Progress Report for
Testing monitoring techniques for wolves in southwest Alberta

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Montana Cooperative Wildlife Research Unit
Wolf Project

Summary

Gray wolf (*Canis lupus*) populations are difficult to monitor because wolves can be elusive and occur in relatively low densities. We developed a population monitoring framework in the U.S. that uses data from hunter surveys and field-based rendezvous site surveys to estimate wolf pack abundance and distribution across large areas. We began testing this framework in southwest Alberta in 2012. In 2012, our study area spanned from the International Border to Highway 1 and was bordered on the east by Highway 22, with the exception of the Porcupine Hills which we included in our surveys. In 2013, we expanded our study area north of Highway 1 along Highway 22 to the Brazeau River, and west to the eastern borders of Banff and Jasper National Parks (hunter surveys only).

We surveyed big-game hunters for wolf observations made in southwest Alberta during the 2012 and 2013 hunting season. Additionally, we conducted field surveys for wolves at predicted rendezvous sites in summers 2012 and 2013 in southwest Alberta. We mailed refrigerator magnets with our contact information to grazing leaseholders and landowners twice in 2013 to obtain wolf sightings made by the public. We also contacted several members of the South Country Trappers Association to obtain recent wolf activity information from trappers during our summer field survey season.

We combined wolf detection data from our survey methods into a patch occupancy model that estimated wolf pack abundance and distribution across our study area. Preliminary results indicate that a patch occupancy model that uses a 1,200 km^2 grid cell size contains the least uncertainty in population estimates. A model that accounts for wolf misidentifications (i.e., false positives) estimated 5.9 (3.4-8.6; 95% CI) wolf packs in our study area in 2012 and 14.5 (9.3-19.7; 95% CI) in our expanded study area in 2013. We did not acquire enough public sightings of wolves or reports of wolf activity from trappers to use as a data source in our model. We were able to use the several reports we did obtain, however, to validate model estimates and found spatial overlap between model predictions and where we received public reports.

We will survey predicted rendezvous sites for wolves in summer 2014 and survey big-game hunters once more after the 2014 hunting season. We plan to have a full study report in 2015 that outlines a framework AESRD can use for periodic wolf population monitoring.

Introduction

Gray wolf (*Canis lupus*) populations are difficult to monitor because wolves tend to be elusive, occur in low densities, and live in remote and inaccessible terrain where surveying is difficult. In addition, wolves are territorial (i.e., maintaining exclusive use of home ranges, excluding conspecifics; Powell 2000), and the challenge of locating an individual, or even sign of an individual within a 390-1200 km^2 territory, can be daunting. Radiotelemetry is an effective tool for monitoring wolves where mortality is relatively low, radiocollars remain deployed for extended periods and funding and manpower are sufficient to collar and track a large proportion of a population. Where turnover is high within the wolf population and resources (staff and funding) to maintain wolf collaring programs are limited, long-term radiotelemetry-based monitoring of wolves has limited application (G. Hale, Alberta Environmental Sustainable Resource Development, [AESRD], pers. comm.). Noninvasive alternatives to radiotelemetry monitoring are available, however, and could provide critical information on the wolf population of southwest AB. Such data would increase the ability of resource managers to make informed and cost-effective management decisions involving wolves. In recent years, a number of noninvasive methods were developed to reliably survey for carnivores (Long et al. 2008). Often these noninvasive techniques do not require highly trained personnel (unlike trapping and collaring) and sampling sites do not have to be checked daily thereby reducing labor costs. This reduction in effort means that more area can be surveyed with given budgets and more data can be obtained about the population as opposed to information about a few collared individuals. Lastly, a region-wide noninvasive monitoring program can provide annual estimates of the abundance and distribution of the population allowing managers to observe trends over time and incorporate this knowledge into management decisions and planning.

We began working collaboratively with the Nez Perce Tribe, Idaho Department of Fish and Game, and Montana Fish, Wildlife and Parks in 2006 on a research project to develop techniques for monitoring gray wolf populations across large scales in the absence of radiotelemetry in the U.S. We tested the use of patch occupancy modeling to monitor wolves at large spatial scales. Patch occupancy modeling provides a means to combine data from multiple different survey methods into one meaningful model of distribution and abundance (MacKenzie et al. 2006). Occupancy models, at their most basic level, can be viewed as presence/absence models that incorporate the reality that species are detected imperfectly (probability of detection < 1.0; MacKenzie et al. 2006). Occupancy models use detection probabilities gathered by repeatedly sampling multiple sites, or spatially replicated visits, to obtain an occupancy estimate that accounts for imperfect detection. Occupancy models use data

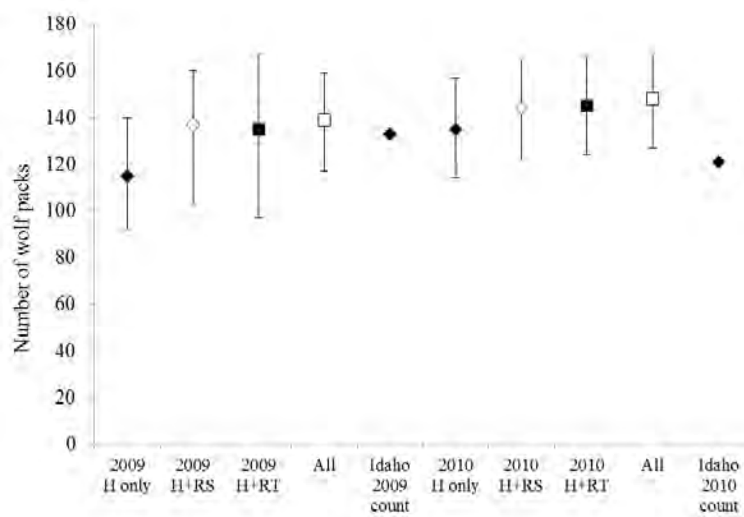

Figure 1. Estimated number of wolf packs using hunter surveys (H), rendezvous site surveys (RS), radiotelemetry locations (RT), and a patch occupancy model compared to the minimum number of packs present in Idaho, USA, 2009-2010 (Ausband et al. 2014).

derived from sampling units to provide a probability of detection and occupancy over a larger area making them ideal for large-scale monitoring programs (MacKenzie et al. 2006). For example, Ausband et al. (2014) used patch occupancy models populated with data from hunter and rendezvous site surveys to accurately estimate wolf pack abundance in Idaho, USA (Fig. 1).

Managers may wish to validate model estimates and, further, may desire more detailed information on packs in areas of high management interest. In addition to testing hunter surveys in Idaho and Montana we developed and tested 3 field-based survey methods for collecting data from wolves without the need for capture and radiocollaring; specifically, rendezvous site surveys and subsequent DNA analyses, rub stations, and howlboxes (Ausband et al. 2011; Brennan et al. 2013; Ausband et al. 2014). Each of these methods is designed to provide different levels of information given management interests and all are designed to provide data necessary to populate a patch occupancy model. We propose using a patch occupancy model populated with data from hunter and rendezvous site surveys as a technique for wolf population monitoring in AB. Additionally, we propose to use existing data sources (e.g. harvested animals, wolf sightings by public and agency personnel) to further populate and validate a patch occupancy model and make use of all available information.

Our objectives for this study are to:

- deploy methods found effective for monitoring wolves in Idaho and Montana in southwest AB
- refine and adjust methods as needed to increase field efficiency and accuracy and precision of population estimates
- develop patch occupancy model that combines multiple data sources into a framework that can be used for continued long-term wolf population monitoring in southwest AB

Introduction to field-based sampling methods

Rendezvous site surveys

Just after the denning period wolves move pups to rendezvous sites. Pups will remain at the rendezvous site for several weeks while adults hunt and return intermittently with food to provision the pups. Rendezvous sites can be occupied for up to several weeks and are often located near, or in, meadows or bogs (Joslin 1967; Mech 1970). Sampling rendezvous sites provides valuable information on breeding packs, which are often the units of management interest, and every individual in the pack spends at least a portion of time at the site and can thus be sampled using genetic tools. Focusing survey efforts at predicted rendezvous sites can narrow the search area for wolves by 89% (Ausband et al. 2010). We used a predictive rendezvous site model to survey for wolves in Idaho and were able to detect 74% of the litters of pups and all study packs without the need for radiotelemetry

