This report presents information on the status, distribution, and management of wolves in the State of Montana, from January 1, 2020 to December 31, 2020.

This report is also available at: http://fwp.mt.gov/fishAndWildlife/management/wolf/

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Montana Gray Wolf Program
2020 Annual Report

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EXECUTIVE SUMMARY

Wolf recovery in Montana began in the early 1980's. The federal wolf recovery goal of 30 breeding pairs for 3 consecutive years in the Northern Rocky Mountains (NRM) of Montana, Idaho and Wyoming was met by 2002. Montana's state Wolf Conservation and Management Plan of 2004 was based on the work of a citizen's advisory council and was approved by the United States Fish and Wildlife Service (USFWS). The wolf population in the NRM tripled between the time recovery goals were met and when wolves were ultimately delisted by congressional action during 2011. At present, Montana Fish, Wildlife and Parks (FWP) implements the 2004 state management plan using a combination of sportsman license dollars and federal Pittman-Robertson funds (excise tax on firearms, ammunition, and hunting equipment) to monitor the wolf population, regulate harvest, collar packs in livestock areas, coordinate and authorize research, and direct problem wolf control under certain circumstances.

The primary means of monitoring wolf distribution, numbers, and trend in Montana is now Integrated Patch Occupancy Modeling, or "iPOM." The iPOM method uses annual hunter effort surveys, known wolf locations, habitat covariates, and estimates of wolf territory size and pack size to estimate wolf distribution and population size across the state. iPOM estimates of wolf population size are the preferred monitoring method due to accuracy, confidence intervals, and cost efficiency. The 2020 iPOM estimate of wolf population size was 1,177 wolves (95% C.I. = 1,069 – 1,290; Fig. 1).

Wolf hunting was recommended as a management tool in the 2004 Montana Wolf Conservation and Management Plan. Calendar year 2020 included parts of two hunting/trapping seasons for wolves. During calendar year 2020, 138 wolves were harvested during the spring, and 167 wolves were harvested during the fall for a total of 305 (Fig. 1). Sales of license year 2020/21 wolf hunting licenses generated $297,487 for wolf monitoring and management in Montana.

Wildlife Services (WS) confirmed the loss of 99 livestock to wolves during 2020, including 62 cattle, 32 sheep, and 5 lamas; 4 livestock guard dogs were also killed by wolves (Fig. 1). This total was similar to numbers during 2011-2019. During 2020 the Montana Livestock Loss Board paid $75,818.75 for livestock that were confirmed by WS as killed by wolves or probable wolf kills. Fifty-two wolves were killed in response to depredation or to reduce the potential for further depredation. Of the 52 wolves, 47 were killed by WS and 5 were lawfully taken by private citizens. FWP's Wolf Specialists radio-collared 9 wolves during 2020 to meet the legislative requirement for collaring livestock packs and to aid in population monitoring and research efforts.

Montana's wolf population grew steadily from the early 1980's when there were less than 10 in the state. After wolf numbers approached 1,250 in 2011 and wolves were delisted, the wolf population has decreased slightly and may be stabilizing at about 1,150 wolves (Fig. 1). Stabilization of population size may be related to the onset of wolf hunting and trapping seasons, whereas reduced livestock depredation in recent years is most likely related to more aggressive depredation control actions (DeCesare et al. 2018). Montana's wolf population remains well above requirements (7 – 8x). Wolf license sales have generated $4.4 million for wolf management and monitoring since 2009.

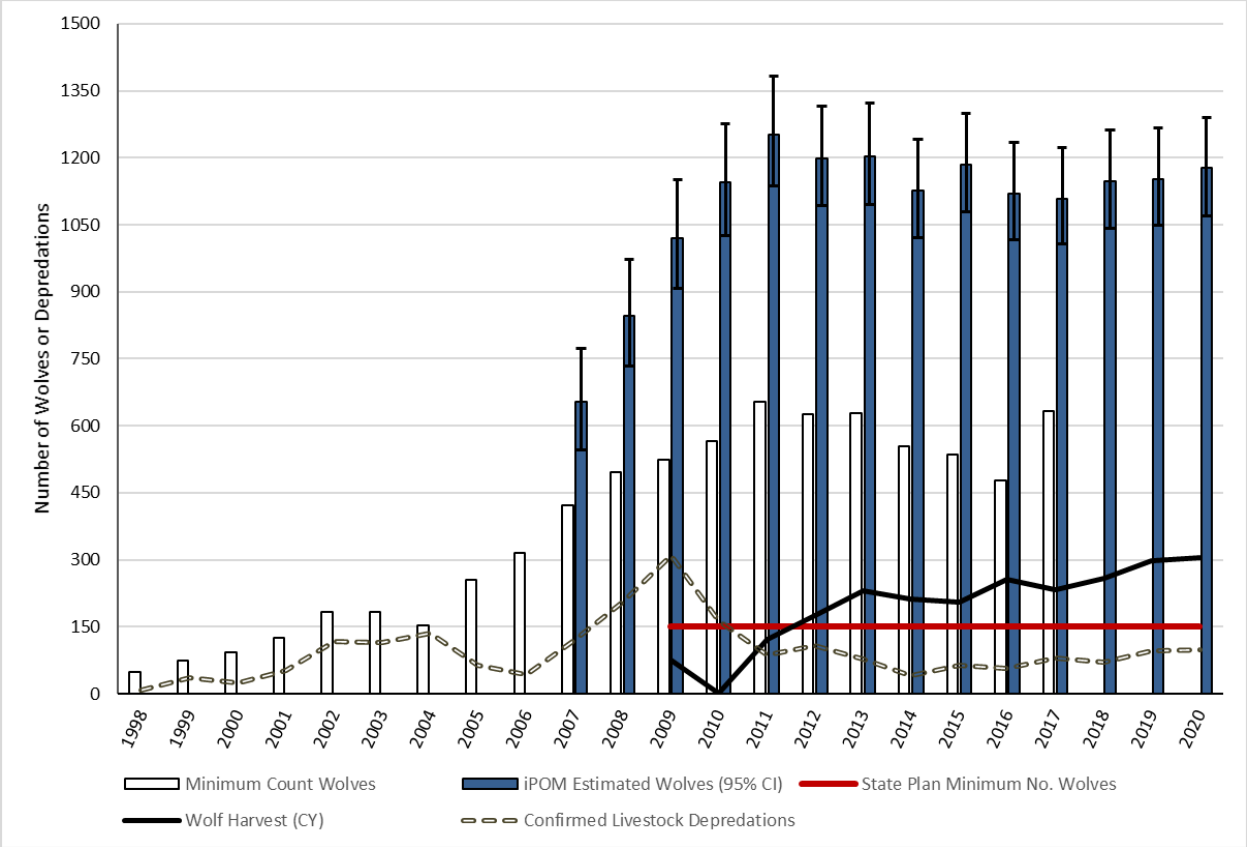

Figure 1. Integrated Patch Occupancy Modeling (iPOM) estimated number of wolves in Montana (including 95% credible intervals) and verified minimum number of wolves residing in Montana in relation to state wolf plan requirements along with trends in wolf harvest and confirmed livestock losses due to wolves, 1998 – 2020.

1. BACKGROUND

Wolf recovery in Montana began in the early 1980's. Wolves increased in number and distribution because of natural emigration from Canada and successful federal and tribal efforts that reintroduced wolves into Yellowstone National Park and the wilderness areas of central Idaho. The federal wolf recovery goal of 30 breeding pairs for 3 consecutive years in Montana, Idaho and Wyoming was met during 2002, and wolves were declared to have reached biological recovery by the U.S. Fish and Wildlife Service (USFWS) that year. During 2002 there were a minimum of 663 wolves and 43 breeding pairs in the Northern Rocky Mountains (NRM).

The Montana Gray Wolf Conservation and Management Plan was approved by the USFWS in 2004. Nine years after having been declared recovered and with a minimum wolf population of more than 1,600 wolves and 100 breeding pairs in the NRM, in April 2011, a congressional budget bill directed the Secretary of the Interior to reissue the final delisting rule for NRM wolves. On May 5, 2011 the USFWS published the final delisting rule designating wolves throughout the Distinct Population Segment (DPS), except Wyoming, as a delisted species.

Beginning with delisting in May 2011, the wolf was reclassified as a Species in Need of Management in Montana. Montana's laws, administrative rules, and state plan replaced the federal framework. The Montana Wolf Conservation and Management Plan is based on the work of a citizen's advisory council. The foundations of the plan are to recognize gray wolves as a native species and a part of Montana's wildlife heritage, to approach wolf management similar to other wildlife species such as mountain lions, to manage adaptively, and to address and resolve conflicts. As noted in the State Plan, "Long-term persistence of wolves in Montana depends on carefully balancing the complex biological, social, economic, and political aspects of wolf management."

At present, Montana Fish, Wildlife and Parks (FWP) implements the state management plan using a combination of sportsman license dollars and federal Pittman-Robertson funds (excise tax on firearms, ammunition, and hunting equipment) to monitor the wolf population, regulate sport harvest, coordinate and authorize research, and direct problem wolf control under certain circumstances. Several state statutes also guide FWP's wolf program. FWP and partners have placed increasing emphasis on proactive prevention of livestock depredation. USDA Wildlife Services (WS) continues to investigate injured and dead livestock, and FWP works closely with them to resolve conflicts. Montana's Livestock Loss Board compensates producers for losses to wolves and other large carnivores.

Montana wolf conservation and management has transitioned to a more fully integrated program since delisting. With wolf population level securely above requirements for over a decade, FWP continues to adapt the wolf program to match resources and needs. For years, when the population was small and wolves were listed, a "wolf weekly" report was issued, detailing all depredations, collaring, control and known mortalities. That level of detail and its

associated expense is no longer warranted, and the information is now reported annually. This allows limited personnel time and conservation dollars to be allocated more effectively.

Population monitoring techniques have also changed. Wolf packs were intensively monitored year-round beginning with their return to the northwestern part of Montana in the 1980's. Objectives for monitoring during the period of recovery were driven by the USFWS's recovery criteria – 30 breeding pairs for 3 consecutive years in Montana, Idaho, and Wyoming. Similar metrics of population status were used from the time recovery criteria were met in 2002, through delisting in 2011, and for the 5 years when the USFWS retained oversight after delisting. These population monitoring criteria and methods were appropriate and achievable when the wolf population was small and recovering. For instance, in 1995, when wolves were reintroduced into Yellowstone National Park and central Idaho, the end-of-year count for wolves residing in Montana was 66. In the early years, most wolf packs had radio-collared individuals and intensive monitoring was possible to identify new packs and most individuals within packs. However, in later years, the minimum count of wolves approached or exceeded 500 individuals distributed across more than 25,000 square miles of mostly rugged and remote terrain in western Montana. Therefore, the ability to count every pack, every wolf, and every breeding pair has become expensive, unrealistic, and unnecessary. Consequently, FWP has moved to more cost-effective methods for monitoring wolves. These methods can be more accurately described as population estimates that account for uncertainty (confidence intervals), as opposed to a minimum count where the end result, at this time when populations are large, reflects total effort (and dollars spent) as much as population numbers.

FWP first began considering alternative approaches to monitoring the wolf population in 2006 through a collaborative effort with the University of Montana Cooperative Wildlife Research Unit. The primary objective was to find an alternative approach to wolf monitoring that would yield statistically reliable estimates of the number of wolves, the number of wolf packs, and the number of breeding pairs (Glenn et al. 2011). Ultimately, a method applicable to a sparsely distributed and elusive carnivore population was developed that used hunter observations as a cost-effective means of gathering biological data to estimate the area occupied by wolves in Montana - "Patch Occupancy Modeling" (POM; Rich et al. 2013a) and most recently "Integrated Patch Occupancy Modeling" (iPOM; Sells et al. (2020a)

iPOM is a modern, scientifically valid, and financially efficient means of monitoring wolves. iPOM is the best and most efficient method to document wolf population numbers and trend at this point in time. FWP is confident that the wolf population estimate and trend that iPOM provides is sufficient and scientifically valid evidence that can be used to assess wolf status relative to the criteria outlined in Montana's Wolf Conservation and Management Plan. Minimum counts and pack tables are no longer reported. Instead, the more appropriate and efficient techniques that have been in development for a decade are being used. If new and improved techniques become available in the future, those methods may be implemented when appropriate.

2. WOLF POPULATION MONITORING

2.1 Wolf Distribution and Numbers via Integrated Patch Occupancy Modeling

We used an Integrated Patch Occupancy Model (iPOM) to estimate the distribution and number of wolves in Montana (Sells et al. 2020). With iPOM, an occupancy model estimates the extent of wolf distribution in Montana, and a territory model predicts territory sizes; together, these models predict the number of packs in a given area (Fig. 2). A group size model predicts pack sizes. Total abundance estimates are derived by combining the estimated number of packs and pack sizes, while also accounting for lone and dispersing wolves.

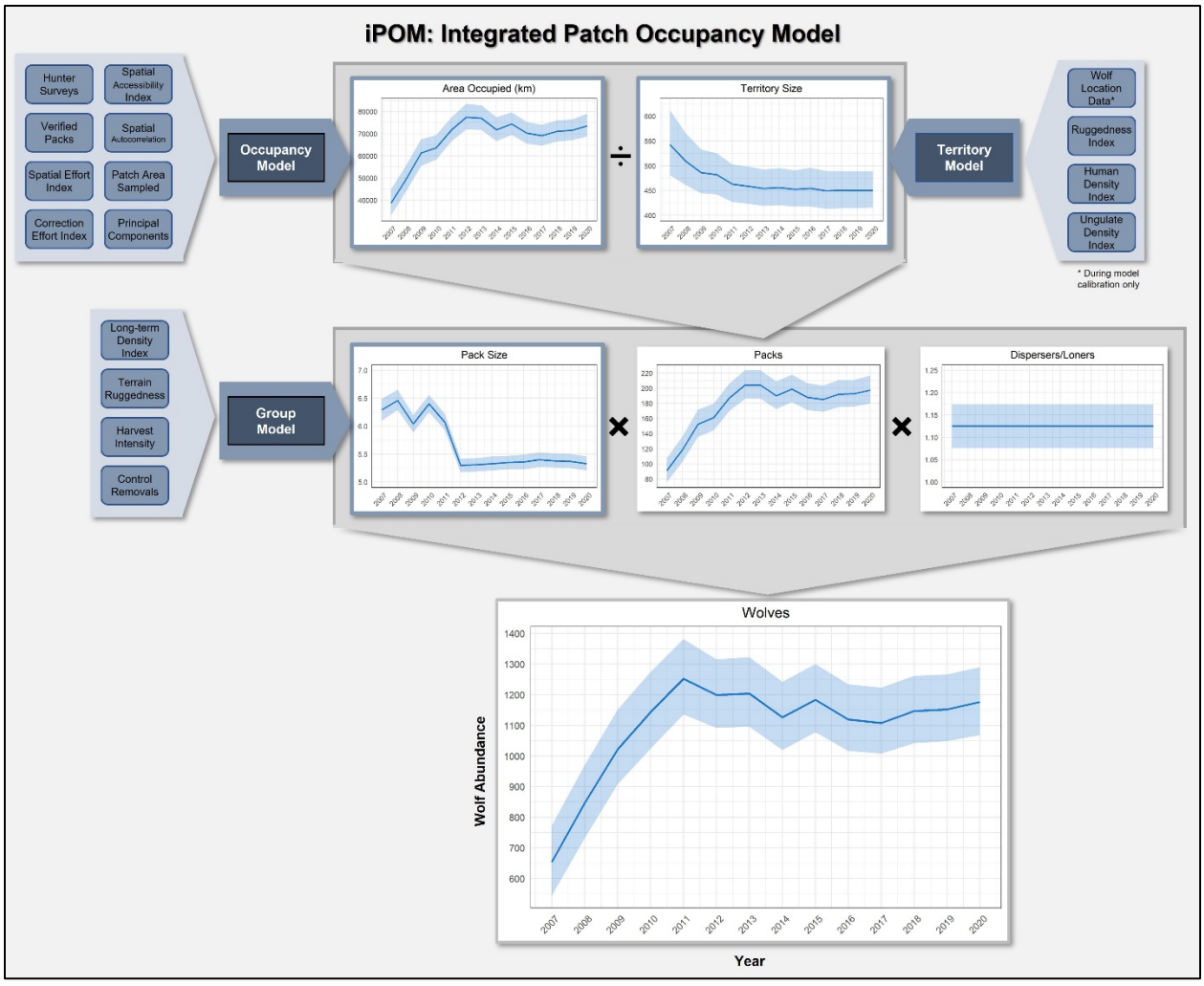

Figure 2. Schematic for method of estimating the area occupied by wolves, number of wolf packs and number of wolves in Montana, 2007 – 2020 using an Integrated Patch Model. Graphs show statewide estimates over time. Ribbons indicate 95% credible intervals.

Integrated Patch Occupancy Modeling Methods

Occupancy Model

To predict where wolves occurred in Montana each year from 2007 – 2019, we fit a multi-season false-positives occupancy model in a Bayesian context (Bassing et al. 2019). This work built on an earlier occupancy model (Miller et al. 2013, Rich et al. 2013, Inman et al. 2020). Following those authors, we created an observation "iPOM grid" for Montana as 600 km^2 cells. We assigned locations of wolves in packs to grid cells, based on monitoring effort by MFWP Wolf Specialists and wolf sightings reported by hunters each fall. Wolf Specialists monitored packs each year to verify presence using trail cameras, visual observations, and telemetry collars, and used these data to demarcate approximate territory centroids for packs. MFWP conducted annual Hunter Harvest Surveys of a random sample of 50,000 – 80,000 resident deer and elk hunters annually to obtain wolf sighting reports. 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.

To develop encounter histories, we divided the 5-week general rifle season (occurring each year around late Oct through Nov or early Dec) into one-week encounter periods and mapped locations of pack centroids and hunter observations for each week. Based on past work (Miller et al. 2013, Rich et al. 2013, Inman et al. 2020), we included model covariates for detection as: 1) hunter days per km^2 in each hunting district (an index to spatial effort), 2) proportion of mapped wolf observations (a correction for effort, accounting for number of hunter observations with coordinates versus total reported, including any sightings with vague location descriptions), 3) densities of low-use forested and non-forested roads (indices of spatial accessibility), 4) a spatial autocovariate (proportion of neighboring cells with wolves seen out to a mean dispersal distance of 100 km), and 5) patch area sampled (because smaller cells on the border of Montana, parks, and tribal lands have less hunting activity and therefore less opportunity for hunters to see wolves). We also included cell size as a nuisance parameter to account for varying cell sizes. Model covariates for occupancy, colonization, and local extinction included a principal component constructed from several autocorrelated environmental covariates (percent forest cover, slope, elevation, latitude, percent low use forest roads, and human population density), and recency (number of years with verified pack locations in the previous 5 years).

Using these pack locations and model covariates, we fit the multi-season false-positives occupancy model to estimate psi, the probability of occupancy (ψ). We used pack centroids to estimate probabilities of false positives, true positives, and false negatives (Miller et al. 2013). We estimated ψ for tribal lands and national parks, where no hunter survey data were available, via modeled covariates.

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 ran 3 chains for 10,000 iterations, after an adaptation phase of 10,000 iterations and a burn-in of 10,000 iterations. We did not thin the MCMC chains.

Territory Model

We used a recently developed mechanistic territory model to predict territory size. Full details are available in Sells and Mitchell 2020 and Sells et al. 2020, 2021. 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. After calibrating the model using wolf location data collected from 2014 – 2018 (Sells et al. 2020), the model provided territory size predictions through simulations in NetLogo 6.1.1 (Wilensky 1999).

The model demonstrated the strong effect of competition on resulting space use (Sells and Mitchell 2020; Sells et al. 2020, 2021). Accordingly, we applied the model to predict territory sizes at a wide range of possible pack densities and resulting levels of competition. We used a density identifier model (Sells et al. 2020) to predict levels of competition in each area of Montana for each year. We then used the territory sizes predicted at the given level of competition as estimates of territory size in each area of the state.

Group Model

We used a recently-developed group size model (Sells et al. 2020) to predict pack sizes in each 600 km^2 iPOM grid cell. The model was based on mechanisms hypothesized to influence wolf pack size and developed using 14 years of wolf pack data. The generalized linear mixed effects model included effects of pack density, terrain ruggedness, harvest intensity, and control removals. Pack density was the long-term (2005 – 2018) mean pack density in the iPOM grid cell, which served as an index to density trends (Sells et al. 2020). Ruggedness was terrain ruggedness in the iPOM grid cell. 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 – 2020 rules were followed (statewide harvest quotas were removed, seasons were longer, bag limits were higher, and trapping was allowed; fwp.mt.gov). Control removals were reported numbers of wolves removed for depredations in the iPOM grid cell that year. Ecoregion defined in which ecoregion the iPOM grid cell fell (epa.gov). The unique identifier for the iPOM grid cell was included as a random effect to account for repeated observations among years. We applied the model to each iPOM grid cell, each year, to predict local pack size.

Model Integration

We estimated numbers of packs and wolves for each year, 2007 – 2020, by combining predictions from the 3 models (Fig. 2). We first calculated mean estimated occupancy ($\bar{\psi}$) across iPOM grid cells, then calculated area occupied ($area_{occupied}$) as:

$$area_{occupied} = \bar{\psi} \times \sum grid_{area}$$

where $\sum grid_{area}$ was the sum of grid cell areas. We calculated number of estimated packs as:

$$N_{packs} = area_{occupied} \div territory_{size}$$

where values for $territory_{size}$ were drawn with replacement for each iteration of the MCMC chain from the distribution of territory sizes predicted by the territory model at the specific grid cell. Values for $territory_{size}$ were therefore spatially explicit and biologically appropriate to local conditions each year and accounted for uncertainty. We then calculated number of wolves as:

$$N_{wolves} = N_{packs} \times pack_{size} \times lone_{rate}$$

where $lone_{rate}$ accounted for lone and dispersing wolves. For $pack_{size}$ we drew for each iteration of the MCMC chain a value from the distribution of group sizes predicted at the specific grid cell. This provided spatially explicit and biologically appropriate values for local conditions each year while incorporating model uncertainty about pack size. We modeled $lone_{rate}$ by drawing for each iteration of the MCMC chain values from a normal distribution assuming a mean of 1.125 and standard deviation of 0.025. This yielded a loner/disperser rate of 12.5% and incorporated variation and uncertainty around this rate, as 95% of values drawn were 7.6 – 17.4%. We selected these values based on studies documenting that 10 – 15% of wolf populations are comprised of lone or dispersing wolves (Fuller et al. 2003). This is consistent with Idaho's calculations for lone wolves (Holyan et al. 2013) and slightly more conservative than Minnesota's calculations, which add 15% (Erb et al. 2018).

To account for uncertainty and calculate credible intervals (CI's) for all parameters, we retained posterior estimates of 10,000 values for each and calculated the median value and 2.5% and 97.5% values (creating 95% CI's) for $area_{occupied}$, $territory_{size}$, $pack_{size}$, N_{packs}, and N_{wolves}. We calculated density of packs per 1,000 km^2, wolves per 1,000 km^2, and population growth (lambda, λ).

We repeated these calculations for MFWP management regions by completing each step described above at each subsetted group of grid cells by region. Grid cells were categorized by the region in which the majority of their areas fell.

Integrated Patch Occupancy Modeling Results

Area Occupied

Each year (2007 – 2020), 50,026 – 82,375 hunters responded annually to the wolf sighting surveys. From their reported sightings, 979 – 3,469 locations of 2 – 25 wolves were mapped each year. Percent of hunters reporting a wolf sighting ranged from 4.4% (2020) to 7.5% (2011).

From 2007 – 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 (Fig. 3).

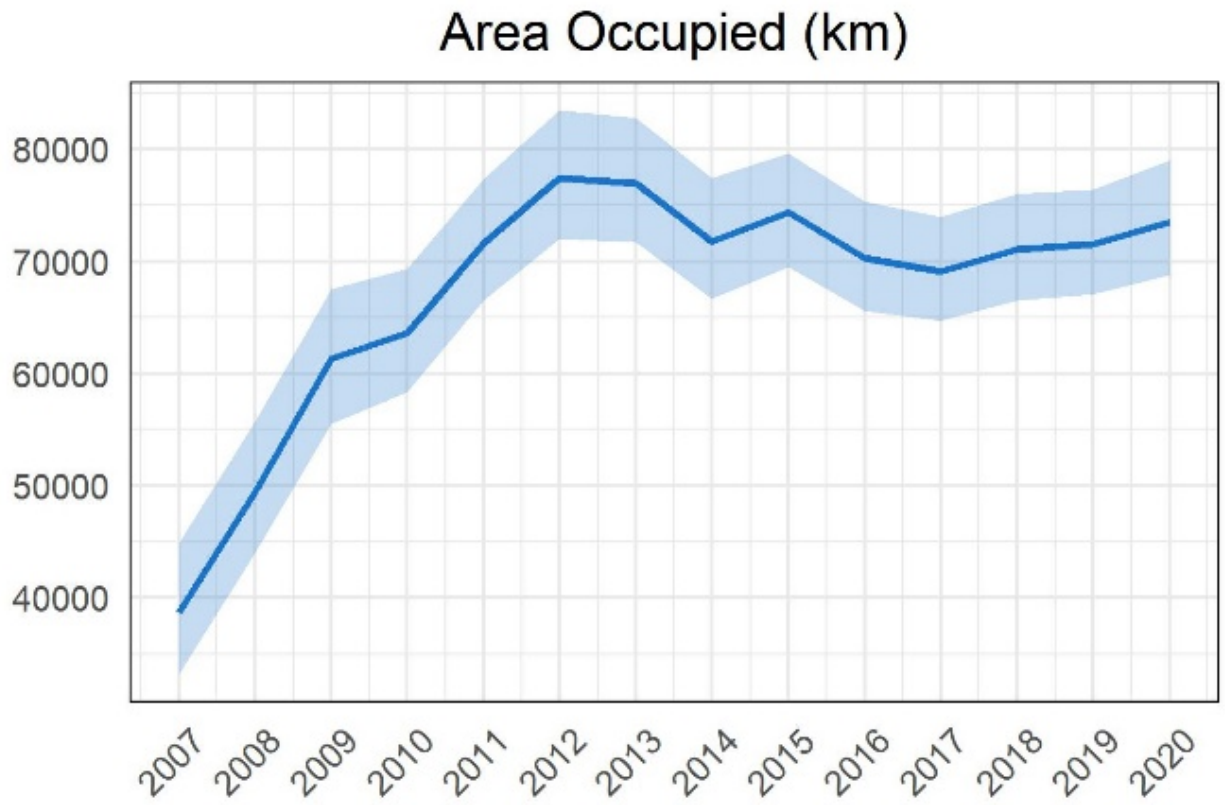

Figure 3. Estimated total area occupied (km^2) by wolves in Montana, 2007 – 2020. Ribbon indicates 95% credible interval.

Territory Size

Estimated territory size varied across time and space (Fig. 4). Overall, territory size was estimated to be largest in southwest MT and second largest in areas in and around Glacier National Park and the Bob Marshall Wilderness. Territories were estimated to be smaller in northwest MT and the Bitterroot. Territory size was greatest in 2007 and dropped thereafter, and has remained largely stable in the past decade.

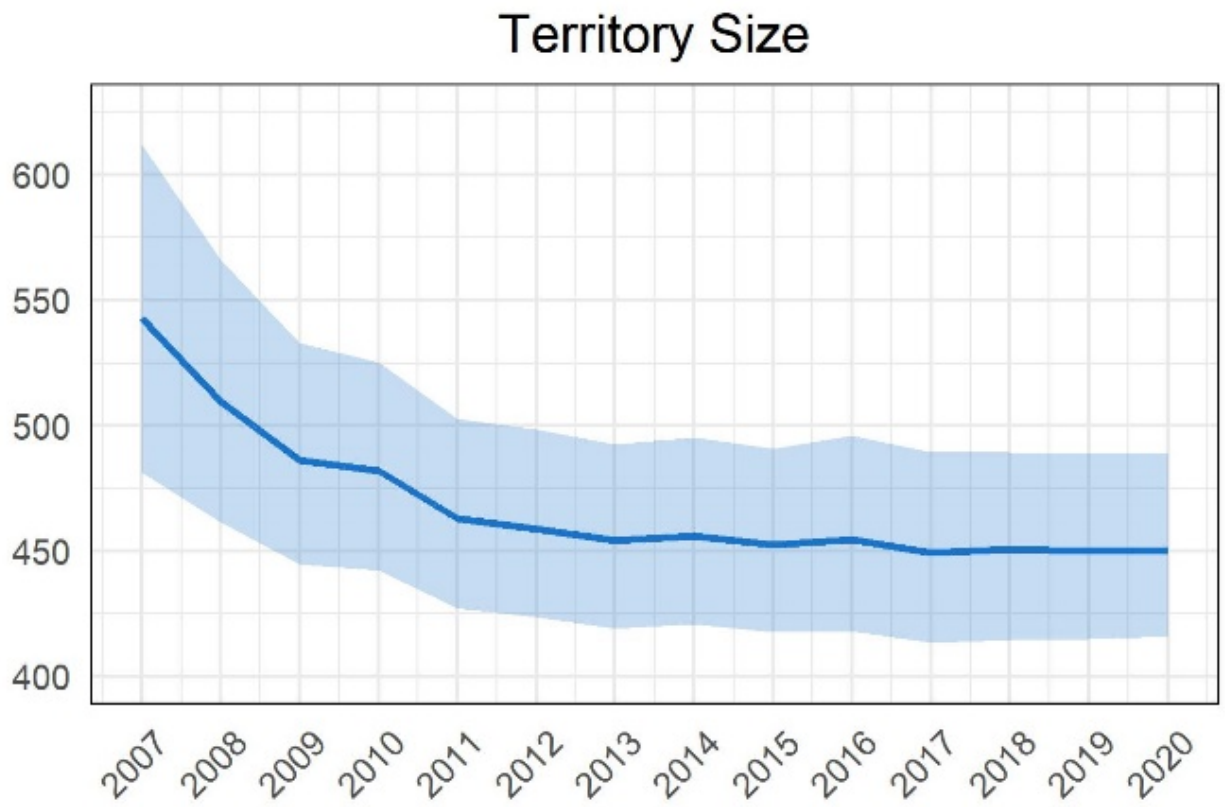

Figure 4. Estimated mean territory size (km^2) of wolves in Montana, 2007 – 2020. Ribbon indicates 95% credible interval.

Group Size

Estimated pack size also varied (Fig. 5). Mean pack sizes were larger in earlier years (prior to harvest) and have since declined by approximately 1 wolf per pack, on average. Mean pack size was estimated to be similar across Montana (an approximate difference of < 1 wolf per pack in most years).

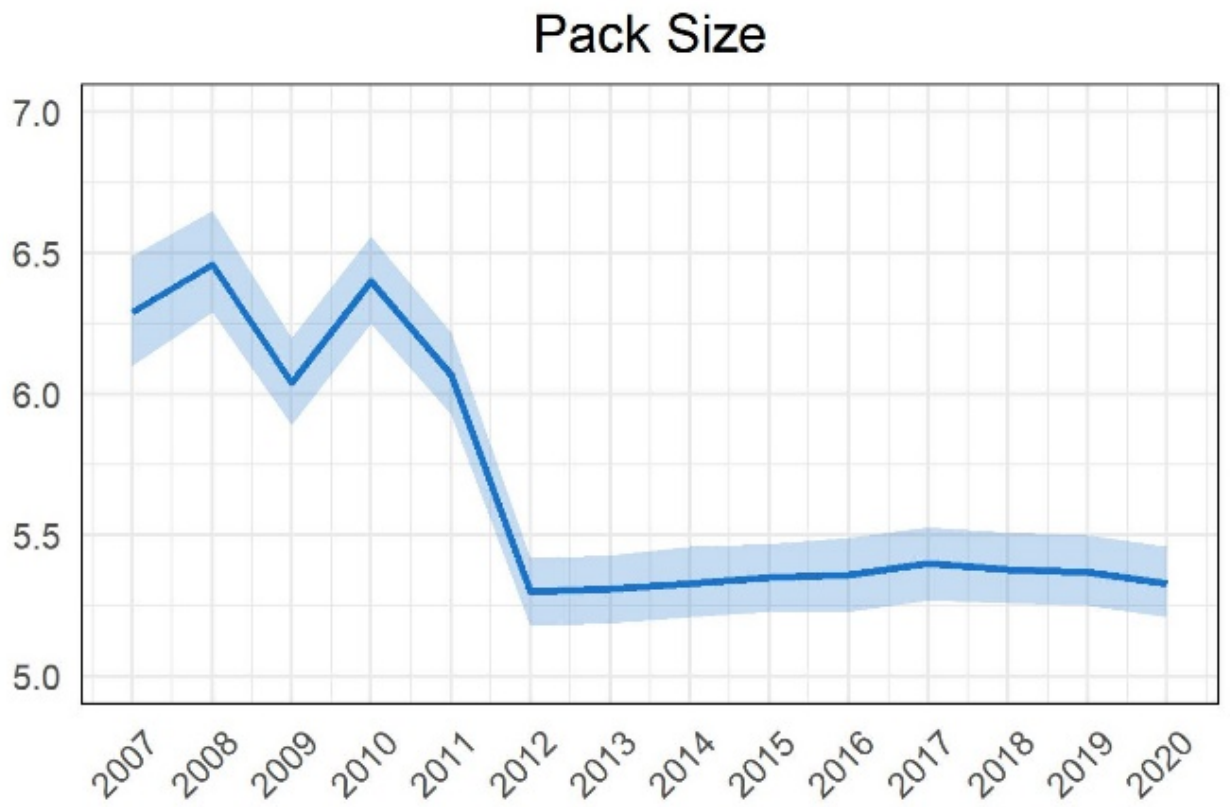

Figure 5. Estimated mean pack size of wolves in Montana, 2007 – 2020. Ribbon indicates 95% credible interval.

Estimated Number of Packs and Wolves

Estimated numbers of packs and wolves varied through time (Fig. 6; Table 1). The population was estimated to have been smallest in the first year of our analysis (2007), with 91 packs (95% CI = 76 – 108) and 654 wolves (95% CI = 545 – 773). Population growth was positive through 2011 (Fig. 6). Total wolf numbers peaked in 2011 with 187 packs (95% CI = 170 – 206) and 1,252 wolves (95% CI = 1,136 – 1,382). This peak coincided with the first years of harvest management in Montana, after which the population declined by 6.0% in total wolf abundance between 2011 and 2020.

Population growth rate alternated from slightly positive and slightly negative each year (Fig. 7). From 2016 – 2020, the population appears to have become somewhat stabilized with an average of 191 packs and 1,141 wolves per year.

Estimated numbers of packs and wolves varied spatially (Fig. 6). Pack and wolf abundances were consistently greater in MFWP Region 1, followed by Regions 2 and 3. Regions 4 – 7 each contained only ≤ 1 – 9% of packs and 1 – 7% of wolves.

Wolf densities varied over space and time (Fig. 8). Densities were estimated to be greatest in MFWP Region 1 (ranging 6.42 – 13.31 wolves per 1,000 km^2 from 2007 – 2020), followed by Region 2 (6.62 – 12.44) and Region 3 (3.24 – 5.07). Regions 4 – 7 had ≤ 1.41 wolves per 1,000 km^2. Maps of pack and wolf densities demonstrate close alignment between known packs, locations of wolf harvests, and predictions from iPOM (Fig. 8).

Table 1. Estimated area occupied by wolves (km^2), number of wolf packs, and number of wolves in Montana, 2007 – 2020. Annual numbers were based on best available information and were retroactively updated as patch occupancy modeling incorporated more information each year.

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	1,021	908	1,151
2010	63,615	58,356	69,367	161	144	180	1,144	1,025	1,275
2011	71,598	66,472	77,317	187	170	206	1,252	1,136	1,382
2012	77,396	72,025	83,472	204	186	224	1,199	1,092	1,316
2013	76,931	71,688	82,796	204	186	224	1,204	1,096	1,323
2014	71,805	66,680	77,413	190	172	209	1,127	1,020	1,242
2015	74,377	69,514	79,661	199	182	218	1,184	1,078	1,300
2016	70,263	65,577	75,293	188	171	207	1,119	1,017	1,234
2017	69,084	64,731	73,984	185	169	203	1,107	1,008	1,223
2018	71,099	66,517	76,027	192	175	211	1,147	1,042	1,262
2019	71,523	67,021	76,426	193	176	211	1,153	1,049	1,266
2020	73,463	68,754	78,958	197	180	217	1,177	1,069	1,290

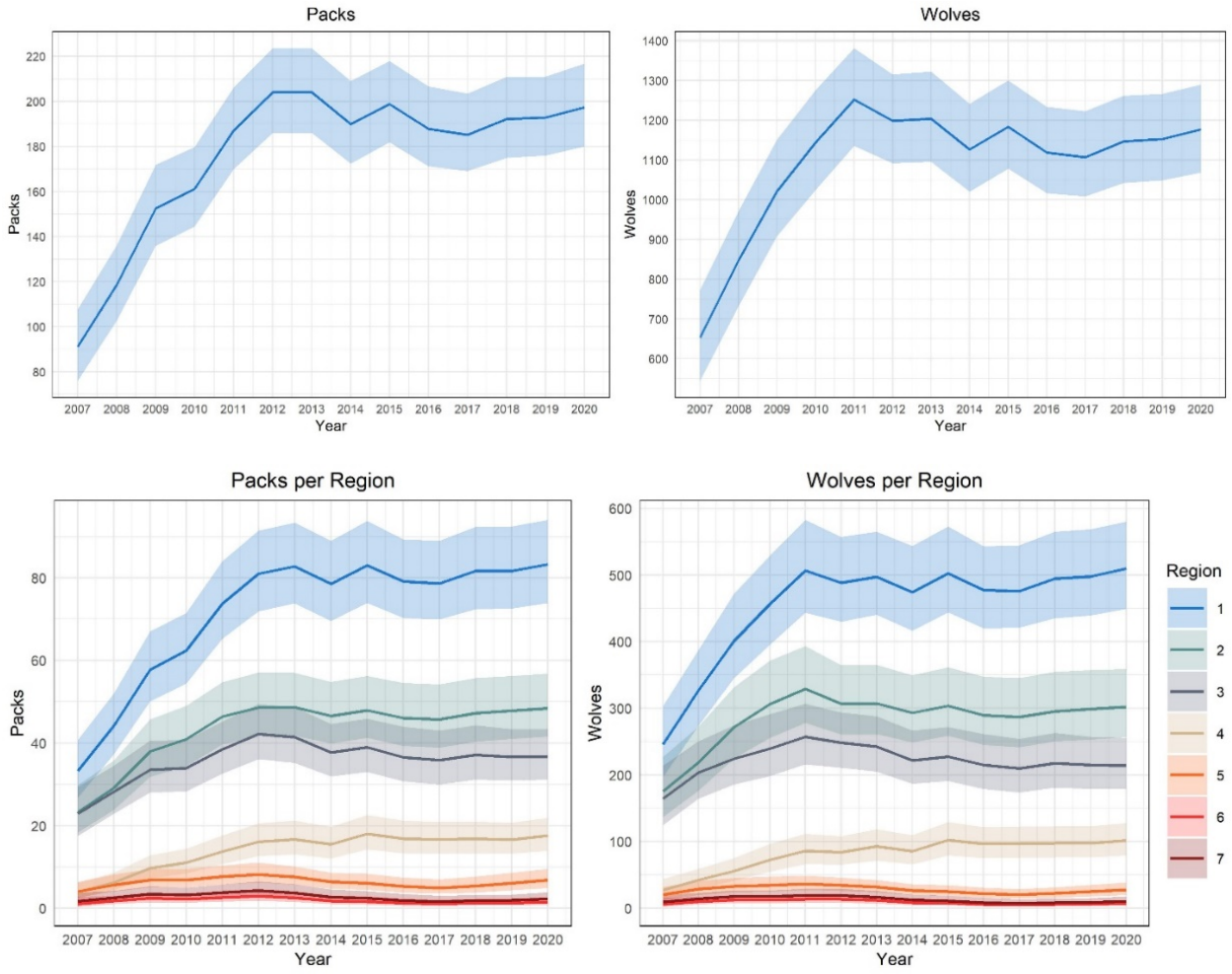

Figure 6. Estimated number of packs and wolves in Montana and by MFWP Administrative Region, 2007 – 2020. Ribbons indicate 95% credible intervals.

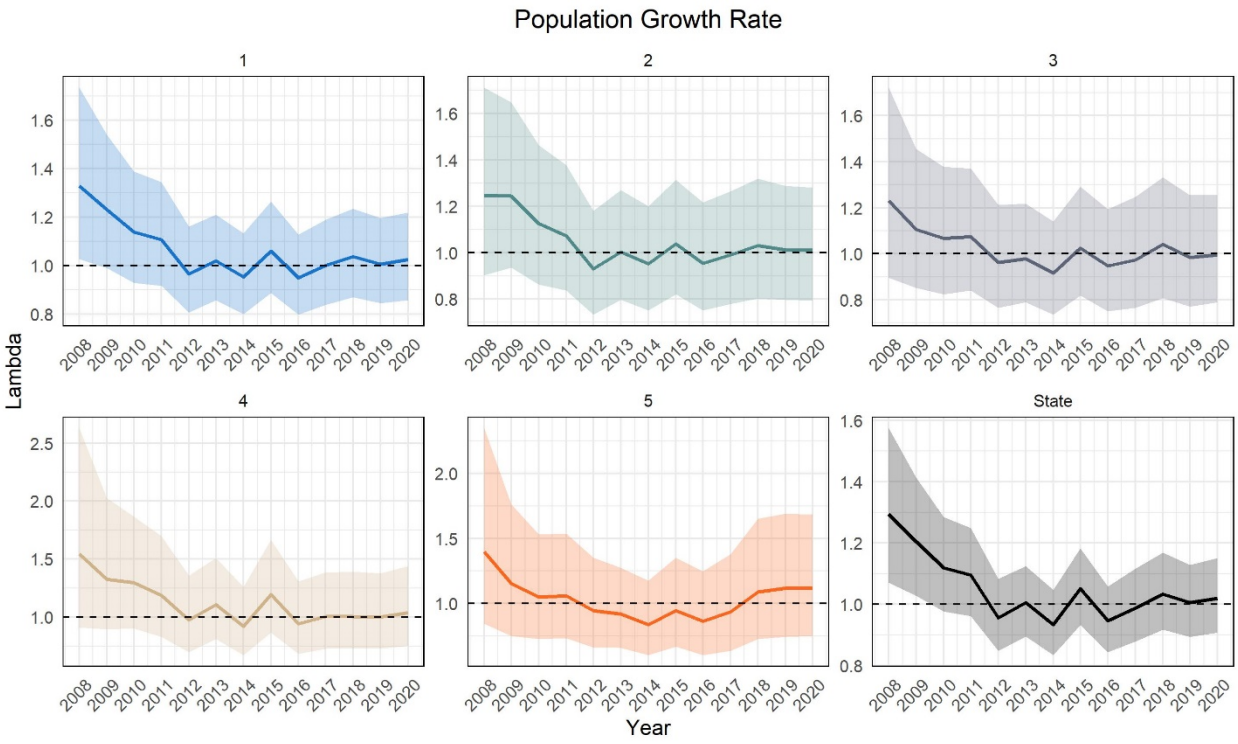

Figure 7. Population growth rate for wolves in MFWP Administrative Regions 1 – 5 and the state, 2008 – 2020. Values <1 indicate a declining population, whereas values >1 indicate a growing population. Ribbons indicate 95% credible intervals.

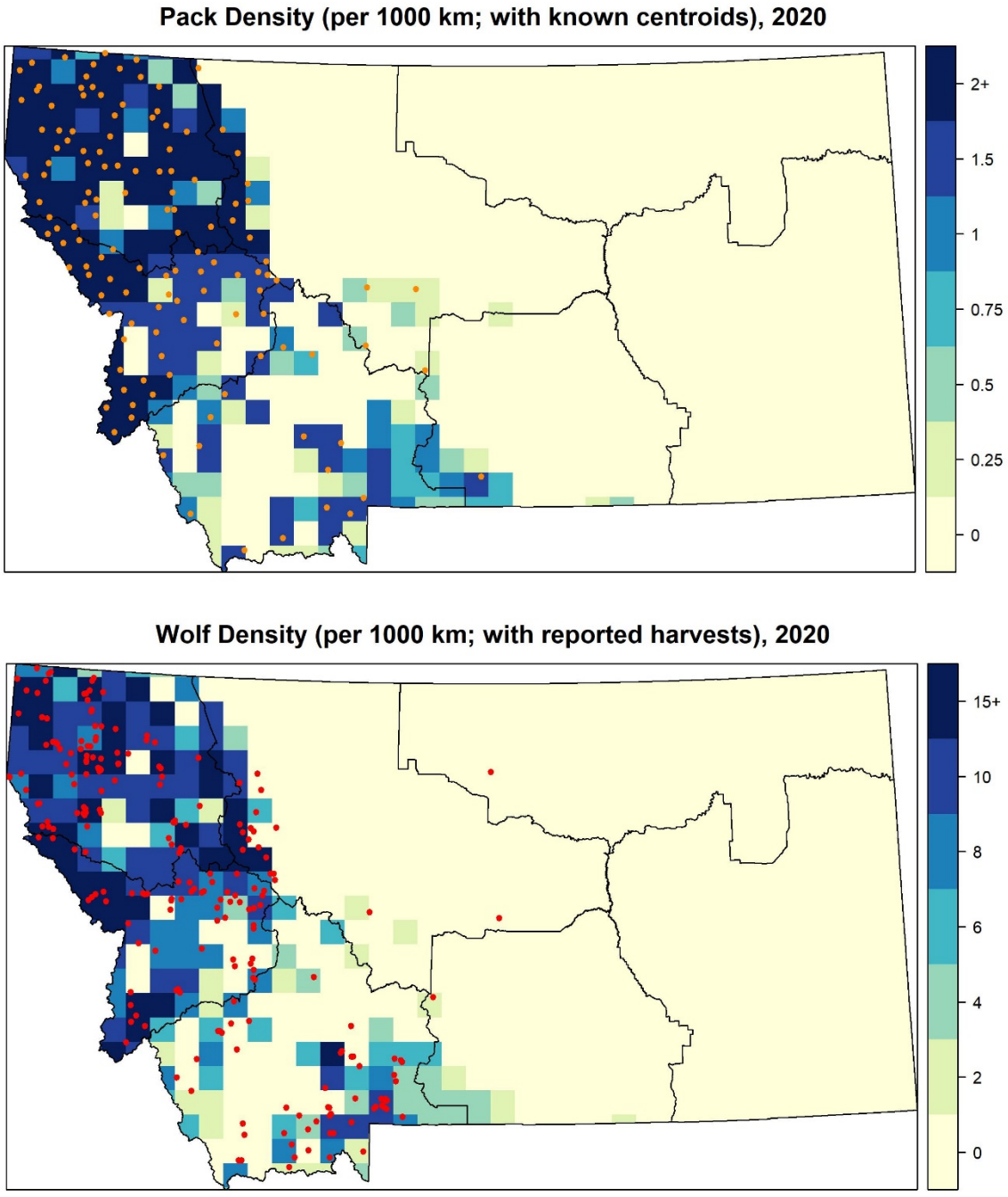

Figure 8. Estimated pack and wolf densities in Montana, 2020, per 1,000 km^2. Orange points demarcate territory centroids identified through monitoring in 2020 (pack density map), whereas red points demarcate reported harvest locations in 2020 (wolf density map).

3. WOLF MANAGEMENT

3.1 Regulated Public Hunting and Trapping

Regulated public harvest of wolves was recommended by the Governor's Wolf Advisory Council and included in Montana's Wolf Conservation and Management Plan that was approved by the USFWS during 2004. FWP has developed and implemented wolf harvest strategies that maintain a recovered and connected wolf population, minimize wolf-livestock conflicts, reduce wolf impacts on low or declining ungulate populations and ungulate hunting opportunities, and effectively communicate to all parties the relevance and credibility of the harvest while acknowledging the diversity of values among those parties. The Montana public has the opportunity for continuous and iterative input into specific decisions about wolf harvest throughout the public season-setting process. Wolf seasons are to be reviewed every other year by the Fish and Wildlife Commission during December (proposals) and February (final decisions). This timing allows discussion of ungulate and wolf seasons during the same Commission meetings.

At the close of the 2020-21 wolf season (2020 License Year) on March 15, 2021, the harvest totaled 327 wolves taken during the 2020-21 season, including 169 taken by hunters (51.6%) and 158 taken by trappers (48.3%). The 2020-21 season yielded the highest wolf harvest on record. Eighty-one more wolves were harvested during 2020-21 season than the average during the previous 8 wolf seasons when both hunting and trapping were allowed (2012-2019). Most of the increase over the 8-year average occurred in Regions 1, 2, and 3 via trapping (Table 2). Statewide wolf population appears to have peaked in 2013 and has declined slightly since then, appearing to stabilize at around 1,150 wolves (Fig. 9). The total calendar-year 2020 wolf harvest in Montana was 305, including 136 wolves harvested during spring of the 2019-20 season and 169 wolves harvested during fall of the 2020-21 season.

Table 2. Change in level of wolf harvest in Montana between the 2012-2019 seasons and the 2020 season by FWP Region and type of harvest.

	2012-2019 Average					**2020 Season**					**Change**				
	R1	**R2**	**R3**	**R4**	**All**	**R1**	**R2**	**R3**	**R4**	**All**	**R1**	**R2**	**R3**	**R4**	**All**
Hunt	46	33	60	10	**149**	48	40	69	12	**169**	2	7	9	2	**20**
Trap	43	31	14	9	**97**	83	37	31	7	**158**	40	6	18	-2	**61**
Total	**89**	**65**	**74**	**19**	**246**	**131**	**77**	**100**	**19**	**327**	**43**	**13**	**27**	**0**	**81**

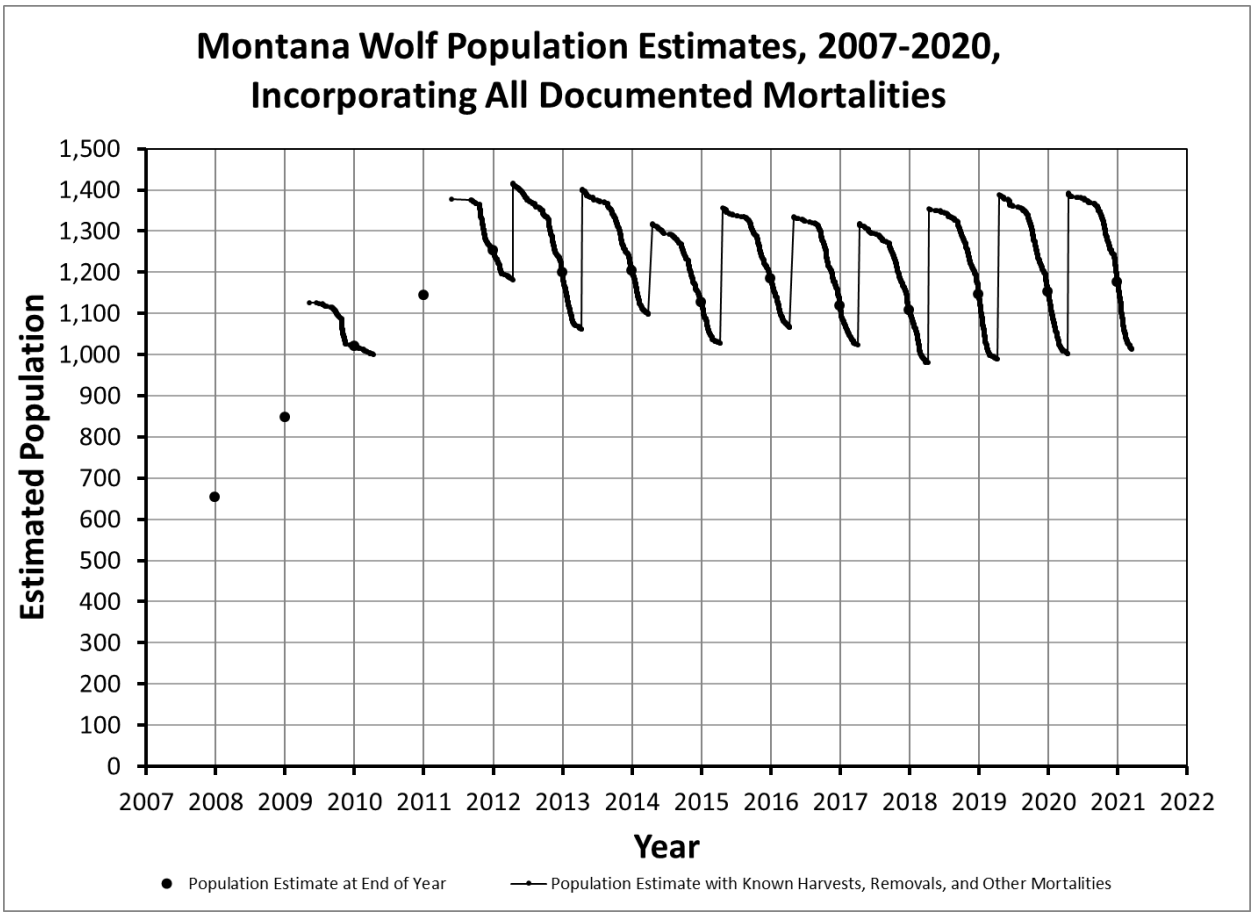

Figure 9. Estimated wolf population size based on known mortalities anchored to December 31 Integrated Patch Occupancy Modeling estimates, 2007-2020.

During 2020, Montana sold 15,994 resident wolf hunting licenses and 2,393 non-resident wolf hunting licenses. Three bills passed by the 2019 legislature lowered the price of wolf hunting licenses in 2020. In calendar year 2020 the price of a resident wolf hunting license dropped from $19 to $12 and a discounted $10 wolf hunting license was offered with the purchase of a sportsman's tag. A nonresident wolf hunting license cost $50 but a discounted nonresident wolf hunting license was offered for $25 with the purchase of a sportsman's tag. Sale of these wolf licenses generated $298,864 for wolf management and monitoring in Montana (Fig. 10). Total funding generated for wolf monitoring and management by the sale of wolf hunting licenses from 2009-2020 is over $4.4 million. Because trapping licenses for both residents and non-residents are not wolf-specific, FWP cannot quantify the financial contribution that wolf trapping generates.

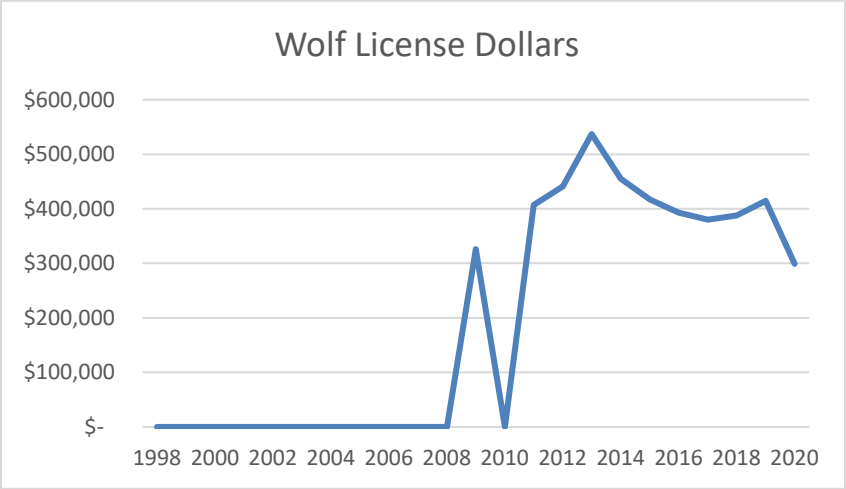

Figure 10. Dollars generated for wolf conservation and management through sales of wolf hunting licenses in Montana, 1998-2020.

3.2 Wolf – Livestock Interactions in Montana

Montana wolves routinely encounter livestock on both private land and public grazing allotments. Wolves are opportunistic predators, most often seeking wild prey. However, some wolves learn to prey on livestock and teach this behavior to other wolves. The majority of cattle and sheep wolf depredation incidents confirmed by USDA Wildlife Services (WS) occur on private lands. The likelihood of detecting injured or dead livestock is probably higher on private lands where there is greater human presence than on remote public land grazing allotments. The magnitude of under-detection of loss on public allotments is unknown. Most cattle depredations occur during the spring or fall months while sheep depredations occur more sporadically throughout the year.

Wolf Depredation Reports

Wildlife Service's workload increased through 2009 as the wolf population increased and distribution expanded (Fig. 11). The number of depredation reports received since those years has declined from 233 in FFY 2009 to approximately 100 or less from FFY14-FFY20. That trend held steady during FFY 2020, when 105 reports were received (Fig. 11). Since 1997, about 50% of wolf depredation reports received by WS have been verified as wolf-caused. During FFY 2020, 60% of reports were verified as wolf depredation, slightly higher than the long-term average.

