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Population Ecology

Estimating Occupancy and Predicting Numbers of Gray Wolf Packs in Montana Using Hunter Surveys

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ABSTRACT Reliable knowledge of the status and trend of carnivore populations is critical to their conservation and management. Methods for monitoring carnivores, however, are challenging to conduct across large spatial scales. In the Northern Rocky Mountains, wildlife managers need a time- and cost-efficient method for monitoring gray wolf (*Canis lupus*) populations. Montana Fish, Wildlife and Parks (MFWP) conducts annual telephone surveys of >50,000 deer and elk hunters. We explored how survey data on hunters' sightings of wolves could be used to estimate the occupancy and distribution of wolf packs and predict their abundance in Montana for 2007–2009. We assessed model utility by comparing our predictions to MFWP minimum known number of wolf packs. We minimized false positive detections by identifying a patch as occupied if 2–25 wolves were detected by ≥3 hunters. Overall, estimates of the occupancy and distribution of wolf packs were generally consistent with known distributions. Our predictions of the total area occupied increased from 2007 to 2009 and predicted numbers of wolf packs were approximately 1.34–1.46 times the MFWP minimum counts for each year of the survey. Our results indicate that multi-season occupancy models based on public sightings can be used to monitor populations and changes in the spatial distribution of territorial carnivores across large areas where alternative methods may be limited by personnel, time, accessibility, and budget constraints. © 2013 The Wildlife Society.

KEY WORDS *Canis lupus*, carnivores, gray wolf, monitoring, northern Rocky Mountains, occupancy, public sightings.

Carnivores are difficult to monitor on large spatial scales because they live at low densities and are often nocturnal, secretive, and difficult to observe (Crete and Messier 1987, Schonewald-Cox et al. 1991, Mills 1996). A variety of effective field survey methods (e.g., aerial counts, scat and track surveys, radiotelemetry, camera trapping, genetic sampling) have been developed for monitoring carnivores (Crete and Messier 1987, Gros et al. 1996, Becker et al. 1998, Gompper et al. 2006), yet most of these techniques are impractical to apply across large spatial scales given constraints on personnel, time, accessibility, and budgets (Potvin et al. 2005). In contrast, public sightings can be used to monitor carnivore populations across large areas (Berg et al. 1983, Crete and Messier 1987, Fanshawe et al. 1991, Gros et al. 1996); public sightings, however, often suffer from misidentifications and unreliable reporting (Gros et al. 1996).

Direct (e.g., live capture) and indirect (e.g., camera traps or track surveys) monitoring techniques provide detection–non-detection data, which can be used in an occupancy model (MacKenzie et al. 2006) to estimate the probability that landscape patches are occupied by a species of interest (i.e., occupancy). Occupancy modeling uses the patterns of detections and non-detections over multiple visits to individual patches on the landscape to estimate occupancy rates while accounting for imperfect detection of the species of interest (MacKenzie et al. 2002, 2006; Bailey et al. 2004). Occupancy models can be developed for a single season, or patch-specific colonization and extinction probabilities can

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be estimated by combining sampling occasions from >1 season in a multi-season model (MacKenzie et al. 2006).

In territorial species, estimates of occupancy can be used to predict the abundance of territorial individuals or groups (MacKenzie et al. 2006). When the total area occupied by a territorial species is divided by mean territory size, the resulting value is an estimate of the number of territorial individuals or groups in the study area. Using estimates of occupancy to predict abundance in this manner is based on the assumptions that mean territory size is constant, minimal overlap occurs among territories, and minimal unoccupied space occurs between territories.

Our goal was to develop a time- and cost-efficient monitoring protocol for gray wolves (*Canis lupus*) across the state of Montana using an occupancy modeling framework. Gray wolves have been a species of conservation interest in the United States since they were listed as endangered in the lower 48 states (except Minnesota where wolves were listed as endangered in 1974 and downgraded to threatened in 1978) by the United States Fish and Wildlife Service (USFWS) in 1973. The recovery goal for wolves in the Northern Rocky Mountains of the United States (Northern Rockies) was ≥300 wolves and ≥30 breeding pairs (i.e., an adult male and female that have produced ≥2 pups that survive until 31 Dec of their birth year) evenly distributed among the recovery areas for 3 consecutive years (USFWS 1994). This recovery goal has been exceeded since 2002 and, as a result, in May 2011 wolves in the Northern Rockies (and subsequently in Wyoming in 2012) were removed from the Federal List of Endangered and Threatened Wildlife (USFWS 2011).

The USFWS and state agencies attempted to capture and radio-collar members of as many wolf packs as possible to monitor wolves in the Northern Rockies during recovery (USFWS et al. 2010). This monitoring technique was assumed to be reliable when a small number of wolf packs inhabited the Northern Rockies, and it produced a near-census of the population. As of 2011, however, the Northern Rockies contained >1,650 wolves in >240 packs (USFWS 2011), and current monitoring now undercounts the true number of wolves and packs to an unknown degree. Radiotelemetry as a comprehensive monitoring technique for this large population is no longer feasible, given the time and financial constraints of state management agencies. To continue monitoring wolves at statewide scales, wildlife managers need a new method for estimating their distribution and abundance.

