Received: 4 December 2021 | Revised: 7 June 2022 | Accepted: 16 June 2022
DOI: 10.1002/eap.2714

ARTICLE

ECOLOGICAL APPLICATIONS
ECOLOGICAL SOCIETY OF AMERICA

Integrating basic and applied research to estimate carnivore abundance

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Funding information
Federal Aid in Wildlife Restoration, Grant/Award Number: W-161-R-1

Handling Editor: Neil Carter

Abstract

A clear connection between basic research and applied management is often missing or difficult to discern. We present a case study of integration of basic research with applied management for estimating abundance of gray wolves (*Canis lupus*) in Montana, USA. Estimating wolf abundance is a key component of wolf management but is costly and time intensive as wolf populations continue to grow. We developed a multimodel approach using an occupancy model, mechanistic territory model, and empirical group size model to improve abundance estimates while reducing monitoring effort. Whereas field-based wolf counts generally rely on costly, difficult-to-collect monitoring data, especially for larger areas or population sizes, our approach efficiently uses readily available wolf observation data and introduces models focused on biological mechanisms underlying territorial and social behavior. In a three-part process, the occupancy model first estimates the extent of wolf distribution in Montana, based on environmental covariates and wolf observations. The spatially explicit mechanistic territory model predicts territory sizes using simple behavioral rules and data on prey resources, terrain ruggedness, and human density. Together, these models predict the number of packs. An empirical pack size model based on 14 years of data demonstrates that pack sizes are positively related to local densities of packs, and negatively related to terrain ruggedness, local mortalities, and intensity of harvest management. Total abundance estimates for given areas are derived by combining estimated numbers of packs and pack sizes. We estimated the Montana wolf population to be smallest in the first year of our study, with 91 packs and 654 wolves in 2007, followed by a population peak in 2011 with 1252 wolves. The population declined ~6% thereafter, coincident with implementation of legal harvest in Montana. Recent numbers have largely stabilized at an average of 191 packs and 1141 wolves from 2016 to 2020. This new approach accounts for biologically based, spatially explicit predictions of behavior to provide more accurate

Diane K. Boyd, Abigail A. Nelson, Robert M. Inman, and Michael S. Mitchell have retired.

estimates of carnivore abundance at finer spatial scales. By integrating basic and applied research, our approach can therefore better inform decision-making and meet management needs.

KEYWORDS
behavioral models, *Canis lupus*, monitoring, Montana, occupancy model, sociality, territoriality, wolves

INTRODUCTION

Wildlife researchers and managers may often assume that basic ecological research that aims to advance scientific theory tends to poorly align with applied management needs (Belovsky et al., 2004; Gavin, 1989; Nudds & Morrison, 1991; Sells et al., 2018). However, basic research that reveals how and why patterns occur in nature can provide an understanding of the levers underlying a system that managers can modify to meet conservation objectives. Compared with research of phenomenological patterns, research focused on biological mechanisms tends to produce inferences that are more reliable beyond the scale of the original study, therefore enhancing utility to conservation (Aarts et al., 2008; Sells et al., 2018).

The recovery of an endangered species presents a unique opportunity to meld basic research and applied management. Endangered populations are typically small and closely monitored, generating detailed data on movement, behavior, and demographics. As an endangered species recovers, their populations ideally grow in abundance and distribution, which often necessitates changes in monitoring methods and therefore the quality and quantity of population-wide data collected. Therefore, integrating basic ecological research into applied management may help address data limitations as the population recovers while also improving the ability to predict population trends and responses to management actions.

Here we present a novel approach to integrating basic research focused on biological mechanisms into wildlife management. Our approach combines an occupancy model, commonly used for wildlife monitoring and conservation, with mechanistic and empirical models based on theory and animal behavior to predict behavioral responses to environmental conditions and resulting space use and population abundance. We use the recovery and long-term management of gray wolves (*Canis lupus*) in the northern Rocky Mountains, USA, as a case study.

After extirpation of gray wolves across most of the contiguous USA in the 20th century, wolf numbers began rebounding in recent decades. Wolf recovery in the United States Northern Rocky Mountains began through natural recolonization of northwest Montana in the 1980s (Ream et al., 1989). Following reintroductions into Yellowstone National Park and Idaho in 1995 and 1996 (Bangs & Fritts, 1996), wolf numbers increased, particularly in Montana and Idaho. Wolves were delisted in those states in 2009 (Bradley et al., 2014; Fritts et al., 1997), relisted in 2010 due to court challenges, and again delisted in 2011 via congressional action. Delisting returned management authority to each state, and harvest seasons were carried out in 2009 and from 2011 onward.

Field monitoring has been an important element of wolf recovery. Intensive monitoring can help managers estimate minimum counts, determine if recovery goals are met, set public harvest seasons, develop livestock depredation policies, evaluate the effects of public harvest and depredation management, and communicate with stakeholders and the public (e.g., Inman et al., 2019). Monitoring elusive large carnivores is challenging, however (Boitani et al., 2012). Minimum counts of packs, wolves, and pups becomes exceedingly difficult and costly once a population recovers to numerous packs spread across wide areas. Furthermore, monitoring often relies on deploying radio collars and Global Positioning System (GPS) collars, which can become increasingly challenging and costly due to the difficulty of capture and frequent collar loss caused by collar failures and mortalities. Public harvest of wolves can increase the frequency in turnover of packs and affect behavioral dynamics (Adams et al., 2008; Brainerd et al., 2008), adding further challenges to monitoring. Importantly, field monitoring alone cannot provide more than a minimum count of wolves in the population.

Wolf abundance estimates remain a key component of monitoring and decision-making in Montana. To date, the state wildlife management agency, Montana Fish, Wildlife and Parks (MFWP), has relied on data from intensive, costly field efforts. Montana's widely distributed, low-density wolf population led MFWP to use a Patch Occupancy Model (POM; Miller et al., 2013; Rich et al., 2013) to estimate annual wolf and pack abundances for 2007–2019, based on area occupied, mean territory size, a territory overlap index, and mean pack size (Inman et al., 2019). Area occupied was estimated annually with an occupancy model, using wolf detections from hunter observations and surveys by MFWP biologists across a statewide observation grid of 600 km^2 cells (Inman et al., 2019; Miller et al., 2013; Rich et al., 2013). Mean territory size was assumed to be 600 km^2 based on past work (Rich et al., 2012). An annual ad hoc overlap index helped account for spatial overlap between neighboring wolf territories, based on the mean number of known packs per 600 km^2 grid cell. Annual mean pack size was estimated from field monitoring using visual surveys, trail cameras, and public reports. Pack abundance was then calculated as the number of territories estimated within the area occupied (i.e., area occupied ÷ 600 km^2 × overlap index). Abundance of wolves living in packs was estimated as the number of packs multiplied by the average pack size. Total wolf abundance was calculated as the abundance of wolves in packs × 1.125 to account for lone and dispersing wolves, based on scientific literature (Fuller et al., 2003).

Whereas estimates of area occupied through POM are reliable (Miller et al., 2013), the reliability of abundance estimates hinge on assumptions about territory size, territory overlap, and pack size (Inman et al., 2019). Assumptions of a fixed territory size with minimal overlap are simplistic; in reality, territories vary spatiotemporally (Sells et al., 2021; Sells & Mitchell, 2020; Sells, Mitchell, Ausband, et al., 2022; Uboni et al., 2015). Furthermore, estimates of mean territory size were largely derived preharvest and at a smaller population size (Rich et al., 2012). Overall abundance estimates would be biased with any temporal changes to mean territory size, as would regional estimates if mean territory size varied spatially. Variations in territory overlap would similarly bias results. Importantly, POM's requirement of developing annual indices for overlap and mean pack size necessitated ongoing intensive monitoring to locate packs and accurately count pack members each year.

Our objective was to integrate basic and applied research to increase accuracy in wolf abundance estimates while reducing reliance on intensive field monitoring. Given a relatively large and secure wolf population size, a more efficient approach would allow limited funding to be used for more pressing conservation needs. We developed an Integrated POM (iPOM) that employs mechanistic and empirical models to incorporate current knowledge about wolf behavior and available data. We used a mechanistic modeling approach that tested hypotheses about how and why wolves select particular territories and predicted territorial behavior across a full range of potential present and future conditions (Sells et al., 2021; Sells & Mitchell, 2020; Sells, Mitchell, Ausband, et al., 2022). We used an empirical model for group size that tested hypotheses about factors influencing pack sizes and enabled predicting patterns in pack sizes across Montana (Sells, Mitchell, Podruzny, et al., 2022). We present here the integration of these models. Our multimodel approach yields estimates of annual wolf population size and characteristics based on the influence of changing conditions on wolf behavior, while drastically reducing costs and intensity of field monitoring efforts. Our approach therefore also provides a case study of the integration of basic research and applied management to inform real-world decision-making for wildlife conservation.

METHODS

Our multimodel approach combined an occupancy model, a mechanistic territory model, and a group size model, as follows (Figure 1).