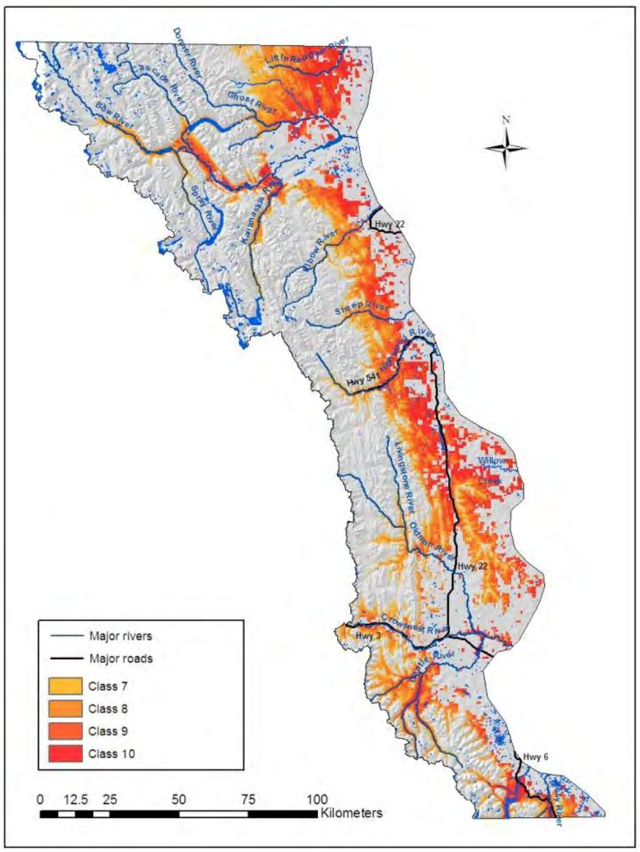

Figure 2. Map of top 4 classes of predicted gray wolf rendezvous site habitat in southwest Alberta.

(Ausband et al. 2010). Additionally, Stenglein et al. (2010a) found that numbers of wolves could be accurately estimated from DNA analyses of scats and hairs collected at predicted sites. Bolstering such data with tissue samples collected from harvested and controlled wolves would provide additional insights and increased monitoring precision. In 2010, we developed a predictive rendezvous site habitat model for southwest AB (Fig. 2). Results of this effort were presented to managers in Pincher Creek, AB in March 2011 and are reported in Ausband and Mitchell (2011). This habitat model was used as the foundation for field surveys of wolves in southwest Alberta 2012 and 2013.

Study Area

The study area in 2012 encompassed 12,950 km^2 in southwest Alberta, spanning the US border to Hwy 1, west to the BC border, and east to Hwy 6 and 22, but included the Porcupine Hills east of Hwy 22 as well (Fig. 3). Based on the 2012 model results we expanded the 2013 hunter survey to further test model performance and precision, encompassing a total of 30,000 km^2 in southwest Alberta by extending the original study area north of Hwy 1 along Hwy 22 to the Brazeau River, and west to the eastern borders of Banff and Jasper National Parks (Fig. 4).

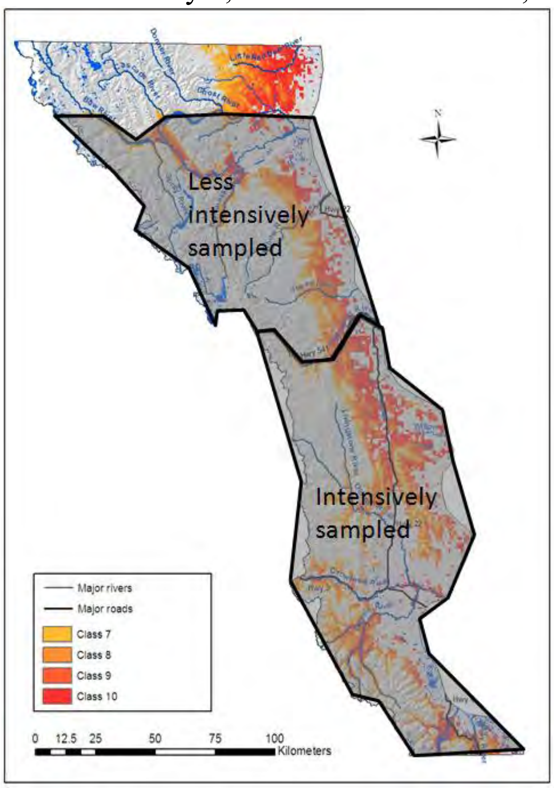

Figure 3. Study area (2012) in southwest Alberta showing intensively and less intensively sampled areas for wolves.

Methods

Rendezvous site surveys

In summer 2012, we surveyed potential rendezvous site locations in the top 3 predicted habitat classes within the intensively surveyed portion of the study area (US border to the Highwood River), with the exception of sites on private lands (Fig. 3). We did not survey the less intensively surveyed portion of the study area (Highwood River to Hwy 1) due to budget constraints in 2012. Most wolf detections and historic rendezvous sites were in predicted habitat classes 7-9 and we refined our survey in 2013 to focus on these habitat classes instead of classes 8-10. In addition, in 2013 we surveyed 25 randomly-selected predicted rendezvous site locations within each 727 km^2 (i.e., average wolf pack territory size in Idaho, USA and southwest Alberta) cell in the less intensively surveyed portion of the study area. We plan to continue surveying in habitat classes 7-9 in both the intensively and less-intensively surveyed portions of the original study area in summer 2014.

We surveyed only sites with contiguous patches $\geq$1.0 ha. At each site a technician gave a series of howls (Harrington and Mech 1982); if wolves responded by howling, technicians attempted to obtain a visual observation. If technicians did not detect wolves after howling, they surveyed for wolf sign along the perimeter of the site where daybeds and high-use areas are commonly found, and on trails leading away from or through the site. If a potential site was too large to survey its entire perimeter and all trails, 2 technicians conducted sign surveys in the site for 30 minutes. Predicted rendezvous sites can sometimes be very large meadow complexes encompassing several square kilometers. We divided such sites into 1.6 km^2 blocks and technicians surveyed alternating blocks because we assume the unsurveyed portions will be within the broadcast range of technicians' howls (Harrington and Mech 1982). When sites contained drivable roads, we conducted sign surveys in vehicles at 20 km/h along all roads within the site (Crete and Messier 1987). The minimum observed distance between historical rendezvous sites of adjacent packs in Idaho was 6.4 km (C. Mack, NPT, unpublished data); we therefore placed a 6.4 km-radius circle around predicted rendezvous sites that were occupied by wolves and did not survey additional sites within that buffer.

We considered canid scats $\geq$ 2.5 cm diameter to be wolf scats (Weaver and Fritts 1979). Because coyote (*C. latrans*) scats and wolf pup scats overlap in size, we did not consider scats < 2.5 cm to be wolf pup scats unless there was abundant wolf sign (e.g., pup play areas; Joslin 1967) or live wolves at the site. We collected a small sample (e.g. pencil-eraser sized) from the side of the scat with sterilized forceps and placed it in DMSO/EDTA/Tris/salt solution buffer (Frantzen et al. 1998; Stenglein et al. 2010b). To provide additional DNA samples and to make use of existing data sources we asked agency personnel to collect tissue samples from harvested or controlled wolves within the study area (Appendix 1). We provided AESRD personnel with sample vials, desiccant, and associated storage envelopes.

We mapped the geographic coordinates of individual wolf genotypes in ArcMap 10.1 (ESRI 2012) to generate detection histories for each grid cell across the entire study area for 2012 and 2013 (Fig. 4). We used the resulting detection/non-detection data (along with hunter survey data – see below) to populate study area-wide patch occupancy models.