To create a time- and cost-effective monitoring protocol for wolves in Montana we set 3 objectives: 1) develop a multi-year occupancy model, using hunter observations of wolves, that estimated statewide occupancy and distribution of wolf packs for 2007–2009; 2) evaluate alternative hypotheses regarding factors that could influence wolf pack detection, occupancy, and local colonization and extinction probabilities across the state (Table 1); and 3) use estimates of occupancy to predict the total area occupied by wolf packs in Montana and statewide numbers of wolf packs for 2007–2009. We evaluated the utility of our models by comparing model predictions to Montana Fish, Wildlife, and Park's (MFWP) minimum known number of wolf packs based on field monitoring.

STUDY AREA

Our study encompassed the entire state of Montana although the majority of gray wolves have been documented in western Montana. Western Montana consists of large valleys and a portion of the Rocky Mountains in the United States. Agricultural lands, rangelands, and grasslands were intermixed with forested areas that tend to occur at higher elevations. The major prey species were elk (*Cervus elaphus*), white-tailed deer (*Odocoileus virginianus*), mule deer (*O. hemionus*), and moose (*Alces alces*; USFWS 1994). Other predators in the area included cougars (*Puma concolor*), coyotes (*C. latrans*), grizzly bears (*Ursus arctos*), bobcats (*Lynx rufus*), and black bears (*U. americanus*). Cattle and sheep occurred throughout the area with the exception of most wilderness areas and Yellowstone and Glacier National Parks (USFWS 1994). Land ownership was a mixture of primarily public and some private lands with hunting permitted on all public land outside of National Parks.

METHODS

Hunter Surveys

We used hunter survey data as the detection–non-detection data for our occupancy model. In Montana, hunters spend

Table 1. Mean values of covariates included in multi-year occupancy models for gray wolf packs in Montana, USA 2007–2009, and hypothesized relationships between covariates and a wolf pack's probability of occupancy (ψ), local colonization (γ), local extinction (ε), and detection by a hunter (p).

	All years		2007		2008		2009		Hypothesized relationship			
Model covariate	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	ψ	γ	ε	p
Elevation (km)	1.29	0.02							−	−	+	
Slope (°)	4.94	0.19							−	−	+	
Forest (%)	0.25	0.01							+	+	−	−/+
Low-use 2-wheel drive roads (km roads/km^2)	0.38	0.01							−/+	−/+	−/+	+
Low-use 4-wheel drive roads (km roads/km^2)	0.14	0.01							−/+	−/+	−/+	+
Bull elk harvest (harvest/km^2)			0.04	0.002	0.03	0.001	0.03	0.001	+	+	−	
Buck deer harvest (harvest/km^2)			0.20	0.004	0.18	0.004	0.17	0.003	+	+	−	
Hunter effort elk (hunter days/km^2)			2.38	0.12	2.55	0.13	2.42	0.12			+	
Hunter effort deer (hunter days/km^2)			2.91	0.11	3.12	0.12	3.01	0.11			+	
Proportion of cell in Montana	0.92	0.01							+	+	−	+

approximately 2 million days every fall hunting deer and elk (MFWP, unpublished results) providing a large number of potential observers of wolves on all public land in Montana (excluding National Parks and Indian Reservations, approx. 10% of state). Annual, random telephone surveys are conducted by MFWP of approximately 50–80,000 resident deer and elk license holders, a sample large enough to ensure hunters from each hunting district across the entire state are sampled (Lukacs et al. 2011). Montana has 161 deer and elk hunting districts, which range in size from 44 km^2 to 18,689 km^2 with a mean of 2,115 km^2. Beginning with the 2007 hunting season, the following questions were asked of any resident sampled for $\geq$1 deer or elk hunting license: 1) "Did you see $\geq$1 live wolf while hunting deer or elk during the archery or rifle season?" and 2) "If yes, provide the hunting district and a landmark close to where wolves were seen, the number of wolves seen, and the date wolves were seen."

We used the 5-week general rifle season as our survey period; each week represented a sampling occasion. In 2007, the survey period was from 21 October to 25 November and in 2008 and 2009, the survey period was from 26 October to 30 November. We dropped observations of single wolves to minimize misidentifications and increase the chance that our inferences referred to established wolf packs. We dropped observations of >25 wolves because they were likely reports of wolves from multiple sighting occasions. We created point locations for individual hunter observations based on the provided landmarks (e.g., creeks and mountains) and the hunting district where wolves were seen using National Geographic TOPO! software (NGHT, Inc., Evergreen, CO). When creeks or minor rivers were provided as landmarks, we plotted point locations at the creek or river's confluence with a larger water body. When we could not clearly find the referenced landmark (e.g., poor description or unknown site), we dropped that observation from the wolf locations database (<5% of locations). We imported point locations into ArcGIS 9.3.1 (ESRI, Redlands, CA) for analyses.

After developing point files of hunter observations, we overlaid these points on a 600-km^2 grid spanning Montana and assigned locations to individual grid cells. We used a 600-km^2 grid cell size because it was equal to the estimated mean wolf pack territory size in Montana (Rich et al. 2012). We assumed the occupancy status of each patch (i.e., 600-km^2 grid cell) remained constant during the 5-week survey period. For each patch, we determined how many hunters observed 2–25 wolves during each sampling occasion in 2007, 2008, and 2009. We assumed $\geq$1 hunter was present in each patch during each sampling occasion (i.e., week) because of the large number of widely distributed deer and elk hunters in Montana (>250,000/year) and because a sample of hunters was included in the surveys from each hunting district.