Study area

Our study area was the state of Montana. Most wolf packs have occurred in western Montana where elevations range from 554–3938 m (Foresman, 2001). In the northwest corner of Montana, the Northern Rockies Ecoregion (NRE) is characterized by dense forests, a maritime-influenced climate, and rugged, mountainous terrain (Figure 2; epa.gov). To the east, the higher-elevation, glaciated terrain of the Canadian Rockies Ecoregion (CRE) transitioned further east to the level and rolling terrain of the northwestern Glaciated Plains Ecoregion (GLPE). In southwestern Montana, the Idaho Batholith Ecoregion (IBE) is mountainous and partially glaciated. To the east, the Middle Rockies Ecoregion (MRE) has rolling foothills with shrubs and grasses along with rugged mountains with conifers and alpine vegetation. Further east, the semiarid, rolling plains of northwestern Great Plains Ecoregion (GRPE) is interspersed with breaks and forested highlands, and the xeric Wyoming Basin Ecoregion (WBE) is dominated by grasses and shrubs. Ungulates include white-tailed deer (*Odocoileus virginianus*), mule deer (*Odocoileus hemionus*), elk (*Cervus canadensis*), and moose (*Alces alces*). Statewide 10-year average abundance estimates were ~201,000 white-tailed deer, 289,000 mule deer, and 177,000 elk (fwp.mt.gov). White-tailed deer are particularly abundant in the northwest Montana, whereas elk and mule deer are more abundant in southwestern and central Montana. Experts estimated there were roughly 5000 moose statewide (N. DeCesare, MFWP, pers, commun.). Other large carnivores include mountain lions (*Puma concolor*), coyotes (*Canis latrans*), grizzly bears (*Ursus arctos*), and black bears (*Ursus americanus*). Most humans live in western Montana, with a statewide population of just more than one million in 2018 (census.gov).

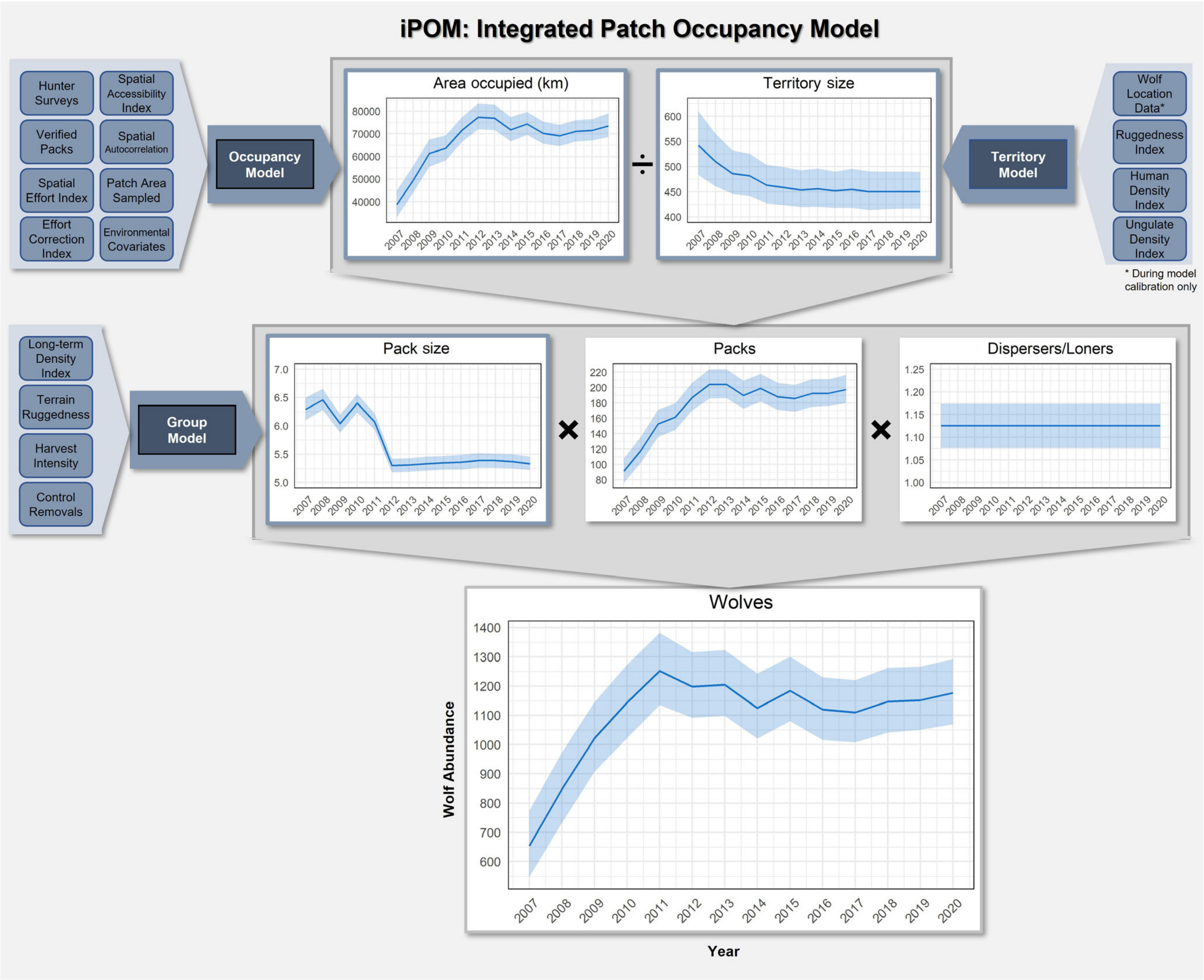

FIGURE 1 The Integrated Patch Occupancy Model (iPOM) combines three separate models into a unified framework for estimating the numbers of packs and wolves in Montana. Graphs display statewide estimates.

Occupancy model

We used a dynamic false-positives occupancy model to predict where wolves occurred in Montana each year from 2007 to 2020 (Inman et al., 2019; Miller et al., 2011, 2013; Rich et al., 2013). Occupancy models use detection/nondetection data and environmental predictors to estimate probabilities of animal occurrence on the landscape while accounting for imperfect detection (MacKenzie et al., 2002). The approach has been used to monitor the presence of many species, including wolves (Ausband et al., 2014; Bassing et al., 2019; Rich et al., 2013; Stauffer et al., 2021). A dynamic occupancy model enables an estimation of transition probabilities for colonization and local extinction between years to better inform occupancy estimates and understand factors that drive changes in occurrence over time (MacKenzie et al., 2003). Accounting for false positives in the detection process addresses concerns of potential misclassification (e.g., a hunter-reported a “wolf” sighting that was a coyote). Public survey data such as wolf sighting reports can be integral to monitoring and occupancy estimation, but accounting for false negatives (nondetection) and false positives (misclassification) is needed to avoid under- or overestimating occupancy (Miller et al., 2013). Our approach maximized available data while properly handling the potential for false reports.

Detection/nondetection data were used to generate encounter histories of the study species within a gridded study area (MacKenzie et al., 2002). In our case, encounter histories included observations for which wolves were not detected (“0”), detected with uncertainty (“1”), and detected with certainty (“2”). Following Rich et al. (2013), we superimposed an observation “iPOM grid”