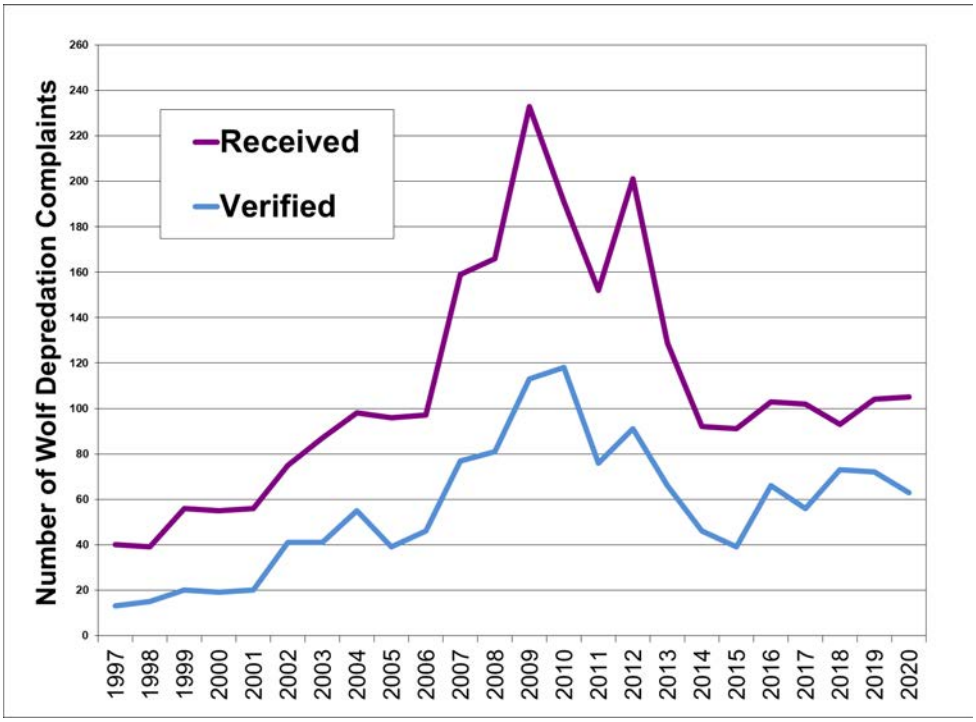

Figure 11. Number of complaints received by USDA Wildlife Services as suspected wolf damage and number of complaints verified as wolf damage, Federal Fiscal Year 1997-2020.

Wolf Depredation Incidents and Responses During 2020

Wildlife Services confirmed that, statewide, 62 cattle, 32 sheep, 5 lamas, and 4 livestock guard dogs were killed by wolves during 2020. Wildlife Services also determined that an additional 14 cattle and 5 lamas were probable wolf kills. Total confirmed cattle and sheep losses were similar to 2011-2019 numbers, however the number of cattle has increased whereas the number of sheep has decreased (Fig. 12). Many livestock producers reported "missing" livestock and suspected wolf predation. Others reported indirect losses including poor weight gain and reduced productivity of livestock. There is no doubt that there are undocumented losses.

To address livestock conflicts and to reduce the potential for further depredations, 52 wolves were killed during 2020 (Fig. 12). This was lower than the average number of wolves removed due to depredation since meeting biological recovery goals in 2002 (Avg. = 70/year) and since delisting in 2011 (Avg. = 67/year). Federal and state regulations since 2009 have allowed private citizens to kill wolves seen in the act of attacking, killing, or threatening to kill livestock; from 2009-2020 an average of 11 wolves have been taken by private citizens each year. Fourty-seven wolves were removed in control actions by USDA Wildlife Services during 2020, five wolves were killed by private citizens when wolves were seen chasing, killing, or threatening to kill livestock. The general decrease in livestock depredations since 2009 (Fig. 12) may be a result of

several factors, primarily more aggressive wolf control in response to depredations (DeCesare et al. 2018).

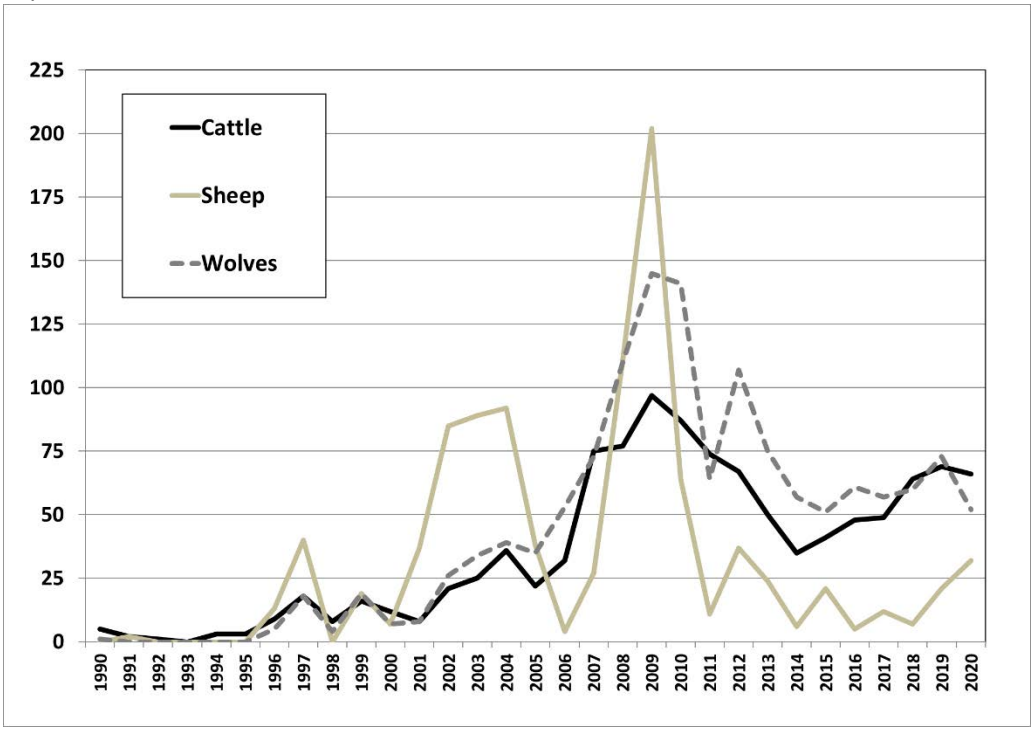

Figure 12. Number of cattle and sheep killed by wolves and number of wolves removed through agency control and legal depredation-related take by private citizens, 2000-2020.

Montana Livestock Loss Board Payments

The Montana Wolf Conservation and Management Plan called for creation of this Montana-based program to address the economic impacts of verified wolf-caused livestock losses. The plan identified the need for an entity independent from FWP to administer the program. The purposes of the MLLB are 1) to provide financial reimbursements to producers for losses caused by wolves based on the program criteria, and 2) to proactively apply prevention tools and incentives to decrease the risk of wolf-caused losses and minimize the number of livestock killed by wolves through proactive livestock management strategies. The Loss Mitigation element implements a reimbursement payment system for confirmed and probable losses that are verified by USDA Wildlife Services. Indirect losses and costs are not directly covered. Eligible livestock losses are cattle, calves, hogs, pigs, horses, mules, sheep, lambs, goats, llamas, and guarding animals. Confirmed and probable death losses are reimbursed at 100% of fair market value. Veterinary bills for injured livestock that are confirmed due to wolves may be covered up to 100% of fair market value of the animal when funding becomes available.

Reimbursement totals for CY2020 wolf depredations were $75,818.75 paid to 40 livestock owners on 101 head of livestock and 4 dogs. These numbers differ slightly from the WS confirmed losses due to wolves because reimbursements are also made for probable wolf

depredations and tallied by calendar year rather than federal fiscal year. By comparison, confirmed and probable losses totaled $97,526.97 from grizzly bears and $14,192.20 from mountain lions during 2020.

FWP Collaring of Livestock Packs

State Statute 87-1-623 requires Montana Fish, Wildlife and Parks to allocate wolf license dollars toward collaring wolf packs in livestock areas. The purpose of these efforts is to be able to more readily understand which wolf pack may have been involved in a livestock depredation and so that USDA Wildlife Services can be more efficient and effective at controlling packs that depredate on livestock. FWP employs five wolf specialists located in Regions 1, 2, 3, 4, and 5 (Appendix 1) along with seasonal technicians in Regions 1 and 2. Wolf specialists and technicians capture wolves and deploy collars during winter helicopter capture efforts and summer/fall trapping efforts. During 2020, FWP wolf specialists captured and collared 9 wolves (Table 3). USDA Wildlife Services also captured and collared 16 additional wolves for a total of 25 statewide by both agencies.

Table 3. Wolves captured and radio-collared by FWP Wolf Specialists during 2020.

	Helicopter	Summer/Fall	**Total**
Region 1	0	1	**1**
Region 2	0	8	**8**
Region 3	0	0	**0**
Region 4	0	0	**0**
Total	**0**	**8**	**9**

Proactive Prevention of Wolf Depredation

In Northwest Montana, proactive depredation prevention work continued in the Trego area with the third grazing season of the Range Rider program. The Trego Range Rider Program was collaboratively funded and staffed by Natural Resources Defense Council; Defenders of Wildlife; Vital Ground; USDA AHPIS Wildlife Services; Montana Fish, Wildlife & Parks; U.S. Forest Service; and six livestock producers. The desired outcomes were to mitigate producer-predator conflicts, reduce cattle losses, reduce wolf and grizzly bear mortalities, find livestock carcasses and remove them, document presence of predators, and alert producers of predators among the herds. Jessianne Castle was the new Ranger Rider, covering 6 allotments in northwestern Montana on the Kootenai National Forest and Jim Creek state lease. Castle traveled the allotments by vehicle and then on horseback, camping out on the allotments during the week. She notified ranchers and FWP about carnivore activity and set survey cameras to help monitor carnivore presence. Cattle were present on the allotments located within the territories of the Lydia pack, the Swamp Creek pack, and the Good Creek Pack. There were no confirmed wolf depredations in any of the allotments, though there was one cow mortality on private land near one of the allotments that remains uncofirmed. The ranchers provided positive feedback of the program, and said they believed having a Range Rider presence in the area was important. They also thought it was a large area for one person to cover and would be interested in

expanding it with additional riders. The Range Rider program is continuing in 2021, and the ranchers expressed optimism at the spring meeting based on their experiences in 2020. Ted North of WS is interested in starting another Ranger Rider program in the Nirada and Hot Springs area west of Flathead Lake due to high livestock-carnivore conflicts in 2020, and is looking for funding and collaboration with the livestock producer in that area. Adam Baca of WS continued preventative work by putting up fladry and electric fencing in 2020, completing calving enclosures at 6 locations (most returning from previous years). He worked with Defenders of Wildlife and NRDC to construct an experimental fence in Marion that is a 6-7 strand alternating-current permanent fence, because they have used fladry at that location for 7 years and want a more permanent fence solution.

In West-Central Montana, FWP was involved in two collaborative proactive risk management projects in the Blackfoot Valley: the Blackfoot Challenge range rider project and carcass pickup program. This was the 13th year that the range rider project was implemented. The project employed four seasonal range riders and one permanent wildlife technician to monitor livestock and predators in areas occupied by the Arrastra Creek, Chamberlain, Morrell Mountain, Inez, and Union Peak wolf packs. The carcass pickup program removed livestock carcasses from Blackfoot Valley ranches and transported them to the carcass compost site to reduce attractants in livestock grazing and calving areas. FWP and the Blackfoot Challenge partnered with Wildlife Services for the third year to deploy fladry in the Blackfoot Valley to deter wolves from livestock calving yards.

FWP was also involved in two collaborative, proactive risk management projects in the Big Hole Valley. The first of these projects, a range rider completed its tenth season in 2020. The second project was a carcass pickup and composting program that was in its sixth year of operation.

In North-Central Montana, a range rider program, initiated in 2017, on private land and USFS grazing allotments in the Augusta area included four livestock producers and employed one full-time and an additional part-time range rider. The program was coordinated by Kyran Kunkel, through the Conservation Science Collaborative, with funding from the Livestock Loss Board, along with several NGOs.

Wildlife Services continued a full-time conflict reduction specialist employee (Adam Baca) in Montana. This is a Wildlife Services position funded collaboratively by Wildlife Services, U.S. Fish and Wildlife Service, Natural Resources Defense Council, Defenders of Wildlife and the American Prairie Reserve. Baca spent his time planning, coordinating, and implementing non-lethal predator damage management tools such as turbo fladry and electric fencing to protect livestock from predation. This position began in February 2018.

3.3 Total 2020 Documented Statewide Wolf Mortalities

FWP detected a total of 368 wolf mortalities during 2020 statewide due to all causes (Fig. 13). Undoubtedly, additional mortalities occurred but were not detected. Documented total wolf mortality in 2020 was 12% greater than 8-year average since 2012 (8-yr avg. = 327). The

majority of the increase was due to higher levels of legal harvest with 305 occurring during calendar year 2020. Control actions were very similar to 2016-2019, and approximately one-third of peak years. Of the 52 wolves removed in 2020 for livestock depredations, 47 were removed by WS and 5 were legally killed by private citizens under the Montana state laws known as the Defense of Property statute (2) or Senate Bill 200 (3). Two wolves were documented as being killed illegally, and 7 wolves were documented as being killed by vehicle or train collision. Three wolves were documented as being killed by natural, other, or unknown causes.

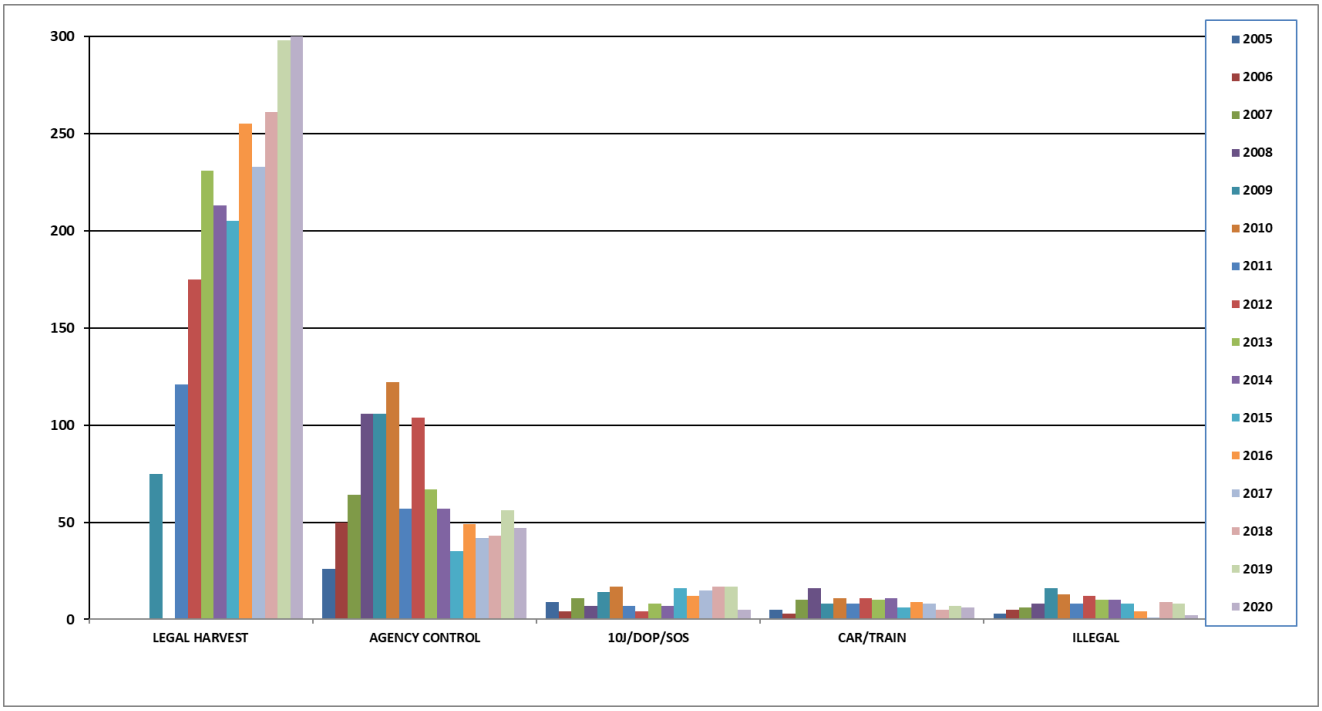

Figure 13. Minimum number of wolf mortalities documented by cause for gray wolves (2005-2020). Total number of documented wolf mortalities during 2020 was 368.

4. OUTREACH AND EDUCATION

FWP's wolf program outreach and education efforts are varied, but significant. Outreach activities take a variety of forms including field site visits, phone and email conversations to share information and answer questions, presentations to school groups and other agency personnel, media interviews, and formal and informal presentations. FWP also prepared and distributed a variety of printed outreach materials and media releases to help Montanans become more familiar with the Montana wolf population and the state plan. The "Report a Wolf" application continued to generate valuable information from the public in monitoring efforts for existing packs and documenting wolf activity in new areas. Several reports were received through the website and others via postal mail and over the phone. Most wolf program staff spent some time at hunter check stations in FWP Regions 1-5 to talk with hunters about wolves, wolf management, and their hunting experiences.

5. FUNDING

5.1 Montana Fish, Wildlife & Parks Funding

Funding for wolf conservation and management in Montana is controlled by laws enacted by the state legislature. State laws also provide detailed guidance on some wolf management activities. The Montana Code Annotated (MCA) is the current law, and specific sections can be viewed at http://leg.mt.gov/bills/mca/index.html. Legislative bill language and history that has created or amended MCA sections can be accessed at http://leg.mt.gov/css/bills/Default.asp. Three sections of the MCA are of primary significance to wolf management and funding. These are:
MCA 87-5-132 Use of Radio-tracking Collars for Monitoring Wolf Packs
MCA 87-1-623 Wolf Management Account
MCA 87-1-625 Funding for Wolf Management

MCA 87-5-132 was created during the 2005 legislative session by Senate Bill 461. It has been amended twice, both times during the 2011 legislative session, by House Bill 363 and Senate Bill 348. This law requires capturing and radio-collaring an individual within a wolf pack that is active in an area where livestock depredations are chronic or likely.

MCA 87-1-623 was created during the 2011 Legislative Session by House Bill 363. This law requires that a wolf management account be set up and that all wolf license revenue be deposited into this account for wolf collaring and control. Specifically, it states that subject to appropriation by the legislature, money deposited in the account must be used exclusively for the management of wolves and must be equally divided and allocated for the following purposes: (a) wolf-collaring activities conducted pursuant to 87-5-132; and (b) lethal action conducted pursuant to 87-1-217 to take problem wolves that attack livestock.

MCA 87-1-625 was created during the 2011 Legislative Session by Senate Bill 348. This law required FWP to allocate $900,000 annually toward wolf management. "Management" in MCA 87-1-625 is defined as in MCA 87-5-102, which includes the entire range of activities that constitute a modern scientific resource program, including but not limited to research, census, law enforcement, habitat improvement, control, and education. The term also includes the periodic protection of species or populations as well as regulated taking. During the 2015 legislative session, Senate Bill 418 reduced this amount to $500,000 of spending authority.

The wolf management budget for state fiscal year 2020 (July 1, 2019 – June 30, 2020) was $753,488.50 and consisted of $236,050 of federal PR funds, $492,437.50 of Montana wolf and general license dollars, and $25,001 from the Rocky Mountain Elk Foundation.

Funding was used to pay for FWP's field presence to implement population monitoring, collaring, outreach, hunting, trapping, and livestock depredation response. During state fiscal

year 2020, the wolf program had 5.5 FTE wolf specialists dedicated to wolf management, and 1 total FTE for 2 seasonal technicians to increase collaring efforts in wolf packs associated with livestock. FWP also renewed the financial agreement with Wildlife Services for their role in wolf depredation management efforts. Other wolf management services provided by FWP include law enforcement, harvest/quota monitoring, legal support, public outreach, and overall program administration. Exact cost figures have not been quantified for the value of these services.

5.2 USDA Wildlife Services Funding

Wildlife Services (WS) is the federal agency that assists FWP with wolf damage management. WS personnel conduct investigations of injured or dead livestock to determine if it was a predation event and, if so, what predator species was responsible for the damage. Based on WS determination, livestock owners may be eligible to receive reimbursement through the Montana Livestock Loss Program. If WS determines that the livestock depredation was a confirmed wolf kill or was a probable wolf kill, the livestock owner is eligible for 100% reimbursement on the value of the livestock killed based on USDA market value at the time of the investigation.

Under an MOU with FWP, the Blackfeet Nation (BN), and the Confederated Salish and Kootenai Tribes (CSKT), WS conducts the control actions on wolves as authorized by FWP, BN, and CSKT. Control actions may include radio-collaring and/or lethal removal of wolves implicated in livestock depredation events. FWP, BN, and CSKT also authorize WS to opportunistically radio-collar wolf packs that do not have an operational radio-collar attached to a member of the pack in order to fulfill the requirements of Montana State Statute 87-1-623.

As a federal agency, WS receives federal appropriated funds for predator damage management activities but no federal funding directed specifically for wolf damage management. Prior to Federal Fiscal Year (FFY) 2011, the WS Program in Montana received approximately $250,000 through the Tri-State Predator Control Earmark, some of which was used for wolf damage management operations. However, that earmark was completely removed from the federal budget for FFY 2011 and not replaced in FFY 2012-2020.

In FFY 2020, WS spent $340,600 conducting wolf damage management in Montana (not including administrative costs). The FFY 2020 expenditure included $230,600 Federal appropriations and $110,000 from FWP.

6. PERSONNEL AND ACKNOWLEDGEMENTS

The 2020 FWP wolf specialist team was comprised of Wendy Cole, Nathan Lance, Tyler Parks, Mike Ross, and Ty Smucker.

Wolf specialists work closely with regional wildlife managers in FWP regions 1-5, including Neil Anderson, Howard Burt, Cory Loeker, Kevin Rose, and Mike Thompson, as well as Carnivore and Furbearer Coordinator, Bob Inman. Wolf technicians Megan Diamond and Brandon Davis provided seasonal assistance monitoring and trapping with the specialists in regions 1 and 2. FWP Helena and Wildlife Health Lab staff contributed time and expertise including Caryn Dearing, Missy Erving, Justin Gude, Anne Howes, Quentin Kujala, Greg Lemon, Ken McDonald, Adam Messer, Kevin Podruzny, Jennifer Ramsey, John Vore, Brian Wakeling, and Smith Wells. The wolf team is part of a much bigger team of agency professionals that make up Montana Fish, Wildlife & Parks including regional supervisors, biologists, game wardens, information officers, front desk staff, and many others who contribute their time and expertise to wolf management and administration of the program.

FWP thanks The Blackfoot Challenge and their range riders: Eric Graham, Jordan Mannix, Vicki Pocha, and Sigrid Olson. The Blackfoot Challenge worked with ranchers and landowners to reduce wildlife conflict in the Blackfoot watershed using fladry and carcass pick-up, and they helped with wolf monitoring.

USDA APHIS WS investigates all suspected wolf depredations on livestock and under the authority of FWP, carries out all livestock depredation-related wolf damage management activities in Montana. We thank them for contributing their expertise to the state's wolf program and for their willingness to complete investigations and carry out lethal and non-lethal damage management and radio-collaring activities in a timely fashion. We also thank WS for assisting with monitoring wolves in Montana. WS personnel involved in wolf management in Montana during 2020 included assistant regional director John Steuber; western district supervisor Kraig Glazier; acting state director Dalin Tidwell; western assistant district supervisor Chad Hoover; eastern assistant district supervisor Alan Brown; wildlife disease biologist Jerry Wiscomb; wildlife biologist Zack May; helicopter pilot Eric Waldorf; helicopter/airplane pilots Tim Graff and John Martin; airplane pilots Guy Terrill, Justin Ferguson, and Scott Snider; wildlife specialists Adam Baca, Jesseanne Castle, Glenn Hall, Micheal "Finny" Helske, Mike Hoggan, Cody Knoop, , John Maetzold, Graeme McDougal, John Miedtke, Kurt Miedtke, Brian Noftsker, Ted North, Scott Olson, Cody Richardson, Jim Rost, Dymond Running Crane, Kirk "Skippy" Sims, Bart Smith, Brian, Smith, Pat Sinclair, and Danny Thomason.

We acknowledge the work of the citizen-based Montana Livestock Loss Board which oversees implementation of Montana's reimbursement program and the conflict prevention grant money, and we thank the LLB's coordinator, George Edwards.

We thank Northwest Connections for their avid interest and help in documenting wolf presence and outreach in the Swan River Valley. We thank Swan Ecosystem Center for their continued interest and support. We thank Kyran Kunkel of Conservation Science Collaborative, Inc. for his continued coordination of a range rider program on private and public land along the Southern Rocky Mountain Front. We also thank Kathy Robinson who was the range rider on this effort and was instrumental in working with local producers to monitor livestock and predator activity in the area.

We thank Confederated Salish and Kootenai Tribal biologists Stacey Courville and Shannon Clairmont, and Blackfeet Tribal biologist Dustin Weatherwax for capturing and monitoring wolves in and around their respective tribal reservations.

The Montana Wolf Management program field operations also benefited in a multitude of ways from the continued cooperation and collaboration of other state and federal agencies and private interests such as the USDA Forest Service, Montana Department of Natural Resources and Conservation ("State Lands"), U.S. Bureau of Land Management, Weyerhauser Company, Stimpson Lumber Company, Southern Pines Plantation, Glacier National Park, Yellowstone National Park, Idaho Fish and Game, Wyoming Game and Fish, Nez Perce Tribe, Canadian Provincial wildlife professionals, Turner Endangered Species Fund, People and Carnivores, Wildlife Conservation Society, Keystone Conservation, Boulder Watershed Group, Big Hole Watershed Working Group, the Madison Valley Ranchlands Group, the upper Yellowstone Watershed Group, the Blackfoot Challenge, Tom Miner Basin Association, and the Granite County Headwaters Working Group.

We deeply appreciate and thank our pilots whose unique and specialized skills, help us find wolves, get counts, and keep us safe in highly challenging, low altitude mountain flying situations. They include Joe Rahn (FWP Chief Pilot), Neil Cadwell (FWP Pilot), Ken Justus (FWP Pilot), Trever Throop (FWP Pilot), Mike Campbell (FWP Pilot), Rob Cherot (FWP Pilot), Jim Pierce (Red Eagle Aviation, Kalispell), Roger Stradley (Gallatin Flying Service, Belgrade), Steve Ard (Tracker Aviation Inc., Belgrade), Dave Horner (Red Eagle Aviation), Joe Rimensberger (Osprey Aviation, Hamilton), and Mark Duffy (Central Helicopters, Bozeman). We also thank Quicksilver Aviation for their safe and efficient helicopter capture efforts.

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APPENDICES

APPENDIX 1

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USDA Wildlife Services

(to request investigations of injured or dead livestock):

John Steuber
USDA WS State Director, Billings
(406) 657-6464 (w)

Kraig Glazier
USDA WS West District Supervisor, Helena
(406) 458-0106 (w)

Dalen Tidwell
USDA WS East District Supervisor, Columbus
(406) 657-6464 (w)

TO REPORT A DEAD WOLF OR POSSIBLE ILLEGAL ACTIVITY:

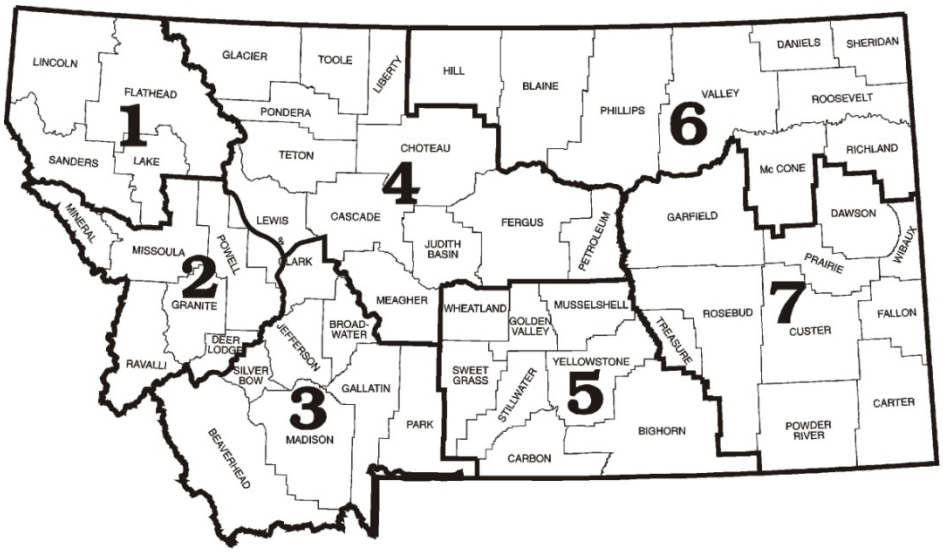
Montana Fish, Wildlife & Parks

- Dial 1-800-TIP-MONT (1-800-847-6668) or local game warden

TO SUBMIT WOLF REPORTS ELECTRONICALLY AND TO LEARN MORE ABOUT THE MONTANA WOLF PROGRAM, SEE:

- http://fwp.mt.gov/fishAndWildlife/management/wolf/

MONTANA FISH WILDLIFE & PARKS
ADMINISTRATIVE REGIONS



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4600 Giant Springs Rd
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LEWISTOWN Area Res Office (LARO)
215 W Aztec Dr
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REGION 5
2300 Lake Elmo Dr
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REGION 6
54078 US Hwy 2 W
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Industrial Site West
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APPENDIX 2

RESEARCH, FIELD STUDIES, AND PROJECT PUBLICATIONS

Each year in Montana, there are a variety of wolf-related research projects and field studies in varying degrees of development, implementation, or completion. These efforts range from wolf ecology and predator-prey relationships to wolf-livestock relationships, policy, or wolf management. In addition, the findings of some completed projects get published in the peer-reviewed literature. The 2019 efforts are summarized below, with updates or project abstracts.

A2.1. IMPROVING ESTIMATION OF WOLF RECRUITMENT AND ABUNDANCE, AND DEVELOPMENT OF AN ADAPTIVE HARVEST PROGRAM FOR WOLVES IN MONTANA.

Improving Estimation of Wolf Recruitment and Abundance, and Development of an Adaptive Harvest Management Program for Wolves in Montana

Federal Aid in Wildlife Restoration Grant W-161-R-1
Final Report, December 2020

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Improving Estimation of Wolf Recruitment and Abundance, and Development of an Adaptive Harvest Management Program for Wolves in Montana

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EXECUTIVE SUMMARY

This research was undertaken from 2014 – 2020 to provide biological insights and tools to enhance conservation and management of wolves in Montana. Gray wolves were extirpated from Montana in the 20th century. Formal protections under the Endangered Species Act, natural recolonization, and reintroduction efforts led to the recovery of the wolf population in the Northern Rocky Mountains. Recovery enabled delisting the population in Montana in 2009 and 2011 (with brief renewed protections during court challenges in these years). This returned management authority to the state, allowing Montana Fish, Wildlife and Parks (MFWP) to manage the population through public harvest seasons.

A major objective of our research was to provide a means to reliably estimate wolf abundance. Abundance estimates are key to management decisions, and to date have relied on challenging, costly field-based monitoring. From 2007 through 2019, MFWP estimated annual population size using a patch occupancy model-based approach. However, this approach was sensitive to sizes of packs and territories, and was developed prior to the implementation of public harvest. Reliability of estimates were contingent on accurate information on territory size, overlap, and pack size. Intensive, field-based monitoring became cumbersome and less effective as the population grew. Furthermore, the cessation of federal funding for wolf monitoring required a reduction in reliance on intensive counts of the wolf population.

We developed a multi-model approach known as the integrated patch occupancy model (iPOM) to estimate wolf abundance. iPOM eliminates the need for intensive field-based monitoring and introduces biological models of wolf behavior. An occupancy model first estimates annual wolf distribution, based on environmental covariates and wolf observations reported by hunters. A mechanistic territory model predicts territory sizes using simple behavioral rules and limited data for prey resources, terrain ruggedness, and human density. Together, these models predict the number of packs in a given area. Finally, a pack size model demonstrates that pack sizes are generally negatively related to terrain ruggedness, local mortalities, and intensity of harvest management. Total abundance estimates are derived by combining the predicted number of packs and pack sizes.

We applied iPOM to estimate wolf abundance for 2007 – 2019. The population was estimated to have been smallest in 2007, with 91 packs (95% CI = 76 – 107) and 650 wolves (95% CI = 547 – 771). A peak appears in 2011, with a high of 187 packs (95% CI = 170 – 206) and 1254 wolves (95% CI = 1136 – 1383). This coincided with the first years of harvest management, after which the population declined by 7.8% in total abundance between 2011 and 2019. From 2016 – 2019, the population appears to have become somewhat stabilized with an average of 190 packs and 1136 wolves per year, even with an estimated annual harvest rate of >20% in this period.

We also sought to develop methods to estimate recruitment in wolf packs in Montana. We developed and tested an integrated population model to estimate the number of pups recruited without recruitment data. Recruitment of wolves in Montana varied annually, and was negatively correlated with wolf abundance and harvest, and positively correlated with pack size. Future application of the recruitment model will require incorporation of iPOM methodology; however, our model provides the foundation for estimating recruitment using collaring and pack count data.

Additionally, we conceptualized a decision tool for wolf management. Management of large carnivore populations with harvest is contentious. Adaptive management incorporates scientific information and associated uncertainty in a transparent process that relates alternative management actions to explicit, quantifiable objectives to guide decision making. Through monitoring, uncertainty can be reduced over time to improve future decisions. We demonstrate how an adaptive management framework explicitly incorporating uncertainty in estimates of harvest, biological and sociopolitical values, and quantitative objectives could guide decisions of harvest regulations of wolves.

Based on these new analytical methods, we provided recommendations for wolf monitoring to inform iPOM and recruitment estimates. Efficient and effective use of limited resources requires targeted monitoring. Because wolves in Montana are managed through harvest, reliable estimates of population size will help inform harvest regulations. Abundance estimation will entail the continuation of hunter harvest surveys and monitoring related to the occupancy model. This includes pack centroids, although potential exists for a reduction from current effort. Approximate locations of wolves removed in response to livestock conflicts will be needed for the pack size model. Future monitoring of pack size may be needed to calibrate the model, such as if changes are made to harvest regulations. Once finalized to include the iPOM methodology, the recruitment model will require collar and pack count data.

INTRODUCTION

Gray wolves (*Canis lupus*) were extirpated from most of the contiguous United States, including Montana, in the 20th century. With formal protections under the Endangered Species Act in 1974 (U.S. Fish and Wildlife Service 1974), wolves began recolonizing northwest Montana in the 1980s (Ream et al. 1989) and nearby areas following reintroductions into Yellowstone National Park and Idaho in 1995 and 1996 (Bangs and Fritts 1996). Wolf numbers increased thereafter, and wolves were delisted via congressional action in Montana in 2009 and 2011 (with a brief re-listing in 2010 due to court challenges; Fritts et al. 1997, Bradley et al. 2014). Delisting returned management authority to the state, and wolves were officially classified as a "species in need of management," enabling harvest seasons as identified in Montana's wolf management plan to be carried out in 2009 and from 2011 onward.

In response to federal delisting criteria, Montana has committed to maintain populations and breeding pairs (a male and female wolf with ≥2 surviving pups by December 31; USFWS 1994) above established minimums of ≥150 wolves and ≥15 breeding pairs. Montana Fish, Wildlife and Parks (MFWP) has estimated population size each year since 2007 using a patch occupancy model-based approach (POM; Miller et al. 2013; Rich et al. 2013; Bradley et al. 2015). However, this approach is sensitive to pack size and territory size and was developed prior to the implementation of public harvest seasons for wolves. Reliability of future estimates will be contingent on accurate information on territory size, overlap, and pack size, which are likely influenced by harvest. Additionally, breeding pairs are determined via direct counts. Federal funding for wolf monitoring has ended in Montana, and future monitoring will not be able to rely on intensive counts of the wolf population. Intensive, field-based monitoring has become cumbersome and less effective since the population has grown. With the implementation of public harvest seasons, predicting the effects of harvest on the wolf population and monitoring the effectiveness of management actions will help inform decisions regarding hunting and trapping seasons.

Objectives & Deliverables

Two PhD students addressed the 4 study objectives, as follows (Fig. 1):

1. **Wolf abundance:** Improve and maintain calibration of wolf abundance estimates generated through POM.

   Deliverables: Models to estimate territory size and pack size that can keep POM estimates calibrated to changing environmental and management conditions for wolves in Montana (Project 1, S. Sells).

2. **Recruitment:** Improve estimation of recruitment.

   Deliverables: A method to estimate recruitment for Montana's wolf population that is more cost effective and biologically sound than the breeding pair metric (Project 2, A. Keever).

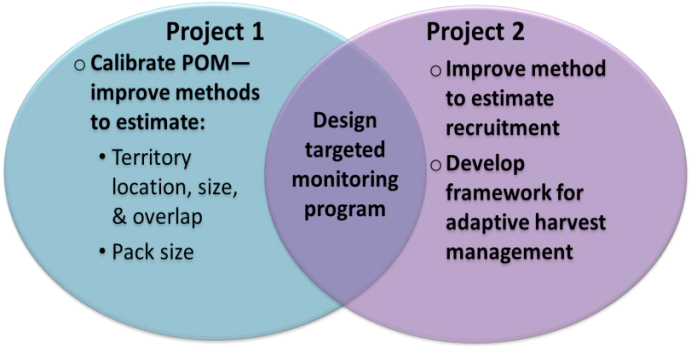

Figure 1. Objectives were addressed by 2 PhD projects.

3. **Adaptive management:** Develop a framework for dynamic, adaptive harvest management based on achievement of Objectives 1 & 2.

   Deliverables: An adaptive harvest management model that allows the formal assessment of various harvest regimes and reduces uncertainty over time to facilitate adaptive management of wolves (Project 2, A. Keever).

4. **Monitoring program:** Design a targeted monitoring program to provide information needed for robust estimates and reduce uncertainty over time.

   Deliverables: A recommended monitoring program for wolves to maintain calibration of POM estimates, determine effectiveness of management actions, and facilitate learning in an adaptive framework (S. Sells and A. Keever).

Project Outcomes

Project 1, S. Sells: The PhD components of this project were completed and defended in December 2019. Project deliverables included a mechanistic territory model, empirical territory and group size models, and a final dissertation (Sells 2019). As a Research Associate through December 2020, S. Sells continued collaboration towards integrating models to estimate wolf abundance for the MFWP Wolf Program.

Project 2, A. Keever: This project was completed in September 2020. Project deliverables included recruitment models, conceptualization for a decision tool in an AHM framework, and a final dissertation (Keever 2020).

Details are provided in subsequent sections of this report.

Acknowledgements

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SECTION 1: ESTIMATION OF WOLF ABUNDANCE

ABSTRACT Our goal under Objective 1 was to develop reliable methods to estimate territory size, territory overlap, and pack size to help improve the reliability of wolf abundance estimates through POM. We developed and applied a mechanistic territory model to produce predictions for the hypothesis that wolves select territories economically based on the benefits of food resources and costs of competition, travel, and predation risk. We summarized territory sizes of real wolves using location data and empirical models to test the mechanistic model's predictions. As predicted, territory sizes in Montana varied inversely with prey abundance, number of nearby competitors, and pack size, and curvilinearly with mortality risk. Parameterizing the mechanistic model with data produced spatially-explicit predictions for territory location, size, and overlap for the Montana wolf population and reliably predicted territories of specific packs. Additionally, we aimed to test mechanisms hypothesized to influence pack size and to develop a predictive model for pack size. Pack size increased with density of packs and decreased with greater terrain ruggedness, control removals, and intensity of harvest management. A predictive model for pack sizes reliably estimated the annual wolf pack sizes observed and illuminated possible underlying mechanisms influencing variation in pack sizes over space and time. Finally, we incorporated these territory and pack size models into an integrated Patch Occupancy Model to estimate wolf abundance in Montana. We applied the models to estimate wolf abundance for 2007 – 2019. The population was estimated to have been smallest in 2007, with 91 packs (95% CI = 76 – 107) and 650 wolves (95% CI = 547 – 771). A peak appears in 2011, with a high of 187 packs (95% CI = 170 – 206) and 1254 wolves (95% CI = 1136 – 1383). This coincided with the first years of harvest management, after which the population declined by 7.8% in total abundance between 2011 and 2019. From 2016 – 2019, the population appears to have become somewhat stabilized with an average of 190 packs and 1136 wolves per year, even with an estimated annual harvest rate of >20% in this period.

1.1 Introduction

Monitoring is a critical yet challenging component of gray wolf management. Throughout wolf recovery in the Northern Rockies, intensive monitoring helped managers estimate numbers of packs, territory locations, and pack sizes. Monitoring results helped MFWP set public harvest seasons, inform livestock depredation policies, evaluate the effects of public harvest and depredation management, and communicate with stakeholders and the public. Monitoring large carnivores is challenging, however, due to their elusive nature and low densities (Boitani et al. 2012). Minimum counts of packs and wolves was achievable during initial stages of wolf recovery when fewer wolves existed on the landscape. This task became exceedingly difficult once wolves became spread across western Montana and federal funding for monitoring ended. Monitoring has also relied on deploying radio- and global positioning system (GPS)-collars, which is increasingly challenging due to difficulty of capture and frequent collar loss caused by collar failures and mortalities. Furthermore, there is frequent turnover of packs, and public harvest can affect behavioral dynamics of wolves (Adams et al. 2008, Brainerd et al. 2008).

Abundance estimates are a key component of monitoring and to date have relied on this challenging, costly field effort. A Patch Occupancy Model (POM) developed a decade ago (Miller et al. 2013, Rich et al. 2013) helped improve the ability to estimate annual wolf and pack abundances (Fig. 1.1). From 2007 – 2019, POM estimated abundance using parameters for area occupied, average territory size, annual territory overlap index, and annual average pack size (Inman et al. 2020). Area occupied was estimated

with an occupancy model, using hunter observations and field surveys on an observation grid of 600 km^2 cells (Miller et al. 2013, Rich et al. 2013, Inman et al. 2020). Average territory size was assumed to be 600 km^2 based on past work (Rich et al. 2012). An ad hoc overlap index was the average number of known packs per 600 km^2 grid cell. Annual average 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 × average pack size, and total wolf abundance was the abundance of wolves in packs × 1.125 to account for lone and dispersing wolves, based on scientific literature (Fuller et al. 2003).

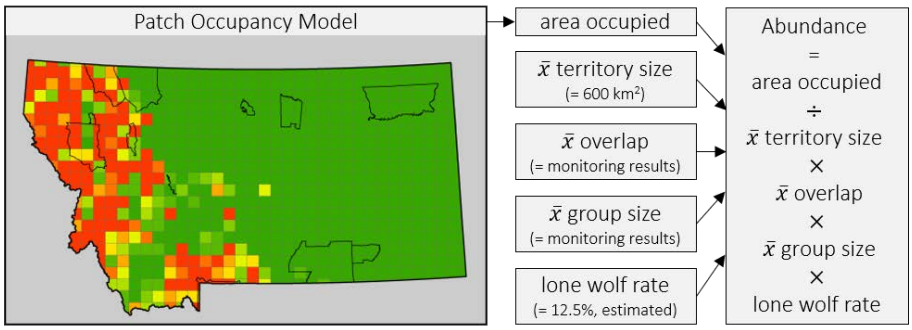

Figure 1.1. Example of POM results (red indicates highest occupancy probability, green lowest), and components of estimated wolf abundance.

Whereas estimates of area occupied through POM are expected to be reliable (Miller et al. 2013), reliability of abundance estimates hinges on assumptions about territory size, territory overlap, and pack size (Inman et al. 2020). Assumptions of a fixed territory size with minimal overlap are simplistic; in reality, territories vary spatiotemporally (Uboni et al. 2015, Sells and Mitchell 2020). Furthermore, estimates of mean territory size were largely derived pre-harvest 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 varies spatially. Variations in territory overlap would similarly bias results. Importantly, POM's requirements of developing annual indices for overlap and mean pack size necessitate intensive monitoring to locate packs and accurately count pack members each year. This became increasingly infeasible given large numbers of packs, limited staff, and declining funding for monitoring (Inman et al. 2020).

Our objective was to improve POM using a multi-model approach to predict territory size, territory overlap, and pack size in a manner that reduced reliance on field monitoring. A more efficient approach would allow limited conservation dollars to be used for other pressing needs. We developed an integrated Patch Occupancy Model (iPOM) that employs mechanistic and empirical models to maximize understanding of behavior and use available data. We used a mechanistic approach to test hypotheses about why wolves select particular territories and enable predicting behavior across a full range of potential present and future conditions. We evaluated the mechanistic model's predictive ability using patterns summarized by empirical territory models. We used empirical models for group size to test hypotheses about factors influencing pack sizes and to develop a predictive model for pack size. This multi-model approach enables annual estimates of wolf population size and characteristics based on changing conditions and enhances understanding of wolf behavior, while drastically reducing costly, intensive monitoring efforts.

Below, we provide overviews of the models developed for iPOM. Section 1.2 provides an overview of the mechanistic model for territory selection (Sells and Mitchell 2020). Section 1.3 introduces how we tested

the model's qualitative predictions using empirical models (Sells et al. *in press*). Section 1.4 introduces how we parameterized the mechanistic model with data for Montana to evaluate the model's capacity to make quantitative, spatially-explicit predictions and to further understand how and why wolf territories vary over space and time (Sells et al. *in review a*). Section 1.5 provides an overview of pack size analyses, and Section 1.6 provides an overview of the resulting predictive model for pack size (Sells et al. *in review b*). Finally, Section 1.7 details the integration of the models into iPOM to estimate wolf abundances (Sells et al. *in prep*). The dissertation produced from this research contains the full details about the territory and pack size models (Sells 2019), as do upcoming manuscripts and those in review.

1.2 Mechanistic Territory Model

Understanding how and why territory sizes vary would help calibrate iPOM. As detailed in Sells and Mitchell (2020), we developed a mechanistic model to enhance understanding of mechanisms driving territory selection. The Sells and Mitchell (2020) model was designed to apply broadly across taxa and used no input data. The model produced qualitative predictions for patterns of territory size and overlap in relation to environmental and social conditions simulated animals encountered.

The model centered on the hypothesis that in general, territories that maximize benefits and minimize costs of ownership should lead to higher fitness (Brown 1964, Emlen and Oring 1977, Krebs and Kacelnik 1991). Accordingly, as a product of natural selection (Darwin 1859), animals are likely adapted to select territories economically. Based on theory and empirical precedent, territoriality should occur only when resources are economically defendable (Brown 1964), i.e., benefits outweigh costs of defense. Economical territories should also be only large enough to provide requisite resources for survival and reproduction, except in cases where additional resources increase fitness (Mitchell and Powell 2004, 2007, 2012). A primary benefit of many territories is likely exclusive access to food resources (Brown 1964, Hixon 1980, Carpenter 1987, Adams 2001) because food is essential to survival and reproduction. Primary costs are likely competition (Brown 1964, Hixon 1980, Carpenter 1987) and travel (Mitchell & Powell 2004, 2007, 2012), because competition is inherent to territoriality and energy is needed to access and defend resources. Territory holders with lower competitive ability may also pay higher costs to compete against more-competitive conspecifics (Packer et al. 1990, Sillero-Zubiri and Macdonald 1998, Cassidy et al. 2015, Sells and Mitchell 2020). Mortality risk may also be a primary cost where predator density is high if it affects how animals select and use their territory (Sargeant et al. 1987, Whittington et al. 2005, Rich et al. 2012).

The mechanistic model was founded on optimal foraging theory and thus an evolutionary approach to understanding the proximate and ultimate mechanisms underlying behavior (Börger et al. 2008). Integration of competitor-interaction modeling (Adams 2001) helped understand how competition affects economical territory selection. The approach strongly differed from previous mechanistic territory models that have typically used partial differential equations to model movement as diffusive with a bias towards the territory center (Börger et al. 2008). That class of mechanistic models focus on movement ecology and third-order selection (space use within the territory; Johnson 1980), whereas Sells and Mitchell (2020) modeled first- and second-order selection through economical behavior. This work thus built on the foundation of a mechanistic model of economical home range selection (Mitchell and Powell 2004), which successfully predicted home ranges of black bears (*Ursus americanus*; Mitchell and Powell 2007, 2012). That earlier work modeled space use with respect to the benefits of food resources and costs of

travel, and was limited to home ranges because it represented competition passively as resource depression. Accordingly, Sells and Mitchell (2020) modeled competition dynamically, whereby territory holders continuously assessed and responded to the decisions made by neighboring conspecifics.

Methods

The Sells and Mitchell (2020) mechanistic model represented the hypothesis that animals from numerous taxa are adapted to select territories economically based on the benefits of food resources and costs of competition, travel, and mortality risk. The mechanistic territory model was developed in NetLogo 6.1.1 (Wilensky 1999) and entailed spatially-explicit simulations. Landscapes for simulations were grids of patches that varied in benefits and costs of ownership.

In the model, territories were selected for simulated animals (agents) to economically meet their resource requirements by maximizing food resources obtained while minimizing costs of territory ownership (Fig. 1.2). Each time an agent was added to the simulated landscape, it selected a starting location for a territory center and then calculated patch values around itself by discounting each nearby patch's food benefits by its associated costs of ownership. It then selected patches for a territory in order of patch value, stopping once sufficient resources were obtained. The agent's selected territory center was next compared to the territory's geographic center. A mismatch between centers indicated patch values were more economical in a particular direction. Accordingly, the agent was repositioned to the geographic center if it did not align with the selected center. The agent then recalculated patch values, reselected patches, and continued this process of territory building and centering until the selected and geographic centers matched, indicating the territory was optimized. After each agent selected its territory, neighboring agents assessed whether their territories were still economical, as any changes in overlap with neighboring territories influenced costs of competition for those patches. Each agent dropped less-valuable patches from its territory and added more-valuable patches to maximize the territory's economic value. This cycle of territory formation and maintenance continued after each new agent was added to the landscape. Once a predefined population target was reached, the simulated ended.

We conducted simulation experiments to provide data for summarizing effects of food, resource requirements, competition, competitive ability, and mortality risk (represented as predator density) on territorial space use. We collected output summaries for each territory formed after initial establishment, at a low population density and after carrying capacity was reached (i.e., the landscape could not

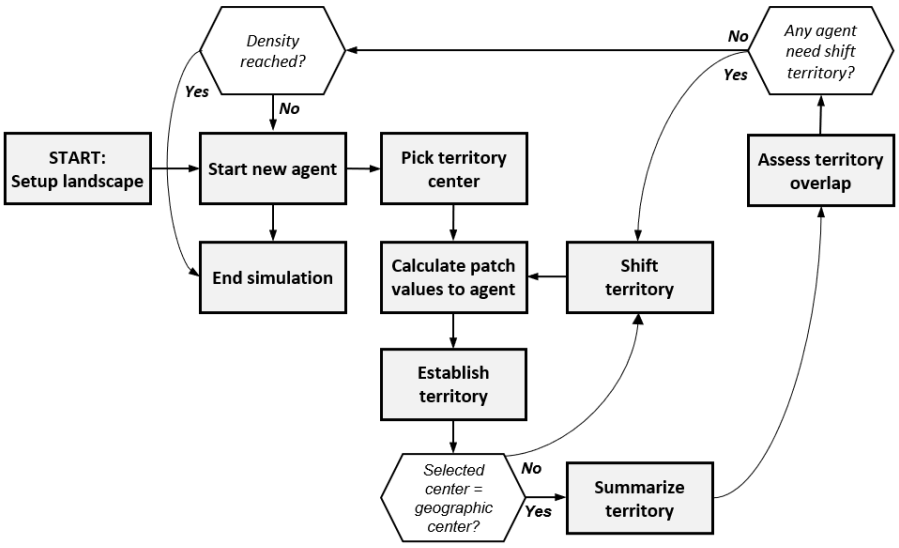

Figure 1.2. Mechanistic territory model schematic.

support more territories). We recorded each agent's final territory size (including travel corridors to reach selected patches from the territory center), territory overlap, number of nearby competitors, and predator density encountered (mean predator presence per territory patch). We used program R Version 3.6.1 (R Core Team 2020) and package dplyr (Wickham et al., 2019) to summarize results.

Results & Discussion

The mechanistic, spatially-explicit, individual-based model produced numerous empirically testable predictions for what may be observed empirically if economical territory selection drives placement and characteristics of territories (Table 1.1). For example, the model predicted that greater food abundance and competitor density would lead to smaller territories, less competitive territory holders encountering high population densities would often have larger territories than more-competitive conspecifics, and territory size would often increase before decreasing curvilinearly in response to greater levels of mortality risk. A curvilinear response to costs of mortality risk suggests there are increasingly-economical trade-offs with other benefits and costs, e.g., through abandoning areas of high mortality risk and accepting higher costs of competition by overlapping other territories. A subsequent literature search demonstrated numerous observations of these patterns in real populations across taxa, contributing evidence for the economical selection of territories as a causal mechanism underlying ecological patterns observed (Sells and Mitchell 2020).

The model can be used to predict the effects of conservation actions. In absence of data, the model provided predictions and a mechanistic understanding of how territorial behavior is likely to vary over space and time. For example, a mechanistic understanding of how a population will respond to prey and predator distributions and abundances can help predict the effects of a species on prey populations, and vice versa. The model can furthermore be parameterized with empirical data to make spatially-explicit predictions, e.g., for locations and sizes of territories across areas of conservation concern (Sect. 1.4).

Table 1.1. Model predictions for mean territory size, overlap, and carrying capacity.

Scenario	Territory size	Territory overlap	Carrying capacity
As food distribution > clumped	−	+	+
As food abundance ↑	−	− or + [a]	+
As resource requirements ↑	+	−	−
As population density ↑, △ in population mean	− or + [a]	+	*NA*
As # neighbors ↑	primarily − [a]	+	*NA*
As competitor density ↑, △ in individual territory	primarily − [a]	+	*NA*
Less competitive individuals or groups	+ [a]	− or + [a]	*NA*
As mortality risk (density of predators) ↑	− or + [b]	variable [b]	−

[a] Trends were variable; details in Sells and Mitchell (2020).

[b] Generally varied curvilinearly by predator density (territory size) or in nuanced ways (overlap).

1.3 Empirical Territory Models

Alignment of the mechanistic model's predictions (Sect. 1.2) with empirically-observable patterns in territories of wolves would contribute evidence that economical territory selection is a causal mechanism underlying space use by wolves (Sells and Mitchell 2020). We therefore sought to determine whether the model suitably predicted and explained patterns in space use of wolves. To accomplish this, we compared patterns predicted by the mechanistic model to patterns observed in territories of wolves in Montana. We used GPS location data collected from 2014 – 2019 as part of this research to estimate the locations of wolf territories.

The mechanistic model's hypotheses are easily extended to wolves (Table 1.2). This strongly territorial species maintains territories year-round (Mech and Boitani 2003). Ungulates comprise the bulk of wolf diets (Mech and Peterson 2003, Peterson and Ciucci 2003). Packs generally comprise a dominant breeding pair and their offspring from multiple years who cooperatively defend the territory, hunt, and raise pups. Larger groups of carnivores may have greater competitive ability (Packer et al. 1990, Sillero-Zubiri and Macdonald 1998, Cassidy et al. 2015) and therefore reduced costs of competition with neighboring groups. Wolves are coursing predators who travel long distances, and such movement is energetically costly. Following the concept of economical territories (Sells and Mitchell 2020), areas costlier to own would necessitate more benefits to offset the cost. For wolves, rugged terrain may increase travel costs whereas roads with low human use may offer less-costly travel routes (Whittington et al. 2005, Zimmermann et al. 2014). It is also possible that high travel costs ultimately become uneconomical

Table 1.2 The mechanistic model's hypotheses and predictions for economical territory selection as applied to wolves, and evidence of these patterns in wolf territories in Montana.

Hypothesis: Wolves select territories economically based on benefits and costs:	Prediction for territory size[a]	Variable	Evidence consistent with hypothesis?
Food resources are a primary benefit structuring space use	↓ where prey abundance ↑	$ungulate_{summer}$	yes
		$ungulate_{winter}$	yes
Competition is a primary cost structuring space use; additionally, smaller groups pay higher costs to compete	↓ as # nearby competitors ↑	$competitor_{density}$	yes
	↓ as group size ↑ at high population densities	$group_{size}$	yes
Travel is a primary cost structuring space use; in our system, rugged terrain is more costly and low-use roads are less costly	↑ where ruggedness ↑ to offset this cost	ruggedness	yes
	alternatively, n-curvilinear response to ruggedness	$ruggedness^{\wedge 2}$	yes
	↓ where road density ↑ given lower costs	$roads_{low\text{-}use}$	yes
Mortality risk is a primary cost structuring space use	n-curvilinear response	$roads_{low\text{-}use}{}^{\wedge 2}$	no
		$density_{humans}{}^{\wedge 2}$	no
		$harvest_{mortalities}{}^{\wedge 2}$	yes

Yes = results consistent with hypothesis (90% confidence intervals [CI's] exclude 0); no = no support (CI overlaps 0).
a. Predictions were from the Sells and Mitchell (2020) mechanistic model (Sect. 1.2). We focused on patterns in territory size rather than overlap because the full territory mosaic and resulting overlap cannot be known (absent simultaneously deploying collars on wolves in every territory, which is infeasible given cost, logistics, difficulty of capture, and frequent collar turnover).

such that territory size declines curvilinearly, as with the response to costs of mortality risk (Sells and Mitchell 2020). Humans are generally a primary source of mortality (Fritts et al. 2003, Musiani and Paquet 2004) and harvest has occurred in our study system for the past decade (Inman et al. 2020). Wolves are intelligent and adaptable (Packard 2003) and often avoid humans (Whittington et al. 2004, Hebblewhite and Merrill 2008, Latham et al. 2011). Whether permanent or limited to specific times of day or seasons, avoidance of sites associated with higher mortality risk could necessitate expansion of the territory to maintain its economic value, until trade-offs in other costs and benefits become more economical (Sells and Mitchell 2020). We hypothesized that costs of mortality risk increased with density of low-use roads (which may provide easier travel for not only wolves, but hunters, trappers, and other recreationists), density of humans, and greater numbers of conspecifics recently killed via harvest.

