.038, 187.581)	174.966 (165.618, 190.441)	16.343 (0.000, 52.134)
	Number of Occupied cells	12.801 (9.000, 18.000)	12.956 (9.000, 19.000)	16.003 (10.000, 26.000)
	Occupancy - Cell	0.354 (0.183, 0.562)	0.358 (0.186, 0.568)	0.437 (0.221, 0.723)
	Occupancy segment *Previous segment not occupied*			0.085 (0.041, 0.145)
	Occupancy segment *Previous segment occupied*			0.643 (0.463, 0.813)
	Detection prob. *Average*	0.139 (0.088, 0.200)	0.139 (0.087, 0.200)	0.971 (0.770, 1.000)
	Detection prob. *Detection on Previous Segment*		0.132 (0.023, 0.321)	
	B detection Intercept	-1.846 (-2.340, -1.389)	-1.848 (-2.353, -1.387)	8.033 (1.209, 22.709)
	B detection DaysSnow	0.086 (-0.245, 0.408)	0.083 (-0.259, 0.404)	4.689 (-7.391, 16.277)
	B detection DetectionPreviousSegment		-0.232 (-1.889, 1.120)	
Deer	Deviance	182.783 (176.707, 194.083)	180.809 (173.954, 192.131)	46.336 (0.007, 92.527)
	Number of Occupied cells	10.317 (8.000, 14.000)	10.551 (8.000, 15.000)	12.426 (8.000, 20.000)
	Occupancy - Cell	0.290 (0.144, 0.473)	0.296 (0.145, 0.485)	0.342 (0.159, 0.592)
	Occupancy segment *Previous segment not occupied*			0.141 (0.062, 0.241)
	Occupancy segment *Previous segment occupied*			0.765 (0.565, 0.925)
	Detection prob. *Average*	0.207 (0.123, 0.303)	0.222 (0.133, 0.322)	0.736 (0.371, 1.000)
	Detection prob. *Detection on Previous Segment*		0.095 (0.021, 0.231)	
	B detection Intercept	-1.369 (-1.968, -0.835)	-1.279 (-1.876, -0.744)	2.780 (-0.526, 15.388)
	B detection DaysSnow	0.631 (0.171, 1.109)	0.696 (0.249, 1.187)	2.528 (-2.772, 11.726)
	B detection DetectionPreviousSegment		-1.142 (-2.473, 0.004)	
Moose	Deviance	318.712 (312.122, 330.486)	314.274 (307.316, 325.585)	65.603 (4.121, 146.168)
	Number of Occupied cells	14.024 (11.000, 18.000)	14.320 (11.000, 19.000)	16.287 (13.000, 21.000)
	Occupancy- Cell	0.387 (0.222, 0.569)	0.394 (0.229, 0.583)	0.443 (0.260, 0.635)
	Occupancy segment *Previous segment not occupied*			0.224 (0.145, 0.326)
	Occupancy segment *Previous segment occupied*			0.723 (0.608, 0.841)
	Detection prob. *Average*	0.248 (0.189, 0.313)	0.263 (0.202, 0.330)	0.863 (0.551, 1.000)
	Detection prob. *Detection on Previous Segment*		0.110 (0.040, 0.223)	
	B detection Intercept	-1.119 (-1.454, -0.787)	-1.038 (-1.377, -0.709)	4.272 (0.205, 15.687)
	B detection DaysSnow	1.015 (0.708, 1.329)	1.104 (0.795, 1.435)	5.818 (1.630, 16.418)
	B detection DetectionPreviousSegment		-1.146 (-2.110, -0.226)	