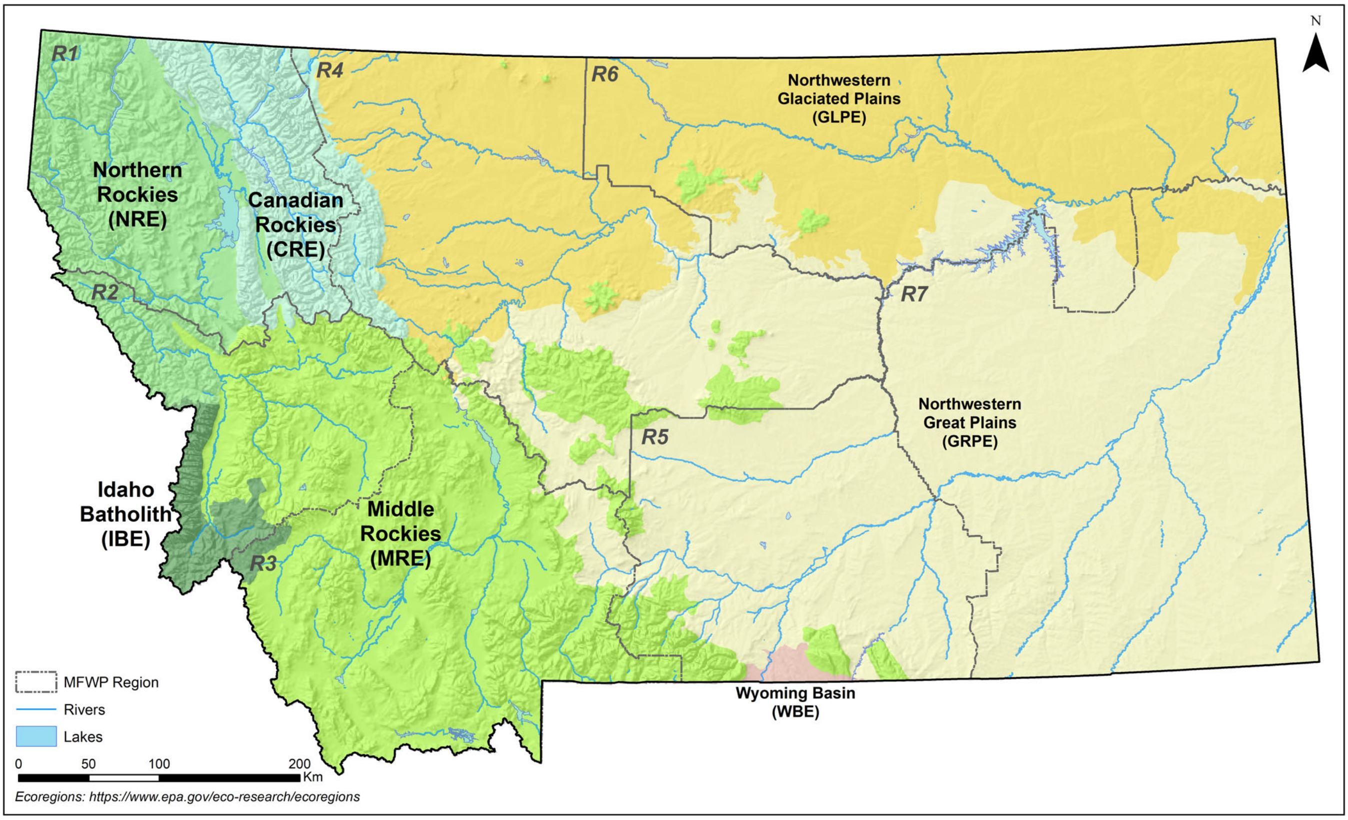

FIGURE 2 The study area encompassed Montana, which is characterized by ecoregions (https://www.epa.gov/eco-research/ecoregions). Wolves are found primarily in the western ecoregions (the Northern Rockies Ecoregion [NRE], Idaho Batholith Ecoregion [IBE], Canadian Rockies Ecoregion [CRE], and Middle Rockies Ecoregion [MRE]). In eastern Montana, only a few verified packs have been documented in the northwestern Glaciated Plains Ecoregion (GLPE) and northwestern Great Plains Ecoregion (GRPE) between 2007 and 2020; no packs have been documented in the Wyoming Basin Ecoregion (WBE) as of 2020. Labels R1–R7 refer to Montana Fish, Wildlife and Parks (MFWP) administrative regions.

across Montana in which each grid cell represented 600 km^2. To generate encounter histories, we divided the 5-week general rifle season (occurring each year around late October through November or early December) into 1-week encounter periods and recorded whether wolves were observed by deer or elk hunters in each iPOM grid cell per week. To obtain wolf sighting reports, MFWP conducted annual Hunter Harvest Surveys of a random sample of 50,000–80,000 deer and elk hunters. Hunters spent 1.8–2.2 million hunter days each fall pursuing deer and elk (fwp.mt.gov), providing many observers across Montana. Hunters were queried about dates and locations of any sightings of groups of 2–25 wolves, which we used as "uncertain" detections of wolves to account for potential misidentification or misreporting (Miller et al., 2011, 2013; Rich et al., 2013).

We used the centroid locations of documented wolf territories to represent "certain" detections of wolf packs. Each year, MFWP wolf specialists monitored packs to verify their presence using a combination of trail cameras, visual observations, track surveys, howl surveys, depredation locations, wolf mortality locations (i.e., wolves removed in response to livestock depredations or harvested by hunters/trappers), and telemetry collars. MFWP's decentralized management allowed each wolf specialist to approach monitoring effort using their expert knowledge. Wolf specialists sought to maximize efficiency by focusing effort, for example, as conditions permitted, based on public tips, and using prior knowledge of when and where to search. At the end of the year, wolf specialists demarcated approximate territory centroids for monitored packs present through autumn.

Covariates helped to account for how habitat and sampling effort influenced spatial and temporal variation in wolf pack occurrence and detection across Montana. We included five covariates on the probability of detection, representing sampling effort: (1) hunter days per km^2 in each hunting district (an index to spatial effort), (2) proportion of hunter observations of wolves with exact location information (a correction to account for the number of hunter observations with coordinates that could be assigned to specific grid cells, versus the total reported),

(3) densities of low-use forested and nonforested roads (total km road length per km^2, serving as indices of spatial accessibility; TIGER Data, 2010, census.gov), (4) a spatial autocovariate (sensu Augustin et al., 1996; the proportion of neighboring cells where wolves were observed within a radius extending to a mean dispersal distance of 100 km; Jimenez et al., 2017), and (5) patch area sampled (because cells overlapping national parks and tribal lands have less hunting activity and therefore less opportunity for hunters to see wolves). We also included patch area to account for varying grid cell sizes, and a covariate for recency (number of years with verified pack locations in the previous 5 years). Finally, we included covariates on the probability of occurrence, colonization (a cell became occupied), and local extinction (a cell became unoccupied) using a principal environmental component constructed from several autocorrelated covariates for each grid cell: percent forest cover (geoinfo.msl.mt.gov); elevation and slope (geoinfo.msl.mt.gov); densities of low-use forested and nonforested roads (TIGER Data 2010, census.gov); and human population density (TIGER Data, 2010, census.gov). Principal components analysis enabled finding a lower-dimensional representation of these correlated variables (Boehmke & Greenwell, 2020). We centered and scaled the six variables and considered principal components (PC) with eigenvalue >1.0. The covariates in the first PC (eigenvalue 3.17) were forest cover, slope, elevation, low-use forested roads, and low-use nonforested roads, which describe environmental covariates or covariates that provide accessibility to wolves. The second PC (eigenvalue 1.02) represented human population density and low-use nonforested roads. We selected the first PC, which explained 53% of the variability in the dataset, as the principal environmental component for the occupancy model.

We fitted the annual encounter histories and model covariates to the dynamic false-positives occupancy model to estimate the probability of occupancy (ψ) per year and probabilities of false-positive detections (i.e., the probability of incorrectly detecting wolves when the site was unoccupied), true positive detections (the probability of detecting wolves given the site was occupied), and certain detections (the probability a detection was classified as certain given the site was occupied and wolves were detected; Miller et al., 2011, 2013). Cells with known territory centroids had a ψ closer to 1. Cells with uncertain observation (i.e., from hunters) and no territory centroids had lower ψ (e.g., despite some hunter observations for eastern Montana, ψ remains very low unless a centroid was also known). We predicted ψ for tribal lands and national parks, where no hunter survey data were available, by extrapolating nearby hunter observations.

We used Markov chain Monte Carlo (MCMC; Brooks, 2003) methods in a Bayesian framework to fit the occupancy model using program R 3.4.1 (R Core Team, 2020) and package *rjags* (Plummer et al., 2019) that calls on program JAGS 4.2.0 (Plummer, 2003). We used $\beta_i \sim \text{Normal}(0, 0.001)$ as a weakly informative prior on the intercept and covariates for all model parameters. We ran three chains for 10,000 iterations without thinning, after an adaptation phase of 10,000 iterations and a burn-in of 10,000 iterations. We assessed convergence by summarizing the Gelman–Rubin convergence statistic (Brooks & Gelman, 1998) across MCMC output for all grid cells, years, and parameters ($n = 19{,}479$) and spot-checked a selection of parameters to ensure a smooth and unimodal posterior and appropriate mixing of chains. Additionally, we validated model results to ensure our Bayesian occupancy model successfully reproduced the original frequentist model by comparing occupancy estimates from POM (Inman et al., 2019) to those from our Bayesian model.

Mechanistic territory model

We used a recently developed mechanistic territory model to predict territory size (Sells et al., 2021; Sells & Mitchell, 2020; Sells, Mitchell, Ausband, et al., 2022). The territory model was a spatially explicit, agent-based model representing the hypothesis that wolves are adapted to select economical territories that maximize food benefits and minimize costs of travel, competition, and mortality risk. Agent-based models focus on how individual behaviors produce population-level patterns. Through simulations in NetLogo 6.1.1 (Wilensky, 1999), individual agents represented wolf packs and sought to select and defend economical territories. During simulations, packs were added to a gridded landscape simulated to represent Montana. Each 1 km^2 grid cell had a food benefit based on an ungulate density index and a measure for terrain ruggedness and human density (Sells, Mitchell, Ausband, et al., 2022). Each time a pack was added, it selected a starting location for a territory center and then calculated cell values around itself by discounting each nearby cell's food benefits by its associated costs of ownership. Food benefits accounted for ungulate densities, based on a spatial index generated from 10 year average densities at hunting district levels using the best available data for deer, elk, and moose (Sells et al., 2021; Sells, Mitchell, Ausband, et al., 2022). Ownership costs accounted for terrain ruggedness, distance from the territory center, number of other packs already in the area, and human density. The pack then selected cells for a territory in order of cell value, stopping once sufficient resources were obtained and the territory was optimized. After each pack selected its territory, neighboring packs assessed whether their territories were still economical, as any changes in overlap with neighboring territories influenced costs of competition for those cells. Each pack dropped less-valuable cells from its territory and added more-valuable cells to maximize the territory's economic value. This cycle of territory formation and maintenance continued after each new pack was added to the landscape. Simulation output provided predictions of what should be observed empirically if the model successfully represented territorial behavior. After calibrating the model using wolf location data from 2014 to 2018, the model successfully predicted observed territory sizes across Montana (Sells, Mitchell, Ausband, et al., 2022).

For our purposes, we used the model to simulate a wide range of pack densities. During simulations, the model continued adding packs until density thresholds were reached in western Montana (comprising the NRE, CRE, IBE, and MRE; Figure 2; Sells, Mitchell, Ausband, et al., 2022). We set density thresholds to {0.1, 0.2, 0.3, ..., 2.5} packs per 1000 km^2 of area in each ecoregion (i.e., totaling 14—329 packs in western Montana) to generate ecoregion-specific predictions of territories under each threshold. As detailed below, this enabled us to then select model predictions appropriate to the density conditions in different areas of Montana each year. This was important because monitoring data indicated that wolf pack densities did not change at the same rate everywhere in Montana through time (fwp.mt.gov/fishAndWildlife/management/wolf/). After all packs optimized their territories and the ecoregion was saturated to the density threshold, territory size was measured as:

$$\text{Territory size} = N_{\text{selected-cells}} + N_{\text{travel-cells}} - N_{\text{cells-shared}} + \sum N_{\text{cells-apportioned}} \tag{1}$$

where $N_{\text{selected-cells}}$ was the number of selected cells, $N_{\text{travel-cells}}$ was the number of cells crossed to reach selected cells from a pack's territory center, $N_{\text{cells-shared}}$ was the number of $N_{\text{selected-cells}}$ and $N_{\text{travel-cells}}$ used by >1 pack, and

$$\sum N_{\text{cells-apportioned}} = \sum_i^n \frac{1}{N_{\text{owners}}} \tag{2}$$

where for each cell $i - n$, N_{owners} was the number of owners at the cell. Territory size therefore accounted for overlap with neighbors by apportioning each overlapping cell by the number of owners.

