Predicting abundance of gray wolves in Montana using hunter observations and field monitoring, 2007-2016.

KEVIN PODRUZNY[1], JUSTIN GUDE[1], BOB INMAN[1], JOHN VORE[1], MICHAEL MITCHELL[2], DIANE BOYD[1], NATHAN LANCE[1], ABIGAIL NELSON[1], TYLER PARKS[1], MIKE ROSS[1], TY SMUCKER[1], AND KERI WASH[1]

[1]**MONTANA DEPARTMENT OF FISH, WILDLIFE AND PARKS**
[2]**UNIVERSITY OF MONTANA, MONTANA COOPERATIVE WILDLIFE RESEARCH UNIT**

Introduction

Since the early 1980s, as wolf populations began recovering in Montana, the numbers of packs, breeding pairs, and total wolves have been documented by attempting to locate and count all individuals. It was assumed that these minimum counts provided an index to the true populations when wolf numbers were small. In the early years, most wolf packs had radio-collared individuals, and intensive monitoring was possible to identify new packs and most individuals within packs. Only verified observations were used, thus these counts represented minimums. In 1995, when the US Fish and Wildlife Service reintroduced wolves into Yellowstone National Park and central Idaho, the end-of-year count for wolves residing in Montana was only 66. By 2011 the minimum count had reached 653 and was 477 in 2016. The capacity for MFWP personnel to monitor a larger and rapidly growing wolf population has been declining given robust wolf population growth since about 2006. The traditional field-based methods yield minimum counts that are conservative and inevitably (and probably increasingly) below the true population sizes, and the degree of undercount is unknown. Consequently, MFWP explored other, cost-effective methods that could more accurately be described as population estimates that account for uncertainty, as opposed to minimum counts.

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

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

Methods

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

Estimating Area Occupied by Wolves in Packs

To estimate the area occupied by wolf packs from 2007 to 2016, we used a multi-season false-positives occupancy model (Miller et al. 2013) in program PRESENCE (Hines 2006). First, we created an observation grid for Montana (Figure 1A) with a cell size large enough to ensure observations of packs across sample periods, yet small enough to minimize the occurrences of multiple packs in the same cell on average (cell size = 600 km^2). We used locations of wolves in packs (2-25 wolves) reported by a random sample of unique deer and elk hunters during MFWP annual Hunter Harvest Surveys (Figure 1B) and assigned the locations to cells (Figure 1C). We modeled detection probability, initial occupancy, and local colonization and local extinction from 5, 1-week encounter periods and verified locations (Figure 1D) using covariates that were summarized at the grid level (Figure 1E). We estimated patch-specific estimates of occupancy (Figure 1F) and estimated the total area occupied by wolf packs by multiplying patch-specific estimates of occupancy by their respective patch size and then summing these values across all patches (Figure 1G). Our final estimates of the total area occupied by wolf packs were adjusted for partial cells on the border of Montana and included model projections for reservations and national parks where no hunter survey data were available.

Model covariates for detection included hunter days per km^2 by hunting district per year (an index to spatial effort), proportion of wolf observations that were mapped (a correction for effort), low use forested and non-forested road densities (indices of spatial accessibility), a spatial autocovariate (the proportion of neighboring cells with wolves seen out to a mean dispersal distance of 100 km), and patch area sampled (because smaller cells on the border of Montana, parks, and Indian Reservations have less hunting activity and therefore less opportunity for hunters to see wolves). Model covariates for occupancy, colonization, and local extinction included a principal component constructed from several autocorrelated environmental covariates (percent forest cover, slope, elevation, latitude, percent low use forest roads, and human population density), and recency (the number of years with verified pack locations in the previous 5 years).

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

Estimating Numbers of Wolf Packs

To predict the total number of wolf packs in Montana from 2007 to 2016 we first established an average territory size for wolf packs in Montana (Figure 1H). Rich et al. (2012) calculated 90% kernel home ranges from radio telemetry locations of wolves collared and tracked by wolf MFWP biologists for research and/or management from 2008 to 2009. We assumed the mean estimate of territory size from these data was constant during 2007-2016. For each year, we estimated the number of wolf packs by dividing our estimates of total area occupied by the mean territory size (Figure 1I). We then accounted for annual changes in the proportion of territories that were overlapping (non-exclusive) using the number of observed cells occupied by verified pack centers.

