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Monitoring Gray Wolf Populations Using Multiple Survey Methods

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ABSTRACT The behavioral patterns and large territories of large carnivores make them challenging to monitor. Occupancy modeling provides a framework for monitoring population dynamics and distribution of territorial carnivores. We combined data from hunter surveys, howling and sign surveys conducted at predicted wolf rendezvous sites, and locations of radiocollared wolves to model occupancy and estimate the number of gray wolf (*Canis lupus*) packs and individuals in Idaho during 2009 and 2010. We explicitly accounted for potential misidentification of occupied cells (i.e., false positives) using an extension of the multi-state occupancy framework. We found agreement between model predictions and distribution and estimates of number of wolf packs and individual wolves reported by Idaho Department of Fish and Game and Nez Perce Tribe from intensive radiotelemetry-based monitoring. Estimates of individual wolves from occupancy models that excluded data from radiocollared wolves were within an average of 12.0% (SD = 6.0) of existing statewide minimum counts. Models using only hunter survey data generally estimated the lowest abundance, whereas models using all data generally provided the highest estimates of abundance, although only marginally higher. Precision across approaches ranged from 14% to 28% of mean estimates and models that used all data streams generally provided the most precise estimates. We demonstrated that an occupancy model based on different survey methods can yield estimates of the number and distribution of wolf packs and individual wolf abundance with reasonable measures of precision. Assumptions of the approach including that average territory size is known, average pack size is known, and territories do not overlap, must be evaluated periodically using independent field data to ensure occupancy estimates remain reliable. Use of multiple survey methods helps to ensure that occupancy estimates are robust to weaknesses or changes in any 1 survey method. Occupancy modeling may be useful for standardizing estimates across large landscapes, even if survey methods differ across regions, allowing for inferences about broad-scale population dynamics of wolves.

KEY WORDS *Canis lupus*, gray wolf, hunter surveys, monitoring, northern Rocky Mountains, occupancy modeling, radiotelemetry, recovery, rendezvous sites.

Large carnivores are often the target of conservation efforts because they can have cascading effects on other species despite their relatively sparse distribution across landscapes (Gompper et al. 2006, O'Connell et al. 2006) and public interest in them is generally high. As a result, an increasing number of studies have focused on assessing carnivore abundance, relative abundance, or distribution and occupancy across large geographical areas (Patterson et al. 2004, Gompper et al. 2006, Long et al. 2007, Johnson et al. 2009). Collecting data to estimate the abundance and distribution

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of carnivores, however, is extremely challenging. Large carnivores generally occupy extensive areas, often live in remote and rugged habitats at low densities, and are elusive (Schonewald-Cox et al. 1991, Gros et al. 1996, Long and Zielinski 2008). Environmental, budgetary, and logistical constraints often limit surveys to small spatial scales. Aerial observations of live animals or their tracks, for example, may be feasible in open habitats but impractical in areas where dense canopy cover results in poor visibility (Ballard et al. 1992, Hayes and Harestad 2000). Camera trap surveys have successfully documented the presence of common and rare carnivores (Karanth and Nichols 1998, Johnson et al. 2009), but deploying cameras over large areas such as an entire state is expensive and logistically demanding (Swann et al. 2004). Acoustic sampling can elicit responses in certain species, but this method also can be labor intensive, biased towards large groups, and affected by topography and weather (Grinnell and McComb 2001, Ausband et al. 2011).

Developing and implementing a single survey methodology that will work across large spatial extents with varying animal distribution, topography, vegetation, and weather conditions can be financially and logistically infeasible. Thus, estimating the abundance and distribution of wide-ranging carnivores accurately across large spatial scales may require multiple survey methods employed at different spatial and temporal scales, and then merging the results. Merging the results from multiple survey methods, however, can be challenging because each method has its own assumptions, the deployment of methods may not take place at the same time, and the probability of detecting a species will vary for each method. Failure to account for the detection probability associated with each survey method also can lead to erroneous estimates of species abundance and distribution (MacKenzie et al. 2006).

Occupancy modeling can provide a useful framework for estimating the abundance and distribution of a species using data from several survey techniques and incorporate their respective detection probabilities (MacKenzie et al. 2006). Each survey method does not need to be employed at each site, and probability of occupancy can be predicted for unsampled sites where information about habitat covariates used in the modeling is available. Occupancy modeling uses detection–non-detection data from repeated visits to sampled units to estimate species occupancy across sampled and unsampled patches. Sample units can be cells within a grid and when cell size is equal to territory size, the sum of the occupancy estimates across cells is roughly equal to the abundance of territorial individuals or groups (MacKenzie et al. 2006).

Methods accounting for species misidentification (i.e., false positive errors; Royle and Link 2006) are necessary when analyses include public survey data and other data sources where misidentification errors are likely to occur (Miller et al. 2012, Rich et al. 2013). Miller et al. (2011, 2013) presented an extension of the multi-state occupancy framework (Royle and Link 2006, Nichols et al. 2008) that allows for the integration of multiple data sources, where some of the observations may include false positive detections. This approach classifies detections based on the degree of certainty about the identification of the species. For example, indirect detections (e.g., tracks) may be classified as uncertain detections (i.e., containing potentially false positive detections), whereas direct observations of the species through aerial surveys may be classified as certain detections. Estimation of occupancy following the methods presented by Miller et al. (2011) can estimate both false negative and false positive errors among uncertain detections, which is an improvement over accounting only for false negative errors where detection is certain.

Our objective was to combine data from multiple survey techniques in an occupancy modeling framework to estimate the number of gray wolves during 2009 and 2010 in Idaho, USA. Gray wolves were reintroduced to Idaho in 1995 and 1996 (Bangs and Fritts 1996). Initially, when the size of the population of wolves was small, it was estimated annually with intensive capturing, radiocollaring, and observation using aerial surveys, which was funded almost entirely by the United States Fish and Wildlife Service (USFWS; USFWS et al. 2010). Since 1995, the wolf population in Idaho has grown to approximately 750 wolves (USFWS et al. 2012), making population estimates difficult to obtain based on a radiotelemetry approach. Wolves in Idaho were removed from the federal list of threatened and endangered species in May 2011 (USFWS 2011). Since then, the state of Idaho has managed wolves as a game species, and is federally mandated to monitor the wolf population, ensuring it continues to exceed federal (10 breeding pairs and 100 wolves; USFWS 2011) and state (15 breeding pairs and 150 wolves; Idaho Legislative Wolf Oversight Committee 2002) relisting thresholds. Monitoring the wolf population in Idaho, however, has become increasingly challenging as its range has expanded and federal funding has declined following delisting. Idaho therefore was faced with relying on limited resources and fewer radiocollared wolf packs to document continued recovery while managing their harvest.

In Montana, Rich et al. (2013) used an occupancy model based on big-game hunter surveys conducted by phone ($n = 50{,}000$–$80{,}000$) to predict the number and distribution of wolf packs. Idaho currently does not survey hunters as intensively as Montana. We therefore developed an occupancy model that made use of a variety of data (hunter surveys, rendezvous site surveys, and radiotelemetry) to estimate the number and distribution of wolf packs across the state of Idaho and extend this approach to estimate the total number of wolves in Idaho, in 2009 and 2010. Further, because widespread use of radiotelemetry is less likely in the future because of budgetary and personnel limitations, we also assessed how estimates from occupancy modeling would be affected if no radiotelemetry data were included in the model. Finally, to evaluate our estimates, we compared them to the number of packs and total number of individual wolves reported by Idaho Department of Fish and Game (IDFG) and the Nez Perce Tribe (NPT) for 2009 and 2010 (Mack et al. 2010, Holyan et al. 2011). We considered the numbers of packs and wolves reported by IDFG and NPT to be minimum counts (i.e., naive estimates; MacKenzie et al. 2006) because not all packs or wolves likely were detected. As a result, we expected our estimates to be greater than the minimum counts, but not substantially so because wolf monitoring in Idaho by IDFG and NPT was intensive in 2009 and 2010.

We expected that wolf occupancy would be positively influenced by prey abundance and forest cover, and negatively influenced by livestock density because of agency control of wolves in response to livestock depredation events. We further expected that increasing slope and elevation would negatively influence wolf occupancy because of the coursing predatory nature of wolves and their affinity for mild terrain roughness (Rich et al. 2013). Additionally, we expected detection of wolves would be positively related to hunter effort (i.e., days) during the fall big game season and the number of predicted rendezvous sites surveyed.

STUDY AREA

The state of Idaho (216,632 km^2) encompassed a wide variety of landscapes. Northern Idaho had a maritime climate and was dominated by western red cedar (*Thuja plicata*) and western hemlock (*Tsuga heterophylla*), whereas southern Idaho had a continental climate and was dominated by Douglas-fir (*Pseudotsuga menziesii*) and ponderosa pine (*Pinus ponderosa*; Mack et al. 2010). Elevations ranged from 457 m to over 3,650 m, annual precipitation ranged from <20 cm at low elevations to >250 cm at high elevations, and temperatures ranged from −34°C in winter to 38°C in summer (Western Regional Climate Center 2010). The majority of southern Idaho was private agricultural lands, central Idaho contained 3 contiguous wilderness areas and several highly productive prairies of mixed native and agricultural lands, and northern Idaho was predominantly public forests and private corporate timber holdings. The primary prey species for wolves in Idaho were largely elk (*Cervus elaphus*) and white-tailed deer (*Odocoileus virginianus*) with moose (*Alces alces*) and mule deer (*O. hemionus*) also likely present in the diet (USFWS 1994).

METHODS

We modeled occupancy of wolves based on a grid spanning the state of Idaho composed of 346 sample units (686-km^2 grid cells). We generated detection histories for each sample unit by combining 3 survey methods (i.e., 1 occasion, 1 Jun–30 Nov, for radiotelemetry; 1 occasion, 10 Jun and 18 Aug, for rendezvous site surveys; and 12 weekly occasions, 1 Sep–30 Nov, for hunter surveys). Grid cell size was equal in area to the mean territory size of wolf packs in Idaho that included ≥1 pack member fitted with a global positioning system (GPS) radio-collar. Territory size of collared wolves was estimated using a kernel-density estimator (smoothing parameter = 80% of reference bandwidths; $n = 27$, 686 km^2, SE = 89 km^2; D. Ausband, Montana Cooperative Wildlife Research Unit, unpublished data).

