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Research Article

Stable Pack Abundance and Distribution in a Harvested Wolf Population

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ABSTRACT Harvesting gray wolves (*Canis lupus*) could affect the abundance and distribution of packs, but the frequency of change in pack occurrence (i.e., turnover) and relative effects of harvest compared to environmental factors is unclear. We used noninvasive genetic sampling, hunter surveys, and occupancy models to evaluate the effect of harvest on occurrence and turnover of packs in a population of wolves managed with intensive harvest in the Canadian Rocky Mountains, 2012–2014. We tested 2 alternative hypotheses: the abundance and distribution of wolf packs were dynamic because of harvest or the abundance and distribution of wolf packs were generally stable regardless of harvest. We found the mean annual probability for wolf pack occupancy ranged 0.72–0.74 and the estimated distribution of wolf packs was consistent over time, 2012–2014. Our top model indicated wolf pack occupancy was positively associated with forest cover and the probability of detecting a wolf pack was positively associated with the intensity of harvest for wolves in that area. We observed frequent turnover of individuals within packs that were genetically sampled consecutive years but not of entire packs. Because turnover of packs occurred infrequently during our study, we could not reject our hypothesis that occurrence of packs was generally stable in a harvested population of wolves. Our results suggest environmental factors have a stronger effect than harvest on the abundance and distribution of wolf packs in southwestern Alberta, but harvest appears to strongly influence turnover of individuals within packs. We hypothesize local dispersal from within the study area and neighboring packs on the periphery of the study area helped promote pack stability. © 2018 The Wildlife Society.

KEY WORDS *Canis lupus*, gray wolves, harvest, noninvasive genetic surveys, occupancy model, pack turnover, social carnivore, wolf group.

Public harvest is commonly used to manage wildlife populations and mitigate human-wildlife conflicts. Harvest can affect the demography of wild populations in various ways, such as altering the age and sex structures (Ginsberg and Milner-Gulland 1994, Milner et al. 2007), reproductive rate (Knowlton 1972, Ausband et al. 2015), and ultimately growth (Pauli and Buskirk 2007) of a population. Understanding how populations respond to harvest can help wildlife managers evaluate the efficacy of management, meet management objectives, and inform future decisions (Williams et al. 2002, Mills 2013).

Populations of gray wolves (*Canis lupus*) are managed with harvest across most of their range in North America (Boitani 2003). Because of the social behavior of wolves, the response of wolf populations to harvest may be more complex than for other exploited species (Rutledge et al. 2010). Typically, only a single pair of adult wolves reproduce per pack (i.e., breeding pair) instead of all reproductively mature individuals in the population; thus, wolf packs are the reproductive units in a wolf population and influence population dynamics (Fuller et al. 2003). The effects of harvest at the pack-level will affect individual pack members (Brainerd et al. 2008) and potentially the larger population (Haber 1996).

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Harvest may affect the abundance and distribution of wolf packs in a population (Jędrzejewska et al. 1996), but the demographic consequences of this relationship are poorly understood. Loss of wolves in a pack can create social instability, leading to pack dissolution and territory abandonment (Meier et al. 1995, Jędrzejewska et al. 1996, Gehring et al. 2003, Brainerd et al. 2008, Smith et al. 2016), and entire packs may be removed through lethal control actions to reduce predation on livestock (Bradley et al. 2015). Frequent loss of packs to harvest can lead to decreased population growth, reproductive success, or relatedness within and among packs (Grewal et al. 2004, Jędrzejewski et al. 2005, Brainerd et al. 2008), which may have long-term effects for populations managed with high harvest (Haber 1996, Brainerd et al. 2008). Alternatively, packs that persist provide a source of dispersing wolves to recolonize vacant territories (Bjorge and Gunson 1985, Ballard et al. 1987, Hayes and Harestad 2000, Mech and Boitani 2003, Brainerd et al. 2008); thus, the loss and reestablishment of packs across space and time (i.e., turnover of packs) may have little effect on demography if dispersers can quickly recolonize unoccupied territories (Larivière et al. 2000, Fuller et al. 2003).

Frequent changes in abundance and distribution of packs may complicate management of harvested populations of wolves even if there are few demographic consequences. Social instability and turnover of packs can change boundaries (Haber 1996, Jędrzejewska et al. 1996, Mech and Boitani 2003), size (Peterson et al. 1984), or use (Haber 1996) of territories. Such changes may affect the quality or quantity of data collected for management because monitoring frequent changes in pack occurrence can be challenging; this may ultimately affect a manager's ability to assess the status of a population, set harvest limits and seasons, or achieve population objectives for wolves. Frequent turnover of packs may also alter the rate of wolf-livestock conflicts. Hayes et al. (1991) reported predation rates on wild prey increased for colonizing pairs and packs severely reduced after lethal removal; this behavior could extend to predation on livestock. If non-depredating packs dissolve in response to harvest, surviving or colonizing wolves may begin to prey on livestock (Bjorge and Gunson 1985). In addition, studies reported lethal removal, particularly of entire packs, reduced the likelihood of future predation events on livestock locally (Bjorge and Gunson 1985, Bradley et al. 2015) but not population-wide (Harper et al. 2008). Frequent turnover of packs may therefore affect conflicts with livestock depending on the frequency of pack replacement (Bradley et al. 2015) and individual traits of wolves recolonizing vacant territories (Bjorge and Gunson 1985). Understanding the frequency of turnover of packs and associated factors will help monitoring efforts provide accurate and sufficient information to managers, and help managers mitigate conflicts and meet population objectives for wolves.

We tested 2 hypotheses to evaluate the effect of harvest on occurrence and turnover of packs in a population of wolves in southwestern Alberta, Canada, where wolves have been managed with public harvest for decades (Gunson 1992, Boitani 2003). We hypothesized that the abundance and distribution of wolf packs were highly dynamic because of harvest and predicted that pack occupancy changed frequently in association with harvest of wolves in southwestern Alberta. Alternatively, we hypothesized that the abundance and distribution of wolf packs were generally stable regardless of harvest and predicted infrequent changes in occupancy associated with harvest of wolves in southwestern Alberta. We then evaluated the relative importance of harvest compared to environmental factors that have already been reported to explain pack occupancy in the Rocky Mountains (e.g., forest cover and cattle density; Rich et al. 2013, Ausband et al. 2014) to determine the dominant factors associated with pack abundance and distribution in a harvested population of wolves.