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

Estimating Numbers of Wolves

To predict the total number of wolves in Montana from 2007 to 2016, we first calculated average pack size from the distribution of packs of known size (Figure 1J). Pack sizes were established by MFWP biologists for packs monitored for research and/or management. We used end-of-year pack counts for wolves documented in Montana from 2007 to 2016; we only used pack counts MFWP biologists considered complete. Typically, intensively monitored packs with radio-collars provided good counts more often than packs that were not radio-marked. For each year, we estimated total numbers of wolves in packs by multiplying the estimate of mean pack size by the annual predictions of number of packs (Figure 1K).

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

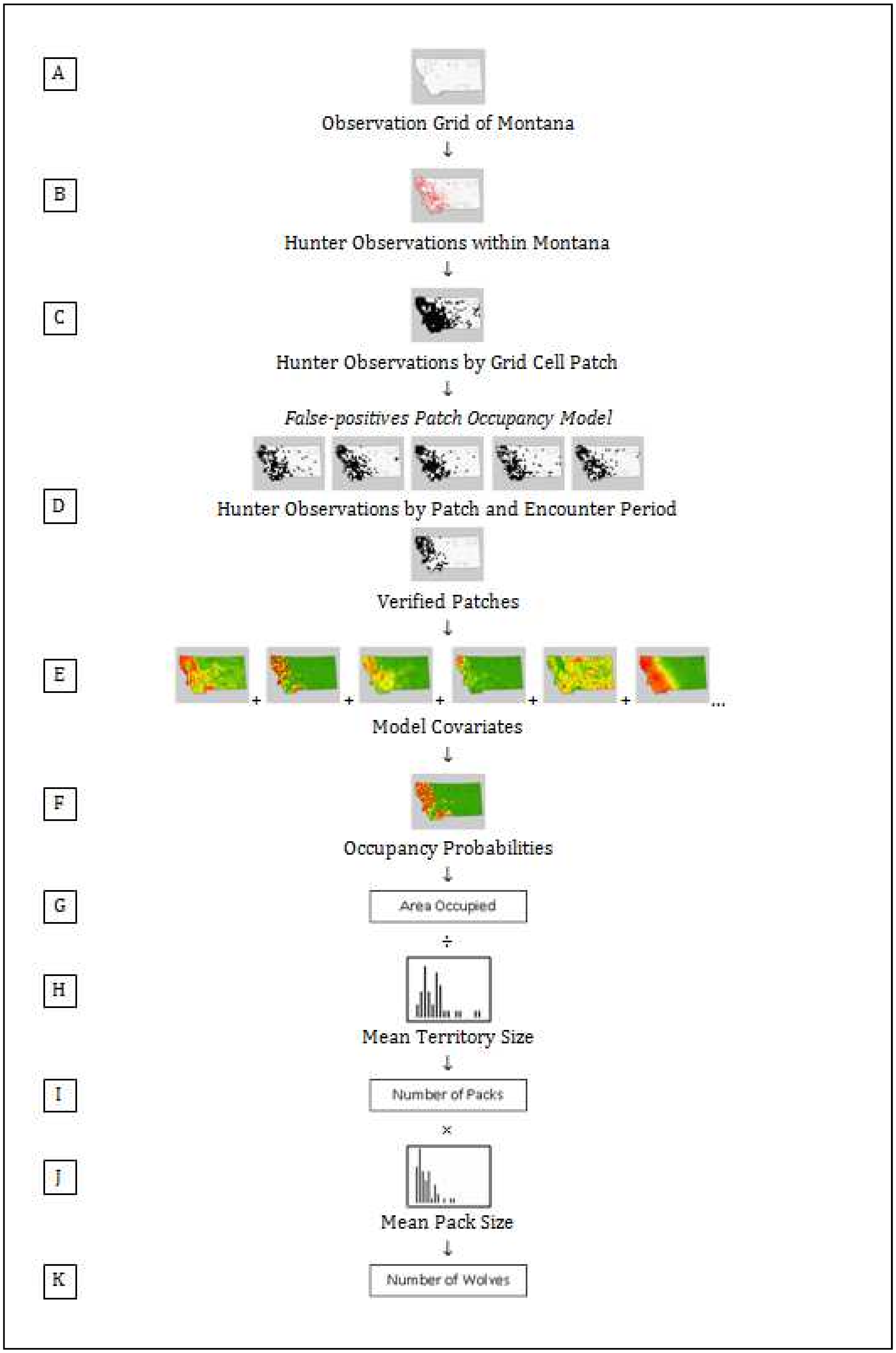

Figure 1. Schematic for method of estimating the area occupied by wolves, number of wolf packs and number of wolves in Montana, 2007-2016.