Methods

Study Area

Our study area was Montana (Fig. 1.3), where elevations range 554 – 3,938 m (Foresman 2001). In the northwest corner of Montana, dense forests and a maritime-influenced climate characterized the rugged, mountainous terrain of the Northern Rockies Ecoregion (NRE, epa.gov). To the east, the Canadian Rockies Ecoregion (CRE) was characterized by higher-elevation, glaciated terrain, which transitioned to the Northwestern Glaciated Plains Ecoregion (GLPE) characterized by level and rolling terrain with seasonal ponds and wetlands. In far southwestern Montana, the Idaho Batholith Ecoregion (IBE) was mountainous, granitic, and partially glaciated. To the east, the large Middle Rockies Ecoregion (MRE) was characterized by rolling foothills where shrubs and grasses transitioned to rugged mountains with conifers and alpine vegetation. The xeric Wyoming Basin Ecoregion (WBE) of south-central Montana

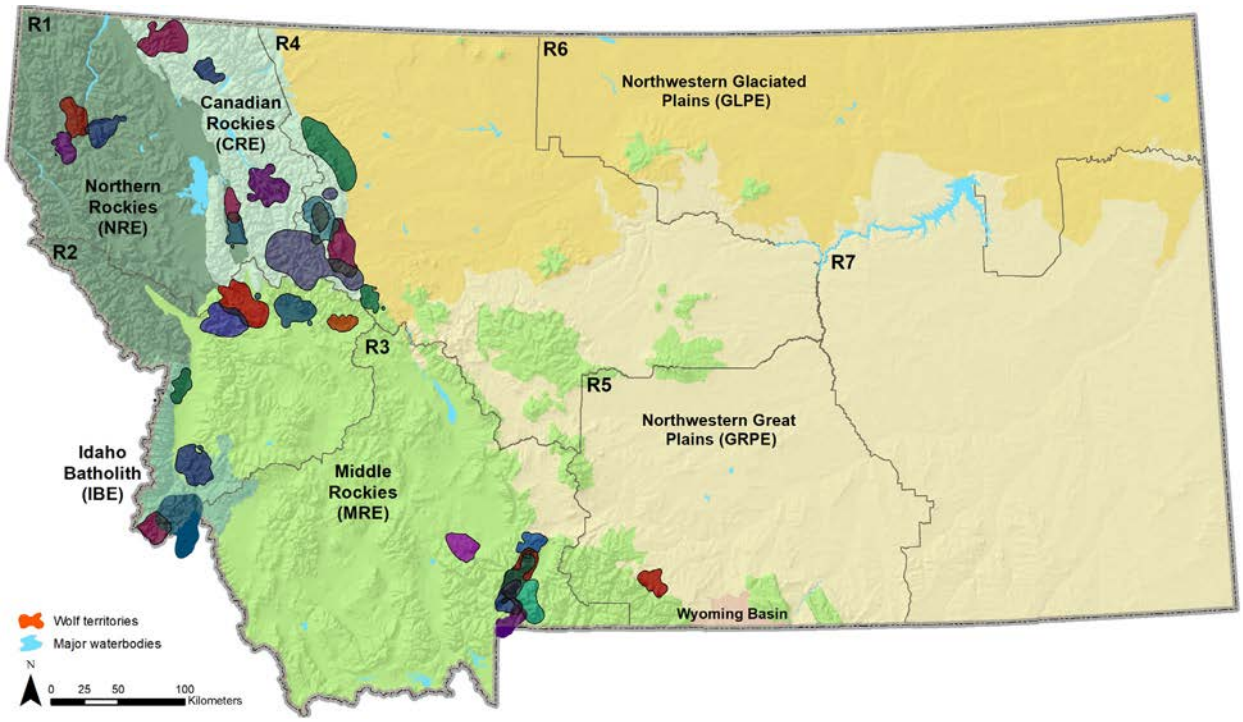

Figure 1.3. Our study area encompassed the state, characterized by various ecoregions (epa.gov). Also shown are the wolf territories estimated as part of this research, and the MFWP regional boundaries (R1 – R7, gray lines).

was dominated by grasses and shrubs. The semiarid, rolling plains of Northwestern Great Plains Ecoregion (GRPE) in southeastern Montana was interspersed with breaks and forested highlands. Wolves were found primarily in the western side of the state within the NRE, CRE, IBE, and MRE, but reported sightings and occasional harvests occurred in eastern Montana. Primary prey for wolves were elk (*Cervus canadensis*), white-tailed deer (*Odocoileus virginianus*), mule deer (*O. hemionus*), and moose (*Alces alces*). Other large carnivores included coyotes (*C. latrans*), mountain lions (*Puma concolor*), black bears (*Ursus americanus*), and grizzly bears (*U. arctos*). The human population in Montana was just over 1,062,000 in 2018 (census.gov). Annual depredation removals for livestock conflicts ranged 51 – 61 from 2014 – 2017 (Coltrane et al. 2015; Bradley et al. 2015; Boyd et al. 2017; Montana Fish Wildlife and Parks 2018). During this same era, harvest through hunting and trapping led to 207 – 295 mortalities per harvest season, which occurred each September 1 – March 15.

Wolf location data

Location data were collected from 2014 – 2019 via GPS collars deployed by MFWP. Wolf captures occurred using foothold traps (EZ Grip # 7 double long spring traps, Livestock Protection Company, Alpine TX), or aerial darting. Wolf anesthetization and handling followed MFWP's 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 from the American Society of Mammalogists (Sikes et al. 2011). GPS collars were Lotek LifeCycle, Lotek Litetrack B 420, Telonics TGW-4400-3, Telonics TGW-4483-3, or Telonics TGW-4577-4, programmed to collect latitude and longitude every 3 – 13 hours.

MFWP Wolf Specialists determined pack membership of each collared individual. A wolf was considered a resident of its pack while its movements were in a localized cluster, including limited forays, defined as departing from and returning to the cluster. We considered a wolf to no longer be a resident if it did not return to its territory, or forays became frequent (this nearly always precipitated full dispersal; frequent forays were defined as starting a new foray < 1 month after returning from a previous one). Upon dispersing, the individual could either die or join a new pack by again localizing its movements. Successful dispersers were identified as a member of the nearest pack or given a new pack identification if the cluster did not overlap a known territory centroid.

We estimated sizes and locations of territories of resident, GPS-collared wolves using Program R (R Core Team 2020). We estimated territory sizes using volume-adaptive kernel density estimates (KDEs; Worton 1989) with package AdehabitatHR (Calenge 2006), with a smoothing parameter of 100% of the reference bandwidth. This smoothing parameter and a 95% KDE best prevented islands and lacunas while excluding extra-territorial forays. We also generated 90% KDEs to enable comparisons to past research in Montana (Rich et al. 2012). We generated KDEs for each year of data for each territory in which the wolf was a resident. We excluded 2 individuals whose territories were mostly or entirely outside of Montana (beyond which covariate data were not readily available), 3 individuals that appeared transient, and 2 individuals whose collars functioned intermittently (transmitting < 1 fix every 5 days on average). We averaged territory size for packs with multiple KDEs, which occurred if > 1 wolf was collared in a pack or a wolf was collared for multiple years. We considered wolves to represent the same pack when their 50% KDEs (i.e., core areas) had any overlap.

Explanatory variables

We generated explanatory variables to represent the benefit of prey resources and costs of competition, travel, and mortality risk using Program R (R Core Team 2020). We represented prey resources as summer and winter ungulate density indices, competition as competitor density and pack size, travel as terrain ruggedness and low-use road densities, and mortality risk as low-use road densities, human densities, and harvest mortalities (Table 1.2). For competitor density, pack size, and harvest mortality, we averaged data from the calendar year in which the collar was deployed (year *T*) and the following year (*T+1*). Because collars were deployed at variable times of year, this 2-year mean better matched the timing of collar deployment. We used the most recent year of data available for these variables in limited cases where data were unavailable in 2018 or 2019.

We developed indices for ungulate densities across our large study area. In each km^2 grid cell *i* delineated as summer deer habitat (http://fieldguide.mt.gov), we calculated a summer deer density index as:

$$deer(summer)_i = (N_R \div \Sigma_{area}) \times (CPUE_i \div CPUE_{\bar{R}}).$$

N_R was MFWP's 10-year average estimate of white-tailed and mule deer abundance in the MFWP administrative region (R) where *i* fell. Σ_{area} was R's estimated area of deer summer habitat. $CPUE_i$ was the mean catch per unit effort (CPUE; male harvest / hunter days) in the MFWP hunting district in which *i* fell, and $CPUE_{\bar{R}}$ was the regional mean CPUE, based on MFWP harvest records from 2008 – 2017. We repeated these calculations for a deer winter density index, and for elk density indices. The long-term regional averages were the most reliable ungulate abundance data for our study area and provided a preliminary density estimate (the first half of the formula). The second half of the formula adjusted this index slightly lower or higher based on the relative CPUE, which generally correlates with deer and elk abundance (Dusek et al. 2006, Rich et al. 2012) and is best compared within administrative regions given spatially similar factors that can affect hunting success (e.g., terrain, vegetation, accessibility, etc.). We calculated a moose density index for each cell *i* delineated as seasonal moose habitat as:

$$moose\ density\ (season)_i = N_{HD} \div \Sigma_{HD\ area}.$$

N_{HD} was MFWP's estimate of moose abundance in the HD in which *i* fell, and $\Sigma_{HD\ area}$ was the area of summer or winter moose habitat in that HD. In limited cases where density estimates were unavailable within territories partially overlapping national parks, tribal reservations, or neighboring states, we interpolated the ungulate indices through inverse distance weighting using the gstat package in R (Pebesma 2004). We smoothed each index using 9×9 km^2 weighted moving windows. We then calculated overall ungulate density indices by summing the indices for deer, elk, and moose for each season, and measured the mean value of these seasonal ungulate indices within each KDE.

Competitor density was based on neighboring packs. Each year, MFWP Wolf Specialists monitored wolf packs to estimate territory centroids. We defined neighbors as packs with territory centroids ≤ 25 km of a pack's KDE (Rich et al. 2012). We calculated the mean number of neighboring packs in year *T* and *T+1*, and scaled this value to number of neighbors per 100 km^2 of the focal pack's territory size to control for territory size (as larger territories tend to have more neighbors; Rich et al. 2012).

Pack size was the mean of sizes reported in year *T* and *T+1*. MFWP Wolf Specialists reported pack sizes each calendar year. We included known removals (harvest, dispersal, etc.) because these individuals were present for part of the year.

We estimated terrain ruggedness with the Vector Ruggedness Measure (Sappington et al. 2007) using R package spatialEco (Evans 2018) and elevation data derived through package elevatr (Hollister and Shah 2017). Ruggedness represented the mean change in elevation between adjacent 1-km^2 raster cells. We calculated the mean ruggedness within each KDE. We calculated the mean density of low-use roads within each KDE using the most recent road dataset (geoinfo.msl.mt.gov).

We calculated the mean human density per KDE based on 2010 census data (geoinfo.msl.mt.gov). We identified the number of hunter-reported harvest locations (wolves killed via hunting and trapping) within the KDE in year *T* and *T+1*.

Analyses

We analyzed patterns in territory size using generalized linear mixed effect models (GLMMs) in R (R Core Team 2020) using package lme4 (Bates et al. 2015) with helper functions from package jtools (Long 2020), AICcmodavg (Mazerolle 2020), and cowplot (Wilke 2020). As a primary analysis we created simple GLMMs for each variable as a single fixed effect plus a random effect for pack identity (family = Gaussian, link = log). We included quadratic terms for ruggedness and each mortality risk variable to test for a curvilinear relationship (Table 1.2). We considered predictions to have support if the 90% confidence intervals (CIs) of the fixed effect's coefficient estimate did not overlap 0.

To further investigate patterns in territory sizes, we created complex GLMMs with multiple fixed effects plus a random effect for pack identity. We started with a global model containing all variables. We next developed 14 reduced models containing each 1-, 2-, and 3-way combination of the benefits and costs (i.e., food alone, food and competition, etc.). No variables were overly correlated (> 0.7 Spearman's rank correlation; Dormann et al. 2013). To avoid fitting overly complex models, we retained 1 quadratic term per model. We included an interaction between competitor density and pack size in some models because we expected pack size could be more important at high competitor densities. We also varied which mortality risk variable received a quadratic term. We identified the most supported models using Akaike's information criterion corrected for small sample size (AICc; Burnham and Anderson 2002) with a cut-off of ΔAICc = 2 (Anderson et al. 2001). Results were based on centered and scaled variables (units accordingly were standard deviations from the mean).

Results

From 2014 – 2019, 93 wolves were captured and GPS-collared. Collar data were collected from January 1, 2014 – May 20, 2019. Mean collar deployment length was 10.20 months, primarily as a result of collar failures (n = 36), harvest (n = 21), and other mortalities (e.g.,

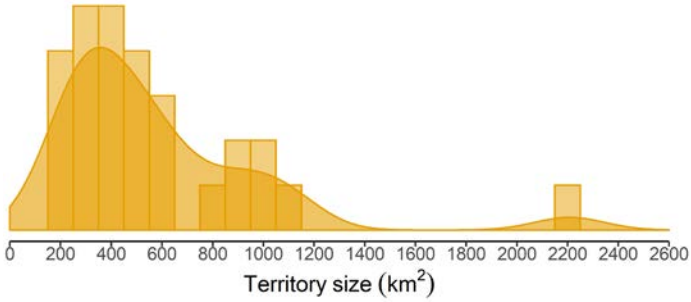

Figure 1.4. Annual territory size estimated for packs in Montana from GPS-collared wolves, 2014 – 2019.

Table 1.3. Mean sizes for wolf territories in Montana, 2014 – 2019.

Measurement	Arithmetic $\bar{x}$ territory size (km^2)	SD (km^2)	Min.	Max.	Geometric $\bar{x}$ (km^2)
95% KDEs	582.02	420.21	187.71	2207.42	483.62
90% KDEs	440.89	390.86	137.82	1592.00	366.50

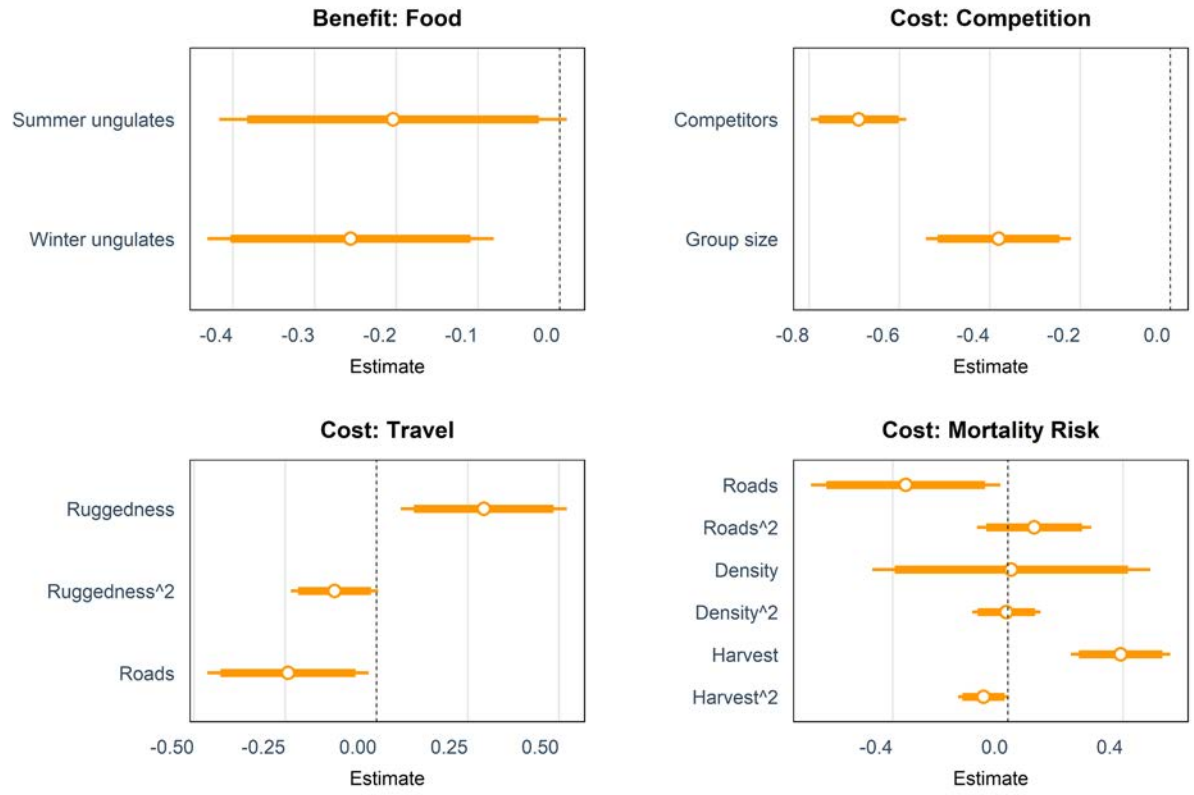

Figure 1.5. Patterns associated with annual and seasonal space use. Lines depict 90% confidence intervals (CIs), thin tails represent 95% CIs, and points represent mean estimates. Variables refer to ungulate density indices ("summer ungulates" and "winter ungulates"), competitor density ("competitors), low-use road density ("roads"), local human density ("density"), and local harvest mortalities ("harvest"). Quadratic terms tested for a curvilinear response.

after livestock depredations or by vehicle strikes, injuries, or poaching; $n = 22$). Of 15 identified dispersals, 9 led to joining or forming other territories. Remaining dispersals yielded 3 mortalities, 2 emigrations to Idaho, and 1 emigration to Wyoming before returning to the wolf's natal territory.

From data for wolves that remained a resident of a pack for ≥ 70% of a year, we estimated 43 territories of 28 packs (Fig. 1.3). After averaging by pack, arithmetic mean territory size was 582.02 km^2 for 95% KDEs and 440.89 km^2 for 90% KDEs (Fig. 1.4; Table 1.3).

Our primary analysis revealed that territories were smaller in areas of greater ungulate densities, in areas with greater competitor densities, and for packs of greater size (Fig. 1.5). Territories had an n-curvilinear response to terrain ruggedness (i.e., initially increasing before decreasing). Greater density of low-use roads was also associated with smaller territories. There was no evidence of a curvilinear response to low-use roads or human densities. Territory size had an n-curvilinear response to harvest mortalities.

The top complex GLMM included the variables for food, competition, and mortality risk (Fig. 1.6). Territory size had a negative relationship with the winter ungulate index, competitor density, and pack

size, and ambiguous relationships with the summer ungulate index, human density, and harvest mortalities.

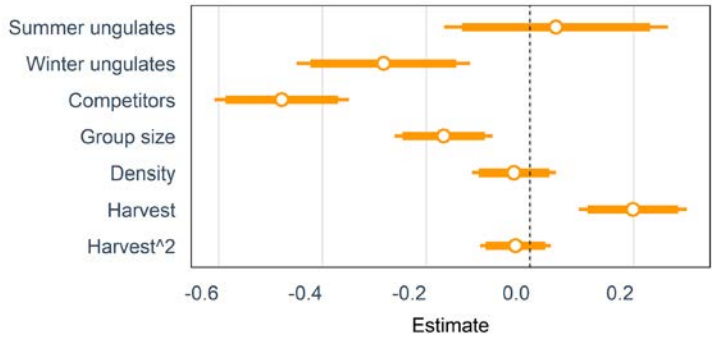

Figure 1.6. Variables in the top complex model for space use. Lines depict 90% CIs, thin tails are 95% CIs, and points are mean estimates.

Discussion

Empirically-observed patterns in space use were consistent with hypotheses and predictions for the economical selection of territories in the Montana wolf population. As hypothesized for many territorial animals (Sells and Mitchell 2020), wolves appear to select territories that maximize benefits of food resources and minimize costs of competition, travel, and mortality risk.

Economical territories should be only large enough to provide requisite resources for survival and reproduction (Mitchell and Powell 2004, 2007, 2012), and exclusive access to food resources has long been expected to be a primary benefit of territoriality (Brown 1964, Hixon 1980, Carpenter 1987, Adams 2001). Results supported the hypothesis that food resources are a primary benefit driving territory selection by wolves. Aligning with predictions of the mechanistic model, space use decreased with greater densities of ungulates (Fig. 1.5), which is consistent with other similar populations (Fuller et al. 2003, Jedrzejewski et al. 2007, Kittle et al. 2015).

Competition is inherent to territoriality and should therefore be a primary cost of space use in territorial animals (Brown 1964, Hixon 1980, Carpenter 1987, Sells and Mitchell 2020). Supporting this hypothesis, territories were smaller in areas of greater densities of neighboring territories (Fig. 1.5; Table 1.2). Matching the prediction that territories would compress with increasing levels of competition, territories were 26% smaller than observed at lower population densities (Rich et al. 2012). Due to territory compression, populations with relatively stable spatial distributions cannot be assumed to have stable dynamics in competition and densities within.

Territory holders with lower competitive ability may pay higher costs to compete against more-competitive conspecifics (Sells and Mitchell 2020). Among social carnivores, competitive ability appears linked to group size (Packer et al. 1990, Sillero-Zubiri and Macdonald 1998, Cassidy et al. 2015). As predicted if cost of competition varies inversely with pack size (Figs. 1.5 – 1.6; Table 1.2; Sells and Mitchell 2020), territories were smaller for packs of greater size in our high-density population (an average estimated 11 – 13 individuals per 1,000 km^2; Inman et al. 2019). Although it might be assumed that larger packs require greater area to provide sufficient food resources, larger territories do not necessarily provide more resources, particularly after accounting for energetic costs of maintaining a large territory. If animals defend areas to satisfy energetic requirements, territories will be smaller in areas with more food resources (Table 1.2).

Travel is likely a primary cost of territoriality because energy is needed to access and defend resources (Mitchell and Powell 2004, 2007, 2012, Sells and Mitchell 2020). Costs of travel are likely to be influenced by numerous environmental variables and a species' evolutionary traits (Shepard et al. 2013,

Wilson et al. 2015). In our study system, we expected costs of travel to increase with terrain ruggedness and decrease with low-use roads (Table 1.2; Whittington et al. 2005, Oakleaf et al. 2006, Zimmermann et al. 2014). As expected, space use increased and then decreased curvilinearly with greater terrain ruggedness (Fig. 1.5), suggesting that larger territories help offset costs of ownership until such trade-offs become uneconomical (Sells and Mitchell 2020). Similarly, territories were smaller in areas with more low-use roads (Fig. 1.5), suggesting that low-use roads decrease cost of territory ownership by reducing cost of travel.

Mortality risk may also be a primary cost of territoriality if it affects how animals select and use their territories. As predicted (Table 1.2; Sells and Mitchell 2020), territories in our system increased and decreased curvilinearly with increasing harvest mortalities (Fig. 1.5). This response suggests that avoiding areas perceived as high mortality risk may necessitate expanding one's territory to offset resources lost by avoidance. Eventually this expansion may become uneconomical, causing territories to contract as other tradeoffs are made (Sells and Mitchell 2020). Variables related to human presence had ambiguous effects (Fig. 1.5), providing evidence that direct mortality hazards may influence the economic valuation of space use more than human presence alone in populations managed through harvest.

1.4 Mechanistic Wolf Territory Model

Our next objective was to parameterize and apply the Sells and Mitchell (2020) model (Sect 1.2) to produce quantitative, spatially-explicit predictions for wolves in Montana. We aimed to use only readily-available data to demonstrate the model's ability to make predictions absent expensive, difficult-to-collect datasets, including data for wolves (e.g., omitting GPS data for wolf locations). The ability to predict wolf space use absent wolf data would help calibrate iPOM and constitute a strong test of the mechanistic model.

We assessed the model's ability to predict first-order selection (the geographic range of wolves in Montana) and second-order selection (the territories of individual packs; Johnson 1980). After ascertaining the model's predictive power, we used the model to predict territory size and location under a range of potential conditions wolves could encounter, such as variable densities of prey and competitors.

Methods

Study area

Our study area was the same as described under Sect. 1.3.

Estimates of truth

Estimates of truth were needed to calibrate and evaluate the model. As detailed in Sect. 1.3, empirically-observed estimates of recent territory sizes (2014 – 2019) were available for 28 packs in Montana. We dropped 2 packs whose territories extended beyond the state boundary because data to run the mechanistic model were limited to Montana. The remaining 26 territory observations formed the primary sample of empirically-estimated territory locations and sizes.

We also estimated the mean density of packs that occurred in each ecoregion from 2014 – 2019. From the territory centroids monitored by MFWP Wolf Specialists each year (Sect. 1.3), we calculated the mean density of packs per ecoregion from this period. The population was largely stable in these years (Inman et al. 2020) with a density of packs per 1000 km^2 equivalent to 1.6 packs in the NRE, 1.4 in the CRE, 1.9 in the IBE, 0.5 in the MRE, 0.02 in the GLPE, and 0.03 in the GRPE, for a total of 127 packs in Montana.

We estimated the distribution of real wolves for 2014 – 2019 from monitoring data. These data included territory centroids and harvest locations, along with wolf collar locations collected from all wolves collared during these years. We plotted locations for territory centroids, harvest locations, and wolf locations together as an approximation of the distribution of wolves in Montana during these years.

As a separate estimate of truth from a different period, we estimated territory size and location using data from 10 GPS-collared wolves from 9 packs in 2008 – 2009 and the same steps outlined in Sect. 1.3. We also estimated the mean density of packs per ecoregion in each year following the steps described above. In 2008, this was equivalent to densities in the NRE, IBE, CRE, MRE, GLPE, and GRPE of 0.9, 1.9, 0.7, 0.4, 0.02, and 0.03 packs per 1000 km^2, respectively. In 2009, respective densities were 1.3, 1.9, 0.9, 0.5, 0.02, and 0.03 packs per ecoregion. Whereas we ultimately use our primary set of 26 locations and sizes of territories for 2014 – 2019 during model calibration and evaluation, we used this secondary set of 9 locations and sizes for 2008 – 2009 during evaluation only.

Mechanistic model

We adapted the mechanistic territory model from Sells and Mitchell (2020) for wolves in Montana. We completed simulations using NetLogo 6.1.1 (Wilensky 1999) and analyzed results in Program R (R Core Team 2020) using helper functions from package dplyr (Wickham et al. 2020), ggplot2 (Wickham 2016), and cowplot (Wilke 2020).

In the model, agents representing wolf packs were added to a landscape parameterized to represent Montana. This consisted of a grid of 1-km^2 patches, 929 × 540 patches in size. Each patch varied in its benefit of food resources and costs of travel and mortality risk (competition arose during simulations through interactions among agents). Our spatial density indices for ungulates represented the seasonal benefit of food for wolves using the same ungulate data described in Sect. 1.3. Travel cost to each patch incorporated distance and a terrain ruggedness index, representing the average change in elevation between adjacent 1-km^2 patches. The cost of mortality risk for each patch was based on human density. A density threshold ($Density_T$) was also set to specify the density of agents per 1000 km^2 to be modeled.

As in the original model, territories were selected and defended (Fig. 1.2). Agents were added to a random starting patch in Western Montana (within the NRE, CRE, IBE, or MRE; Fig. 1.3). Because wolves in Montana rely on migratory ungulates, seasonal territories were selected to meet resource requirements for summer and winter. The full territory constituted the sum of these selected patches and travel corridors to reach them from the agent's territory center. The cycle of steps proceeded as in the original model (Fig. 1.2, Sect. 1.2), whereby agents continued selecting, modifying, and defending territories in response to decisions made by neighboring agents. Throughout each simulation, the density of agents per ecoregion was tracked. Once $Density_T$ was reached in an ecoregion, no new agents could settle there. Once $Density_T$ was reached in all ecoregions, the simulation ended.

Model output included territory size, overlap, and spatial extent. Territory size was the number of 1-km^2 patches in the territory and territory overlap was the percentage of the territory overlapping other territories. The model saved a raster dataset of the spatial extent and sizes of territories. To do so, each agent transmitted its territory size onto patches it owned; shared patches were assigned the mean territory size of the agents claiming them. This created a spatial layer of locations and sizes of predicted territories at a 1-km^2 resolution. The model also recorded each agent's number of nearby competitors (# of other agent territory centers ≤ 25 patches from the territory border) and mean human density per territory patch.

Model calibration

Because resource requirements and the costs of competition, travel, and mortality risk for wolves was unknown, calibration was required to identify parameter values for wolves (Sells et al. *in review a*; Grimm and Railsback 2005). This calibration step involved a substantially different application of the model than used for drawing inferences and assessing the model's predictive performance. As outlined above, in the primary model application agents were added randomly to the landscape. Agents had no information about locations of real territories. In contrast, during calibration we adjusted the model to manually settle an agent at the center of each of the 26 empirically-observed territories from 2014 – 2019. The 26 agents selected optimal territories with respect to their locations on the landscape and the parameter values encountered. We then calculated the mean squared error (MSE) in the size of each predicted versus observed territory. We repeated these steps as we iteratively varied each parameter over a wide range. We then identified the set of parameter values that produced the smallest average MSE across the 26 packs, and used the identified parameter values when applying the model.

Model application

Our primary model application evaluated its predictive power. We simulated conditions experienced by packs in Montana from 2014 – 2019. We set $Density_T$ per ecoregion to the mean density of packs that occurred in the respective ecoregion during these years. We repeated 50 iterations of the simulation to capture variability in results. We assessed the model's predictive ability by comparing accuracy in predicted versus observed territory distributions, territory sizes, and patterns in relation to food, competition, and human density. For the comparison of territory distributions, we merged the raster datasets from the 50 model runs to identify where the predicted territories occurred, then overlaid this with the estimated distribution of real territories. For the comparison of individual territory sizes, we calculated the mean of the 50 raster datasets. We then measured the mean size predicted within each of the 26 real territory boundaries and compared this to the observed size. We also plotted the sizes of the simulated territories versus the 26 real territories in relation to prey density, competition, and human density.

We next evaluated the model's predictive capacity for an earlier period. We set $Density_T$ per ecoregion to the density of packs that occurred in the respective ecoregion during 2008 and ran 50 iterations of the model. We calculated the mean of the 50 rasters and measured the predicted territory sizes for wolves collared in 2008. We then repeated this using the identified $Density_T$ per ecoregion for 2009. We compared observed versus predicted territory sizes of the 9 packs with collared wolves from 2008 – 2009.

We next applied the model to predict outcomes under alternate environmental and social conditions. We first predicted outcomes under changing densities of prey in Western Montana. We retained the settings from the primary model application but scaled the density of prey to 50%, 75%, 125%, and 150% of the main prey densities estimated. We repeated 50 iterations at each relative prey density. We next simulated increasingly intense competition among packs for space in Western Montana. We set $Density_T$ incrementally from 0.1 – 2.5 agents per 1000 km^2, in increments of 0.1. We repeated 50 simulations per $Density_T$ and summarized the predicted territory sizes under these densities.

Results

The model successfully predicted the distribution of wolves in Montana. The observed locations of wolves versus predicted distribution of territories from 2014 – 2019 were broadly aligned (Fig. 1.7). Areas not known to be used by real wolves in Western Montana were largely avoided by simulated packs, such as in the Flathead and Bitterroot Valleys. The distribution of real wolf locations was noticeably

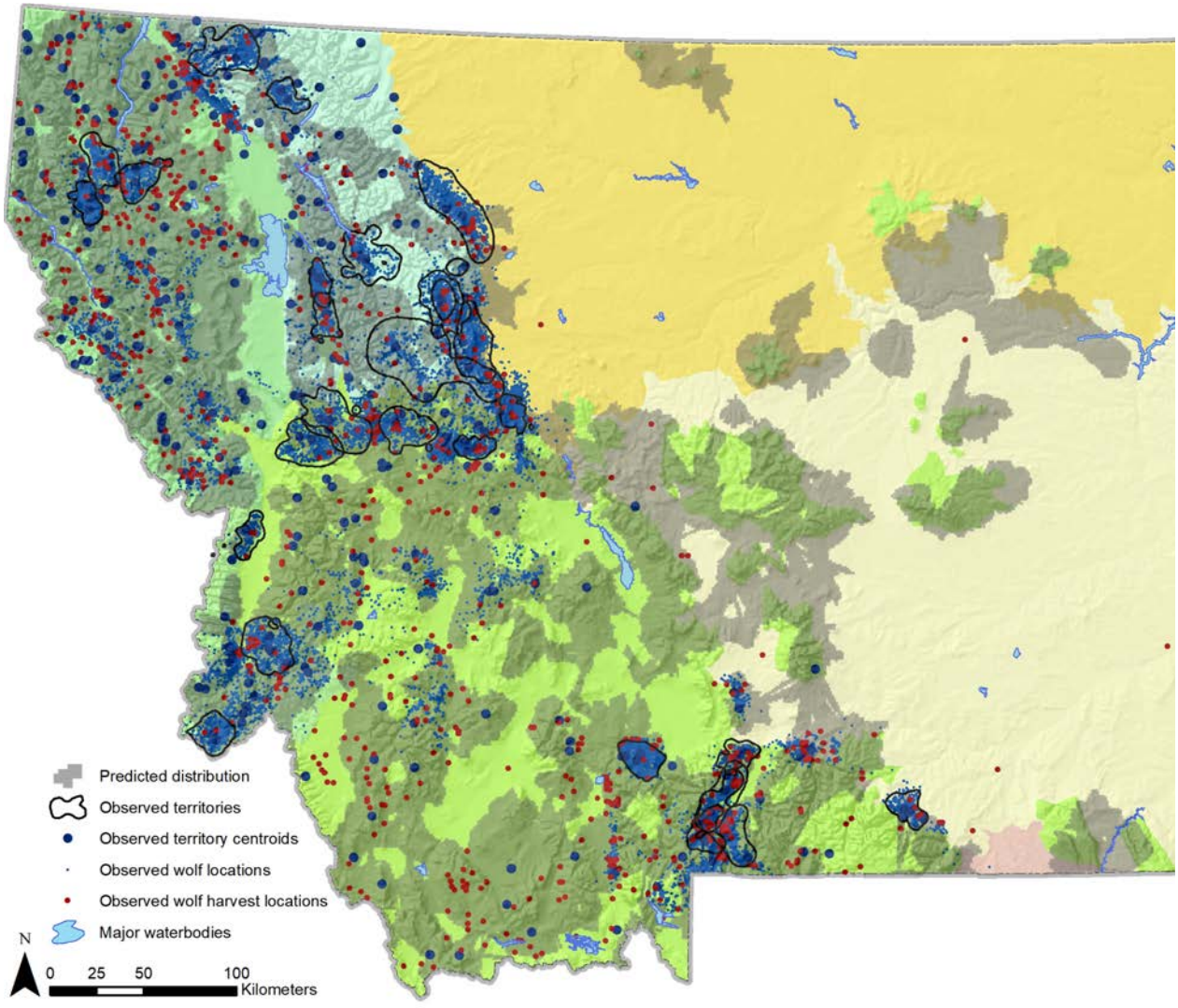

Figure 1.7. Predicted distribution of territories for 2014 – 2019 on a 1-km^2 grid (gray shading), alongside observed locations of wolves during this period (territory centroids, GPS locations for collared individuals, and harvest mortality locations).

patchy in the MRE (southwestern Montana), and the model replicated the approximate locations of used space well. The model predicted a slightly broader distribution of territories in central Montana (including parts of the GLPE and GRPE) than were known to occur there. This was expected because agents were randomly initiated in Western Montana and small sections of the MRE fell within this area. Placement of territories varied by simulations, and these areas of central Montana were not commonly predicted to hold territories. Nonetheless, these areas may have been missed by past monitoring efforts or forecast sites that may be selected by wolves in the future.

The model successfully predicted the territory sizes observed in real packs (Fig. 1.8). The mean difference in predicted versus observed territory size for the 26 real territories was 202 km^2. Omitting one large outlier territory resulted in a mean difference of 146 km^2. Of the 26 territories, 42.3% predicted territory sizes were within 100 km^2 of the observed size and 80.8% were within 200 km^2. Interestingly, the 19.2% of territories with lower accuracy (>200 km^2 difference in predicted versus observed sizes) were generally those with visible extra space estimated around the wolf locations (Fig. 1.7). This byproduct of kernel density estimation represented uncertainty in the exact extent of the territory boundaries; the primary space used by all but 1 of this subset of wolves was both predicted and observed to be smaller than the full territory boundary that was estimated as truth.

The model successfully predicted the sizes of territories from 2008 – 2009

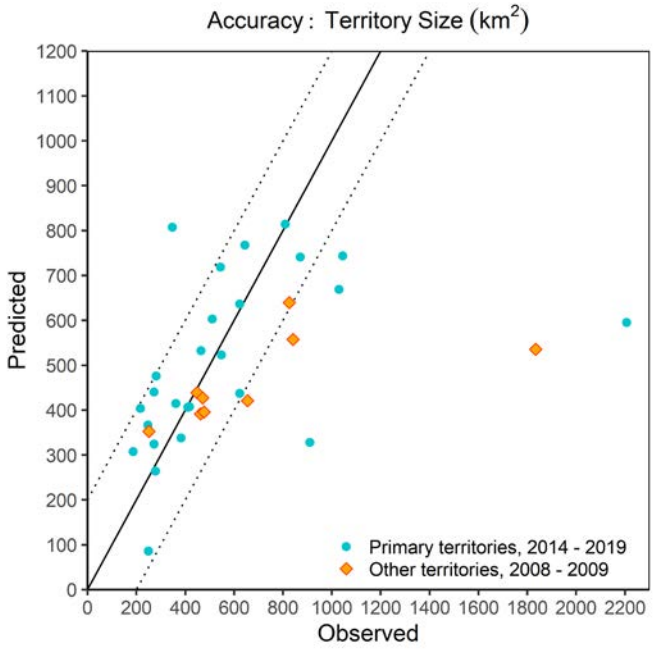

Figure 1.8. Comparison of predicted versus observed territory sizes for 26 GPS-collared packs (2014 – 2019), as well as 9 packs from 2008 – 2009. The solid line represents perfect precision, and dotted lines represent estimates with a difference of ≤ 200 km^2 in predicted versus observed territory size.

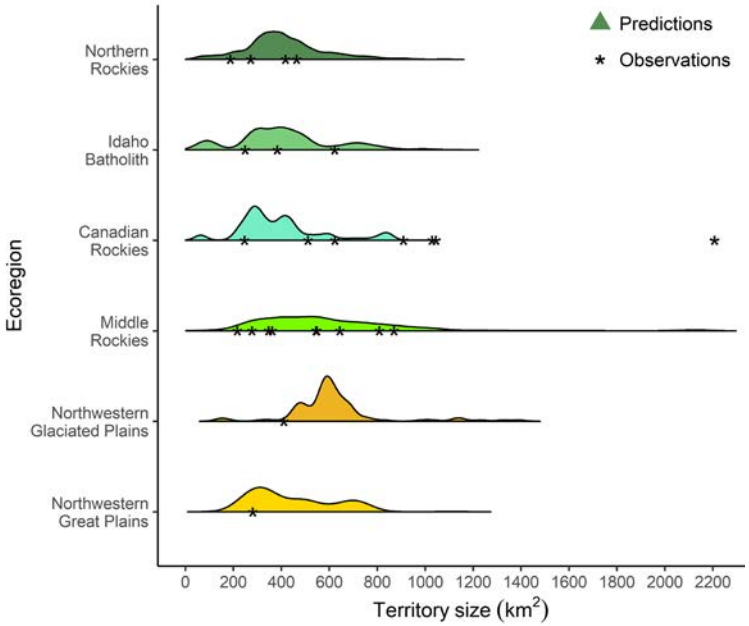

Figure 1.9. Territory sizes from 2014 – 2019 were predicted to vary by ecoregion (Fig. 1.3). These predictions aligned well with observations.

(Fig. 1.8). The mean difference in predicted versus observed territory size for these 9 earlier territories was 256 km^2. Omitting one large outlier territory resulted in a mean difference of 127 km^2. Of the 9 territories, 44.4% were within 100 km^2 of the observed size, and 66.7% were within 200 km^2; all but the one outlier territory were within 300 km^2.

Predictions by ecoregion tracked trends observed empirically (Fig. 1.9). The same was true for predictions in response to food abundance (Fig. 1.10), competitor density (Fig. 1.11), and human density (Fig. 1.12). As originally predicted (Sells and Mitchell 2020) and demonstrated statistically for wolves (Sect. 1.3; Sells et al. *in press*), territory size declined with increasing food abundance and more neighboring packs. Territory overlap was predicted to increase under the same circumstances. Similar to predictions from Sells and Mitchell (2020), territory size was predicted to increase and then decrease curvilinearly with an increase in mortality risk (Fig. 1.12).

The model also predicted outcomes in space use under changing environmental and social conditions. It predicted that territories would increase in size and decrease in overlap if prey densities declined (Fig. 1.13). Mean territory size was predicted to be 515 km^2 or 487 km^2 at prey densities of 50% or 75% of current levels, respectively, with mean overlap decreasing to 3.4% and 7.9%. Conversely, mean sizes

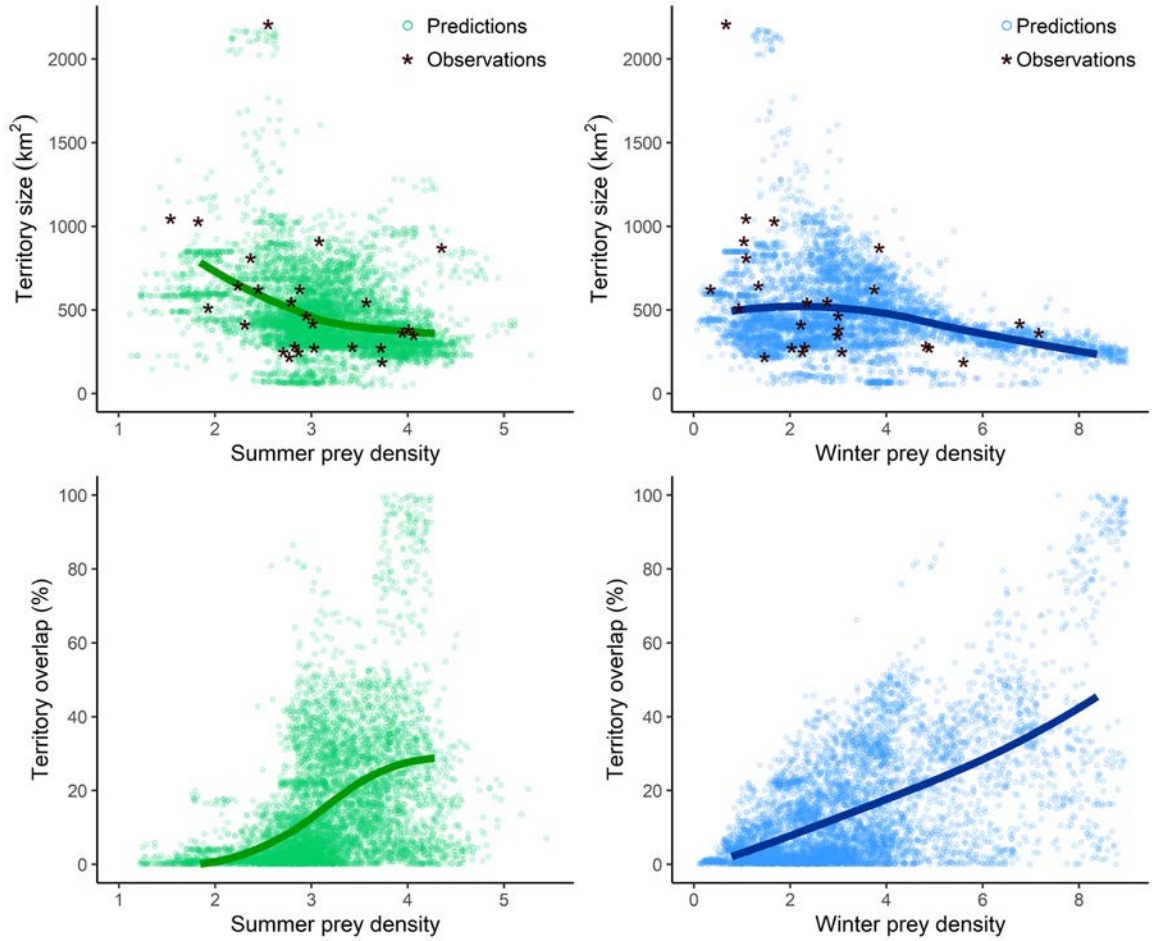

Figure 1.10. Territory size was predicted to decline whereas overlap was predicted to increase with greater summer and winter densities of ungulates. These predictions were closely aligned with empirical observations. Lines depict smoothed conditional means (method = local polynomial regression) for predictions.

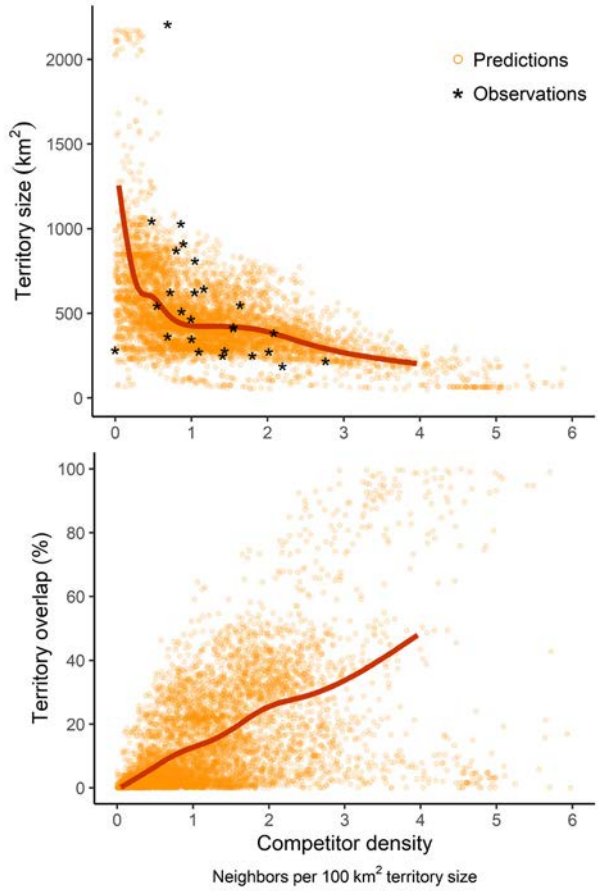

Figure 1.11. The model predicted territory size would decline and overlap increase with increasing competitor density (measured as the # of neighbors per 100 km^2 in territory size), as observed empirically. Lines depict smoothed conditional means (method = generalized additive model) for predictions.

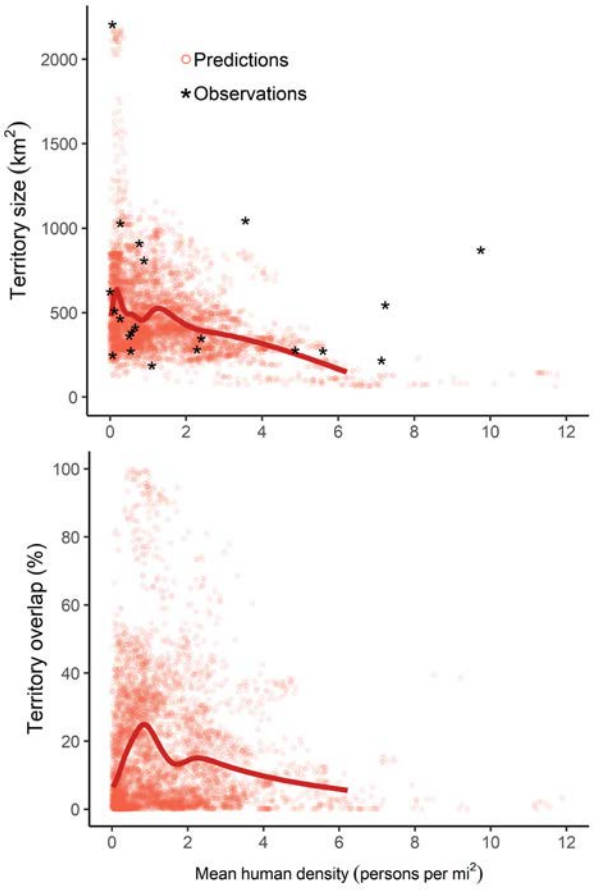

Figure 1.12. The model predicted territory size and overlap would increase and then decrease in response to increasing human densities. Lines depict smoothed conditional means (method = generalized additive model) for predictions. 3 outlier observations are omitted (densities of 26 – 72 humans per mi^2).

were predicted to decline to 449 km^2 or 410 km^2 at prey densities of 125% and 150% of current levels, respectively, with mean overlap increasing to 22.0 and 25.2%. Changes in social conditions also affected space use (Fig. 1.14). Territory size on average declined with an increase in pack density. As an exception, territory size in the NRE initially increased as pack densities transitioned from 0.1 to 1.0 packs per 1000 km^2 before again declining at pack densities > 1.0. The range in territory sizes was consistently greatest at low pack densities. Differences in mean territory sizes by ecoregions were initially pronounced but became more uniform across ecoregions at approximately 1.0 packs per 1000 km^2.

Discussion

We demonstrated the strong potential for a mechanistic modeling approach centered on optimal foraging theory to predict space use and advance scientific understanding of mechanisms driving spatial behavior. Our mechanistic model based on simple rules for economical territory selection successfully predicted locations and sizes of real wolf territories using limited data. Demonstrating the model's ability to predict first-order selection, the distribution of predicted territories closely matched the estimated distribution of

real space use of wolves in Montana (Fig. 1.7). At the second-order level, the model predicted individual territory sizes (Fig. 1.8) and replicated empirically-observed patterns in relation to variable ecoregions, prey densities, competitor densities, and mortality risk (Figs. 1.9 – 1.12). Ability to predict space use provides strong evidence that wolves select territories economically based on the benefits and costs of territory ownership.

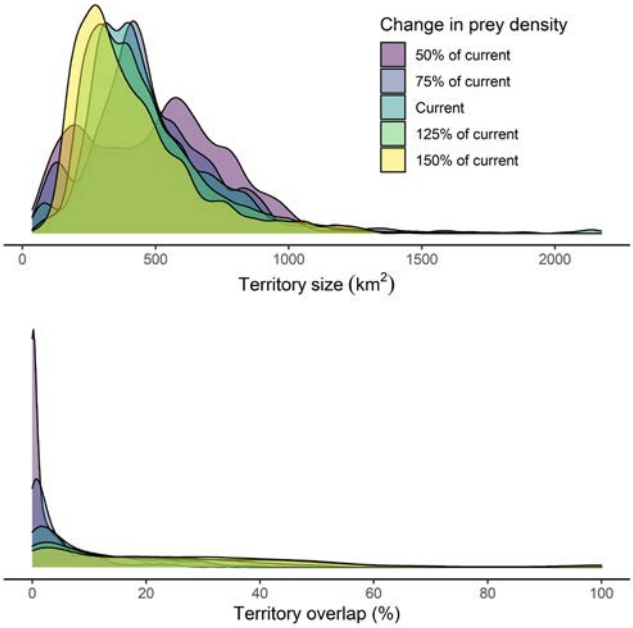

Figure 1.13. Example predictions under potential conditions wolves may encounter whereby prey densities have decreased or increased from current levels. Density plots show that mean territory size increased and overlap decreased as prey density declined; the range in territory sizes also increased. As prey density increased, mean territory size declined and overlap increased.

The model's first-order predictions replicated the distribution of real wolves while also revealing areas where territories may have gone undetected in the recent past and where they may occur in the future (Fig. 1.7). Territories predicted in areas where few have been confirmed (e.g., in some mountain ranges in central Montana) may have been used by real wolves who did not successfully sustain territories, as territories had to be identified and remain occupied through each calendar year to be recorded (Inman et al. 2020). These areas include island mountain ranges surrounded by ranchlands where human-wolf conflicts can be high, potentially decreasing the odds a pack persisted. Wolves are commonly reported by the public to occur and have occasionally been harvested in these areas (Fig. 1.7), indicating that real wolves do use them during extra-territorial forays, dispersal, or as sites of attempted territories. As wolves continue expanding their range, new territories may be successfully settled in the areas predicted.

The model successfully predicted individual territory sizes, both for our original dataset of 26 observed territories from 2014 – 2019, and for a former dataset of 9 territories from 2008 – 2009 (Fig. 1.8). The original dataset was used briefly to help calibrate the model whereas the former dataset was held out of model calibration entirely, demonstrating the need for only a limited location dataset for model calibration to enable successful prediction of second-order space use.

The model's mechanistic approach to understanding space use and its successful replication of patterns observable in nature reveal how differing conditions will influence spatial behavior. Economical territory selection leads to differences in territory sizes by ecoregion (Fig. 1.9). These density plots are expected to better depict the true variation in territories in Montana than could be summarized from limited empirical observations. Spatial variation in territories can arise through disparities in any one benefit or cost of territory ownership (e.g., prey or pack densities), or as an outcome of the interacting effects of these benefits and costs. Spatial variation in mean territory size will influence the local densities of packs and abundance estimates from iPOM. Accordingly, this spatial variation in territory sizes can be incorporated into iPOM to improve accuracy of abundance estimates.

Predictions related to the density of prey (Fig. 1.10) demonstrate the important effects of food resources on space use. By maintaining economical territories, wolves can be expected to generally compress their territories and increase territory overlap in response to greater prey abundances. Smaller territories with more overlap mean that densities and numbers of packs are likely to be relatively high where prey populations are high. Fluctuating prey populations can be expected to cause territory size and overlap to also fluctuate. Altogether these effects could influence the accuracy of abundance estimates from iPOM if not unaccounted for, particularly when estimating wolf abundances at finer spatial scales than the statewide level, where local prey populations can be highly variable. Using this understanding of how prey populations influence space use, iPOM estimates can be calibrated for finer spatial scales (e.g., at MFWP regional management levels) and into the future as prey populations fluctuate.

By maintaining economical territories, wolves can be expected to compress their territories and increase territory overlap in response to greater inter-pack competition (Fig. 1.11). Packs may therefore reach higher densities than would be estimated using a snapshot of average observed territory sizes alone. For example, Rich et al. (2012) reported an average territory size of 599.8 km^2 for packs in 2008 – 2010.

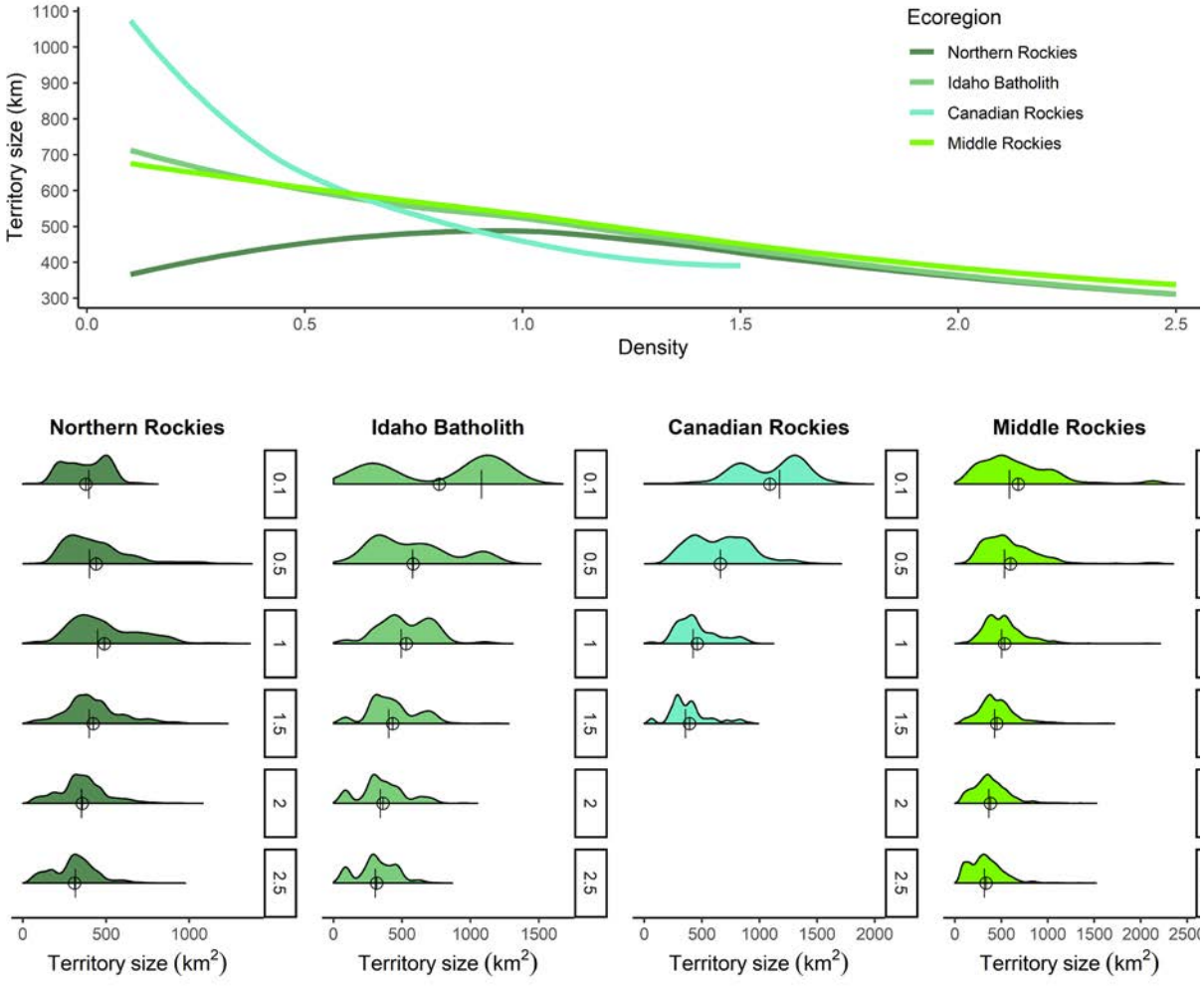

Figure 1.14. Example predictions under potential conditions wolves may encounter whereby group densities have decreased or increased from current levels. The lower panel contains density plots and the mean (circle) and median (line) territory sizes observed. The predictions for the CRE end at 1.5 because no additional simulated packs successfully established territories past this density.