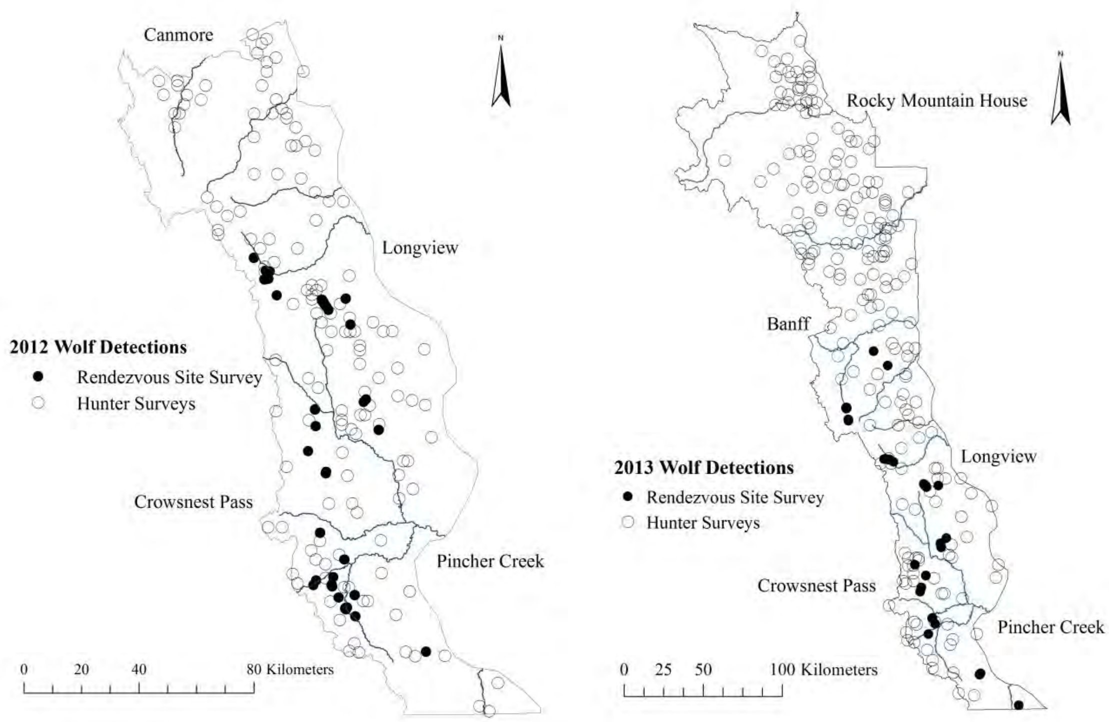

Figure 4. Wolf detection locations from our two sampling methods in the original 2012 study area (L) and the expanded 2013 study area (R). In 2012 and 2013, we extracted DNA to identify individuals from collected wolf scats and distributed online questionnaires to hunters for wolf observations made during the big game hunting season. Rendezvous site surveys were only conducted in the intensively surveyed portion of the study area in 2012 and were expanded throughout the full original study area in 2013. We created detection histories for our patch occupancy models using these data.

Hunter Surveys

In early 2013 and 2014, we surveyed hunters for any observations of live wolves made during the respective 2012 and 2013 big game hunting seasons. We added 4 questions (Fig. 5) to the existing online hunter reporting form currently used by Alberta ESRD to survey big game hunters (Rich et al. 2013; Ausband et al. 2014). Based on the 2012 model results we expanded the 2013 hunter survey to further test model performance and improve precision, encompassing a total of 30,000 km^2 in southwest Alberta by expending the original study area north of Hwy 1 along Hwy 22 to the Brazeau River, and west to the eastern borders of Banff and Jasper National Parks (Fig. 4). We also implemented an interactive map in the 2013 hunter survey so hunters could select the exact section within a Wildlife Management Unit (WMU) where they observed wolves, providing us with more accurate wolf-sighting locations. We recorded the geographic coordinates and mapped the resulting hunter sightings in ArcMap 10.1 (ESRI 2012; Fig. 4). Wolf sightings were used to generate detection histories for each grid cell across the entire study area. We used the resulting detection/non-detection data in combination with the rendezvous site survey data to populate a study area-wide patch occupancy model. We will continue to survey hunters in January 2015 for any observations of live wolves made during the 2014 big game hunting season.

1. Did you see wolves?
2. When did you see wolves?
3. Where did you see wolves?
4. How many wolves did you see?

Figure 5. Questions added to the online hunter survey conducted annually by Alberta ESRD. Resulting wolf detection/non-detection data were used to populate a patch occupancy model and estimate wolf abundance in southwest Alberta.

Patch Occupancy Model

We populated our occupancy models with detection data using genetic results from rendezvous site surveys and wolf sightings from hunter surveys to estimate wolf occupancy in southwest Alberta in 2012 and 2013. Both detection methods generated multiple detection states (i.e., certain and uncertain) as described by Miller et al. (2011). Our annual survey period was 1 June to 31 December. We assumed the population was closed to changes in pack occupancy during each sampling season (i.e, no pack colonizations or local extinctions) and detection of a pack in one site was independent of detections in another site. We fit our detection data to a basic single-season occupancy model and one that incorporates false positive detections. The false positive detection occupancy model allowed us to address the third model assumption that packs were not falsely detected (MacKenzie et al. 2006; Miller et al. 2011; Miller et al. 2013).

Based on our detection methods, we created alternate detection histories by condensing the 16-week hunting season into weekly wolf sightings, biweekly wolf sightings, and monthly wolf sightings to maximize sample size while retaining sufficient wolf detections for best model performance. We used the preliminary models to inform our final model design with 9 sampling occasions per sampling season, 1 from rendezvous site surveys, and 8 from hunter surveys. The rendezvous site survey sampling occasion included the entire summer field season (June-Aug). The hunter survey detections were condensed into 8, two-week sampling occasion (Sept-Dec).

In the rendezvous site survey sampling occasion, the *i*th grid cell was treated as being a certain detection if individual genotypes indicated the presence of ≥2 adults and ≥1 pups (i.e., a reproductive pack), an uncertain detection if only ≥2 adult wolves were present, and a non-detection if only 1 adult wolf was present. Uncertain detections were only incorporated in the false positive detection models. In some instances, one individual wolf genotype was detected in ≥2 grid cells. To avoid overestimating detection frequencies, we only counted the detection in one cell using one of the following rules. If the same wolf was detected multiple times in the *i*th cell we counted the detection in that cell and all other cells ignored the presence of that individual. If the same wolf was detected equally in multiple cells then we chose to ignore the detection in one cell at random. Hunter survey detections for the *i*th grid cell in the *t*th sampling occasions were treated as being certain if ≥3 hunters observed ≥2 wolves, uncertain if ≥2 hunters observed ≥2 wolves, and a non-detection if hunters observed 1 wolf. For both sampling methods, we assigned a missing data value to grid cells that were not surveyed during the *t*th sampling occasion. We were interested in estimating the presence of wolf packs as opposed to individual wolves. Public observations can include misidentifications and both our survey methods can detect transient wolves unassociated with established packs (Miller et al. 2013; Rich et al. 2013). We excluded detections of single wolves (Ausband et al. 2014) to ensure fewer false positive detections occurred in our single season occupancy models (Rich et al. 2013).

We assessed 9 site-specific covariates (Table 1), including 3 habitat and landscape covariates. We calculated percent forest cover from ABMI Wall-to-wall Land Cover Map (2010) based on digital classification of 30 m spatial-resolution Landsat satellite imagery (Alberta Biodiversity Monitoring Institute, University of Alberta) in each grid cell to assess the effects of percent forest cover on wolf occupancy and detection. We derived elevation and slope data from 25 m^2 resolution digital elevation models (DEM; Alberta ESRD) and calculated mean elevation and slope for each grid cell to evaluate landscape effects on occupancy. We estimated the effects of human density, 4wd-road density, wolf trapping harvest, and the presence of grizzly bear intercept feed sites (Alberta ESRD) in each grid cell. We assessed the effects of human density on occupancy using Alberta Municipal Affairs 2012 and 2013 population list statistics and Alberta municipal boundaries to calculate area-weighted mean number of humans in each grid cell (Alberta ESRD). We estimated area-weighted mean road length in each grid cell based on cut lines and OHV trails to assess the effects of 4wd roads on wolf occupancy and detection (Alberta ESRD). Preliminary modeling with 2012 data informed our decision to retain the road density covariate from further analyses due to correlations with other covariates. We calculated the number of wolves trapped per year per grid cell based on the area-weighted number of harvested wolves reported in each Registered Fur Management Area (RFMA; Alberta ESRD) to evaluate trapping effects on occupancy. We also assessed the effects of grizzly bear (*Ursus arctos*) intercept feeding sites on wolf occupancy by summing the number of feed sites present in each grid cell (Alberta ESRD). Finally, we estimated the effects of summer surveying effort and hunter effort on detection. We evaluated the effects of summer field sampling effort by summing the number of rendezvous sites surveyed in each grid cell. We used responses from the online hunter surveys to estimate area-weighted hunter effort per grid cell, standardized by the proportion of Wildlife Management Units (WMU) in each grid cell. Lastly, we estimated the differences in detection for hunter surveys by month and by season (archery and general).

Table 1. Mean values of covariates tested in a patch occupancy analysis for gray wolves in southwest Alberta, 2012 and 2013, and expected relationships between covariates and a wolf pack's probability of occupancy (ψ), detection (p_{11}), false positive detection (p_{10}), and certain detection (b).

	2012		2013		Hypothesized relationship			
Model Covariates	$\bar{x}$	**SE**	$\bar{x}$	**SE**	ψ	p_{11}	p_{10}	b
Forest cover (%)	0.41	0.044	0.50	0.035	+	-	+	-
Elevation (km)	1.67	0.066	1.61	0.054	-			
Slope (°)	0.15	0.016	0.13	0.012	-			
Human density (humans/km^2)	1.35	0.378	1.17	0.210	-			
No. wolves harvested/grid cell[a]	0.70	0.240	---	---	-/+			
No. grizzly bear intercept feed sites/grid cell	0.45	0.290	0.30	0.208	+			
Road density (total road length/km^2)[b]	0.92	0.115	---	---	-/+			
No. rendezvous site surveyed/grid cell[c]	18.22	6.098	6.38	1.720		+	-	+
Hunter effort for big game (hunter days/km^2)[d]	1.29	0.119	0.70	0.060		+	-	+

[a]Covariate data from registered furbearer traplines
[b]Covariate data from 4wd roads and cutlines only, correlated with hunter effort so not used in models
[c]Covariate data for sampling occasions from rendezvous site field surveys
[d]Covariate data for sampling occasions from online hunter surveys

We tested the effect of grid cell size (i.e., average territory size) on occupancy estimates. We used a 727km^2 grid based on the combined average pack territory size in central Idaho and 2008-2009 GPS radio collar data from southwest Alberta. We then increased the grid cells to 1,000km^2 and 1,200km^2 based on unpublished estimates of wolf pack territory size in western Alberta (N. Webb, Alberta ESRD, pers. comm). We derived unique detection histories and calculated covariates for all 3 grid cell sizes.