Survey Methods

Hunter surveys.—Big game hunters in Idaho are required to report the results of their hunts and IDFG maintains an annual statewide database of deer and elk hunter activities during hunting season (i.e., days afield, successful or not). We mailed surveys to approximately 12,000 randomly selected, licensed deer and elk hunters during spring 2010 and 2011. To sample evenly across the 75 Game Management Units (GMUs) that included potential wolf habitat, we identified hunters who had reported hunting for deer and elk in each GMU in September–November 2009 and 2010. For each year, we randomly selected 500 hunters from the largest GMU (6,400 km^2) and then allocated sample sizes proportionally based on GMU size. We mailed surveys to the selected hunters and sent a second survey to non-respondents to account for reporting bias. The mail surveys included the following questions: 1) In what GMU did you hunt for big game during the previous hunting season and for how many days in each month? 2) Did you observe any wolves (not wolf sign) while hunting? 3) If you observed wolves, please identify the week in which you saw wolves, the GMU, a description of the location, and the number of wolves observed.

Hunting seasons occurred from 1 September to 30 November in 2009 and 2010. We assigned each observation of ≥2 wolves provided by the hunters to 1 of 12, 1-week sampling occasions. We dropped observations of single wolves to restrict our inferences to established packs and to minimize false positives. We created point locations for each hunter observation based on the descriptions of where wolves were observed using National Geographic TOPO! software (NGHT, Inc., Evergreen, CO). We dropped hunter sightings from the database when the description was insufficient to identify a point location, when wolves were observed outside of hunting season, or when wolf sign, not live wolves, was observed. We imported point locations into ArcGIS 9.3.1 (ESRI, Redlands, CA) and used the point locations to populate the 686-km^2 grid cells. We assigned missing values to grid cells that were not surveyed and allowed detection for hunter surveys to vary by week and month. We assumed occupancy was constant during the survey period, the same pack of wolves was present in each grid cell during the hunting season, and that the probability a hunter detected wolves at 1 site was independent of the probability wolves were detected at all other sites (MacKenzie et al. 2002).

Rendezvous site surveys.—To predict rendezvous site locations, we characterized historical rendezvous sites based on habitat and landscape characteristics and then used a resource selection function to map similar sites within each GMU (Ausband et al. 2010). We then surveyed predicted rendezvous sites in GMUs 6, 28, 33, 34, and 35 between 10 June and 18 August 2009 and in GMUs 1 and 6 between 12 June and 20 July 2010 (Figs. 1 and 2). We surveyed the top 3 equal-area bins of highly suitable predicted rendezvous sites on public land (Ausband et al. 2010). We recorded the presence and abundance of wolf tracks, scat, hair, daybeds, kills, and when possible, we collected genetic samples (i.e., scat and hair). We analyzed genetic samples to verify species and determine the number of unique individuals at a site (Stenglein et al. 2010, 2011). We surveyed each individual

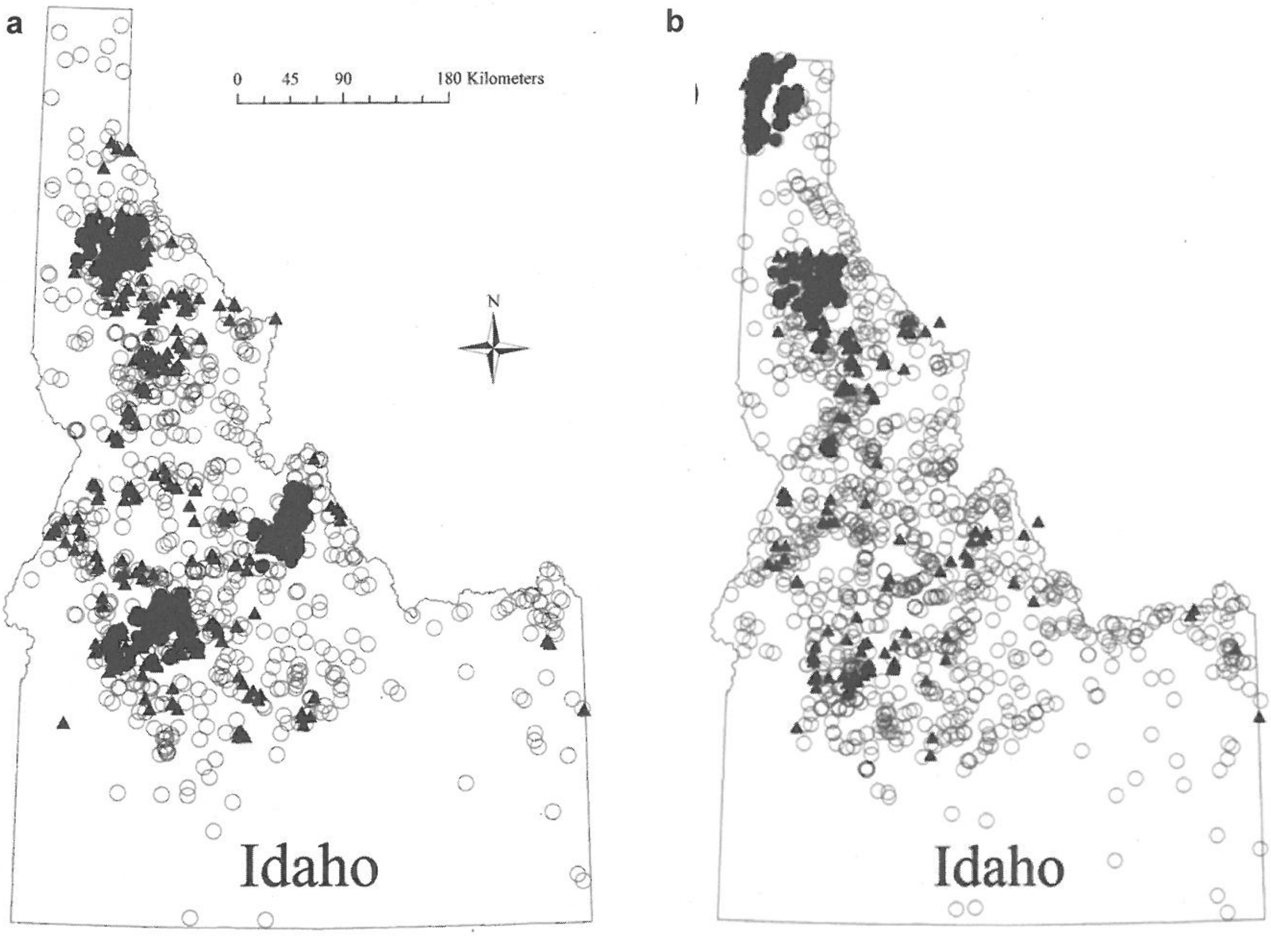

Figure 1. Distribution of gray wolf detections in Idaho in (a) 2009 and (b) 2010. Open circles = hunters observed ≥2 live wolves, dark circles = detections at predicted wolf pack rendezvous sites, and dark triangles = radiocollared wolf locations.

rendezvous site once and removed detections of single wolves because we were targeting packs. If we sampled >1 rendezvous site within a single 686 km^2-cell on the grid in the same year, we combined observations into a single sampling occasion based on whether we observed ≥2 wolves at ≥1 of the sites.

Radiotelemetry data.—We used locations of all very high frequency (VHF) radiocollared wolves located in Idaho between 1 June and 30 November 2009 and 2010 collected by IDFG and the NPT. We combined the location data into a single sampling occasion for each year and used only locations from wolves that were members of a pack. If a radiocollared wolf was located >1 time during our annual survey period, then we randomly selected a single location from that pack to use in our analysis to meet the occupancy assumption of independence (MacKenzie et al. 2002). We imported locations into ArcGIS, overlaid locations on the 686-km^2 grid, and determined which grid cells contained ≥1 location from a radiocollared wolf.

Model Covariates

We assessed 6 survey-specific covariates (Table 1). We used number of male deer (white-tailed and mule deer combined) and male elk harvested/km^2 by GMU as indices of deer and elk density because population estimates of deer and elk were not uniformly available across Idaho. Furthermore, harvest of antlered deer and elk has been used as an index of population size because they are generally correlated with deer and elk abundance (Wood et al. 1989, Hamlin and Ross 2002, Dusek et al. 2006). We calculated a GMU area-weighted mean harvest/km^2 for grid cells that overlapped GMU boundaries. We also used harvest statistics from IDFG (2012) to estimate hunter days for elk, divided it by the size (km^2) of each GMU, and used this as a measure of GMU area-weighted mean hunter effort in each grid cell. We used United States Department of Livestock statistics to obtain coarse estimates of annual domestic cattle and sheep densities by county (U.S. Department of Agriculture 2013) to calculate the county area-weighted mean density of cattle and sheep for each grid cell. We excluded wilderness areas from counties to ensure estimates of cattle and sheep density only encompassed areas where grazing was generally present. Lastly, for rendezvous site survey data, we estimated the effect of sampling effort on detection by summing the number of rendezvous sites that were surveyed in each grid cell.

We also included 3 habitat and landscape covariates (Table 1). We derived elevation and slope data from 200-m^2