Results

Estimating Area Occupied by Wolves in Packs

From 2007 to 2016, 50,039, 81,479, 80,493, 82,387, 81,532, 76,996, 76,862, 59,747, 56,973, and 59,060 hunters responded to the wolf sighting surveys. From their reported sightings, 1,200, 2,859, 3,056, 3,469, 3,320, 2,391, 1,774, 1,254, 1,309, and 1,064 locations of 2 to 25 wolves were determined during the 5, 1-week sampling periods.

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

From 2007 to 2016, estimated area occupied by wolf packs in Montana increased from 42,098 km^2 (95% CI = 42,096 to 44,881) to 69,092 km^2 (95% CI = 68,788 to 69,776), with a maximum of 76,215 km^2 (95% CI = 75,952 to 76,865) in 2012 (Table 1). The predicted distribution of wolves from the occupancy model closely matched the distribution of field-confirmed wolf locations (verified pack locations and harvested wolves; Figure2).

Table 1. Estimated area occupied by wolves, number of wolf packs, and number of wolves in Montana, 2007-2016. Annual numbers were based on best available information and were retroactively updated as new information was obtained.

	2007	2008	2009	2010	2011	2012	2013	2014	2015	2016
Estimated Area Occupied (km^2)	42,098	51,702	61,730	63,283	70,629	76,215	75,219	70,022	72,508	69,092
(95% C.I.)	(42,096 - 44,881)	(51,377 - 52,459)	(61,420 - 62,391)	(62,958 - 63,946)	(70,295 - 71,246)	(75,952 - 76,865)	(74,938 - 75,907)	(69,699 - 70,733)	(72,181 - 73,195)	(68,788 - 69,776)
Territory Size (km^2)	599.83	599.83	599.83	599.83	599.83	599.83	599.83	599.83	599.83	599.83
(95% C.I.)	(493.36 - 740.35)	(493.36 - 740.35)	(493.36 - 740.35)	(493.36 - 740.35)	(493.36 - 740.35)	(493.36 - 740.35)	(493.36 - 740.35)	(493.36 - 740.35)	(493.36 - 740.35)	(493.36 - 740.35)
Estimated Packs (600 km^2 territories w/overlap)	79	93	117	123	149	161	167	145	152	152
(95% C.I.)	(66 - 99)	(76 - 113)	(95 - 142)	(99 - 150)	(121 - 181)	(131 - 197)	(136 - 204)	(117 - 176)	(123 - 186)	(124 - 186)
Average Pack Size (complete counts)	7.03	6.65	6.37	6.16	5.71	4.96	5.66	5.39	5.61	4.96
(95% C.I.)	(6.15 - 7.97)	(5.96 - 7.35)	(5.69 - 7.04)	(5.51 - 6.86)	(5.23 - 6.17)	(4.49 - 5.46)	(5.16 - 6.22)	(4.86 - 5.93)	(5.08 - 6.15)	(4.44 - 5.44)
Estimated Wolves Including Lone Wolves	623	694	836	849	955	899	1065	878	961	851
(95% C.I.)	(501 - 815)	(553 - 870)	(663 - 1,063)	(667 - 1,055)	(757 - 1,166)	(713 - 1,105)	(849 - 1,313)	(698 - 1,098)	(759 - 1,193)	(673 - 1,062)