We fit occupancy models to the 2012 and 2013 detection data with Program PRESENCE 6.2 (Hines 2013) and used Akaike's information criterion value corrected for small sample size (AIC_c; Burnham and Anderson 2002) to identify the best supported model for each grid cell size and model type. We assessed alternative parameterizations for occupancy and detection covariates for both single season and false positive detection occupancy models. We tested alternatives where detection varied among survey methods, rendezvous site survey detections varied as a function of survey effort, and hunter survey detections varied as a function of hunter effort, hunting season, month, biweekly observations, and monthly observations. We also tested alternative methods to address the lack of wolf detections in the 2012 December sampling occasions by fixing these sampling occasions to equal 0, as well as by removing the December sampling occasions entirely. We used the 2012 results to inform our 2013 model design and excluded the last sampling occasion from late December 2013 due to a lack of hunter observations.

We ran Goodness of Fit tests on global models (most parameterized model) to assess over-dispersion and model structure in the single season occupancy models. We calculated $QAIC_c$ values for single season occupancy models with over-dispersion parameters >1 ($\hat{c}$; Burnham and Anderson 2002) to account for over-dispersion in the model estimates. Currently, there is no Goodness of Fit test for false positive detection occupancy models so we could not assess over-dispersion in these models.

We excluded models with fully constrained detection parameters from our model selection process (i.e. no difference in detection methods was considered in the model design). These models were used to test model design and program performance but are unreasonable in practice because the two survey methods were disparate in design and had dissimilar detection probabilities. We did consider models with constrained occupancy parameters when selecting models. Once we excluded models with fully constrained detection parameters, we considered models with the lowest AIC_c or $QAIC_c$ value as our best model (Appendix 2). Models within 2 AIC_c values of the lowest AIC_c or $QAIC_c$ also had substantial support and were considered in model selection and used to infer covariate effects (Appendix 2; Burnham and Anderson 2002).

To help account for over-dispersion in our best models we employed a non-parametric bootstrap approach to all models within 2 AIC_c values of the top model in R (R Core Team 2014) to estimate pack abundance and 95% confidence intervals (95% CI; Ausband et al. 2014). This involved resampling the detection histories and associated covariates from the top models 10,000 times to calculate the variance from the simulated distributions (Ausband et al. 2014). We used the bootstrapped 50% confidence interval as our estimate of wolf pack abundance.

Results

Rendezvous Site Surveys

We surveyed 420 potential wolf rendezvous sites in 2012. We detected 3 litters of pups in the study area and located 3 unoccupied rendezvous sites from 2011. In addition, we collected 439 genetic samples (278 adult, 161 pup). The majority (62%) of the samples were collected in occupied rendezvous sites. Scats were the most common form of wolf sign detected with tracks and howling following, respectively. Fecal samples collected during our surveys yielded 45 individual wolf genotypes.

In summer 2013, we surveyed 301 potential wolf rendezvous sites. We detected 3 litters of pups in the study area. The Bob Creek litter was detected by the presence of pup tracks only; no pup scats were detected. We detected 2 adults but no pups in the Oil Basin pack during rendezvous site surveys but Park scientists supplied us remote-sensing camera photos that confirmed pups in Waterton Park (B. Johnston, Waterton Lakes National Park of Canada, pers. comm). In addition, we collected 415 genetic samples (201 adult, 214 pup) in 2013. The majority (69%) of the samples were collected in occupied rendezvous sites. Scats were the most common form of wolf sign detected with tracks and howling following, respectively. Fecal samples collected during our surveys yielded 38 individual wolf genotypes. Of those, 7 were genetic recaptures from 2012, 2 of which were members of the Castle/Carbondale pack. Rendezvous site survey sampling effort was greater in 2012 due to access difficulties associated with flooding in the study area in 2013 (Table 1).

Hunter Surveys

We received 2,227 responses to our 2012 online survey in January 2013. Of those responding, 161 hunters (7.2%) reported seeing ≥2 live wolves during the 16-week survey period of the 2012 big game hunting season. In February 2014, we received 2,843 responses to our 2013 online hunter survey. Of those, 242 hunters (8.5%) observed ≥2 live wolves during the 16-week survey period of the big game hunting season. The 2013 online hunter survey included the late-winter hunting season in January 2014, but we excluded these hunter responses and wolf sightings to avoid violating population closure assumptions. These few reports from January spatially overlapped hunter reports from earlier in the season. Locations of hunter sightings were similar to summer wolf detection locations throughout most of the intensively surveyed portion of the study area (Fig. 4). Hunter survey sampling effort was greater in 2012 (Table 1).

Patch Occupancy Model

We tested over 10,000 models with unconstrained detection probabilities using the 2012 and 2013 data (3,200 single season models and 7,200 false positive detection models). Many models were unable to converge on estimates likely due to sparse detections, too few sampling occasions, or too few cells. The 2012 data was only able to support simpler models with few covariates. After expanding the study area and the hunter surveys in 2013, the data was able to support more complex models (Table 2; Appendix 2). Percent forest cover and human density influenced wolf pack occupancy and hunter survey detection probabilities were influenced by percent forest cover and month (Table 2).

Table 2. Top occupancy models predicting gray wolf distribution and estimated wolf pack abundance in southwest Alberta based on a 1,200km^2 grid where Ψ = occupancy, p = detection probability, p_{10} = probability of a false positive detection, b = detection probability given a certain detection, FC = percent forest cover, HUMAN = human density (humans/km^2), rnd = rendezvous site survey and hunter surveys unconstrained from each other but all hunter surveys constrained together, Full_ID = All surveys unconstrained from each other (full identity), month = rendezvous site survey and hunter surveys unconstrained from each other but hunter surveys constrained by month, FChunt = percent forest cover applied to hunter surveys only, -2Log-likelihood (-2LL), number of parameters (K), Akaike's Information Criterion Value corrected for small sample size (AIC$_c$), change in (Δ) AIC$_c$ value, Akaike's weight (w_i), estimated wolf pack abundance (Est. #of Packs), and 95% Confidence Interval (95% CI). 2012 estimates are for area from International Border to Highway 1, bordered on the east by Highway 22, with the exception of the Porcupine Hills. 2013 estimates are for 2012 area plus area north of Highway 1 along Highway 22 to the Brazeau River, and west to the eastern borders of Banff and Jasper National Parks.

Top False Positive Detection Models, 2012

Model	-2LL	K	AIC$_c$	Δ AIC$_c$	AIC$_c$ w	Est. # of Packs	95% CI
ψ(FC),*p*(rnd),*p*10(rnd),*b*(rnd)	**203.28**	**8**	**229.57**	**0.00**	**0.99**	**5.9**	**3.42-8.59**
[1]ψ(FC),*p*(Full_ID),*p*10(rnd),*b*(rnd)	190.41	13	256.85	27.29	0.00	---	---

[1]Model presented for comparison but not considered a top model.

Top False Positive Detection Models, 2013

Model	-2LL	K	AIC$_c$	Δ AIC$_c$	AIC$_c$ w	Est. # of Packs	95% CI
ψ(HUMAN),*p*(month, FChunt),*p*10(rnd),*b*(rnd)	**317.90**	**15**	**363.38**	**0.00**	**0.47**	**14.47**	**9.32-19.73**
[1]ψ(HUMAN),*p*(month),*p*10(rnd),*b*(rnd)	337.14	11	366.68	3.30	0.09	---	---

[1]Model presented for comparison but not considered a top model.

We estimated 5.90 (3.42-8.59; 95% CI) wolf packs in the original study area in 2012 (Table 2; Fig. 6). We estimated 14.47 (9.32-19.73; 95% CI; Table 2; Appendix 3) wolf packs in the expanded study area in 2013, of which 9.13 (6.03-11.35; 95% CI) were in the original portion of the 2012 study area (Table 3; Fig. 6). Predicted distribution in the original portion of the study area was similar in 2012 and 2013, with one exception (Fig. 7). The 2012 model predicted a medium to high probability of pack occupancy in the Kananaskis Valley, while the 2013 model predicted a low probability of occupancy in these cells likely due to limited sampling because of flooding (Fig. 7). We found estimated wolf pack abundance varied by grid cell size. Models using the 727km^2 grid as the average pack territory size had high variance around estimated abundance (Fig. 6; Appendix 3). Models using the 1,000km^2 and 1,200km^2 grids estimated similar wolf pack abundance with similar variance around the estimates in both years (Fig. 6; Appendix 3).