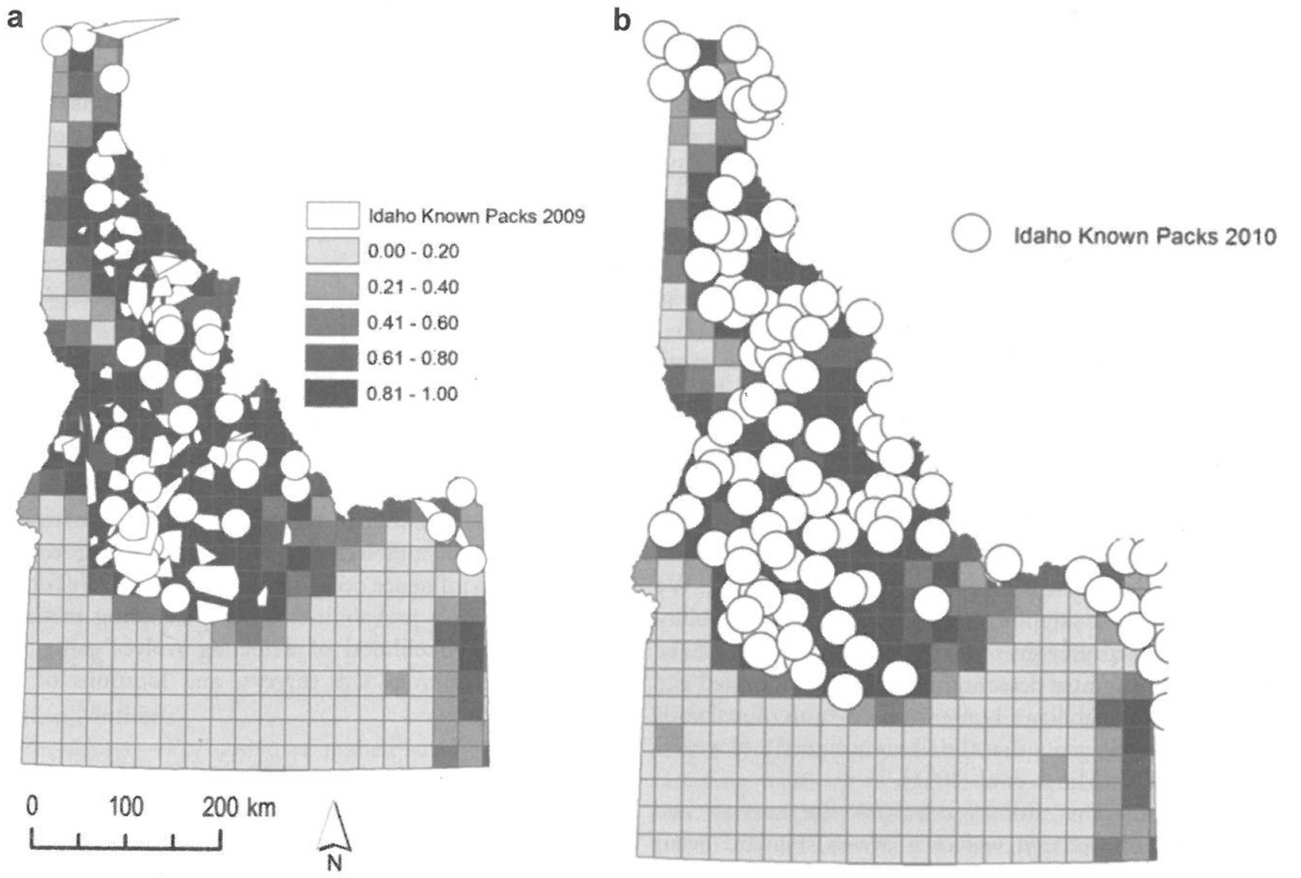

Figure 2. The probability each 686-km^2 patch in Idaho was occupied by a wolf pack in (a) 2009 and (b) 2010. Patch size was equal in area to mean territory size of wolf packs in Idaho ($n = 27$). We estimated occupancy probabilities using multiple detection state and method models (Miller et al. 2011) with mail surveys of hunters, surveys of predicted rendezvous sites, and locations of radiocollared wolves as the sampling methods. White circles and polygons indicate known wolf territories with shaded grid cells indicating increasing probability of occupancy. Wolf pack territory polygons were only available for 2009.

resolution digital elevation models (DEM; U.S. Geological Survey, National Elevation Dataset) and calculated mean elevation and slope in each grid cell. We calculated percent forest cover for 90-m^2 land cover pixels (Gap Analysis Project, Wildlife Spatial Analysis Lab, University of Montana) in each grid cell.

Estimating Occupancy

We used models populated with multiple survey data each with multiple detection states (i.e., certain and uncertain) as described by Miller et al. (2011) to estimate the probability of occurrence of wolf packs in Idaho in 2009 and in 2010. Our annual survey period was 1 June to 30 November. Whereas individual wolves may have died, joined, or left a particular pack, the majority of dispersal does not occur during June–November (M. Jimenez, U.S. Fish and Wildlife Service, unpublished data). Also, our focus was on estimating occupancy of packs and we assumed the occupancy status of an entire pack remained constant during the survey period. We assumed constant mean territory size and little overlap or

Table 1. Mean values of covariates included in an occupancy analysis for gray wolf packs in Idaho, 2009 and 2010, and expected relationships between covariates and a wolf pack's probability of occupancy (ψ), detection (p_{11}, r_{11}), false positive detection (p_{10}), and certain detection (b).

	2009		2010		Hypothesized relationship			
Model covariate	$\bar{x}$	SE	$\bar{x}$	SE	ψ	p_{11}, r_{11}	p_{10}	b
Bull elk harvest (harvest/km^2)	0.04	0.002	0.04	0.002	+			
Buck deer harvest (harvest/km^2)	0.14	0.006	0.11	0.004	+			
Cattle density (cattle/km^2)	9.70	0.875	9.97	0.908	–			
Sheep density (sheep/km^2)	0.32	0.044	0.29	0.044	–			
Elevation (km)	1.57	0.026	1.57	0.026	–			
Slope (°)	11.32	0.362	11.32	0.362	–			
Forest (%)[a]	34.78	1.613	34.78	1.613	+	–/+	–/+	–/+
Hunter effort for elk (hunter days/km^2)[a]	2.60	0.131	2.43	0.125		+	–	+
No. rendezvous sites/grid cell[b]	1.21	0.348	0.70	0.220		+		

[a] Covariate for sampling occasions from hunter surveys.
[b] Covariate for sampling occasion from rendezvous site surveys.

unoccupied space between territories. Our 3 sources of data (hunter surveys, rendezvous site surveys, locations of radiocollared wolves) yielded a total of 14 sampling occasions per year, 12 from hunter surveys, 1 from rendezvous site surveys, and 1 from radiocollar locations.

Although we rarified data by excluding detections of single wolves, we also accounted for false positive detections in the hunter surveys because public sightings can suffer from misidentifications (Gros et al. 1996). In Montana, the estimated probability of a false positive detection was <0.0001% when grid cells of roughly the same size (i.e., 600 km^2) were classified as occupied if ≥ 2 wolves were detected by ≥ 3 hunters in a 1-week period (Rich et al. 2013). As a result, in sampling occasions based on hunter observations of wolves, the ith grid cell in the tth sampling occasion was treated as being a certain detection if ≥ 3 hunters observed ≥ 2 wolves, an uncertain detection if 1–2 hunters observed ≥ 2 wolves, a 0 if hunters observed ≤ 1 wolf, and a missing data value if the grid cell was not surveyed. We parameterized these sampling occasions using the probability of a hunter detecting wolves at an unoccupied site (p_{10}), the probability of a hunter detecting wolves at an occupied site (p_{11}), and the probability a hunter's observation of wolves is classified as certain given that the site is occupied and wolves were detected (b; Miller et al. 2011).

Sampling occasions from rendezvous site surveys and locations of radiocollared wolves followed standard occupancy design where false positive detections were assumed not to occur (MacKenzie et al. 2002). In the sampling occasion based on surveys of predicted rendezvous sites, a certain detection was recorded for the ith grid cell if ≥ 2 adult wolves or ≥ 1 pup was detected at ≥ 1 surveyed rendezvous site, and non-detection was recorded for a cell if ≤ 1 adult wolf was detected. We assigned unsurveyed cells missing values. For the rendezvous site sampling occasion, q_{11} represented the probability we detected wolves at an occupied rendezvous site. In the sampling occasion based on locations of radiocollared wolves, a certain detection was recorded for the ith grid cell if it contained ≥ 1 wolf location and a non-detection was recorded if it did not. For the radiotelemetry sampling occasion, r_{11} represented the joint probability a wolf was captured, radiocollared, and located during our survey period.

We fit single season models to detection data for 2009 and 2010 using PRESENCE v 4.1 (Hines 2010) and we used Akaike's Information Criterion (AIC; Burnham and Anderson 2002) to identify the most supported model. We first examined alternative parameterizations for detection covariates. When selecting among detection models, we used the most global parameterization of occupancy parameters (all factors were included in the model). We considered alternatives where detection (p_{11}, r_{11}, q_{11}) varied among survey methods, where detection (q_{11}) for rendezvous sites varied as a function of the number of rendezvous sites surveyed in a grid cell, and where detection for hunter surveys (p_{11}, p_{10}, and b) varied with respect to forest cover, hunter effort for elk, week observed, and month observed. We assumed detections based on surveys of predicted rendezvous sites or locations of radiocollared wolves were certain (Ausband et al. 2010). We accounted for this in PRESENCE by fixing q_{10} and r_{10} equal to 0 and b equal to 1 for these sampling occasions. We considered all combinations of the detection covariates and selected the model with the lowest AIC value as our best detection model. We compared estimates of wolf abundance and associated precision among models populated with data from 1) the hunter survey only, 2) hunter survey and rendezvous site data, 3) hunter survey and radiotelemetry data, and 4) all data.

We then examined pair-wise correlations between our grid cell covariates (Table 1); if a pair was highly correlated ($|r| > 0.60$) we chose to retain the covariate with the larger influence on occupancy. We kept the parameterization of our best detection model and selected among alternative models for the remaining occupancy parameters. We considered all combinations of the remaining covariates predicted to influence occupancy probabilities. We compared mean detection probabilities among sampling methods to evaluate the likelihood of detecting wolves using hunter surveys, rendezvous site surveys, and locations of radiocollared wolves.

Predicting Distribution and Number of Wolves

We did not conduct surveys in 17% ($n = 99$) of GMUs in southern Idaho that have not been recolonized by wolves. Our occupancy model estimated occupancy for these cells, however, through the use of habitat covariates. We calculated cell-specific estimates of occupancy from the model with the lowest AIC value. We used cell-specific estimates of occupancy to evaluate the annual distribution of wolf packs in Idaho. Because some cells overlapped state borders and were only partially contained within Idaho we estimated the total area occupied by wolf packs in Idaho during 2009–2010 by multiplying cell-specific estimates of occupancy by their respective size (i.e., 686 km^2) and then summing these values across all cells. Our final estimates of total area occupied were adjusted for partial cells on the state border when we multiplied occupancy probabilities by the percent of the cell that was contained within our study area. To assess the influence of radiotelemetry data on model estimates, we repeated the occupancy analysis as described above but withheld radiotelemetry data from the model.

To estimate the number of wolf packs in Idaho from 2009 to 2010, we divided the total area occupied (estimated with and without detections from radiotelemetry) by mean size of wolf pack territories in Idaho (686 km^2, SD = 460). To estimate abundance of wolves, we multiplied the number of estimated packs by mean size of packs monitored via radiotelemetry. To calculate mean pack size, we used only packs where IDFG and NPT observers indicated accurate year-end counts. We used single-season occupancy models and employed a non-parametric bootstrap approach to estimate 95% confidence intervals (95% CI) for our estimates of total area occupied by wolf packs using Program R (Fiske and Chandler 2011) to bootstrap the top model in PRESENCE. This approach entailed resampling the encounter histories and associated covariates 10,000 times, running the top model structure to obtain estimates of occupancy probabilities, and calculating the upper and lower bounds from the simulated distribution. We compared our estimates of the numbers of packs and wolf abundance to the minimum known number of wolf packs and estimated number of wolves in Idaho (Mack et al. 2010, Holyan et al. 2011). Minimum number of wolf packs included wolf packs residing in the state, packs that overlapped state borders, groups of wolves ($\geq$2 wolves with no history of reproduction), and packs that were removed because of livestock depredations between 1 June and 30 November. IDFG and NPT then estimated individual wolf abundance by multiplying the minimum number of packs by the average pack size for packs where biologists determined they had a reliable year-end (31 Dec) count. Minimum counts of packs represent year-end knowledge with the understanding that not all wolf packs could be adequately surveyed (Mack et al. 2010, Holyan et al. 2011).