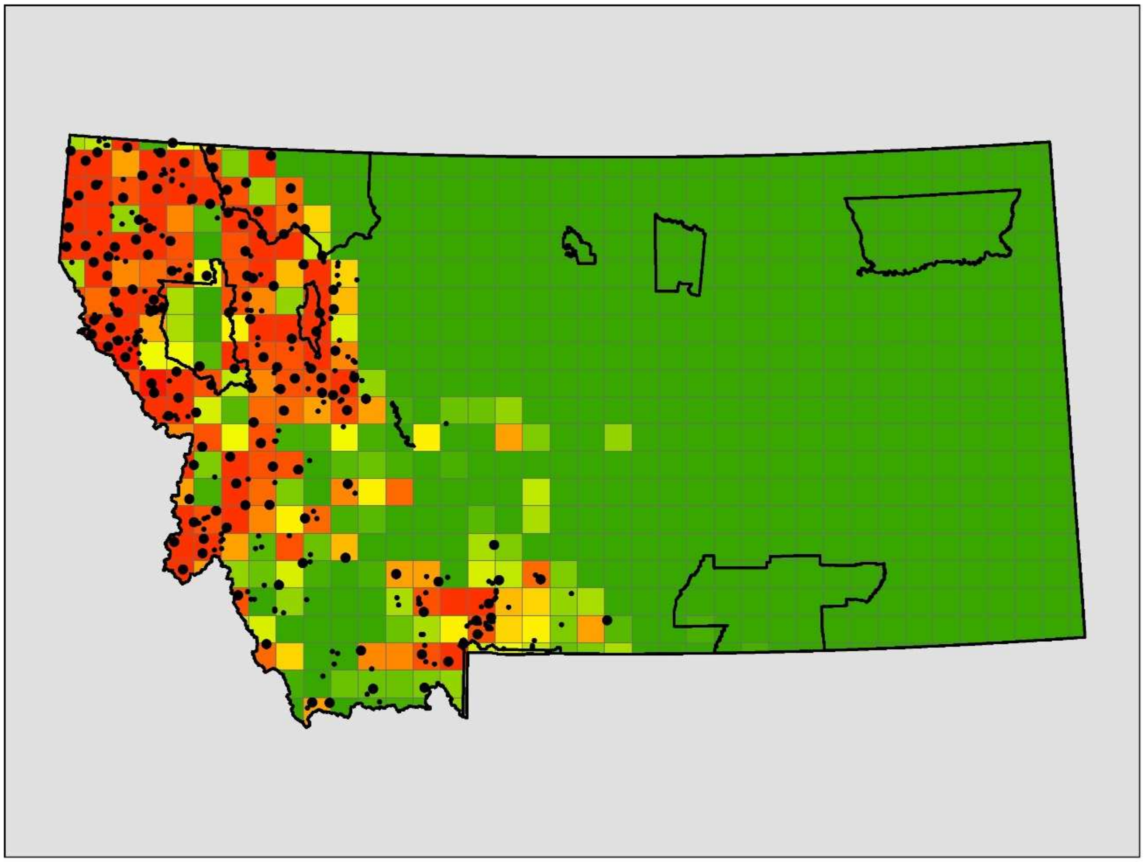

Figure 2. Model predicted probabilities of occupancy (ranging from low to high [green to red]), verified pack centers (large dots), and harvest locations (small dots) in Montana, 2016.

Estimating Numbers of Wolf Packs

In 2008 and 2009, territory sizes from 38 monitored packs ranged from 104.70 km^2 to 1,771.24 km^2. Mean territory size was 599.83 km^2 (95% C.I. = 478.81 to 720.86; Rich et al. 2012). Dividing the estimated area occupied by mean territory size resulted in an estimated number of packs that increased from 70 (95% C.I. = 59 to 88) in 2007 to 115 (95% C.I. = 93 to 141) in 2016, with a maximum of 127 (95% C.I. = 103 to 155) in 2012 (Table 1). We adjusted these estimates to account for annual changes in the number of verified pack centers per grid from 2007 to 2016 (1.12, 1.08, 1.13, 1.16, 1.26, 1.27, 1.33, 1.24, 1.26, and 1.32 for each respective year during 2007-2016) as an index of territory overlap. Accounting for territory overlap, estimated numbers of packs increased from 79 (95% C.I. = 66 to 99) in 2007 to 152 (95% C.I. = 124 to 186) in 2016, with a maximum of 167 (95% C.I. = 136 to 204) in 2013 (Table 1). The estimated number of wolf packs ranged from 7% larger than the minimum verified number of packs residing in Montana in 2016 to 21% larger in 2015 (Figure 3).