Assessing False Positives

Standard occupancy estimation procedures assume that false positive detections do not occur (MacKenzie et al. 2006). However, because our data were based on hunters' observations of wolves, false positive detections (e.g., misidentifications or unreliable reports) were likely. We used 3 criteria to assemble 3 different sets of detection–non-detection encounter histories. We recorded a 1 for each patch where 2–25 wolves were seen by 1) $\geq$1 hunter, 2) $\geq$2 hunters, or 3) $\geq$3 hunters in a sampling occasion and a 0 for sampling occasions where detection criteria were not met. For example, if 2 wolves were detected by 2 hunters in week 1, 1 hunter in week 2, 0 hunters in week 3, and 4 hunters in week 4, the corresponding encounter histories would be 1) 1101, 2) 1001, and 3) 0001. For each encounter history, if the detection criterion was met in any 1-week sampling occasion, we recorded a positive identification in that patch for that week. We then estimated false positive detection probabilities for each criterion using the methods of Miller et al. (2011). The Miller et al. (2011) estimator relied on 2 data sets; the primary data set included false positive detections and the secondary data set, based on known locations of radio-collared wolf packs (Sime et al. 2008, 2009, 2010), that was assumed to not include false positive detections. We used the approach of Miller et al. (2011) with the secondary data set to estimate false positive detections in the primary data set based on each of the 3 sets of encounter histories. We then selected the criteria that maintained the greatest amount of information while minimizing false positive detections for our occupancy analyses.

Model Covariates and Associated Hypotheses

We developed a suite of a priori hypotheses regarding factors that could influence wolf pack detection, occupancy, and local colonization and extinction probabilities across Montana (Table 1). We hypothesized that environmental features including forest cover, elevation, and slope could influence occupancy and local colonization and extinction probabilities of wolf packs because wolves are associated with forested areas (Mladenoff et al. 1995, Oakleaf et al. 2006, Jedrzejewski et al. 2008) with low elevations and slopes (i.e., low levels of ruggedness; Paquet et al. 1996, Oakleaf et al. 2006, Whittington et al. 2008) where ungulates are more accessible and abundant during winter (Table 1). We also anticipated that forest cover could influence detection probability, either positively because hunters are more abundant in forests or negatively because wolves are less visible in forests (Table 1). We estimated percent forest cover in each patch by reclassifying 90-m^2 land cover pixels into forest and non-forest (Gap Analysis Project, Wildlife Spatial Analysis Lab, University of Montana). We derived slope and elevation data from 200-m^2 resolution digital elevation models (DEM; U.S. Geological Service National Elevation Dataset) and calculated mean slope and elevation in each patch.

We hypothesized that occupancy and local colonization and extinction probabilities of wolf packs could also vary with road densities, either negatively because wolves are often less abundant in areas with high road densities (Mech et al. 1988, Mladenoff et al. 1995, Jedrzejewski et al. 2008; Table 1) or positively because wolves often use low-use roads as travel

corridors (Thurber et al. 1994, Paquet et al. 1996, Whittington et al. 2008; Table 1). Additionally, we expected that road densities could positively influence detection because roads increase hunter access (Table 1). We divided roads (U.S. Census Bureau Geography Division 2003, U.S. Department of Agriculture Forest Service 2007) into 4-wheel drive (4WD) or 2-wheel drive (2WD). We assumed roads in areas with human population densities >25 people/km^2 represented high-use roads and removed these roads from our analysis. We then calculated patch-specific low-use 4WD and low-use 2WD road densities.

We hypothesized that occupancy and local colonization probabilities would be positively related to prey density and local extinction probabilities would be negatively related to prey density (Fuller et al. 2003; Table 1). We used buck deer and bull elk harvest/km^2 as indices of deer and elk density because estimates of deer and elk abundance were not uniformly available across Montana. Harvest of antlered deer and elk are often positively correlated with deer and elk abundance and can be an index of population size (Wood et al. 1989, Hamlin and Ross 2002, Dusek et al. 2006). We calculated annual buck deer and bull elk harvest density for each hunting district using harvest statistics from MFWP. In reservations and national parks we estimated indices of deer and elk density by averaging buck deer and bull elk harvest densities in hunting districts along their respective borders. We then calculated area-weighted mean harvest densities of deer and elk for each patch. We also hypothesized detection of wolves by hunters would increase with hunter effort (Table 1). We used estimates of hunter effort for deer and elk from MFWP, normalized by the size (km^2) of each hunting district, and calculated area-weighted hunter effort for each patch. We assumed our estimates of bull elk harvest, buck deer harvest, and hunter effort were constant across their respective hunting districts.

We also included the proportion of the cell in Montana (i.e., area) as a covariate for each of the model parameters to evaluate whether partial cells on the border of Montana had an effect on our estimates. We hypothesized that occupancy, local colonization, and detection probabilities would be positively related to area (Table 1); the larger the area the greater the likelihood it will be occupied or colonized by a wolf pack and the greater the likelihood wolves will be observed by hunters. Lastly, we considered differences in detection among weeks.