RESULTS

Detection Methods

Hunter surveys.—For 2009, we mailed surveys to 11,878 hunters; 4,093 (34%) hunters returned fully completed surveys of which 610 (15% of responding hunters) reported seeing $\geq$2 live wolves during our 3-month survey period (Fig. 1a). For 2010, we mailed surveys to 11,834 hunters; 3,789 (32%) hunters returned fully completed surveys of which 967 (25% of responding hunters) reported seeing $\geq$2 live wolves during our 3-month survey period (Fig. 1b).

Rendezvous site surveys.—We surveyed 437 predicted rendezvous sites in 5 GMUs in 2009 (Fig. 1a) and 252 sites in 2 GMUs in 2010 (Fig. 1b). At least 2 adult wolves or $\geq$1 pup were detected at 7.8% ($n = 34$) and 6.4% ($n = 16$) of the sites in 2009 and 2010, respectively. In 2009, 25 grid cells each contained 1 to 73 ($\bar{x} = 17$, SD = 19) surveyed rendezvous sites. In 2010, 15 grid cells each contained 1 to 38 ($\bar{x} = 17$, SD = 13) surveyed rendezvous sites.

Radiotelemetry data.—Personnel from IDFG and the Nez Perce Tribe located 89 radiocollared wolves from 61 packs $\geq$1 time in 2009 (Fig. 1a) and 71 radiocollared wolves from 46 packs $\geq$1 time in 2010 (Fig. 1b). In 2009, 292 locations of collared wolves were collected across 73 grid cells; each grid cell contained 1–17 locations ($\bar{x} = 4$, SD = 2.9). In 2010, 222 locations of collared wolves were collected across 58 grid cells; each grid cell contained 1 to 15 locations ($\bar{x} = 4$, SD = 3.5).

Model Covariates and Estimating Occupancy

The parameter estimates from our best overall model for 2009 were similar with and without radiotelemetry data (Table 2). Detection probability (p_{11}, r_{11}, q_{11}) varied among sampling methods (Table 3) and detection at rendezvous sites was positively related to the number of sites surveyed in a grid cell (Table 2). Weekly detection probabilities by hunters varied by sampling week and the probability of a false detection (p_{10}) varied by sampling month (Table 2). Forest

Table 2. Parameter estimates for occupancy analysis of gray wolf packs in Idaho, 2009 and 2010. Models included 3 detection methods: mail surveys of hunters, surveys of predicted rendezvous sites, and locations of radiocollared wolves. We conducted separate analyses for each year and analyzed data sets that did and did not include observations of radiocollared wolves. Month, forest and effort were not in the 2009 model and sheep density was not in the 2010 model.

		2009		2009 (no telemetry)		2010		2010 (no telemetry)	
Parameter	Variable	β	SE	β	SE	β	SE	β	SE
Occupancy[a]	Intercept	−4.68	0.900	−3.37	0.994	−5.78	1.235	−6.05	1.246
	Slope (°)	0.19	0.033	0.14	0.036	0.21	0.043	0.21	0.046
	Elevation (km)	0.99	0.358	1.00	0.390	1.58	0.455	1.62	0.505
	Sheep density (sheep/km^2)	−4.23	2.140	−5.47	2.646				
	Cattle density (cattle/km^2)	0.002	0.04	−0.17	0.053	−0.17	0.051	−0.21	0.061
	Bull elk harvest (harvest/km^2)	29.01	6.841	26.86	7.895	44.35	12.22	50.36	12.963
p_{11}, r_{11}[b]									
Hunter surveys	Sampling method Hunter effort, elk (days/km^2)					−0.05	0.021	−0.06	0.023
Rendezvous surveys	No. surveys	0.15	0.071	0.15	0.071	0.27	0.160	0.47	0.428
p_{10}[c]									
Hunter surveys	Sep	−5.71	0.878	−6.00	0.961	−4.57	0.409	−4.65	0.431
	Oct	−4.44	0.538	−4.29	0.431	−3.76	0.279	−3.86	0.310
	Nov	−3.27	0.268	−3.27	0.278	−3.53	0.276	−3.44	0.269
	Hunter effort, elk (days/km^2)					0.24	0.089	0.31	0.121
b[d]									
Hunter surveys	Intercept	−3.00	0.224	−3.00	0.224				
	Sep					−3.20	0.600	−3.20	0.595
	Oct					−2.32	0.504	−2.31	0.502
	Nov					−3.32	0.604	−3.28	0.606
	Forest					0.02	0.008	0.02	0.008
	Hunter effort, elk (days/km^2)					−0.18	0.074	−0.18	0.074

[a] Probability a wolf pack occupied an area.
[b] Probability a wolf pack was detected at an occupied site.
[c] Probability a wolf pack was detected at an unoccupied site.
[d] Probability an observation of wolves was classified as certain given that the site was occupied and wolves were detected.

Table 3. Estimates for the mean probabilities wolf packs were detected (p_{11}, q_{11}, r_{11}) through surveys of hunters (H), surveys of predicted rendezvous sites (RS), and by having a radiocollared pack member located via telemetry (RT); the mean probabilities a hunter detected wolves at an unoccupied site (p_{10}); and the mean probability a hunter's observation of wolves was classified as certain given that the site was occupied and wolves were detected (b). Probabilities were estimated using multiple detection state and method occupancy models (Miller et al. 2011).

	p_{11}, q_{11}, r_{11} (SE)					
Year	H	RS	RT	Overall mean	p_{10} (SE) Hunter surveys	b (SE) Hunter surveys
2009 (all data)	0.23 (0.031)	0.59 (0.109)	0.46 (0.042)	0.25 (0.039)	0.04 (0.006)	0.05 (0.010)
2009 (no RT)	0.24 (0.032)	0.60 (0.111)		0.24 (0.040)	0.02 (0.006)	0.05 (0.010)
2010 (all data)	0.31 (0.037)	0.54 (0.110)	0.34 (0.038)	0.30 (0.039)	0.04 (0.016)	0.08 (0.026)
2010 (no RT)	0.32 (0.039)	0.60 (0.111)		0.30 (0.038)	0.06 (0.024)	0.08 (0.026)

cover ($\beta = 0.04$, SE $= 0.004$) and slope ($\beta = 0.22$, SE $= 0.027$) were correlated ($r = 0.74$), thus we retained slope in subsequent analyses. Occupancy was positively influenced by slope, elevation, and bull elk harvest density and negatively influenced by domestic sheep density (Table 2). When we excluded radiotelemetry data, the best model also included a negative effect of cattle density on occupancy (Table 2).

For 2010, model results were similar to 2009 with and without radiotelemetry data (Table 2). As with 2009, detection varied among sampling methods (Table 3), and was positively related to the number of rendezvous sites surveyed (Table 2). Detection by hunters varied by sampling week and in 2010 was negatively associated with hunter effort (Table 2). False positive detection probabilities were positively associated with hunter effort and did not vary significantly by sampling month (Table 2). The probability that a true positive detection was classified as certain (b) was positively influenced by forest cover, negatively associated with hunter effort and varied by sampling month although with no discernible pattern. In 2010, occupancy was positively related to slope, elevation, and bull elk harvest density and negatively related to cattle density.

Overall, probabilities of occupancy were highest in central and northern Idaho and along the eastern border of the state, adjacent to Montana (Fig. 2). Additionally, our estimates of the distribution of wolf packs in 2009 and in 2010 were consistent with the distribution of known wolf packs in Idaho (Fig. 2). We found detection probability varied among sampling methods and was highest when using rendezvous site surveys (only including grid cells surveyed for predicted rendezvous sites), followed by locations from radiocollared wolves, and lastly hunter surveys (Table 3). The estimated probability that hunters falsely reported wolves in unoccupied cells (p_{10}) averaged 4.0% across years (Table 3). The percentage of actual observations of wolves that were classified as certain increased from 5.0% in 2009 to 8.0% in 2010 (b; Table 3).

Predicting Distribution and Number of Wolves

We estimated 44.0% (95,358 km^2; 95% CI: 73,668–117,047 km^2) and 47.0% (101,369 km^2; 95% CI: 83,310–119,428 km^2) of Idaho was occupied by wolf packs, when including radiotelemetry, in 2009 and 2010, respectively. When we excluded the radiotelemetry sampling occasion, our overall estimates decreased only slightly to 42.3%; (91,732 km^2; 95% CI: 70,272–113,191 km^2) and 45.5% (98,566 km^2; 95% CI: 83,472–113,660 km^2) in 2009 and 2010, respectively.

Mean number of packs from all 4 models ranged 115–139 and 135–148 for 2009 and 2010, respectively (Fig. 3a). Models using only hunter survey data estimated the least number of packs and models using all data generally estimated a marginally greater number of packs (Fig. 3a). Precision ranged from 16–28% of mean estimates in 2009 to 14–16% in 2010. Models that used all data sources generally provided the most precise estimates (Fig. 3a). When using all available data, we estimated 139 (95% CI: 117–159) and 148 (95% CI: 127–167) wolf packs in Idaho in 2009 and 2010, respectively. When we excluded radiotelemetry data, our estimates declined slightly to 137 (95% CI: 103–160) and 144 (95% CI: 122–165) wolf packs in 2009 and 2010, respectively. IDFG and NPT estimated 133 and 121 wolf packs (i.e., resident, border, and non-reproductive groups) occupied Idaho in 2009 and 2010, respectively (Fig. 3a; USFWS et al. 2010, 2011).