Although this mean territory size has been presumed to date to be unchanged, territory sizes have considerably declined when estimated for 2014 – 2019 using comparable methods (Sect. 1.3). Territory compression explains why the estimated distribution of wolves has not increased at comparable rates as the estimated number of packs. For example, an estimated ~65% increase in the number of packs from the years of Rich et al. (2012)'s study to ours yielded an estimated 41% increase in area occupied (Inman et al. 2019). Packs are thus likely to have more neighboring territories in recent years than they did a decade ago, increasing the costs of competition and leading to territory compression. Fritts and Mech (1981) also reported that territories shrank by as much as 68% as density of packs increased during recolonization in Minnesota. Occupancy and wolf distribution can be expected to be more stable than territory sizes and pack densities as packs adjust their space use in response to levels of intraspecific competition. Understanding these dynamics will be important for keeping iPOM estimates calibrated as the wolf population fluctuates. Assessing wolf occupancy without also accounting for territory sizes within the occupied area could easily over- or under-estimate wolf abundance estimates.

Predictions related to human density support the hypothesis that the cost of mortality risk affects territory selection by wolves in Montana (Fig. 1.12). We observed that running the model without a cost of mortality risk led some simulated wolves to settle relatively urban areas (e.g., the broad Flathead and Mission Valleys in northwestern Montana), whereas they avoided urban areas if this cost contributed to the values of potential territory patches. As no data exist for how costs of mortality risk affect the economic value of patches for wolves, we had to assume that we suitably represented these costs in the model. Our results are intuitive, however. Human settlements often occur along Montana's valley bottoms, which also attract ungulates. These areas were likely used by wolves prior to heavy habitation and mortality risk by humans. Wolves in our study area faced risk of mortality through harvest and control removals in response to livestock depredations. We expect that in areas with lower human-caused mortality risk, e.g., national parks, the risk of mortality from humans is relatively less important to how wolves select territories.

We know of no other model for animal space use capable of accurately predicting territory sizes of individual animals or groups and a population's distribution, particularly absent extensive data for movements and resource availability. Ultimately, the dynamic fluctuations and large variations in territory sizes within a population make it difficult to draw inferences about a population's spatial requirements absent approaches such as ours. Any empirically-observed territory is a snapshot in time and assumes an individual's movements revealed the full extent of the territory and no extraneous movements (e.g., during extra-territorial forays prior to dispersal). The true territory mosaic at any given time could only be observed empirically if all individuals in a population were simultaneously collared. Our approach uniquely enabled predicting these mosaics for the full population using limited data and under varying conditions.

Management implications

Wildlife conservation agencies like MFWP require information about animal behavior, numbers, and the anticipated effects of conservation actions. Such information is challenging, costly, and time-consuming to gather. Efforts often include the use of radio- or GPS-transmitters to track movements, but particularly for elusive large carnivores like wolves, it can take weeks or more to successfully capture a single individual. Post-capture, equipment failures and mortalities can easily cut short the lifespan of a

transmitter, challenging efforts to gather ongoing data to understand and monitor spatial behavior. Furthermore, inferences from empirical approaches are generally limited to the time and place from which data were collected, as such approaches tend to describe space use but do not reveal the causal mechanisms underlying behavior.

Our mechanistic approach to modeling animal space use provided a linkage between theory and conservation and made predictions applicable to ecology absent extensive data for animal movements or resource availability. Model parameterization used only readily available data, i.e., indices for ungulate densities, terrain ruggedness, and human densities. Our approach enabled simulating a suite of potential conditions to produce predictions for the full population and potential future conditions, absent any additional data. The model is expected to be predictive and reliable across a full range of current and future conditions because it was founded on hypothesized drivers of behavior (Sells et al. 2018). The model's spatially-explicit predictions can be used to estimate the abundance of territories, carrying capacity, and effects of conservation actions or environmental change. Linking the model's estimates of territory size and overlap with the spatially-explicit occupancy probabilities produced through iPOM (Sect. 1.1) will enable summarizing the estimated number of packs at finer spatial scales, e.g., at MFWP regional levels. Ability to predict the effects of changing conditions will enable calibrating iPOM into the future, absent intensive monitoring efforts.

We expect this mechanistic approach centered on optimal foraging theory and explicit modeling of economical behavior has far-ranging potential. Primary challenges of our approach include the necessity of strong coding skills and sufficient data, including indices representing the hypothesized benefits and costs of space use, and location data for initial model calibration and evaluation. We demonstrated the utility of even simple indices from readily-available datasets. The foundation provided by Sells and Mitchell (2020) and this study are adaptable to different contexts or to further improve predictive capacity, such as by modifying model rules or data inputs. Similar approaches could be taken to not only predict first- and second-order habitat selection by wolves in other areas, but for other species. The approach is not limited to territorial species; minor changes to the model would extend it to home ranges in general, further expanding the opportunity to study and understand animal spatial behavior.

1.5 Group Size Models

To help calibrate iPOM, we aimed to better understand mechanisms influencing wolf pack size. As with populations, groups and group sizes are shaped by births, deaths, and social decisions about group membership. The outcome of these decisions can strongly shape demographic processes, particularly for species like wolves, in which only a dominant pair generally breeds (Clutton-Brock 2016). Behaviors as fundamental as group living should be strongly shaped by natural selection (Emlen 1982, 1994, 1995; Krebs and Kacelnik 1991). Decisions about group membership are thought to ultimately be driven by factors related to resource competition, kin interactions, inbreeding avoidance, or habitat quality (Emlen 1982, 1995; Bowler and Benton 2005). Whereas in some carnivorans dominant individuals enforce eviction of subordinates (Cant et al. 2001; Grinnell et al. 1995; Stephens et al. 2005), in other species like wolves, decisions to emigrate are likely influenced by economic considerations for both dominants and subordinates. In such cases, subordinates should be accepted when the benefits to dominant individuals outweighs the costs of a subordinate's presence, and otherwise encouraged to leave. Subordinates should likewise remain only while the benefits they gain by staying exceed their costs (Emlen 1982, 1994, 1995).

Similarly, given an option, dominant individuals should only accept immigrants when in the dominant's economic interest; likewise, immigrants should only join groups when in their economic interest.

We hypothesized competition is a primary factor influencing the size of groups. By reducing per capita resources, larger groups may experience fewer births and more deaths. Mortality rates may also rise through conspecific aggression within or among groups. Competition likely also influences the economics of social decisions (Emlen 1982, 1994, 1995). An increase in the density of nearby groups may signal less space for new home ranges and greater risk of conspecific mortality while emigrating, causing a positive effect on group size as subordinates delay leaving. Additionally, dominant individuals may be more accepting of subordinates and immigrants at high group densities, when territorial disputes may increase and having a larger group can increase the odds of winning confrontations (Mosser & Packer 2009; Cassidy et al. 2015). Accordingly, if there is a large positive effect on social decisions, group size may increase with competition even if birth rates fall and death rates rise (Table 1.4). Delayed dispersal may also lead to greater birth rates through multiple breeders (Ausband 2018), further contributing to a positive effect of competition. Alternatively, a negative or null relationship between competition and group size would occur if individuals leave at greater rates to avoid this competition, or social decisions simply do not offset effects on births and deaths.

We hypothesized that conditions related to prey also influence births, deaths, and social decisions. Birth rates may fall and death rates rise if prey acquisition falls below per capita requirements (Fuller et al. 2003). If subordinates cannot meet their food requirements, leaving is likely the optimal decision; additionally, dominant individuals might increase aggression or withhold resources to further encourage emigration (Mech 1999, Peterson and Ciucci 2003). Conversely, in addition to potentially increasing birth rates and reducing death rates, greater access to food resources may increase the group sizes that can be maintained, allowing dominants to tolerate subordinates and accept immigrants, and enticing subordinates to stay. For these reasons we expected that group size would positively correlate with prey abundance and availability (Table 1.4; Mech & Boitani, 2003). We alternatively hypothesized that higher prey abundance may signal subordinates that conditions are conducive to forming one's own group in which to breed, increasing emigration and resulting in a weak or nonexistent relationship between group size and prey.

Mortalities directly decrease group size, but we hypothesized they also have wider effects. Deaths of parents or helpers may lead to further deaths of dependent young (Ausband et al. 2017). Survivors may also have more difficulty hunting prey (Creel and Creel 1995), defending territories (Cassidy et al. 2015), and assisting injured or sick group members (Almberg et al. 2015). We also expected that mortalities or even a perceived risk of mortality could influence the economics of social decisions. As the risk of dying increases locally, subordinates might leave to avoid this risk and the consequences of losing group members. Subordinates may also be pressured or opt to leave if larger groups are more easily detected by predators. Emigration may be economical if dominant individuals are replaced by non-relatives, reducing inclusive fitness benefits (Emlen 1995). Smaller groups would be the outcome of these mortalities and behavioral responses (Table 1.4). Alternatively, mortalities could cause group size to stabilize or increase if decreased survival leads to compensation through increased reproduction or larger litters. Similarly, emigration may decrease and immigration increase if predation risk is diluted in larger groups.

We evaluated our hypotheses about group size using a 14-year dataset of wolf pack sizes observed in Montana. We used our previously-developed index for prey abundance (Sect. 1.3), and terrain ruggedness

as an index for prey availability. We expected that greater terrain ruggedness could negatively influence pack size by decreasing the availability of ungulates because wolves are coursing predators (Peterson and Ciucci 2003) who may make more kills at lower elevations (McPhee et al. 2012) and may have lower hunting success in rugged terrain (Rich et al. 2012). We expected that several factors would influence mortality risk to wolves, including hunting, trapping, deaths in response to livestock depredations (i.e., control removals), and intensity of harvest management (Table 1.4). Additionally, greater human densities could mean more hunters and mortalities, plus greater perceived mortality risk given the natural wariness of wolves towards humans (Hebblewhite & Merrill 2008; Latham et al. 2011; Whittington et al. 2004). Mortality risk could also increase in human-dominated landscapes (e.g., agricultural areas), and with low-use roads, which humans may use while hunting or otherwise recreating.

Table 1.4. Hypothesized relationships between wolf pack size and variables related to competition, prey, and mortality risk (o denotes neutral outcome expected for group size). We considered hypotheses to be supported when 90% confidence intervals did not overlap 0.0, as determined by variables included in the top models (Fig. 1.16[1]) or through secondary analyses of models with single fixed effects (denoted by *). Bold text signifies the hypotheses with support.

Variables hypothesized to influence group size	Expected relationship	Alternative expected relationship	ß	CI_{lower}	CI_{upper}
Competition					
Density of groups	**H_1: +**	$H_{1\text{-alt}}$: o	0.082	0.039	0.124
Prey					
Summer ungulate density	H_{2a}: +	**$H_{2a\text{-alt}}$: o / −**	0.014	−0.028	0.055
Winter ungulate density	H_{2b}: +	**$H_{2b\text{-alt}}$: o / −**	0.008	−0.031	0.046
Summer deer density	H_{2c}: +	**$H_{2c\text{-alt}}$: o / − ***	0.007	−0.033	0.048
Winter deer density	H_{2d}: +	**$H_{2d\text{-alt}}$: o / −**	0.014	−0.029	0.058
Summer elk density	H_{2e}: +	**$H_{2e\text{-alt}}$: o / −**	0.018	−0.027	0.063
Winter elk density	H_{2f}: +	**$H_{2f\text{-alt}}$: o / −**	0.013	−0.027	0.054
Terrain ruggedness	**H_3: −**	$H_{3\text{-alt}}$: o / +	−0.051	−0.092	−0.010
Mortality risk					
Harvest mortality density	H_{4a}: −	**$H_{4a\text{-alt}}$: o / +**	−0.012	−0.063	0.039
Control removals	**H_{4d}: −**	$H_{4d\text{-alt}}$: o / +	−0.061	−0.098	−0.027
Intensity of harvest management (restricted)	H_{4e}: −	**$H_{4e\text{-alt}}$: o / +**	−0.089	−0.183	0.004
Intensity of harvest management (liberal)	**H_{4f}: −**	$H_{4f\text{-alt}}$: o / +	−0.193	−0.298	−0.087
Human density	H_{4g}: −	**$H_{4g\text{-alt}}$: o / +**	0.025	−0.009	0.059
Human-dominated area	H_{4h}: −	**$H_{4h\text{-alt}}$: o / + ***	0.000	−0.035	0.035
Density of low-use roads	H_{4i}: −	**$H_{4i\text{-alt}}$: o / +**	−0.013	−0.053	0.027

1. The variable values shown are from the highest-ranked model with the given variable.

Methods

Study area

Our study area was the same as described under Sect. 1.3 (Fig. 1.3).

Data

Wolf Specialists from MFWP monitored packs through radio-tracking, camera-trapping, and aerial surveys each year from 2005 – 2018 to verify pack presence, count pack members, and estimate year-end pack sizes. We retained for analysis only good quality counts, which were from packs documented multiple times each year using trail cameras, visual sightings, or track surveys. Wolf Specialists estimated an annual territory centroid for each pack.

We estimated local conditions related to competition, prey, and mortality risk using relevant spatial data and program R (R Core Team 2020), as follows. In each case, we measured the mean value of the covariate within the local vicinity of the pack's annual territory centroid (defined as 12.41 km around the centroid, based on the 484 km^2 geometric mean territory size for wolves in Montana, 2014 – 2019, Sect. 1.3) using R package raster (Hijmans 2020) and helper functions from packages dplyr (Wickham et al. 2020), tidyr (Wickham 2020), and AICmodavg (Mazerolle 2020).

We represented competition as the density of packs. Within each pack's local vicinity, we measured the density of territory centroids per 1000 km^2 using the kernel smoothed intensity function in R package spatstat (Baddeley et al. 2015) with sigma set to 25 km.

To represent prey abundance, we used the spatial density indices developed in Sect. 1.3. We included the individual indices for deer and elk to measure their separate effects. To represent prey availability, we calculated terrain ruggedness using the steps described under Sect. 1.4. Within each pack's local vicinity, we estimated mean ruggedness, representing the mean elevation change among adjacent 1 km^2 grid cells.

For mortality risk, we first estimated the annual density of harvest mortalities (hunting and trapping combined) per 1000 km^2 using reported locations of harvested wolves and the kernel smoothed intensity function in R package spatstat (Baddeley et al. 2015) with a sigma of 25 km. Pack-specific control removals were reported in MFWP annual reports (fwp.mt.gov). We classified the intensity of harvest management as hunting seasons with no harvest ($\leq$ 2008 and 2010), restricted harvest (2009 and 2011; when statewide harvest was limited by a quota, seasons were shorter, bag limits were low, and trapping was prohibited), and liberal harvest (2012 on, when statewide harvest quotas were removed, seasons were longer, bag limits were higher, and trapping was allowed; fwp.mt.gov). Within each pack's local vicinity, we measured the mean density of humans using 2010 census data (geoinfo.msl.mt.gov), the percentage of human-dominated areas using existing vegetation type to identify agricultural and developed areas (LANDFIRE 2014), and the mean density of low-use roads using the most recent road dataset (geoinfo.msl.mt.gov).

Analyses

We tested our hypotheses using GLMMs (family = Poisson) with R package lme4 (Bates et al. 2015). We designed 20 competing models (Sells et al. *in review b*) to focus on competition, prey, or mortality risk, as well as their combined effects, representing different hypotheses for which factors best predicted pack size. We included variables for the density of harvest mortalities, number of control removals, and intensity of harvest management in each model because these mortality variables directly influence pack size. We avoided combining overly-correlated variables in the same model (> 0.6 Spearman's rank correlation; Dormann et al. 2013). We also added a random effect for pack identity to each model. We identified the most supported models using Akaike's information criterion (AIC; Burnham & Anderson 2002) with a cut-off of 2 ΔAIC (Anderson et al. 2001) and Akaike weights (ω_i; Burnham & Anderson 2002). We reported results based on centered and scaled variables, with resulting units representing standard deviations from the mean. We considered a hypothesis to have support if the 90% confidence intervals (CIs) of the coefficient estimate (ß) excluded 0. Where covariates were omitted from the top models identified, we ascertained other evidence of support for hypotheses using GLMMs with a single fixed effect for the covariate of interest. To display results, we used R packages ggplot2 (Wickham 2016) and jtools (Long 2020), with helper functions from cowplot (Wilke 2020).

Results

From 2005 – 2018, MFWP monitored 46 – 152 packs per year for a total of 1531 pack-years. Of these, 26 – 68 packs per year had good quality counts, yielding 660 total pack-years from 220 packs for analysis. Annual mean pack size ranged 4.86 – 7.03 and overall mean pack size was 5.92 (Fig. 1.15). Most packs were relatively small, with 80% containing ≤ 8 members.

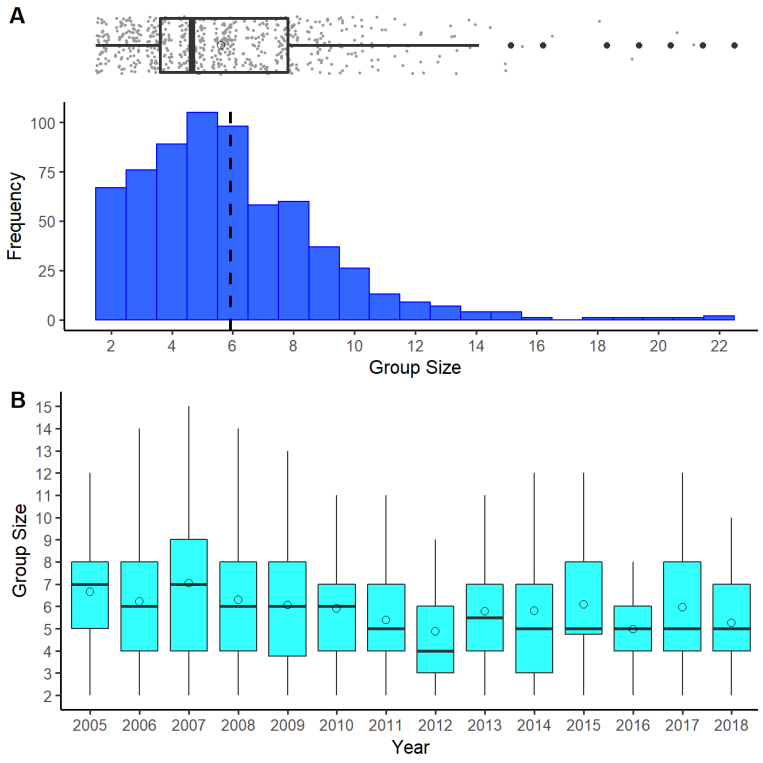

Figure 1.15. Observed wolf pack sizes, 2005 – 2018. Pack sizes ranged 2 – 22, with a mean of 5.92 and a 50% interquartile range of 4 – 8 members. Gray points in Panel A depict observations whereas black points depict outliers. Boxplot whiskers in both panels extend 1.5 times the interquartile range.

Six models had support (Fig. 1.16). These models differed by prey indices and mortality risk factors included, and revealed similar effects on group size. Group size increased with density of groups and decreased with greater terrain ruggedness and control removals (Table 1.4). Liberal harvest had a negative effect whereas restricted harvest had an uncertain effect. Group size had no clear relationship with densities of prey, harvest

mortalities, humans, or low-use roads. Further assessment of covariates excluded from the top models found no measurable effect for remaining variables (Table 1.4).

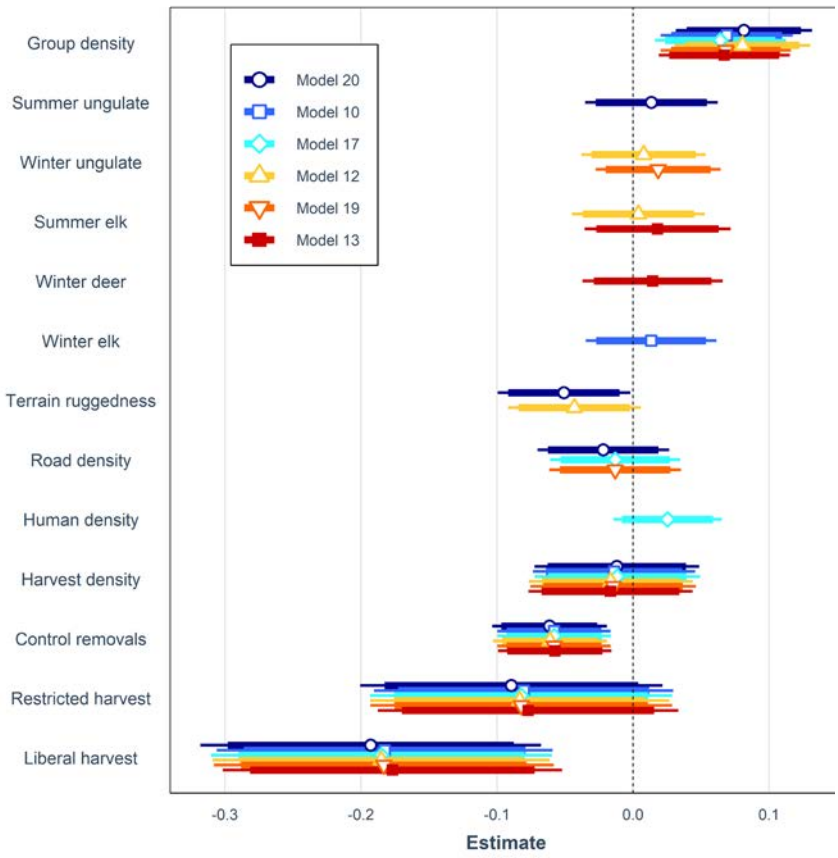

Figure 1.16. The top predictive models for pack sizes included variables related to competition, prey, and mortality risk. Thicker line segments represented 90% CIs, full lines the 95% CIs, and points represented mean estimates.

Discussion

Sociality in carnivores is relatively uncommon but associated with many potential benefits, including increased ability to acquire resources, decreased risk of mortality, and increased reproductive success. Group size may affect these benefits and is driven not only by births and deaths, but the social decisions of group members, including whether to stay with or leave the group.

A positive relationship between the density of packs and pack size supported the hypothesis that group densities influence the economics of social decisions (Fig. 1.16, Table 1.4). Under that hypothesis, we predicted that even if births fell or deaths rose with increased competition, group size would increase if social decisions favored staying in the group. Our results align with Emlen (1982)'s hypothesis that group living evolved as a result of delayed dispersal in response to habitat saturation, and suggest that, as habitat becomes saturated, inclusive fitness may become increasingly important such that subordinates decide to stay and help rather than emigrate. Local group densities may serve as an important cue to the costs and benefits of staying versus leaving. Detection of local densities of conspecific groups may occur through direct interactions and signals such as scent marks or howling (Mech and Boitani 2003). Pre-disposal forays may also help an individual investigate the costs and benefits of emigrating. Emigration may lead to injury and death through increased encounters with conspecifics at high group densities (Jimenez et al. 2017). Our results also suggest that dominants may be more accepting of subordinates and immigrants at high densities of groups, particularly when a group's competitive ability and success in defending their territory increases with group size (Cassidy et al. 2015, Sells and Mitchell 2020). The patterns we observed may have also been driven by enhanced fitness, such as through multiple breeders per group (Ausband 2018). Declines in rates of dispersal, however, have been attributed to wolf population increases (Jimenez et al. 2017), greater numbers of neighboring prides of lions (*Panthera leo*; VanderWaal et al. 2009), and saturated habitats for Ethiopian wolves (*C. simensis*; Sillero-Zubiri et al.

1996). Similarly, clans of spotted hyenas (*Crocuta crocuta*) may be prone to fission when there is more vacant habitat nearby (Holekamp et al., 1993).

Wolf packs were smaller where food availability was low (Fig. 1.16, Table 1.4), demonstrating that the advantages of sociality may be reduced when food availability declines. Terrain ruggedness served as an index to food availability because hunting success may increase in less rugged terrain (McPhee et al. 2012, Rich et al. 2012). Decreased food availability may reduce a group's ability to meet its resource requirements, potentially reducing births and survival. In similar systems, litter size and pup survival appear to correlate with prey biomass (Fuller et al. 2003) and availability (Mech et al. 1998). Smaller carnivore groups may likewise occur in response to decreased prey availability if dominants become less tolerant of subordinates and subordinates decide to leave (Table 1.4; Ekman et al. 2004). Increased emigration may be a contributing mechanism for observed correlations between food and carnivore densities (Fuller et al. 2003; Fuller 1989; Mech & Peterson 2003).

Contrary to our index for prey availability, our indices for prey abundance were not associated with wolf pack size (Fig. 1.16, Table 1.4). This supports our alternative hypothesis that an increase in births or reduction in deaths with greater prey abundance is offset by a higher rate of emigration because prey abundance is a cue to greater odds of finding sufficient resources. Other studies have however reported evidence that carnivore dispersal increases in response to low prey availability instead (Messier 1985; Peterson & Page 1988; Gese et al. 1996; Fuller et al. 2003). Because deer and elk numbers for our large study area were at coarse resolutions, our results may have been a product of the prey data available for analysis. Whereas this information successfully helped predict territory sizes (Sect. 1.4), we suspect more detailed data tracking temporal trends in prey abundance may be required to detect effects on pack sizes.

Mortalities may both directly and indirectly influence group size (Fig. 1.16, Table 1.4). Our results suggest that control removals, hunting, and trapping may not just directly decrease group size but also depress survival of remaining group members (e.g., via higher mortality of young after the death of a parent or helper; Ausband et al. 2017). Smaller groups in areas of greater mortalities could also be an outcome of emigration by surviving subordinates in response to increased local mortality risk, or reduced inclusive fitness after the death of a parent (Emlen 1995). In similar systems, groups appear more likely to disband after loss of dominant individuals (Brainerd et al. 2008). Although it might be expected that emigration in response to mortalities would lead to voids of groups in high-mortality areas, later immigrants would likely not immediately know that mortality risk was locally high, nor have freedom to select low-mortality areas (e.g., in protected reserves) if already defended by existing groups.

Evidence suggests that wolves may partially compensate for a relatively low level of mortality through increased births, decreased emigration, or increased immigration. Restricted harvest occurred in 2 years punctuated by a year without harvest and had no appreciable effect on wolf pack size during this period (Fig. 1.16, Table 1.4). This could have been an outcome of the restricted harvest regulations (which entailed statewide quotas, lower bag limits, and no trapping) or a recovery year absent harvest. More liberal harvest regulations (which entailed no quotas, higher bag limits and both hunting and trapping), however, had a measurable effect on pack size, potentially because of direct mortality or increased emigration. Increased emigration in response to greater harvest intensity would serve to replenish breeder or territory vacancies quickly, which in turn could lead to more compensation under intensive harvest

than may otherwise be expected. This may help explain the apparent overall stability of some harvested carnivore populations like ours despite years of intensive harvest (Inman et al. 2019).

Data for group-specific births, deaths, immigration, and emigration are rarely available, especially where large carnivores coexist alongside humans outside protected reserves. We employed a large, long-term dataset to test our hypotheses. Although smaller groups could conceivably be more difficult to find and count, 80% of packs monitored contained ≤ 8 members and 51% had ≤ 5 members (Fig 1.15). Undetected packs would lead to locally-underestimated densities and likely weaken measurable relationships with pack size. We assumed that terrain ruggedness was a credible index to prey availability (Peterson and Ciucci 2003, McPhee et al. 2012, Rich et al. 2012), and although its observed relationship with pack size could have been related to other factors (e.g., mortality risk), ruggedness had < 0.4 correlation with other variables (Sells 2019). Imprecise reports of harvest locations or control removals could also weaken relationships between group size and mortality variables. We assumed that data for human density, human-dominated areas, and low-use roads did not appreciably change from 2005 – 2018; finer-resolution data for these variables may reveal relationships with pack size.

1.6 Predictive Pack Size Model

Pack size has been integral to MFWP's abundance estimates since 2007. These data, however, have been derived through intensive monitoring efforts to date. Absent annual monitoring data, total wolf abundance could be estimated with a model that predicts pack size. A useful model for MFWP would predict pack sizes with as few data as possible given the costs and difficulties of monitoring an elusive large carnivore.

Methods

We adapted our top group size model (Sect. 1.5) into a predictive model. We aimed to make the model as parsimonious as possible, and to require minimal monitoring effort for covariates. We therefore first dropped summer ungulate density, harvest density, and low-use road density, which had CIs overlapping 0 (Fig. 1.16). Because obtaining pack centroids through monitoring is costly, we used the mean pack density observed from 2005 – 2018 as an index to long-term density trends. Because control removals were pack-specific and this level of detail may not always be available, we used the observation grid of 600 km^2 cells (Sect. 1.1), then summarized the total number of control removals reported in each cell. To capture additional environmental effects, we added a covariate representing the pack's ecoregion (Fig. 1.3). We included a random effect for the 600 km^2 grid cell in which the pack fell in place of a pack-specific random effect to account for repeated observations among years. We then refit the GLMM.

We tested our model by comparing predicted versus observed mean pack size each year (2005 – 2018). We first measured mean values for model covariates in each 600 km^2 POM observation grid cells, then predicted pack size per cell by applying the model covariates to each cell. We next obtained the probability of occupancy in each cell for each year from 2007 – 2018 (when occupancy data were available) from MFWP's occupancy model (Sect. 1.1; Inman et al. 2019). We calculated the annual mean predicted pack size of cells with ≥50% probability of occupancy. For 2005 and 2006 (when occupancy estimates were unavailable), we predicted pack size per cell known to have a pack. We estimated a linear regression of these predicted versus observed annual mean pack sizes. If the regression slope estimate's

95% CI overlapped 1.0 (Rich et al. 2012), we considered the model to reliably estimate annual mean pack size.

Table 1.5. The predictive model for wolf pack sizes. Variables and their 95% confidence intervals (CIs) are reported on the log scale.

Coefficients	Estimate	Lower CI	Upper CI
intercept	1.56	1.324	1.803
mean pack$_{density}$	0.44	0.259	0.624
ruggedness	−67.28	−99.661	−34.892
harvest intensity$_{restricted}$	−0.06	−0.158	0.043
harvest intensity$_{liberal}$	−0.18	−0.257	−0.100
grid-level control$_{removals}$	−0.03	−0.049	−0.005
ecoregion: IBE	−0.06	−0.245	0.120
ecoregion: MRE	0.04	−0.095	0.166
ecoregion: CRE	0.13	−0.019	0.286
ecoregion: GLPE	0.03	−0.327	0.390
ecoregion: GRPE	0.00	−0.320	0.317

Results & Discussion

The predictive model revealed a positive relationship of pack size with pack density, and negative relationships with ruggedness, harvest intensity, and control removals (Table 1.5). The model reliably estimated annual mean pack size, as the linear regression of observed versus predicted pack sizes included 1.0 (ß = 0.81, 95% CI = 0.319, 1.307, R^2 = 0.52, $F_{1,12}$ = 12.84, P = 0.004).

Despite omitting direct information for births, immigration, dispersal, and deaths, our model successfully predicted annual mean pack size for wolves in Montana (Fig. 1.17). The model can be used alongside the mechanistic territory model (Sells and Mitchell 2020) and existing occupancy model (Miller et al. 2013, Rich et al. 2013) to estimate wolf abundance with limited data. Our predictive model for pack size therefore directly fulfills a conservation need by facilitating estimates of wolf abundance with limited data.

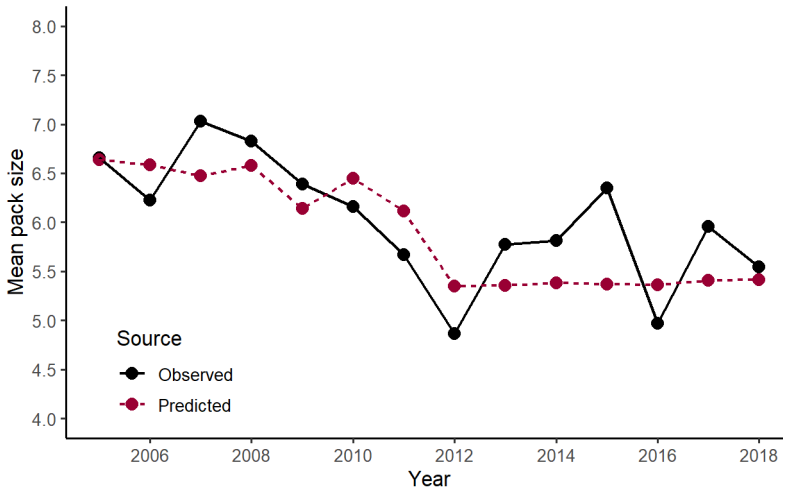

Figure 1.17. Predicted annual mean pack sizes reflected observed mean pack sizes for wolves in Montana from 2005 – 2018. Predictions were derived using our model for wolf pack sizes.

1.7 Integration of Models: iPOM

As our final step under Objective 1, we incorporated the territory and pack size models into iPOM to estimate wolf abundance.

Methods

Occupancy

To predict where wolves occurred in Montana each year from 2007 – 2019, we fit the multi-season false-positives occupancy model from POM in a Bayesian context (Bassing et al. 2019). Details of the original

model are provided in past publications (Miller et al. 2013, Rich et al. 2013, Inman et al. 2020). We retained the original observation grid for Montana as 600 km^2 cells (hereafter, the iPOM grid). We assigned to grid cells the locations of wolves based on monitoring effort by MFWP Wolf Specialists and wolf sightings reported by hunters each fall. To demarcate approximate territory centroids for packs, Wolf Specialists monitored packs each year to verify presence using a combination of trail cameras, visual observations, and telemetry collars. MFWP conducted annual Hunter Harvest Surveys of a random sample of 50,000 – 80,000 deer and elk hunters annually to obtain wolf sighting reports. 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.

To develop encounter histories, we divided the 5-week general rifle season (occurring each year around late Oct through Nov or early Dec) into one-week encounter periods and mapped locations of pack centroids and hunter observations for each week. Based on past work (Miller et al. 2013, Rich et al. 2013, Inman et al. 2020), we included model covariates for detection as: 1) hunter days per km^2 in each hunting district (an index to spatial effort), 2) proportion of mapped wolf observations (a correction for effort, accounting for the number of hunter observations with coordinates versus the total reported, including any sightings with vague location descriptions), 3) densities of low-use forested and non-forested roads (indices of spatial accessibility), 4) a spatial autocovariate (the proportion of neighboring cells with wolves seen out to a mean dispersal distance of 100 km), and 5) patch area sampled (because smaller cells on the border of Montana, parks, and tribal lands have less hunting activity and therefore less opportunity for hunters to see wolves). We also included cell size as a nuisance parameter to account for varying cell sizes. Model covariates for occupancy, colonization, and local extinction included a principal component constructed from several autocorrelated environmental covariates (percent forest cover, slope, elevation, latitude, percent low use forest roads, and human population density), and recency (the number of years with verified pack locations in the previous 5 years).

Using these pack locations and model covariates, we fit the multi-season false-positives occupancy model to estimate psi, the probability of occupancy (ψ). We used pack centroids to estimate probabilities of false positives, true positives, and false negatives (Miller et al. 2013). We estimated ψ for tribal lands and national parks, where no hunter survey data were available, via modeled covariates.

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, Stukalov and Denwood 2019) that calls on program JAGS 4.2.0 (Plummer 2003). We ran 3 chains for 10,000 iterations, after an adaptation phase of 10,000 iterations and a burn-in of 10,000 iterations. We did not thin the MCMC chains.

Territory size

We used the mechanistic wolf territory model (Sect. 1.4) to predict territory size each year from 2007 – 2019. Monitoring data indicated that pack densities in Montana changed at different rates in different places. The mechanistic model demonstrated the strong effect of competition on resulting space use (Sect. 1.2 – 1.4). Accordingly, as described in Sect. 1.4, we applied the model to predict territory sizes at a wide

range of possible pack densities ($Density_T$) and resulting levels of competition. We used the model to also generate a modified measure of territory size for each pack that accounted for overlap:

$$Territory_{size} = N_{selected-patches} + N_{travel-patches} - N_{patches-shared} + \sum N_{patches-apportioned}$$

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

$$\sum N_{patches-apportioned} = \sum_{i}^{n} \frac{1}{N_{owners}}$$

where for each patch *i* - *n*, N_{owners} was the number of owners at the patch. This slightly modified measure of territory size negated the need for specific estimates of territory overlap in the final iPOM calculations. Model output was saved as tables of each pack's territory size and location.

To identify the appropriate level of competition to use for iPOM, we developed a density identifier model. In earlier model applications, we modeled competition by simulating territories at the set of known pack centroids each year. The resulting iPOM estimates were highly comparable to our final iPOM results. In the future, however, this application of the mechanistic model would have required the time-consuming task of re-running simulations every year. Our density identifier model provided the alternative, simpler link to identifying the approximate degree of competition each year. For each ecoregion and year from 2007 – 2018, we tallied the number of verified packs ($N_{packs\text{-}verified}$) from field monitoring and calculated area occupied ($\sum area_{occupied}$), which was $\bar{\psi}$ multiplied by the area of the ecoregion ($ecoregion_{area}$). We then fit a linear model in the form of:

$$N_{packs-verified} \sim \sum area_{occupied} \times ecoregion_{ID}$$

This formalized the strong relationship between total area occupied per ecoregion and known packs within ($R^2 = 0.98$; Table 1.6). Accordingly, the model enabled identifying the appropriate density for each ecoregion in each year ($density_{identified}$), solved for as:

$$density_{identified} = N_{packs-verified} \div ecoregion_{area} \times 1000$$

Finally, we subset the mechanistic model's estimated $territory_{size}$ to the $Density_T$ matching the $density_{identified}$ per ecoregion, per year. This provided $territory_{size\text{-}distribution}$, 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.

Table 1.6. Density identifier model results. Ecoregions refer to codes on Fig. 1.3.

Coefficients:	Estimate	SE	Pr(>|t|)
Intercept	-6.849	3.998	0.092
$area_{occupied}$	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
$area_{occupied}$ × IBE	-0.003	0.003	0.294
$area_{occupied}$ × MRE	-0.001	0.000	0.012
$area_{occupied}$ × NRE	0.000	0.000	0.416
$area_{occupied}$ × GLPE	-0.002	0.001	0.034
$area_{occupied}$ × GRPE	-0.003	0.001	<0.001

Importantly, the density identifier model provides a means to easily apply the mechanistic model beyond 2019. Even if minimum pack counts become unavailable or less accurate 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 account for observational uncertainty in the number of packs reported each year.

Pack size

We applied the predictive pack size model (Sect. 1.6) to each iPOM grid cell each year. We used the resulting mean and standard deviation estimated for each grid cell in each year to create gamma distributions that were spatially and temporally explicit estimates of pack size and its uncertainty. These distributions, $group_{size\text{-}distribution}$, informed abundance calculations during final steps.

Abundance estimates

We estimated numbers of packs and wolves for each year, 2007 – 2019, by combining predictions from the 3 models (Fig. 1.18). We calculated results at the state and MFWP regional levels. To do so, we calculated mean estimated occupancy ($\bar{\psi}$) across iPOM grid cells, then calculated area occupied ($area_{occupied}$) as:

$$area_{occupied} = \bar{\psi} \times \sum grid_{area}$$

where $\sum grid_{area}$ was the sum of grid cell areas. We calculated the number of estimated packs as:

$$N_{packs} = area_{occupied} \div territory_{size}$$

where values for $territory_{size}$ were drawn with replacement from $territory_{size\text{-}distribution}$ for each iteration of the MCMC chain. Values for $territory_{size}$ were therefore spatially explicit and biologically appropriate to the local conditions each year and accounted for uncertainty. We then calculated the number of estimated wolves as:

$$N_{wolves} = N_{packs} \times pack_{size} \times lone_{rate}$$

where $pack_{size}$ was drawn from $group_{size\text{-}distribution}$ and $lone_{rate}$ accounted for lone and dispersing wolves. For $pack_{size}$ we drew for each iteration of the MCMC chain a random value from $group_{size\text{-}distribution}$. This provided spatially explicit and biologically appropriate values for local conditions each year while incorporating model uncertainty about pack size. We modeled $lone_{rate}$ by drawing for each iteration of the MCMC chain values from a normal distribution assuming a mean of 1.125 and standard deviation of 0.025. This yielded a loner/disperser rate of 12.5% and incorporated variation and uncertainty around this rate, as 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 are comprised of lone or dispersing wolves (Fuller et al. 2003). This is consistent with Idaho's calculations for lone wolves (Holyan et al. 2013) and slightly more conservative than Minnesota's calculations, which add 15% (Erb et al. 2018).

To account for uncertainty and calculate credible intervals (CI's) for all parameters, we retained posterior estimates of 10,000 values for each and calculated the median value and 2.5% and 97.5% values (creating 95% CI's) for $area_{occupied}$, $territory_{size}$, $pack_{size}$, N_{packs}, and N_{wolves}. We calculated density of packs per 1000 km^2, wolves per 1000 km^2, and population growth (lambda, λ). We also calculated harvest rate as the annual number of wolves harvested divided by N_{wolves}. As with all harvested populations, harvest rate would appear somewhat lower if the annual population peak was used in the denominator; however, this peak cannot be known without data for all births, deaths, and dispersals.

We repeated these calculations for MFWP management regions by completing each step described above at each subsetted group of grid cells by region. Grid cells were categorized by the region in which the majority of their areas fell.

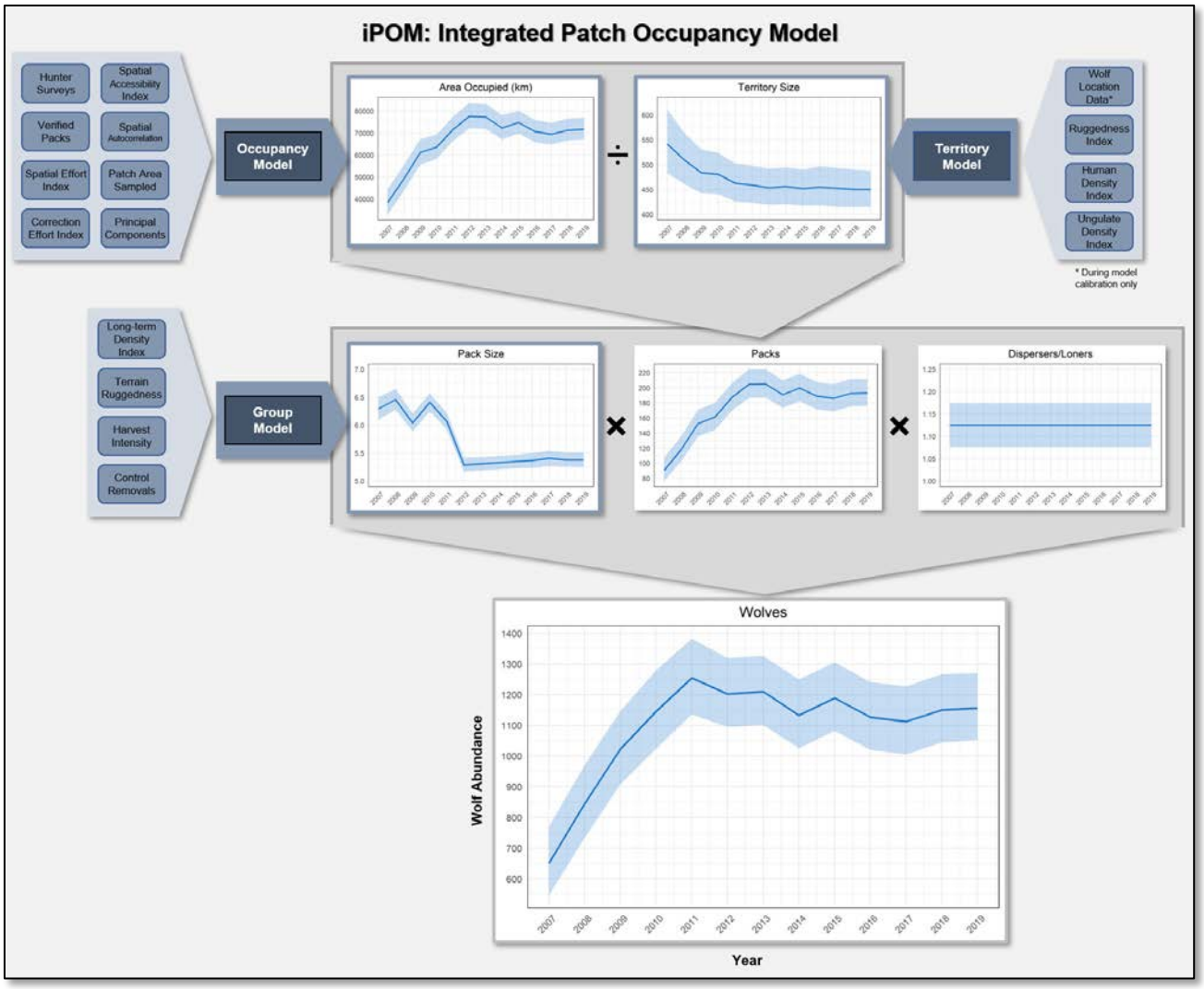

Figure 1.18. The iPOM approach combines 3 separate models to estimate the numbers of packs and wolves in Montana. Statewide estimates are shown.

Results

Each year (2007 – 2019), 50,026 – 82,375 hunters responded annually to the wolf sighting surveys. From their reported sightings, 1,064 – 3,469 locations of 2 – 25 wolves were mapped each year. Percent of hunters reporting a wolf sighting ranged from 4.5% (2017) to 7.5% (2011).

From 2007 – 2019, estimated area occupied by wolf packs in Montana ranged from 38,424 km^2 (95% CI = 33,041 – 44,642) in 2007 to 77,563 km^2 (95% CI = 72,209 – 83,739) in 2012 (Table 1.7). The estimated distribution of wolves from the occupancy model closely matched the distribution of field-confirmed wolf locations (verified pack locations and harvested wolves; e.g., Fig. 1.7).

Table 1.7. iPOM results, 2007 – 2019.

Year	Area Occupied	LCI Area Occupied	UCI Area Occupied	Packs	LCI Packs	UCI Packs	Wolves	LCI Wolves	UCI Wolves
2007	38424	33041	44642	91	76	107	650	547	771
2008	49264	43808	55574	118	103	136	845	734	970
2009	61148	55620	67198	153	136	171	1023	908	1147
2010	63594	58365	69332	161	145	180	1145	1024	1280
2011	71594	66458	77392	187	170	206	1254	1136	1383
2012	77563	72209	83739	205	187	224	1203	1095	1320
2013	77247	71901	83259	205	187	224	1210	1102	1326
2014	72244	67074	78056	191	173	210	1132	1026	1250
2015	74764	69780	80176	200	182	219	1189	1082	1306
2016	70674	65859	75914	189	172	208	1126	1020	1242
2017	69374	64824	74526	186	169	205	1113	1005	1227
2018	71218	66661	76574	193	175	211	1150	1045	1267
2019	71723	67183	76986	193	176	212	1156	1052	1270

Estimated territory size varied (Fig. 1.19). Considering grid cells likely occupied by packs (defined as $\psi \geq 0.5$), territory size was estimated to be largest in the 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 (Fig. 1.19). Considering only grid cells with $\psi \geq 0.5$, mean pack size was estimated to be similar across ecoregions (an approximate difference of < 1 wolf per pack in most years). Pack size was estimated to generally be slightly larger than average in the NRE, approximately equal to average in the CRE and MRE, and slightly smaller than average in the IBE. Pack sizes

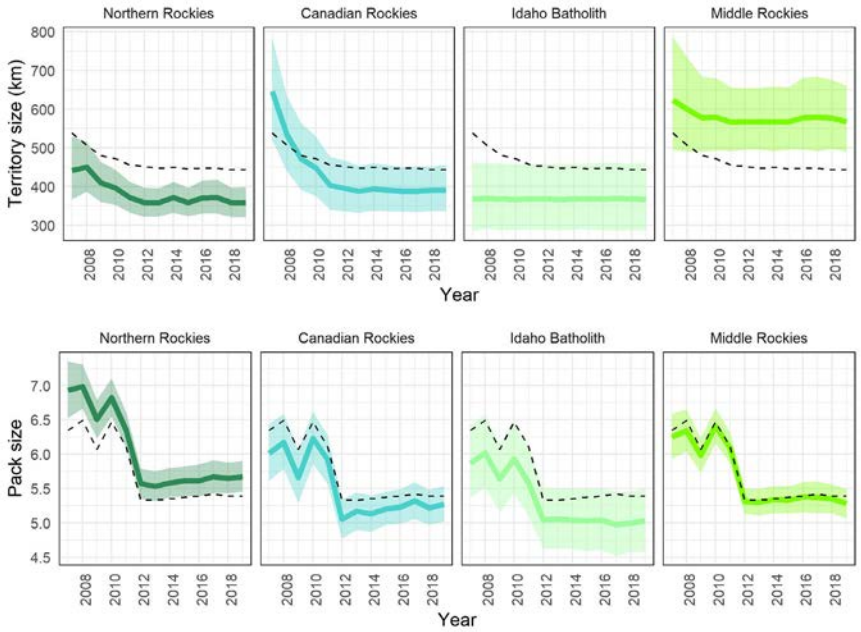

Figure 1.19. Estimated territory size and pack size in western Montana for cells with $\psi \geq 0.5$ (i.e., having higher likelihood of being occupied). Ribbons indicate 95% credible intervals. Dashed line is the overall mean for western Montana. (Eastern Montana ecoregions were estimated to have few packs each year and are not shown.)

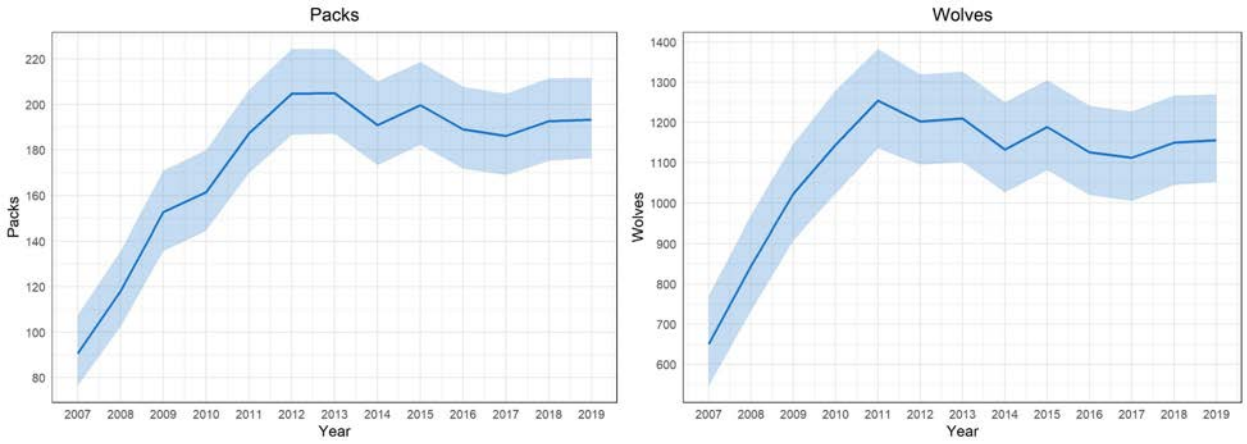

Figure 1.20. Estimated number of packs and wolves statewide, 2007 – 2019. Ribbons indicate 95% credible intervals.

were larger in the earlier years (prior to harvest) and have since declined by approximately 1 wolf per pack, on average.

Estimated numbers of packs and wolves varied through time (Fig. 1.20; Table 1.7). The population was estimated to have been smallest in the first year of our analysis (2007), with 91 packs (95% CI = 76 – 107) and 650 wolves (95% CI = 547 – 771). Population growth was positive through 2011 (Fig. 1.21). A peak in total wolves appears that year, with a high of 187 packs (95% CI = 170 – 206) and 1254 wolves (95% CI = 1136 – 1383). This 2011 peak coincided with the first years of harvest management in Montana, after which the population declined by 7.8% in total wolf abundance between 2011 and 2019.

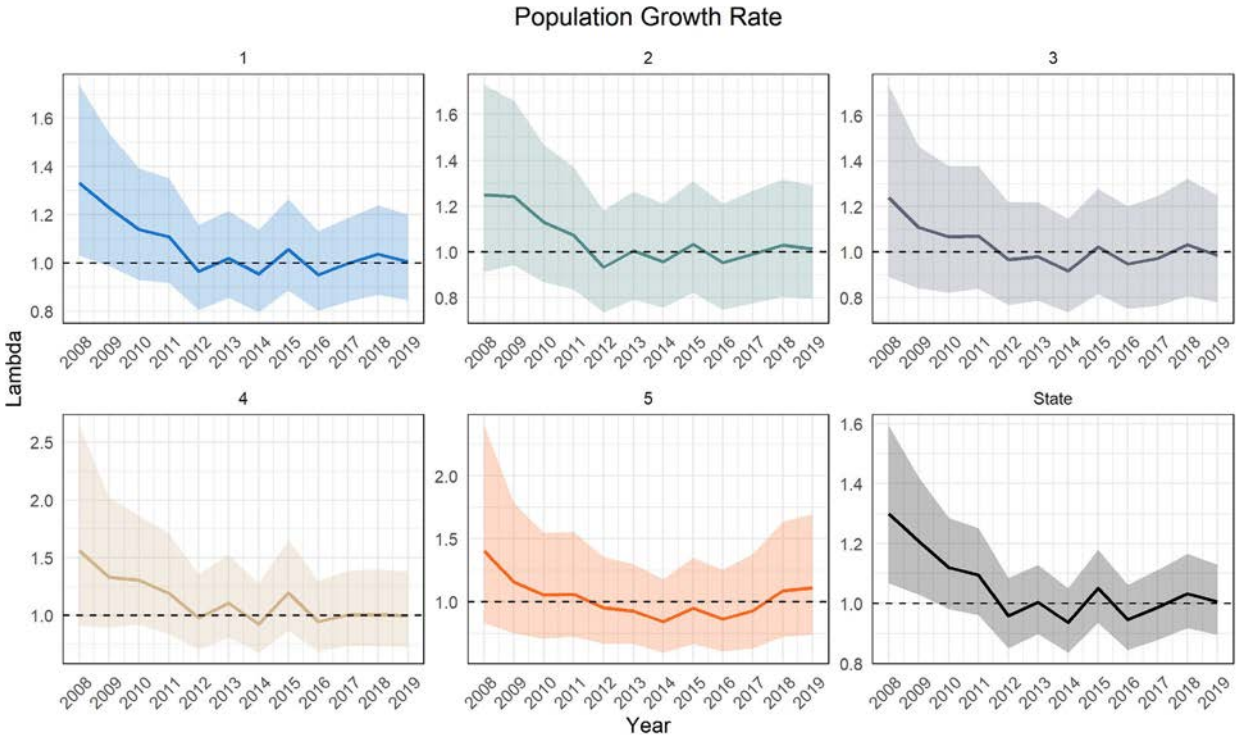

Figure 1.21. Population growth rate varied over time and space. Facets show lambda by MFWP region (regions 1 – 5) and the full state ($\lambda > 1.0$ = increasing population, < 1.0 = decreasing population.

λ alternated from slightly >1.0 to slightly <1.0 (positive and negative growth rates, respectively) during this time. From 2016 – 2019, the population appears to have become somewhat stabilized with an average of 190 packs and 1136 wolves per year. This was despite a harvest rate estimated at >20% per year over this same period (Fig. 1.22).

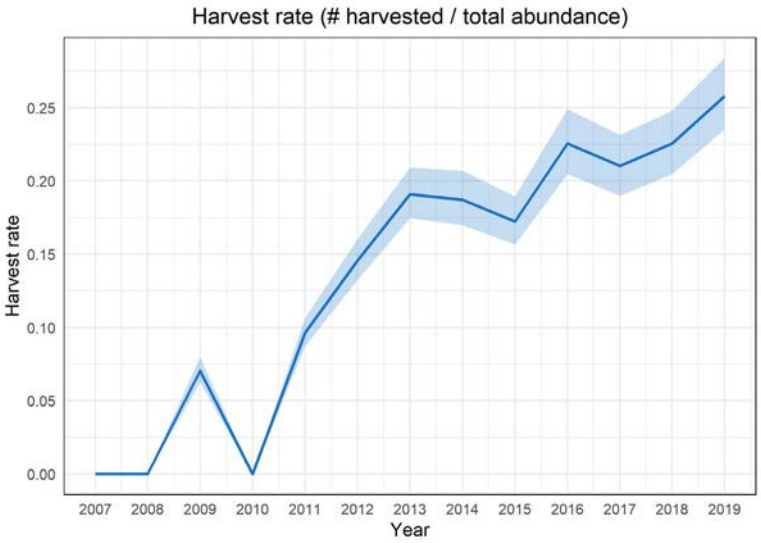

Figure 1.22. Estimated statewide harvest rate, 2007 – 2019. Ribbons indicate 95% credible intervals.