STUDY AREA

We conducted our study in southwestern Alberta, Canada, 2012–2014. Our 30,000-km^2 study area extended from the Canadian-United States border north to the Brazeau River but excluded Banff and Jasper National Parks (Fig. 1). Elevation ranged 429–3,560 m, annual temperatures averaged >11°C in summer and <−5°C in winter, and mean annual precipitation ranged 420–1,700 mm (Alberta Government 2018). The study area featured mountains in the west along the British Columbia border, dominated by Douglas-fir (*Pseudotsuga menziesii*), lodgepole pine (*Pinus contorta*), and spruce (*Picea engelmannii*) mixed forests that

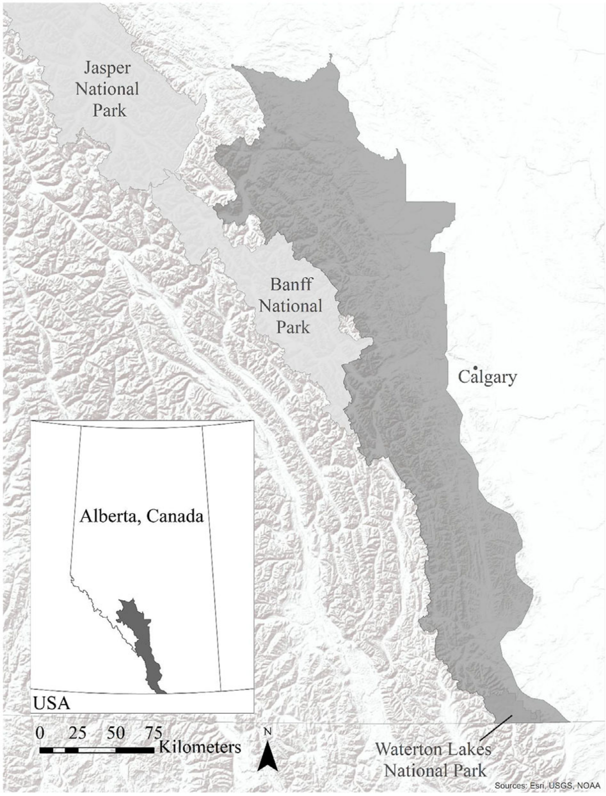

Figure 1. Area surveyed for wolf packs in southwestern Alberta, Canada, 2012–2014. Study area shaded in gray.

abruptly transition through aspen (*Populus tremuloides*) stands to fescue (*Festuca* spp.)-dominated grassland and agricultural land in the east (Natural Regions Committee 2006, Desserud et al. 2010). In addition to gray wolves, black bears (*Ursus americanus*), cougars (*Puma concolor*), coyotes (*C. latrans*), and grizzly bears (*U. arctos*) occurred throughout the study area and were sympatric with native ungulate species including bighorn sheep (*Ovis canadensis*), elk (*Cervus canadensis*), moose (*Alces alces*), mule deer (*Odocoileus hemionus*), and white-tailed deer (*O. virginianus*; Natural Regions Committee 2006, Morehouse and Boyce 2016). The study area was predominantly public federal Crown land under the jurisdiction of the Alberta provincial government but included Waterton Lakes National Park. Oil and gas extraction, timber harvest, outdoor recreation, and livestock and crop production occurred throughout the study area, except for within Waterton Lakes National Park (Natural Regions Committee 2006).

Wolves in Alberta, Canada have been managed with public harvest for decades (Gunson 1992, Boitani 2003). Residents could hunt wolves without license year-round on private and leased lands, on public land 1 September–15 June (varied regionally), and trap with license 1 October–31 March (Alberta Government 2014*a*, *b*). Some counties in our study area also offered bounties for wolves (Cardston County Council 2012). Annual wolf harvest was concentrated primarily in November–March (Government of Alberta-Alberta Environment and Parks [AEP], unpublished data). In southwestern Alberta, harvest mortality was consistently high for wolves, although the exact harvest rate was unknown because not all public harvest was reported. Harvest mortality in this region was likely similar to that in adjacent west-central Alberta, where the annual harvest rate for wolves was reported to be approximately 35% of the regional wolf population (Robichaud and Boyce 2010, Webb et al. 2011). Given that population growth appears to decline once harvest mortality exceeds approximately 29% of a wolf population (Adams et al. 2008), we considered the harvest rate in southwestern Alberta to be relatively high.

METHODS

Rendezvous Site Surveys and Genetic Analyses

We surveyed for wolves in southwestern Alberta in 2012–2014. We collected DNA from wolves in collaboration with Government of Alberta-Alberta Environment and Parks (AEP) following methods described by Ausband et al. (2010) and Stenglein et al. (2011). We followed University of Montana animal use protocols (001-15MMMCWRU-011315 and 008-12MMMWCRU-021412) during surveys. We used a predictive habitat model to identify potential wolf rendezvous sites (i.e., pup-rearing sites used in summer; Ausband et al. 2010, Ausband and Mitchell 2011) and conducted noninvasive genetic surveys between mid-June and late-August of each year (Ausband et al. 2010, Ausband and Bassing 2015). We recorded the presence and geographic location of wolf sign and collected a genetic sample from scat when detected (Ausband et al. 2010; Stenglein et al. 2010*b*, 2011). We classified canid scats as adult wolf if $\geq$2.5 cm in diameter and canid scats in active rendezvous sites as wolf pup if $<$2.5 cm in diameter (Weaver and Fritts 1979). We collected a small sample (pencil eraser sized) from the side of each scat using sterilized forceps and stored it in DMSO/EDTA/Tris/salt solution buffer (Frantzen et al. 1998, Stenglein et al. 2010*a*). Because of budgetary constraints, we surveyed for wolves across the southern third of our study area in 2012 and the southern half of our study area in 2013 and 2014 (Ausband and Bassing 2015).

We analyzed fecal samples at the Laboratory for Ecological, Evolutionary and Conservation Genetics at the University of Idaho, Moscow, USA, to identify individuals sampled each year. We followed DNA extraction and analysis protocols described by Stenglein et al. (2010*b*, 2011) and Stansbury et al. (2014). We used a mitochondrial DNA species-identification test to screen and remove non-target species and low-quality samples (De Barba et al. 2014, Stansbury et al. 2014). We genotyped the remaining samples using 9–10 nuclear DNA microsatellite loci. We used GENALEX (Peakall and Smouse 2006, 2012) to sort matching and unique genotypes and used RELIOTYPE (Miller et al. 2002) to test the accuracy of single-capture genotypes. We required a minimum of 8 loci to confirm a match and estimated the probability of identity (PID) genotypes for siblings ranged 3.54×10^{-4} to 1.18×10^{-3} (Waits et al. 2001, Stansbury et al. 2014). We genotyped samples matching at all but 1 loci with an additional 8–9 microsatellite loci to verify matches or mismatches (Stenglein et al. 2011, Stansbury et al. 2014). We allowed a 1 locus mismatch when it was due to allelic dropout (Adams and Waits 2007). We used STRUCTURE (Pritchard et al. 2000) to estimate percent coyote, domestic dog, and gray wolf ancestry of each genotype to test for and remove samples with highly probable coyote or dog ancestry (Stansbury et al. 2014).

Hunter Surveys

We surveyed registered ungulate hunters for observations of live wolves made during the hunting season through an online hunter reporting form used by AEP at the end of each hunting season (Rich et al. 2013, Ausband et al. 2014, Ausband and Bassing 2015). Ungulate hunting seasons occurred from 1 September–20 January each year (Alberta Government 2014*a*) and hunters reported observations made within each week of the hunting season (Ausband and Bassing 2015). We surveyed hunters who hunted in the southern half of our study area after the 2012 season and the entire study area after the 2013 and 2014 seasons.

We excluded hunter observations when only single wolves were reported, only wolf sign (i.e., tracks or howling) was reported, inadequate location data were reported, or an observation was made outside the hunting season (Rich et al. 2013, Ausband et al. 2014). We truncated hunter survey data to include only observations of wolves made September–December to minimize violating the assumption of population closure (MacKenzie et al. 2002). We then estimated point locations for hunter observations of wolves based on the centroid of the Section, Township, Range, and Meridian reported for each sighting using Program R 3.2.5 (R Core Team 2016).