We used this framework to generate predictions of territory sizes in each ecoregion at each density threshold. To allow for stochastic variation in model runs, we repeated 50 simulation iterations at each density threshold in western Montana, for a total of 1250 simulations. We processed results using program R (R Core Team, 2020) and *tidyverse* (Wickham et al., 2019). For each density threshold we calculated the mean of territory sizes in each ecoregion. Because ≤4 packs have been verified in each eastern Montana ecoregion each year (fwp.mt.gov/fishAndWildlife/management/wolf/), we also modeled 50 iterations at a density of 0.02 and 0.03 packs per 1000 km^2 for the GLPE and GRPE, respectively.

To identify the appropriate level of competition to use for generating predictions in the iPOM framework, we developed a density identifier formula. During iPOM development, we originally modeled competition by simulating territories at the set of known pack centroids each year, and results were comparable with our final iPOM results. To avoid rerunning simulations every year, our density identifier formula identified the approximate degree of competition each year. For each ecoregion and year from 2007 to 2018, we tallied the number of verified packs ($N_{\text{packs-verified}}$) from field monitoring and calculated area occupied ($\sum \text{area}_{\text{occupied}}$) as mean ψ for the ecoregion multiplied by the area of the ecoregion ($\text{ecoregion}_{\text{area}}$). We then fit a linear model in the form of:

$$N_{\text{packs-verified}} \sim \sum \text{area}_{\text{occupied}} \times \text{ecoregion}_{\text{ID}} \tag{3}$$

This formalized the strong relationship between total area occupied and known packs per ecoregion ($R^2 = 0.98$; Table 1), that is, verified minimum packs. Accordingly, the model enabled identifying the appropriate density to model in each ecoregion each year ($\text{density}_{\text{identified}}$), solved for as:

$$\text{density}_{\text{identified}} = N_{\text{packs-verified}} \div \text{ecoregion}_{\text{area}} \times 1000 \tag{4}$$

Finally, we subset the mechanistic model's results for $\text{territory}_{\text{size}}$ to the density threshold matching the $\text{density}_{\text{identified}}$ per ecoregion, per year. This provided $\text{territory}_{\text{size-distribution}}$, the spatially explicit distributions of territory size estimates appropriate to local conditions over time. We assigned each distribution of values to the iPOM grid cells within that ecoregion for that year.

The density identifier formula provides a means to apply the mechanistic model in future years. Even if minimum pack counts from field monitoring become reduced in future years through reduced monitoring effort, the estimated area occupied in each ecoregion will enable predicting the yearly, ecoregional-specific level of competition. This approach also helps to account for observational uncertainty in the number of packs reported from field monitoring each year.

TABLE 1 Density identifier formula results. Ecoregions are defined by the EPA (epa.gov) and refer to codes in Figure 2.

Coefficients	Estimate	SE	Pr(>|t|)
Intercept	−6.849	3.998	0.092
$\text{Area}_{\text{occupied}}$	0.003	0.000	<0.001
IBE	16.580	9.649	0.091
MRE	10.650	6.262	0.094
NRE	−10.660	6.421	0.102
GLPE	6.671	5.031	0.190
GRPE	9.815	5.623	0.086
$\text{Area}_{\text{occupied}}$ × IBE	−0.003	0.003	0.294
$\text{Area}_{\text{occupied}}$ × MRE	−0.001	0.000	0.012
$\text{Area}_{\text{occupied}}$ × NRE	0.000	0.000	0.416
$\text{Area}_{\text{occupied}}$ × GLPE	−0.002	0.001	0.034
$\text{Area}_{\text{occupied}}$ × GRPE	−0.003	0.001	<0.001

Abbreviations: GLPE, Northwestern Glaciated Plains Ecoregion; GRPE, Northwestern Great Plains Ecoregion; IBE, Idaho Batholith Ecoregion; MRE, Middle Rockies Ecoregion; NRE, Northern Rockies Ecoregion.

Group size model

We used a wolf group size model (Sells, Mitchell, Podruzny, et al., 2022) to predict pack sizes in each 600 km^2 iPOM grid cell. The model, which was based on mechanisms hypothesized to influence wolf pack size, was developed using 14 years of wolf pack data and formalized as a generalized linear mixed effects model (family = Poisson) with variables on original scales:

$$\begin{aligned}\text{pack}_{\text{size}} = \exp(&1.56 + 0.44 \times \text{pack density} - 67.28\\ &\times \text{ruggedness} - 0.06\\ &\times \text{harvest intensity}_{\text{restricted}} - 0.18\\ &\times \text{harvest intensity}_{\text{liberal}} - 0.03\\ &\times \text{control removals} - 0.06\\ &\times \text{ecoregion}_{\text{IBE}} + 0.04\\ &\times \text{ecoregion}_{\text{MRE}} + 0.13\\ &\times \text{ecoregion}_{\text{CRE}} + 0.03\\ &\times \text{ecoregion}_{\text{GLPE}} + 0.00\\ &\times \text{ecoregion}_{\text{GRPE}} + (1|\text{Grid}_{\text{ID}}))\end{aligned} \tag{5}$$

Pack density was the mean pack density in the iPOM grid cell based on field monitoring from 2005 to 2018 (Sells, Mitchell, Podruzny, et al., 2022). Ruggedness was the terrain ruggedness in the iPOM grid cell (ranging 0–0.05 using Sappington et al., 2007's Vector Ruggedness Measure). Harvest intensity was categorized as "none" when no harvest was allowed, "restricted" if 2009 and 2011 rules were followed (statewide harvest was limited by a quota, seasons were shorter, bag limits were low, and trapping was prohibited), and "liberal" if 2012–2021 were followed (statewide harvest quotas were removed, seasons were longer, bag limits were higher, and trapping was allowed; fwp.mt.gov). Control removals was the reported number of wolves removed for depredations in the iPOM grid cell in the calendar year. Ecoregions were defined by the EPA (Figure 2) with a reference category set to the NRE. Grid_{ID} was the unique identifier for the iPOM grid cell, included as a random effect to account for repeated observations among years.

The group size model was developed using only good quality counts (i.e., pack size counts for which wolf specialists had a high degree of confidence, $n = 660$ pack-years) and intended to minimize monitoring effort (Sells, Mitchell, Podruzny, et al., 2022). Whereas their initial group size model relied on annual estimates of pack density based on each pack's territory centroid, the predictive model used long-term average pack density to eliminate this intensive monitoring requirement. This adaptation captured the long-term trends in pack densities and still enabled the model to reliably estimate annual pack size (Sells, Mitchell, Podruzny, et al., 2022).

We applied the model to each iPOM grid cell, each year, to predict local pack size ($\text{pack}_{\text{size}}$) and confidence intervals. These estimates provided group size distributions ($\text{group}_{\text{size-distribution}}$) for each grid cell.

Abundance estimates

We calculated annual numbers of packs and wolves for 2007–2020 by combining predictions from the three models (Figure 1). We simulated 10,000 predictions for each grid cell from each model (matching the length of the MCMC iterations from the occupancy model) and summarized results at statewide and MFWP regional levels, as follows. (Grid cells were categorized by the region in which the majority of their areas fell.)

Iterating across the 10,000 predictions for each grid cell, we first calculated area occupied ($\text{area}_{\text{occupied}}$) as:

$$\text{area}_{\text{occupied}} = \psi \times \text{grid}_{\text{area}} \tag{6}$$

where $\text{grid}_{\text{area}}$ was area of the grid cell. We calculated the number of estimated packs as:

$$N_{\text{packs}} = \text{area}_{\text{occupied}} \div \text{territory}_{\text{size}} \tag{7}$$

where values for $\text{territory}_{\text{size}}$ were drawn 10,000 times per grid cell with replacement from $\text{territory}_{\text{size-distribution}}$. Values for $\text{territory}_{\text{size}}$ were therefore spatially explicit, biologically appropriate to the local conditions each year, and accounted for uncertainty. We calculated the number of wolves as:

$$N_{\text{wolves}} = N_{\text{packs}} \times \text{pack}_{\text{size}} \times \text{lone}_{\text{rate}} \tag{8}$$

where values for $\text{pack}_{\text{size}}$ were drawn 10,000 times per grid cell from $\text{group}_{\text{size-distribution}}$. This provided spatially explicit and biologically appropriate values for local conditions each year while incorporating model uncertainty about pack size. Finally, $\text{lone}_{\text{rate}}$ accounted for lone and dispersing wolves. We sampled $\text{lone}_{\text{rate}}$ by drawing 10,000 values per grid cell from a normal distribution assuming a mean of 1.125 and standard deviation of 0.025. This yielded a mean loner/disperser rate of 12.5%, and 95% of values drawn were 7.6%–17.4%. We selected these values based on studies documenting that on average, 10%–15% of wolf populations consist of lone or dispersing wolves (Fuller et al., 2003). This is consistent with Idaho's calculations for lone wolves (Idaho Department of Fish and Game and Nez Perce Tribe, 2013) and slightly more conservative than Minnesota's calculations, which add 15% (Erb et al., 2018).