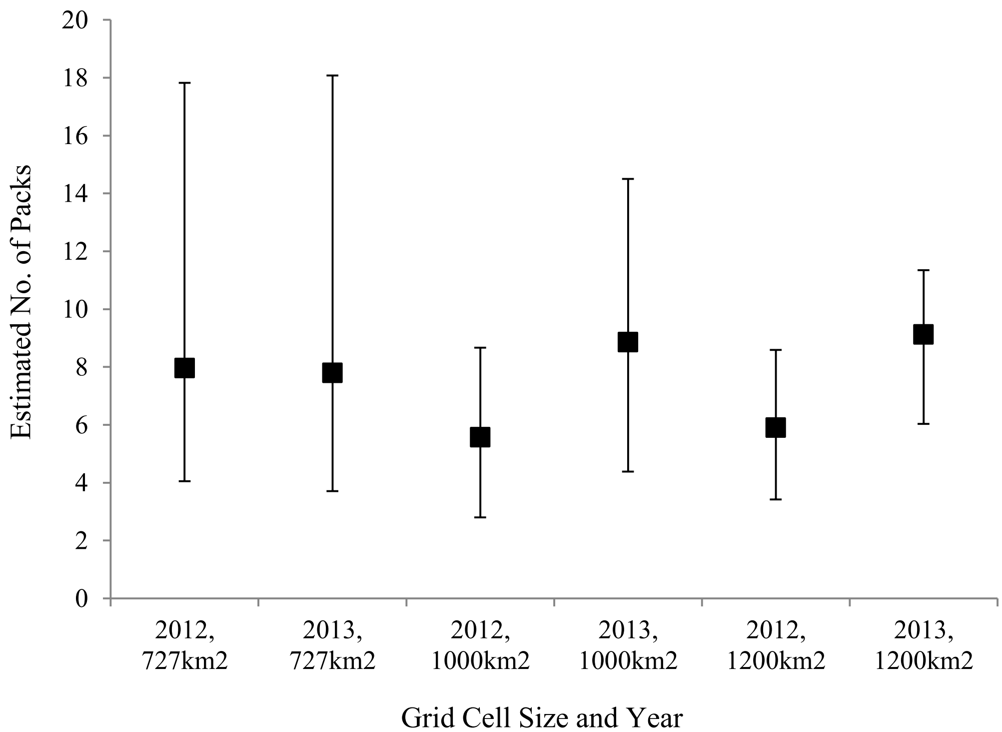

Figure 6. Estimated abundance (±95% CI) of wolf packs in the original study area (roughly International Border to Highway 1, bordered east by Highway 22). Estimates used 3 different average wolf pack territory sizes (727km^2, 1,000km^2, and 1,200km^2) from the top false positive detection occupancy models, 2012 and 2013.

Table 3. Estimated pack abundance and 95% Confidence Intervals for original study area (US border to Hwy 1 west of Highway 22, includes Porcupine Hills) using a non-parametric bootstrap approach for the top false positive detection models and a 1,200km^2 estimated average territory size. Ψ = occupancy, p = detection probability, p_{10} = probability of a false positive detection, b = detection probability given a certain detection, FC = percent forest cover, HUMAN = human density (humans/km^2), rnd = rendezvous site survey and hunter surveys unconstrained from each other but all hunter surveys constrained together, month = rendezvous site survey and hunter surveys unconstrained from each other but hunter surveys constrained by month, FChunt = percent forest cover applied to hunter surveys only.

Year	Model	Est. # of Packs	95% CI
2012	ψ(FC),p(rnd),p10(rnd),b(rnd)	5.90	3.42-8.59
2013	ψ(HUMAN),p(month,FChunt),p10(rnd),b(rnd)	9.13	6.03-11.35

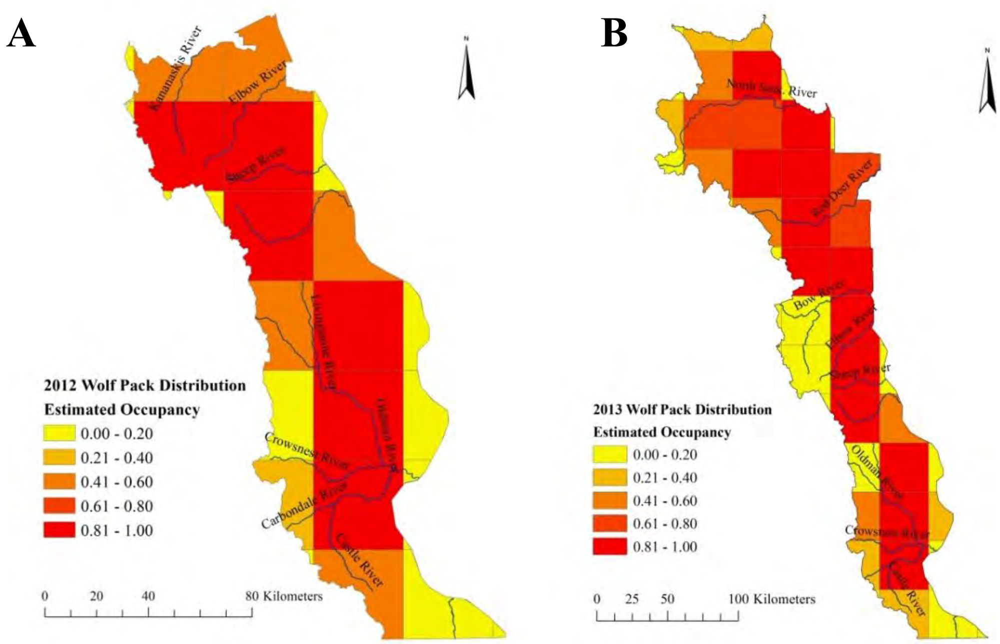

Figure 7. The predicted probability each 1,200km^2 cell in southwest Alberta, Canada was occupied by wolves in (A) the original study area in 2012 and (B) the expanded study area in 2013. We estimated occupancy probabilities using a single season model that accounts for false positive detections with rendezvous site surveys and hunter surveys as the sampling methods and percent forest cover and human density as predictor variables.

Detection probabilities varied among sampling methods and across years. In 2013, hunter survey detections varied by sampling month and were positively related to percent forest cover (Table 4; Table 5). The probability that wolves were considered falsely detected (i.e., 1 wolf detected; p_{10}) and the probability that a true positive detection was classified as certain (b) also varied by sampling method (Table 4). We found detection probabilities (p_{11}) and false positive detection probabilities (p_{10}) were highest in rendezvous site surveys across years (Table 4). True positive detection probabilities (b) were greater in rendezvous site surveys in 2012 but were greater in hunter surveys in 2013. The percentage of true wolf observations that were classified as certain in rendezvous site surveys decreased from 59.0% in 2012 to 30.0% in 2013, while it remained constant with hunter surveys at 52.0% across years (b; Table 4). Occupancy was positively related to percent forest cover in 2012. In 2013, wolf pack occupancy was positively related to human density (Table 5).

Table 4. Estimates for the mean probabilities wolf packs were detected (p_{11}) through surveys of predicted rendezvous sites and hunter surveys; the mean probabilities wolves were detected in unoccupied sites (p_{10}) during rendezvous site surveys and hunter surveys depending on percent forest cover (FC) and month; and the mean probability wolf detections during rendezvous site surveys or hunter observations were considered certain given that the site was occupied and wolves were detected (b) in 2012 and 2013 using false positive detection occupancy models with a 1,200km^2 estimated average territory size.

Parameter	Variable	2012	2013
		p (S)	p (S)
p_{11}			
Rendezvous site survey		0.62 (0.171)	0.67 (0.155)
Hunter survey		0.45 (0.064)	
	FC in September		0.19 (0.014)
	FC in October		0.37 (0.025)
	FC in November		0.63 (0.028)
	FC in December		0.09 (0.022)
p_{10}			
Rendezvous site survey		0.50 (0.369)	0.27 (0.022)
Hunter survey		0.01 (0.019)	0.03 (0.017)
b			
Rendezvous site survey		0.59 (0.220)	0.30 (0.181)
Hunter Survey		0.52 (0.086)	0.52 (0.072)

Table 5. Parameter estimates for occupancy analysis of gray wolf packs in southwest, Alberta, 2012 and 2013. Models include two detection methods: summer rendezvous site surveys and online hunter surveys. We tested false positive detection occupancy models to estimate wolf pack occupancy, probability a wolf pack was detected in an occupied site (p_{11}), probability a wolf pack was detected in an unoccupied site (p_{10}), and probability wolf observations were classified as a certain detection given the site was occupied and wolves were detected (*b*).