Table 1. Mean and standard error for covariates included in occupancy analysis of wolf packs in southwestern Alberta, Canada, 2012–2014, and predicted relationships between covariates and the probability a wolf pack occupied a sample unit (ψ) and was detected (p) by either noninvasive genetic or hunter surveys.

	Annual covariate summaries							
	2012		2013		2014		Predicted relationship	
Model covariate	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	ψ	p
Forest cover (%)	0.45	0.23	0.45	0.23	0.45	0.23	+	
Mean ruggedness (TRI[a])	4.39	2.90	4.39	2.90	4.39	2.90	−	
Wolves harvested[b]	2.23	2.65	2.35	2.50	0.47[c]	0.64	−/+	−
Wolves harvested previous year[b]	2.12	2.08	2.23	2.65	2.35	2.50	−	−
Reported cattle density (number of cattle/km^2)[d]	18.93	31.41	20.12	32.00	16.61	24.40	−/+	
Rendezvous sites surveyed[e]	8.40	20.40	6.02	10.76	6.40	10.72		+
Hunter effort (hunter days/km^2)[f]	0.54	0.80	0.94	0.68	0.96	0.64		+
Proportion of sample unit in study area	0.60	0.32	0.60	0.32	0.60	0.32		+

[a] TRI = terrain ruggedness index

[b] Reported number of wolves harvested per sample unit. Area-weighted values (number of wolves harvested/km^2) were categorized as low (≤0.001), medium (≤0.003), or high (0.015) harvest intensity.

[c] Reported harvest from 2014 was an incomplete dataset that underrepresents total harvest.

[d] Reported cattle density was categorized as low (≤3.22), medium (≤25.57), or high (≤129.81) density (number of cattle/km^2).

[e] Number of predicted rendezvous sites surveyed for noninvasive genetic observations of wolves.

[f] Number of reported days spent hunting by ungulate hunters, area-weighted by size of sample unit.

Detection Histories and Covariates

We used observation data from both survey methods to generate detection histories of wolf packs in southwestern Alberta following methods described by Rich et al. (2013) and Ausband et al. (2014). We arbitrarily superimposed a grid of 1,000-km^2 cells across the study area; each cell represented a sample unit. The cell size was based on the estimated average territory size of wolf packs (Rich et al. 2013, Ausband et al. 2014) in southwestern Alberta based on limited global positioning system (GPS) collar location data (A. T. Morehouse, University of Alberta and AEP, unpublished data) and published estimates from wolf packs within the southwest and west central regions of Alberta (Hebblewhite 2006, Webb 2009, N. F. Webb, [AEP], personal communication). We plotted observations from both survey methods across the gridded study area using the rgdal (Bivand et al. 2017) and raster (Hijmans 2017) packages in Program R 3.2.5 (R Core Team 2016) to generate detection histories for each year (i.e., 3 primary sampling periods, 1 Jun–31 Dec). Each annual detection history consisted of 9 sampling occasions; 1 based on unique genotypes observed through rendezvous site surveys (Ausband et al. 2014), and 8 from hunter surveys where we consolidated weekly observations of wolves into 2-week sampling periods. For the genetic sampling occasion, we considered a pack detected if individual genotypes indicated the presence of ≥2 adult wolves or ≥1 wolf pups (i.e., indicating a reproductive pack was present; Ausband et al. 2014). For each hunter survey sampling occasion, we considered a pack detected if ≥2 hunters observed ≥2 live wolves (Rich et al. 2013). If a sample unit was not surveyed during a given sampling occasion, we recorded NA in its detection history. To account for potential false-positive detections of wolf packs in our data (Royle and Link 2006, Miller et al. 2011), we allowed for multiple detection states (i.e., uncertain and certain) in the hunter survey data (Miller et al. 2011, 2013; Ausband et al. 2014). We then relaxed this requirement because analyses indicated little evidence of false-positive detections in our dataset. For both survey methods, we assumed detecting a pack in 1 sample unit was independent of detections in other sample units, the probability of detecting wolves was not correlated between survey methods, and the population was closed to changes in pack occupancy during each primary sampling period (i.e., no colonization or local extinction of packs from Jun–Dec each year; MacKenzie et al. 2002, 2003, 2006).

We assessed the relationship of 6 environmental and management covariates and 2 survey effort covariates on wolf pack occupancy and detection (Table 1). We estimated and categorized harvest intensity of wolves (i.e., low [≤0.001], medium [≤0.003], or high [0.015]) based on the area-weighted reported number of wolves trapped in Registered Fur Management Areas (RFMA) and shot in Wildlife Management Units each year (wolves harvested/km^2; 2011–2014). We tested for immediate and 1-year lag effects (Robichaud and Boyce 2010) of harvest intensity on occupancy and detection probabilities of wolves. We estimated and categorized area-weighted density of reported cattle (i.e., low [$\leq$3.22], medium [$\leq$25.57], or high [$\leq$129.81] density [number of cattle/km^2]) using a combination of reported stocking rates for non-overlapping grazing allotments and leases on public (AEP) and private lands (Agriculture and Agri-Food Canada 2011) to test the relationship between wolf occupancy and density of a potential prey item. We calculated percent forest cover from the ABMI Wall-to-wall Land Cover Map (2010) based on 30-m^2 spatial-resolution Landsat satellite imagery (Alberta Biodiversity Monitoring Institute 2012) in each sample unit. We derived mean elevation, slope, and ruggedness (terrain ruggedness index [TRI]) for each sample unit from 25-m^2 resolution digital elevation models (DEM; AEP). We also included the proportion of sample unit within the study area (i.e., the area surveyed) as a covariate to test whether partial cells on the edge of the study area influenced the detection of wolf packs in southwestern Alberta (Rich et al. 2013). We evaluated the relationship between survey effort and detection probability by summing the number of predicted rendezvous sites surveyed and estimating the area-weighted number of hunter days in each Wildlife Management Unit (hunter days/km^2) per year for each sample unit as measures of rendezvous site survey and hunter effort, respectively (Rich et al. 2013, Ausband et al. 2014). We centered and scaled all covariates based on their individual means and standard deviations per year. Finally, we tested for collinearity among the covariates and excluded elevation and slope because they were highly correlated ($|r| \geq 0.6$; Zuur et al. 2010); we retained ruggedness because it combines information on elevation and slope.

Occupancy Models

We used occupancy models to estimate the abundance and distribution of wolf packs in southwestern Alberta and evaluate the frequency with which pack occurrence changed. Occupancy models use detection and non-detection data to estimate the probability landscape patches (i.e., sample units) are occupied by a species of interest given imperfect detection of that species (MacKenzie et al. 2002). Previous occupancy-based studies reported close agreement between independent model and radio-telemetry-based estimates of occupancy, abundance, and distribution of wolves, demonstrating the ability of occupancy modeling frameworks to monitor wolves across broad-spatial scales (Rich et al. 2013, Ausband et al. 2014). We estimated and compared the effects of harvest and environmental factors on the probability of occupancy to evaluate the relative influence of harvest on abundance and distribution of packs. As an independent test of whether occupancy models could adequately measure the frequency of turnover of packs in a population managed with public harvest, we then compared site-specific estimates of occupancy to individual wolf genotypes derived from the genetic data. This allowed us to compare predicted changes in occupancy to the dynamics of genetically marked wolf packs and evaluate the efficacy of using occupancy models to monitor the frequency of turnover of packs in a harvested population of wolves.