We summarized results at the statewide and regional levels for $\text{area}_{\text{occupied}}$, $\text{territory}_{\text{size}}$, $\text{pack}_{\text{size}}$, N_{packs}, and N_{wolves}. To do so, we used the median value to generate a point estimate, and 0.025 and 0.975 sample quantile values to account for uncertainty (creating 95% credible intervals, CI's). We calculated density of packs per 1000 km^2, wolves per 1000 km^2, and population growth (lambda, λ). We also calculated the human-caused mortality rate as the annual number of human-caused wolf mortalities divided by N_{wolves}. Known mortalities were from legal harvest, control removals, vehicle/train collisions, illegal killings, euthanasia, and other or unknown causes, with totals ranging 100–394/year during our study (2007–2020; mean = 277/year; fwp.mt.gov).

RESULTS

Each year (2007–2020) 50,026–82,375 hunters responded to wolf sighting surveys. From their reported sightings, we recorded 979–3469 detections of 2–25 wolves each year. The percentage of hunters reporting a wolf sighting ranged from 4.4% (2020) to 7.5% (2011).

The occupancy model converged (99.99% of Gelman–Rubin convergence statistics were <1.1) and produced occupancy estimates similar to the original frequentist POM estimates (Inman et al., 2019). The model showed that from 2007 to 2020, estimated area occupied by wolf packs in Montana ranged from 38,719 km^2 (95% CI = 33,162–44,909) in 2007 to 77,396 km^2 (95% CI = 72,025–83,472) in 2012 (Table 2). The estimated distribution of wolves from the occupancy model closely matched the distribution of field-confirmed wolf locations (verified pack locations and harvested wolves; Appendix S1).

Estimated territory size varied (Figure 3). Considering grid cells that were most likely to be occupied by packs ($\psi \geq 0.5$), territory size was estimated to be largest in the

TABLE 2 iPOM results, 2007–2020.

Year	Area occupied	LCI area occupied	UCI area occupied	Packs	LCI packs	UCI packs	Wolves	LCI wolves	UCI wolves
2007	38,719	33,162	44,909	91	76	108	654	545	773
2008	49,409	43,922	55,658	119	103	136	847	733	972
2009	61,284	55,507	67,562	152	136	172	1021	908	1151
2010	63,615	58,356	69,367	161	144	180	1144	1025	1275
2011	71,598	66,472	77,317	187	170	206	1252	1136	1382
2012	77,396	72,025	83,472	204	186	224	1199	1092	1316
2013	76,931	71,688	82,796	204	186	224	1204	1096	1323
2014	71,805	66,680	77,413	190	172	209	1127	1020	1242
2015	74,377	69,514	79,661	199	182	218	1184	1078	1300
2016	70,263	65,577	75,293	188	171	207	1119	1017	1234
2017	69,084	64,731	73,984	185	169	203	1107	1008	1223
2018	71,099	66,517	76,027	192	175	211	1147	1042	1262
2019	71,523	67,021	76,426	193	176	211	1153	1049	1266
2020	73,463	68,754	78,958	197	180	217	1177	1069	1290

Abbreviations: LCI, lower credible interval; UCI, upper credible interval (95%).

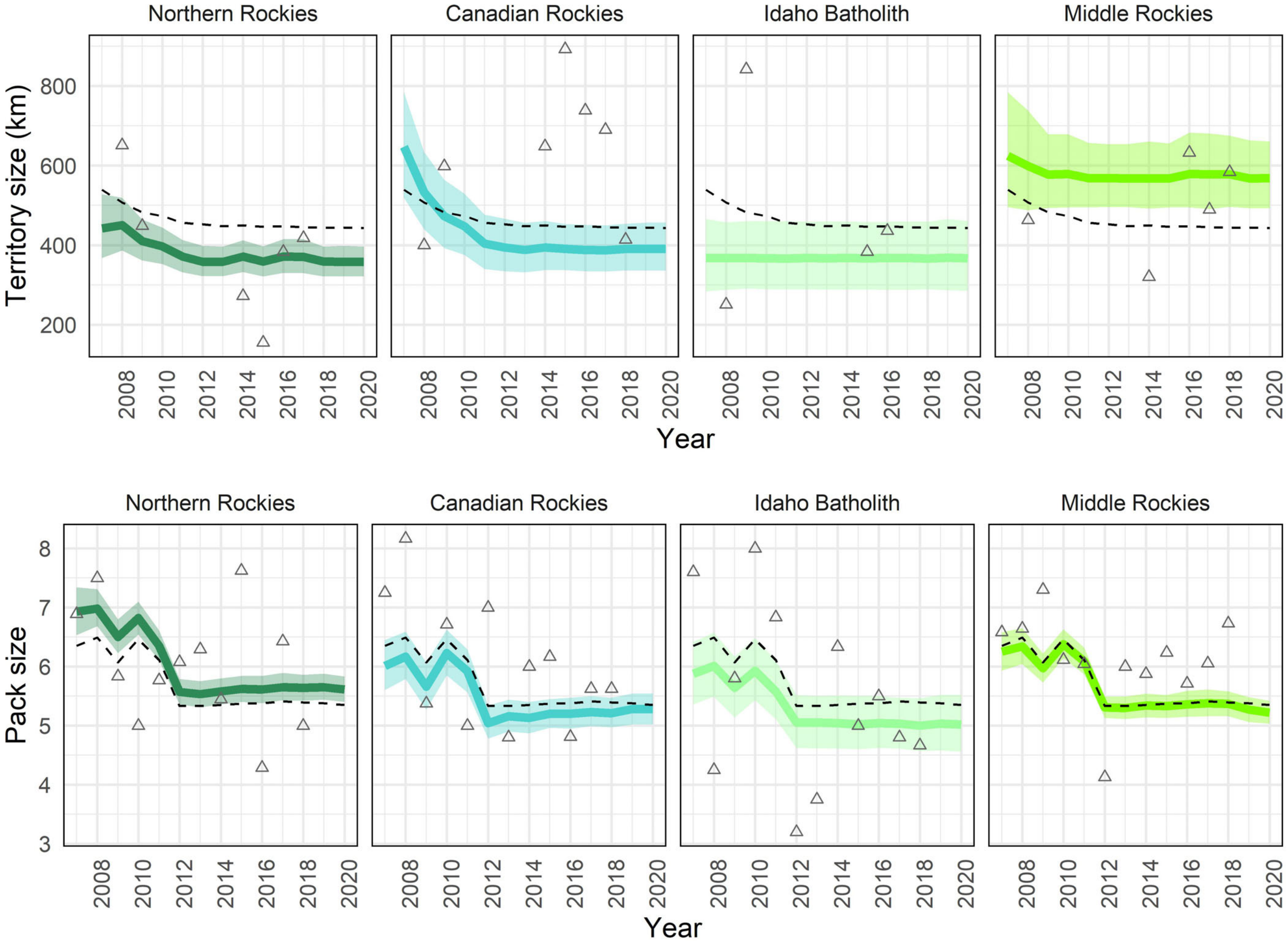

FIGURE 3 Estimated territory size and pack size in western Montana, by year and ecoregion, for cells with $\psi \geq 0.5$ (i.e., having higher likelihood of being occupied). Dashed lines represent the means across ecoregions, and ribbons indicate 95% credible intervals. (Eastern Montana ecoregions are omitted here because they had very few packs each year.) Triangles indicate mean observed territory and pack sizes per year, per ecoregion. Observations were relatively limited; within the Northern Rockies Ecoregion (NRE), Canadian Rockies Ecoregion (CRE), Idaho Batholith Ecoregion (IBE), and Middle Rockies Ecoregion (MRE), respectively, territory sizes were based on a mean of 1.7, 2.3, 1.25, and 2.2 packs per year after omitting two outlier packs with territories >1800 km^2, and pack sizes were based on a mean of 15, 9, 4, and 20 packs with good quality counts annually. However, no clear bias or trends over time are evident in observed versus predicted territory or pack sizes, with the possible exception of some territory estimates for the CRE. Several packs that increased the mean observed territory sizes in the CRE in these years reduced their space use by ~50% the following years, and the CRE was estimated to contain ≤9% of total packs within Montana.

Middle Rockies (the MRE, southwest MT) and second largest in the Canadian Rockies (the CRE, including Glacier National Park and the Bob Marshall Wilderness), followed by the Northern Rockies (the NRE, northwest MT) and the Idaho Batholith (the IBE, the Bitterroot area). Territory size was greatest in 2007 and dropped thereafter, except in the IBE where territory size remained stable.

Estimated pack size also varied (Figure 3). Considering grid cells most likely occupied by packs, mean pack size was estimated to be similar across ecoregions (an approximate difference of <1 wolf per pack in most years). We estimated pack size to generally be slightly larger than average in the NRE, approximately equal to the average in the CRE and MRE, and slightly smaller than average in the IBE. Pack sizes were larger in the earlier years (prior to harvest) and then declined by approximately one wolf per pack, on average.