Parameter	Variable	2012		2013	
		β	SE	β	SE
Occupancy					
	Forest Cover (%)	4.29	2.513		
	Human Density			3.32	1.680
p_{11}					
Sampling method					
Rendezvous surveys		0.51	0.730	0.69	0.697
Hunter surveys		-0.20	0.259		
	FC in September			4.59	2.561
	FC in October			5.85	2.193
	FC in November			6.13	2.011
	FC in December			14.01	16.505
p_{10}					
Sampling method					
Rendezvous surveys		-0.01	1.478	-0.98	1.095
Hunter surveys		-4.60	1.880	-3.39	0.545
b					
Sampling method					
Rendezvous surveys		0.38	0.913	-0.83	0.857
Hunter surveys		0.09	0.346	0.08	0.288

We found only subtle differences in model performance when 2012 December sampling occasions were fixed to equal 0 and when they were excluded entirely. Preliminary modeling indicated road density and hunter effort were correlated (r = 0.5) and road density had no effect on occupancy in single-season models with the 727 km^2 grid and we removed road density from further analyses.

Discussion

Wolves, like many large carnivores, are territorial, wide-ranging, and occur at low densities, making large-scale monitoring challenging (Royle and Dorazio 2008; Rich et al. 2013; Ausband et al. 2014). Additionally, previous studies found that when wolf turnover is high implementing common single-method monitoring programs, like radio-telemetry monitoring, are not practical (Ausband et al. 2014). Occupancy models can address this challenge by using presence/absence detection data collected from a range of survey methods at different temporal and special scales to estimate species distribution and abundance, making them an ideal statistical tool on which to build a wolf monitoring framework (MacKenzie et al. 2006; Nichols et al. 2008). Occupancy models can produce reliable population estimates even when detection varies and the species occurs at low densities (MacKenzie et al. 2006), which is ideal for monitoring large carnivore populations like wolves (Rich et al. 2013; Ausband et al. 2014). Unique sets of covariates can help predict occupancy probabilities in unsampled sites within the study area, as well as estimate detection probabilities for each detection method (MacKenzie et al. 2006; Nichols et al. 2008).

We collected presence/absence detection data in 2012 and 2013 to populate and test patch occupancy model design and performance for the gray wolf population in southwest Alberta. Much of this work was exploratory to determine ideal model type, model structure, and test covariate data. Similar wolf occupancy studies encompassed large study areas (Miller et al. 2013; Rich et al. 2013; Ausband et al. 2014). Because our study area was small by comparison we were unsure what to expect for model estimates. We found evidence of lack-of-fit in our 2012 basic single season occupancy models. A lack-of-fit can be a result of structural inadequacy in the model or over-dispersion in the data (Burnham and Anderson, 2002). We suspected the lack-of-fit in our models was due to a combination of both issues, so we expanded our hunter survey in 2013 to improve model performance. As a result, we found no evidence of lack-of-fit in our 2013 basic single season models.

Similar to other wolf patch occupancy studies, we found that single season false positive occupancy models are more appropriate for the southwest Alberta wolf population than basic single season occupancy models. Miller et al. (2011; 2013) demonstrated that false positive detection errors can have a significant effect on occupancy estimates if unaccounted for and results in over-estimating occupancy. Being that hunter observations can include species misidentifications and both our survey methods may misinterpret transient animals as evidence of a pack, it is necessary to account for false positive detections. In doing so, we can reduce bias and increase precision in our occupancy estimates (Miller et al. 2011). Our results support the need to incorporate false positive detections in our models as single season occupancy models estimated more wolf packs with a wider variance than models that incorporated false positive detections (Table 6; Appendix 3).

Our preliminary models suggest 1,200km^2 is likely the best estimate of average wolf pack territory size, although this estimate could be developed further. There are no radiocollared wolves in our current study area and little data exists on current average pack territory size. The most recent territory size estimates use GPS collar location data from 2008 and 2009 but are based on 3 wolf packs and partial annual movements (A. Morehouse, Alberta ESRD, unpublished data). It was therefore necessary to test several grid cell sizes to find the best estimate for average wolf pack territory size. Although our 727km^2 grid incorporated the 2008/2009 territory data the variance around abundance estimates were so large we suspected we were underestimating average pack territory size and thus overestimating pack abundance (Adams et al. 2008). Models based on 1,000km^2 and 1,200km^2 grids estimated relatively similar pack abundance and variance, making it difficult to discern the best average pack territory size. Ultimately, we chose to present results from models using the 1,200km^2 grid because the variance was least in these models and previous AESRD studies in west-central Alberta demonstrated pack territories increased in size on a gradient from northeast to southwest (Webb et al. 2009), reaching 1,200km^2 in the western-most portion of their range in Alberta (N. Webb, Alberta ESRD, pers. comm). Further research is necessary to estimate a more accurate average pack territory size for our study. Using GPS collar location data from historic packs in southwest Alberta, we estimated average territory size was 1,982km^2 (95% Kernel Density Estimates; Spatial Ecology LLC 2012; ESRI 2012) between 2004 and 2005 (Alberta ESRD, unpublished data). Wolf density and pack composition may have been different than in

2008/2009 and may explain discrepancies in average territory size between these years. Wolf pack territory size is more variable in populations that experience human exploitation (Ballard et al. 1987; Haber 1996; Rich et al. 2012) and are more directly related to pack size than in unexploited wolf populations (Peterson et al. 1984; Haber 1996). We currently lack the biological context for these historic packs to evaluate the influences of pack size and harvest pressure on these territory size estimates.

Our models included several other assumptions beyond assuming our grid cell size is a reliable estimate of average territory size. We assumed the distribution and abundance of wolf packs did not change during our sampling season, 1 June to 31 December, and that detections were independent of each other (MacKenzie et al. 2006; Rich et al. 2013; Ausband et al. 2014). Although individual wolves were lost from the population due to mortality or emigration, and added to the population through births and immigration, we assumed occupancy in each cell was stable and that packs did not move into adjacent cells during a sampling season. To our knowledge, registered trapping and control actions did not remove entire wolf packs during our sampling seasons in either 2012 or 2013. In addition, we assumed no territory overlap within our study area and minimal gaps between territories. Previous wolf research supports this assumption (Mech and Boitani 2003; Robichaud and Boyce 2010) and results from similar occupancy studies found this assumption to hold true (Rich et al. 2013; Ausband et al. 2014). However, as with our average territory size estimate, it is necessary to monitor the level of overlap and interstitial space between wolf pack territories over time as these characteristics in wolf populations can change (Rich et al. 2013; Ausband et al. 2014).

Covariate effects on occupancy and detection probability varied by year. Percent forest cover had a positive influence on wolf pack occupancy in 2012 and on monthly hunter survey detection probabilities in 2013. Human density had a positive influence on wolf pack occupancy in 2013. We suspect there is a positive relationship between human density and occupancy because humans, prey, and wolves alike tend to congregate in the lower elevations of our study area. We were unable to fully test the effects of several covariates, including wolf trapping. We tested incomplete wolf harvest data in the 2012 models but were unable to test trapping at all in the 2013 models due to lack of data. The 2012 trapping covariate was most influential to occupancy in models with an estimated average territory size of 727km^2, despite the incomplete data. As a result, we suspect the complete dataset will influence occupancy estimates in the future. Previous wolf occupancy studies found prey densities and livestock densities were influential to wolf occupancy (Rich et al. 2013; Ausband et al. 2014). We believe this is likely true in our study area as well, especially when we consider Morehouse and Boyce (2011) found cattle made up almost 75% of the biomass consumed by wolves during the grazing season (summer and early fall) in southwest Alberta. We were unable to obtain the necessary data to include these covariates but hope to in the future.

Detection probabilities varied by method, sampling effort, and sampling season. Similar to results from Ausband et al. (2014), we showed that rendezvous site surveys yield higher detection probabilities than hunter surveys. Rendezvous site surveys had higher false positive detection probabilities than hunter surveys likely due to our definition of "certain detections". For example, if we detected two adult wolves from genetic sampling but not their pups the cell was classified as an "uncertain" detection. Survey effort was greater in 2012 for both hunter and rendezvous site survey methods but its influence on detection probability was ambiguous (i.e., survey effort had a positive influence on hunter detection probability and the probability of false positive detections in rendezvous site surveys, but negatively influenced rendezvous site detection probability and the probability of false positive detections in hunter surveys).

Pack abundance and distribution estimates varied between year and across grid cell size. Our false positive detection occupancy models with a 1,200km^2 grid estimated approximately 3 more wolf packs in the original portion of the study area in 2013 than in 2012. We attribute this greater pack estimate in part to our increased sampling effort in the Waterton Biosphere Area in 2013. This area went relatively unsampled in 2012 as we did not conduct rendezvous site surveys in this area and hunting, and thus hunter survey data, is not allowed in Waterton Lakes National Park. It is possible that additional packs established territories within the original portion of the study area between 2012 and 2013. For example, the 2013 wolf genotypes from the Willow Creek pack showed they are comprised of entirely different individuals than the 2012 Willow Creek pack. It is therefore reasonable to assume other new packs have established themselves in our study area.