NPT and IDFG documented end of year pack size for 24 packs in 2009 ($\bar{x} = 8.0$ wolves, SD $= 2.8$) and 20 packs in 2010 ($\bar{x} = 7.0$ wolves, SD $= 3.4$). Using the product of estimated number of packs and mean pack size, we estimated 1,112 (95% CI: 936–1272) and 1,036 (95% CI: 889–1169) wolves occupied Idaho in 2009 and 2010, respectively. Our estimates of wolf abundance without radiotelemetry data were 1,096 (95% CI: 824–1280) and 1,008 (95% CI: 854–1155) wolves for 2009 and 2010, respectively. IDFG and NPT estimated 958 and 847 wolves (i.e., resident, border, and non-reproductive groups) occupied Idaho in 2009 and 2010, respectively (Fig. 3b). Because estimates of individual wolf abundance were derived in part from the estimated number of packs, trends in estimates of abundance and associated precision of individual wolves across the 4 models was identical to those observed on estimates of pack numbers. Generally, hunter survey data alone provided the lowest abundance estimates and models using all data had increased precision. The precision of our estimates may be overestimated because the non-parametric bootstrap method we used was unable to fully incorporate all sources of variation (i.e., occupancy, territory size, pack size).

DISCUSSION

Methods for estimating the size of large carnivore populations are financially and logistically challenging

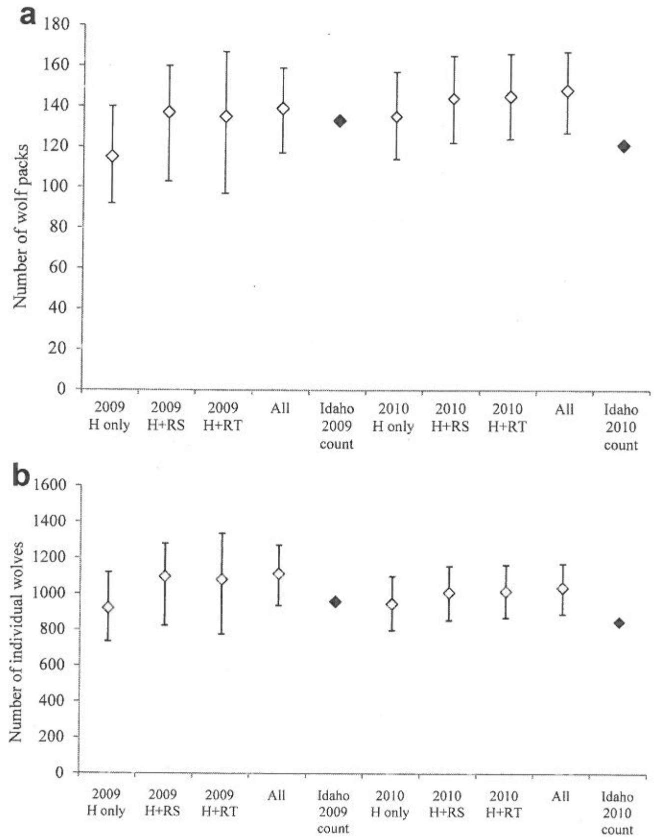

Figure 3. Abundance (±95% CI) of (a) wolf packs and (b) individual wolves in Idaho (2009–2010) estimated from occupancy models populated with data from hunter surveys (H), rendezvous site surveys (RS), and radiotelemetry (RT) data. Dark diamonds represent Idaho count data for packs and non-reproducing groups, and individual wolves (Mack et al. 2010, Holyan et al. 2011).

(Gros et al. 1996, Patterson et al. 2004, Potvin et al. 2005, Gompper et al. 2006). Whereas a variety of survey methodologies are available for estimation at fine spatial scales and for specific sampling conditions, no approach has been developed to combine these methods for estimation at the large spatial scales commensurate with the dynamics of large carnivore populations and their management by state agencies. This can be particularly problematic for carnivores such as wolves in the U.S. northern Rocky Mountains, where state agencies are required to document the recovery of previously endangered wolf populations while also implementing public harvest. To address this problem, we developed an occupancy model based on data from 3 survey methods that produced annual estimates of number and distribution of wolf packs and wolf abundance, with associated measures of precision, for the state of Idaho in 2009 and 2010.

As we expected, our modeled estimates were greater than the minimum numbers documented by IDFG and NPT. Our estimates of number of wolf packs were an average of 12.0% (SD = 9.0) greater than the IDFG and NPT estimates based on monitoring using radiotelemetry, except for the 2009 model based only on hunter survey data, which underestimated the IDFG and NPT combined estimate by 13.5%. Estimated distribution of packs from the occupancy model were commensurate with known wolf distribution in the state (Fig. 3). Our estimates of wolf abundance were an average of 17.0% (SD = 4.0) greater than IDFG and NPT estimates based on monitoring using radiotelemetry (Mack et al. 2010, Holyan et al. 2011) except for the 2009 model based only on hunter survey data which underestimated the IDFG and NPT combined estimate by 4.0%. Our estimate of the number of wolf packs increased from 2009 to 2010 yet the average pack size declined between years leading to a decrease in estimated number of individual wolves in 2010. We do not know if the decline in pack sizes recorded in 2010 was due to the first harvest season implemented in fall 2009.

We showed that a model populated with hunter sightings and rendezvous site survey data provided similar estimates of wolf abundance even in the absence of extensive radiotelemetry data. With the relatively widespread, contiguous distributions of wolves we observed and the statewide hunter surveys and focused rendezvous site surveys we implemented, withholding radiotelemetry data from our model did not strongly affect our estimates. Furthermore, comparisons of models populated with varying survey methods indicated radiotelemetry data did little to improve model performance over models populated with hunter survey data alone. The inclusion of radiotelemetry data did not appreciably change the occupancy estimates, likely because hunter sighting locations were widespread across Idaho and therefore overlapped areas where wolves were radiocollared. Where use of widespread sampling such as hunter surveys is limited, the importance of radiotelemetry data to estimation using an occupancy model would likely increase. Radiotelemetry data may compliment a monitoring program based on occupancy modeling where it could be used to test and validate other less certain data streams (e.g., hunter surveys, territory sizes) and refine the model over time.

We assumed that hunter survey data would contain a relatively high number of false positive detections compared to data collected using our other sampling methods. We found that increased hunter effort (i.e., hunter days/km^2) did lead to more false detections (p_{10}) although our estimated false detection rate was relatively low (4.0%). Hunter surveys yielded the lowest percentage of certain detections of all methods considered (Table 3). Because our definition of certain was $\geq$3 hunters reporting $\geq$2 wolves in a cell, our low certain detection rate may in part be, an artifact of relatively small sample sizes (approx. 12,000) of surveyed hunters across the state. Although hunter survey data were the workhorse in our models and relatively inexpensive to obtain, the 4% false detections and 5–8% certain detections may explain why models using only hunter survey data provided the lowest estimates of abundance (markedly in 2009); hunter survey data underestimated the state's known minimum count by 18 packs. We therefore suggest caution when using only public sightings to estimate population size; augmenting public survey data with observations collected using methods with more certain detections may improve both accuracy and precision of modeled estimates.

Detection probabilities varied by sampling method and effort. For example, the probability of detecting a wolf at an occupied site was influenced by sampling method. Increased effort in rendezvous site surveys led to higher detection rates, whereas results from increased hunter effort were equivocal (i.e., positive influence on detection rates in 2009 and a negative influence in 2010). Overall, detection probabilities across our survey methods were relatively high ($\bar{p} = 0.42$, SE = 0.05). Among the survey methods, rendezvous site surveys had the highest detection probability (in grid cells where $\geq$1 rendezvous site was surveyed) but this could be because of the intensity of our sampling ($\bar{x} = 17$ sites per cell; SD = 17).

As we predicted, increasing prey density positively influenced wolf occupancy and livestock density negatively influenced occupancy. Contrary to our expectations and results from Rich et al. (2013), however, wolf occupancy was positively influenced by slope, presumably because wolves primarily inhabited relatively mountainous portions of Idaho. Wolves in Idaho generally do not persist in areas of high livestock abundance (i.e., valley bottoms) because of subsequent agency control in response to livestock depredations (USFWS et al. 2012) and this may explain in part why wolves have not recolonized the southernmost portion of Idaho as they have other portions of the state. In contrast, we found wolves occupy mountainous areas where prey is abundant in Idaho as predicted by Oakleaf et al. (2006), and they do not persist in areas dominated by livestock production.

We assumed wolf packs did not leave cells during the hunting season and that detections were independent of one another. Detections in adjacent cells would lead to overestimates of wolf population size particularly if wolf distribution is patchy and not contiguous, but this was not the case for our study (USFWS et al. 2010, 2011). Predicting wolf abundance from an occupancy model requires 3 further assumptions: 1) average territory size is known, 2) average pack size is known, and 3) territories do not overlap. Because each of these characteristics of a wolf population can change over time, one must periodically estimate pack and territory size using field data to ensure occupancy estimates remain reliable (Rich et al. 2013).

The use of multiple survey methods can help ensure that occupancy estimates are robust to weaknesses or changes in any 1 method. Occupancy models populated, in part, with public sighting data will require regular calibration with field data, otherwise estimates could lose accuracy over time where public participation wanes or becomes unreliable. To keep an occupancy model calibrated, focal areas could be identified where periodic, intensive sampling (e.g., radiotelemetry, rendezvous site surveys) can be used to obtain independent estimates of population characteristics such as territory size and pack size. These estimates could be compared to hunter survey reports to test assumptions of the occupancy model, maintain data quality, and revise sampling approaches, if necessary (e.g., increased sampling, discarding ineffective techniques). Importantly, data from the focal areas could be used to update estimates of size of packs and territories, which are critical for generating reliable estimates of wolf abundance from the occupancy model.

MANAGEMENT IMPLICATIONS

Estimates of wolf abundance at statewide scales are required under the Endangered Species Act and necessary for the transition from federal to state management in the U.S. northern Rocky Mountains and in the midwestern United States (Beyer et al. 2009). Further, where wolves are a game species, management for public harvest requires understanding population dynamics that take place on broad spatial scales. In addition to providing reliable population estimates over large areas, the approach we present exploits other strengths of occupancy modeling useful to monitoring, that is, estimating occupancy for unsampled areas, understanding how terrain and habitat influence probabilities of occupancy and detection, and predicting cell-specific probabilities of colonization and extinction (MacKenzie et al. 2006). Conservation efforts routinely attempt to address populations of animals that overlap political boundaries. We suggest that occupancy modeling can provide a means for standardizing estimates of abundance and spatial distribution across ecologically arbitrary boundaries (e.g., state lines, international borders) to a scale that better reflects the dynamics of large, transboundary populations. Jurisdictional boundaries can be problematic for occupancy estimation because they can bisect cells and animals occupying those cells can be double-counted if estimates are being made independently on both sides of the border. Close collaboration between transborder agencies would be necessary to avoid such double-counting and overestimation of populations along border regions.