We fit dynamic (multiple-season) and single-season occupancy models using a Bayesian framework (Royle and Kéry 2007, Kéry and Schaub 2012) in JAGS (Plummer 2013) and Program R 3.2.5 (R Core Team 2016) with the R2jags package (Su and Yajima 2015) to test for changes in occupancy of wolf packs in southwestern Alberta. Only dynamic models could estimate transition probabilities between years (MacKenzie et al. 2003). We allowed both parameterizations of the model to account for false-positive detections in the data (Miller et al. 2011); based on initial model results, we refit the models assuming no false-positive detections in the data. We then tested the effects of environmental, management, and survey effort covariates on abundance and distribution of packs using the best performing model type (i.e., dynamic vs. single-season model). We first tested covariates on detection probability, allowing detection probability to vary by survey method, and then used the best-supported model for detection probability to test hypothesized effects of covariates on occupancy. We retained only models that successfully converged to compute the Watanabe-Akaike Information Criterion (or Widely Applicable Information Criteria; WAIC) for model comparison and selection (Watanabe 2010, Gelman et al. 2014, Hooten and Hobbs 2015) using the loo package (Vehtari et al. 2017). We considered models within 10 ΔWAIC and considered covariates in each model supported if the 95% credible interval (CRI) posterior distributions did not include zero (Kéry 2010). We ran 3 independent chains of 300,000 Markov chain Monte Carlo (MCMC) iterations, discarding the first 150,000 iterations, with a thinning rate of 4 for all models.

Estimating Mean Pack Size and Turnover of Packs

We estimated number of packs and minimum abundance of wolves for each year based on area occupied and the mean territory and pack size in southwestern Alberta (Bradley et al. 2014). We assumed mean territory size was 1,000 km^2, minimal overlap between territories, and territory and pack size did not change per year (Rich et al. 2013, Ausband et al. 2014). We estimated mean pack size with a linear mixed-effects model and a random effect of pack across years ($n = 14$ pack-years) using the lme4 package (Bates et al. 2015) in Program R (R Core Team 2016) based on the number of unique individuals genetically assigned to packs in southwestern Alberta each year. Because we genetically sampled packs in summer, mean pack size was based on when abundance was highest in the annual cycle of the population.

Following methods described by Stansbury et al. (2016), we assigned an individual to a putative pack if it was sampled at $\geq$1 common locations with other wolves and STRUCTURE (Pritchard et al. 2000) analyses estimated it shared common ancestry ($q \geq 0.7$) with wolves it was sampled with, or ML-RELATE (Kalinowski et al. 2006) analyses estimated it was related to $\geq$50% of the wolves it was sampled with at the parent-offspring or full-sibling ($r \geq 0.5$) level. If an individual did not meet the genetic requirements but was sampled at $\geq$1 common locations with other wolves it was also assigned to the pack. We compared putative pack assignments to pack pedigree analyses (Ausband 2015) to evaluate pack membership for each pack in each year and

Table 2. Results from surveys of wolf rendezvous sites and hunters for observations of wolf packs in southwestern Alberta, Canada. We report the number of predicted and active wolf rendezvous sites surveyed, unique genotypes identified from genetic samples, online responses from ungulate hunters, and observations of ≥ 2 live wolves made by hunters, 2012–2014.

Year	Number of sites surveyed	Number of active sites detected	Number of samples collected	Number of unique genotypes detected	Number of hunter responses[a]	Number of hunter observations ≥ 2 wolves
2012	420	3	439	45	2,227	189
2013	301	2	441	37	2,844	372
2014	321	10	829	76	3,256	408

[a] Included hunters that responded no to question, "did you hunt in the study area?"

determined if whole pack turnover occurred (i.e., entirely new individuals assigned to a pack each year). We only considered packs in years when we detected the active rendezvous site (i.e., did not include partially sampled packs). We did not include detected lone wolves in estimating mean pack size or minimum abundance.

RESULTS

Rendezvous Site and Hunter Surveys

We surveyed 1,042 predicted rendezvous sites in southwestern Alberta from 2012 to 2014 (annual $\bar{x} = 347 \pm 64$ [SD]). We located 15 active rendezvous sites and collected 1,709 genetic samples (Table 2). The majority (85%) of the genetic samples were collected in active rendezvous sites. We identified 129 unique genotypes, 20 of which we genetically recaptured ≥ 2 times across years. We identified 53 ± 21 unique wolves/year on average (Table 2).

We received 8,327 responses to our hunter surveys, 2012–2014 ($\bar{x} = 2{,}776 \pm 518$ hunters/year; Table 2). Of those responses, 762 hunters reported seeing ≥ 2 live wolves during the ungulate hunting season ($\bar{x} = 254 \pm 97$ hunters/year). Forty-nine hunter observations of ≥ 2 live wolves did not provide adequate data for analyses and were excluded. Between 10% and 15% of the reported observations of wolves were made on private land.

Occupancy Models

Precision of model estimates and convergence success indicated the single-season models best described occupancy of wolf packs in southwestern Alberta (Table 3). Dynamic model estimates were more variable than single-season

Table 3. Model type, parameters, annual estimates, and 95% Bayesian credible intervals (CRI) used to test changes in abundance and distribution of wolf packs in southwestern Alberta, Canada, 2012–2014. We estimated the probabilities a sample unit was occupied, became colonization, and remained occupied (i.e, survival) by a wolf pack over time. We tested the probability a wolf pack was detected when not present (FP = false-positive detection) by estimating the probabilities of detecting (p_{11}), falsely detecting (p_{10}), and detecting with certainty (b) a wolf pack in each sample unit for single-season and dynamic occupancy models. These models did not include covariates.

			Estimated parameter values					
			2012		2013		2014	
Model	FP[a]	Parameter[b]	$\bar{x}$	95% CRI	$\bar{x}$	95% CRI	$\bar{x}$	95% CRI
Single	No							
		Occupancy	0.68	0.46–0.89	0.70	0.54–0.84	0.71	0.55–0.86
		Detection, genetic	0.59	0.29–0.86	0.49	0.25–0.74	0.55	0.31–0.78
		Detection, hunt	0.28	0.12–0.37	0.27	0.21–0.34	0.26	0.20–0.32
Single	Yes							
		Occupancy	0.67	0.45–0.90	0.68	0.52–0.83	0.70	0.54–0.85
		Detection (p_{11})	0.30	0.22–0.39	0.29	0.23–0.35	0.28	0.22–0.34
		Detection (p_{10})	0.01	0.00–0.01	0.00	0.00–0.03	0.00	0.00–0.01
		Detection (b)	0.57	0.42–0.72	0.56	0.45–0.66	0.62	0.51–0.72
Dynamic	No							
		Occupancy[c]	0.88	0.64–0.99	0.64	0.46–0.81	0.68	0.53–0.83
		Colonization	0.31	0.01–0.99	0.17	0.01–0.52		
		Survival	0.70	0.48–0.92	0.97	0.87–0.99		
		Detection, genetic	0.51	0.23–0.80	0.60	0.30–0.87	0.63	0.37–0.85
		Detection, hunt	0.11	0.06–0.16	0.16	0.11–0.21	0.15	0.11–0.20
Dynamic	Yes							
		Occupancy[c]	0.64	0.44–0.83	0.63	0.47–0.78	0.69	0.55–0.82
		Colonization	0.20	0.01–0.55	0.26	0.03–0.53		
		Survival	0.87	0.62–0.99	0.94	0.80–0.99		
		Detection (p_{11})	0.30	0.22–0.39	0.30	0.24–0.37	0.28	0.22–0.33
		Detection (p_{10})	0.00	0.00–0.01	0.02	0.00–0.06	0.00	0.00–0.01
		Detection (b)	0.57	0.42–0.72	0.58	0.47–0.69	0.62	0.51–0.72

[a] Indicates whether we accounted for potential false-positive (FP) detections in the data.