Ausband et al. (2014) demonstrated that the use of multiple survey methods helps ensure occupancy estimates are robust to changes in any one method (Nichols et al. 2008). Hunter surveys can become less reliable over time as public interest wanes or if individuals attempt to influence estimates by misrepresenting sightings (Rich et al. 2013; Ausband et al. 2014). Because hunter sightings are the workhorse of our models, additional survey methods help calibrate these occupancy models by ensuring hunter sightings are still a reliable indicator of wolf pack presence (Nichols et al. 2008; Rich et al. 2013; Ausband et al. 2014). In addition, fine-scale survey methods can provide population characteristics, like pack size or territory size, which are necessary for accurate distribution and abundance estimates, but difficult to obtain with hunter surveys (Ausband et al. 2014). Finally, public sightings, trapper reports, hunter reports of wolf howls, remote-sensing camera photos, and harvested wolves can provide additional forms of model verification. Our efforts to acquire public sightings in addition to hunter surveys and trapper information on wolf activity did not yield an abundance of data. We were able to compare estimated wolf pack distributions from our models with the sparse location data submitted by the general public and found spatial overlap between model estimates and public reports.

Future Work

Our final sampling season will include the 2014 rendezvous site field survey and the 2015 online hunter survey following the conclusion of the 2014 big game hunting season. We will incorporate these data into our existing model structure to further evaluate the use of occupancy modeling as a monitoring framework for wolf packs in southwest Alberta.

In addition, we hope to continue exploring and testing our assumptions and model parameters. Primarily, we want to address the uncertainty in our grid cell size and incomplete covariate data. One possible avenue to estimate a more accurate grid cell size is to relax the assumption that there is one average territory size across the entire study area (Rich et al. 2013). Rich et al. (2012) found territory size can vary due to a number of influencing factors, including prey availability, terrain, and anthropogenic mortality. These factors can be measured and accounted for by incorporating spatial variation in grid cell sizes in our model (Rich et al. 2013). In addition, we can use wolf genotypes derived from scat samples to assign individual wolves to specific packs using assignment tests (Pritchard et al. 2000; Manel et al. 2003; Vonholdt et al. 2010). Once pack membership is determined we can use scat detection locations to estimate territory sizes in each sampling season, providing our models with study specific territory and grid cell size estimates. We also hope to use this genetic data and the unique capabilities of occupancy modeling to assess trends in southwest Alberta's wolf population, including colonization and extinction probabilities and genetic movement.

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Appendix 1

Instructions for Collecting Tissue Samples

1) Sterilize a razor or knife with a lighter by burning the blade for $\geq$ 5 seconds.

2) Cut a small piece of tissue, 4 mm x 4 mm, (no larger than a kernel of corn) from the tongue of the animal using the sterilized razor blade or knife. If the animal has been dead for some time and is substantially decayed a sample can be taken from the footpad (if available) because it is the last tissue to rot.

3) Place tissue into sample vial that is filled with silica desiccant. Tissue should be fully covered by desiccant beads.

4) Record on vial:

    a. Date
    b. Personnel name
    c. Sex of animal

5) Place sample vial into coin envelope and fill out the fields on the envelope label.

6) Samples can be stored at room temperature.

Appendix 2

Appendix 2, Table 1.
Top occupancy models (within 2 AIC_c values) predicting gray wolf distribution and abundance in southwest Alberta, 2012 and 2013, based on an estimated average wolf pack territory size of 727 km^2, where Ψ = occupancy, p = detection probability, p_{10} = probability of a false positive detection, b = detection probability given a certain detection, FC = Percent Forest Cover, ELEV = mean elevation, TRAP = number of wolves harvested in registered traplines, HUMAN = human density (humans/km^2), INTER = number of grizzly bear intercept feed sites, FChunt = percent forest cover applied to hunter surveys only, rnd = rendezvous site survey and hunter survey detections unconstrained from each other but all hunter surveys constrained together, method = rendezvous site survey and hunter surveys unconstrained from each other but hunter surveys constrained by hunting season (archery or general), month = rendezvous site survey and hunter surveys unconstrained from each other but hunter surveys constrained by month, -2Log-likelihood (-2LL), number of parameters (K), Quasi-Akaike's Information Criterion Value corrected for small sample size ($QAIC_c$), change in (Δ) $QAIC_c$ value, Quasi-Akaike's weight (w_i), Akaike's Information Criterion Value corrected for small sample size (AIC_c), change in (Δ) AIC_c value, Akaike's weight (w_i), wolf pack abundance (Est. # of Packs), and 95% Confidence Intervals (95% CI).

Single Season Models, 2012

Model	-2LL	K	$QAIC_c$	Δ $QAIC_c$	$QAIC_c$ w	Est. # of Packs	95% CI
ψ(.),*p*(rnd)	**120.48**	**4**	**24.87**	**0.00**	**0.34**	**8.47**	**4.43-17.82**
ψ(.),*p*(method)	111.41	5	26.57	1.75	0.14	8.01	4.32-13.18

False Positive Detections Models, 2012

Model	-2LL	K	AIC_c	Δ AIC_c	AIC_c w	Est. # of Packs	95% CI
ψ(FC_ELEV),*p*(month),*p*10(month),*b*(month)	**205.33**	**15**	**237.47**	**0.00**	**0.95**	**7.96**	**4.05-17.82**
[1]ψ(FC_ L V_TRAP),*p*(month),*p*10(month),*b*(month)	205.26	16	244.47	6.99	0.03	---	---

[1]Model presented for comparison but not considered a top model.

Single Season Models, 2013

Model	-2LL	K	AIC_c	Δ AIC_c	AIC_c w	Est. # of Packs	95% CI
ψ(ELEV),*p*(method)	**179.24**	**5**	**190.29**	**0.00**	**0.11**	**9.86**	**5.43-16.76**
ψ(FC_ L V),*p*(method)	177.90	6	191.40	1.11	0.06	17.24	9.53-31.45

ψ(L V),*p*(method,FChunt)	175.49	7	191.53	1.23	0.06	16.81	9.73-32.10
ψ(L V_HUMAN),*p*(method,FChunt)	173.16	8	191.83	1.53	0.05	18.19	10.34-28.96
ψ(HUMAN),*p*(method,FChunt)	175.84	7	191.88	1.58	0.05	18.42	10.69-27.57
ψ(L V),*p*(month)	178.79	6	192.29	2.00	0.04	16.41	9.41-32.66

False Positive Detection Models, 2013

Model	-2LL	K	AIC_c	ΔAIC_c	AIC_c *w*	Est. # of Packs	95% CI
ψ(ELEV_INTER),*p*(month),*p*10(rnd),*b*(rnd)	**383.78**	**12**	**414.02**	**0.00**	**0.39**	**12.97**	**8.00-19.11**
ψ(L V),*p*(month),*p*10(rnd),*b*(rnd)	387.57	11	414.75	0.73	0.27	14.84	8.95-23.00

Appendix 2, Table 2.
Top occupancy models predicting gray wolf distribution in southwest Alberta, 2012 and 2013, based on an estimated average wolf pack territory size of 1,000 km^2, where Ψ = occupancy, p = detection probability, p_{10} = probability of a false positive detection, b = detection probability given a certain detection, TRAP = number of wolves harvested (trapping), FC = percent forest cover, ELEV = mean elevation, SLOPE = mean percent slope, rnd = rendezvous site survey and hunter surveys unconstrained from each other but all hunter surveys constrained together, month = rendezvous site survey and hunter surveys unconstrained from each other but hunter surveys constrained by month, -2Log-likelihood (-2LL), number of parameters (K), Akaike's Information Criterion Value corrected for small sample size (AIC$_c$), change in (Δ) AIC$_c$ value, Akaike's weight (w_i), Quasi-Akaike's Information Criterion Value corrected for small sample size (QAIC$_c$), change in (Δ) QAIC$_c$ value, Quasi-Akaike's weight (w_i), wolf pack abundance (Est. # of Packs), and 95% Confidence Intervals (95% CI).