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Montana Gray Wolf
Conservation and Management
2013 Annual Report

A cooperative effort by Montana Fish, Wildlife & Parks, USDA Wildlife Services, Glacier National Park, Yellowstone National Park, Blackfeet Nation, and The Confederated Salish and Kootenai Tribes

This report presents information on the status, distribution, and management of wolves in the State of Montana, from January 1, 2013 to December 31, 2013.

It is also available at: http://fwp.mt.gov/wolf

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TABLE OF CONTENTS

Predicting abundance of gray wolves in Montana using hunter observations and field monitoring
Principal Investigator: Kevin Podruzny

Since the early 1980's, as wolf populations began recovering in Montana, the numbers of packs, breeding pairs, and total wolves have been documented by attempting to locate and count all individuals. It was assumed that these minimum counts provided an index to the true populations when wolf numbers were small. In the early years, most wolf packs had radio-collared individuals, and intensive monitoring was possible to identify new packs and most individuals within packs. Only verified observations were used, thus these counts represented minimums. In 1995, when the US Fish and Wildlife Service reintroduced wolves into Yellowstone National Park and central Idaho, the end-of-year count for wolves residing in Montana was only 66. By 2012 the minimum count had reached 625. The capacity for MFWP personnel to monitor the wolf population has been declining given robust wolf population growth and range expansion since about 2006. The traditional field-based methods yield minimum counts that are conservative and inevitably (and probably increasingly) below the true population sizes. The degree of this undercounting is unknown. Consequently, MFWP explored other, cost-effective methods that could more accurately be described as population estimates that account for uncertainty, as opposed to minimum counts.

In anticipation of an increased work load and declining federal funding, MFWP first began considering alternative approaches to monitoring the wolf population in 2006. Preliminary work focused on developing a more reliable and cost-effective method to estimate the number of breeding pairs based on the size of a wolf pack using logistic regression models (Mitchell et al. 2008). Subsequent work focused on finding ways to utilize wolf observations by hunters in a more systematic way. A collaborative research effort with the University of Montana Cooperative Wildlife Research Unit was initiated in 2007. The primary objective was to find an alternative approach to wolf monitoring that would yield statistically reliable estimates of the number of wolves, the number of wolf packs, and the number of breeding pairs (Glenn et al. 2011). Ultimately, a method applicable to a sparsely distributed and elusive carnivore population was developed that used hunter observations as a cost effective means of gathering biological data to estimate the area occupied by wolves in Montana, and additional information gathered from field monitoring by biologists to estimate the number of packs (Rich et al. 2013).

This transitioning from labor intensive minimum counts that are biased low to an unknown degree to obtaining population estimates can be fine tuned and modified as new data and methodologies become available, new techniques are developed, and new research answers key uncertainties. This technique bypasses the need to count every individual in every pack, and instead relies on public reported wolf observations, field-documented territory size, and a small number of monitored packs and pack sizes.

Methods

The general method we used to estimate the number of gray wolves in Montana was to 1) estimate the area occupied by wolves in packs, 2) estimate the numbers of wolf packs by dividing area occupied by average territory size and correcting for overlapping territories, and 3) estimate the numbers of wolves by multiplying the number of estimated packs by average annual pack size (Figure 2).

Estimating Area Occupied by Wolves in Packs

To estimate the area occupied by wolf packs from 2007 to 2012, we used a multi-season false-positives occupancy model (Miller et al. 2013) using program PRESENCE (Hines 2006). First, we created an observation grid for Montana (Figure 2A) with a cell size large enough to ensure observations of packs across sample periods, yet small enough to minimize the occurrences of multiple packs in the same cell on average (cell size = 600 km^2). We used locations of wolves in packs (2-25 wolves) reported by a random sample of unique deer and elk hunters during MFWP annual Hunter Harvest Surveys (Figure 2B) and assigned the locations to cells (Figure 2C). We modeled detection probability, initial occupancy, and local colonization and local extinction from 5, 1-week encounter periods and verified locations (Figure 2D) using covariates that were summarized at the grid level (Figure 2E). We estimated patch-specific estimates of occupancy (Figure 2F) and estimated the total area occupied by wolf packs by multiplying patch-specific estimates of occupancy by their respective patch size and then summing these values across all patches (Figure 2G). Our final estimates of the total area occupied by wolf packs were adjusted for partial cells on the border of Montana and included model projections for reservations and national parks where no hunter survey data were available.

Model covariates for detection included hunter days per hunting district per year (an index to spatial effort), low use forested and non-forested road densities (indices of spatial accessibility), a spatial autocovariate (the proportion of neighboring cells with wolves seen out to a mean dispersal distance of 100 km), and patch area sampled (because smaller cells on the border of Montana, parks, and Indian Reservations have less hunting activity and therefore less opportunity for hunters to see wolves). Model covariates for occupancy, colonization, and local extinction included a principal component constructed from several autocorrelated environmental covariates (percent forest cover, slope, elevation, latitude, percent low use forest roads, and human population density), and recency (the number of years with verified locations in the previous 5 years).

To estimate area occupied in each year, we calculated unconditional estimates of occupancy probabilities which provided probabilities for sites that were not sampled by Montana hunters (such as National Parks and Reservations). We accounted for uncertainty in occupancy estimates using a parametric bootstrap procedure on logit distributions of occupancy probabilities. For each set of bootstrapped estimates we calculated area occupied. The 95% confidence intervals

(C.I.s) for these values were obtained from the distribution of estimates calculated from the bootstrapping procedure.

Estimating Numbers of Wolf Packs

To predict the total number of wolf packs in Montana from 2007 to 2012, we first established an average territory size for wolf packs in Montana (Figure 2H). Rich et al. (2012) calculated 90% kernel home ranges from radio telemetry locations of wolves collared and tracked by wolf MFWP biologists for research and/or management from 2008 to 2009. We assumed the mean estimate of territory size from these data was constant during 2007-2012. For each year, we estimated the number of wolf packs by dividing our estimates of total area occupied by the mean territory size (Figure 2I). We then accounted for annual changes in the proportion of territories that were overlapping (non-exclusive) using the number of observed cells occupied by verified pack centers.

We accounted for uncertainty in territory areas using a parametric bootstrap procedure and a log-normal distribution of territory sizes, and for each set of bootstrapped estimates we calculated mean territory size. The 95% C.I.s for these values were obtained from the distribution of estimates calculated from the bootstrapping procedure.

Estimating Numbers of Wolves

To predict the total number of wolves in Montana from 2007 to 2012, we first calculated average pack size from the distribution of packs of known size (Figure 2J). Pack sizes were established by MFWP biologists for packs monitored for research and/or management. We used end-of-year pack counts for wolves documented in Montana from 2007 to 2012. We only used pack counts MFWP biologists considered complete. Typically, intensively monitored packs with radio-collars provided good counts more often than packs that were not radio-marked. For each year, we estimated total numbers of wolves in packs by multiplying the estimate of mean pack size by the annual predictions of number of packs (Figure 2K).

We accounted for uncertainty in pack sizes using a parametric bootstrap procedure and a Poisson distribution of pack sizes, and for each set of bootstrapped estimates we calculated mean pack size. The 95% C.I.s for these values were obtained from the distribution of estimates calculated from the bootstrapping procedure. We allowed pack sizes to vary by year but not spatially.

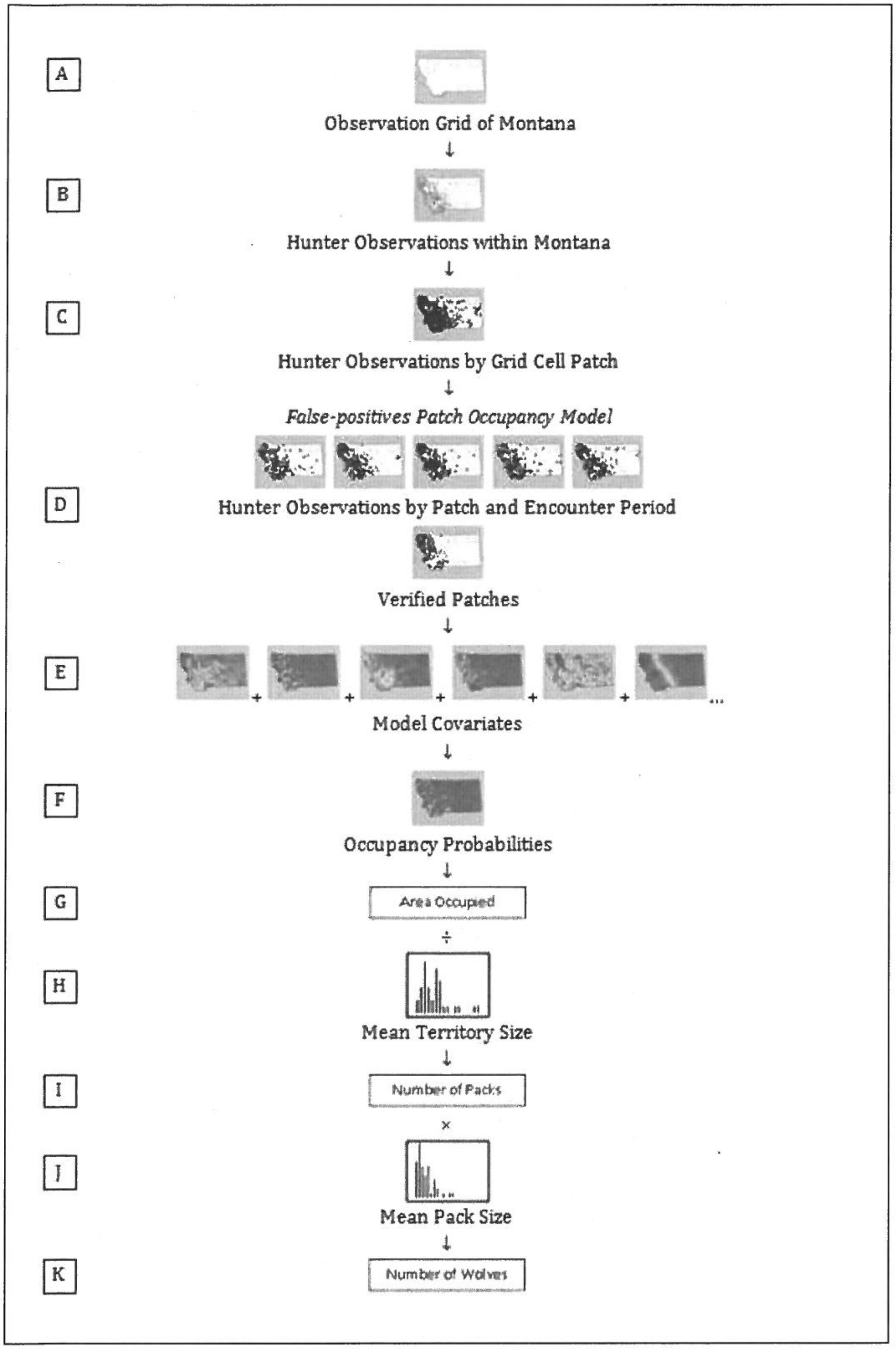

Figure 2. Schematic for method of estimating the area occupied by wolves, number of wolf packs and number of wolves in Montana, 2007-2012.