The estimated numbers of packs and wolves varied spatially (Fig. 1.23). Pack and wolf abundances were consistently greater in MFWP Region 1 (which contains most of the NRE and CRE; Fig. 1.3). Annually from 2007 – 2019, 37 – 43% of packs in Montana were found in Region 1, which also contained an average of 41% of the wolf population (Fig. 1.24). The next most populous area was Region 2, with 24 – 26% of total packs and 26% of the wolf population. Region 3 contained 19 – 25% of packs and 21% of the wolf population. Regions 4 – 7 each contained only ≤ 1 – 9% of packs and 1 – 7% of wolves. As the number of packs and wolves changed through time (Fig. 1.23), 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 (Fig. 1.24).

Wolf densities varied over space and time (Fig. 1.25; Appendix A). Densities were estimated to be greatest in MFWP Region 1 (ranging 6.41 – 13.30 wolves per 1000 km^2 from 2007 – 2019), followed by Region 2 (6.62 – 12.44) and Region 3 (3.23 – 5.06). Regions 4 – 7 had ≤ 1.42 wolves per 1000 km^2. Regions 1 and 2 saw the greatest increase in densities from 2007 through the population peak, with a

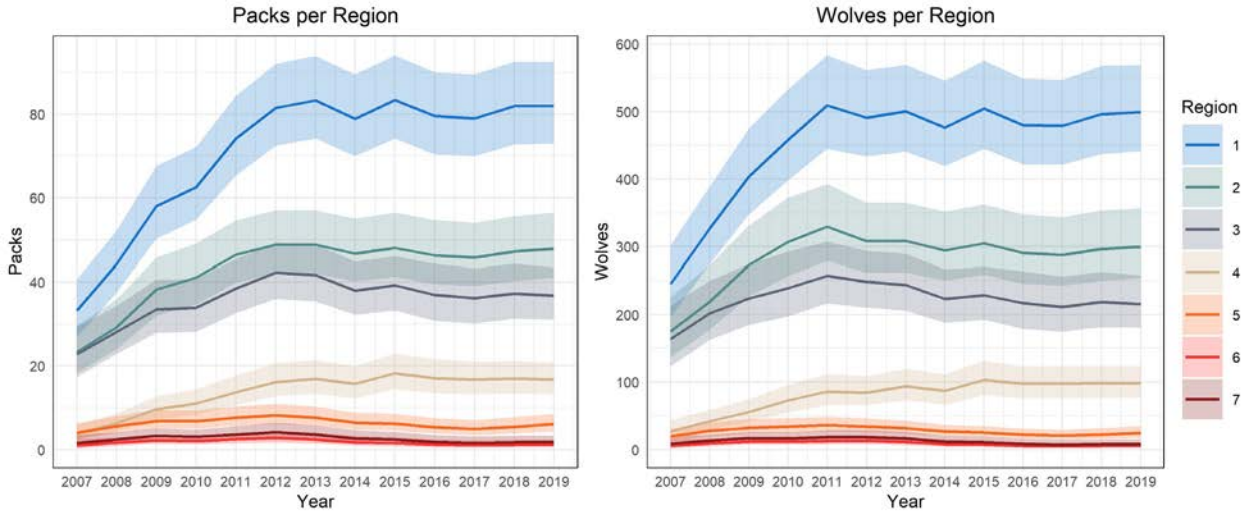

Figure 1.23. Estimated number of packs and wolves by MFWP region, 2007 – 2019. Ribbons indicate 95% credible intervals.

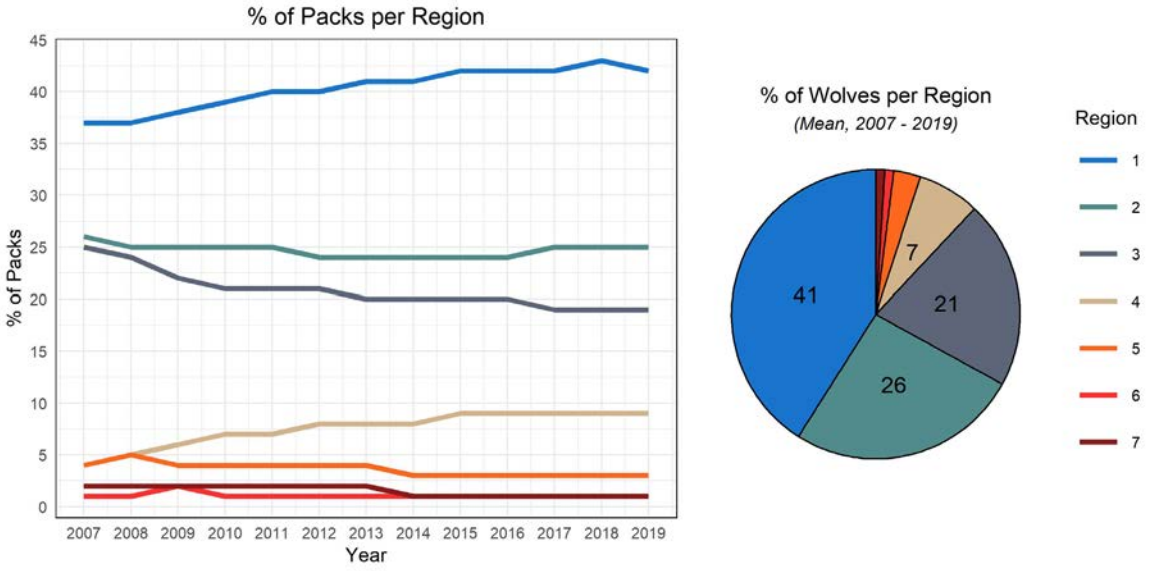

Figure 1.24. Proportion of packs estimated per MFWP region and year, and total mean % of wolves per region. (Annual % of wolves followed similar trends to that of packs shown in the left panel.)

smaller change in density in Region 3 and largely consistent densities in Regions 4 – 7. Annual maps of pack and wolf densities demonstrate close alignment between known packs, locations of wolf harvests, and predictions from iPOM (Appendix A).

Discussion

We developed a multi-model approach to estimate wolf abundance in Montana. This approach addresses important assumptions of original methods for estimating wolf abundance by incorporating an occupancy model (Miller et al. 2013; Rich et al. 2013; Inman et al. 2020) and biologically-based models for territory and pack size (Sells et al. *in press*; Sells et al. *in review a, b*). Although monitoring has been a central component to Montana's wolf recovery efforts for > 3 decades, it became increasingly challenging as wolf populations grew and limitations in staff time and funding were reached. In contrast, our models for territory and group size provided accurate estimates with limited data. This reduces monitoring needs while providing more accurate abundance estimates founded on biology and behavior of wolves. (A recommended monitoring program is provided in Section 4.)

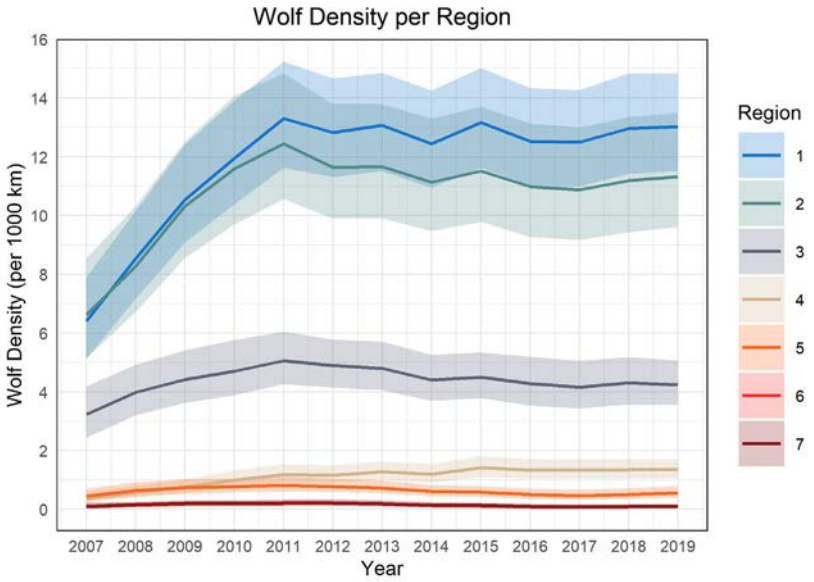

Figure 1.25. Wolf densities varied by region and year. Ribbons indicate 95% credible intervals.

Statewide estimates of abundance from iPOM were consistently greater than numbers reported from monitoring, as expected given that monitoring provided only minimum counts (Fig. 1.26). iPOM estimates were likewise greater than previous POM estimates. This was expected because POM assumed territory size was consistent over space and time, and this assumption was clearly violated (Sect. 1.3 – 1.4). POM also incorporated an overlap index in 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 spatiotemporally-specific estimates of territory and pack size (Fig. 1.27). In contrast, behavioral models informed iPOM to incorporate biologically appropriate estimates of territory and pack size at both statewide and finer spatial scales.

The ability to predict abundances at regional scales will enable managers to make decisions using the best available estimates for the local population. Regional estimates from iPOM demonstrate large variations in pack and wolf abundances across space and time (Figs. 1.23 – 1.25). These estimates align with the expectations of MFWP Wolf Specialists familiar with local pack dynamics. They also reveal how many packs may have been unverified each year. Generally, only a small number of additional packs were estimated to been excluded from verified minimums (Fig. 1.28). The largest differences occurred in Region 1 in recent years; this is attributable in part to a change in field personnel (Coltrane et al. 2015). This area has also received numerous public comments that the wolf population was higher than the annual minimum counts.

Because population dynamics are in constant flux, pack and wolf abundances will fluctuate through the year. Our estimates are thus approximate and expected to be closest to truth in the late fall and early winter (when hunter surveys and final monitoring efforts occur). Importantly for management decisions, not all estimated packs may have existed through each calendar year due to pack dissolutions or extirpations (e.g., arising from mortalities, competition among packs, etc.). Breeder mortalities may particularly influence pack dissolution (Brainerd et al. 2008) and these mortalities have likely increased under harvest. Large populations such as estimated in Montana in the past decade also likely experience intensive competition, which may cause greater pack turnover due to dynamic fluctuations in territory mosaics (Sells et al. *in review a*).

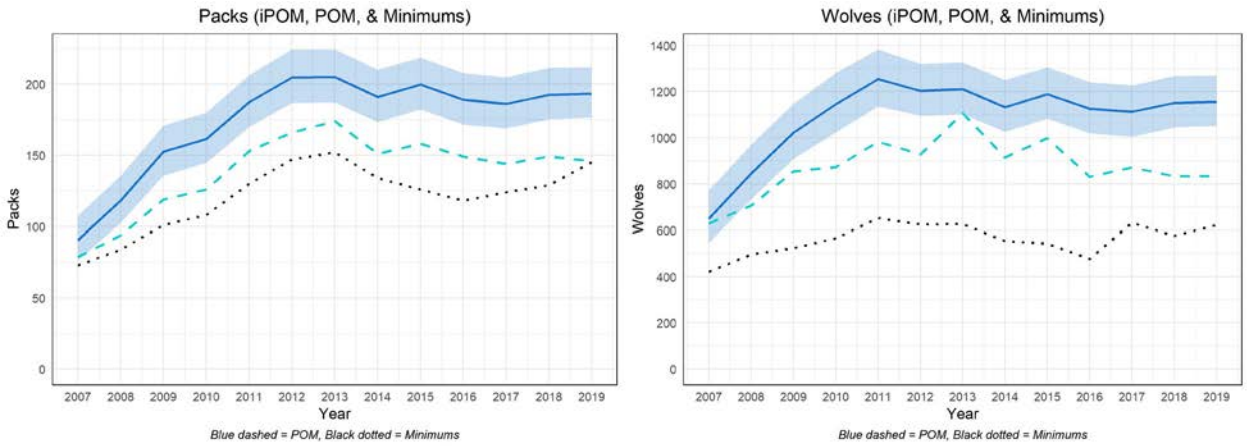

Figure 1.26. Estimated number of packs and wolves from iPOM versus previous POM estimates and minimum counts, 2007 – 2019. Ribbons indicate 95% credible intervals for iPOM.

Although the estimated area occupied doubled from 2007 to 2012, area occupied has largely stabilized since 2012 at slightly lower values from this peak. The extent to which this stabilization represents a population responding to density dependent factors versus hunting and trapping 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 (Sect. 1.2 – 1.4). Accordingly, the 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 (Sect. 1.5). Both features point to density dependence, but effects of harvest cannot be ruled out, particularly given that area occupied largely plateaued coincident with increased intensity of harvest. It also remains likely that human social tolerance has prevented the successful long-term expansion of wolves into central and eastern Montana, as new packs are often discovered and may be removed through harvest.

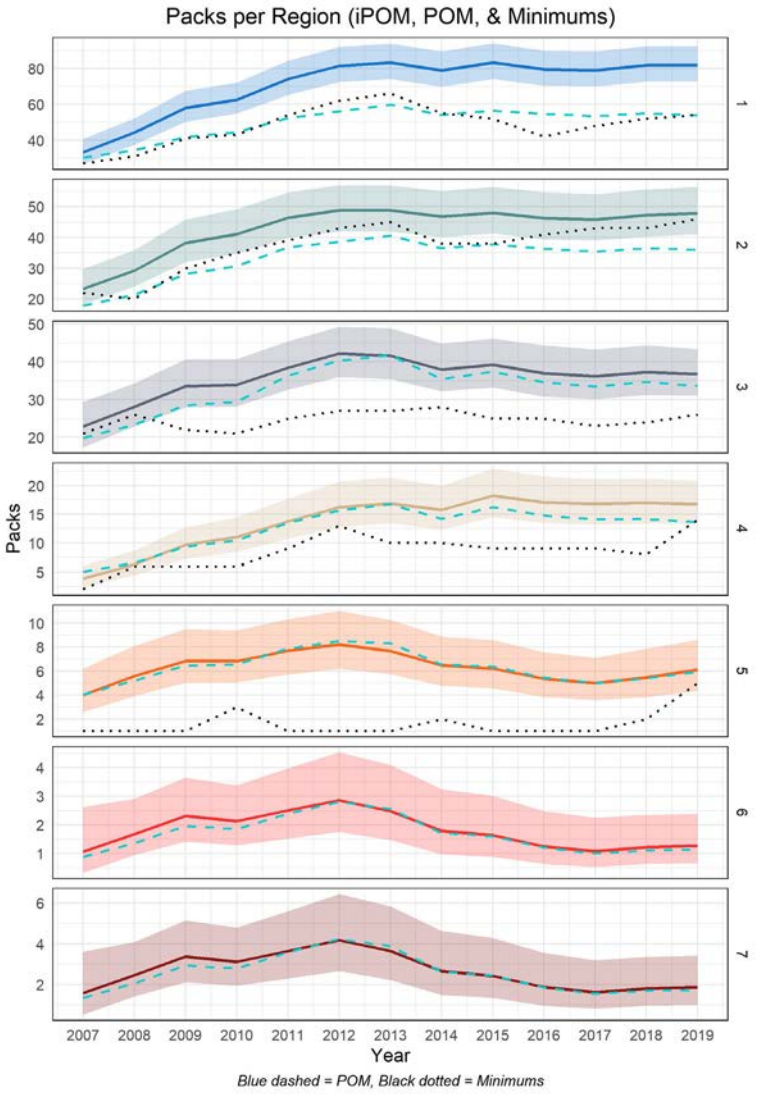

Figure 1.27. Estimated number of packs and wolves per MFWP region from iPOM versus previous POM and minimum counts. Ribbons indicate 95% credible intervals for iPOM. Based on what is known from minimum counts and expert knowledge of MFWP Wolf Specialists, POM appears to cause over- and under-counts relatively frequently. (E.g., any estimate < minimum counts is clearly underestimated.)

The occupancy model carries important assumptions. Grid cells are assumed to be independent such that the same wolves do not overlap multiple grid cells, and any movement into the cell is assumed to be equal to movement out of the cell. Although individual territories do not fall within grid cell boundaries, most territories are smaller than the cell areas (i.e., < 600 km^2). Furthermore, because the model employs territory centroids to help inform the true and false detections, the cell predicted to have the greatest occupancy contains the core of the territory. Future work might consider designing a new occupancy model with grid cells that vary in size according to the more localized territory size estimates.

Although hunter surveys could theoretically bias occupancy estimates given sufficient mistaken or falsified reports, there is limited evidence this occurs, and it is unlikely to affect results. The false

positives nature of the model accounts for these possibilities. Furthermore, 95% of hunters surveyed did not report seeing wolves, and suspect reports (e.g., >25 wolves sighted at one time) are rare and automatically omitted. Sightings furthermore align strongly with the distribution of wolves known from monitoring, with exception of sporadic reports in eastern Montana. 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 drive the estimates of abundance.

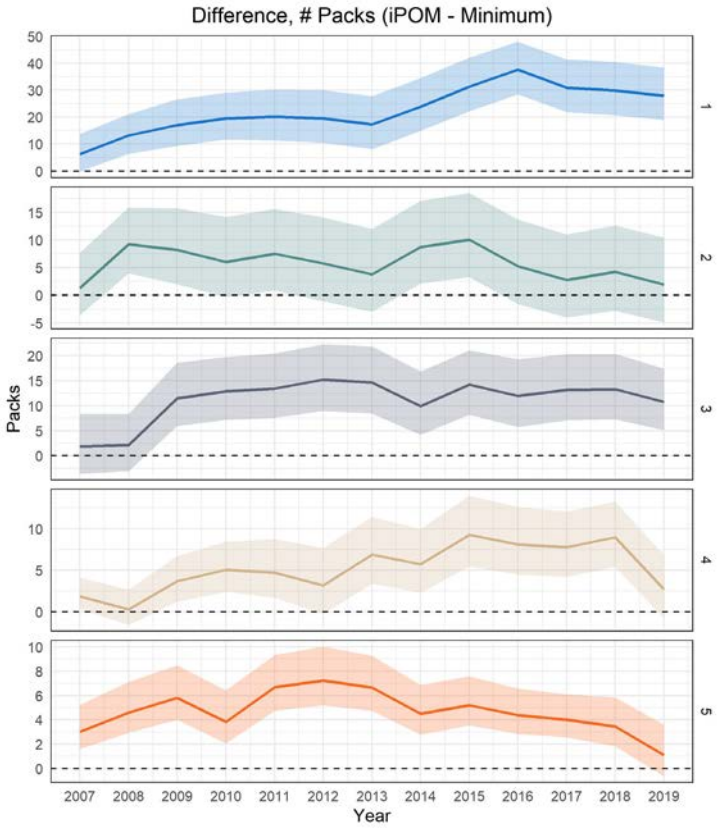

Figure 1.28. Difference in number of packs from iPOM versus minimum counts, 2007 – 2019. Difference of 0 would indicate all packs were identified and reported. Ribbons indicate 95% credible intervals.

The territory and pack size models also carry various assumptions (Sects. 1.2 – 1.6). As with POM, consistent bias in estimated territory or pack sizes would also bias results. Were territory size estimates biased low or pack size estimates biased high, the overall population 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, while others were underestimated). 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 easily biased estimates if these components were wrongly estimated.

To account for dispersing and lone wolves, iPOM includes a disperser/loner rate of 12.5% of the estimated number of wolves living in packs. This is consistent with POM and scientific literature (Fuller et al. 2003), and similar to methods used in other states (Holyan et al. 2013, Erb et al. 2018). In the future, models for dispersal and lone wolf rates could be incorporated into iPOM to improve this component. Such models would likely require intensive, expensive monitoring (e.g., collaring a high number of young wolves to obtain sufficient data during future dispersal). To date, such efforts have been infeasible given the difficulty of capture and high mortality and collar failure rates. iPOM can easily incorporate dispersal and lone wolf models in the future should they be successfully developed.

Our iPOM approach is unique among the various approaches taken to monitor wolves and estimate their abundance. Like Montana in early phases of recovery, intensive efforts may be employed 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 areas rely on models

designed to estimate population parameters from monitoring data. In Finland, e.g., winter track surveys are used to estimate the number of litters (Kojola et al. 2014). This estimation technique was effective in only some areas 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 all pairs, packs, and reproductions were detected. Scandinavia has also used open population spatial capture-recapture models to estimate recent and future abundance (Bischof et al. 2020). Such approaches appear highly 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 such models may be most conducive in small areas with concentrated field effort. 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 (Moeller et al. 2018; Loonam et al. 2020). Employing 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) and Wisconsin (Wiedenhoeft et al. 2020; https://dnr. wisconsin.gov/newsroom/release/38041) also use patch occupancy modeling-based estimation approaches. Neither state has incorporated 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.

SECTION 2: ESTIMATION OF RECRUITMENT

ABSTRACT Our objective was to develop methods to estimate recruitment in wolf packs in Montana. A model for estimating recruitment needed to produce accurate estimates and require less field data. We developed and tested an empirical model to estimate the number of pups recruited without recruitment data. Recruitment of wolves in Montana varied annually, and was negatively correlated with wolf abundance and harvest, and positively correlated with pack size. Future application of the recruitment model will require incorporation of the iPOM methodology; however, our model provides the foundation for estimating recruitment using collaring and pack count data.

Introduction

Recruitment (i.e., number of young produced that survive to an age at which they contribute to the population) affects population growth and may be influenced by intrinsic and extrinsic factors. Because each breeding pair of wolves produce an average of 4 – 6 pups per year, pups tend to be the largest age class in the population (Fuller et al. 2003). The number of non-breeding helpers influences recruitment in many species that cooperatively breed, including wolves (Solomon and French 1997; Courchamp et al. 2002, Stahler et al. 2013, Ausband et al. 2017). Population density may also affect recruitment (Gude et al. 2012, Stenglein et al. 2015*a*). Forest cover may be associated with greater recruitment because it is associated with occupancy of wolves (Rich et al. 2013, Bassing et al. 2019) and may serve as security cover (Llaneza et al. 2012). Winter severity may also affect recruitment by increasing the vulnerability of ungulates to predation by wolves (Huggard 1993, Post et al. 1999, Mech and Peterson 2003). Fluctuations in wolf populations have furthermore been linked to winter severity (Peterson 1974, Mech et al. 1998, Mech and Fieberg 2015). Harvest both directly and indirectly reduces recruitment, as well (Ausband et al. 2015, 2017*a*).

Estimating recruitment of wolves is difficult. To date, MFWP has documented recruitment using the number of breeding pairs (a male and female wolf with at least 2 surviving pups by December 31; U.S. Fish and Wildlife Service 1994). A breeding pair estimator (Mitchell et al. 2008) could be used to estimate breeding pairs but requires knowing pack size. Recruitment could alternatively be estimated by comparing den site counts to winter counts (Mech et al. 1998), marking pups at den sites (Mills et al. 2008), or using non-invasive genetic sampling (Ausband et al. 2015) at predicted rendezvous sites (Ausband et al. 2010). Each of these options are intensive, costly, and bound to be incomplete due to the large number of wolves in the population. Accordingly, a new model for estimating recruitment needed to produce accurate estimates and require less field data.

We developed an empirical recruitment model using the framework of an integrated population model. Integrated population models can be a useful tool for demographic analyses from limited datasets and can increase precision in estimates (Besbeas et al. 2002). These models generally use time-series count data to inform changes in abundance over time, mark-recapture data to inform survival, and survey data to inform recruitment (Abadi et al. 2010, Schaub and Abadi 2011). With this approach it is possible to estimate recruitment with only survival and count data because changes in abundance over time contain information on changes in vital rates.

We adapted the integrated population model to account for the social structure of wolves. Traditional integrated population models ignore social structure, which can greatly affect demography (Al-Khafaji et al. 2009). A wolf population is a collection of packs and packs are collections of individuals. Within a pack, wolves can survive, disperse, or be recruited. Packs can dissolve and new packs can form. The processes that occur within a pack (e.g., dispersal) can affect the processes that occur among packs (e.g., pack formation).

We used the model to evaluate how recruitment in wolves varied across Montana. We tested hypotheses that variation in recruitment was driven by intrinsic versus extrinsic factors. For intrinsic factors, we expected recruitment would 1) increase with pack size given the importance of non-breeding helpers (Ausband et al. 2017, Ausband 2018); and 2) decline with population size because conspecific aggression can negatively affect survival (Cubaynes et al. 2014). We alternatively hypothesized that extrinsic factors drive variation in recruitment. We expected that recruitment would 3) increase with forest cover given its association with wolf occupancy and security cover (Llaneza et al. 2012, Rich et al. 2013, Bassing et al. 2019); 4) increase with prey abundance and winter severity by increasing the vulnerability of ungulates (Huggard 1993, Post et al. 1999, Mech and Peterson 2003); 5) decrease with harvest via direct and indirect effects on survival (Ausband et al. 2015, 2017*a*); and 6) decrease with low-use road density given the increased access such roads provide to hunters and trappers (Person and Russell 2008).

Methods

To account for social structure of wolves, we modeled the processes that occur both within and among packs (Fig. 2.1). We used 1) estimates of abundance from POM to inform changes in abundance over time, 2) estimates of colonization and extinction from POM to inform group formation and extinction, 3) group counts from monitoring to inform changes in pack size over time, 4) GPS and VHF collar data to estimate survival, and 5) data from the literature to model dispersal (Jimenez et al. 2017). As our study was concurrent with Project 1 (Objective 1), we used POM rather than the new iPOM approach and its resulting estimates. We ignored adoption of individuals into the pack because we assumed it was rare. We estimated survival using a discrete-time proportional hazards model with a complementary log-log (cloglog) link function. We used 4 discrete periods for survival analyses: the denning period (April – May), rendezvous period (June – August), the hunting-only period (September – November), and the hunting/trapping period (December – March). GPS and VHF collared adult wolves from 2007 – 2018 provided the

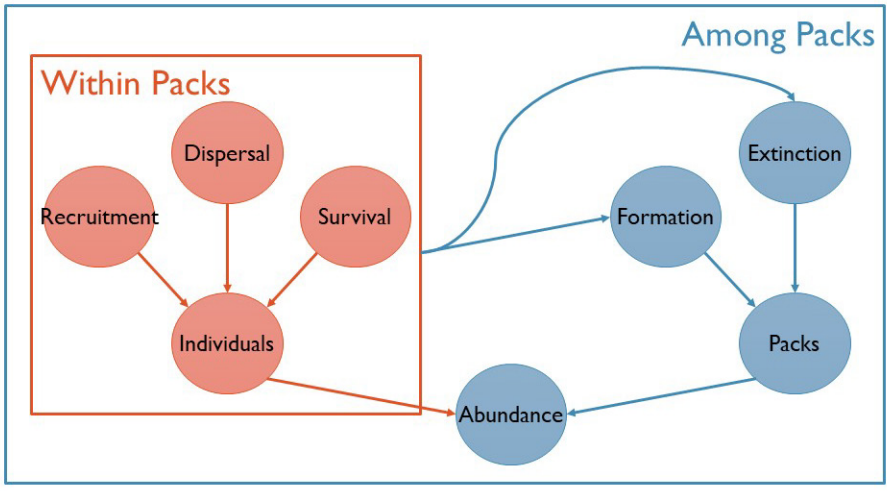

Figure 2.1. The recruitment model accounts for the hierarchy of demography in wolf population dynamics. Blue circles represent processes that occur among packs and red circles represent processes that occur within packs.

known-fate data to estimate survival. We did not include wolves that were removed for livestock depredation as these have inherent sampling bias. Recruitment was the only parameter without data and could therefore be estimated. We modeled recruitment as the number of pups per pack using generalized linear models with a log link function. The linear predictor could then be described using covariates to test hypotheses about factors influencing recruitment. We included a random year effect on survival to account for yearly variation.

Table 2.1. Model selection results and # of parameters (K) from integrated population models to estimate wolf recruitment from 2007-2018. Lower deviance suggests more model support, and we considered those within a standard deviation (SD) of the top model to have support. Explanatory variables included intrinsic factors (population and pack size) and extrinsic factors related to risk of mortality (harvest, forest cover, 4WD and 2WD road density) or prey availability (average daily snow depth and elk catch-per-unit-effort).

Model	K	Deviance	SD
$\gamma \sim Population\ Size + \varepsilon_{Year}$	3	998	300.7
$\gamma \sim Harvest + \varepsilon_{Year}$	3	1000	313.3
$\gamma \sim Pack\ Size + \varepsilon_{Year}$	3	1200	433.3
$\gamma \sim Forest + \varepsilon_{Year}$	3	1484	314.2
$\gamma \sim 4WD + 2WD + \varepsilon_{Year}$	4	1964	309.1
$\gamma \sim Snow + Elk + \varepsilon_{Year}$[a]	4	2013.9	384.4

[a] Failed to converge; coefficient values not included in results.

We used the recruitment model to estimate and evaluate variation in recruitment of wolves in Montana. For intrinsic factors, we used pack sizes reported by MFWP Wolf Specialists and the estimated population size. We retained good and moderate quality pack size observations (Inman et al. 2019). For extrinsic factors, we first buffered pack centroids by 600 km^2, representing the average territory size of wolves assumed under POM (Rich et al. 2012, 2013). We calculated the proportion of the buffer covered by forest using ArcGIS (ESRI 2011) and data from the Gap Analysis Project (Wildlife Spatial Analysis Lab, University of Montana). We also classified low-use road density as either 4-wheel-drive or 2-wheel-drive roads in areas with ≤ 25 people/km^2 (Rich et al. 2013, Montana Fish Wildlife and Parks 2018) and calculated road density within the buffer. Data for forest cover and road density were from 2013, and we assumed this varied little over time. We used winter severity and catch-per-unit-effort (CPUE) of antlered elk as an index of prey abundance (Lancia et al. 1996). For winter severity we used the average daily snow depth for the water year (October 1 – September 30) from SNOTEL (https://www.wcc.nrcs.usda.gov/snow/). We estimated CPUE for elk in each administrative region as the number of harvested antlered elk divided by the number of hunter days using harvest statistics from MFWP (fwp.mt.gov). Harvest was a binary variable (1 in years with harvest and 0 in years without harvest).

Two candidate models represented the intrinsic hypothesis, and 4 candidate models represented the extrinsic hypothesis (Table 2.1). Each model also included a random effect of year to account for temporal variation. We used Markov chain Monte Carlo (MCMC; Brooks 2003) methods in a Bayesian framework to fit the model using program R 3.4.1 (R Core Team 2020) and package R2Jags (Su and Yajima 2015) that calls on program JAGS 4.2.0 (Plummer 2003). We ran 3 chains for 300,000 iterations, discarded the first 50,000 iterations as a burn-in period, and used a thinning rate of 3. We ran an additional 100,000 iterations until convergence was reached or a maximum of 500,000 additional iterations. We monitored convergence using visual inspection of the MCMC chains and the Gelman-Rubin diagnostic (Gelman and Rubin 1992). Model selection was based on posterior deviance. All results are presented with mean and 95% credible intervals unless otherwise specified.

Results

Table 2.2. Mean coefficient estimates (95% CRI) of covariate effects on recruitment to 5 and 17 months of age for wolves in Montana (2007-2018).

Coefficient	5 months	Pr	17 months	Pr
Harvest	0.06 (-0.309 – 0.464)	0.62	-0.48 (-1.490 – 0.098)	0.91
2WD road density	-0.07 (-0.287 – 0.141)	0.70	0.01 (-0.747 – 0.356)	0.67
4WD road density	0.01 (-0.086 – 0.098)	0.65	-0.26 (-0.778 – 0.038)	0.95
Forest cover	0.10 (-0.076 – 0.227)	0.92	-0.41 (-0.709 – -0.055)	0.98
Abundance	0.001 (-0.002 – 0.001)	0.68	-0.003 (-0.006 – 0.000)	0.97
Pack size	0.06 (0.043 – 0.072)	1.00	-0.02 (-0.644 – 0.516)	0.48

From 2007 – 2018, 163 adult wolves were collared (95 females and 68 males, 19 – 47 collars per year). Of these wolves, 81 had an unknown fate and were censored the period of their last known location. Mortality sources for the remaining 82 wolves included legal harvest (n=31), control removals (n=21), poaching (n=9), other human-caused mortality (e.g., vehicle collision or livestock conflicts; n=3), non-human mortality (e.g., natural mortality or conspecific aggression; n=6), and unknown cause of mortality (n=7).

We excluded 358 group count observations (24.8%) classified as poor quality. The final dataset included 816 observations from 2007 – 2018. The mean observations per year was 68 (SD=21.8, range 27 – 102). On average, each pack had 4.5 observations (SD=2.48).

The model with the lowest mean deviance included a density-dependent effect on recruitment (Table 2.1). There was a 0.97 probability of a negative correlation between population size and recruitment rate to 17 months (Table 2.2). There was a 2.5% (0 – 5.92%) decline in recruitment with a 10% increase in

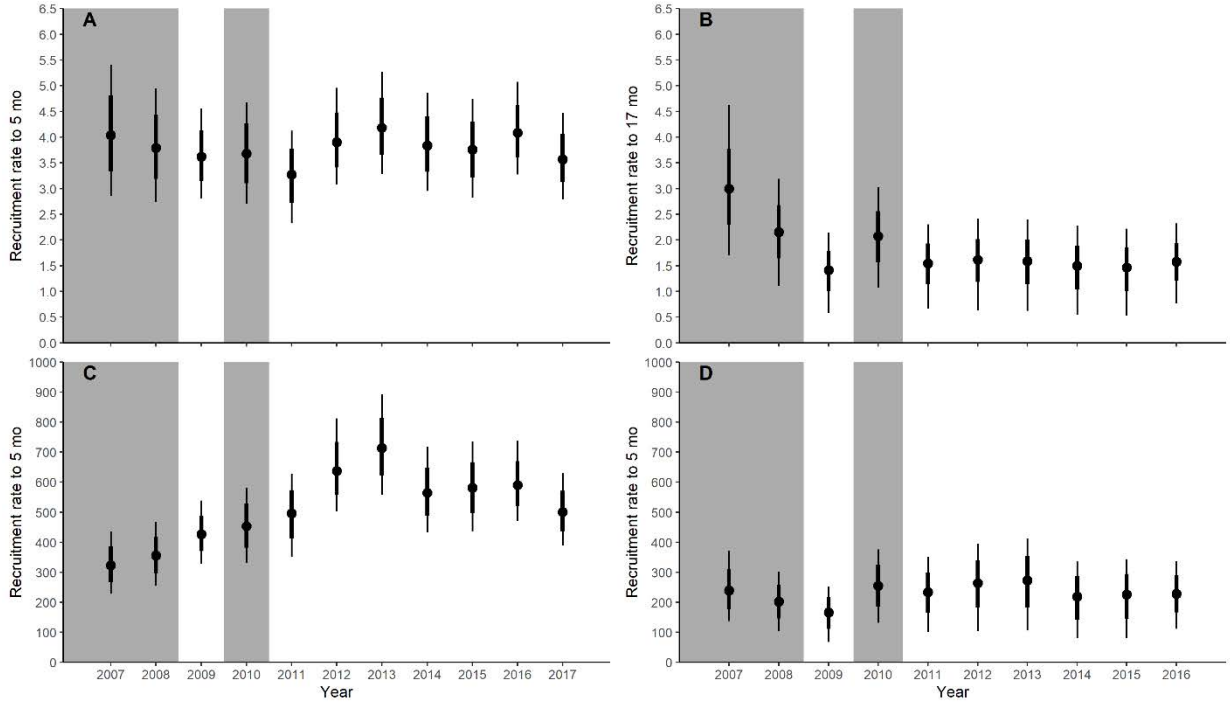

Figure 2.2. Estimates of recruitment rate (A, B; mean # of pups per pack) and total # of pups recruited (C, D) for wolves in Montana to 5 (A, C) and 17 months of age (B, D). Line widths represent the 66% and 95% CRI. Shaded areas represent years in which wolves were protected under the Endangered Species Act and not harvested.

population size. The effect of population size on recruitment rate to 5 months was positive, however this relationship was uncertain (Table 2.2). Two competing models within the standard deviation of the top model included 1) harvest and 2) pack size (Table 2.1). We found a 0.91 probability that harvest was correlated with decreased recruitment to 17 months. Recruitment decreased by 49% (149% decrease – 9.8% increase) in years with harvest (Table 2.2). The correlation between harvest and recruitment to 5 months of age was positive; however, the relationship was uncertain. Pack size had a positive effect on recruitment to 5 months of age. For each additional wolf added to the pack, recruitment rate to 5 months of age increased by 6% (4.4 – 7.5%). The relationship between recruitment rate to 17 months and pack size was uncertain.

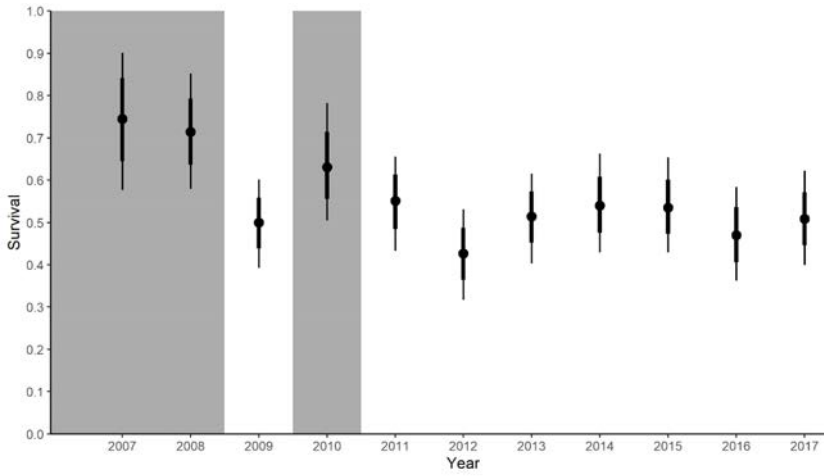

Figure 2.3. Estimates of annual survival rate and 66% and 95% credible intervals of adult wolves. Shaded areas represent years in which wolves were protected under the Endangered Species Act and not harvested.

Recruitment rate of pups to 5 months of age and to 17 months of age varied little across years. Mean recruitment rate to 5 months of age ranged from 3.25 (2.32 – 4.13) to 4.21 (3.28 – 5.26) wolves per pack whereas mean recruitment rate to 17 months of age ranged from 1.40 (0.57 – 2.15) to 3.06 (1.70 – 4.63; Fig. 2.2) wolves per pack. During years without harvest, mean recruitment rate to 5 and 17 months of age was 3.86 (2.92 – 4.82) and 2.57 (2.14 – 3.48) wolves per pack, respectively. During years with harvest, however, mean recruitment rate to 5 and 17 months of age was 3.80 (3.14 – 4.55) and 1.51 (0.76 – 2.13) wolves per pack, respectively. Mean annual total number of pups recruited to 5 and 17 months was 516 (389 – 653) and 229 (103 – 347), respectively (Fig. 2.2).

Adult survival rates varied annually, and were greatest during years without harvest (0.70, 0.585 – 0.814) than years with harvest (0.50, 0.434 – 0.555; Fig. 2.3). The biological period with the greatest survival rate, based on non-overlapping CRIs, was the denning period (April – May; 0.99, 0.972 – 0.998) and rendezvous period (June – August; 0.91, 0.868 – 0.947), whereas survival for the hunting-only period (September – November; 0.78, 0.745 – 0.807) and the hunting and trapping period (December – March; 0.77, 0.701 – 0.833) were similar. The greatest difference in survival by period during years with and without harvest, based on non-overlapping CRIs, was during the hunting and trapping period. Survival during the hunting and trapping period for years with harvest was 0.74 (0.660 – 0.814) compared to 0.86 (0.786 – 0.919) during years without harvest.

Discussion

Using available data from monitoring of wolves in Montana from 2007 – 2018, we found that recruitment was primarily affected by intrinsic factors. Both abundance and pack size appeared to affect recruitment, suggesting density dependent effects of population size and pack size; however, these processes had

opposite effects. Abundance had a negative correlation with recruitment to 17 months of age, suggesting a negative density dependent effect. Pack size had a positive correlation with recruitment of pups to 5 months of age and indicates positive density dependence within a pack.

The evidence that recruitment to 17 months is density dependent suggests that wolves may have saturated available habitat (Oakleaf et al. 2006) and reached some carrying capacity, whether biological or social (i.e., human tolerance; Murray et al. 2010). Density dependence in recruitment could be due to decreasing per capita food availability affecting pup survival, litter size, or both (Boertje and Stephenson 1992, Sidorovich et al. 2007). We found no support for a negative effect of abundance on recruitment to 5 months of age (Table 2.2), suggesting that density dependence may not influence litter size or neonatal pup survival in our study. This suggests that food availability, at least through September, may not be limiting. Instead, as the population grew and prime habitat became saturated, wolves may have expanded into marginal habitat with more human activity, potentially resulting in density dependence in survival and recruitment to 17 months (Fig. 2.2). Gude et al (2012) and Stenglein et al. (2015*a*) also found negative density dependence in recruitment of wolves in the Northern Rockies and Wisconsin, respectively.

The evidence that presence of non-breeding helpers increases recruitment to 5 months (i.e., positive density dependence with pack size) corroborates findings of increased survival and recruitment of pups with increasing pack size in wolves (Ausband et al. 2017) and other species that cooperatively breed (Koenig 1995, Solomon and French 1997, Courchamp and Macdonald 2001, Courchamp et al. 2002). By helping guard and provision pups (Ausband et al. 2016), non-breeders may increase pup survival and recruitment. Alternatively, the increase in recruitment with group size could be due to increased production of pups instead of survival. Typically, only the breeding pair reproduces, but increases in both pack size and abundance are positively correlated with multiple breeding females in a pack (Ausband 2018). Therefore, increased recruitment in larger packs could be a result of multiple breeding females and larger litter sizes per pack.

Our results suggest that the benefit of larger packs for recruitment to 5 months did not translate to higher recruitment to 17 months. After 5 months of age, pups begin moving with the pack and are less dependent on care from adults (Fuller et al. 2003, Mech and Boitani 2003). Additionally, harvest mortality occurs after pups are 5 months old, and any increase in recruitment to 5 months old in larger packs may be negated by harvest mortality.

Although we did not find evidence of negative density dependence within groups, we only tested for a monotonic relationship, and both positive and negative density dependence may occur (Creel and Creel 1995, Bateman et al. 2012, Stenglein et al. 2015*a*). There could be a threshold beyond which increasing pack size results in decreased recruitment. In African wild dogs (*Lycaon pictus*), the per capita food intake adjusted for costs was greatest at intermediate pack sizes (Creel and Creel 1995), and less food available per individual could negatively affect recruitment of offspring.

We found support for our hypothesis that harvest negatively affected recruitment. The probability that harvest reduced 17-month recruitment was 0.91, but this relationship was uncertain (95% credible intervals contained zero). Uncertainty in the estimated coefficient for harvest is also likely an artifact of our binary variable for harvest (i.e., years with and without harvest). Recruitment rate to 17 months

included survival through the harvest season, therefore we could not account for variation in harvest rate. Harvest rates varied annually and spatially. We attempted to account for spatial variation in risk of harvest using increased road density as an index to increased risk. Roads provide easy access for hunters and have been correlated with increased risk of mortality (Person and Russell 2008, Stenglein et al. 2015*b*). Our results suggest that this increased risk of mortality also translated to reduced recruitment, however the negative correlation between 4-wheel-drive road density and recruitment to 17 months was uncertain (Table 2.2). Like Horne et al. (2019), we did not find an effect of harvest on recruitment to 5 months. This was unsurprising as recruitment to 5 months precedes the harvest season.

Our estimates of recruitment and survival were comparable to other studies for wolves. Recruitment estimates for wolves in Idaho averaged 3.2 and 1.6 pups per pack to 15 months without harvest and with harvest, respectively (Ausband et al. 2015). Our estimates of recruitment to 17 months of age were similar (2.57 and 1.51, without and with harvest). Recruitment of wolves in Idaho to 6 months was 4 (3.5 to 4.6) pups per pack, similar to our estimates of recruitment to 5 months during years with and without harvest (3.80 versus 3.86 pups per pack). Survival rate for wolves in the Northern Rockies prior to harvest implementation averaged 0.75 (Smith et al. 2010), slightly greater than we estimated during years without harvest (0.70, Fig. 2.3). Similarly, survival rate for wolves in an unharvested population in Wisconsin was 0.76 (Stenglein et al. 2015*a*). Survival rates for wolves in harvested populations in Yukon and Alaska averaged 0.56 and 0.59, respectively (Ballard et al. 1987, Hayes and Harestad 2000), similar to our estimates for Montana during years with harvest (0.50, Fig. 2.3). The greatest decline in survival was during the hunting and trapping period in years with harvest, suggesting that harvest has decreased survival in adult wolves in Montana; however, we did not explicitly test this.

Various model assumptions may have affected estimates of recruitment. We assumed that dispersal was constant across packs and consistent with past research. Wolves appear to disperse in response to competition for food resources and mating opportunities (Mech and Boitani 2003). Density dependence in dispersal with group size has also been observed in wolves (Hayes and Harestad 2000) and other group living species (Bateman et al. 2018, Woodroffe et al. 2019). Mean dispersal greater than we assumed would likely bias our recruitment estimates low, whereas mean dispersal less than we assumed would likely bias estimates high. We also omitted adoption of unrelated individuals into packs and assumed this did not affect pack dynamics; if untrue, our estimates of recruitment could be biased high. Adoption of non-breeding adults may be infrequent (Bassing 2017), however most male breeder vacancies in Idaho are filled by non-related males (Ausband et al. 2017). Because we assumed estimates of recruitment were predominately a result of pup production and survival, immigration into packs would also be included in those estimates, which would bias results. We also did not account for or evaluate the effects of disease (e.g., canine parvovirus, distemper, Mech and Goyal 1995, Mech et al. 2008), which can cause declines in pup recruitment and contribute to spatial and temporal variation in recruitment rate (Almberg et al. 2009).

Our estimates have the potential to be biased given that we omitted collared wolves killed via control actions because they represented a non-random sample. During this study, 10% (SD = 4.2%) of wolves were removed for control actions annually, and relatively more were removed during years without harvest (15%, SD = 2.1%) than during years with harvest (7%, SD = 1.8%). Therefore, our estimates of survival may be biased high, and, consequently, our estimates of recruitment may be biased low. This is likely a small effect because only 35% of packs had a control removal, and only 25% of packs had a

control removal during years with harvest. Additionally, we accounted for control removals by subtracting wolves removed from group count data in our model.

We used POM estimates of abundance, the number of packs, and pack growth rate (Inman et al. 2019). These estimates rely on assumptions of a constant average territory size and may be biased (Sect. 1). Future application of the recruitment model will necessitate integrating iPOM (Sect. 1.7) into the recruitment model structure.

SECTION 3: ADAPTIVE HARVEST MANAGEMENT FRAMEWORK

ABSTRACT: Management of large carnivore populations with harvest is contentious. Adaptive management incorporates scientific information and associated uncertainty in a transparent process that relates alternative management actions to explicit, quantifiable objectives to guide decision making. Through monitoring, uncertainty can be reduced over time to improve future decisions. Our objective was to conceptualize a decision tool for wolf management. We demonstrate how an AM framework explicitly incorporating uncertainty in estimates of harvest, biological and sociopolitical values, and quantitative objectives could guide decisions of harvest regulations of wolves.

Introduction

Balancing viable large carnivore populations with stakeholder needs is often challenging. Predation on livestock and competition for ungulates are a main source of conflict (Muhly and Musiani 2009, Laporte et al. 2010, Macdonald and Loveridge 2010, Treves et al. 2013). Livestock losses and non-lethal effects of carnivores on livestock have negative socioeconomic impacts (Muhly and Musiani 2009, Laporte et al. 2010), and disproportionately affect rural communities. Hunters may have concerns that carnivores will negatively affect ungulate populations and reduce opportunities for hunting (Ericsson and Heberlein 2003). Conversely, large carnivores can generate interest and revenues due to ecotourism (Tortato et al. 2017) or positive attitudes due to perceived ecosystem services and their role in wildlife communities (Ritchie et al. 2012, Treves et al. 2013).

Management of wolves in Montana is subject to many similar challenges. The Montana Wolf Conservation Strategy (MFWP 2002) requires a minimum of 15 breeding pairs (a male and female wolf with ≥ 2 pups that survive until December 31) and 150 wolves to have a regulated, public harvest season. Harvest has accordingly occurred since delisting in 2011; however, harvest decisions are challenging due to conflicting values and objectives from stakeholders, which include federal and state agencies, hunters, the general public, wildlife enthusiasts, and livestock producers. Surveys have shown that many Montanans feel that wolves negatively affect the economy, likely due to livestock losses and the perceived or realized loss of hunting revenues from decreased elk populations (Berry et al. 2016). Private landowners and ungulate hunters have more positive opinions and tolerance for wolf hunting and trapping (Lewis et al. 2012, 2018, Berry et al. 2016). Conversely, some Montanans feel wolves positively affect tourism (Berry et al. 2016), and visitors to Yellowstone consider wolves to be a top species to view (Duffield et al. 2006). Respondents to a general household survey of Montanans tended to agree that wolves help maintain balance in nature (Lewis et al. 2018), and a slightly greater percentage of Montanans had a positive opinion of wolves on the landscape than not (Berry et al. 2016 Lewis et al. 2018), though this was not true of private landowners or hunting license holders (Lewis et al. 2018).

Management of wolves through harvest is also challenging because managers cannot directly control harvest rates. Changes in harvest regulations do not necessarily change harvest rates (Bischof et al. 2012). Harvest rates can vary based on many factors, including weather, regulations, hunter and trapper effort and success, and prey availability (Kapfer and Potts 2012).

There is no consensus for how harvest affects wolves (Fuller et al. 2003, Adams et al. 2008, Creel and Rotella 2010, Gude et al. 2012). Harvest appears to be mostly an additive source of mortality for yearlings

and adults (Creel and Rotella 2010, Murray et al. 2010, Horne et al. 2019) and to reduce pup survival and recruitment (Ausband et al. 2015, 2017). However, wolf abundance has remained relatively stationary despite harvest rates estimated at 0.17 to 0.36 (Inman et al. 2019). This may be due to increased immigration into Montana or decreased dispersal (i.e., positive net immigration). Immigration and dispersal can be important processes in dynamics of wolf populations (Hayes and Harestad 2000, Fuller et al. 2003, Adams et al. 2008, Bassing 2017). It is unclear, however, whether net immigration occurs in Montana and if so, how it affects wolf population dynamics.

Structured decision making (SDM) can help managers address the conflicting objectives surrounding management of wolves. This value-focused approach provides a transparent process to relate objectives of management to alternative actions while accounting for uncertainty (Gregory and Keeney 2002, Gregory and Long 2009). MFWP developed objectives for wolf management in Montana during an SDM workshop in 2010 (Runge et al. 2013) and has used the objectives to guide management since then.

Adaptive management (AM) is a special case of SDM when decisions are iterated over time or space and outcomes uncertain. Because decisions are iterated, AM can be used to learn and reduce uncertainty to improve future decisions (Fig. 3.1). AM entails clearly defined objectives, alternative management actions, models to predict outcomes of actions, evaluation of tradeoffs, and a monitoring program to learn over time (Williams et al. 2009). Objectives help determine whether management was successful (McGowan et al. 2011, Conroy and Peterson 2013). Management actions are alternatives available to help meet objectives. Models are used to predict consequences or outcomes of different management actions. When there is uncertainty in how the system (e.g., population) functions, multiple models can represent competing hypotheses. These competing models each have a corresponding model weight, representing the support or confidence in each model. The decision model is then solved to select the management action that best meets objectives. After management is implemented, the change in system state is estimated via monitoring. Comparison of model predictions to monitoring data provides support for some models over others. When time to make a new decision, the new model weights and population size are incorporated to determine the optimal management action.

Given the multiple, conflicting objectives of wolf management, a decision model could evaluate how well different management actions (i.e., harvest regulations) meet objectives for wolf management. Our objective was to conceptualize a flexible decision tool for wolf management.

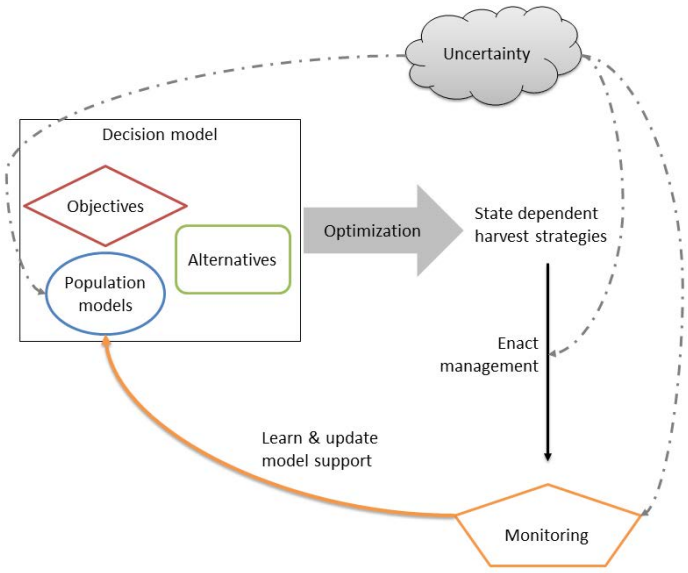

Figure 3.1. The adaptive management framework.

Methods

We developed a prototype AM framework to demonstrate how such an approach could guide decisions regarding harvest regulations for wolves in Montana (Keever 2020). Using objectives from a 2010 SDM workshop, we simulated AM. We used population models to

describe changes in abundance and formalized relationships between population size of wolves, recruitment, depredation events, impacts of wolves on ungulates, and the harvest regulations and management objectives. We considered alternative models of population dynamics, whereby Model 1 assumed net immigration of wolves into Montana was 0 and not partially compensating for harvest, and Model 2 assumed net immigration was positive and partially compensating for harvest. We used estimates from the literature to estimate livestock depredation events from wolf abundance (DeCesare et al. 2018) and public acceptance of wolf harvest (Lewis et al. 2012, 2018). We used stochastic dynamic programing (SDP; Bellman 1957, Williams et al. 2002), to determine optimal sequences of harvest regulation decisions.

Objectives and utility functions

We used the objectives previously deemed critical to the decision, as defined during the 2010 SDM workshop (Runge et al. 2013):

1) Reduce wolf impacts on ungulate (i.e., elk and deer) populations.
2) Reduce wolf impacts on livestock.
3) Maintain hunter opportunity for ungulates.
4) Maintain a viable and connected wolf population in Montana.
5) Maintain hunter opportunity for wolves.
6) Increase broad public acceptance of harvest and hunter opportunity as part of wolf conservation.
7) Maintain positive and effective working relationships with livestock producers, hunters, and other stakeholders.

A reward (or objective) function helps determine how well a management action meets multiple objectives (Conroy and Peterson 2013). We converted the values of each objective into a common scale using utilities that ranged 0 (worst) – 1 (best). We then combined the utility values into a single value that included the weights (relative importance) of each objective. We elicited utility functions and weights for objectives from MFWP representatives. We also determined their risk attitudes as either risk adverse, risk neutral, or risk tolerant. For the reward function, we combined utility values:

$$Reward = w_i U_i + \cdots w_I U_I$$

where w_i is the weight and U_i the utility value for objective i (Conroy and Peterson 2013). Weights for objectives were averaged from the responses by MFWP representatives (Table 3.1). We described the metrics, utility functions, and risk attitude for each objective below.

Reduce Impacts of Wolves on Ungulate Populations.— We measured the impact of wolves on ungulates using a scale from 0 (no impact) to 1 (wolves are reducing ungulate populations). Wolf impacts on ungulate populations in Montana vary greatly, even over short distances, for several reasons (Garrott et al. 2005, Hamlin et al. 2008). For simplicity, we assumed that the impact of wolves on ungulates was only a

Table 3.1. Objectives, measurable attributes, and objective weights (relative importance) for an adaptive management framework for gray wolves in Montana. Objectives were developed in 2010 as part of a structured decision making workshop (Runge et al. 2013) and weights were assigned by MFWP representatives which included supervisors, wildlife managers, and wolf specialists.

Objective	Measurable Attribute	Weight
Reduce wolf impacts on big game populations	Scale: 0 (no impact) – 1 (reducing populations)	0.246
Reduce wolf impacts on livestock	# depredation events/year	0.205
Maintain viable and connected wolf population	# wolves and pups recruited	0.255
Maintain hunter opportunity for wolves	# wolves, season length, bag limit	0.183
Increase acceptance of wolf harvest and opportunity	Percent Montanans satisfied with regulations	0.111

function of the statewide number of wolves. For application of this decision framework and tool, further work would be required to refine the spatial scale for decision-making related to this objective, refine the spatial scale for predicting wolf impacts on ungulate populations, or to translate statewide wolf population size to cumulative impacts on local ungulate herds. We assumed if there were no wolves, then there was no impact on ungulates (utility value of 1), and that an increase in the wolf population was associated with a greater impact on ungulates and lower utility values. We used a combination of value elicitation and function elicitation (Conroy and Peterson 2013) to determine the relationship between wolf population size and the impact on ungulates. The most frequently selected risk attitude was risk tolerant.