Single Season Models, 2012

Model	-2LL	K	QAIC$_c$	Δ QAIC$_c$	QAIC$_c$ w	Est. # of Packs	95% CI
ψ(.),p(rnd)	**105.79**	**4**	**57.88**	**0.00**	**0.37**	**5.77**	**2.86-10.04**
ψ(TRAP),p(rnd)	101.44	5	59.14	1.26	0.19	5.37	2.61-8.79

False Positive Detection Models, 2012

Model	-2LL	K	AIC$_c$	Δ AIC$_c$	AIC$_c$ w	Est. # of Packs	95% CI
ψ(.),p(rnd),p10(rnd),b(rnd)	**214.74**	**7**	**235.74**	**0.00**	**0.40**	**5.57**	**2.80-8.67**
ψ(TRAP),p(rnd),p10(rnd),b(rnd)	210.60	8	236.20	0.46	0.32	5.54	2.65-8.80

Single Season Models, 2013

Model	-2LL	K	AIC$_c$	Δ AIC$_c$	AIC$_c$ w	Est. # of Packs	95%CI
ψ(FC),p(month)	**154.86**	**7**	**171.47**	**0.00**	**0.17**	**9.13**	**5.10-15.55**
ψ(.),p(month)	158.74	6	172.65	1.18	0.10	9.00	5.02-13.34
ψ(FC_SLOP),p(month)	153.65	8	173.08	1.61	0.08	9.12	5.12-16.01
ψ(FC_ L V),p(month)	153.65	8	173.08	1.61	0.08	9.15	5.12-15.94

False Positive Detection Models, 2013

Model	-2LL	K	AIC$_c$	Δ AIC$_c$	AIC$_c$ w	Est. # of Packs	95% CI
ψ(.),p(month),p10(rnd),b(rnd)	**346.05**	**10**	**371.55**	**0.00**	**0.23**	**12.43**	**7.75-18.57**
ψ(FC),p(month),p10(rnd),b(rnd)	343.33	11	372.10	0.55	0.18	12.22	7.56-18.67

ψ(L V),*p*(month),*p*10(rnd),*b*(rnd)	344.70	11	373.47	1.92	0.09	12.48	7.70-19.33

Appendix 2, Table 3.
Top occupancy models predicting gray wolf distribution in southwest Alberta, 2012 and 2013, based on a 1,200 km^2 grid where Ψ = occupancy, p = detection probability, p_{10} = probability of a false positive detection, b = detection probability given a certain detection, FC = percent forest cover, HUMAN = human density (humans/km^2), FChunt = percent forest cover applied to hunter surveys only, rnd = rendezvous site survey and hunter surveys unconstrained from each other but all hunter surveys constrained together, method = rendezvous site survey and hunter surveys unconstrained from each other but hunter surveys constrained by hunting season (archery or general), Full ID = rendezvous site survey and hunter surveys are fully unconstrained from each other (Full Identity), month = rendezvous site survey and hunter surveys unconstrained from each other but hunter surveys are constrained by month, -2Log-likelihood (-2LL), number of parameters (K), Quasi-Akaike's Information Criterion Value corrected for small sample size ($QAIC_c$), change in (Δ) $QAIC_c$ value, Quasi-Akaike's weight (w_i), Akaike's Information Criterion Value corrected for small sample size (AIC_c), change in (Δ) AIC_c value, Akaike's weight (w_i), wolf pack abundance (Est. # of Packs), and 95% Confidence Intervals (95% CI).

Single Season Models, 2012

Model	-2LL	K	$QAIC_c$	Δ $QAIC_c$	$QAIC_c$ w	Est. # of Packs	95% CI
ψ(.),*p*(rnd)	**115.56**	**3**	**25.79**	**0.00**	**0.70**	**6.89**	**3.68-10.79**
[1]ψ(.),*p*(method)	110.70	4	28.44	2.65	0.18	---	---

False Positive Detection Models, 2012

Model	-2LL	K	AIC_c	Δ AIC_c	AIC_c w	Est. # of Packs	95% CI
ψ(FC),*p*(rnd),*p*10(rnd),*b*(rnd)	**203.28**	**8**	**229.57**	**0.00**	**0.99**	**5.9**	**3.42-8.59**
[1]ψ(FC),*p*(Full_ID),*p*10(rnd),*b*(rnd)	190.41	13	256.85	27.29	0.00	---	---

[1]Model presented for comparison but not considered a top model.

Single Season Models, 2013

Model	-2LL	K	AIC_c	Δ AIC_c	AIC_c w	Est. # of Packs	95% CI
ψ(HUMAN),*p*(method,FChunt)	**158.26**	**7**	**175.13**	**0.00**	**0.16**	**11.93**	**7.44-16.44**
ψ(HUMAN),*p*(month,FChunt)	145.83	11	175.37	0.24	0.15	11.73	7.12-16.28
ψ(HUMAN),*p*(month)	159.19	7	176.06	0.93	0.10	10.62	6.13-15.83
ψ(FC_HUMAN),*p*(month)	156.84	8	176.63	1.50	0.08	10.52	6.03-17.14

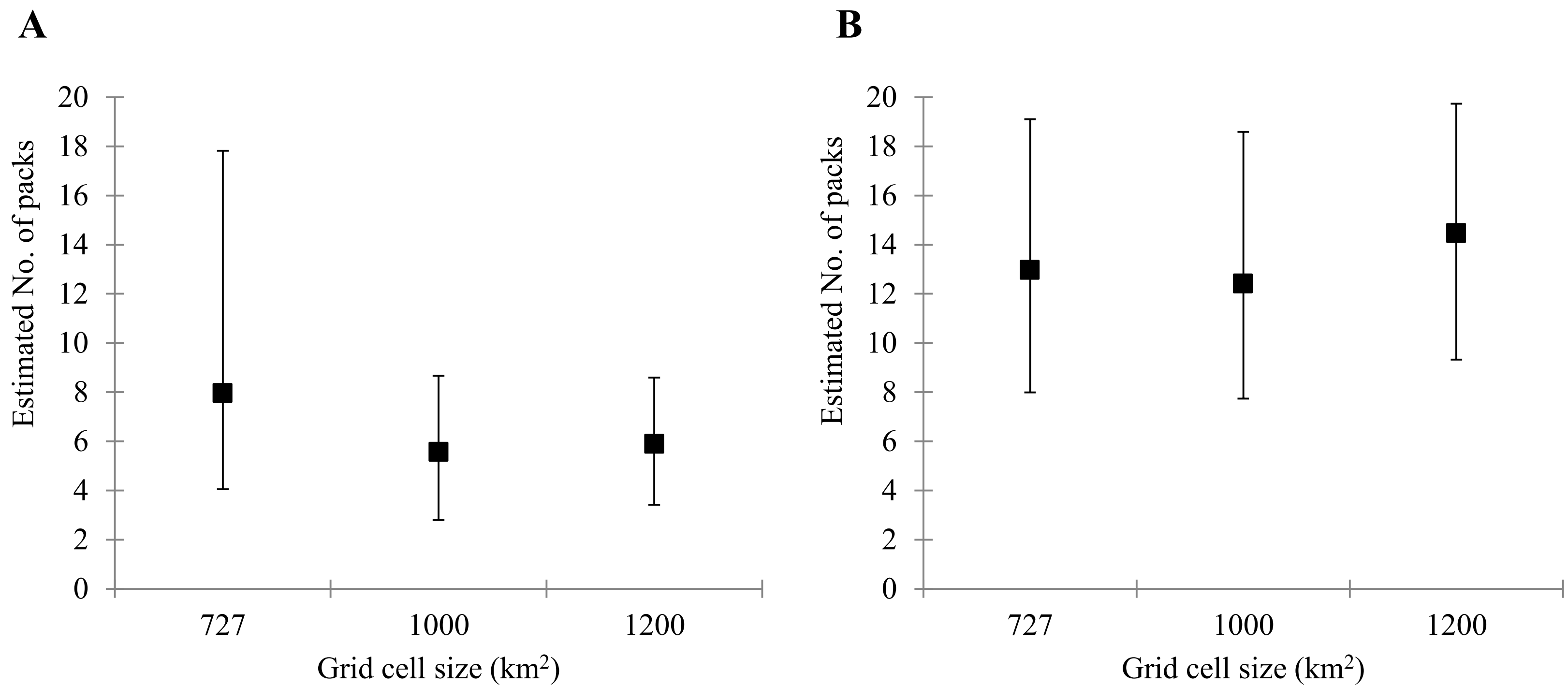
False Positive Detection Models, 2013

Model	-2LL	K	AIC_c	Δ AIC_c	AIC_c w	Est. # of Packs	95% CI

ψ(HUMAN),*p*(month,FChunt),*p*10(rnd),*b*(rnd)	**317.90**	**15**	**363.38**	**0.00**	**0.47**	**14.47**	**9.32-19.73**
[1]ψ(HUMAN),*p*(month),*p*10(rnd),*b*(rnd)	337.14	11	366.68	3.30	0.09	---	---

[1]Model presented for reference but not considered a top model

Appendix 3



Abundance (±95% CI) of wolf packs in (A) 2012 in the original study area and (B) 2013 in the expanded study area, estimated with three different average wolf pack territory sizes ($727 km^2$, $1,000 km^2$, and $1,200 km^2$) from the top false positive detection occupancy models, 2012 and 2013.