[b] We estimated detection probability separately for different survey methods when we assumed false-positive detections did not occur. Different survey methods included noninvasive genetic surveys for wolves (genetic), and hunter observations of live wolves made during the ungulate hunting season (hunt).

[c] We estimated probability of occupancy directly in year 1 and derived it from the probabilities of colonization and survival for years 2 and 3.

Table 4. Single-season occupancy models tested to estimate abundance and distribution of wolf packs in southwestern Alberta, Canada. We modeled occupancy (ψ) and detection probability (p) and present Watanabe-Akaike Information Criterion (WAIC), standard error of WAIC value, and change (Δ) in WAIC. We evaluated covariate effects on detection probability and then used the most-supported parameterization of detection probability to evaluate covariate effects on occupancy probability. We considered models within 10 ΔWAIC values of the top model for inference.

Parameter of interest	Model[a]		WAIC	SE	ΔWAIC
Occupancy	ψ (forest)	p (harvest)	232.8	1,050.7	0.0
Occupancy	ψ (forest+harvest)	p (harvest)	449.4	993.2	216.6
Occupancy	ψ (lag-harvest)	p (harvest)	921.5	1,336.8	688.7
Occupancy	ψ (harvest)	p (harvest)	1,307.1	1,188.4	1,074.3
Occupancy	ψ (ruggedness)	p (harvest)	1,313.8	1,031.0	1,081.0
Occupancy	ψ (livestock)	p (harvest)	2,301.7	1,733.4	2,068.9
Occupancy	ψ (harvest+livestock)	p (harvest)	3,310.6	1,377.1	3,077.8
Detection	ψ (.)	p (harvest)	442.9	1,470.7	0.0
Detection[b]	ψ (.)	p (hunter effort)	447.3	1,477.6	4.4
Detection	ψ (.)	p (.)	520.9	1,458.5	78.0
Detection	ψ (.)	p (lag-harvest)	588.3	1,501.9	145.4
Detection[b]	ψ (.)	p (rendezvous effort+hunter effort)	619.6	1,502.3	176.7
Detection[b]	ψ (.)	p (rendezvous effort)	755.4	1,527.3	312.5

[a] Forest = percent forest cover; harvest = density of reported number of wolves harvested in current year (wolves/km^2), categorized as low, medium, or high density; lag-harvest = density of reported number of wolves harvested in previous year (wolves/km^2), categorized as low, medium, or high density; ruggedness = mean terrain ruggedness index (TRI); livestock = density of reported livestock per year (reported cattle/km^2), categorized as low, medium, or high density; hunter effort = hunter survey effort per sample unit (hunter days/km^2); rendezvous effort = number of rendezvous sites surveyed per sample unit. Models that included the covariate for the proportion of sample unit in the study area on detection probability failed to converge and were not included in the final results.

[b] Hunter effort and rendezvous effort were tested on respective detection parameters only.

estimates and precision of transition probabilities (e.g., colonization) were highly variable. Dynamic models indicated the mean probability an unoccupied sample unit would become occupied (i.e., colonization) was low, whereas the mean probability an occupied sample unit remained occupied the next year (i.e., patch survival) was high (Table 3).

Based on our top model (Table 4), the probability of detecting a wolf pack was generally consistent across years and increased with harvest intensity (Tables 5 and 6; Appendix A). We were more likely to detect a wolf pack through rendezvous site surveys than hunter surveys (Tables 3 and 5). The mean probability of falsely detecting a wolf pack in an unoccupied sample unit was zero (annual 95% CRIs ranged 0.00–0.03) when false-positives detections were accounted for in the single-season occupancy model (Table 3). The mean probability of falsely detecting a wolf pack in an unoccupied sample unit ranged 0.00–0.02 over the 3-year study period when false-positives detections were accounted for in the dynamic model (Table 3).

Our top model (Table 4) estimated the mean annual probability a sample unit was occupied by a wolf pack (i.e., occupancy) ranged 0.72–0.74 over the 3-year study period (Table 5). Probabilities of occupancy were generally highest in the north and through the center of the study area where the Rocky Mountains transition into foothills (Fig. 2). The estimated distribution of wolf packs was consistent over time, with little variation in the probability of occupancy for individual sample units, 2012–2014 (Table 5; Appendix A). On average, we estimated 23.41 (95% CRI = 20.32–26.34) wolf packs occupied approximately 23,406 km^2 (95% CRI = 20,322–26,338 km^2) each year in southwestern Alberta. Pack size averaged 6.76 (95% CI = 5.53–9.45) wolves across years. Based on the estimated number of packs and mean pack size, we estimated at minimum 160 (95% CRI = 123–186), 156 (95% CRI = 126–183), and 160 (95% CRI = 129–187) wolves occupied our study area in 2012, 2013, and 2014, respectively. The top model indicated the probability a sample unit was occupied by a wolf pack was positively related to forest cover (Tables 4 and 6). For example, we considered the probability a wolf pack occupied sample units where percent forest cover was 1 standard deviation above and below the standardized mean percent forest cover. We predicted wolf pack occupancy was 0.53 (95% CRI = 0.25–0.81) in sample units with lower percent forest cover (21.6%) and 0.92 (95% CRI = 0.73–0.99) in sample units with higher percent forest cover (68.0%; Fig. 3). The probability of detecting a wolf pack with either survey method was positively related to harvest intensity; we predicted wolf packs occurring in sample units where high harvest intensity occurred had 1.62 (95% CRI = 0.96–2.74) times greater odds of being detected compared to wolf packs in sample units with low intensity harvest (Tables 4 and 6). The 95% credible intervals for the medium and high harvest intensity coefficients included 0 in this final model (Table 6). Using the MCMC samples from the posterior distribution,

Table 5. Estimates for the mean probabilities and 95% Bayesian credible intervals (CRI) a sample unit was occupied by a wolf pack and a wolf pack was detected through rendezvous site surveys and hunter surveys in southwestern Alberta, Canada, 2012–2014.