Estimation of Wolf Pack Occupancy and Distribution

To estimate the occupancy and distribution of wolf packs from 2007 to 2009 in Montana, we used multi-season occupancy models. Rather than develop an initial comprehensive model set to estimate the probabilities of detection, occupancy, and local colonization and extinction, we used a multi-step process to identify our top model(s); we conducted model selection using the UNMARKED package in Program R (Fiske and Chandler 2011). We focused on models for detection probability first, followed by initial occupancy, local colonization, and local extinction. For each parameter, we identified the best model (while the other parameters were held constant using their most general parameterizations) and used that model structure when evaluating alternative model forms for each additional parameter. To identify the best models, we first evaluated univariate models for each parameter where we had a priori hypotheses. After determining the best univariate model for a given parameter, we then considered combinations of covariates in the top univariate models that may have had biological relevance and did not include covariates that were highly correlated ($r < 0.70$). In all cases, we used Akaike's Information Criterion (AIC) to rank models (Burnham and Anderson 2002). We selected the model with the lowest AIC value as our top model.

We used our top model to generate patch-specific estimates of occupancy (2007–2009), local colonization (2007–2008, 2008–2009), local extinction (2007–2008, 2008–2009), and detection (2007–2009) probabilities using the UNMARKED package in Program R (Fiske and Chandler 2011). For unsurveyed areas, including reservations and national parks, we estimated unconditional occupancy (i.e., the probability that grid cell i is occupied based on covariate values associated with the cell; MacKenzie et al. 2006). For sampled sites, we calculated conditional estimates using finite sampling inference (Royle and Dorazio 2008). These estimates assumed no false positives and were conditional on the encounter history. For sampled sites where wolves were seen, the probability of occupancy was 1. For sampled sites where wolves were not seen, estimates of occupancy (i.e., probability wolves were there but not seen) were made conditional on the encounter history and the associated covariate values.

To evaluate our estimates of the distribution of wolf packs, we compared patch-specific estimates of occupancy to the distribution of known wolf packs in 2007, 2008, and 2009 (Sime et al. 2008, 2009, 2010). For each year, we divided the patch-specific estimates of occupancy into 3 classes based on natural breaks; mean values for the upper and lower class breaks were 0.6 and 0.2. We determined how many patches with occupancy probabilities >0.6 (i.e., high probability wolf pack occupied patch) overlapped or were within 13.82 km of a known wolf pack territory; 13.82 km is the radius of an average-sized, circular territory in Montana (Rich et al. 2012). We also determined how many patches with occupancy probabilities <0.2 (i.e., low probability wolf pack occupied patch) overlapped or were within 13.82 km of a known wolf pack territory.

Prediction of Total Area Occupied and Number of Wolf Packs

We assumed minimal overlap occurred among pack territories and minimal unoccupied space between territories. This type of spacing typically results from territorial behavior in established wolf populations (Mech and Boitani 2003). To estimate the total area occupied by wolf packs in Montana in 2007, 2008, and 2009, we multiplied patch-specific estimates of occupancy by their respective patch size (e.g., 600 km^2) and summed these values across the state. To estimate the number of wolf packs, we divided our estimates for the total

area occupied by the mean territory size of wolves in Montana (600 km^2; Rich et al. 2012). Because our patch sizes were equal to the mean territory sizes of wolves in Montana, this was equivalent to multiplying the predicted occupancy for each patch by the size of the patch, then summing these values for each year. We obtained confidence intervals for patch-specific estimates of occupancy probabilities using the parametric bootstrap function "parboot" in UNMARKED. For each set of bootstrapped estimates, we calculated area occupied and the number of wolf packs. We obtained the 95% confidence intervals for these values from the distribution of estimates calculated from the bootstrapping procedure. The parametric bootstrap simulates encounter histories for each site and each bootstrap sample using the estimated sampling uncertainty associated with the model coefficient estimates as well as the binomial processes associated with initial occupancy, local colonization and extinction, and detection based on our top model. Our inference was conditional on the years we surveyed and the detection histories we observed, such that uncertainty in our estimates of the number of packs arose from cells where wolves were not observed or where surveys were not conducted.

We compared predictions of the numbers of wolf packs to MFWP minimum known number of wolf packs. Minimum counts were made by MFWP by 31 December of every year based on aerial surveys of radio collared wolf packs; howl, track, and scat surveys; and field verifications of reports from the public, private landowners, and natural resource agency personnel (Sime et al. 2010). Our minimum counts included wolf packs residing in the state, border packs, and packs that were removed because of livestock depredations from October to December (Sime et al. 2008, 2009, 2010).

We assessed the utility of our model predictions of the number of wolf packs by the degree to which predictions exceeded minimum counts. We did not expect differences between minimum counts and the true number of wolf packs to be large but did expect model predictions to be greater than minimums. We could not measure utility by placing a practical limit on the degree to which model predictions exceeded minimum counts because we could not quantify the difference between minimum counts and the true population size of wolves. For example, all wolf packs undetected in a given year were not necessarily detected in subsequent years. Thus, we could not account for the degree to which minimum counts underrepresented actual population sizes by comparing our model predictions to the number of new packs discovered in subsequent years. Despite this limitation, minimum counts represented the best available information, which was of sufficient quality to meet federal Endangered Species recovery criteria standards.

RESULTS

In 2007, 2008, and 2009, MFWP personnel surveyed 50,370, 82,411, and 81,117 deer and elk hunters, respectively; 2.40%, 3.48%, and 3.07% saw 2–25 wolves during the 5-week survey period, respectively. Of the hunters who saw $\geq$1 wolf, <1% reported seeing >25 wolves from 2007 to 2009. Of the hunters who reported seeing 1–25 wolves, the median number of wolves observed was constant among the years (median = 2, range = 1–25).