Reduce Impacts of Wolves on Livestock.— We measured wolf impacts on livestock (i.e., cattle and sheep) as number of depredation events. We estimated the events per year using the mean and variance of per-wolf depredation rates before and after harvest (DeCesare et al. 2018), multiplied by the statewide wolf population size. The frequency and number of wolf depredations on livestock are highly concentrated in certain areas within Montana (DeCesare et al. 2018), and the statewide per-wolf depredation rate masks this variation. To apply this decision framework, more work would be needed to refine the spatial scale for decision-making, refine the spatial scale for predicting the number of depredations, or to translate the statewide per-wolf depredation rate to depredation impacts in specific areas. We assumed that 0 depredation events had a utility value of 1 and an increase in the number of depredation events was associated with smaller utility values. MFWP representatives selected a risk tolerant attitude.

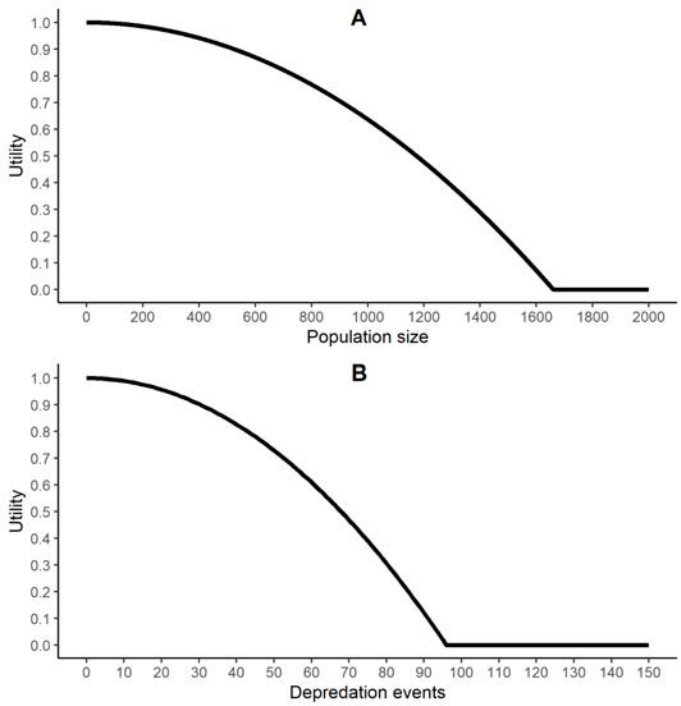

Figure 3.2. Utility functions representing the relationship between A) wolf population size and the utility for reducing impacts of wolves on ungulates, and B) the # of depredation events and the utility for reducing impacts of wolves on livestock.

Maintain Hunter Opportunity for Ungulates.— We assumed the main effect of wolves on ungulate hunter opportunity was through an impact on ungulate populations. Wolves likely

had little effect on other factors associated with maintaining hunter opportunity for ungulates, such as public access, and would likely not be influenced by decisions for wolf harvest regulations. Therefore, we assumed that reducing impacts of wolves on ungulates would maintain sufficient hunter opportunity.

Maintain Viable Wolf Population.— We measured maintaining a viable and connected wolf population by the number of wolves and pups recruited. We assumed that recruitment of < 150 wolves or 30 pups yielded 0 utility (i.e., a penalty function), and utility increased with increasing recruitment. We combined utilities by taking their product (Fig. 3.3). MFWP representatives were risk averse for abundance and risk neutral for recruitment.

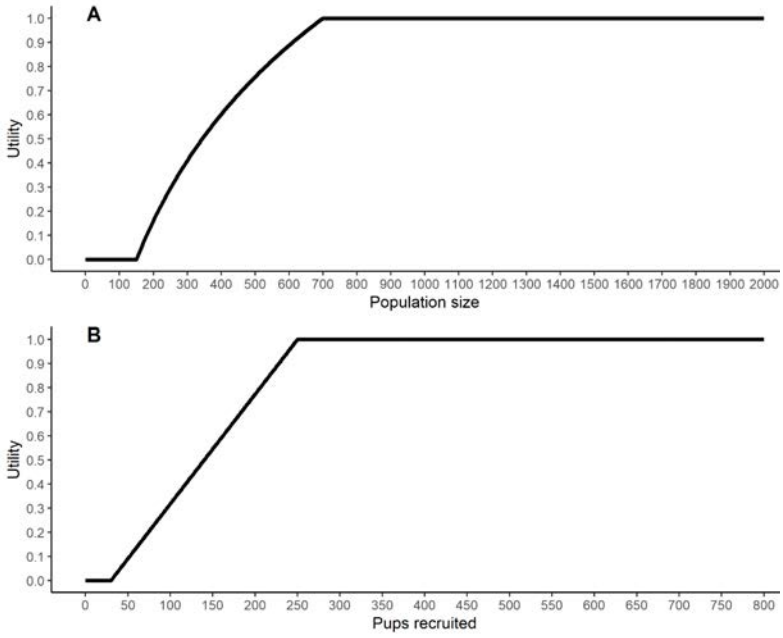

Figure 3.3. Utility functions representing the relationship between A) wolf population size and the utility for maintaining a viable wolf population, and B) the # of pups recruited and the utility for maintaining a viable wolf population.

Maintain Hunter Opportunity for Wolves.— We used the abundance of wolves, bag limit, and hunting and trapping season lengths as a metric for hunter opportunity for wolves. We assumed wolf numbers or recruitment rates below the required minimum yielded no hunter opportunity and a utility value of 0, whereas an increase in wolf abundance increased hunter opportunity (Fig. 3.4). MFWP representatives were risk tolerant and risk neutral for bag limit and season length, respectively. We multiplied utility values for abundance, bag limit, and season length together.

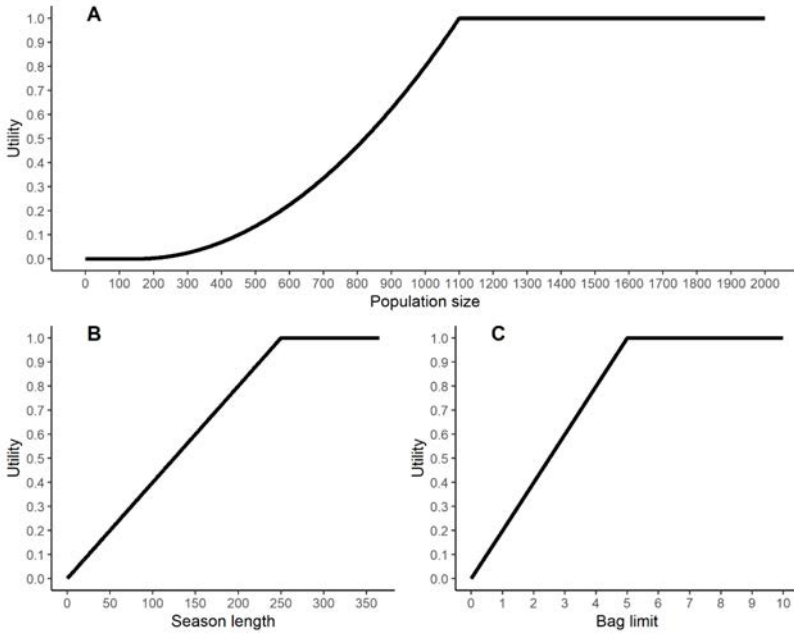

Figure 3.4. Utility functions representing the relationship between A) wolf population size, B) season length, and C) bag limit and the utility for maintaining hunting opportunity for wolves.

Increase Public Acceptance of Wolf Harvest.— We considered the

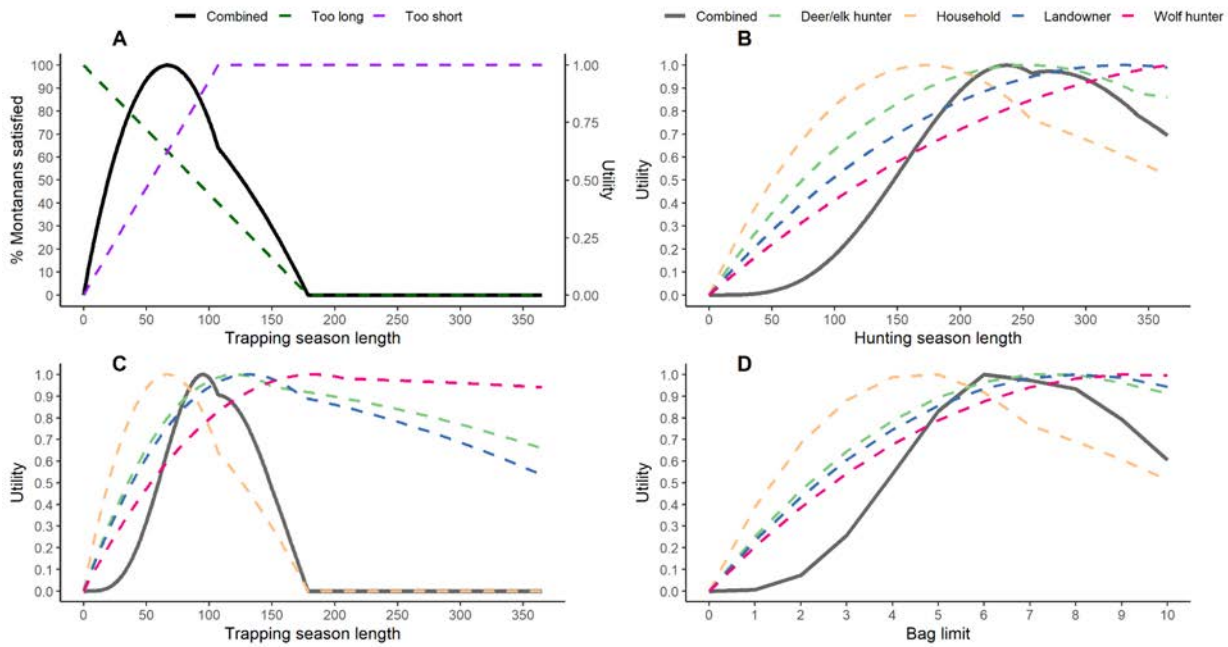

Figure 3.5. Utility functions representing the relationship between B) hunting season length, C) trapping season length, and D) bag limit and the utility for increasing acceptance of harvest and hunting opportunity for wolves. Figure A demonstrates how utility functions were created from the percent Montanans that thought the season was too long or too short.

percentage of Montanans satisfied with season length and bag limit as the metric for acceptance of wolf harvest. We used survey data to predict satisfaction (Lewis et al. 2012, 2018). Survey data were categorized as resident private landowners, resident wolf hunting license holders, resident deer/elk license holders, and general household. We developed utility functions for satisfaction with hunting season length, trapping season length, and bag limit separately for the 4 stakeholder groups. Survey data included the percent of respondents that thought the season or bag limit was too short/low (suggesting they would be more satisfied with a longer/greater season or bag limit and thus a positive relationship with season length or bag limit), and the percent that thought season or bag limit was too long/high (suggesting they would be more satisfied with a shorter/smaller season or bag limit and thus a decreasing line). We used these relationships to convert satisfaction into utility values for each respondent group. We assumed that if 0% of Montanans were satisfied with the regulations, the utility value was 0, and an increase in the percent satisfaction was associated with an increase in utility values. MFWP representatives were risk neutral.

For each regulation and stakeholder group, we combined utility values using the negative squared-error loss function (Williams and Kendall 2017). This balanced competing interests of respondents, as utility values increased with increasingly similar percentages of Montanans who thought the season was too long versus too short. We combined the utility values of the 4 survey groups for each regulation type using the weighted sum method with equal weights for each group. To combine the three regulation types into a final utility value for the objective (U_{Public}), we used a weighted sum with equal weights (Fig. 3.5):

$$U_{r,g} = -\left(U.short_{r,g} - U.long_{r,g}\right)^2$$

$$U_r = 0.25 * \left(U_{r,landower} + U_{r,wolf} + U_{r,deer} + U_{r,household}\right)$$

$$U_{Public} = 0.33 * \left(U_{bag} + U_{hunting} + U_{trapping}\right)$$

where $U.short$ and $U.long$ were the utility values for the percentage of respondents who said the season or bag limit was too short/low or too long/high, respectively. U was the utility value for hunting regulation r (bag limit, hunting season length, trapping season length) and survey group g (landowner, wolf license holder, deer/elk license holder, household).

Maintain Positive Working Relationships.— We did not consider a utility function for maintaining positive working relationships with stakeholders as we assumed that increasing acceptance of wolf harvest would also increase positive relationships with stakeholders. Maintaining positive working relationships may also require management actions beyond harvest regulations (e.g., public outreach).

Management actions

We considered 4 management actions consisting of different bag limits, hunting season lengths, and trapping season lengths:

1) *No harvest:* if the population fell below established minimums.
2) *Restricted:* bag limit of 1 (wolves/year), 2 weeks archery, 2 weeks firearm, 4 weeks trapping.
3) *Status quo:* bag limit of 5, 2 weeks archery, 26 weeks firearm, 11 weeks trapping.
4) *Liberal:* bag limit of 10, 2 weeks archery, 38 weeks firearm, 17 weeks trapping.

Actions 2 and 4 were created from the average responses of MFWP representatives for restricted and liberal management actions.

We predicted wolf harvest for each license-year (Keever 2020). We fitted negative binomial mixed-effects models of the relationship between number of wolves harvested and harvest regulations, social factors (e.g., hunting and trapping effort), and ecological factors (e.g., winter severity or wolf density). The top models for hunting included season length, method (archery or firearm), and type of season (i.e., archery, general, trapping, post-trapping). The top model for trapping was a function of trapping season length. We used the mean and standard deviation (SD) of the posterior predictive distribution in a normal distribution to draw values of the total wolves harvested for each year for each management action.

Models of population dynamics

We developed 2 per capita population models to estimate future population size and calculate the probability of transition from one system state to any other, given an action. We predicted future population size for the following year (i.e., annual time-step) as:

$$N.adult_t \sim Binomial(N_{t-1}, \phi_{t-1})$$
$$N.pup_t \sim Poisson(N_{t-1}\rho_{t-1})$$
$$N_t = N.adult_t + N.pup_t - H_t,$$

where ϕ_t was annual survival, ρ_t was per capita recruitment, N_t was population size, and H_t was number of wolves harvested. We did not include age or sex structure because monitoring data could not distinguish between sexes and age classes. We assumed yearlings and adults of both sexes had equal survival, and that harvest mortality was additive. In Model 1, we assumed that net immigration into Montana was 0. For Model 2 representing the hypothesis that net immigration was positive, we included a term for net immigration (δ_t), and adjusted the above equation for adults to:

$$N.imm_t \sim Poisson(N_{t-1} * (1 + \delta_{t-1}))$$
$$N.adult_t \sim Binomial(N.imm_t, \phi_{t-1}).$$

We used estimates of survival and recruitment for wolves in Montana to parameterize the population models (Keever 2020, Smith et al. 2010). Because we assumed additive harvest mortality, we used the mean and variance of non-harvest survival rates (mean = 0.73, variance = 0.003). We included stochasticity in survival by drawing random values from a beta distribution based on the mean and variance. For recruitment rate, we included density dependence (Keever 2020). We used a maximum recruitment rate of 0.05 and a slope coefficient for the effect of density of -0.00114 in a generalized linear model with a log-link function as:

$$\rho_t = \exp\left(0.05 - 0.00114 \times N_{t-1}\right)$$

We included stochasticity in recruitment by drawing random values for the intercept and slope coefficient from a gamma distribution based on the mean and variance. We assumed a mean of 0.10 and a variance of 0.005 for net immigration and drew random values from a beta distribution to incorporate stochasticity. We included partial controllability in harvest by drawing the annual total number of wolves harvested from the posterior predictive distribution described above.

To estimate the probability of transitioning from one population state to another given a management action, we initiated the population size randomly within each discretized population state for 50,000 iterations. We used the 2 population models and their respective model weights to predict abundance the next year. We discretized population size by rounding to the nearest 10 wolves and used the frequencies of predicted population size to create state transition matrices. We derived probability mass functions describing the probability of transitioning from one system state to another. We discretized model weights in increments of 0.1, from 0.1 to 0.9. This yielded 10,000,000 simulations (200 population states × 50,000 iterations) for each of the 4 harvest management actions under each model weight state.

Optimization and simulation

We used SDP to compute the optimal set of management actions (Bellman 1957, Williams et al. 2002, Puterman 2014). We solved the problem by maximizing the expected cumulative reward value over the infinite time horizon using policy iteration in R v3.6.1 (R Core Team 2020) with package MDPtoolbox (Chadès et al. 2017). We assumed a discount factor close to 1 (i.e., 0.99999; Puterman 2014), indicating the value of a resource in the future is the same as the value now. Because the optimal management actions depended on population size and model weight, uncertainty could be reduced by implementing the optimal management actions and updating model weights. We used a passive adaptive framework and updated model weights using Bayes' theorem in 2 simulations to predict median annual population size, number of pups recruited, number of depredation events, and reward values for how well each management action met objectives.

We first simulated a population for 100 years. Each year, the optimal management action was selected and enacted, and the population and model weight states were updated. We updated model weights assuming Model 1 was correct, then Model 2 was correct. E.g., we used abundance estimates from Model 1 as the mean in a normal distribution with an SD of 20% to draw an estimate for the observed data, then determined its normal likelihoods given the estimates for each model with an SD of 20%.

We next simulated the Montana wolf population from 2011 – 2018 using the management actions enacted by MFWP each year. We used the status quo for 2012 – 2018, and restricted management for 2011 – 2012. To update model weights, we compared predictions from the competing models to the estimated

abundance of wolves from original POM estimates (Inman et al. 2019). To account for uncertainty in estimated abundance, we resampled the estimates 1000 times for each year and replication from a normal distribution using the reported mean and SD. We took the mean model weight for each replication and resampling run to get the annual weight for both models.

Sensitivity analyses

We evaluated model performance and sensitivity of results to uncertainty in parameter values, construction of utility functions, and weights of objectives (Keever 2020). We used one-way sensitivity analysis (Conroy and Peterson 2013) to test sensitivity of the optimal decision reward value to uncertainty in parameter estimates. We also used response profile sensitivity analysis (Conroy and Peterson 2013) to identify how the optimal decision changed across a range of parameter values. To assess sensitivity of results to utility functions and risk attitude, we compared the reward values for each risk attitude. We evaluated sensitivity of the expected reward values to weights for objectives using indifference curves. Lastly, we evaluated the sensitivity of evolving model weights to bias in abundance estimates of wolves. Estimates of wolf abundance from POM hinge on assumptions about territory size (Sect. 1). Therefore, we tested the sensitivity of model weights to a 15% change in annual estimates of abundance.

Results

Median population size, number of pups recruited, number of depredation events, and the reward value differed for the 4 management actions (no harvest, restricted harvest, status quo, and liberal harvest) when the weights of the 2 population models were equal. No harvest had greater median number of depredation events per year (Fig. 3.6A). Restricted harvest was expected to have slightly more depredation events than the status quo or liberal harvest. Total pups recruited was expected to be greatest under more restrictive harvest (Fig. 3.6B). Total harvest was a median of 66 wolves under restricted harvest, 225 under status

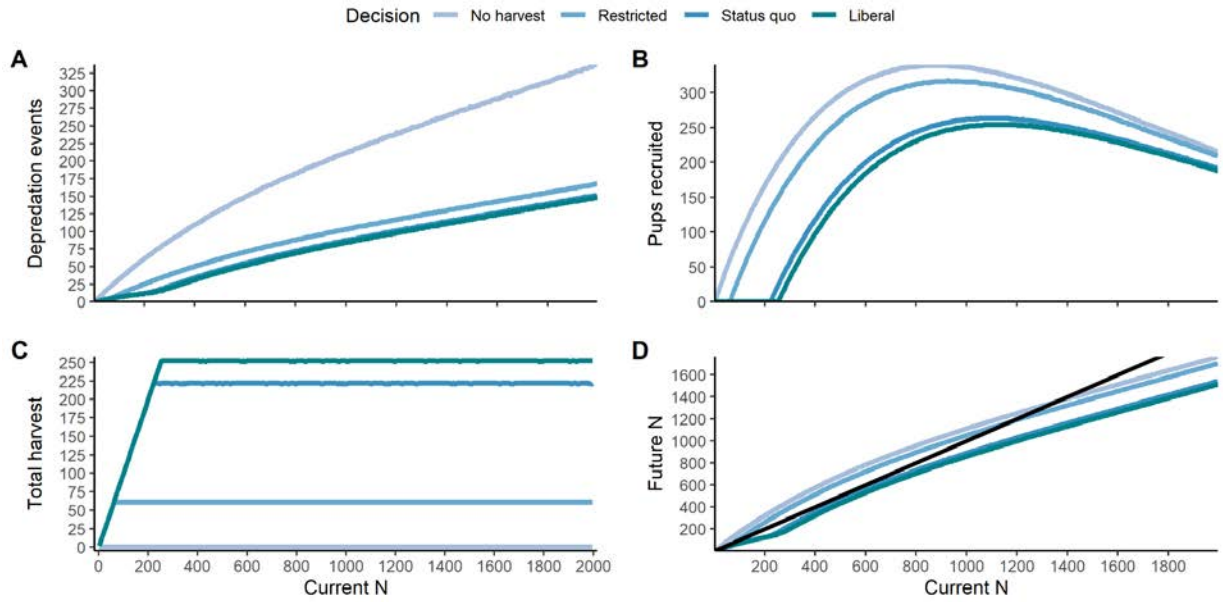

Figure 3.6. Expected annual performance from 2 competing models of wolf population dynamics with equal model weight under 4 management actions: no harvest, restricted harvest, status quo, and liberal harvest. The figures show the median expected A) # of depredation events, B) # of pups recruited, C) total harvest, and D) future population size as a function of the current state (i.e., abundance) of the population and management action. The black line in D represents a stationary population.

quo, and 253 under liberal harvest (Fig. 3.6C). Generally, no or restricted harvest yielded greater expected future population sizes (Fig. 3.6D).

More liberal harvest regulations had greater utility than no or restricted harvest for the objectives to reduce impacts of wolves on ungulates, reduce impacts of wolves on livestock, maintain hunter opportunity for wolves, and increase public acceptance of wolf harvest (Fig. 3.7). Conversely, utility for maintaining a viable wolf population was greatest under no or restricted harvest. The median reward for each management action differed across population states.

Policy plots showed that the optimal management action varied little with different model weights (varied by ~ 150 wolves for 0.1 and 0.9 model weight; Fig. 3.8). In general, the optimal management action was no harvest when population size was < 170 wolves, restricted harvest when the population was 170 – 280 wolves, status quo harvest when 280 – 1330 wolves, and liberal harvest when >1330 wolves (Fig. 3.8).

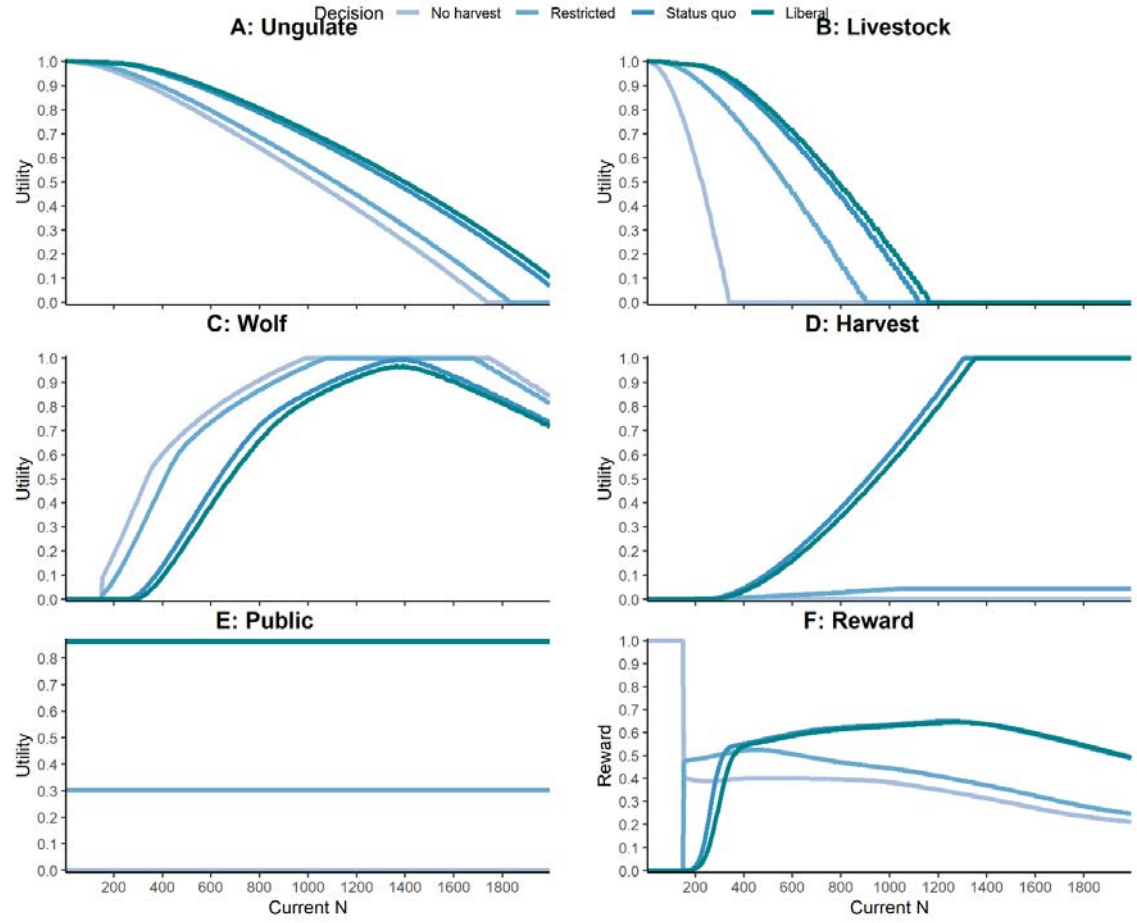

Figure 3.7. Utility values for the objectives (A-E) and the mean expected reward value for meeting all objectives (F) for harvest management of wolves in Montana, 2011-2018, as a function of current abundance (Current N). Objectives included: A) reduce impact of wolves on ungulate populations, B) reduce impact of wolves on livestock, C) maintain viable and connected wolf population, D) maintain hunter opportunity for wolves, and E) increase public acceptance of wolf harvest. The management action with the greatest utility or reward does best at meeting that objective. given population size.

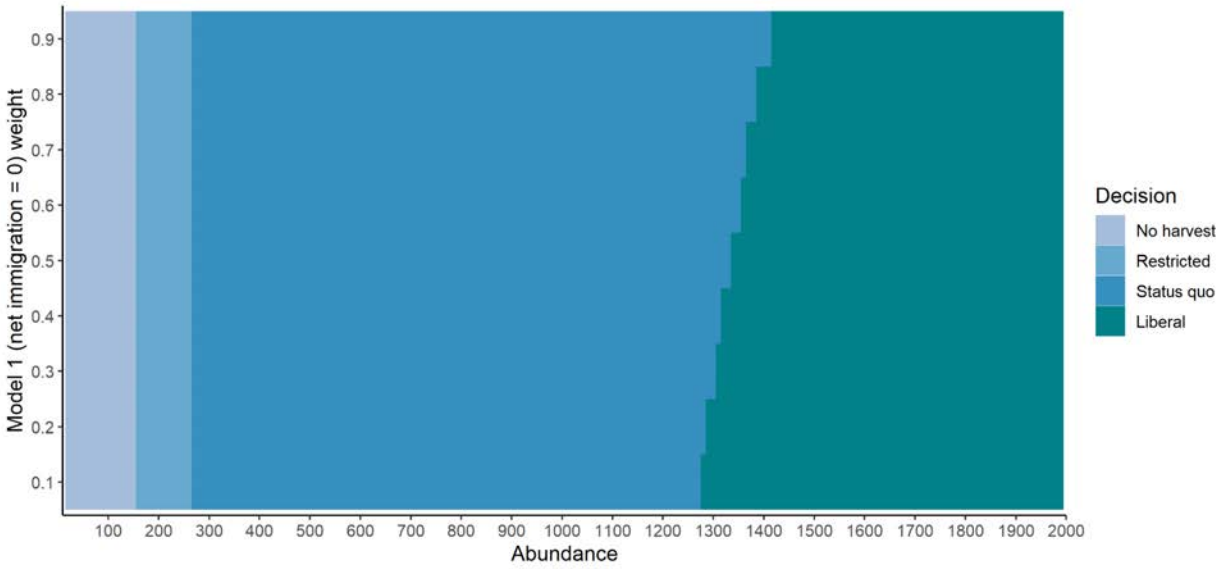

Figure 3.8. Optimal harvest management strategies for wolves as a function of current abundance and support for the model with no net immigration (Model 1 weight). Decisions included no harvest, restricted harvest, the status quo, and liberal harvest.

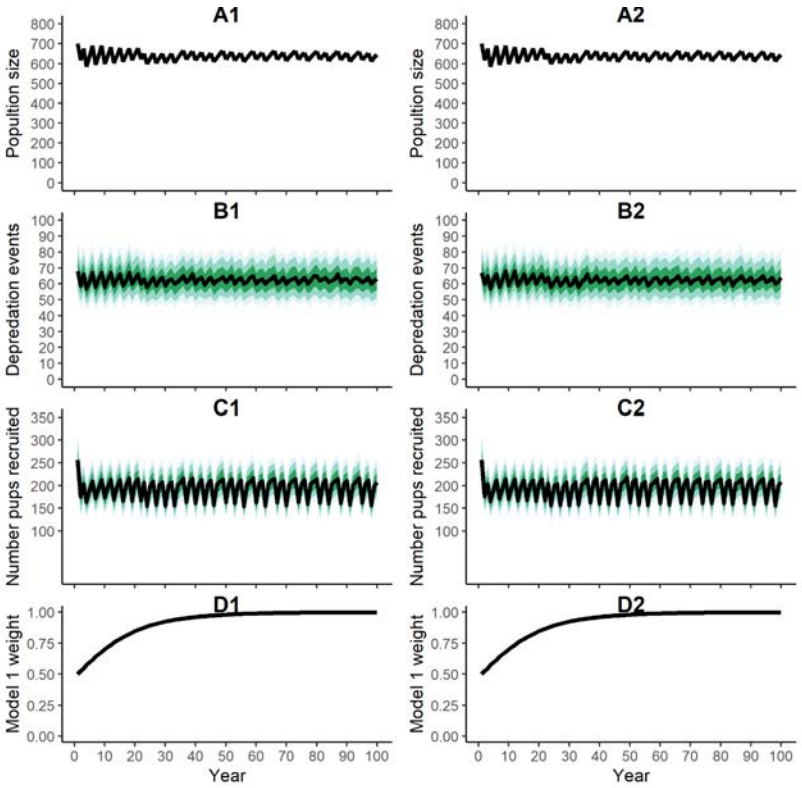

Figure 3.9. Expected annual performance from simulations of passive adaptive harvest management of wolves. The expected performance metrics were derived from the weighted average of 2 models of wolf population dynamics (Model 1: no net immigration, left column; Model 2: positive net immigration, right column). Performance included expected A) population size, B) # of annual depredation events, C) # of pups recruited, and D) change in Model 1 weight. Shaded areas are 50, 80, and 95% quantiles.

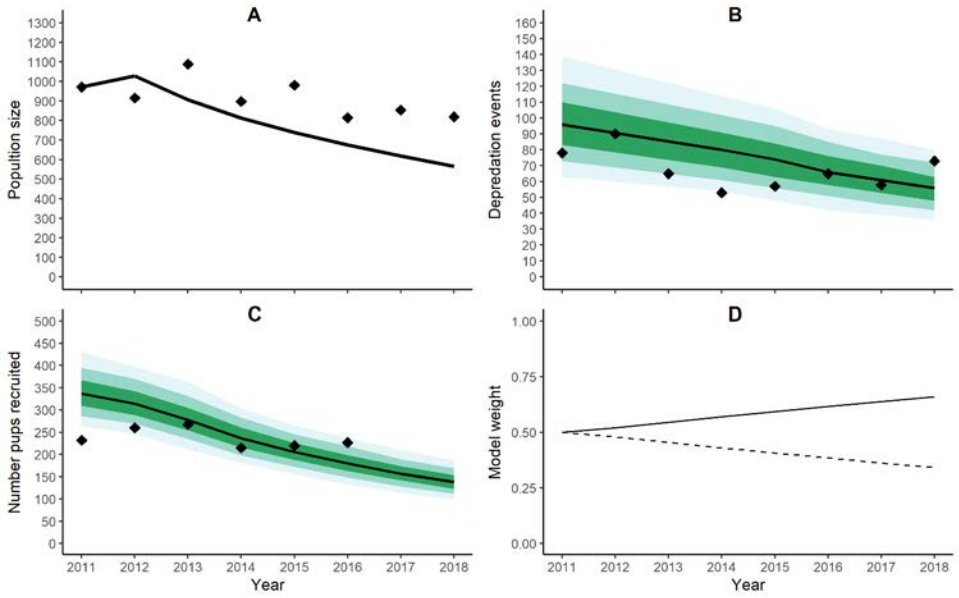

Figure 3.10. Expected annual performance from simulations of passive adaptive management for wolves in Montana from 2011 – 2018 based on harvest decisions implemented by MFWP. The expected performance metrics were derived from the weighted average of 2 models of wolf population dynamics (Model 1: no net immigration, Model 2: positive net immigration). Figures include A) predicted population size (line) compared to estimates of abundance (points), B) median # of annual depredation events (line) compared to # of verified depredation events (points), C) median # of pups recruited (line) compared to estimates of recruitment (points), and D) change in model weights with no immigration (solid) and positive immigration (dashed). Shaded areas are 50, 80, and 95% quantiles.

The expected annual performance was similar when we assumed Model 1 and Model 2 were true. When we simulated a population under the optimal management actions, wolf population size fluctuated around 650 wolves under both scenarios (Fig. 3.9). The expected number of depredations was ~60 events per year, and the annual number of pups recruited was 256. Under both scenarios, weight for Model 1 increased over 100 years.

By simulating AM for the Montana wolf population from 2011 – 2018 based on the decision construct and utility functions outlined above, we found that expected population size, number of pups recruited, and depredation events declined (Fig. 3.10). This follows general patterns for estimates of abundance of wolves and the number of verified depredation events in Montana (Inman et al. 2019). Over the 8-year period, weight for Model 1 (net immigration = 0) increased from 0.50 to 0.67, and weight for Model 2 (net immigration > 0) decreased from 0.50 to 0.33 (Fig. 3.10).

Sensitivity analyses

The expected reward for meeting objectives was most sensitive to depredations per wolf, mean recruitment of offspring, and harvest (Keever 2020). The model was least sensitive to uncertainty in immigration rate or changes in coefficient values for the effect of harvest regulations on percentage Montanans satisfied. As mean recruitment rate decreased, the supported management action became more restricted (e.g., at a wolf abundance of 350, optimal management changed from status quo to restricted harvest). As wolf abundance increased, this relationship become less pronounced. Uncertainty in adult

survival also altered the optimal management action, but only when the population was small; the same was true of uncertainty in total harvest and depredation rate.

The optimal management action was most sensitive to the construction of the utility function for the objectives to maintain a viable wolf population and reduce the impact of wolves on livestock. This effect was only observed when abundance was around 350 wolves (Keever 2020). To convert to utility values, we assumed there was a maximum threshold beyond which the utility value was 1 (highest utility) for an increasing function or 0 (lowest utility) for a decreasing function. For example, for the objective to maintain a viable wolf population we assumed that beyond the threshold of 700 wolves the population was viable and utility was 1 (Fig. 3.3A). When the maximum threshold for the viable wolf population decreased, more conservative regulations performed better at meeting objectives.

The expected reward for meeting objectives was most sensitive to the objective weights for reducing impacts on ungulates, reducing impacts on livestock, and increasing public acceptance of wolf harvest (Keever 2020). Changes in weights for these objectives did not alter the optimal management action. The optimal management action was most sensitive to objective weights for maintaining a viable wolf population and increasing public acceptance of harvest opportunity. Although changing the weights of the other objectives resulted in slight changes in the recommended management action, the overall reward values for the different management actions remained close, suggesting that changes in weights would not result in a clearly superior decision.

Reduction of uncertainty in the role of immigration to wolf population dynamics was not sensitive to a systematic bias in estimates of abundance. We found similar change in model support with a 15% increase or decrease in estimates of abundance (Keever 2020). When estimates were biased low, support for no net immigration increased to 0.67 compared to 0.66 when the estimates were biased high.

Discussion

Management of large carnivore populations can be particularly challenging due to conflicting values of stakeholders, debated science, and ecological complexity. We demonstrate how an AM framework explicitly incorporating uncertainty in estimates of harvest, biological and sociopolitical values, and quantitative objectives could guide decisions of harvest regulations of wolves.

From our conceptual model, we found that the optimal management actions became more liberal as the population grew (Fig. 3.8), and the management actions differed in expected effects on wolf population size, number of livestock depredations, and total harvest (Fig. 3.6). This result stems from the weights placed on objectives, the models we employed to predict wolf population size, and the utility functions that tied wolf population size to the extent to which objectives were achieved. This combination of factors that we used to define the decision framework leads to a slightly declining statewide population producing the best overall results. Our conceptual framework could be improved by determining optimal management actions at finer spatial scales (e.g., by MFWP administrative regions). Whereas we evaluated objectives and considered management actions at a statewide scale, metrics used to evaluate objectives may vary spatially. For example, most livestock depredation events (95%) occur in 22% of Montana (DeCesare et al. 2018), and most harvest (60%) occurs in northwestern Montana. Spatial variation in depredation events, harvest, ungulate populations, and wolf impacts on ungulate populations would likely

influence weight of objectives as well as the expected performance metrics (e.g., number of depredation events) if we accounted for such variation more fully.

Optimal harvest regulations are dependent on the objectives we used, their quantification, and the set of management actions considered. Accurately translating objectives into reward values may be the most important component. As a metric for the objective to reduce impacts of wolves on ungulates, we used an expert opinion-based scale from 0 (no impact statewide) – 1 (wolves reduce ungulate populations statewide). This simplification of how wolves affect ungulates ignores functional and numerical responses (Mech and Peterson 2003, Hebblewhite 2013, Zimmermann et al. 2015), the confounding effects of other predators on ungulates (e.g., Hamlin et al. 2008, Rotella et al. 2018), and the documented spatial variation in wolf impacts on ungulate populations (Garrott et al. 2005, Hamlin et al. 2008). For the objective to increase public acceptance of wolf harvest and harvest opportunity, we used survey data to relate hunting season length, trapping season length, and bag limit to the percent Montanans satisfied. There are other metrics or considerations we could have included, such as overall tolerance of wolves in Montana (Lewis et al. 2018). We made this decision because we did not have a clear way of predicting how tolerance changed with metrics of the wolf population or harvest regulations, but it is also not clear that a changing wolf population size or harvest regulations govern Montanans' tolerance for wolves in Montana.

In addition to more explicit treatment of spatial variation and utility functions, objective weights affect the optimal management decisions. Our results were sensitive to objective weights for maintaining a viable wolf population and for increasing public acceptance of harvest as part of wolf management. Ideally, the objective weights will reflect the values of stakeholders. However, in situations such as harvest management for large carnivores, one set of objectives and weights that accurately reflect the values of all stakeholders is not guaranteed. The objectives we used were established during a 2010 SDM workshop among agency professionals and decision makers, and some stakeholder groups may not feel their values are adequately represented in the list of objectives we used. Situations where objectives and objective weights cannot be agreed to by all stakeholders may be better addressed with conflict transformation (Madden and McQuinn 2014) or other decision-making approaches focused on conflict management.

Using AM, we found evidence that net immigration of wolves into Montana was 0. From 2011 to 2018, our model for no net immigration gained support (increasing from 0.5 to 0.67). Other wolf population models assume that immigration and emigration sum to 0 (Schmidt et al. 2015, Stenglein et al. 2015*b*, Horne et al. 2019), and this assumption may be valid. A study in Idaho also found evidence that immigration does not compensate for harvest (Bassing et al. 2020). The wolf population in Montana may have saturated much of the prime available habitat. Immigration may be more important for colonizing or isolated, small subpopulations (Bull et al. 2009).

Reduction of uncertainty in AM is contingent on the accuracy of the monitoring data. An assumption in many optimization methods is that the state (here, the population size) is observed without error (Williams 2009, Conroy and Peterson 2013). This is clearly violated in this and most ecological applications. Estimates of abundance of wolves in Montana also rely on accurate estimates of territory and group size (Sect. 1). We used POM estimates for our conceptual AM framework, whereas the newer iPOM estimates may change weights of the 2 competing models. Although we found model support was insensitive to a 15% change in abundance estimates, we did not test the effects of greater changes, and iPOM represents a >15% increase over POM estimates. Changes in bias over time could also influence

results. Our sensitivity analyses also revealed that at small population sizes (<350 wolves), optimal management actions were sensitive to uncertainty in recruitment, survival, depredation, and harvest.

When uncertainty impedes effective decision making, AM can facilitate learning and reduce uncertainty (Williams et al. 2002; Conroy and Peterson 2013). Importantly, AM can improve future decisions to manage populations more effectively. Furthermore, as demonstrated in this AM conceptualization, AM can include public survey data (Lewis et al. 2018). Public opinion is an influential component in wildlife management, yet it is rarely explicitly incorporated into the decision process (McCool and Guthrie 2001). When there is a transparent link between public input and management decisions, satisfaction with management often increases (McCool and Guthrie 2001).

SECTION 4: RECOMMENDED MONITORING PROGRAM

ABSTRACT Monitoring is central in wildlife management, but efficient and effective use of limited resources requires targeted monitoring. Because wolves in Montana are managed through harvest, reliable estimates of population size will help inform harvest regulations. We therefore recommended a monitoring program and considerations for MFWP's Wolf Program. Abundance estimation will entail the continuation of hunter harvest surveys and monitoring related to the occupancy model. This includes pack centroids, although potential exists for a reduction from current effort. Approximate locations of wolves removed in response to livestock conflicts will be needed for the pack size model. Future monitoring of pack size may be needed to calibrate the model, such as if changes are made to harvest regulations. Once finalized to include the iPOM methodology, the recruitment model will require collar and pack count data.

Introduction

Monitoring plays a central role in wildlife management. Monitoring allows managers to detect changes in wildlife populations or habitats, evaluate effectiveness of management actions, make decisions based on status of the resource, and facilitate learning to improve efficacy of future management actions (Nichols and Williams 2006). Monitoring is often most useful when it is directly linked to objectives and targets key uncertainties that impede management (Gibbs et al. 1999; Nichols and Williams 2006). Targeted monitoring can be more efficient and a better use of limited resources compared to surveillance monitoring (i.e., monitoring not guided by *a priori* hypotheses and including all aspects of a population's demographic and ecological factors; Nichols and Williams 2006).

Because wolves in Montana are managed through harvest, reliable estimates of population size are needed to make informed decisions for harvest regulations. As the final step of this project, we recommended a targeted monitoring program to provide reliable estimates of population size and inform decisions. Below, we discuss the recommendations for iPOM and the recruitment model.

iPOM

As detailed in Section 1, the integrated Patch Occupancy Model (iPOM) is a multi-model approach incorporating models for occupancy, territory size, and pack size (Sect. 1.7; Sells et al. *in prep*). The original POM approach required numerous data inputs, including annual statewide mean group size, a territory overlap index calculated from the statewide set of pack centroids identified each year, and a decade-old estimate of mean territory size. These data inputs are now omitted from iPOM, enabling monitoring to be targeted more efficiently and effectively to provide reliable estimates of wolf abundance.

Occupancy model

The occupancy model is a key element of the abundance estimates and will serve as the primary focus for monitoring effort. Annual Hunter Harvest Surveys will continue to be needed to collect observations of wolves each year. These surveys are conducted as part of larger MFWP operations and require minimal added effort to include questions specific to wolf sightings.

The occupancy model was designed to use pack centroids as a measure of true positive detection (Sect. 1.7; Rich et al. 2013, Miller et al. 2013). This will entail continued monitoring by Wolf Specialists to verify packs each year and report approximate locations of pack centroids. Effort to detect new and existing packs can be focused in the areas predicted by the territory model given its demonstrated predictive ability (Fig. 1.7). Empirical data collected in past years can also help guide search effort, as many areas continue to be used each year by wolves (Fig. 1.7). The expert knowledge of the Wolf Specialists will continue to be invaluable for efficient and effective monitoring of pack centroids. Remote cameras deployed strategically at suspected den and rendezvous sites or along wolf travel routes are likely to be helpful in detecting packs. Drones may also prove useful for remotely visiting these sites to unobtrusively search for wolves (T. Smucker, MFWP, pers. comm.). Cameras, drones, or visual surveys could also be deployed opportunistically at kill sites of any collared ungulates.

Once a pack is detected, its centroid can be estimated using the Wolf Specialists' expert knowledge. Because any 600 km^2 grid cell containing a centroid becomes a true positive detection regardless of the placement of the centroid within, precise coordinates of territory centroids are unnecessary. As such, the most efficient monitoring will entail verifying only whether a grid cell contains a pack. If a pack appears to use > 1 cell, the cell that appears to contain the greatest use should be the one reported.

There is potential for alternative data sources to be used in place of pack centroids for true positive detections. MFWP has expressed interest, for example, in using mortality locations of wolves harvested by trapping and hunting to indicate cells that contain packs. Because lone or dispersing wolves may also be harvested, safeguards will be needed to avoid over-estimation of true positive detections. For example, a true positive detection might require ≥2 harvest locations in the cell to reduce the likelihood of including lone or dispersing individuals. These locations might also be paired with the mapped territory predictions and past empirical observations (Fig. 1.7); harvest locations in areas not used in the past or predicted to hold territories could trigger independent verification of pack presence by Wolf Specialists.

We suggest that MFWP conduct sensitivity analyses to evaluate monitoring effort associated with pack centroids and understand potential biases that might arise. Such analyses might involve gradually thinning the pack centroid inputs into the model (e.g., 10% fewer centroids, 20% fewer, etc.) and rerunning the occupancy model to determine effects on occupancy estimates. Harvest locations could also be included as true positives to again compare resulting occupancy estimates. We suspect a combination of monitoring for pack centroids and harvest locations might serve to reduce monitoring effort while incorporating available data from harvest.

Territory model

The territory model was designed to significantly reduce monitoring effort and improve accuracy of abundance estimates from iPOM (Sells and Mitchell 2020; Sells et al. *in press*; Sells et al. *in review a*). In addition to the estimated area occupied, territory size has strong effects on overall abundance estimates. The territory model's mechanistic approach maximizes predictive ability across time and space (Aarts et al. 2008, Sells et al. 2018) and enables predicting territorial behavior across changing environmental and social conditions (Sect. 1.4).

Changing levels of competition among packs are an important driver of territory size (Sells and Mitchell 2020, Sells et al. *in press*; Sells et al. *in review a*). We simulated widely ranging levels of competition to provide a suite of predictions that can be used in future years. Higher pack densities are predicted to yield more consistency in means and ranges in territory sizes across Western Montana (Fig. 1.14). Less spatial and temporal variation in territory size means that a given unit of area occupied will contain a similar estimated pack abundance regardless of where that area occurs. This is not true at low pack densities due to the greater spatial variation in territory sizes under these conditions. Although consistently small territories will produce higher estimates of pack abundances under iPOM, it is arguably most important to successfully predict territory size at low pack densities both due to the spatial variation involved and risk of over-estimating abundance for a population that might be imperiled with extirpation. Our application of the model to conditions a decade ago demonstrates our ability to accurately predict territory sizes even at relatively low pack densities (Sect. 1.4).

Major shifts in prey populations will also have implications for territory size. We designed our prey indices to be general and stable by using long-term datasets to model average densities across space and time. Where local prey abundances change sharply from the densities estimated for the previous decade, the model's predictions for changing prey densities can be used to calibrate territory size estimates (Sect. 1.4). This would likely have limited effects on the total abundance estimates if prey populations increase in some areas and decrease in others (as some territories would increase in size while others decrease). Should prey populations undergo widespread, long-term, directional changes, the territory model could be updated and ran with new prey indices to update estimates of spatial requirements for wolves.

Many studies of space use to date have relied on deploying GPS collars, but as we discovered for wolves in our study system, this yields a low return on investment given the costs and challenges involved. A GPS collar costs >$2000 upfront, must be carefully maintained before and after capture, and involves hundreds of dollars in annual data charges, along with costly battery replacements and regular servicing. Collars more importantly require intensive effort to deploy. Trapping efforts to deploy collars occur spring through fall (freezing injuries make winter trapping unsafe for wolves). Wolf Specialists and their field crews may spend weeks in a pack's territory to capture a single individual. These efforts may fail altogether, despite these crews' expertise. All indications point to declining capture success in recent years, regardless of investment in effort. Wolves may be wiser to these efforts now that trapping is employed pervasively across wolf habitat by both MFWP and recreational trappers. The alternative method to capturing wolves is via helicopter darting, which cost approximately $3000 – $4000 or more per wolf in contract costs, not including MFWP personnel time or collar costs. Helicopter captures require intensive advance monitoring effort by MFWP to locate wolves, and successful aerial capture is far from guaranteed. These efforts are furthermore dangerous both for humans and wolves; aviation accidents are a primary cause of job-related deaths among wildlife professionals in the US (Sasse 2003) and wolves may be injured or killed during or shortly after capture.

For this study, a substantial investment in time and resources to capture wolves using both ground and aerial methods yielded 93 total captures over a 5-year period (Sect. 1.3; Sells et al. *in press*). After a successful capture, a wolf must survive long enough with a functional collar to provide the data needed to estimate space use. Of the 93 wolves captured, only 46% yielded sufficient data to delineate 28 pack territories. This low rate of return on investment was due to collar failure (39% of wolves captured had collar failure, largely within the first year or so after capture) and mortalities from harvest or other causes

(46% of wolves captured), as well as the fact that pups and yearlings often disperse before sufficient data can be collected (16% of captured wolves dispersed).

We designed the mechanistic territory model to maximize the utility of the data collected during this study, and critically, to preempt a need for continued capturing and collaring for estimation of space use. No additional monitoring data are required for territory size. If in the future there are drastic changes to conditions related to prey or competition, however, collar data could help assess the model's predictive capacity, especially if any modifications are made to the model. We demonstrated the strong predictive capacity of the model for recent and past years and expect it to continue to be predictive in future years given its mechanistic nature (Aarts et al. 2008). Despite the challenges of collaring wolves, collaring efforts are likely to continue into the future at least at some level for livestock conflict prevention and response, and potentially for estimating recruitment (below). Collar data may also be collected for future studies on wolves. Sufficient location data may thus eventually be opportunistically available to again verify the territory model's predictive capacity, if desired. Any apparent changes in accuracy of the model estimates would be most problematic if consistent directional biases are observed, otherwise a combination of both under- and over-estimation in territory size would likely cancel any major effects on estimated wolf abundances.

Pack size

The pack size model was likewise designed to significantly reduce monitoring effort and improve accuracy of abundance estimates from iPOM (Sect. 1.5 – 1.6; Sells et al. *in review b*). Pack size affects the overall abundance of wolves during the final calculations in iPOM (Sect. 1.7). We designed the pack size model to be general and involve minimal monitoring effort. We attempted to include the best available data representing hypothesized connections to mechanisms driving pack size. However, the model's empirical nature and use of proxies will make it more susceptible to bias under changing future conditions. Applying an empirical model beyond the conditions for which the data existed during model development entails extrapolation based on patterns (Aarts et al. 2008). If future conditions (e.g., intensity of harvest management) shift beyond the conditions experienced within our 14-year dataset, the effects on pack size will be unknown, making predictions less reliable.

The only annually-changing input required for the pack size model is the number of wolves removed for livestock conflicts in each grid cell. This will entail timely and accurate reporting to MFWP by Wildlife Services and the public for approximate locations of wolves killed each year in response to human-wolf conflicts (ideally, township, range, and section for sites of removals). When removals are unreported, the grid cell's pack size estimate will be biased slightly high, leading to a slight positive bias in overall wolf abundance estimates. Wolf abundance estimates from iPOM could be adjusted by the sum of the approximate number of depredation removals without coordinates plus those assumed to be unreported.

Various conditions will trigger a need to increase pack size monitoring in the future. Increased liberalization of harvest regulations could influence pack sizes in unknown ways. Harvest regulation (no harvest, restricted harvest, and liberal harvest) is furthermore a main driver of the pack size model. Other conditions that may trigger increased monitoring include, e.g., a widespread disease outbreak within the wolf population. As no data exist to model these relationships, future monitoring effort will need to increase if such conditions occur. As with the implications of assumptions for POM (Sect. 1.1), if actual

pack sizes drop below that estimated by the pack size model, estimated abundance would be biased higher than the true population size. The opposite would occur if pack sizes increased from model estimates.

We conducted a simulation analysis to determine the monitoring effort needed to accurately estimate mean pack size if conditions change in the future. We represented truth using the 2005 – 2018 pack size dataset for good quality observations (i.e., the data used in Sect 1.5). We used these observations to calculate the true pack size observed for each harvest intensity. We conducted the simulation by creating

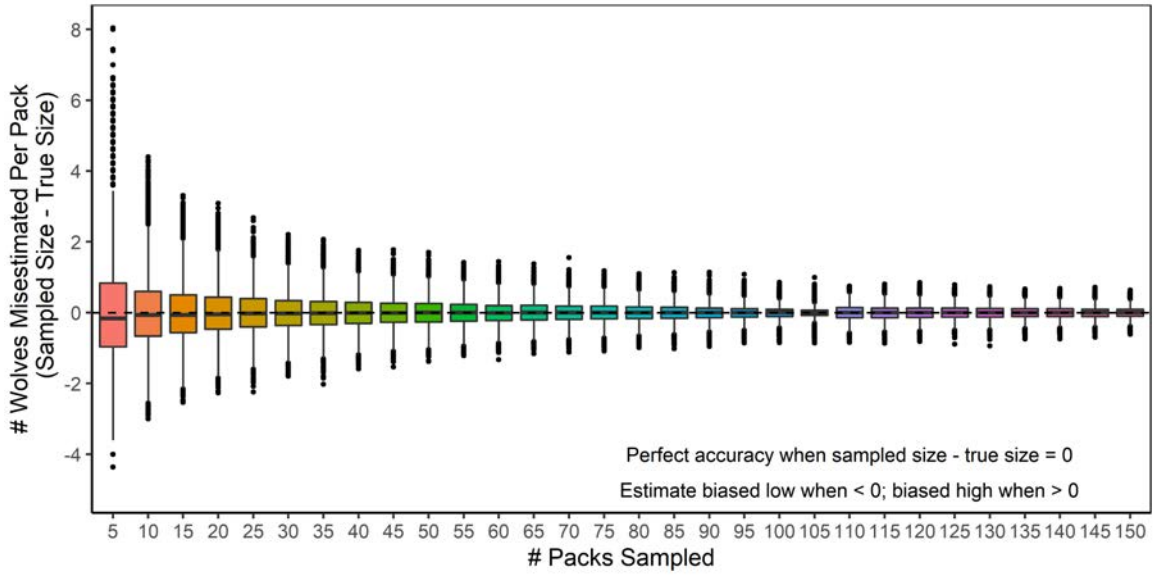

Figure 4.1. Boxplots for the difference in estimated pack size from truth given the # of packs sampled. Accuracy quickly increased with added monitoring effort. Lower and upper box edges are the 25th and 75th percentiles, respectively; whiskers extend the smallest and largest values within 1.5 the inter-quartile range, and outliers are displayed as points. (As results were similar across harvest regulations, we combined results for this plot.)

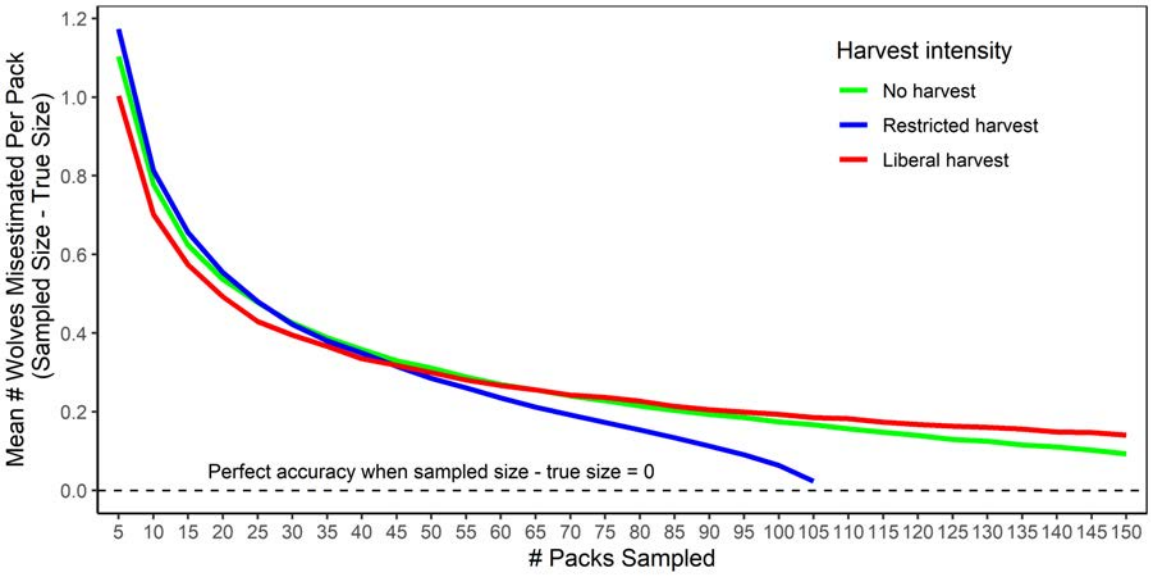

Figure 4.2. The mean number of wolves misestimated per pack quickly dropped towards 0 with additional monitoring effort. (Restricted harvest more quickly reaches truth because only 106 packs were available to represent truth, so a sample of 105 packs includes nearly the entire population.)

monitoring schemes of {5, 10, 15...150 packs}. In the first round, 5 packs were sampled without replacement from the dataset partitioned for the no harvest regulation. We calculated the mean estimated pack size from this sample of 5 packs, then calculated the difference from truth. We repeated this 10000 times per monitoring scheme. We then repeated these steps for the restricted and liberal harvest regulations. (As the restricted harvest data partition contained 106 observations, we ended the monitoring scheme at 105 packs for this regulation.)