	Estimated probability					
	Occupancy		Rendezvous detection		Hunter detection	
Year	$\bar{x}$	95% CRI	$\bar{x}$	95% CRI	$\bar{x}$	95% CRI
2012	0.74	0.56–0.89	0.61	0.31–0.86	0.30	0.21–0.40
2013	0.72	0.57–0.86	0.53	0.27–0.77	0.27	0.21–0.33
2014	0.74	0.59–0.89	0.56	0.32–0.78	0.25	0.19–0.31

Table 6. Parameter estimates and 95% Bayesian credible intervals (CRI) for occupancy analysis of wolf packs in southwestern Alberta, Canada, 2012–2014. The model included 2 survey methods: rendezvous site surveys for noninvasive wolf DNA and surveys for observations of wolves made by hunters during the ungulate hunting season. We estimated annual probabilities of occupancy and detection within a single model.

		Estimated coefficients					
		2012		2013		2014	
Parameter	**Variable**	$\bar{x}$	**95% CRI**	$\bar{x}$	**95% CRI**	$\bar{x}$	**95% CRI**
Occupancy[a]	Intercept	1.29	0.20–2.71	1.15	0.25–2.56	1.30	0.34–2.90
	Forest cover	1.19	0.46–2.30	1.19	0.46–2.30	1.19	0.46–2.30
Detection[b]							
Rendezvous surveys	Intercept	0.19	−1.14–1.60	−0.17	−1.29–0.95	0.16	−0.84–1.21
	Med harvest[c,d]	0.23	−0.21–0.67	0.23	−0.21–0.67	0.23	−0.21–0.67
	High harvest[c,d]	0.48	−0.05–1.01	0.48	−0.05–1.01	0.48	−0.05–1.01
Hunter surveys	Intercept	−1.15	−1.66 to −0.67	−1.32	−1.79 to −0.89	−1.21	−1.57 to −0.87
	Med harvest[c,d]	0.23	−0.21–0.67	0.23	−0.21–0.67	0.23	−0.21–0.67
	High harvest[c,d]	0.48	−0.05–1.01	0.48	−0.05–1.01	0.48	−0.05–1.01

[a] Probability a wolf pack occupied a sample unit.

[b] Probability a wolf pack was detected in an occupied sample unit.

[c] Effect of medium (med) and high harvest of wolves were compared to the effect of low harvest of wolves.

[d] The 95% credible intervals of the harvest coefficients included 0; based on 112,500 Markov chain Monte Carlo repetitions, the probability that the harvest effect was greater than 0 was 0.94 for high harvest and 0.80 for medium harvest.

we therefore computed the probability that the harvest effect was greater than zero and found the probability was 0.94 for high harvest intensity and 0.80 for medium harvest intensity.

We detected few instances of whole-pack turnover but frequent turnover of individuals within 3 different packs sampled consecutive years, based on genetic analyses. We detected whole-pack turnover in only 1 pack when we genetically sampled a group of wolves (*n* = 12) in 2012 but did not detected them genetically again; we detected an entirely new group of wolves (*n* = 9) in the same area the next year. We detected turnover of breeders in 6 pack-years; dispersers from other packs replaced 4 breeders, a subordinate pack member replaced 1 breeder, and 1 breeder's replacement was unknown but the pack successfully reproduced that year.

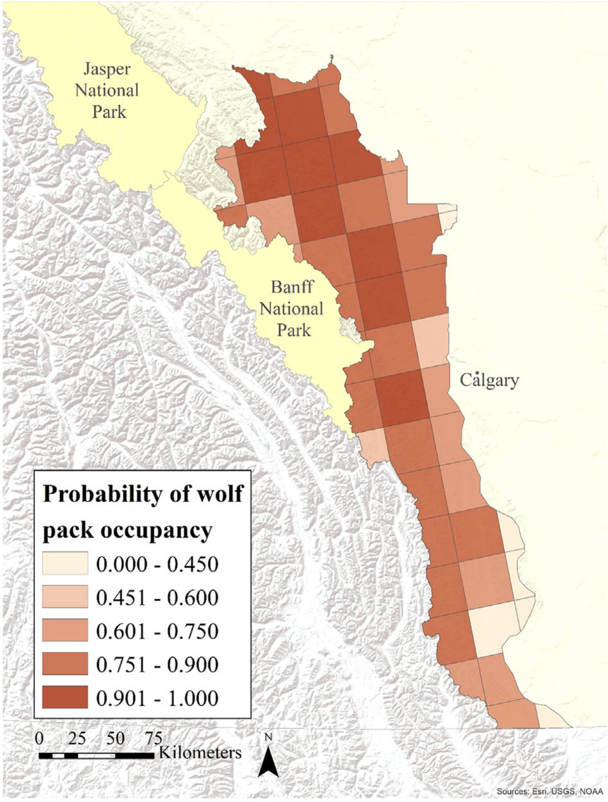

Figure 2. Distribution of the mean probability sample units were occupied by a wolf pack in southwestern Alberta, Canada, 2012–2014. Occupancy estimates were based on a model that included the effects of forest cover on the probability of occupancy and intensity of wolf harvest on detection probability. The probability a sample unit was occupied by a wolf pack was greater in areas with higher percent forest cover and the probability of detecting a wolf pack in a sample unit was greater where more intensive harvest of wolves occurred. Occupancy estimates were similar for an individual sample unit across years.

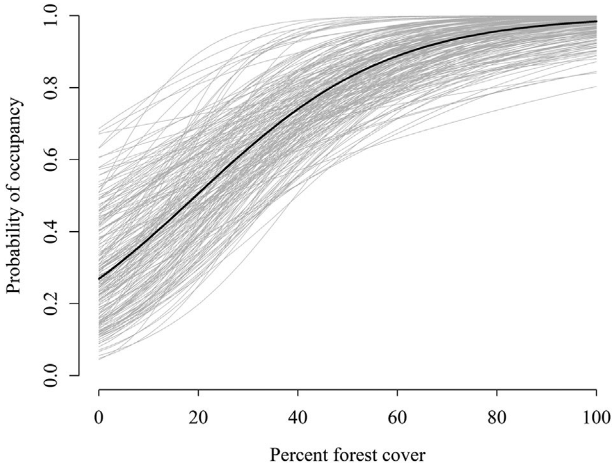

Figure 3. Predicted relationship between percent forest cover and probability of occupancy for wolf packs in southwestern Alberta, Canada, 2012–2014. Gray lines represent 200 predictions randomly drawn from the posterior distribution of the probability of occupancy.

DISCUSSION

Harvest of large carnivores is controversial, particularly for species with complex social structures (Packer et al. 2009, Creel and Rotella 2010, Gude et al. 2012, Ordiz et al. 2013). Understanding the demographic, genetic, and social effects of harvest on group living species is necessary to make informed management and conservation decisions (Haber 1996). Harvest of wolves, for example, may lead to frequent changes in abundance and distribution of packs, which may affect demography (Haber 1996, Jędrzejewska et al. 1996) or the ability to effectively manage their populations. We found occupancy of wolf packs was stable in a population managed with public harvest, but turnover of individuals within packs was common, suggesting habitat, and possibly social structure or dispersal, were more influential in determining the abundance and distribution of wolf packs than harvest in this system. Evaluating the relative effect of harvest on pack occurrence and frequency of turnover therefore allows managers to assess the efficacy of harvest and inform decisions for wolf management.