Using the approach of Miller et al. (2011), we estimated the rate of false positive detections as 0.063–0.087, 0.004–0.005, and <0.001 when classifying a patch as occupied if 2–25 wolves were seen by $\geq$1, $\geq$2, or $\geq$3 hunters in a week, respectively. For occupancy analyses, we therefore classified patches as occupied if 2–25 wolves were seen by $\geq$3 hunters in a week to minimize false positive detections.

The top model of wolf pack occupancy (Table 2) showed a positive association between the initial probability that a wolf pack occupied an area and forest cover, elevation, low-use 2WD roads, and the proportion of the cell in Montana (Table 3). The probability that an unoccupied patch became occupied by a wolf pack in the following year was positively related to forest cover, low-use 2WD roads, bull elk harvest, and the proportion of the cell in Montana (Table 3). The probability that an occupied patch became unoccupied in the following year was negatively related to forest cover and elevation (Table 3). Lastly, the probability that a wolf was seen by a hunter during a 1-week sampling occasion was positively related to hunter effort for elk, forest cover, and the

Table 2. Top models from a multi-year occupancy analysis for gray wolf packs in Montana, 2007–2009; ψ = initial occupancy, γ = local colonization, ε = local extinction, p = detection by a hunter. We considered models within 4 ΔAIC to have support; log(l) = maximized log-likelihood, K = number of estimable parameters, ΔAIC = differences in Akaike's Information Criterion, and ω_i = Akaike weights

Model[a]	−2Log(l)	K	ΔAIC	ω_i
ψ(forest + elev + 2wd rds + area*) γ(forest + bull elk harvest + 2wd roads + area) ε(forest + elev) p(hunter effort elk + forest +area + week*)	3,026.43	31	0	0.41
ψ(forest + elev + 2wd rds + area*) γ(forest + bull elk harvest + 2wd roads + area) ε(forest) p(hunter effort elk + forest + area + week*)	3,030.48	30	2.05	0.15
ψ (forest + elev + 2wd rds + area*) γ(forest + bull elk harvest + 2wd roads + area) ε(forest + area*) p(hunter effort elk + forest + area + week*)	3,029.27	31	2.84	0.10

* 95% CI overlapped 0.00.

[a] Forest = % forest cover; elev = elevation (km); 2wd rds = km of low-use 2-wheel drive roads/km^2; area = proportion of grid cell inside of Montana; bull elk harvest = harvest/km^2; hunter effort elk = hunter days/km^2.

proportion of the cell in Montana, and this probability changed among sampling occasions (Table 3). The mean probability of detection (i.e., detection during a 1-week sampling occasion for average hunter effort and forest cover in a patch occupied by wolves) was 0.11 (SE = 0.022, 95% CI = 0.08–0.17) across Montana for 2007–2009.

Overall, occupancy estimates of the distribution of wolf packs were consistent with the field-documented distribution of wolf packs in Montana (Fig. 1). Eighty-seven percent, 89%, and 85% of patches with occupancy probabilities >0.6 overlapped known wolf pack territories or were within 13.82 km in 2007, 2008, and 2009, respectively. Comparatively, 14%, 13%, and 13% of patches with occupancy probabilities <0.2 overlapped or were within 13.82 km of known wolf pack territories in 2007, 2008, and 2009, respectively.

We predicted 18%, 24%, and 25% of Montana was occupied by wolf packs in 2007, 2008, and 2009, respectively (Table 4). The minimum number of wolf packs known to be in Montana fell below the 95% confidence intervals for our predictions in 2007, 2008, and 2009 (Fig. 2; Table 4). The predicted numbers of wolf packs were 1.34–1.46 times the minimum counts for each year of the survey (Fig. 2; Table 4). The estimated 95% confidence intervals had the largest range in the first year (2007) of the study when fewer wolves were observed by hunters and approximately 30,000 fewer hunters were surveyed than in 2008 or in 2009.

DISCUSSION

Methods for directly or indirectly monitoring carnivore populations are costly and time-intensive, especially at large spatial scales (Crete and Messier 1987, Gros et al. 1996, Potvin et al. 2005, Gompper et al. 2006). We found occupancy models based on hunter observations of wolves can provide wildlife managers with information to estimate the distribution of wolf packs and predict the number of wolf packs at scales commensurate with state-run wildlife management programs. These models can provide a time- and cost-effective alternative to historical monitoring of wolves in the Northern Rockies and help state agencies monitor wolf population status and distribution at large scales.

Occupancy models assume that detection of a species indicates presence and formally account for imperfect detection (MacKenzie et al. 2002). False positive detections, however, are an inherent component of many datasets (Gros et al. 1996, McClintock et al. 2010). When using avian and anuran calls, highly trained observers can misclassify species as present (McClintock et al. 2010), and when using public sightings of a species, the public can misidentify the species or provide false claims of seeing the species (Gros et al. 1996). We hypothesized that by requiring a greater number of hunters to see wolves in a patch during a given week, we would reduce the number of false positive observations. By only classifying a patch as occupied if ≥3 hunters saw 2–25 wolves, we reduced false positive detections to very low levels while retaining sufficient observations to generate estimates of occupancy comparable to the known occupancy of wolf packs based on field monitoring. As a result, we provide dependable estimates indicating that 30 years after wolf recovery began in Montana and 15 years after wolves were reintroduced into neighboring jurisdictions, wolves now occupy approximately 25% of Montana.

