# Monitoring and Assessment of Wolf-Ungulate Interactions and Population Trends within the Greater Yellowstone Area, Southwestern Montana, and Montana Statewide

## FINAL REPORT

2009

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Montana Fish, Wildlife & Parks

Wildlife Restoration

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# FOREWORD

The impacts of wolves on elk and other ungulates is perhaps one of the most controversial wildlife-related issues faced by people that co-inhabit landscapes with these species. This is certainly true in Montana, where the issue often involves widely disparate opinions and values. In the Greater Yellowstone Area (GYA) and southwest Montana in particular, public interest is heightened in this issue. The GYA and southwest Montana generate approximately half of the Montana statewide elk hunter days afield and elk harvest annually. The impacts of wolves on elk populations are front and center in the minds of many elk hunters and elk enthusiasts in the region. The region is also close to Yellowstone National Park, where wolf conservation efforts were bolstered in 1995-96 with the experimental restoration of wolves to an ecosystem that had been without wolves for much of the previous century. The region holds particular significance for wolf conservation enthusiasts, and the impacts of wolves on elk are fresh in their minds as well.

Montana Fish, Wildlife, and Parks (MFWP) is entrusted to conserve and manage wildlife in the GYA and in southwest Montana. The state of Montana has been successful in efforts toward this endeavor since statehood was enacted in 1889. With the re-establishment of wolves in the region around the turn of the 21st century, however, wildlife managers were faced with a new challenge. Before this occurred, wildlife conservation and management programs were implemented without a thought given to wolves or their impacts on the ungulate populations the agency managed. Facts and data about the impacts of wolves on elk in the region were sorely needed for wildlife conservation and management programs to adapt and remain successful.

With the intense public interest and the data needs of wildlife managers in mind, MFWP began a wolf-ungulate research project in 2001 to fill some large gaps in our knowledge base. This was a collaborative project with the Ecology Department at Montana State University, with involvement from Drs. Bob Garrott and Scott Creel. The project was designed to incorporate both intensive and extensive data collection efforts. Intensive study sites were identified, and individual project cooperators ran efforts at these sites. Data collection at the intensive study sites was intended to provide the detailed comparisons needed to understand the range of effects that wolves can have on elk population dynamics and behavior. Additionally, as a part of this overall effort, MFWP agreed to bolster ungulate monitoring efforts in a more extensive region in southwest Montana, as well as to continue monitoring programs elsewhere in the state to provide insights regarding the effects of wolves on ungulate populations over a larger area.

Due to the immediate need for information to inform the public conversation, scientific debates, and wildlife management programs, much of what has been learned from this research effort was published during the course of the project, in scientific journals and in agency annual reports. A list of scientific publications resulting from this project is contained in this final report. Further, Hamlin et al. (2008) summarizes much of the knowledge gained via comparisons between data collected at the intensive study sites through 2007. This report updates these comparisons with more recent data, and provides a more in-depth look at wolf-elk interactions in the Northern Yellowstone elk herd, which was lacking in previous publications and reports. This report also provides summaries from more extensive data collection efforts and MFWP monitoring programs, which have been absent from previous publications and reports, including summaries of data collected for deer and moose populations.

The major, overriding result from this research effort has been that one-size-fits-all explanations of wolf-elk interactions across large areas do not exist. However, we have learned that elk populations tend to become limited by predators when high ratios of predators to elk are reached, and this typically has occurred when multiple predator species are numerous within the range of one elk population. This limitation of elk populations in areas with numerous predators appears to become manifest through direct impacts on elk calf survival and recruitment.

The research presented in this report results from an active MFWP applied wildlife research program. Montana's wildlife management programs have long been built upon the scientific investigations of a dependable team of research scientists working in close conjunction with very talented and dedicated staff wildlife biologists and managers. This particular research project is no exception to that trend, and it will undoubtedly serve as the basis of wildlife management programs and decisions well into the future.