We found little evidence wolf pack occupancy changed frequently in our study area from 2012 to 2014; thus, we rejected our hypothesis that abundance and distribution of packs were highly dynamic in a heavily harvested population of wolves during this time period. Despite intensive harvest occurring during our study ($\bar{x} = 114.75 \pm 56.94$ harvested wolves reported/year within the study area), we found there was a low probability the occupancy state of an individual sample unit changed over a 3-year sampling period. In addition, most packs genetically sampled during consecutive years persisted even when some individuals were likely lost to harvest. Because turnover of packs occurred infrequently during our study, we could not reject our hypothesis that abundance and distribution of packs would remain generally stable in a harvested population of wolves over several years.

Contrary to expectations, our best-supported models did not include harvest on the probability of occupancy. Models that did include harvest suggested a weak negative relationship between harvest intensity and occupancy of wolf packs, but this relationship was uncertain (95% CRIs contained zero and models converged poorly). This suggests that public harvest had little influence on the abundance or distribution of wolf packs in southwestern Alberta during our study. Human density and anthropogenic disturbances (e.g., road or building density) have been negatively associated with habitat selection and use by wolves at fine spatiotemporal scales (i.e., within kms or hrs; Whittington et al. 2005, Hebblewhite and Merrill 2008, Llaneza et al. 2012), but our results suggest human activity, specifically public harvest, may not be strong enough to influence occurrence of wolf packs in southwestern Alberta over several years. In addition, most packs likely experienced some harvest mortality each year (Webb et al. 2011); if the harvest rate was not high enough to remove all pack members, packs likely persisted because surviving members could maintain their territories (Ballard et al. 1987). Alternatively, if harvest generally targeted dispersing wolves over residents (Peterson et al. 1984, Person and Russell 2008), harvest of wolves may have had relatively little effect on established packs.

Even under intensive harvest management, environmental factors had a stronger influence than harvest on the distribution and abundance of wolf packs in southwestern Alberta. Similar to Rich et al. (2013), we found forest cover was positively associated with the probability of occupancy. We hypothesize high forest cover provides security habitat for wolves inhabiting human-dominated landscapes (Llaneza et al. 2012). Alternatively, we hypothesize forest cover is associated with the distribution of wild prey (Llaneza et al. 2012, Kittle et al. 2015) in southwestern Alberta. Prey availability generally determines wolf distribution and densities (Fuller 1989, Boitani 2003, Fuller et al. 2003) and was strongly predictive of wolf occupancy in Idaho and Montana, USA (Rich et al. 2013, Ausband et al. 2014). We were unable to estimate prey density or distribution in southwestern Alberta, but research in the Rocky Mountains in the United States found elk selected for forests and shrublands over grasslands as snowpack decreased (Proffitt et al. 2011); wild ungulates may prefer forested habitats to grasslands and agricultural lands during summer and fall in southwestern Alberta. In addition, previous research documented wild prey densities were highest at lower elevations in the foothills of west-central Alberta (Webb 2009), which corresponded with the highest probabilities of occupancy in our study.

Once harvest reaches a certain intensity, logically it should have a strong negative effect on the occurrence of wolf packs. Thus, at some point beyond the harvest level we observed, we hypothesize the relative effect of harvest may become more important for determining the abundance and distribution of packs than our results suggest. This could be particularly true for colonizing populations and ones on the edge of their range that are at low densities or poorly connected to other populations (Fuller et al. 2003, Gehring et al. 2003, Brainerd et al. 2008).

Harvest appeared to have a stronger effect on turnover of individuals within packs (Webb et al. 2011) compared to turnover of entire packs. We genetically identified 129 unique wolves in the southern half of our study area but recaptured only 20 in >1 year and only 4 in all 3 years; hunters and trappers reported harvesting 71 wolves in the same area during our study. We observed frequent turnover of breeders in packs genetically sampled in consecutive years and packs appeared more receptive to adopting nonbreeding adults than in other portions of the Rocky Mountains (Bassing 2017). Although frequent breeder loss may lead to pack dissolution (Gehring et al. 2003, Brainerd et al. 2008), we found little evidence of this in southwestern Alberta, and we hypothesize rapid replacement of breeding adults may explain how packs appeared to persist despite frequent turnover of individuals (Gehring et al. 2003). Most breeding adults were replaced by local dispersers or by an individual within the pack (Ausband 2015, Bassing 2017). In addition, most harvest coincided with the breeding season and the pulse in dispersal typical for wolves in the Rocky Mountains (i.e., late winter–early spring; Mech and Boitani 2003, Webb et al. 2011, Jimenez et al. 2017). Replacement of breeding adults can occur rapidly under these conditions (Rothman and Mech 1979, Fritts and Mech 1981, Stahler et al. 2002, Mech and Boitani 2003); thus, breeder turnover may have occurred quickly, preventing some destabilizing effects of breeder loss on the pack (Ballard et al. 1987). Contrary to the hypothesis that harvested populations of wolves are often sustained by immigrants dispersing into the population (Ballard et al. 1987, Haight et al. 1998, Hayes and Harestad 2000, Fuller et al. 2003), most individuals adopted into the packs that we genetically sampled dispersed from neighboring packs (i.e., packs within the study area or ones on the periphery; Bassing 2017). This suggests pack stability and occupancy were generally maintained from within the population, supporting the hypotheses that reduced emigration can offset harvest mortality (Adams et al. 2008).

We found a weak positive relationship between detection probability and harvest of wolves. Contrary to concerns that harvest may reduce density (Gasaway et al. 1983, Fuller 1989) or influence behaviors (Gunson 1992, Webb et al. 2009) of wolves to the point that detecting wolf packs was more difficult than in unharvested populations, we found detection probability was highest in areas where high intensity harvest occurred. We hypothesize this is because harvest intensity may be positively associated with density of wolves. Abundance can strongly affect detection probability (Royle and Nichols 2003, MacKenzie et al. 2006) and surveys may be more likely to detect wolf packs in sample units where wolf densities, and associated harvest intensity, are highest. Alternatively, we hypothesize harvest intensity may reflect areas of higher quality habitat that attract wolves regardless of mortality risk (i.e., attractive sinks; Delibes et al. 2001, Novaro et al. 2005). Even if harvest removes a high proportion of wolves in these areas, dispersers may quickly backfill and maintain local wolf densities enough that the probably of detecting wolves with surveys is still high.

We made several assumptions in our study that, if violated, could have affected our ability to detect turnover or evaluate the influence of harvest on the occurrence of packs. We assumed we would be able to detect turnover of packs using occupancy models. Although harvest occurred year-round, winter trapping is the primary source of harvest-related mortality for wolves in Alberta (Robichaud and Boyce 2010, Webb et al. 2011). If trapping led to the dissolution of packs, it likely occurred between our primary sampling periods. If a wolf pack recolonized a vacant territory faster than the rate at which sampling occurred (i.e., rescue effect; Brown and Kodric-Brown 1977), sample units would appear continuously occupied over time and we would have failed to detect turnover of packs. We detected 1 instance of whole-pack turnover with genetic analyses that was not detected by the occupancy models; the time within or between primary periods may be biologically irrelevant in an intensively harvested population of wolves and unsuitable for testing our hypotheses about turnover of packs. Genetic analyses and occupancy model estimates were generally consistent; thus, the data suggest occupancy was generally stable during our study. We also assumed the number of harvested wolves reported by hunters and trappers accurately reflected harvest in southwestern Alberta. Because not all public harvest of wolves was reported (Gunson 1992, Robichaud and Boyce 2010, Webb et al. 2011) and was reported by Wildlife Management Units (not precise harvest locations; AEP), our estimated intensity of wolf harvest may have biased the estimated relationships between harvest, occupancy, and detection of wolves. Finally, we were unable to acquire harvest data for part of 2014; the reported harvest is an underestimate of the actual harvest for that year. The lack of data from 2014 may have reduced our ability to detect an effect of harvest intensity on the probability of occupancy. Previous research and documentation of wolf distribution and harvest in this region (Robichaud and Boyce 2010, Webb et al. 2011) suggest the estimated relationships are reasonable, however.