Overall, our estimates of the occupancy and distribution of wolf packs were consistent with the known occupancy and distribution of wolf packs in Montana based on field monitoring (Fig. 1; Sime et al. 2008, 2009, 2010). Our model predicted high probabilities of occupancy in areas where no known wolf packs existed such as west-central (i.e., between Helena and Butte) and far southwestern Montana (Fig. 1). Hunters reported sighting wolves in these areas; current field efforts, however, have not documented packs in these areas.

Table 3. Parameter estimates ($\hat{\beta}$) from the top model of a multi-year occupancy analysis for gray wolf packs in Montana, USA 2007–2009; ψ = initial occupancy, γ = local colonization, ε = local extinction, p = detection by a hunter.

Parameter	Variable	$\hat{\beta}$	$\hat{SE}$
ψ	Intercept	−10.42	1.90
	% Forest	3.86	0.81
	Elevation (km)	2.32	0.52
	Low-use 2-wheel drive roads (km/km^2)	5.31	1.35
	Proportion of cell in Montana	2.01	1.11
γ	Intercept	−8.09	1.33
	% Forest	5.31	0.78
	Low-use 2-wheel drive roads (km/km^2)	2.44	1.04
	Bull elk harvest/km^2	17.48	4.20
	Proportion of cell in Montana	2.57	1.08
ε	Intercept	2.77	1.65
	% Forest	−3.71	1.14
	Elevation	−1.69	0.84
p	Intercept	−5.31	0.63
	Hunter effort elk/km^2	0.18	0.02
	% Forest	1.54	0.25
	Proportion of cell in Montana	2.33	0.56
	Week[a]		

[a] Fourteen-week parameters and a reference category represented the 3 years with 5 sampling occasions each.

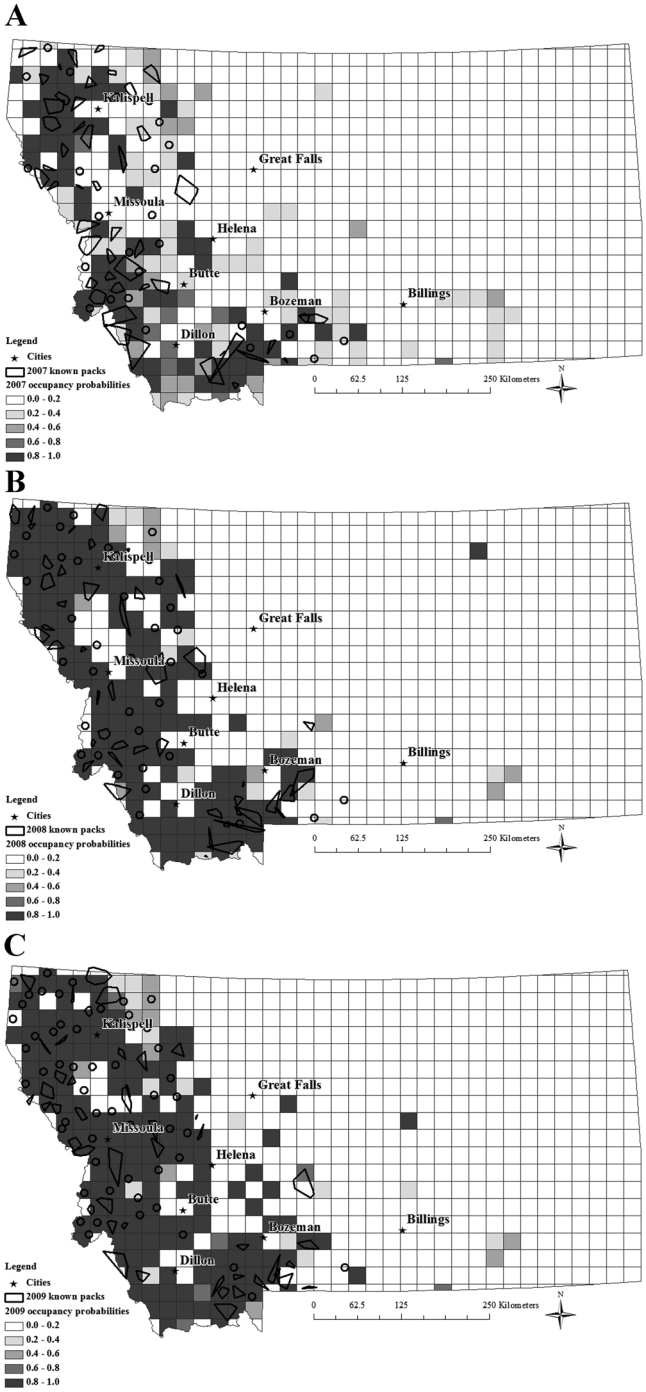

Figure 1. The predicted probability each 600-km^2 patch in Montana, USA was occupied by wolves in (A) 2007, (B) 2008, and (C) 2009. We estimated occupancy probabilities using multi-season occupancy models with hunter surveys as the sampling method and forest cover, low-use 2-wheel drive road density, elevation, and proportion of the cell in Montana as predictor variables. Conditional probabilities of occupancy are displayed for the 633 sampled sites and unconditional probabilities are displayed for the 55 unsampled sites (i.e., National Parks and reservations). Montana Fish, Wildlife and Parks (MFWP) known wolf packs were based on field monitoring; pack territories displayed as small circles had insufficient relocation data to estimate territory boundaries.