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Because of the time constraints in finishing this final report before the senior author's retirement, neither Julie Cunningham nor the RTS Supervisor have had time for a thorough final review. **Therefore, any errors in presentation, conclusions, or interpretations are by Kenneth L. Hamlin and not associated with other project personnel.**

In addition to MFWP employees, this study was the beneficiary of cooperation among many landowners, ranch managers, private citizens, state and federal agencies, and university researchers. Unfortunately, with so much help and cooperation, acknowledgments usually leave out others who should also be listed. Below, we list those who provided extra help and apologize to those inadvertently left out.

Project funding and support was provided by the sale of hunting and fishing licenses in Montana, Montana Fish, Wildlife and Parks Federal Aid in Wildlife Restoration grants, GYIBC brucellosis funding through Dr. Tom Linfield and Montana Dept. of Livestock, The National Science Foundation, MSU EPSCoR, the Big Sky Institute, MSU-UM Transboundary Research Fellowship Program, Rocky Mountain Elk Foundation, Roger and Cindy Lang of the Sun Ranch, and Bob and Annie Graham of Elk Meadows Ranch.

**All MFWP wildlife biologists and Wildlife Managers risked their lives collecting this data and provided help in assembling the data.** Following, we mention those who provided extra time, effort, and information: Kurt Alt, Neil Anderson, Mark Atkinson, Keith Aune, Lydia Bailey, Bob Brannon, Tom Carlsen, John Firebaugh, Kevin Frey, Justin Gude, Jeff Herbert, Craig Jourdonnais, Fred King, Quentin Kujula, Tom Lemke, Adam Messer, Magaret Morelli, Coleen O'Rourke, Dave Pac, Mike Ross, Carolyn Sime, Shawn Stewart, Tom Stivers, Mike Thompson, Jenifer Verschyul, John Vore, Harry Whitney, and Jim Williams.

Major contributions were made by Montana State University professors Dr. Robert Garrott and Dr. Scott Creel and their students John Winnie, Jr., Justin Gude, Julie Fuller (Cunningham), Dave Christianson, Jamin Grigg, and Kelly Proffitt. Ed Bangs and Joe Fontaine of the U. S. Fish and Wildlife Service, Val Asher of USFWS, Turner Endangered Species Fund and MFWP, Dave Hunter, DVM of TESF, and P.J. White and Doug Smith of NPS, Yellowstone National Park have all been very helpful. Chad Dickinson, Kyran Kunkel, and Kris and Bob Inman provided help with telemetry equipment. None of this work would have been possible without the skill of SuperCub pilots Roger Stradley and Steve Ard; helicopter pilots Mark Duffy, Noel Boyd, and Steve Collins; and other pilots statewide who provided skilled and safe flights for biologists.

Much help in the Madison Valley studies was provided by the Sun Ranch, Carroll Brothers' Ranch, CB Ranch, Corral Creek Ranch, Elkhorn Guest Ranch, Elk Meadows Ranch and Sun West Ranch and ranch managers Todd Graham, David Henderson, Peggy and Mark Jasmann, Scott McClintok, Alan and Linda Padgett, Steve Smelser, Marina Smith, and Sonny and Jan Smith. The Madison Valley Ranchlands Group, especially Lane Adamson, also provided help.

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# PREVIOUSLY PUBLISHED RESULTS

Fifteen professional publications on wolf-ungulate relationships have been directly associated with, or the result of partial funding by, MFWP and the Wolf-Ungulate Research Project. Due to the nature of the collaboration among cooperators working on the project, some of these products were produced with little input from MFWP staff. Additionally, 4 other professional publications, not directly related to wolf-ungulate relationships, were completed based on data collected or summarized as a result of the Wolf-Ungulate Research Project. All publications are listed below. Hamlin et al. (2008) is an overall summary of wolf-elk population interactions in the Greater Yellowstone Area through 2007. Additional manuscripts are in preparation.