Estimated numbers of packs and wolves varied through time (Figure 4; Table 2). The population was estimated to have been smallest in the first year of analysis (2007), with 91 packs (95% CI = 76–108) and 654 wolves (95% CI = 545–773). Total wolf numbers peaked in 2011 with 187 packs (95% CI = 170–206) and 1252 wolves (95% CI = 1136–1382). This peak coincided with the first years of harvest management in Montana,

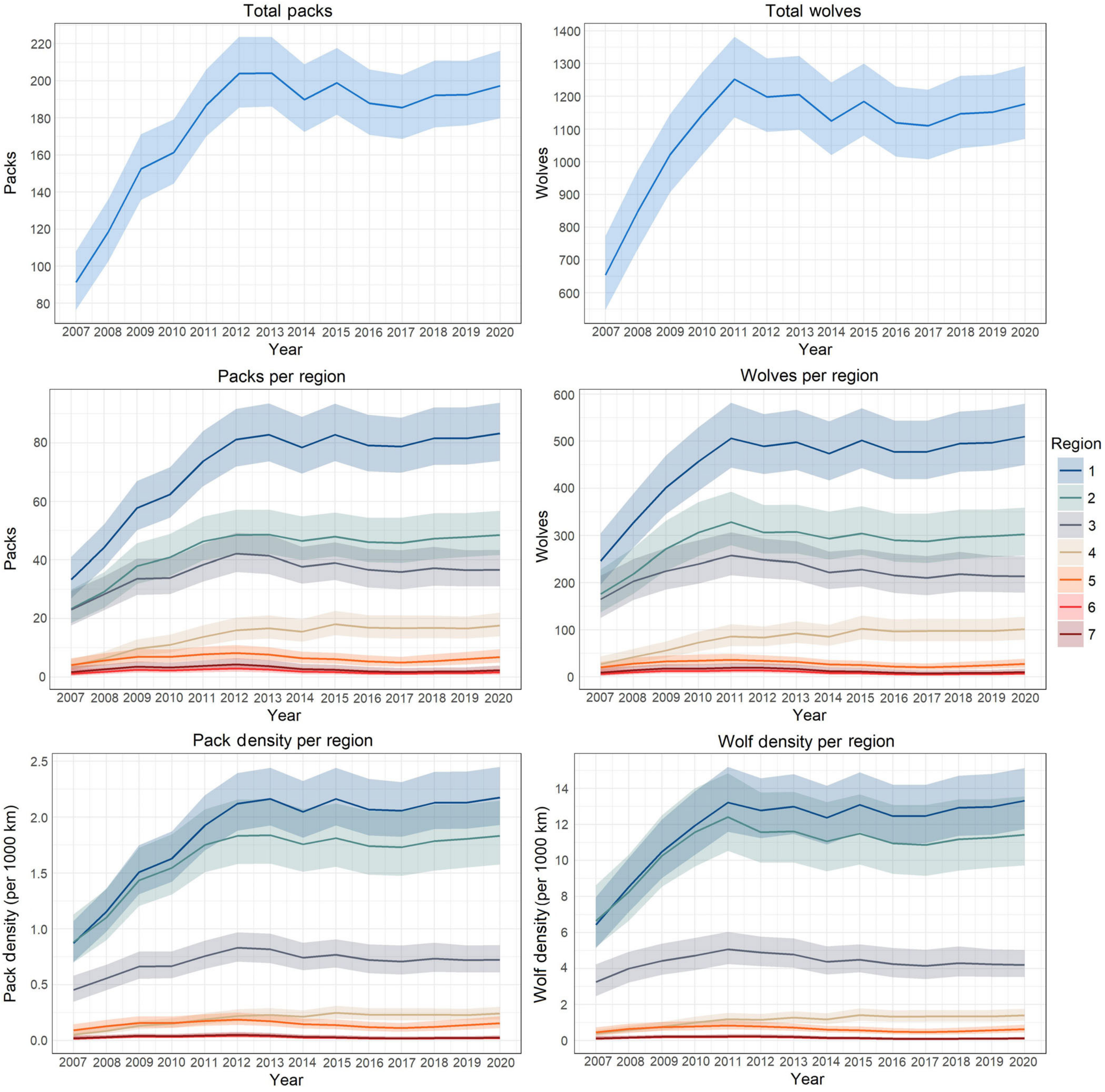

FIGURE 4 Estimated abundances and densities of packs and wolves statewide and per region, 2007–2020. Ribbons indicate 95% credible intervals.

after which the population declined by 6.0% in total wolf abundance between 2011 and 2020. These estimates were consistently greater than numbers reported from monitoring or POM (Appendix S1: Figure S1).

Population growth rate was initially >1.0 through 2010 or 2011 in each region and then alternated from slightly positive and slightly negative during each year of harvest (Figure 5). From 2016 to 2020, however, the population appears to have become relatively stabilized with an average of 191 packs and 1141 wolves per year. This was despite a human-caused mortality rate estimated at 30.4% per year on average over this same period (Figure 5).

The estimated numbers of packs and wolves varied spatially. Pack and wolf abundances were consistently greater in the MFWP Region 1 (which contains most of the NRE and CRE; Figure 2). Annually from 2007 to 2020, 37%–42% of packs in Montana were found in Region 1, which also contained an average of 41% of the wolf population (Figure 6). The next most populous area

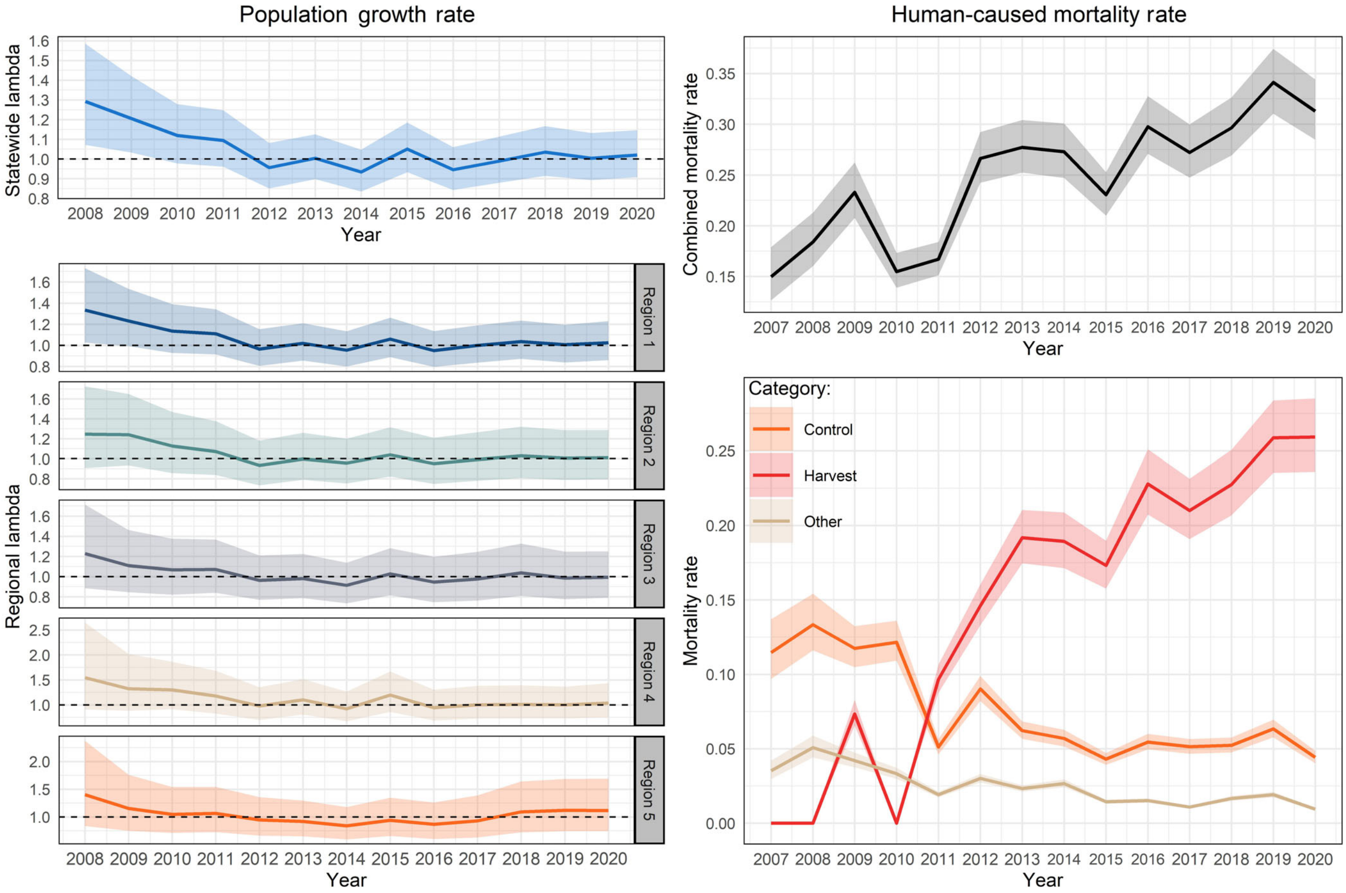

FIGURE 5 Estimated population growth rate per region (lambda) and human-caused mortality rate (number of human-caused mortalities/total abundance) per year. Ribbons indicate 95% credible intervals.