Hunter sightings may have been of transient wolves and these areas may not be able to sustain packs. Alternatively, transient wolves may be the front edge of a colonization process or hunters could have seen wolf packs in areas where packs have yet to be documented or monitored by current field efforts. Continued field monitoring efforts can be used to evaluate the likelihood of each of these possibilities.

The probability that an animal will occupy, colonize, or become extinct from an area is not constant across time or space and may vary predictably with local ecological factors. As expected, we found the probability a site was occupied and the probability an unoccupied patch was colonized by a wolf pack in the following year increased with the proportion of the cell in Montana (i.e., area), forest cover, and low-use 2-wheel drive road density (Tables 2 and 3) suggesting wolves prefer to establish territories in areas with cover and possibly where travel is facilitated by forest roads. Alternatively, roads could have been positively related to occupancy and local colonization because they represented low-use areas as we only included roads from areas with $\leq$25 people/km^2. We also found wolf packs were more likely to colonize areas that had high densities of bull elk harvest (Tables 2 and 3). Our finding that occupancy and elevation were positively correlated and that local extinction and elevation were negatively correlated (Table 3) is likely because the majority of wolves observed by hunters were in western Montana, where elevations are relatively high. Elevation is likely a surrogate for a suite of other, unmeasured covariates that distinguish western and eastern Montana.

Bull elk and buck deer harvest densities did not explain much variation in initial occupancy (2007) probabilities (Table 2). Harvested ungulate densities may not have been accurate indices of deer and elk density if human access, weather conditions, and harvest regulations overrode ungulate population levels in influencing annual harvest (Hamlin and Ross 2002). Additionally, ungulate densities, as indexed by harvest estimates, may not have influenced wolf pack occupancy if ungulate densities were high enough to support wolves across western Montana (i.e., not limiting).

Detection probability may be influenced by local density of the study species, behavior, seasonality, environment, weather, or sampling effort (Royle and Nichols 2003, Bailey et al. 2004). Our results showed wolf packs were more likely to be seen by hunters in forested areas where hunter effort was high (Table 3). Detection was also positively related to the proportion of the cell that was in Montana and varied among sampling weeks (Table 3). We did not detect any year-to-year differences in detection probabilities for 2007–2009.

To evaluate our predictions of the number of wolf packs, we compared them to MFWP's annual minimum known number of wolf packs. When we used a detection criterion that minimized false positives and accounted for false negatives (i.e., classifying a patch as occupied only if $\geq$3 hunters saw 2–25 wolves), our predictions of numbers of wolf packs were 1.40, 1.46, and 1.34 times greater than minimum counts in 2007, 2008, and 2009, respectively (Table 4). We did not expect differences between minimum counts and the true number of wolf packs to be substantial because of the intensive monitoring of wolves in Montana during this period (Sime et al. 2008, 2009, 2010). We did expect, however, that our predictions would be greater than

Table 4. Predicted area occupied by wolf packs and predicted numbers of wolf packs in Montana from 2007 to 2009. We calculated mean predictions based on the average territory size of 600 km^2 and conditional probabilities of occupancy for the 633 sampled sites and unconditional probabilities from the 55 unsampled sites. We obtained median and upper and lower 95% confidence intervals from the parametric bootstrap. We compared predicted numbers of wolf packs to the Montana Fish, Wildlife and Parks minimum known number of wolf packs in the state (FWP min).

	Predicted area occupied (km^2)				Predicted no. of wolf packs				
	Mean	Median	Lower CI	Upper CI	FWP min	Mean	Median	Lower CI	Upper CI
2007	69,000	68,400	55,800	85,800	82	115	114	93	143
2008	89,400	85,200	77,400	95,400	102	149	142	129	159
2009	94,800	93,600	84,000	102,600	118	158	156	140	171

minimum counts as perfect documentation of wolf packs in the field is improbable. Our findings support the perception that wolf populations in Montana are in fact larger than the MFWP minimum counts at the statewide scale. Our method for predicting the abundance of wolf packs, however, required us to make several assumptions and had associated limitations.

Close examination of the inferential limitations of predicting numbers of wolf packs from occupancy data is warranted. Our method of predicting numbers of wolf packs included 3 key assumptions. The first assumption was that our use of 600-km^2 as the mean territory size of wolf packs in Montana was accurate and constant from 2007 to 2009. Territory sizes should be monitored if occupancy estimates are used to predict wolf pack numbers. This assumption could be relaxed by incorporating models that explain spatial variation in wolf territory sizes, in particular, influential factors that are likely to vary through time such as anthropogenic mortality (e.g., Rich et al. 2012). Our estimates of uncertainty could also be improved by incorporating uncertainty in estimates of mean territories sizes. Secondly, we assumed minimal overlap occurred among territories of adjacent wolf packs as has been demonstrated by previous field-based wolf research (Mech and Boitani 2003). We do not believe this assumption was violated as data from radio-collared wolf packs and field efforts in Montana have shown minimal overlap among adjacent pack territories. Our third assumption was that unoccupied space between pack territories was minimal. Some spatial separation of wolf packs along territory borders is common due to their territorial nature (Mech and Boitani 2003). By not accounting for inter-pack buffer space within occupied wolf habitat, our predictions of the number of wolf packs would have been positively biased. An approach to correcting our predictions for inter-pack buffer space could be to inflate mean territory sizes to account for unoccupied buffers (e.g., Erb and DonCarlos 2009). Buffers could be estimated using local field studies that determine the proportion of the known, general wolf distribution that is truly occupied by wolf packs (Fuller et al. 1992). Montana-specific estimates of inter-pack buffer space do not currently exist and should be the focus of future research given its potential impact on wolf population estimates.