**Wolf-Ungulate Relationship Products** *(using wolf-ungulate project funding, logistical support, and with substantial input from MFWP staff in product development)*

Christianson, D. A., and S. Creel. 2007. A review of environmental factors affecting winter elk diets. Journal of Wildlife Management 71:164-176.

Creel, S and J. A. Winnie, Jr. 2005. Responses of elk herd size to fine-scale spatial and temporal variation in the risk of predation by wolves. Animal Behavior 69:1181-1189).

Creel, S., J. A. Winnie, Jr., B. Maxwell, **K.L. Hamlin** and M. Creel. 2005. Elk alter habitat selection as an antipredator response to wolves. Ecology 86:3387-3397.

Garrott, R. A., **J. A. Gude**, E. J. Bergman, C. Gower, P. J. White, and **K. L. Hamlin**. 2005. Generalizing wolf effects across the Greater Yellowstone Area: a cautionary note. Wildlife Society Bulletin 33:1245-1255.

**Gude, J. A**., R. A. Garrott, J. Borkowski, and **F. King**. 2006. Prey risk allocation in a grazing ecosystem. Ecological Applications 16:285-298.

**Hamlin, K. L**., R. A. Garrott, P. J. White, and **J. A. Cunningham**. 2008. Contrasting wolf-ungulate interactions in the Greater Yellowstone Ecosystem. Chapter 25. *in* R. A. Garrott, P. J. White, and F. Watson, eds., The Ecology of Large Mammals in Central Yellowstone. Elsevier (Academic Press).

Proffitt, K. M., J. L. Grigg, **K. L. Hamlin**, and R. A. Garrott. 2009 (*in press)*. Contrasting effects of wolves and human hunters on elk behavioral responses to predation risk. Journal of Wildlife Management 73: April.

White, P. J., R. A. Garrott, J. J. Borkowski, **K. L. Hamlin**, and J. G. Berardinelli. 2008. Elk nutrition after wolf recolonization of Central Yellowstone. Chapter 22. *in* R. A. Garrott, P. J. White, and F. Watson, eds., The Ecology of Large Mammals in Central Yellowstone. Elsevier (Academic Press).

**Wolf-Ungulate Relationship Products** *(using wolf-ungulate project funding and logistical support, but with little or no input from MFWP staff in product development)*

Christianson D., and S. Creel. 2008. Risk effects in elk: sex-specific response in grazing and browsing due to predation risk from wolves. Behavioral Ecology 19: 1258-1266.

Creel S., and D. Christianson. 2008. Relationships between direct predation and risk effects. Trends in Ecology & Evolution 23: 194-201.

Creel S., D. Christianson, S. Liley, and J.A. Winnie, Jr. 2007. Effects of predation risk on reproductive physiology and demography in elk. Science 315: 960.

Creel S., J. A. Winnie, Jr.., D. Christianson D., and S. Liley. 2008. Time and space in general models of antipredator response: tests with wolves and elk. Animal Behavior 76: 1139-1146.

Liley, S., and S. Creel. 2008. What best explains vigilance in elk: characteristics of prey, predators, or the environment? Behavioral Ecology 19:245-254.

Winnie, J. A., Jr., D. Christianson, B. Maxwell, and S. Creel. 2006. Elk decision-making rules are simplified in the presence of wolves. Behavioral Ecology and Sociobiology 61:277-289.

Winnie, J. A., Jr. and S. Creel. 2007. Sex-specific behavioral responses of elk to spatial and temporal variation in the threat of wolf predation. Animal Behavior 73:215-225.

**Other Publications Resulting From Data Compiled For Wolf-Ungulate Project** *(all with substantial input from MFWP staff in product development)*

**Cunningham, J. A., K. L. Hamlin**, and T. O. Lemke. 2009 (*in press)*. Fetal sex ratios in southwestern Montana elk. Journal of Wildlife Management 73:

Cross, P. C., E. K. Cole, A. P. Dobson, W. H. Edwards, **K. L. Hamlin**, G. Luikart, A. D. Middleton, B. M. Scurlock, and P. J. White. *In review*. Disease in the 'New West': effects of changing elk demography on brucellosis dynamics.