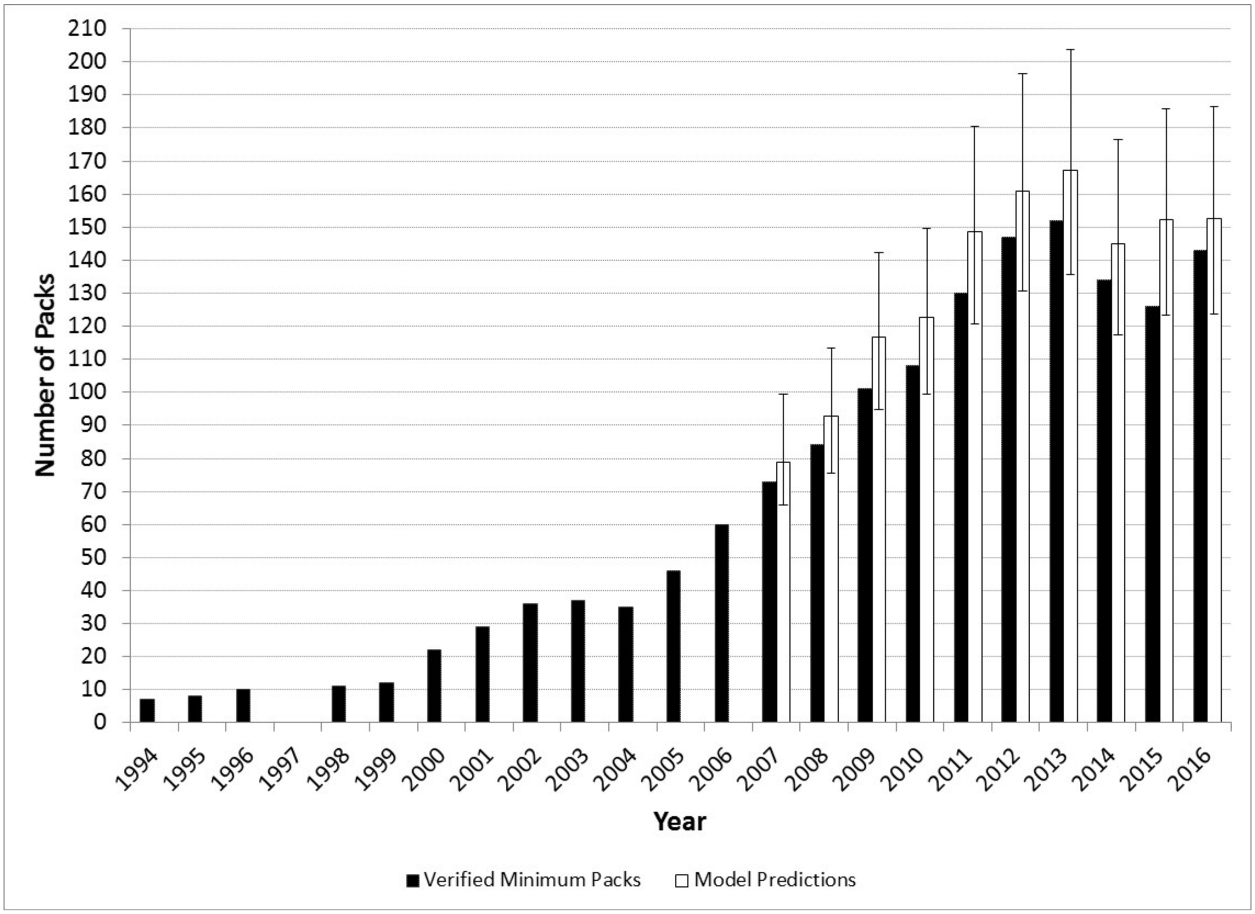

Figure 3. Estimated number of wolf packs in Montana compared to the verified minimum number of packs residing in Montana, 2007-2016. Annual numbers were based on best available information and were retroactively updated as new information was obtained.