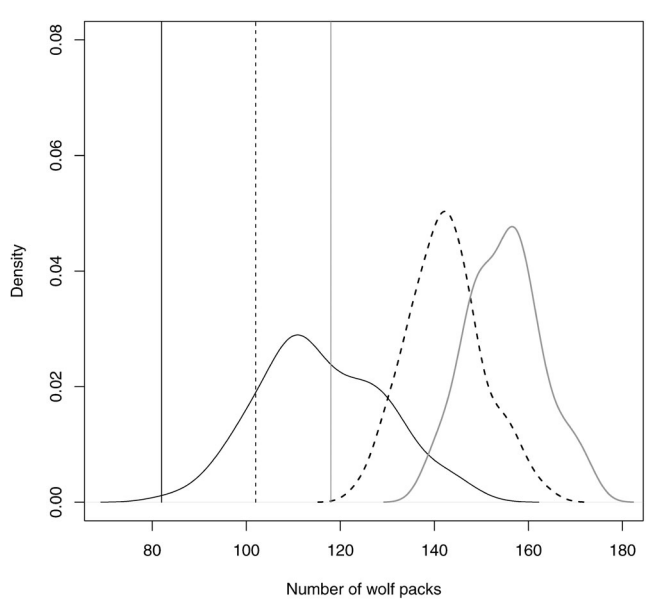

Figure 2. Predicted distribution of number of wolf packs in Montana, USA in the years 2007 (black sold line), 2008 (black dotted line), and 2009 (gray solid line) obtained from the parametric bootstrap. Vertical lines represent minimum counts in 2007 (solid black), 2008 (black dotted), and 2009 (sold gray).

Another possible limitation in our method of predicting numbers of wolf packs from estimates of occupancy is that our predictions apply to the entire state of Montana. The eastern portion of Montana is thought to be unoccupied by wolves, yet each 600-km^2 patch has an associated non-zero probability of occupancy (Fig. 1). In Montana, the wolf population has grown rapidly in recent years and as a result, expanded in distribution. As such, determining the spatial extent at which to estimate occupancy and predict the number of wolf packs is difficult until growth slows and the population becomes well-established.

Although we were confident that our predictions of the number of packs should exceed minimum counts, we could not quantify the utility of our model predictions by placing a defendable upper bound on the number of packs that exist in Montana. We do not have a quantitative estimate of the degree to which minimum counts under-represent the true number of packs in Montana, and we could not reliably generate such an estimate from the field monitoring data. This is a consistent issue for most applications of methods to estimate abundance of free-ranging populations, in that the actual population size is rarely, if ever, known (Seber 1982:561). For this reason, application of methods to estimate population sizes must include examination of the underlying assumptions (Seber 1982:1). We have used

formal, rigorous modeling techniques to produce estimates that are accompanied by measures of precision, building upon similar efforts to estimate wolf distribution and populations across large areas (e.g., Fuller et al. 1992, Erb and DonCarlos 2009). We have also carefully described our methods, their limitations, and the underlying assumptions in our models to estimate wolf pack occupancy and the number of wolf packs, such that these assumptions can be evaluated by our and future work. Therefore, our method is refutable and can be improved as it is applied over time.

MANAGEMENT IMPLICATIONS

Occupancy models based on public sightings offer a monitoring technique for territorial carnivores across large spatial scales where alternative methods may be limited by personnel, time, accessibility, and budget constraints. In addition to documenting the occupancy and distribution of carnivores, multi-season occupancy models can be used to monitor population trends and record changes in spatial distribution (MacKenzie et al. 2006). Occupancy models based on public sightings, however, should not be considered temporally static models that can be used perpetually with confidence. Monitoring is needed to verify whether public sightings continue to be dependable indicators of presence of the carnivore of interest. Information provided by the public may become less reliable over time because of waning interest or attempts to influence estimates by mischaracterizing sightings. We can deal with such change to some degree, as our methods permit estimation of year-specific detection probabilities. Territory sizes also need to be monitored because the use of an occupancy estimate to predict the number of territorial individuals or groups is dependent on the assumption that mean territory size is known (MacKenzie et al. 2006). We recommend occupancy models based on multiple survey methods (Nichols et al. 2008), such as fine-scale survey methods (Stenglein et al. 2010) used in conjunction with hunter surveys, which would help ensure that occupancy estimates and predictions of abundance are robust to weaknesses or changes in any one methodology.

State agencies within the Northern Rockies are legally required to annually document $\geq$100 wolves and $\geq$10 breeding pairs within their respective states for the 5 years following delisting (USFWS et al. 2010). To meet these requirements, we encourage the development of an occupancy model that may also be used to predict the total number of wolves and breeding pairs within a state. We also encourage the development of multi-season occupancy models that directly address false positive observations. This would allow the use of a greater proportion of wolf sighting data for modeling occupancy than we included in our models.

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