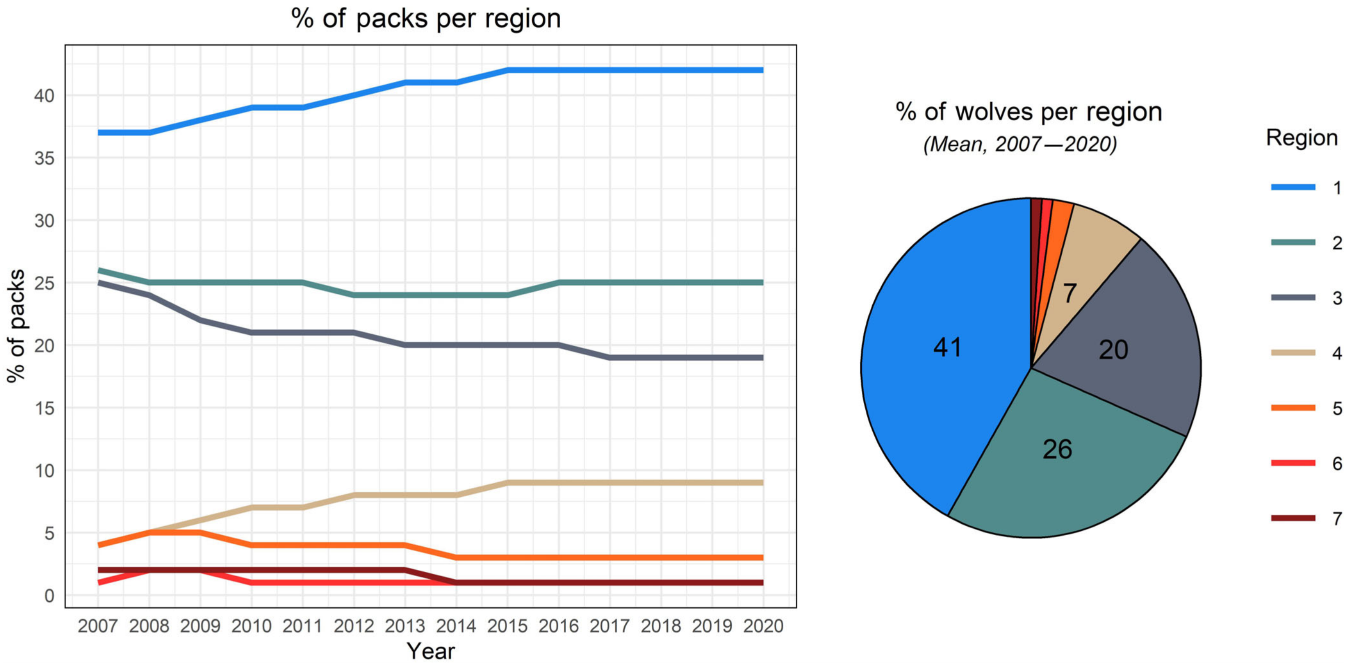

FIGURE 6 Proportion of packs estimated per Montana Fish, Wildlife and Parks (MFWP) region, and total mean % of wolves per region (annual % of wolves were nearly identical to that of packs).

was Region 2 (encompassing parts of the IBE, MRE and NRE), with 24%–26% of total packs and 26% of the wolf population. In contrast, Region 3 (comprised mostly by the MRE) contained 19%–25% of packs and 20% of the wolf population. Regions 4–7 (containing mostly the eastern Montana ecoregions) each contained only ≤1%–9% of packs and 1%–7% of wolves. As the abundance of packs and wolves changed through time (Figure 4), the proportion of packs and wolves in each region stayed relatively consistent, with slight increases in Regions 1 and 4, and slight declines in Regions 3 and 5 (Figure 6).

Wolf densities varied over space and time (Figure 4; Appendix S1). Estimated densities were greatest in MFWP Region 1 (ranging 6.42–13.31 wolves per 1000 km^2 from 2007 to 2020), followed by Region 2 (6.62–12.44) and Region 3 (3.24–5.07). Regions 4–7 had ≤1.41 wolves per 1000 km^2. Regions 1 and 2 saw the greatest increase in densities from 2007 through the population peak, with a smaller change in density in Region 3 and largely consistent densities in Regions 4–7. Maps of pack and wolf densities demonstrate close alignment between known packs, locations of wolf harvests, and predictions from iPOM (Appendix S1).

DISCUSSION

We demonstrate the integration of basic and applied research to meet management needs by developing a multimodel approach to estimate wolf abundance in Montana. This approach addresses important assumptions of existing methods for estimating wolf abundance by incorporating an occupancy model (Inman et al., 2019; Miller et al., 2013; Rich et al., 2013) and biologically based models for territory and pack size (Sells et al., 2021; Sells, Mitchell, Ausband, et al., 2022; Sells, Mitchell, Podruzny, et al., 2022). Our approach reduces monitoring needs while providing more accurate abundance estimates founded on the biology and behavior of wolves. This is beneficial and timely given the continued expansion of wolf populations across the American west, liberalization of harvest management in the Rocky Mountains, and limited monitoring budgets.

Our multimodel approach provides a unique, biologically based means for estimating abundance of an elusive large carnivore. As expected given that monitoring provided only minimum counts, statewide estimates of abundance from iPOM were consistently greater than numbers reported from monitoring (Appendix S1: Figure S1). iPOM estimates were similarly greater than previous POM estimates, which assumed territory size was constant over space and time. This assumption was clearly violated (Figure 3). Empirical data alone show that wolf territories have not averaged 600 km^2 in recent years (Sells et al., 2021), demonstrating the bias of approaches such as POM if the territory size estimates mismatch the reality. POM also incorporated an overlap index in an attempt to account for changing spatial dynamics over time, but this ad hoc approach was not tested or biologically based and its effects on accuracy were unknown. Additionally, POM could not accurately estimate regional abundances due to the lack of spatiotemporal estimates of territory and pack size (Appendix S1: Figure S1).

By integrating basic and applied research, our iPOM approach improves accuracy in estimates of wolf abundance. The mechanistic territory model maximizes predictive ability across time and space (Aarts et al., 2008; Sells et al., 2018; Sells, Mitchell, Ausband, et al., 2022) and enables predicting territorial behavior across changing environmental and social conditions. Changing levels of ungulate densities or intrapack competition are important drivers of territory size (Sells et al., 2021; Sells & Mitchell, 2020; Sells, Mitchell, Ausband, et al., 2022), and our approach provided predictions across a range of conditions, which can be used in future years as conditions change.

Importantly, our iPOM approach reduces field-based monitoring requirements. Annual hunter surveys about wolf sightings are part of a larger program by MFWP to survey hunters, and wolf-related questions add minimal extra effort for MFWP staff. Wolf specialists will continue to monitor packs to document known detections each year, but this can rely on established methods such as well placed remote cameras, visits to past den sites, howl surveys, or drone flights to document definitive wolf presence through autumn. Several decades of wolf monitoring effort and close communication with the local public provide wolf specialists with a wealth of knowledge of when and where to most efficiently invest effort to detect packs. Because the original assumption of 600 km^2 territory sizes biased POM estimates, without our mechanistic territory model the MFWP would need to collar many wolves to continuously estimate territory size for POM across space and time. This task was clearly not feasible as wolves became more difficult to trap, and collars yielded less data due to failures and mortalities (Sells et al., 2021). This field-intensive approach would also fail to explain why spatial requirements of packs vary. By contrast, our territory model required substantial upfront investment, but now provides a simple means to calibrate territory size estimates based on the biology and behavior of wolves. The pack size model was similarly designed to significantly reduce monitoring effort and improve the accuracy of abundance estimates from iPOM

(Sells, Mitchell, Podruzny, et al., 2022). Annual monitoring to collect data on pack sizes is no longer required unless future conditions (e.g., intensity of harvest, disease events, etc.) shift beyond conditions experienced within our 14-year dataset, in which case the effects on pack size will be unknown. For example, increased liberalization of harvest methods since 2012 and, especially in 2022, would necessitate re-calibration of the model if total harvest increases substantially beyond that observed in previous years. However, the most recent (2021–2022 season) liberalization of wolf harvest regulations have not resulted in an increase in wolf harvest compared with prior years (fwp.mt.gov/hunt/regulations/wolf), indicating that the existing model remains useful. Regardless of temporary increases in monitoring efforts to re-calibrate the pack size model as needed in future years, its existence provides a substantial saving in monitoring requirements by negating the need to continuously monitor sizes of as many packs as possible each year.

Incorporation of biologically appropriate estimates of territory size at both statewide and regional spatial scales allows for regional scale estimates of the number of packs and wolves. This will enable managers to make decisions using estimates for regional populations. Regional estimates from iPOM demonstrate large variations in pack and wolf abundances across space and time (Figure 4). These estimates accord with expert knowledge of MFWP wolf specialists familiar with local pack dynamics. They also reveal how many packs may have been unverified each year. Generally, iPOM estimated that only a small number of additional packs had been omitted from verified minimums in each region (Appendix S1: Figure S1). The largest differences occurred in Region 1 in recent years; which was attributed in part to a change in field personnel (Coltrane et al., 2015) and consistent with recent public and field staff input.

The extent to which the population's stabilization over recent years (Figure 1) represents a response to density-dependent factors versus human-caused mortality (particularly hunting, trapping, and depredation removals) is uncertain. However, our territory model demonstrated that increasing levels of competition generally result in territory compression as desirable areas are competed for and claimed (Sells et al., 2021; Sells, Mitchell, Ausband, et al., 2022). Accordingly, the spatial distribution of territories may not appreciably change even as territory dynamics fluctuate within. Our group size model also demonstrated evidence of large packs in areas of greater pack densities, suggesting less dispersal in response (Sells, Mitchell, Podruzny, et al., 2022). Both features point to density dependence, but effects of human-caused mortalities cannot be ruled out, particularly given that the area occupied largely plateaued coincident with increased intensity of harvest. Recent human-caused mortality rates (Figure 5) are approximately at the level that has led to population stability in other, smaller areas (Adams et al., 2008; Fuller et al., 2003). It also remains likely that human intolerance has prevented the successful long-term expansion of wolves into central and eastern Montana, as new packs may be removed, for example, through harvest or livestock depredation control events. Future monitoring may help to reduce uncertainty about the extent to which density dependence or human-caused mortality is limiting wolf population growth in Montana, especially if recent liberalization of harvest regulations results in additional mortality.