From our simulation analysis, we determined that accuracy quickly increases with small added investments in monitoring. Boxplots demonstrate a strong potential for bias and low precision in estimated pack size if few packs are sampled (Fig. 4.1). In particular, mean pack size could be strongly over-estimated if only 5 packs are sampled. However, the chances of this extensive bias quickly diminish with additional packs sampled. Summarized as mean effects on accuracy, sampling 5 packs will misestimate 1 wolf per pack on average, and average accuracy quickly improves with additional pack sampled (Fig. 4.2). Projecting these misestimates out to an example population of 150 packs enables estimating the overall implications for estimated abundance (Fig. 4.3). This information can be used to help balance tradeoffs in monitoring costs and accuracy of pack size estimates when choosing how many packs to monitor. As the rate in gained accuracy declines at a sample of ≥30 packs, we suggest this cutoff as a reasonable starting point for monitoring effort.

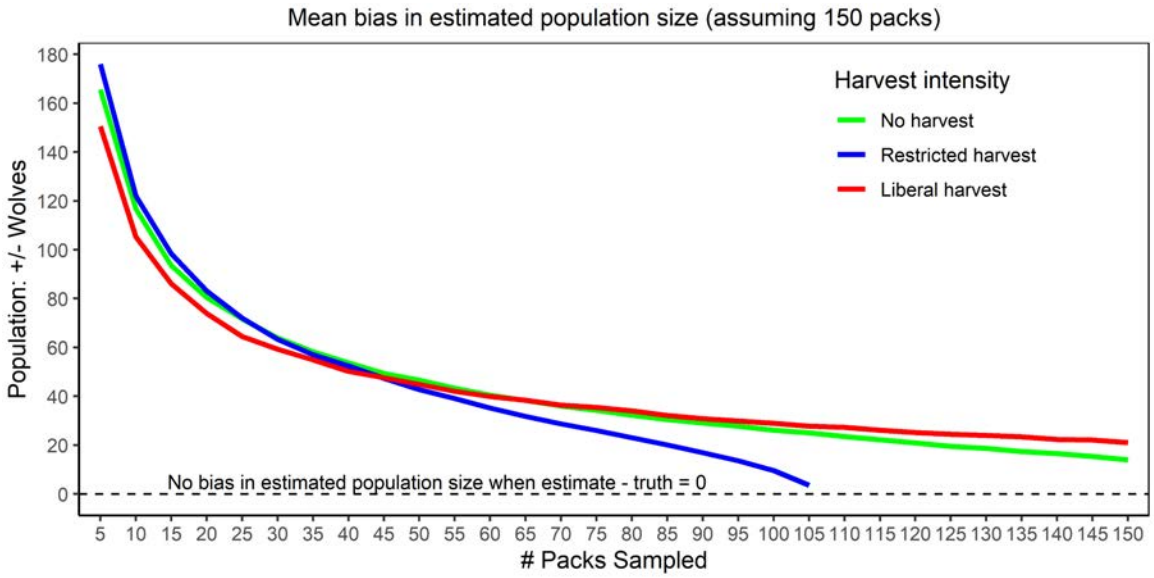

Figure 4.3. The overall population effect of misestimating pack size, assuming a population of 150 packs.

Recruitment Model

As detailed in Section 2, the recruitment model was designed using an integrated population modeling approach (Keever 2020). The model inputs included POM estimates, collar data, and group count data.

To assess usefulness of the recruitment model, we conducted a simulation analysis to determine the accuracy of recruitment estimates with variable amounts of group count and collar data. For the analysis, we simulated a wolf population for 15 years and then sampled from the population. We first generated 100 wolf packs with group counts using a Poisson distribution with an average pack size of 7 wolves. We

then randomly generated survival, recruitment, and dispersal rates using a uniform distribution with a range of biologically realistic rates for each year (Murray et al. 2010, Smith et al. 2010, Ausband et al. 2015, Stenglein et al. 2015*b*). This allowed for yearly variation in the demographic rates, which we recorded as truth. The simulated wolves in the initial 100 packs survived and reproduced based on these demographic rates. We included stochasticity using a Poisson distribution for reproduction and a binomial distribution for survival and dispersal. The number of packs was determined by generating random patch occupancy, colonization, and extinction rates from biologically realistic rates for each year and calculating the area occupied by wolves. We divided the area occupied by wolves by 600 km^2 (Rich et al. 2012) to determine the number of packs for our truth to which estimates could be compared.

We sampled from the simulated packs and population to create datasets representing variable monitoring effort. For group counts we randomly sampled 50, 25, and 12 packs per year. We added observation error to these counts so that the data were also a sample of wolves within the pack. We also tested the model without any group data. This yielded 4 total datasets (50, 25, 12, and 0 pack counts per year). For collar data we sampled 20 and 10 wolves per year to generate known-fate observations. We then sampled and created datasets for 20 and 10 collars every year, every 2 years, and every 5 years (6 datasets). We used every combination of the collar and group count datasets for a total of 24 scenarios. For each scenario we generated occupancy data by sampling 500 sites with 5 occasions per year.

We estimated recruitment using the model for all 24 scenarios. We compared estimates of recruitment to truth and calculated the percent error for each of the scenarios. We used MCMC (Brooks 2003) methods in a Bayesian framework to fit the model using program R 3.4.1 (R Core Team 2020) and package R2Jags (Su and Yajima 2015) that calls on program JAGS 4.2.0 (Plummer 2003). We ran 3 chains for 100,000 iterations, discarded the first 50,000 iterations as a burn-in period, and used a thinning rate of 2.

Table 4.1. Mean percent error and standard deviation of estimates from truth for a simulated wolf population with different amounts of collar and group count data. The greater the percent error, the less accurate the estimate. The mean and SD were calculated as the mean from all group count datasets for the # of collars, and the mean from all collar datasets for group counts.

# of collars	recruitment, $\bar{\gamma}$ (SD)	group size, $\bar{G}$ (SD)	abundance, $\bar{N}$ (SD)	survival, $\bar{\phi}$ (SD)
10 per yr	29.5 (22.90)	5.7 (3.05)	9.9 (8.23)	8.6 (6.46)
10 per 2 yr	30.6 (26.35)	5.7 (3.05)	9.7 (8.02)	11.3 (8.41)
10 per 5 yr	55.1 (28.99)	5.8 (3.06)	8.9 (7.05)	31.6 (21.58)
20 per yr	27.8 (22.08)	5.7 (3.05)	9.3 (7.95)	8.1 (6.05)
20 per 2 yr	30.7 (21.41)	5.7 (3.05)	9.4 (7.98)	10.1 (6.97)
20 per 5 yr	63.7 (29.36)	5.8 (3.05)	8.6 (7.68)	36.3 (22.01)
# of group counts				
0	54.5 (33.27)	NA	15.9 (7.81)	20.0 (18.64)
15	39.8 (29.75)	5.8 (3.33)	7.3 (7.36)	19.5 (20.16)
25	40.8 (26.53)	5.5 (3.15)	6.7 (5.60)	21.0 (20.13)
50	23.2 (13.78)	5.9 (2.55)	7.2 (6.16)	10.2 (8.61)

The models for all scenarios using group count data converged and had Gelman-Rubin statistics < 1.1 for each parameter. The scenarios with 50 group counts were most accurate in estimating recruitment across collar datasets (Table 4.1). Scenarios with 25 and 15 group counts had lower accuracy in estimated recruitment across collar datasets. Recruitment estimates with 15 and 25 group counts and 20 or 10 collars at least every 2 years were similar to recruitment estimates with 50 group counts and the same collar data (Fig. 4.4). Models for scenarios without group count data (not

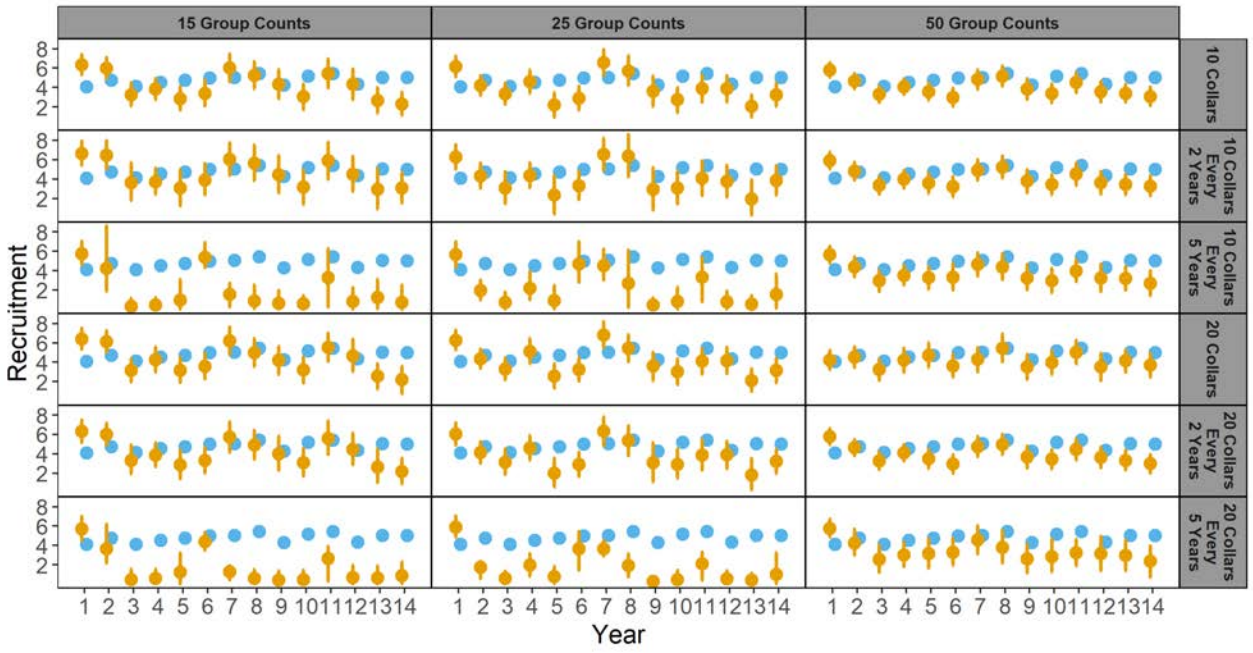

Figure 4.4. Estimates of recruitment in # of pups per pack that survive 1 year (orange circles) from an integrated population model compared to truth (blue circles) for a simulated wolf population with different amounts of group count and collar data.

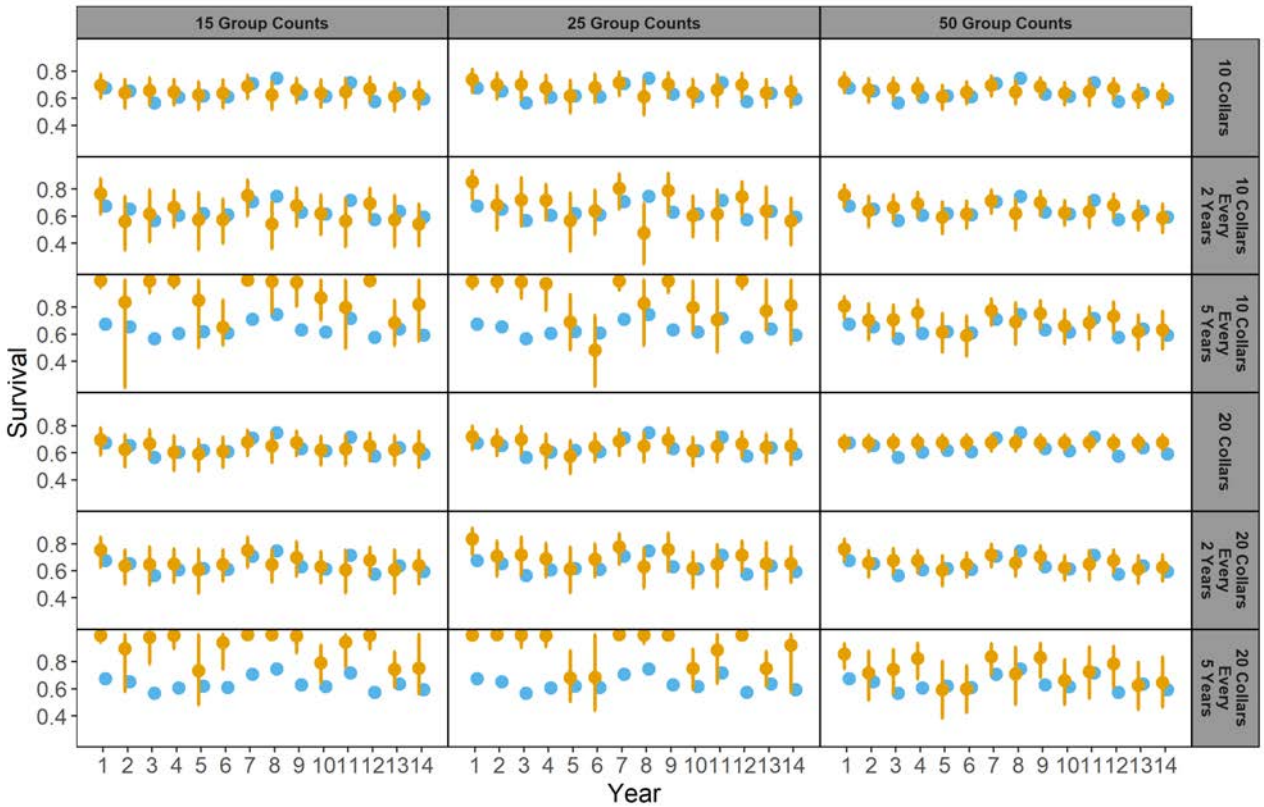

Figure 4.5. Estimates of survival (orange circles) from an integrated population model compared to truth (blue circles) for a simulated wolf population with different amounts of group count and collar data.

accounting for social structure) had trouble converging, and those that did converge were less precise and accurate than scenarios with group counts. Survival estimates for scenarios with 10 or 20 collars at least every 2 years were relatively accurate for all amounts of group count data, and survival estimates were inaccurate for 10 or 20 collars every 5 years with 25 group counts or less (Fig. 4.5). Estimates of abundance were similarly accurate for all scenarios, however the scenarios without group counts were less precise (Table 4.1).

We demonstrated that the recruitment model enables estimating the number of pups recruited per pack and into the population (Sect. 2). Field effort to collect group counts and deploy collars would remain at relatively high levels that may not be feasible given costs, constraints, and tradeoffs involved in this investment. Group count data greatly increase the precision and accuracy of estimates. There appears to be minimal gains in accuracy of estimates by increasing monitoring efforts from 15 group counts and 10 collars every 2 years to either 20 collars every 2 years, or 10 or 20 collars every year. Similarly, there appears to be little increase in accuracy from increasing monitoring from 15 group counts and 10 collars every 2 years to 25 group counts with the same collar data. If the recruitment model is used to estimate and report recruitment, we therefore recommend monitoring to produce 15 group counts and monitoring the fate of 10 collared wolves every 2 years. Importantly, because it was developed using the original POM estimation methods, the recruitment model would have to be updated to include the iPOM framework to make the model fully functional. Additional evaluation is warranted to test model assumptions that may influence accuracy in estimates (Sect. 2; Keever 2020).

General Suggestions for Montana's Wolf Program

It will be important to manage the wolf population in a manner to account for uncertainty. We suggest that MFWP set threshold population sizes that would trigger additional monitoring effort and management responses. In response to federal delisting criteria, the Montana Wolf Conservation Strategy (MFWP 2002) requires a minimum of 15 breeding pairs and 150 wolves to have a regulated public harvest season. Protections will be renewed under the Endangered Species Act if numbers drop too low. A population of 150 wolves thus provides a definitive minimum population threshold that will trigger cessation of public harvest. Selection of additional thresholds and resulting responses will necessitate careful consideration of tolerance within MFWP for the risk of dropping below minimum population targets. Presence of ≥15 breeding pairs is a safe assumption for a large and relatively stable population; however, population thresholds could also be selected to trigger investment in the effort necessary to update the recruitment model as a means for estimating recruitment.

Importantly, selected thresholds should be sufficiently high to allow time for both data collection and resulting changes in management to take effect. Estimated rates of population change from iPOM could possibly help forecast whether and when thresholds might be crossed (including by the bounds of uncertainty from iPOM). Monitoring effort should be increased before a threshold is projected to be reached. If the presumed cause of the decline is harvest, changes to harvest regulations represent a lever relatively within MFWP control. In contrast, disease outbreaks in wild populations are likely to remain beyond human control. A greater buffer of time and population size may thus be required to prevent a population at risk of disease from falling below minimum thresholds. The same is true for large-scale declines in prey resources. In these and other scenarios relatively beyond human control, harvest regulations are still likely to remain an important lever for helping a population remain above selected

thresholds. If necessary, uncertainty in iPOM estimates could be reduced through various means, perhaps most obviously by increasing monitoring effort to verify >150 wolves on the landscape (e.g., through trail cameras, drones, or collar deployment paired with added surveys at current wolf locations). Other methods could also or alternatively be employed to provide estimates alongside iPOM, such as camera trap estimation (e.g., Loonam et al. 2020) or genetic analyses (e.g., Bischof et al. 2020).

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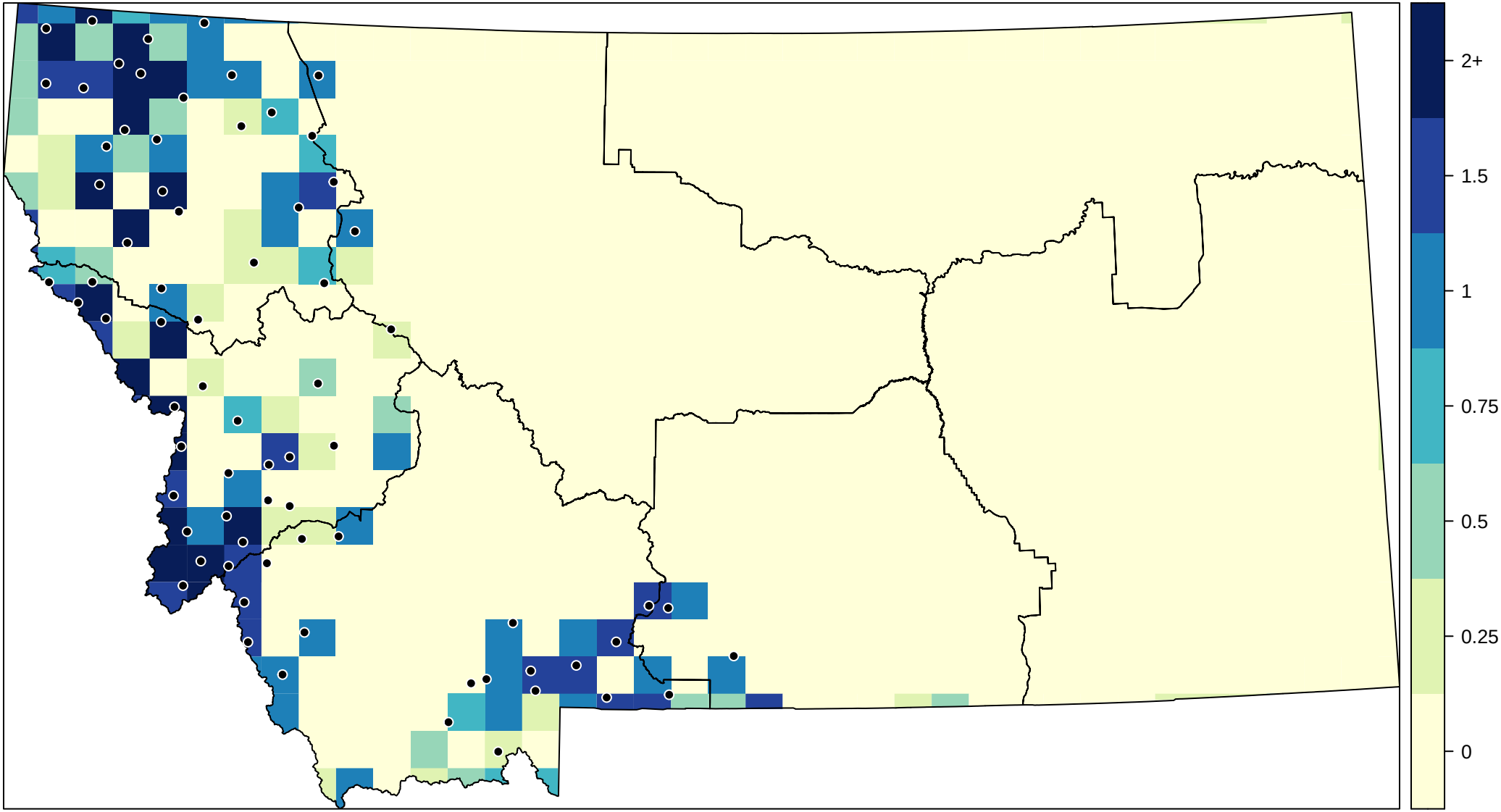
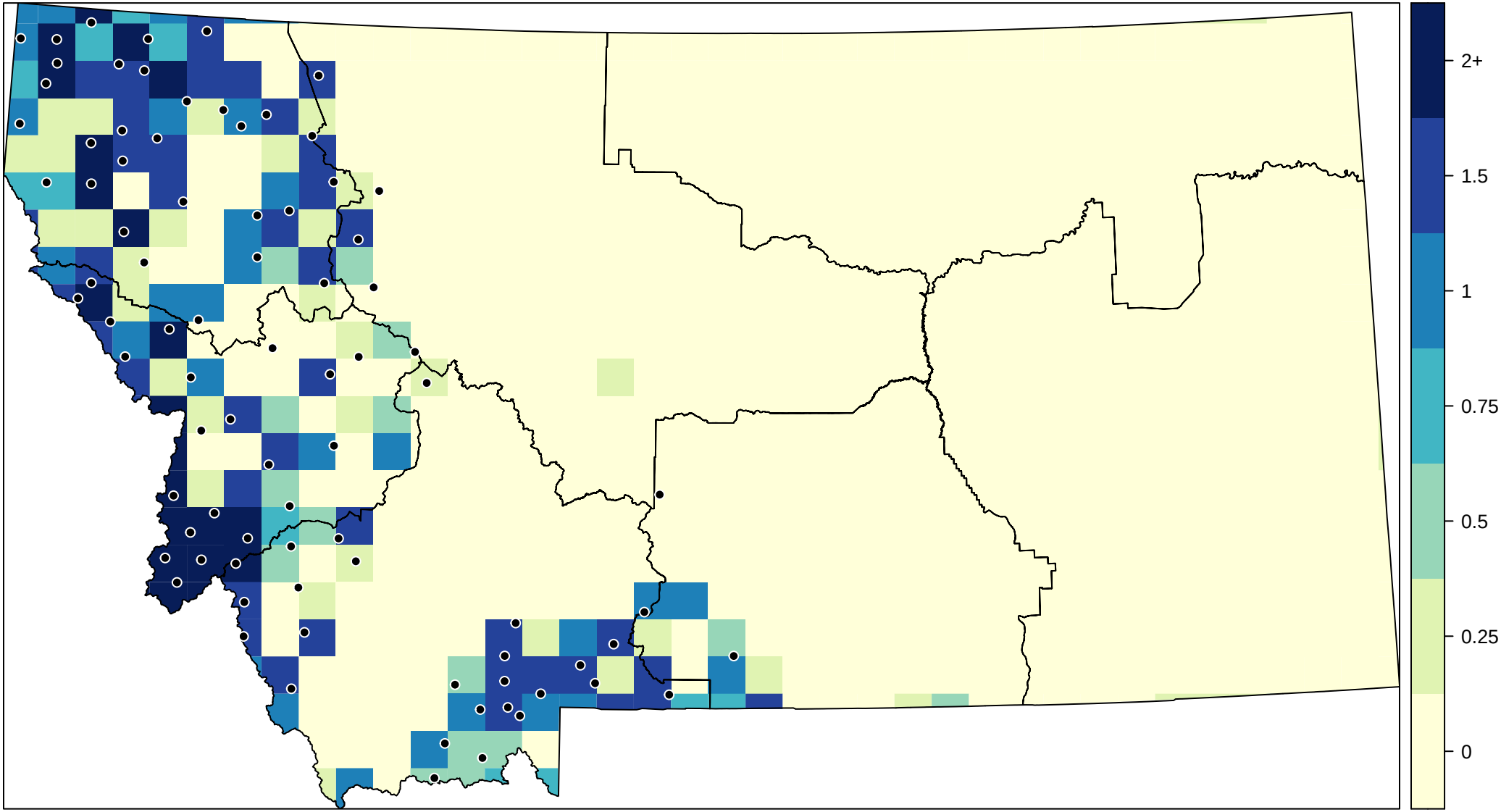
APPENDIX A. PREDICTED DENSITY

On the following pages, iPOM's annual predictions for densities of packs and wolves per 1000 km^2 are shown. Also included are the known pack centroids (black dots on pack density maps) and reported harvest locations (red dots on wolf density maps), demonstrating strong alignment between known wolf activity and iPOM predictions.

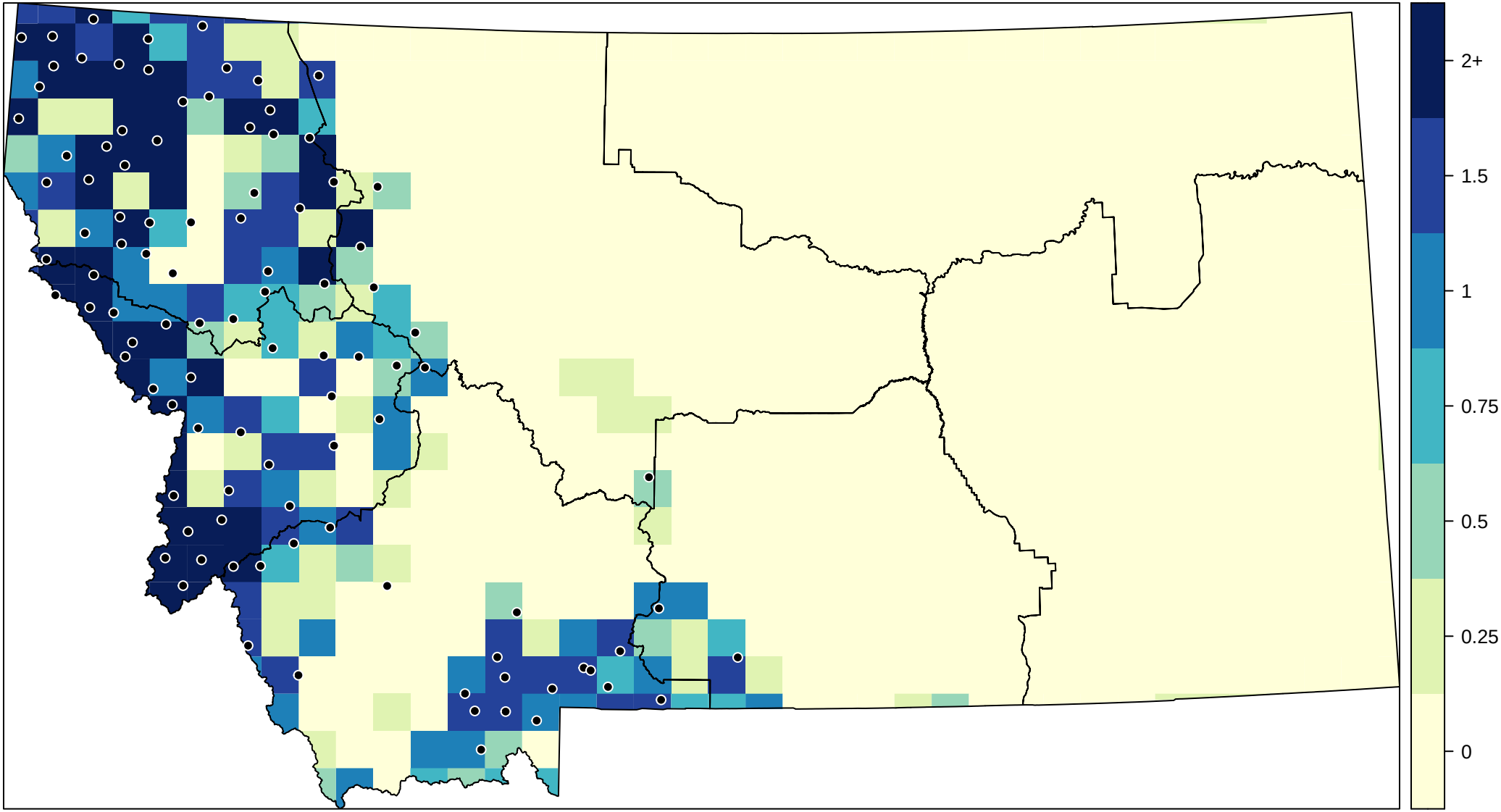
Pack Density (per 1000 km; with known centroids), 2007



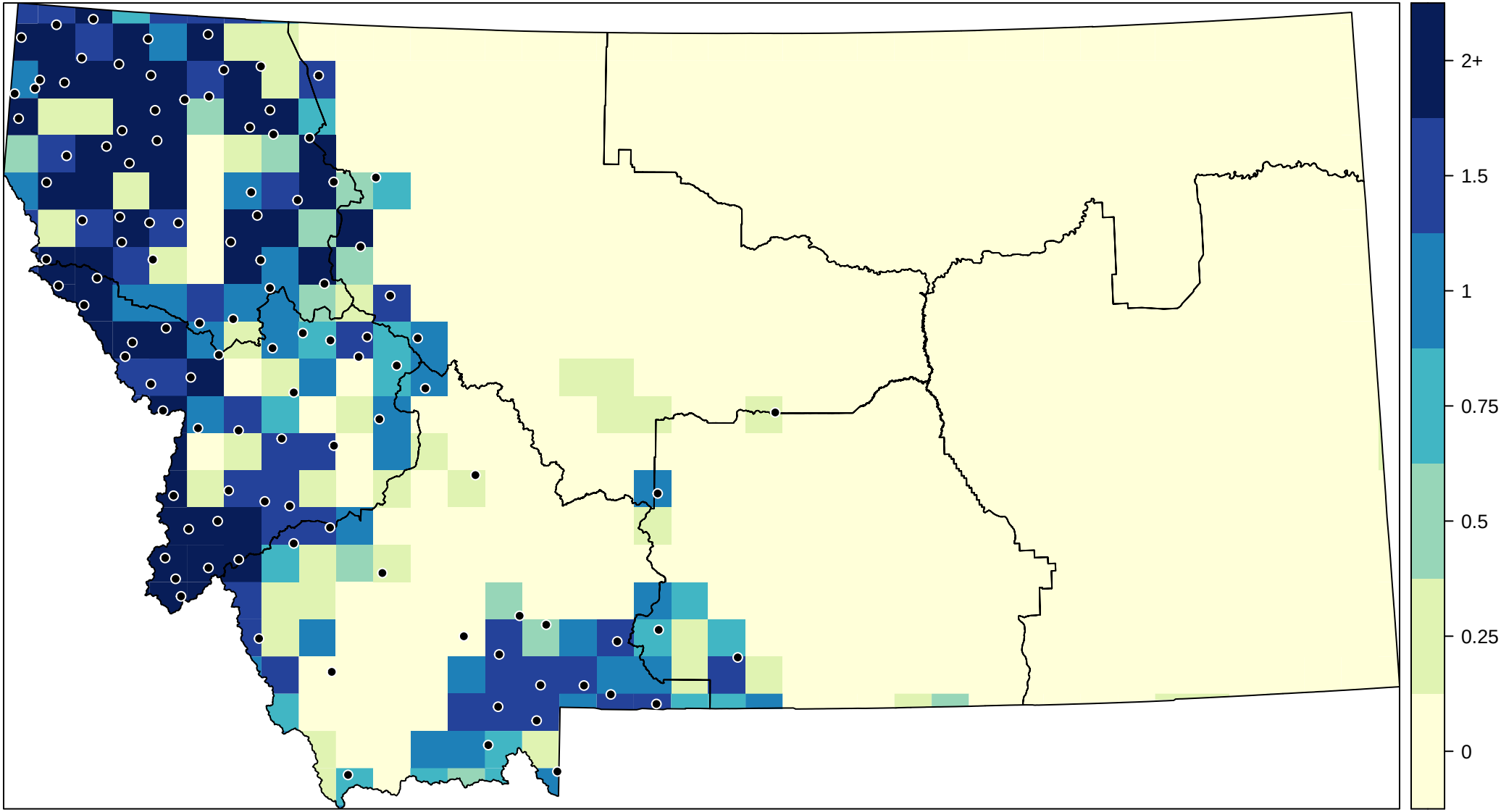
Pack Density (per 1000 km; with known centroids), 2008



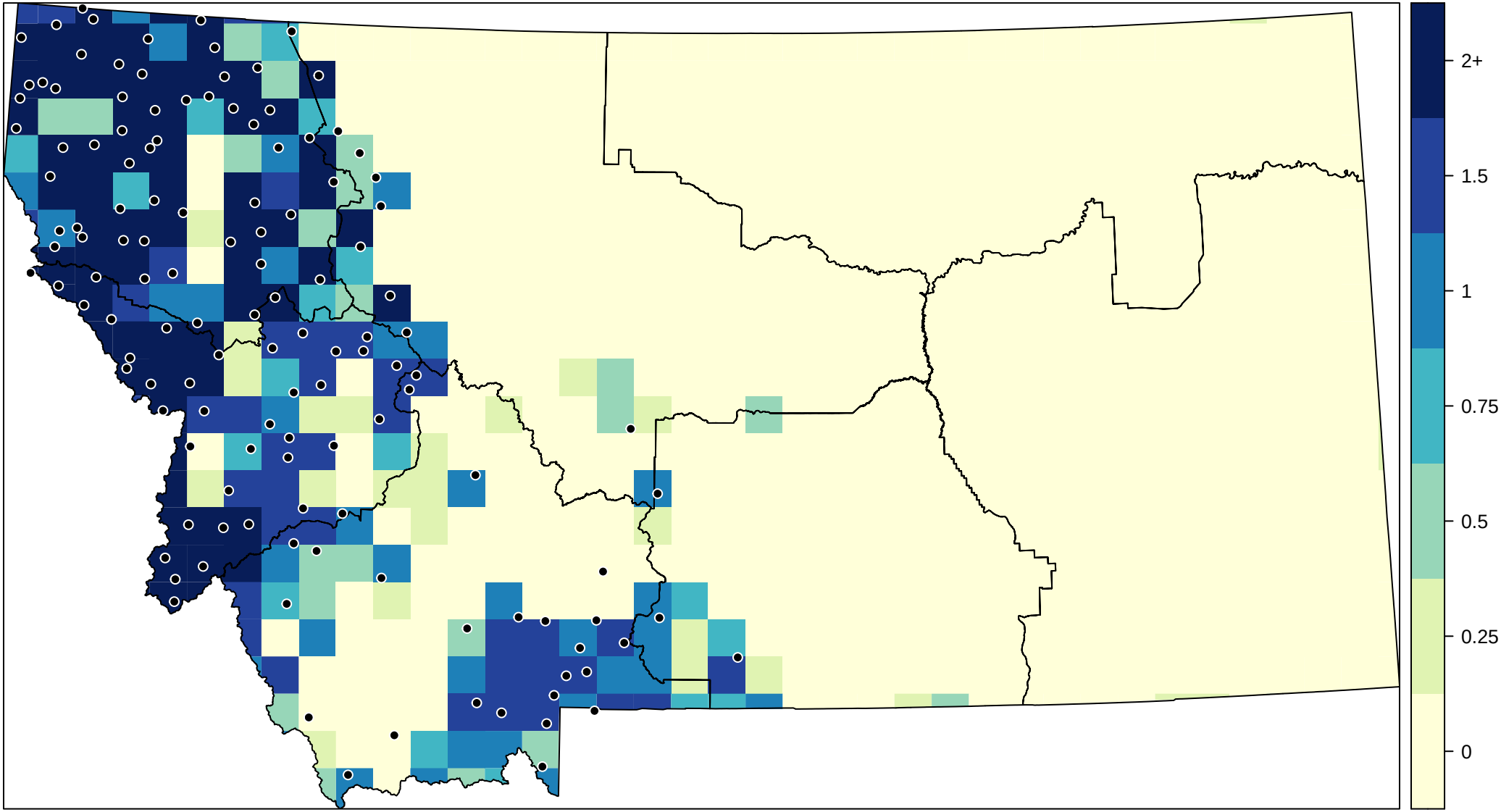
Pack Density (per 1000 km; with known centroids), 2009

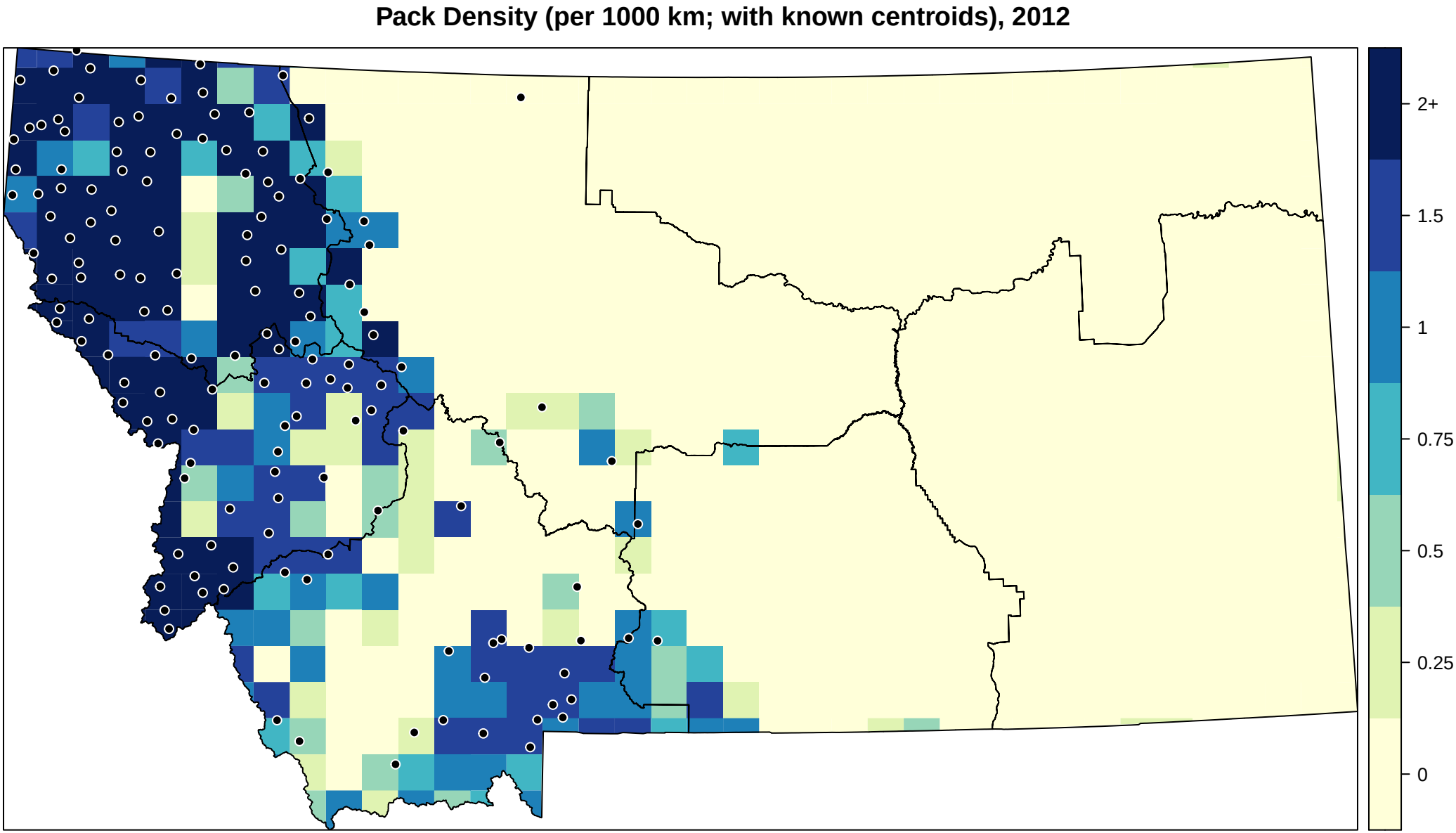


Pack Density (per 1000 km; with known centroids), 2010

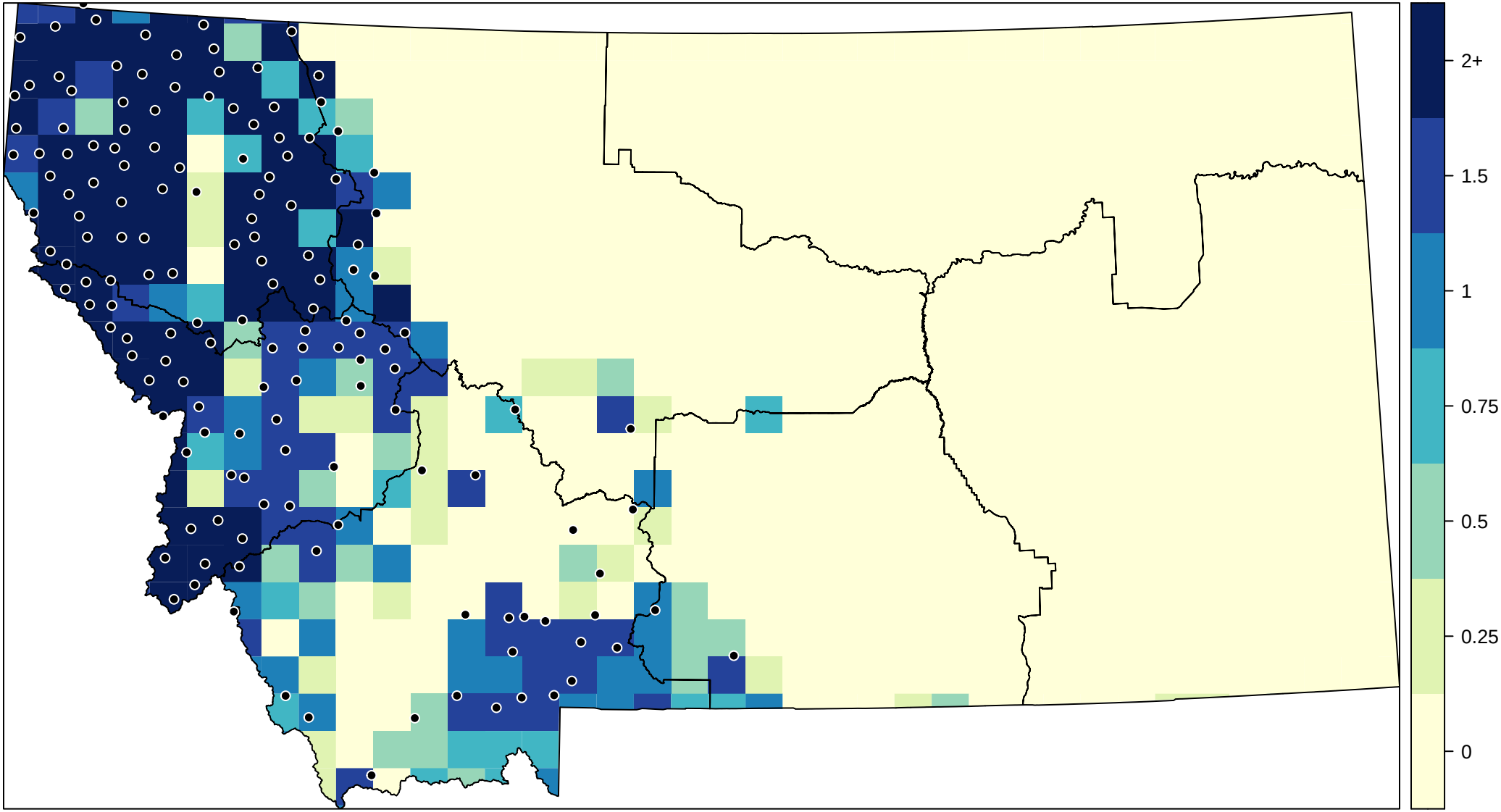


Pack Density (per 1000 km; with known centroids), 2011

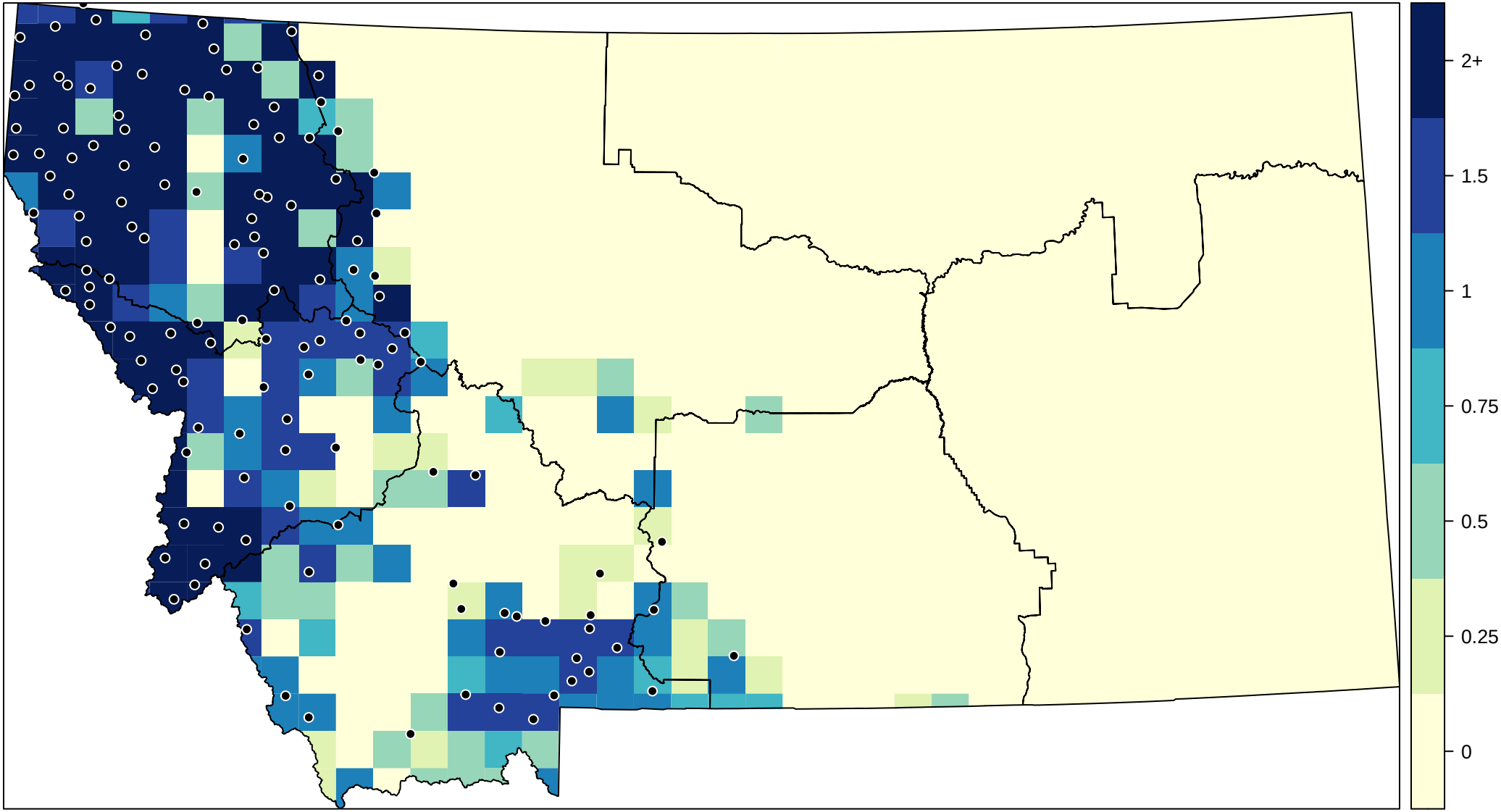



Pack Density (per 1000 km; with known centroids), 2012
2+
1.5
1
0.75
0.5
0.25
0

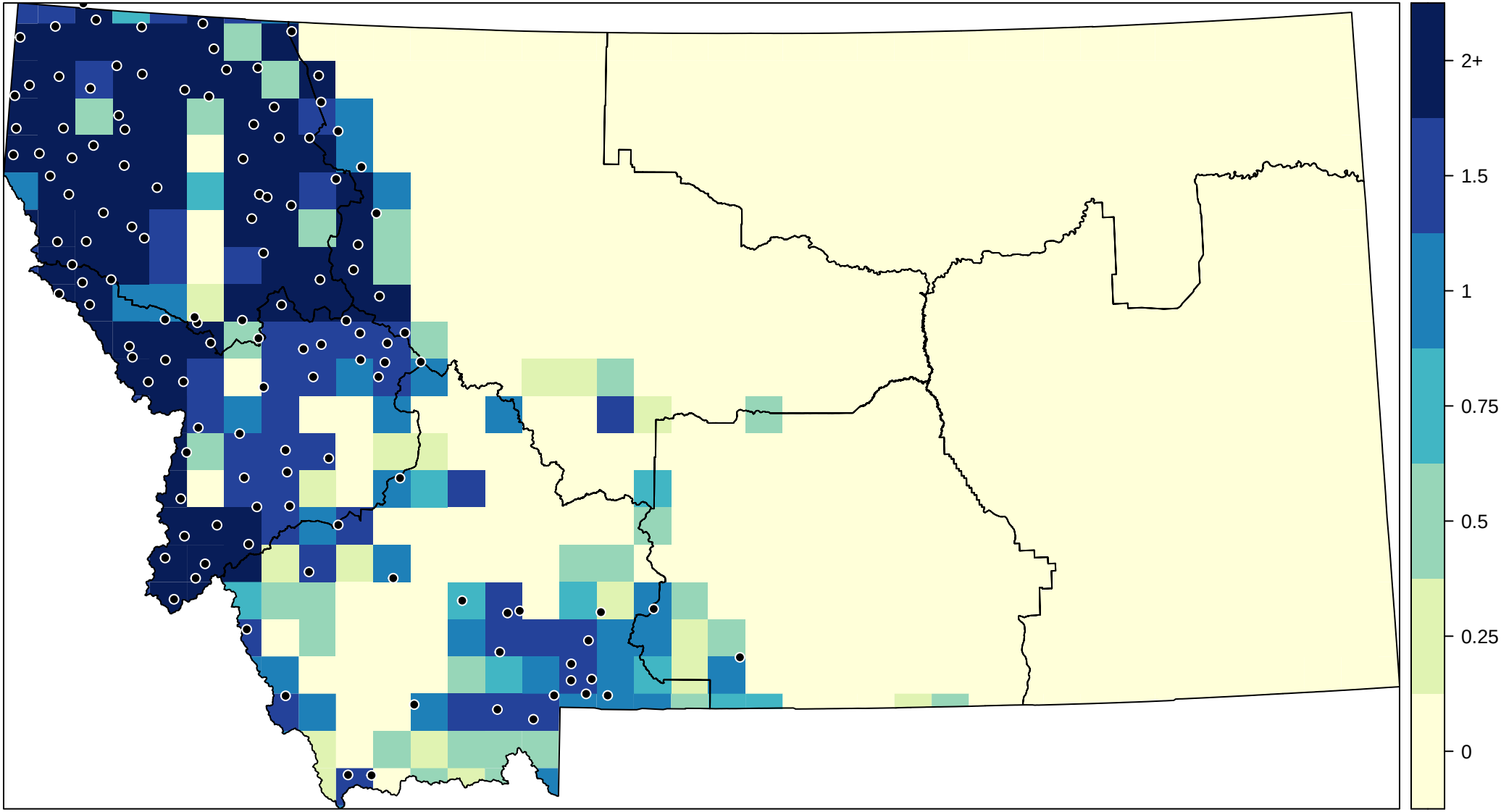
Pack Density (per 1000 km; with known centroids), 2013



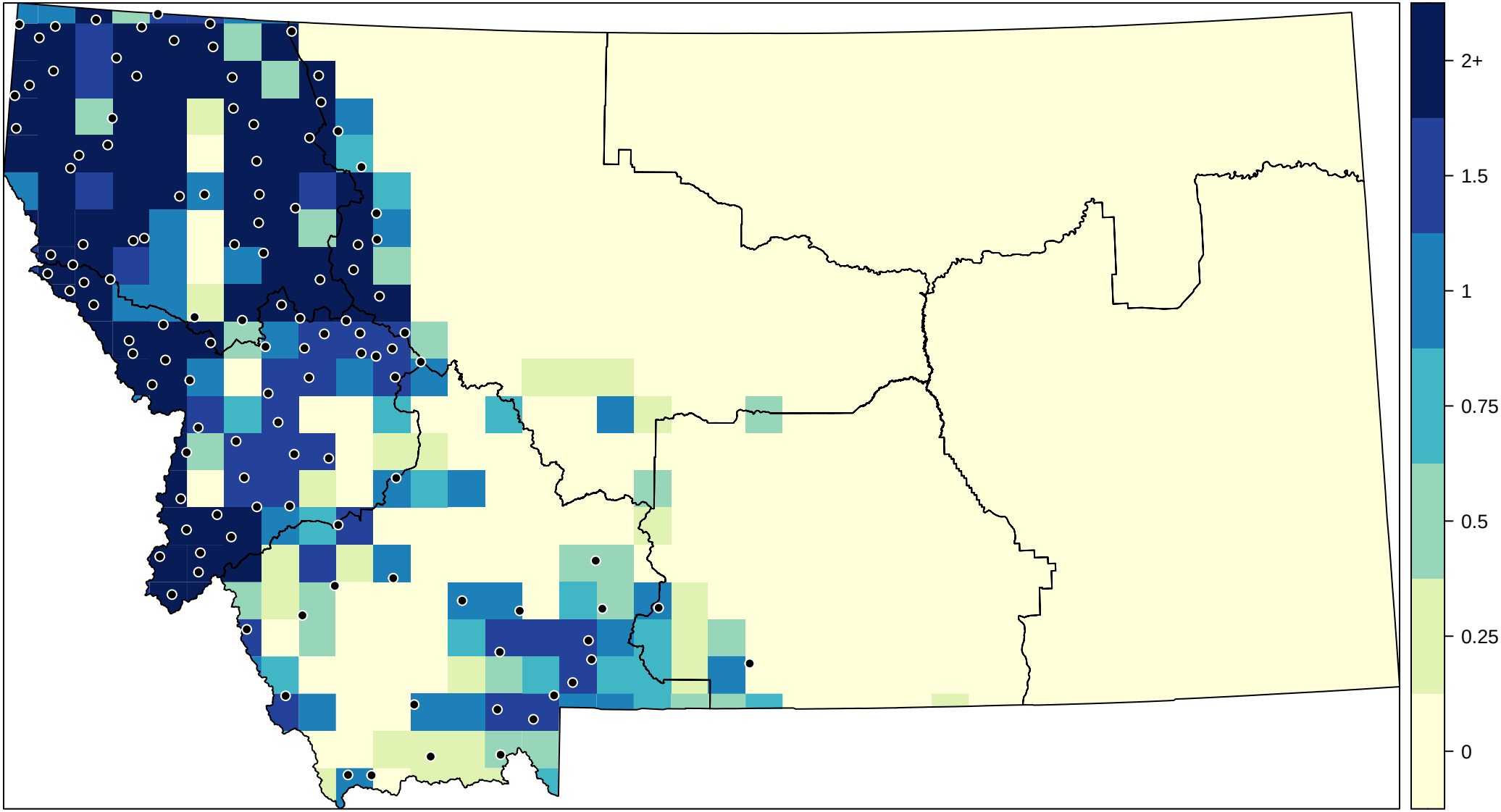
Pack Density (per 1000 km; with known centroids), 2014