Estimating Numbers of Wolves

From 2007 to 2016, complete counts were obtained from 664 packs within Montana. Pack sizes ranged from 2 to 22 and mean pack sizes decreased from 7.03 (95% C.I. = 6.15 to 7.97) in 2007 to 4.96 (95% C.I. = 4.44 to 5.44) in 2016 (table 1). Pack sizes for complete counts ranged from 13% larger than for minimum verified counts in 2008 to 39% larger in 2013 (Figure 4). Multiplying the number of estimated packs by mean pack size and a multiplication factor of 1.125 to account for the percentage of the population presumed to be lone wolves (Mech and Boitani 2003, p. 170) resulted in an increase of estimated wolves from 623 (95% C.I. = 501 to 815) in 2007 to 851 wolves in 2016 (95% C.I. = 673 to 1,062) in 2016, with a maximum of 1,065 (95% C.I. = 849 to 1,313) in 2013 (Table 1). The estimated number of wolves ranged from 40% larger than the minimum verified number of wolves in Montana in 2008 to 78% larger in 2016 (Figure 5).

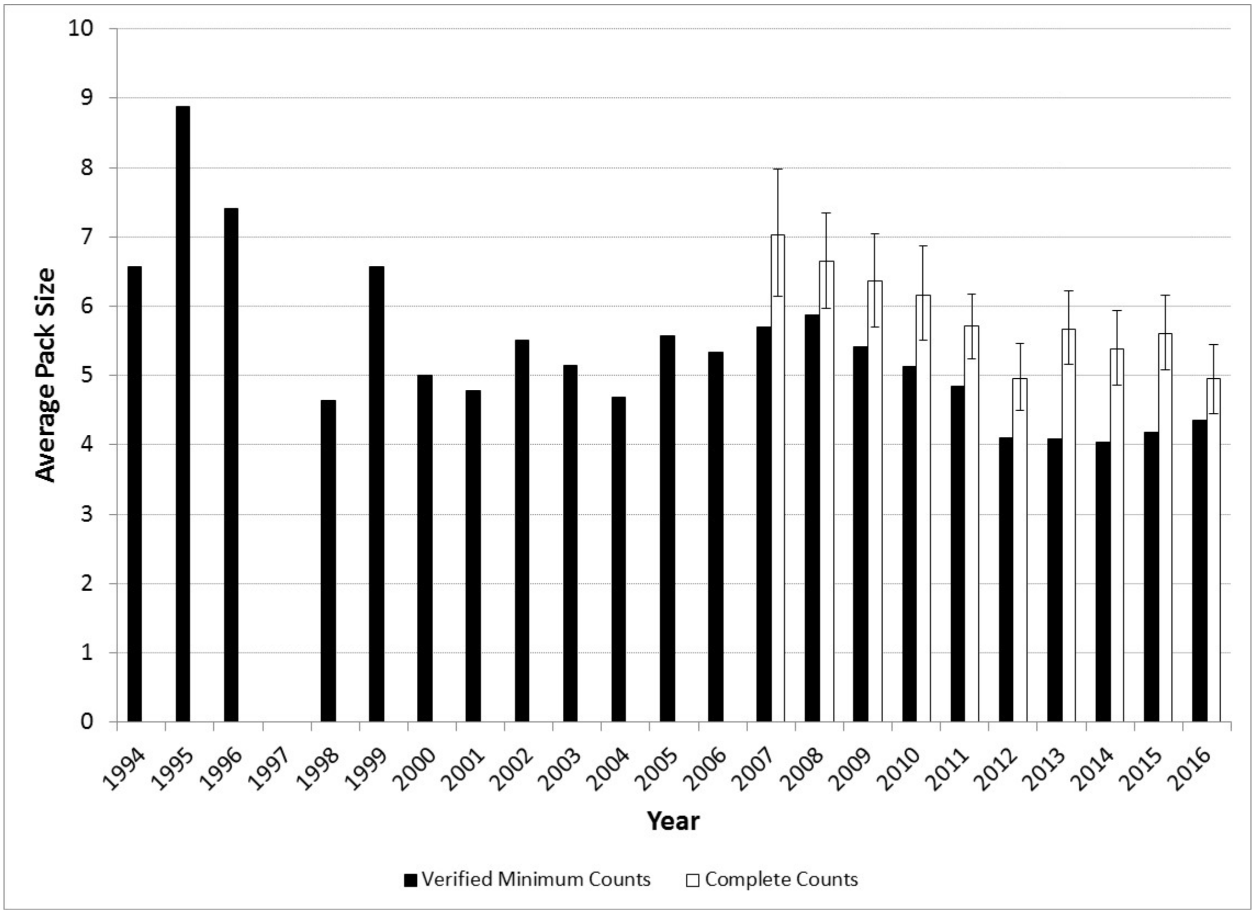

Figure 4. Mean number of wolves per pack with complete counts in Montana compared to the mean number of wolves per pack with verified minimum counts in Montana, 2007-2016. Annual numbers were based on best available information and were retroactively updated as new information was obtained.

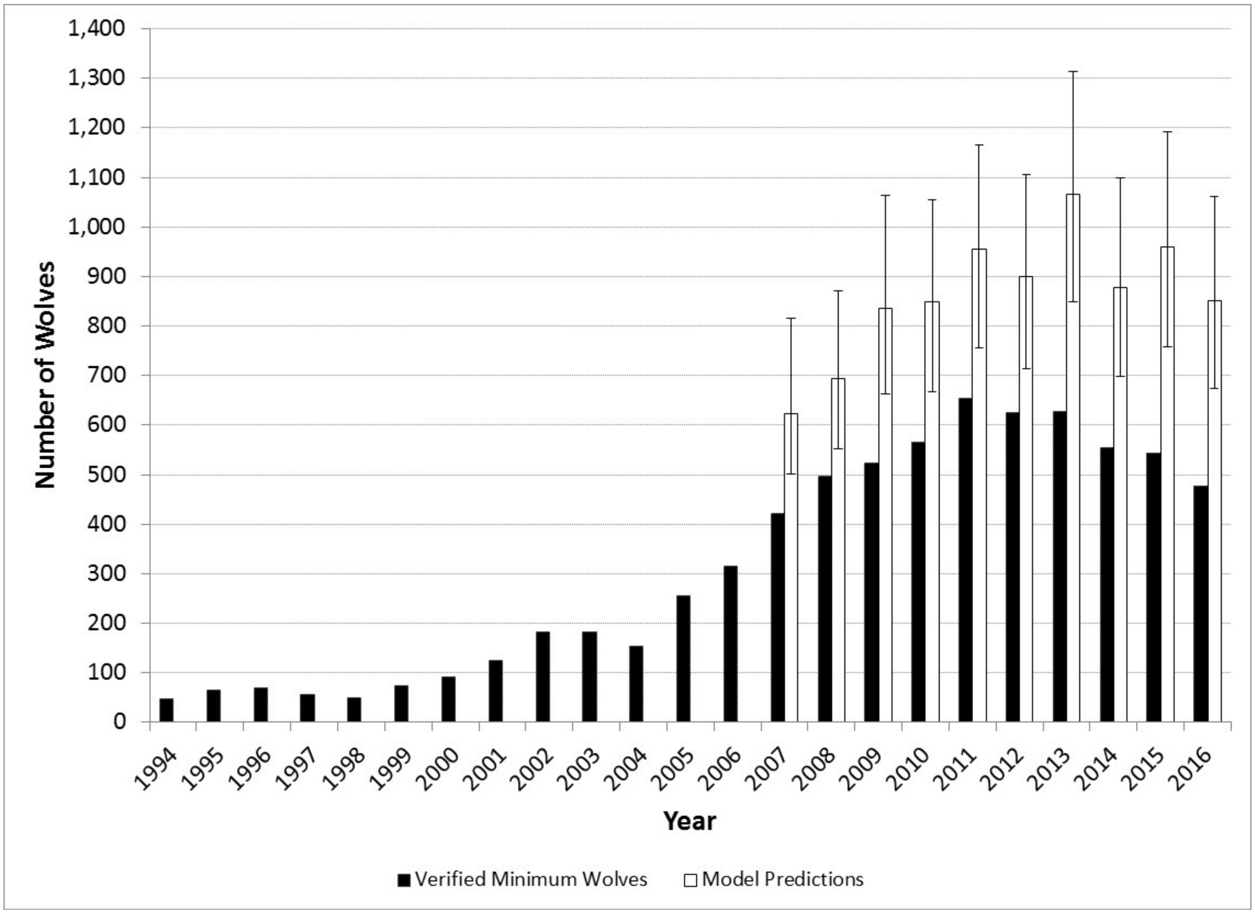

Figure 5. Estimated number of wolves in Montana compared to the verified minimum number of wolves residing in Montana, 2007-2016. Annual numbers were based on best available information and were retroactively updated as new information was obtained.