Researchers recently used simulations to identify the conditions likely to most bias estimates of abundance using a POM approach without spatially explicit, biologically based estimates for territory and pack sizes (Stauffer et al., 2021). Occupancy models assume that packs do not overlap multiple grid cells, and any movement into the cell is equal to movement out of the cell. Stauffer et al. (2021) found that abundance estimates were most biased when using a static occupancy model for a small population with small territories and a detection grid composed of large grid cells (where territories were assumed to be 100 km^2, grid cells were 324 km^2, and population size was 100 wolves). Abundance estimates were conversely the least biased for larger populations of wolves in larger territories, defined as 324 km^2. Based on these results, POM estimates should have comparatively low bias due to use of a dynamic false-positives occupancy model with large grid cells (600 km^2), large territories (600 km^2), and a population far exceeding 100 individuals. Estimates generated from iPOM further reduced the potential for bias by incorporating spatial and temporal variation in territory and pack sizes. In the future, iPOM could be modified to include a new detection grid with cells that vary in size according to more localized territory sizes, which would probably further minimize bias by better matching grid cell and territory size estimates (Stauffer et al., 2021).

Although wolf conservation advocates have expressed concerns that hunter surveys could bias occupancy estimates given sufficient mistaken or falsified reports, for several reasons there is little evidence that this occurs or would be likely to affect results. First, the false-positive nature of the model accounts for these possibilities by explicitly treating hunter observations as uncertain detections. Furthermore, 92.5%–95.6% of hunters surveyed each year did not report seeing wolves, and suspect reports (e.g., >25 wolves sighted at one time) were rare and automatically omitted. Lone wolves and potential misidentifications were also automatically excluded (sightings of <2 wolves). Sightings also aligned strongly with the distribution of wolves known from agency monitoring, with the exception of sporadic reports in eastern Montana (Appendix S1). These reports neither drive up the estimates of occupancy nor affect overall abundance estimates in appreciable ways, further demonstrating the inability of hunter reports to singly influence the estimates of abundance.

Consistent bias in estimated territory or pack sizes would bias results. If territory size estimates were biased low or pack size estimates were biased high, the overall population estimate would be biased high. Unless territory or pack size estimates were consistently biased in the same direction across large spatial extents, however, regional- and population-level biases are likely to partially or fully wash out (as some areas would be slightly overestimated and others underestimated). Although challenging to compare due to limited observation data in each ecoregion per year, no bias in observed versus predicted territory or pack sizes across ecoregions was clearly evident (Figure 3). A possible exception occurred in the CRE, where territories were observed to be larger in some years than estimated by the territory model. Several packs that increased the mean observed territory sizes in the CRE in these years reduced their space use by ~50% the following years, and the CRE was estimated to contain ≤9% of total packs within Montana (Figure 6). Accordingly, any change to the territory size inputs for this ecoregion would have limited overall effect on abundance estimates. Altogether, iPOM's incorporation of spatially explicit estimates for territory and pack size therefore has a strong advantage over POM. By assuming a single estimate for territory and pack size was accurate each year, POM had more potential to generate biased estimates if these components were inaccurately estimated (e.g., Stauffer et al., 2021). iPOM also carries uncertainty in estimates across the full set of calculations to provide credible intervals that account for uncertainty from each component (occupancy, territory size, pack size, and lone wolf rate).

Our approach is unique among the various approaches taken globally to monitor wolves and estimate their abundance. Like Montana in early phases of recovery, intensive efforts may be used to monitor as many wolves as possible, particularly where wolf populations remain relatively small (e.g., California, Oregon, and Washington; wildlife.ca.gov, dfw.state.or.us, wdfw.wa.gov). Many management and research groups rely on models designed to estimate population parameters from wolf monitoring data. In Finland, for example, winter track surveys were used to estimate the number of litters in an effort to track population growth (Kojola et al., 2014). This estimation technique was effective in only some regions and involved intensive effort (over a 2 decade period, 200,000 km of transects surveyed primarily by ski to obtain <900 wolf track observations). Scandinavian countries have also used individual-based models with highly informative priors to estimate population size (Chapron et al., 2016). These priors were uniquely available for one of the most intensively studied populations of large carnivores in the world, and the model assumed that all pairs, packs, and reproductions were detected. Open population spatial capture–recapture models have also been used to estimate recent and future abundance of wolves in Scandinavia (Bischof et al., 2020). These approaches appear to be effective when extensive genetic datasets are available. In less well studied populations, genetic spatial capture–recapture models may be unable to produce estimates for some time periods, despite intensive field effort (e.g., as demonstrated for cougars in Idaho; Loonam et al., 2020). Loonam et al. (2020) concluded that these models may be most conducive in small areas with concentrated field effort and therefore not appropriate for statewide monitoring, such as in Montana. An integrated population model to estimate wolf abundance in Idaho was recently developed using an extensive dataset (including 10 years of data with >1300 pack counts and nearly 200 GPS collars; Horne et al., 2019). Time- and space-to-event modeling with cameras have received great interest in recent years and can effectively estimate abundance and densities of populations for some large mammalian species (Loonam et al., 2020; Moeller et al., 2018). Using these approaches over large areas would be costly and field intensive, and the approaches are sensitive to camera placement and rely on accurate estimates of animal movement speeds. Idaho (Ausband et al., 2014), southwestern Alberta (Bassing et al., 2019), and Wisconsin (Stauffer et al., 2021; Wiedenhoeft et al., 2020) have also used POM-based estimation approaches. These approaches did not incorporate spatially explicit, biologically based models for territory and pack size. As demonstrated, integrating these types of models is important for estimating population size from estimates of area occupied.

iPOM meets the broadscale monitoring needs of a large wolf population while integrating wolf biology and reducing the amount of detailed monitoring data required by many previous estimation methods. It has already demonstrated its effectiveness in revealing changes in population size (Figure 4). Although recent developments in mark–recapture methods offer alternative approaches to estimating population size, applying these methods to elusive large carnivores over vast areas is not feasible with current technology. Intensive marking and counting over multiple years may provide an estimate of population size over smaller areas. However, these methods fail to generate estimates once intensive field effort drops. Mark–recapture or other modeling approaches may become feasible in future years if the wolf population substantially declines. The Montana Gray Wolf Conservation and Management Plan specifies that wolf population monitoring will be more limited when the population contains more than 15 breeding pairs (defined as packs that produce at least two young that survive to 31 December), and that monitoring will be enhanced when the population is between 10–15 breeding pairs (Montana Fish, Wildlife and Parks, 2003). We developed iPOM to fulfill the need for monitoring methods for the current large, well distributed population. Monitoring methods that are more effective for smaller populations distributed over smaller areas will become more appropriate if the population approaches, or declines below, the 15 breeding pair threshold.

ACKNOWLEDGMENTS

This project is made possible with the generous assistance of biologists and managers at Montana Fish, Wildlife and Parks. We thank L. Bradley, B. Dunne, K. Laudon, M. Ross, and W. Cole, as well as technicians and volunteers, for their invaluable support, including by trapping and collaring wolves for this work. We also thank landowners for allowing access for trapping and collaring efforts. Other MFWP staff also provided support, including J. Vore, K. Proffitt, J. Coltrane, N. DeCesare, Q. Kujala, N. Anderson, M. Lewis, and numerous area biologists. S. Courville provided ungulate data from the Confederated Salish and Kootenai Tribes. We also thank D. Ausband, D. Emlen, A. Luis, D. Pletscher, H. Robinson, A. Keever, K. Barker, and C. Waters for advice and assistance, and D. MacNulty, T. Avgar, K. Manlove, and E. Stubner for helpful discussion on this work. This work was supported by revenues from the sale of Montana hunting and fishing licenses, and Federal Aid in Wildlife Restoration grant W-161-R-1 to MFWP.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data supporting this research are sensitive and not available publicly but are available to qualified researchers by request to MFWP. Occupancy model code (Sells, Nowak, et al., 2022) is available on Zenodo at https://doi.org/10.5281/zenodo.6672368. Territory model code (Sells, 2022a) is available on Zenodo at https://doi.org/10.5281/zenodo.5802243. Group size model code (Sells, 2022b) is available on Zenodo at https://doi.org/10.5281/zenodo.5838722.

ETHICAL APPROVAL

All wolves were captured, anesthetized, and handled in accordance with MFWP biomedical protocol for free-ranging wolves (Montana Fish, Wildlife and Parks, 2005), guidelines from the Institutional Animal Care and Use Committee for the University of Montana (AUP #070–17), and guidelines approved by Sikes et al. (2011).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Sells, Sarah N., Kevin M. Podruzny, J. Joshua Nowak, Ty D. Smucker, Tyler W. Parks, Diane K. Boyd, Abigail A. Nelson, et al. 2022. "Integrating Basic and Applied Research to Estimate Carnivore Abundance." *Ecological Applications* e2714. https://doi.org/10.1002/eap.2714