Proffitt, K. M., J. L. Grigg, R. A. Garrott , **K. L. Hamlin, J. A. Cunningham**, **J. A. Gude, and C. S. Jourdonnais**. *In review.* Changes in elk resource selection and distributions associated with a late-season elk hunt on a Greater Yellowstone Area wintering range. Journal of Wildlife Management.

Wang, G., N. T. Hobbs, R. B. Boone, A. W. Illius, I. J. Gordon, J. E. Gross, and **K. L. Hamlin**. 2006. Spatial and temporal variability modify density dependence in populations of large herbivores. Ecology 87:95-102.

# EXECUTIVE SUMMARY

The first section of this report presents summaries and results from data collected at intensive study sites in the Greater Yellowstone Area (GYA) and southwestern Montana during 2001-2008. Hamlin et al. (2008) summarizes much of the knowledge gained via comparisons between data collected at the intensive study sites through 2007. This section updates these comparisons with more recent data, with a more in-depth focus on wolf-elk interactions in the Northern Yellowstone elk herd, and with data concerning ungulates other than elk. Major findings from this section can be characterized as follows.

1. Wolf numbers have increased rapidly in all of western Montana since wolf restoration began in 1995, at rates of approximately 10% to 34% annually. In the range of the Northern Yellowstone elk herd, wolf numbers increased by an average of approximately 13% annually during 1995-2007.

2. Elk are the primary prey species for wolves in southwest Montana and the GYA, though there is limited evidence that the portion of elk in wolf diets may decline during summer months. Most data indicate that wolves preferentially select for elk calves and against adult female elk. Some data indicate that wolves preferentially select for adult male elk, and the degree to which this happens appears to be influenced by the number of adult male elk that reside within the territory of a particular pack or population of wolves.

3. Winter elk kill rates of wolves have varied widely across southwest Montana and the GYA, from approximately 7 to 23 elk killed per wolf during November through April. There is little data on summer elk kill rates of wolves, but it appears that wolves kill fewer elk during summer than during winter.

4. The number of grizzly bears in southwest Montana and the GYA has increased more than 3-fold since 1987, concurrently with the increase in wolf numbers, affecting the total elk predation rate.

5. Most data that have directly measured elk pregnancy rates since wolf restoration began indicate that elk pregnancy rates are unaffected by wolves, in contrast to some indirect evidence from average hormone concentrations in elk feces. Indirect evidence from hunter-collected samples also indicates that elk pregnancy rates have been unaffected by wolves.

6. In most of southwest Montana and the GYA, calf survival rates following wolf restoration have been similar to rates prior to wolf restoration. Declines in calf per 100 cow ratios have occurred in the Northern Yellowstone, Gallatin- Madison, and Madison- Firehole elk herds, where both wolf and grizzly bear densities have been high. In the Northern Yellowstone and Gallatin- Madison elk herds, calf per 100 cow ratios have recently been approximately half or less than levels recorded prior to wolf restoration.

7. Adult female elk survival rates have remained high in most areas during the wolf population increase. In the Northern Yellowstone elk herd, adult female survival has ranged from approximately 75% to 85% since the mid-1980s. In earlier years, most adult female mortality in this herd was due to hunting. During 2000-2004, major mortality sources included hunting and predation. Since 2005, hunter harvest has been minimal and adult female survival rates appear to have remained in the low 80% range.

8. In areas with high predator (grizzly bear and wolf) to prey ratios, including the Northern Yellowstone, Gallatin Canyon, and Madison-Firehole winter ranges, elk numbers have declined substantially since wolf reintroduction. In most areas with lower predator to prey ratios, elk numbers have remained stable or have increased since wolf restoration began.

9. In the Northern Yellowstone elk herd, we estimate that since 2004 wolves have killed more elk than hunters, since 2005 wolves have killed more adult female elk than hunters, and in all but one year since 2002 wolves have killed more bull elk than hunters.