Discussion

Estimated Area Occupied by Wolves in Packs

Although the estimated area occupied has nearly doubled between 2007 and 2016, the rate of growth for the area occupied has been declining. The extent to which this declining rate of increase represents a population responding to density dependent factors as available habitats become filled, versus a response to hunting and trapping harvest or livestock depredation removals, is unknown.

Estimated Numbers of Wolf Packs

Our estimate for total numbers of wolf packs exceeded the minimum count by 7 to 21% between 2007 and 2016. Such a level of undercount is not unreasonable for elusive carnivores and is within the range of imperfect detection recorded for many other wildlife species and population estimation methods. For example, detection rates of elk during aerial surveys can be less than 20% (e.g., Vander Wal et al 2011), and detection rates of elk during winter surveys on the open winter ranges in southwestern Montana have been estimated at 44-89% (Hamlin and Ross 2002). Becker et al. (1998) produced a population estimate 48% higher than the number of individual wolves they observed, even though they assumed that they detected all wolf tracks in the area they surveyed.

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

The estimated number of packs exceeded the minimum number of verified packs to some degree because verified packs did not include border packs attributed to other states or Canada that spent time in Montana and could have been recorded by hunters. We only included verified border packs included in the Montana summaries in comparing our estimates to minimum counts. Also, the minimum number of packs verified was for the end of the year, and wolf population estimates derived from hunter observations represented the deer and elk hunting season in October- November, a period of time before some natural and human-caused wolf mortalities occurred. Because natural mortality and public harvest of wolves rarely results in the loss of full packs, this issue likely did not result in excessive bias. But in general, this would lead to negative bias in our estimate of the number of packs.

Estimated Numbers of Wolves

Our estimate for total numbers of wolves exceeded the minimum count by 40 to 78% between 2007 and 2016. The degree of difference exceeds that of packs because in addition to undocumented packs, it incorporates undocumented individuals within known packs. This degree of difference between minimum counts and our population estimate remains within that observed in other studies of wolves (Becker et al. 1998) or more common ungulate species (e.g., Hamlin and Ross 2002, Vander Wal et al. 2011).

Our estimate of the number of wolves is dependent on several assumptions that need to be examined further. First, our population estimate assumes that missed packs are the same size as verified packs. If missed packs are smaller (e.g., recently established packs or packs interspersed among known packs), then our estimated number of wolves would be biased high. Also, our estimate assumes that pack size is constant and equal across space. Pack sizes that were actually larger in some years or some areas would induce a negative bias in our estimates of wolves in those years or areas, and pack sizes that were actually smaller in some years or some areas would induce a positive bias in our estimates of wolves in those years or areas. Finally, our population estimate for wolves in groups of 2 or more also accounts for lone or dispersing wolves by using an inflation factor of 12.5%. Various studies have documented that on average 10-15% of wolf populations are composed of lone or dispersing wolves (Fuller et al. 2003). The state of Idaho inflates their estimates by 12.5% to account for lone wolves (Idaho Department of Fish and Game and Nez Perce Tribe 2012) and Minnesota inflates their estimate by 15% (Erb 2008). In the future, more direct estimates of lone or dispersing wolves could be made and spatial or temporal variation could be incorporated into the Montana population estimate in various manners.

The estimated number of wolves exceeded the minimum number of verified wolves to some degree because verified wolves did not include individuals associated with border packs attributed to other states or Canada that spent time in Montana and could have been observed by hunters. As with packs, the minimum number of wolves verified was for the end of the year, and wolf population estimates derived from hunter observations represented a period of time before some natural and human-caused mortalities occurred. Because of wolf mortality during the October- November time period, this likely results in a negative bias in our population estimate because wolves harvested during October and November were alive when the deer and elk hunting season started.

Management Implications

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

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