MANAGEMENT IMPLICATIONS

Where intensive wolf harvest takes place, habitat features appear more influential than harvest in determining where wolf packs occur. Harvest does not reduce the ability to detect wolf packs with noninvasive survey methods and occupancy model-based annual monitoring is reliable for estimating the abundance and distribution of wolf packs at broad spatial scales, even in harvested populations of wolves but may not be reliable for estimating the frequency of turnover of packs if changes in occupancy occur faster than an annual time step. If managers are interested in monitoring turnover of packs in heavily harvested populations of wolves, we recommend reducing the duration of time between primary sampling periods to increase the likelihood of observing changes in occupancy probabilities, if they occur. In addition, if managers desire to explicitly estimate transition probabilities between primary sampling periods and evaluate covariates associated with temporal changes in occupancy, dynamic models are required instead of single-season models. Although occupancy was stable during our study, genetic sampling indicated dispersal was important for population persistence. Thus, for populations managed with heavy harvest, it would be beneficial to use genetic or other tools that also provide information on recruitment and movement in the population.

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APPENDIX A. PROBABILITY OF WOLF PACK OCCUPANCY BY SAMPLE UNIT.

Table A1. Estimated annual probability of occupancy and 95% Bayesian credible intervals (CRI) of wolf packs for each sample unit in southwestern Alberta, Canada, 2012–2014. Estimates are based on the top single-season occupancy model, which included percent forest cover on occupancy and intensity of wolf harvest on annual detection probability.

	Probability of occupancy					
	2012		2013		2014	
Unit	$\bar{x}$	95% CRI	$\bar{x}$	95% CRI	$\bar{x}$	95% CRI
1	0.93	0.77–1.00	0.92	0.78–1.00	0.93	0.79–1.00
2	0.89	0.71–0.99	0.88	0.72–0.99	0.89	0.73–0.99
3	0.88	0.70–0.99	0.87	0.71–0.99	0.88	0.72–0.99
4	0.69	0.46–0.89	0.66	0.47–0.87	0.69	0.49–0.90
5	0.94	0.80–1.00	0.94	0.80–1.00	0.94	0.82–1.00
6	0.91	0.74–0.99	0.90	0.75–0.99	0.91	0.76–1.00
7	0.88	0.69–0.99	0.87	0.70–0.98	0.88	0.72–0.99
8	0.70	0.47–0.90	0.67	0.48–0.87	0.70	0.50–0.91
9	0.92	0.76–1.00	0.92	0.77–1.00	0.93	0.78–1.00
10	0.94	0.78–1.00	0.93	0.79–1.00	0.94	0.80–1.00
11	0.93	0.78–1.00	0.92	0.78–1.00	0.93	0.79–1.00
12	0.72	0.50–0.91	0.70	0.51–0.90	0.72	0.53–0.92
13	0.76	0.54–0.93	0.74	0.55–0.92	0.76	0.57–0.94
14	0.72	0.50–0.91	0.70	0.51–0.90	0.72	0.53–0.92
15	0.92	0.75–0.99	0.91	0.76–0.99	0.92	0.77–1.00
16	0.89	0.71–0.99	0.88	0.72–0.99	0.89	0.73–0.99
17	0.68	0.44–0.88	0.65	0.45–0.86	0.68	0.48–0.89
18	0.37	0.11–0.69	0.34	0.12–0.62	0.37	0.14–0.67
19	0.68	0.44–0.88	0.65	0.45–0.86	0.68	0.48–0.89
20	0.80	0.59–0.96	0.78	0.60–0.95	0.80	0.62–0.96
21	0.91	0.74–0.99	0.90	0.74–0.99	0.91	0.76–0.99
22	0.81	0.60–0.96	0.79	0.61–0.95	0.81	0.63–0.97
23	0.44	0.17–0.73	0.40	0.18–0.66	0.44	0.20–0.71
24	0.80	0.59–0.96	0.78	0.60–0.95	0.80	0.62–0.96
25	0.93	0.78–1.00	0.93	0.78–1.00	0.93	0.80–1.00
26	0.80	0.58–0.95	0.78	0.60–0.95	0.80	0.62–0.96
27	0.78	0.57–0.95	0.76	0.58–0.94	0.78	0.60–0.96
28	0.83	0.62–0.97	0.81	0.64–0.96	0.83	0.65–0.97
29	0.54	0.28–0.80	0.50	0.29–0.74	0.54	0.31–0.79
30	0.82	0.61–0.96	0.80	0.62–0.96	0.82	0.64–0.97
31	0.92	0.75–0.99	0.91	0.76–0.99	0.92	0.77–1.00
32	0.63	0.38–0.85	0.60	0.39–0.81	0.63	0.42–0.89
33	0.58	0.33–0.82	0.55	0.34–0.78	0.58	0.36–0.83
34	0.89	0.70–0.99	0.87	0.71–0.99	0.86	0.73–0.99
35	0.75	0.53–0.93	0.73	0.54–0.92	0.75	0.56–0.94
36	0.83	0.62–0.97	0.81	0.64–0.96	0.83	0.65–0.97
37	0.60	0.36–0.84	0.57	0.37–0.80	0.60	0.39–0.84
38	0.80	0.59–0.96	0.78	0.60–0.95	0.80	0.62–0.96
39	0.87	0.68–0.98	0.86	0.69–0.98	0.87	0.71–0.99
40	0.36	0.10–0.68	0.32	0.10–0.60	0.35	0.12–0.65
41	0.79	0.58–0.95	0.77	0.59–0.94	0.79	0.61–0.96
42	0.72	0.50–0.91	0.70	0.51–0.90	0.72	0.53–0.92
43	0.35	0.09–0.67	0.31	0.10–0.60	0.34	0.11–0.64
44	0.77	0.56–0.94	0.75	0.57–0.93	0.77	0.59–0.95
45	0.42	0.15–0.72	0.38	0.16–0.65	0.41	0.17–0.70
46	0.33	0.08–0.66	0.30	0.08–0.58	0.32	0.10–0.63
47	0.69	0.46–0.89	0.66	0.47–0.87	0.69	0.49–0.90
48	0.70	0.47–0.90	0.67	0.48–0.87	0.70	0.50–0.91
49	0.63	0.38–0.85	0.60	0.39–0.81	0.63	0.42–0.86
50	0.42	0.15–0.72	0.38	0.16–0.65	0.41	0.17–0.70