Results

Estimating Area Occupied by Wolves in Packs

From 2007 to 2012, 50,039; 81,475; 80,486; 82,386; 81,532 and 76,996 hunters responded to the wolf sighting surveys. From their reported sightings, 1,202; 2,859; 3,056; 3,469; 3,320, and 2,391, locations of 2 to 25 wolves could be determined during the 5, 1-week sampling periods.

The top model of wolf occupancy showed positive associations between the initial probability that wolves occupied an area and an environmental principal component and recency. The probability that an unoccupied patch became occupied in subsequent years was positively related to an environmental principal component and recency. The probability that an occupied patch became unoccupied in the following year was constant. The probability that wolves were detected by a hunter during a 1-week sampling occasion was positively related to hunter days per hunting district per year, low use forest road density, low use non-forest road density, a spatial autocovariate, and area sampled. The probability that wolves were falsely detected by a hunter during a 1-week sampling occasion was positively related to hunter days per hunting district per year, low use forest road density, low use non-forest road density, and a spatial autocovariate

From 2007 to 2012, estimated area occupied by wolf packs in Montana increased from 39,521 km^2 (95% CI = 39,144 to 40,562) to 79,275 km^2 (95% CI = 78,696 to 79,944; Table 1). The predicted distribution of wolves from the occupancy model closely matched the distribution of field-confirmed wolf locations (verified pack locations and harvested wolves; Figure 3).

Table 1. Estimated area occupied by wolves, number of wolf packs, and number of wolves in Montana, 2007-2012.

	2007	2008	2009	2010	2011	2012
Estimated Area Occupied (km^2)	39,521	49,831	59,067	64,810	72,134	79,275
(95% C.I.)	(39,144 - 40,562)	(49,298 - 50,593)	(58,542 - 59,814)	(64,277 - 65,476)	(71,606 - 72,871)	(78,696 - 79,944)
Territory Size (km^2)	599.83	599.83	599.83	599.83	599.83	599.83
(95% C.I.)	(493.35 - 740.34)	(493.35 - 740.34)	(493.35 - 740.34)	(493.35 - 740.34)	(493.35 - 740.34)	(493.35 - 740.34)
Estimated Packs (600 km^2 territories)	66	83	98	108	120	132
(95% C.I.)	(54 - 81)	(67 - 101)	(80 - 120)	(87 - 131)	(97 - 146)	(107 - 160)
Territory Overlap Index	1.17	1.11	1.13	1.16	1.24	1.25
Estimated Packs (600 km^2 territories w/overlap)	77	93	112	126	149	165
(95% C.I.)	(63 - 95)	(75 - 113)	(90 - 136)	(102 - 153)	(121 - 181)	(134 - 201)
Average Pack Size (complete counts)	7.03	6.82	6.39	6.16	5.67	4.86
(95% C.I.)	(6.06 - 7.97)	(6.18 -7.65)	(5.75 - 7.10)	(5.46 - 6.86)	(5.05 - 6.28)	(4.27 - 5.51)
Estimated Wolves	542	631	713	774	843	804
(95% C.I.)	(422 - 688)	(503 - 796)	(570 - 888)	(612 - 965)	(664 - 1,056)	(636 - 1,019)

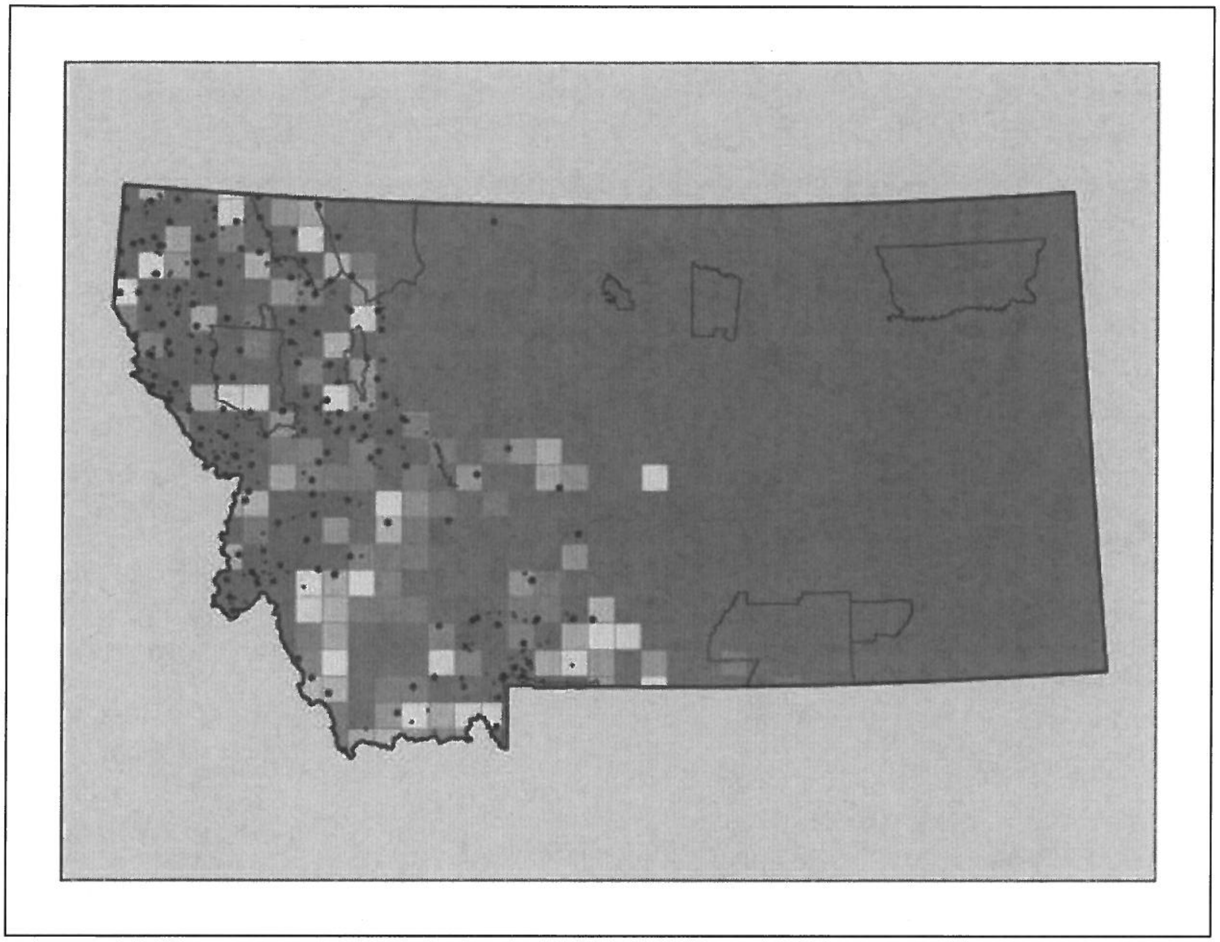

Figure 3. Model predicted probabilities of occupancy (ranging from low to high [green to red]), verified pack centers (large dots), and harvest locations (small dots) in Montana, 2012.

Estimating Numbers of Wolf Packs

In 2008 and 2009, territory sizes from 38 monitored packs ranged from 104.70 km^2 to 1771.24 km^2. Mean territory size was 599.83 km^2 (95% C.I. = 478.81 to 720.86; Rich et al. 2012). Dividing the estimated area occupied by mean territory size resulted in an estimated number of packs that increased from 66 (95% C.I. = 54 to 81) to 132 (95% C.I. = 107 to 160) from 2007 to 2012 (Table 1). We adjusted these estimates to account for annual changes in the number of verified pack centers per grid from 2007 to 2012 (1.17, 1.11, 1.13, 1.16, 1.24, and 1.25 for each respective year during 2007-2012) as an index of territory overlap. Accounting for territory overlap, estimated numbers of packs increased from 77 (95% C.I. = 63 to 95) to 165 (95% C.I. = 134 to 201) from 2007 to 2012 (Table 1). The estimated number of wolf packs ranged from 6% larger than the minimum verified number of packs residing in Montana in 2007 to 16% larger in 2010 (Figure 4).