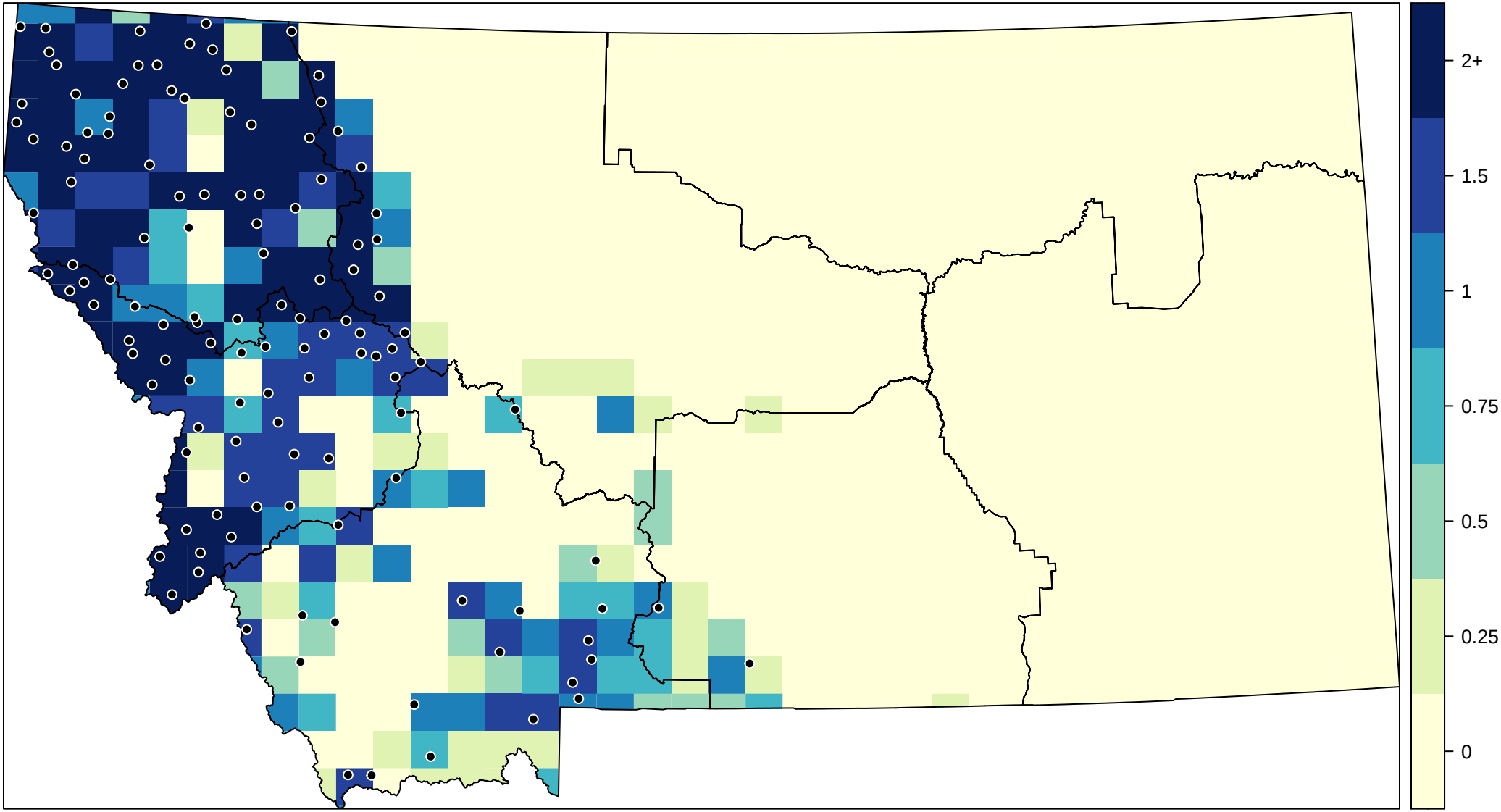
Pack Density (per 1000 km; with known centroids), 2015



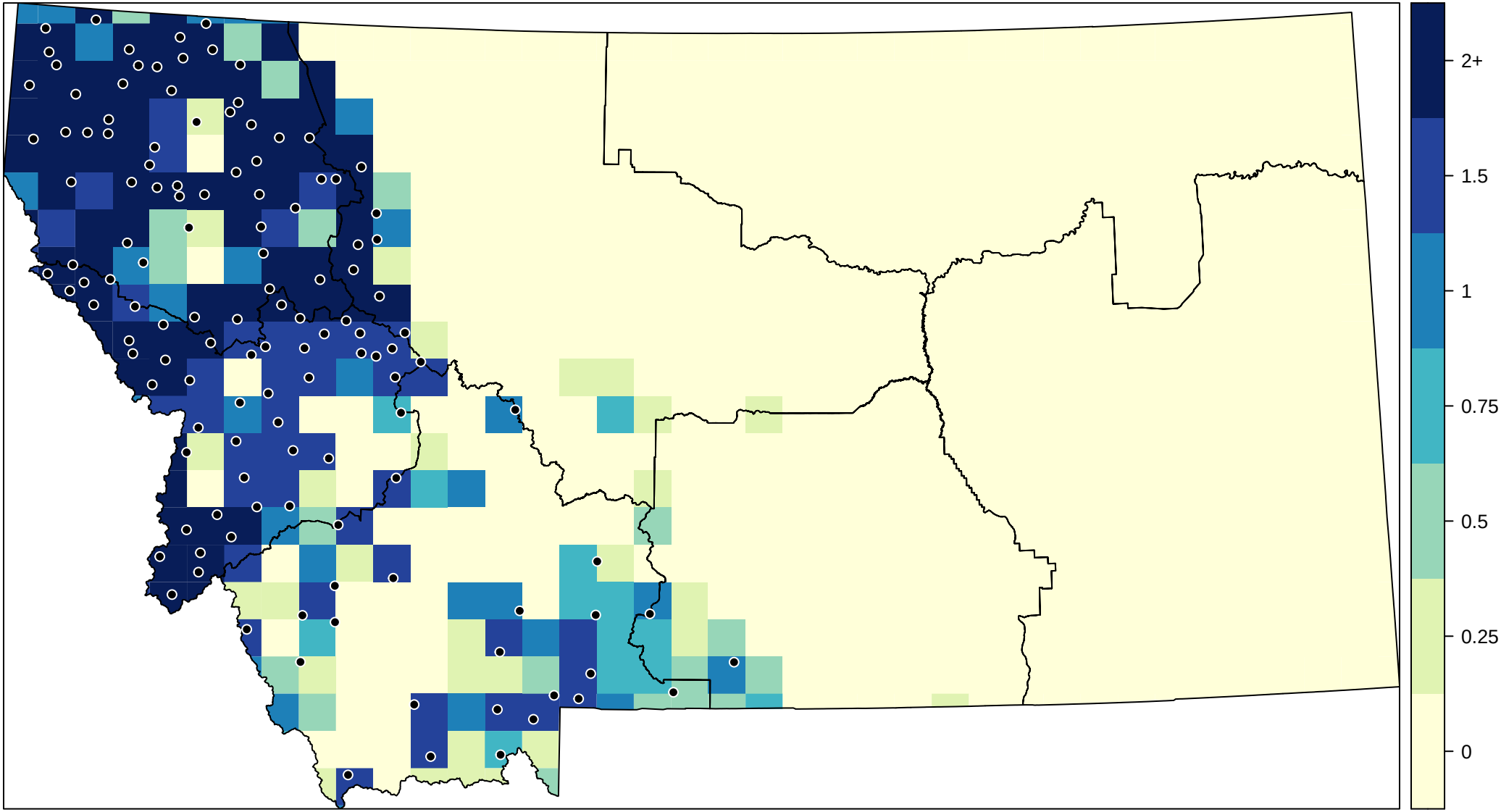
Pack Density (per 1000 km; with known centroids), 2016



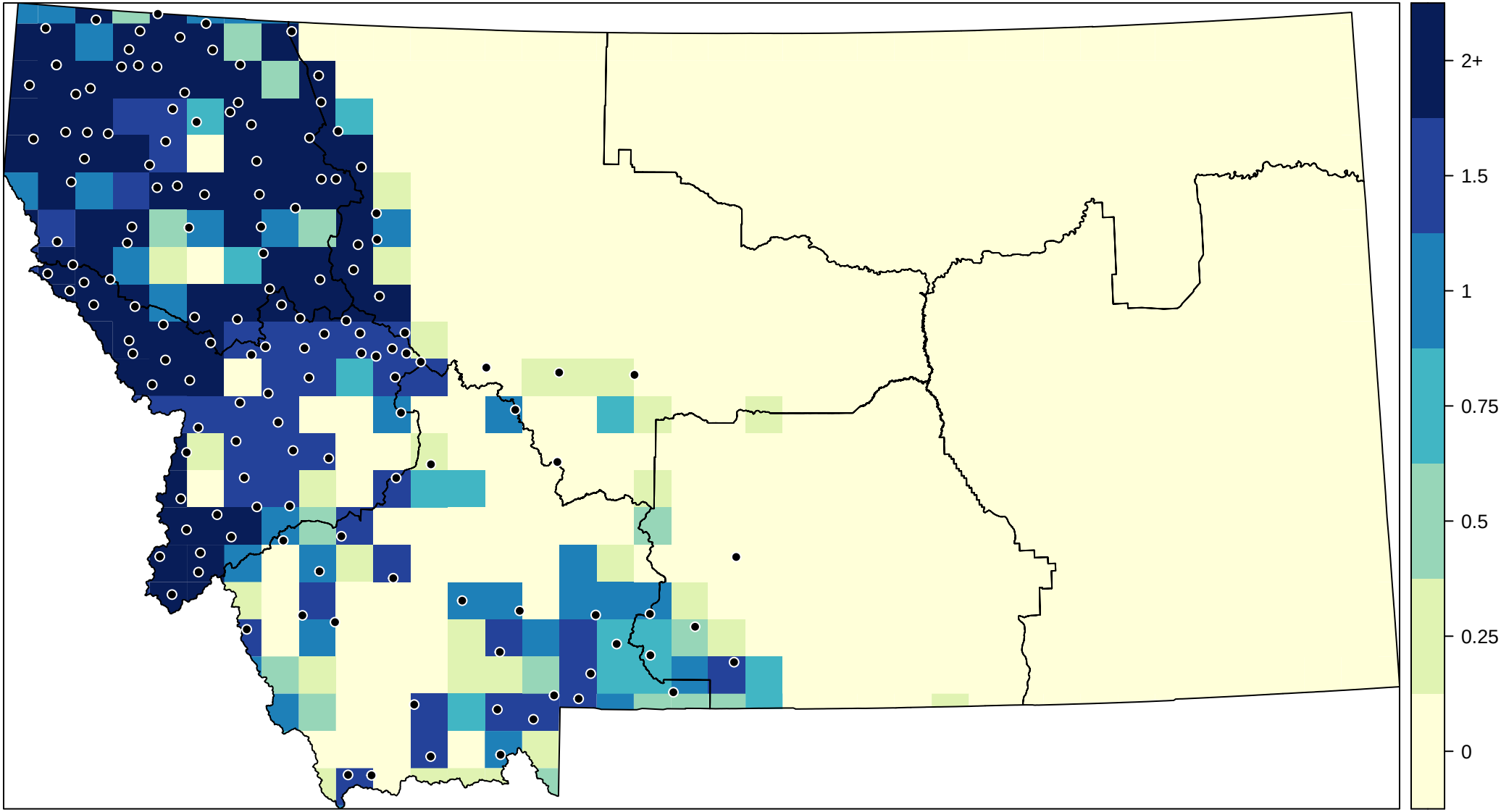
Pack Density (per 1000 km; with known centroids), 2017



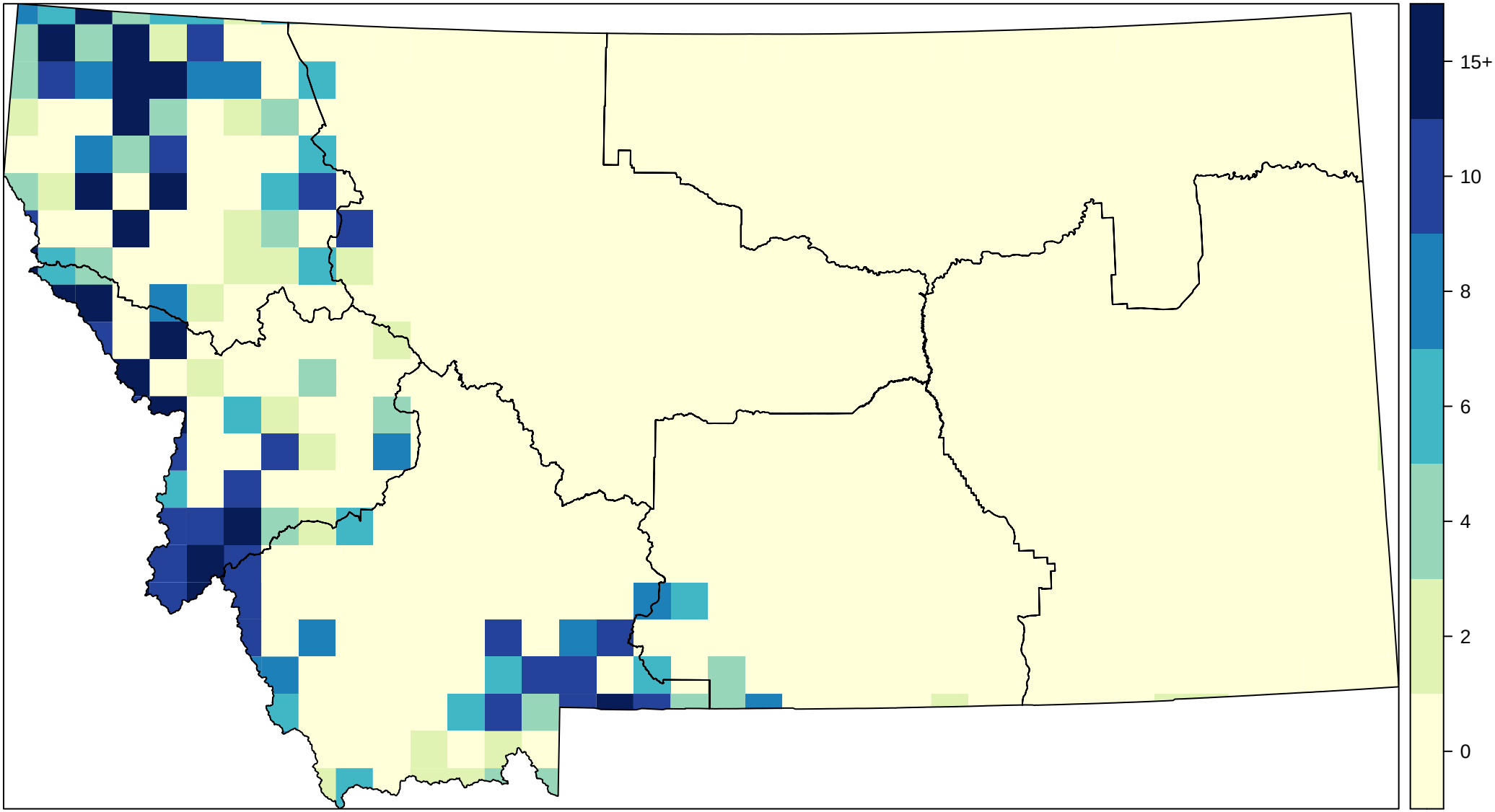
Pack Density (per 1000 km; with known centroids), 2018



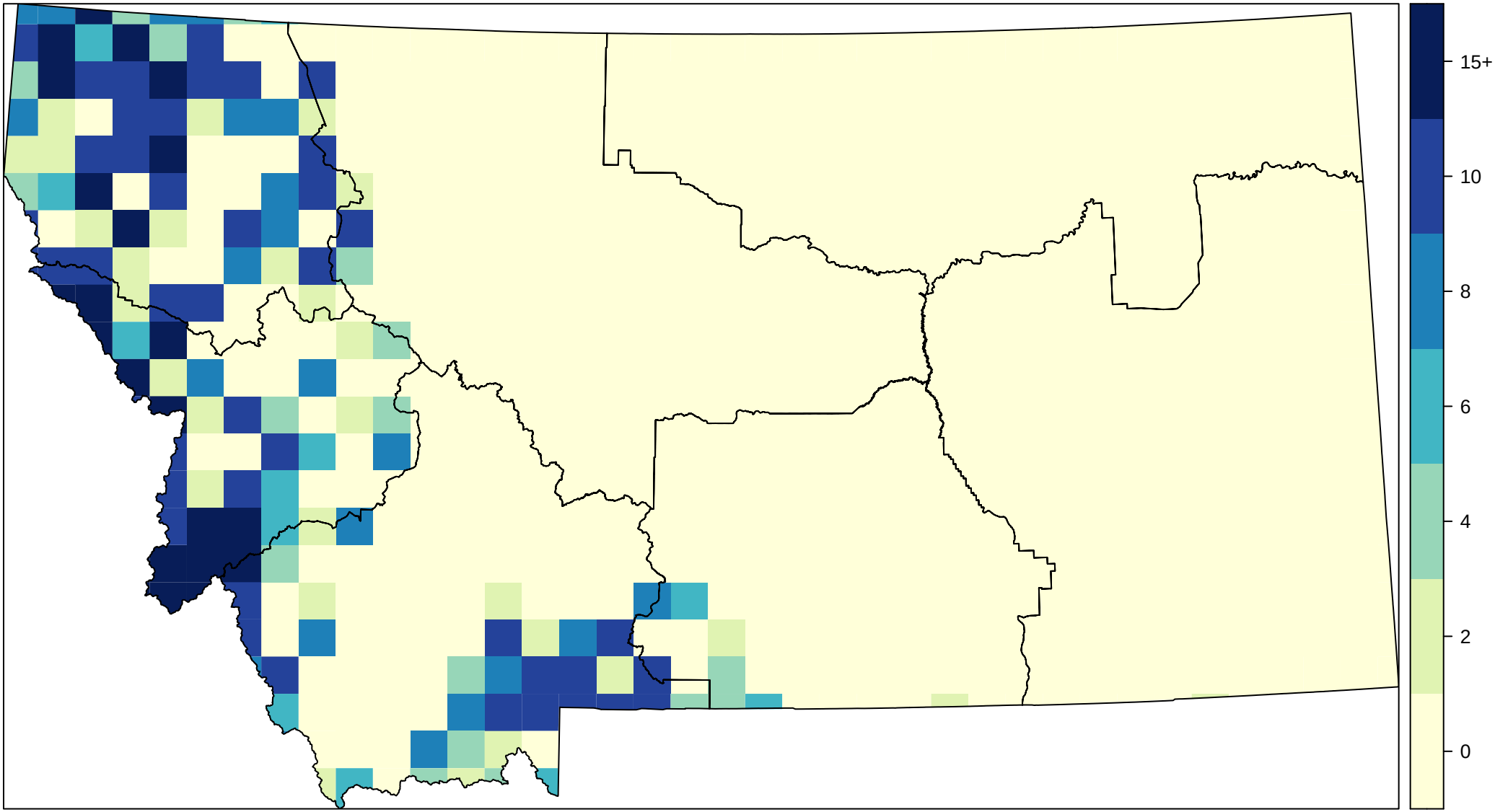
Pack Density (per 1000 km; with known centroids), 2019



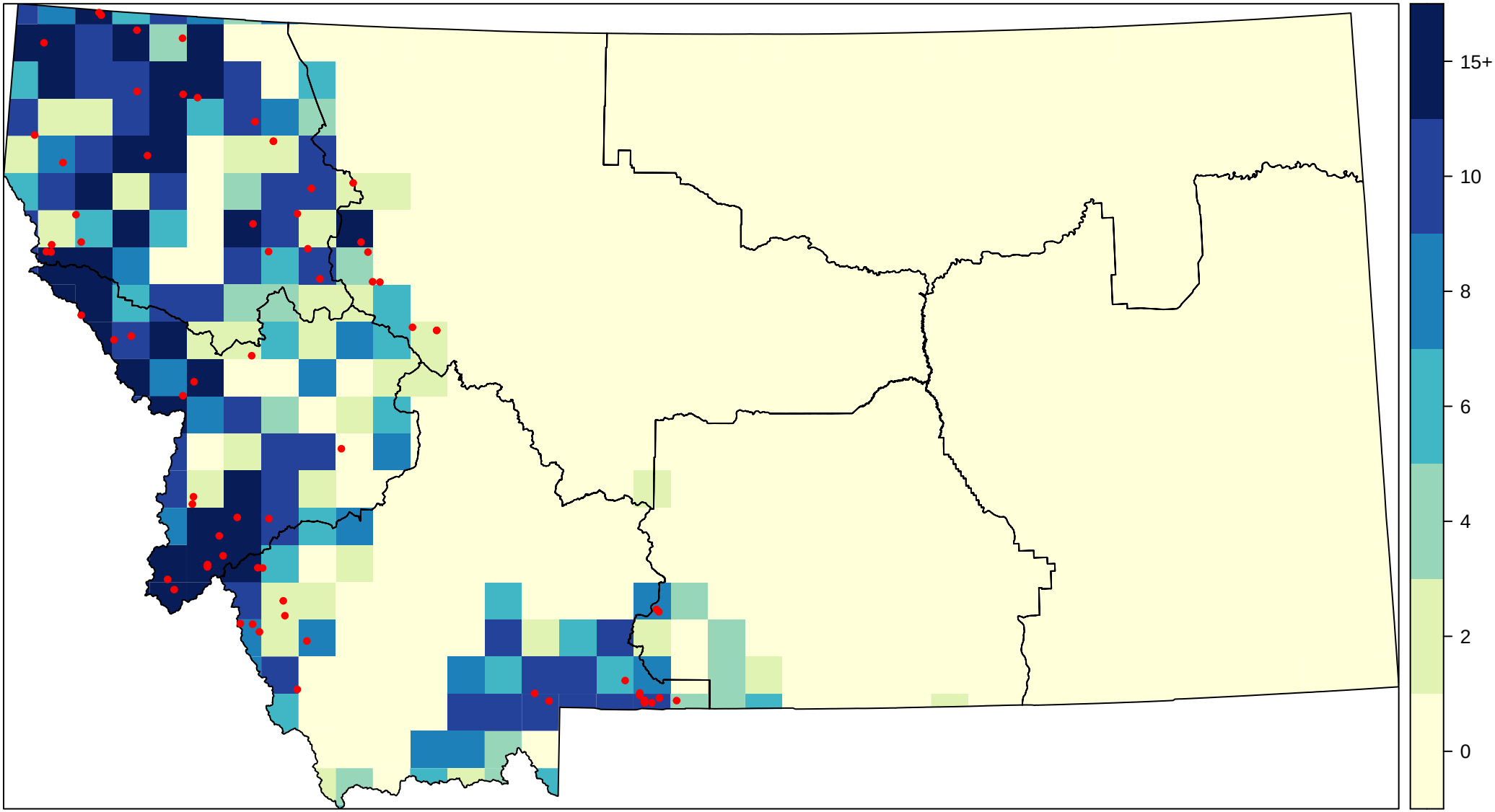
Wolf Density (per 1000 km), 2007



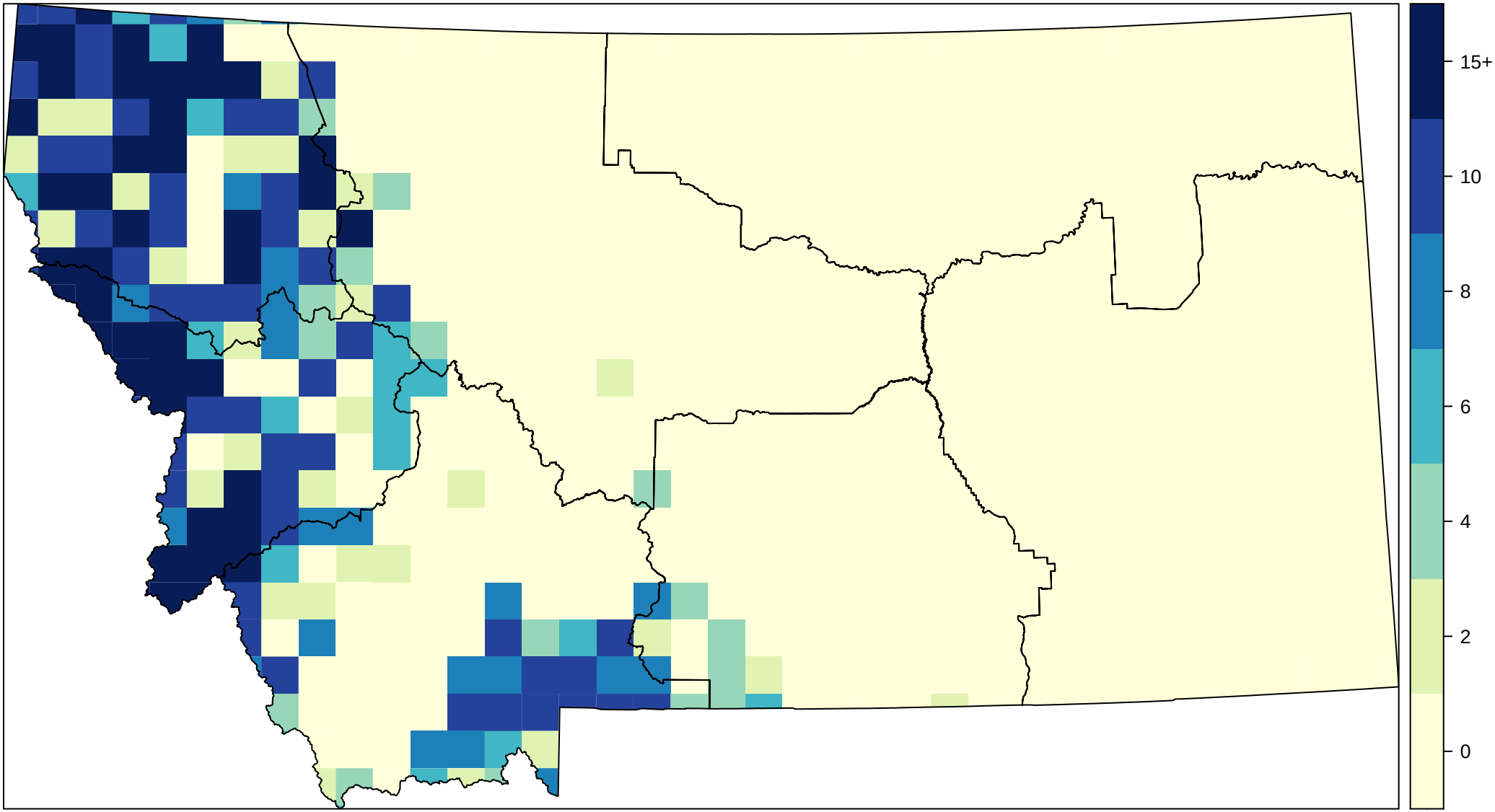
Wolf Density (per 1000 km), 2008



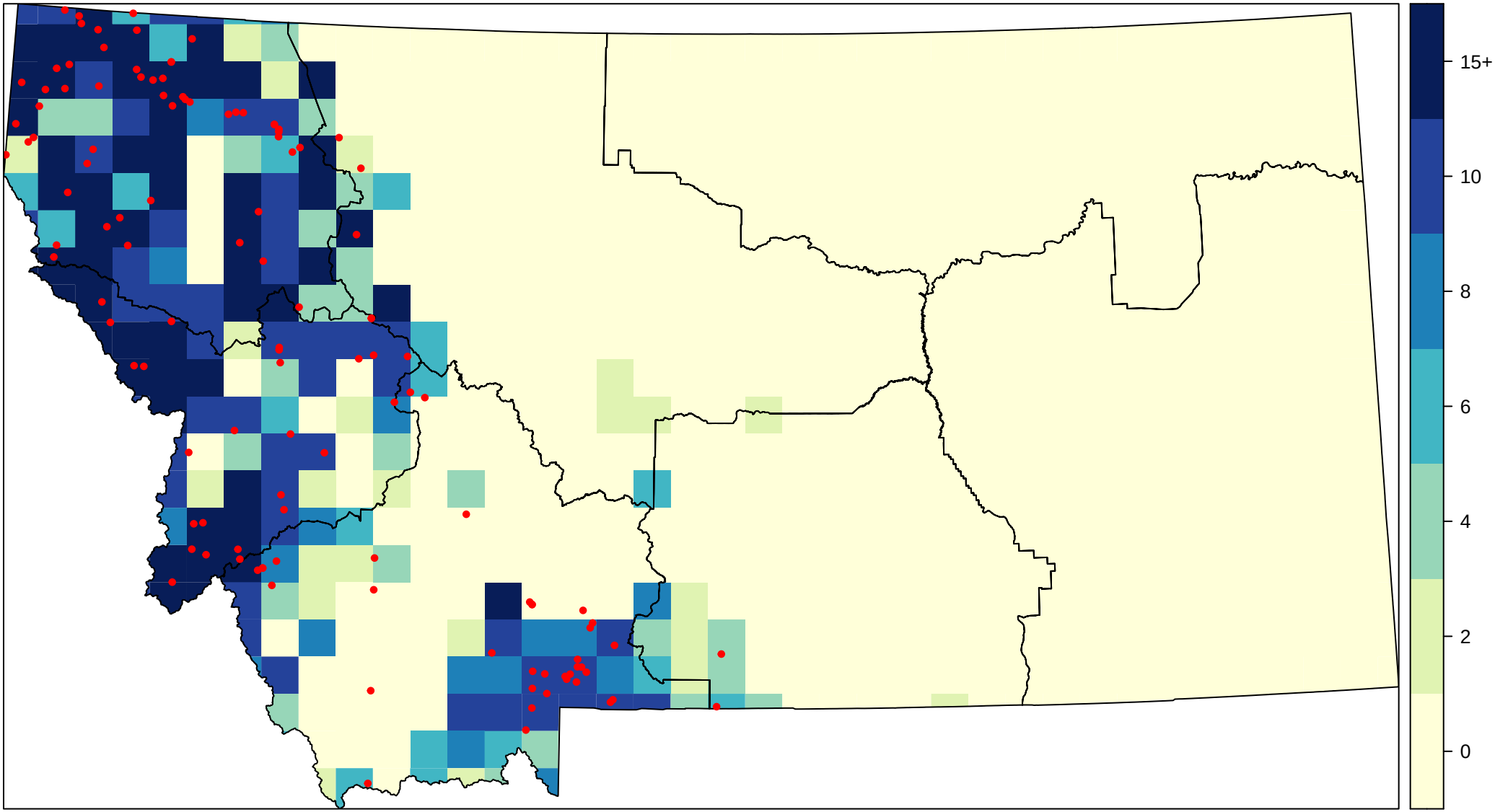
Wolf Density (per 1000 km; with reported harvests), 2009



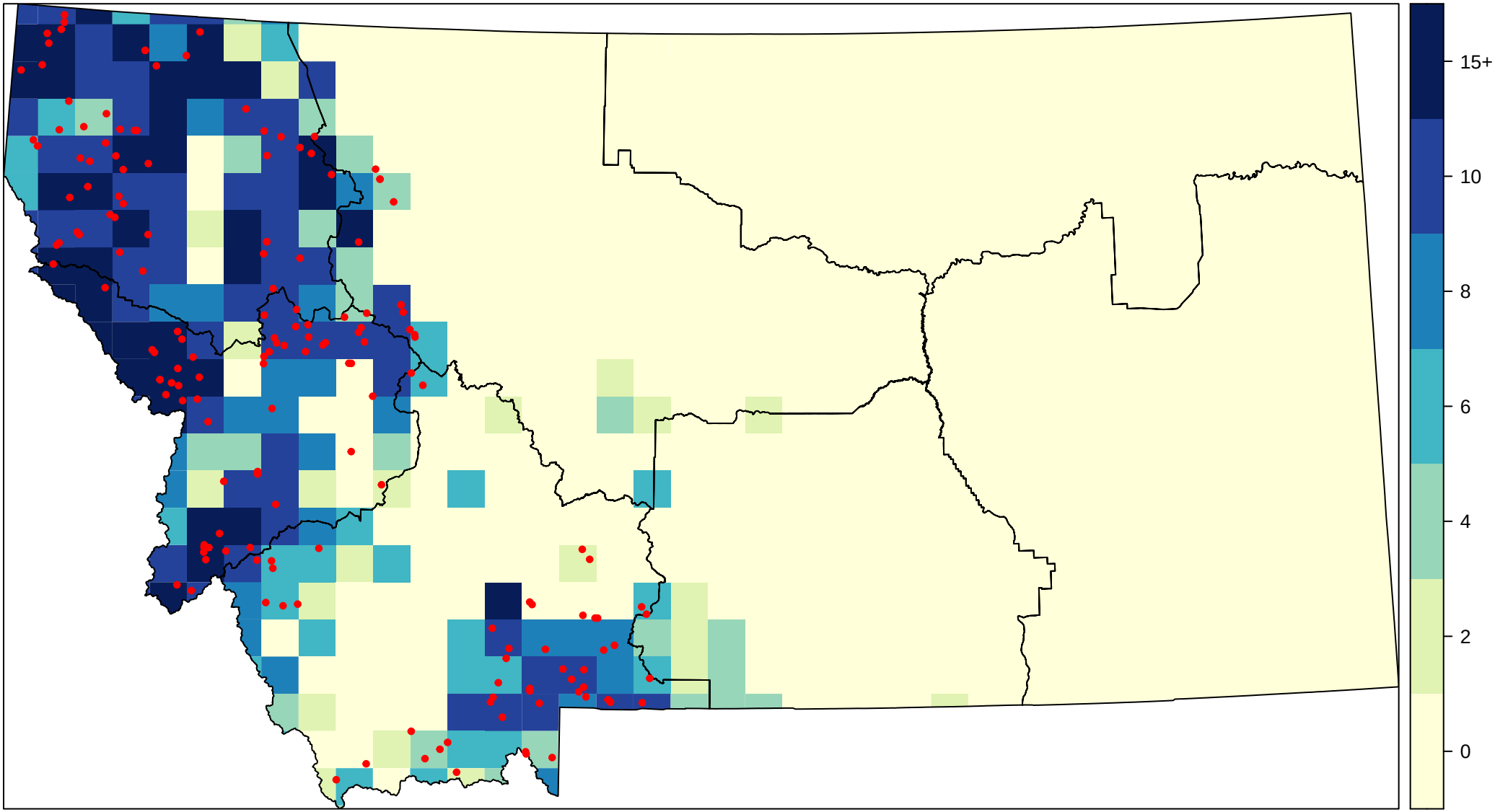
Wolf Density (per 1000 km), 2010



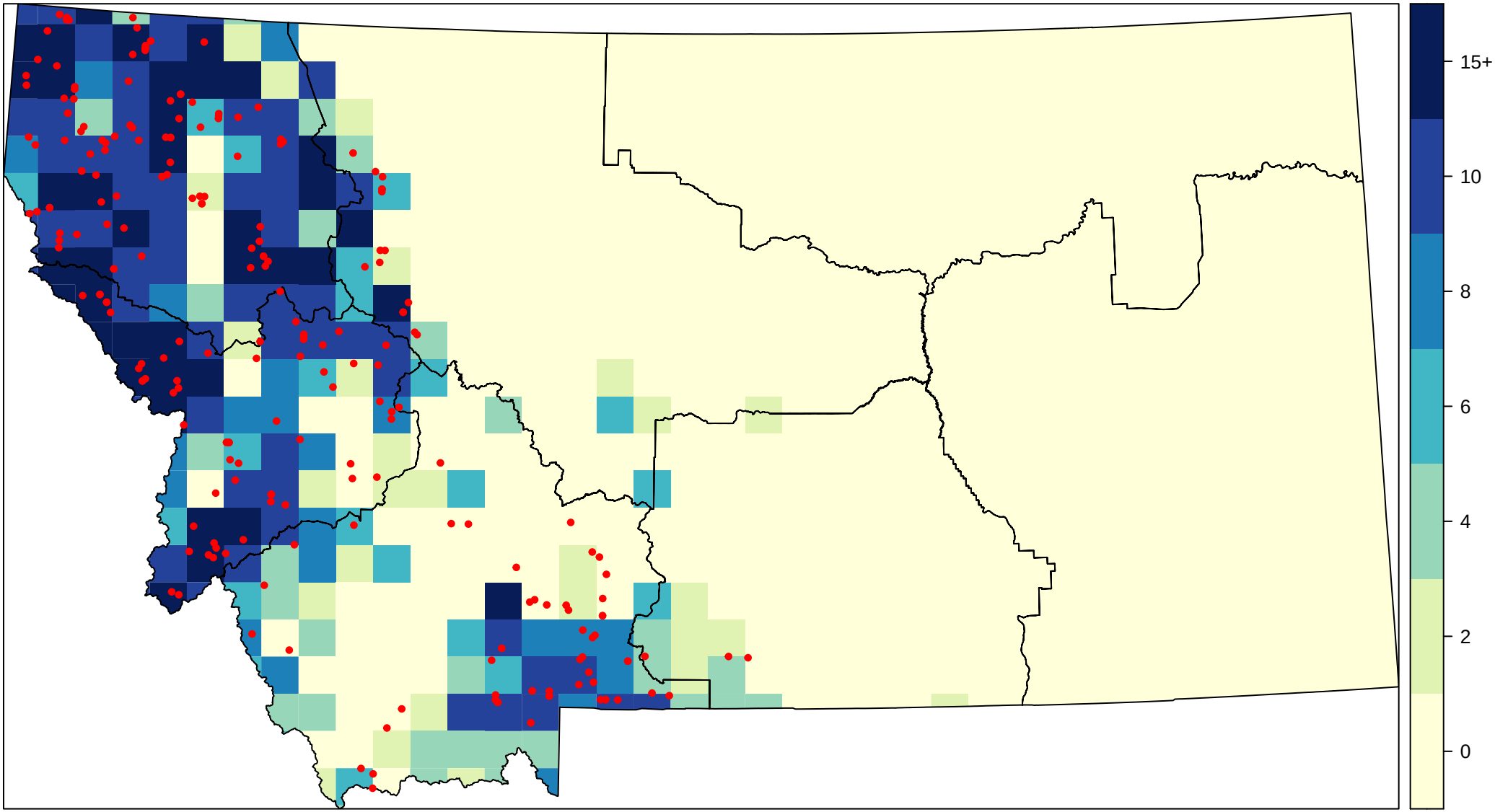
Wolf Density (per 1000 km; with reported harvests), 2011



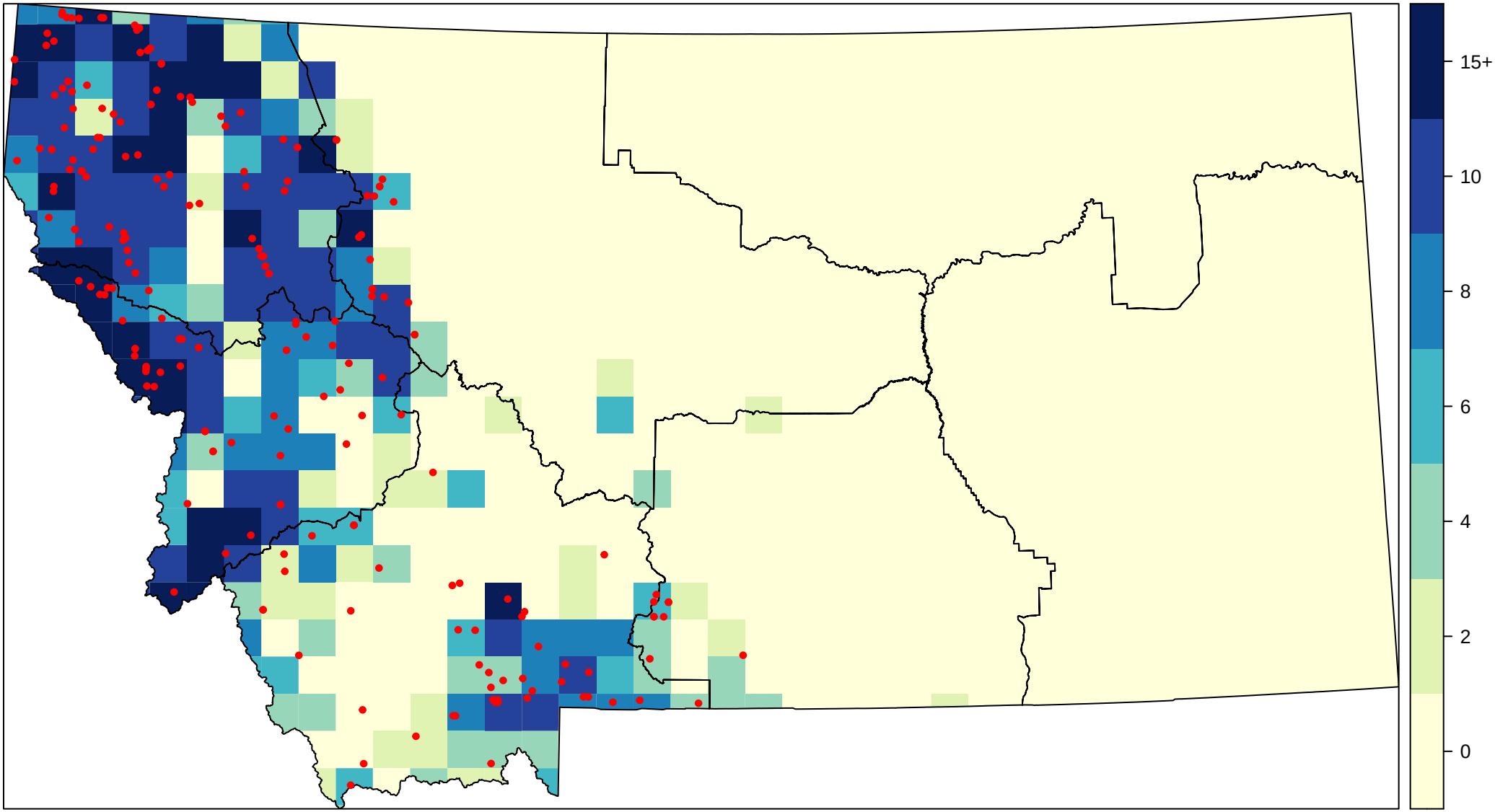
Wolf Density (per 1000 km; with reported harvests), 2012



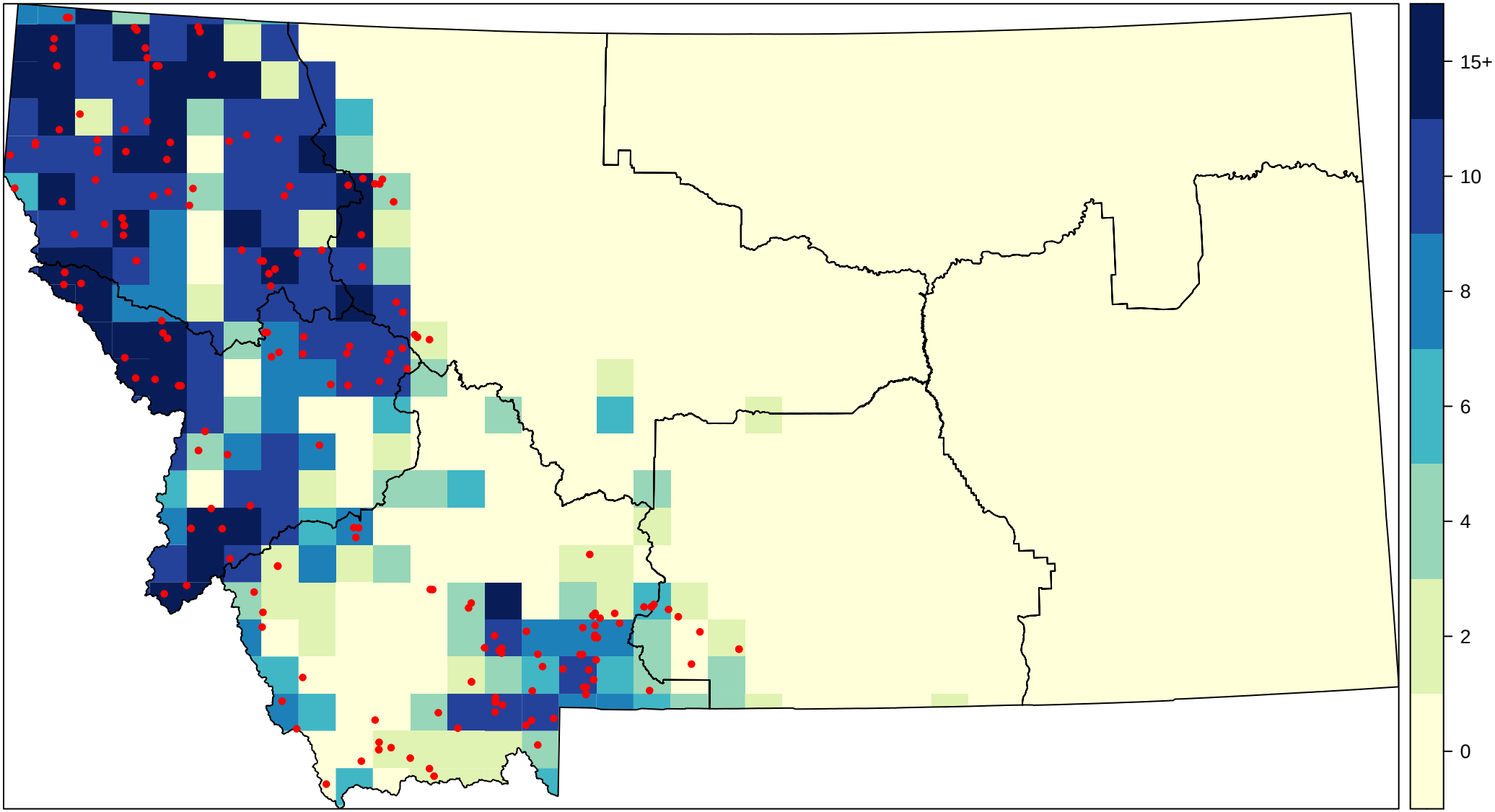
Wolf Density (per 1000 km; with reported harvests), 2013



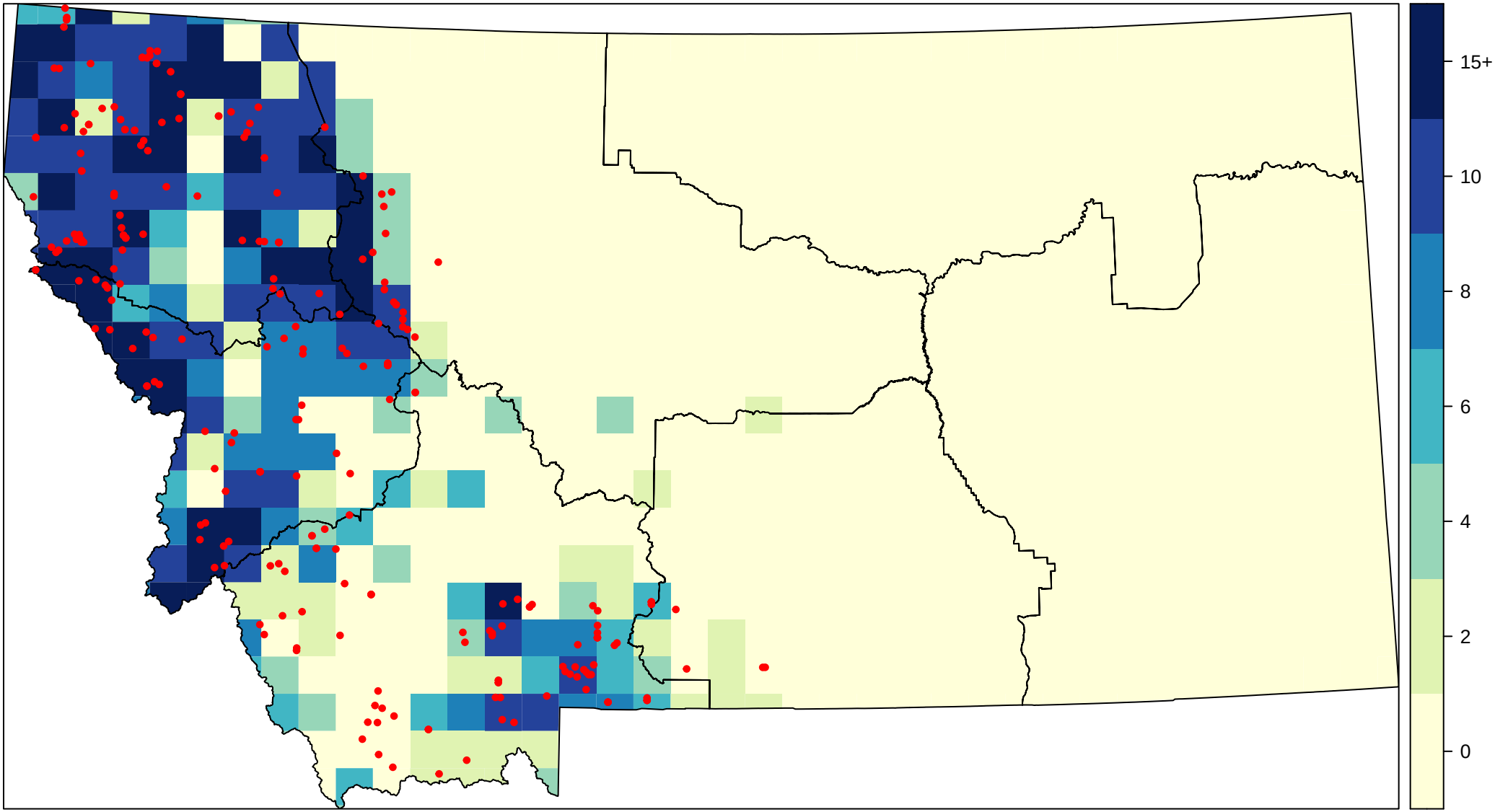
Wolf Density (per 1000 km; with reported harvests), 2014



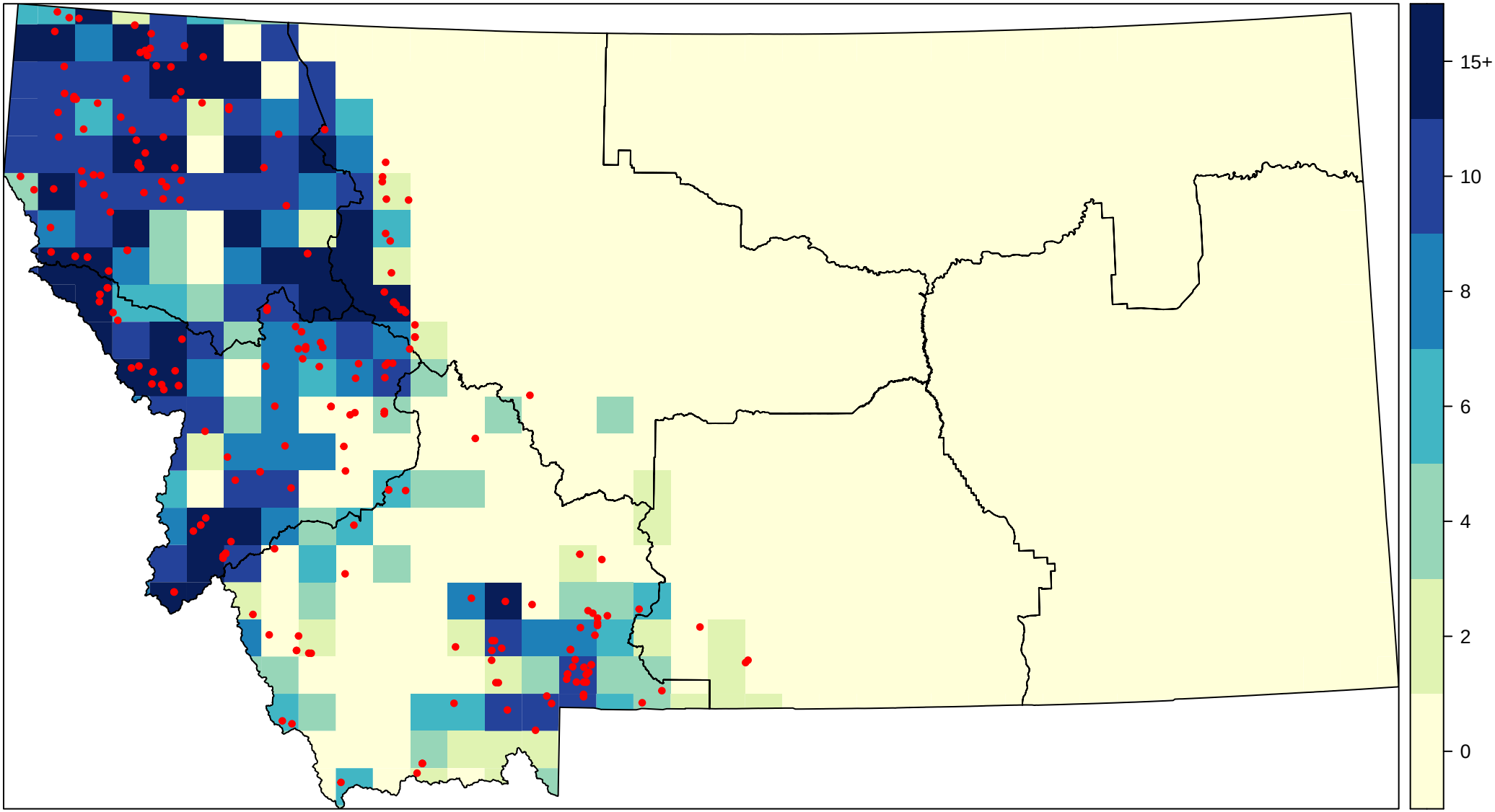
Wolf Density (per 1000 km; with reported harvests), 2015



Wolf Density (per 1000 km; with reported harvests), 2016



Wolf Density (per 1000 km; with reported harvests), 2017



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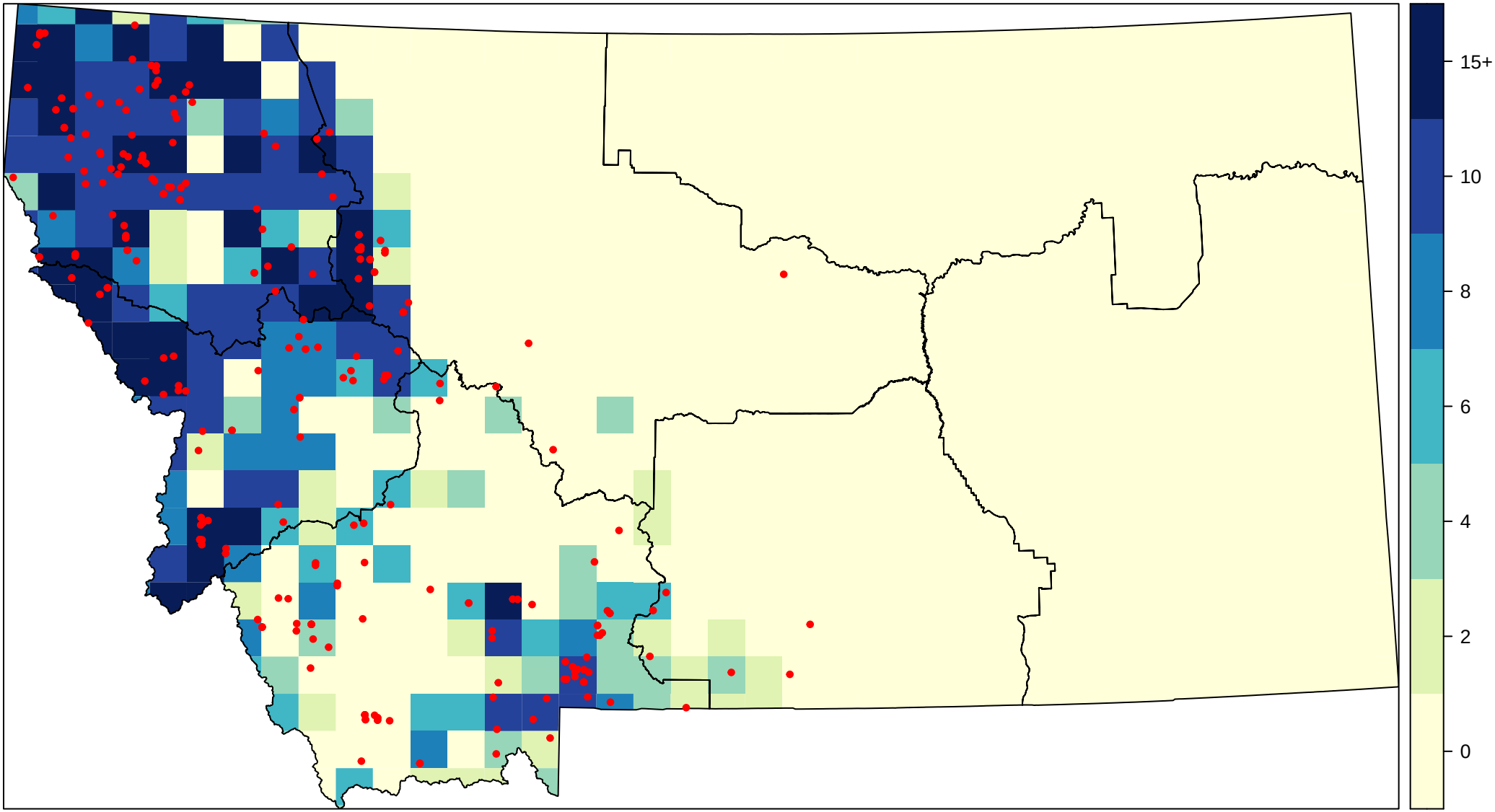

Wolf Density (per 1000 km; with reported harvests), 2019