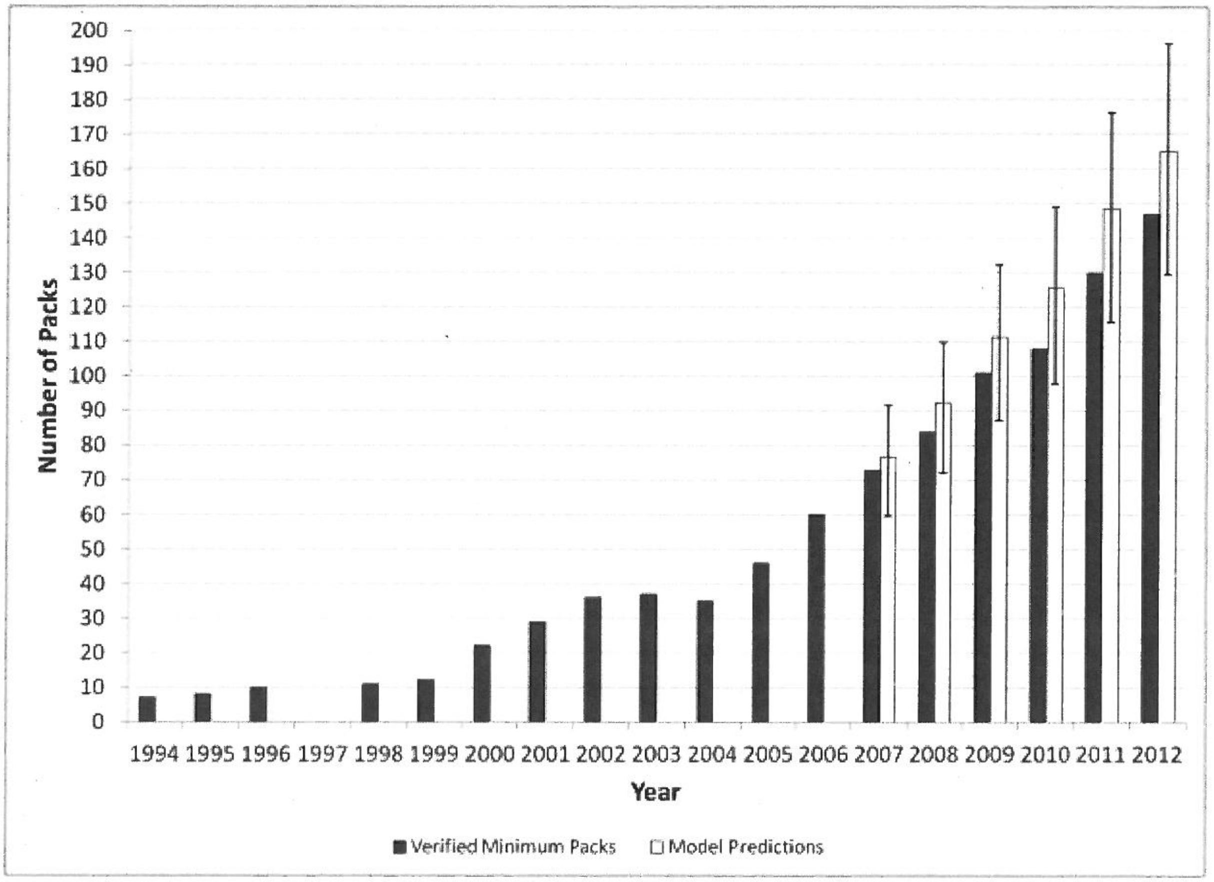

Figure 4. Estimated number of wolf packs in Montana compared to the verified minimum number of packs residing in Montana, 2007-2012.

Estimating Numbers of Wolves

From 2007 to 2012, complete counts were obtained from 314 packs within or bordering Montana. Pack sizes ranged from 2 to 22 and from 2007 to 2012 mean pack sizes decreased from 7.03 (95% C.I. = 6.06 to 7.97) to 4.86 (95% C.I. = 4.27 to 5.51). Multiplying estimated packs by mean pack size resulted in an increase of estimated wolves from 542 (95% C.I. = 422 to 688) to 804 from (95% C.I. = 636 to 1,019) 2007 to 2012 (Table 1). The estimated number of wolves ranged from 27% larger than the minimum verified number of wolves in Montana packs in 2008 to 37% larger in 2010 (Figure 5).

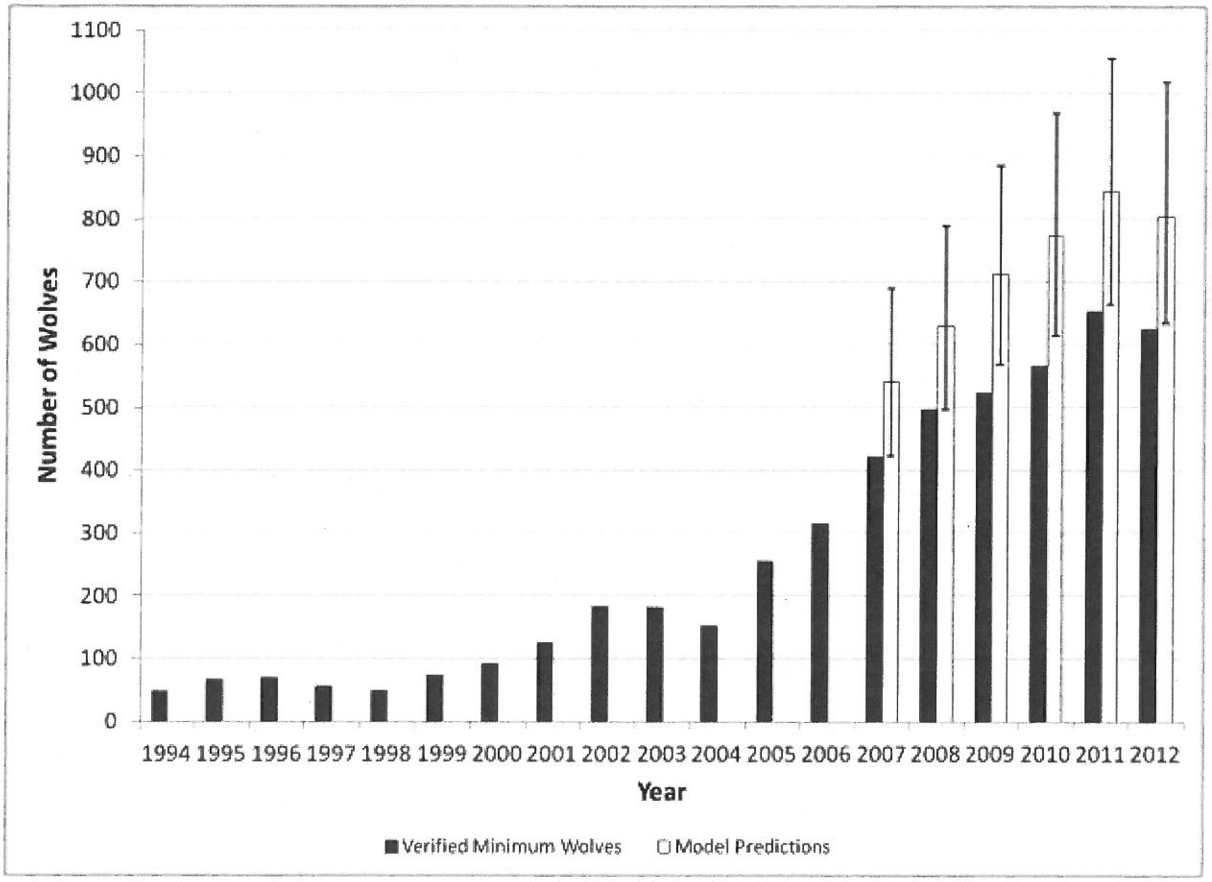

Figure 5. Estimated number of wolves in Montana compared to the verified minimum number of wolves residing in Montana, 2007-2012.

Discussion

Estimated Area Occupied by Wolves in Packs

Although the estimated area occupied has doubled between 2007 and 2012, the rate of growth for the area occupied has been declining. The extent to which this declining rate of increase represents a population responding to density dependent factors as available habitats become filled, versus a response to hunting and trapping harvest, is unknown.

Estimated Numbers of Wolf Packs

Our estimate for total numbers of wolf packs exceeded the minimum count by 6 to 16% between 2007 and 2012. Such a level of undercount is not unreasonable for elusive carnivores and is within the range of imperfect detection recorded for many other wildlife species and population estimation methods. For example, detection rates of elk during aerial surveys can be less than 20% (e.g., Vander Wal et al 2011), and detection rates of elk during winter surveys on the open winter ranges in southwestern Montana have been estimated at 44-89% (Hamlin and Ross 2002). Becker et al. (1998) produced a population estimate 48% higher than the number of individual wolves they observed, even though they assumed that they detected all wolf tracks in the area they surveyed.

Our estimate of the number of wolf packs assumes that territory size is constant and equal across space. If territory sizes were actually larger in some years or some areas, then the estimated number of packs in those years or areas would have been biased high, and if territory sizes were actually smaller in some years or some areas, then the pack estimates would have been biased low in those years or areas. Similarly, our estimates of territory overlap were indirect indices rather than field-based observations based on high-quality telemetry data. In future applications of this technique, the assumption of constant territory sizes could be relaxed by modeling territory size as a flexible parameter, incorporating estimates of inter-pack buffer space or territory overlap into estimates of exclusive territory size, and incorporating spatially and temporally variable territory size predictions into estimates of pack numbers.

The estimated number of packs exceeded the minimum number of verified packs to some degree because verified packs did not include border packs attributed to other states or Canada that spent time in Montana and could have been recorded by hunters. We only included verified border packs included in the Montana summaries in comparing our estimates to minimum counts. Also, the minimum number of packs verified was for the end of the year, and wolf population estimates derived from hunter observations represented the deer and elk hunting season in October- November, a period of time before some natural and human-caused wolf mortalities occurred.

Estimated Numbers of Wolves

Our estimate for total numbers of wolves exceeded the minimum count by to 37% between 2007 and 2012. The degree of difference exceeds that of packs because in addition to undocumented packs, it incorporates undocumented individuals within known packs. This degree of difference between minimum counts and our population estimate remains within that observed in other studies of wolves (Becker et al. 1998) or more common ungulate species (Hamlin and Ross 2002, Vander Wal et al. 2011).

Our estimate of the number of wolves is dependent on several assumptions that need to be examined further. First, our population estimate assumes that missed packs are the same size as verified packs. If missed packs are smaller (e.g., recently established packs or packs interspersed among known packs), then our estimated number of wolves would be biased high. Also, our estimate assumes that pack size is constant and equal across space. Pack sizes that were actually larger in some years or some areas would induce a negative bias in our estimates of wolves in those years or areas, and pack sizes that were actually smaller in some years or some areas would induce a positive bias in our estimates of wolves in those years or areas. Finally, our population estimate is for wolves in groups of 2 or more and does not factor lone or dispersing wolves into the population estimate. Various studies have documented that on average 10-15% of wolf populations are composed of lone or dispersing wolves (Fuller et al. 2003). The state of Idaho inflates their estimates by 12.5% to account for lone wolves (Idaho Department of Fish and Game and Nez Perce Tribe 2012) and Minnesota inflates their estimate by 15% (Erb 2008). In the future, lone or dispersing wolves could be incorporated into the Montana population estimate in various manners.

The estimated number of wolves exceeded the minimum number of verified wolves to some degree because verified wolves did not include individuals associated with border packs attributed to other states or Canada that spent time in Montana and could have been observed by hunters. As with packs, the minimum number of wolves verified was for the end of the year, and wolf population estimates derived from hunter observations represented a period of time before some natural and human-caused mortalities occurred.

Future applications of this modeling and population estimation technique will include incorporation of harvest (locations and number of harvested wolves) effects on wolf occupancy, territory sizes and overlap, and pack sizes. Incorporation of harvest as a model covariate for each of these aspects of wolf population size will enable a formal assessment of the effects of harvest on wolf populations in Montana. This strategy will also allow for predictions of the effects of different seasons or harvest quotas on wolf populations, to provide information to decision makers as they set wolf hunting and trapping seasons in coming years. Therefore, in addition to its use for monitoring and wolf population estimation, the technique described here also will provide utility for directly informing decisions about public harvest of wolves.