10. Our analyses of elk vital rates in the Northern Yellowstone elk herd indicate that a continued decline in elk numbers in coming years is likely until predator to prey ratios decline, even if hunting pressure remains low or is decreased further.

11. Most data collected during winter indicate that wolves have small-scale effects on elk distribution (displacement of up to approximately 1 km upon contact) and movement rates (increased movement rates of approximately 1.23 km per every 4 hours). Wolves may also affect elk habitat selection and group sizes, but the magnitude and direction of these effects is widely variable among wintering areas and even among habitats in the same wintering area. Where the impacts of hunting, hunter access, and wolves have been studied simultaneously, the impacts of hunting and hunter access on elk distribution, movements, group sizes, and habitat selection have been larger than the effects of wolves.

12. Data concerning the effect of wolves on large-scale elk distribution are equivocal. Based on research data collected during this project, there is little or no indication that wolves affect larger-scale elk seasonal distribution or the timing of migration in some areas in southwest Montana. Anecdotal information suggests that this may occur in some other areas in southwest Montana, however. Additionally, research data from the Madison-Firehole elk herd suggest that wolf predation pressure affects large-scale migration patterns or seasonal range selection for some elk.

13. In the areas of southwest Montana and the GYA that have shown declines in elk calf survival, recruitment, and population size since the wolf reintroduction, mule deer recruitment and numbers have increased.

14. Little data exist on moose populations in southwest Montana and the GYA due to inconsistent monitoring. Recruitment and population sizes appear to have declined in some areas, while numbers have increased in other areas. We can currently provide little insight into the causes of these disparities, and increased monitoring efforts or research efforts might provide more insight.

The second section of this report provides summaries of data from routine MFWP statewide monitoring programs, including aerial survey, harvest survey, and species management programs, which have been absent from previous publications and reports. Conclusions in this section are more general and can be characterized as follows.

1. Elk populations in MFWP Administrative Region 1 appear to be stable or increasing, and all areas with consistent, long-term aerial counts have few wolves at present.

2. Moose numbers appear to be stable in the sole hunting district of Region 1 that has consistent, long-term data on moose population trend.

3. In most of northwestern Montana, including Administrative Region 1 and the northern portion of Administrative Region 2, white-tailed deer are likely the major prey of wolves, rather than elk.

4. Using buck harvest as an index of population trend for white-tailed deer, in most hunting districts numbers appeared to increase steadily until 2006 following the large decline in 1996-97. Recent highs were slightly lower than previous highs despite relatively smaller anterless harvests, and the entire increase occurred during a phase of increasing wolf numbers.

5. Since 2006, and beginning as early as 2004 in some areas of Region 1, white-tailed deer population sizes, indexed by buck harvest, have been decreasing. The decrease has coincided with record high antlerless deer harvests in most hunting districts.

6. It appears that factors other than predation have played major roles in recent white-tailed deer population declines in Administrative Region 1. However, predation may have played a role in initiating the declines, prolonging the recovery periods, and/ or limiting total deer numbers below the previous highs. In much of Region 1, it appears to be possible that predator and prey fluctuations or cycles may develop, rather than more consistent, low numbers of white-tailed deer in the presence of wolves, because white-tailed deer numbers were able to increase following major declines in 1996-97.

7. In MFWP Administrative Region 2, white-tailed deer numbers, as indexed by buck harvest, increased through 2006 following the major declines in 1996-97. However, in HDs 201 and 202 where wolves have been present longest, buck harvest has remained below historic pre-wolf levels.

8. Since 2006, white-tailed deer numbers have decreased concurrently with record or near-record high antlerless harvest, following a pattern very similar to the pattern in

Administrative Region 1. The declines in Region 2 have been also influenced by factors other than predation, and most populations recovered following the major declines in 1996-97. This again leads to the possibility that predator and white-tailed numbers will fluctuate in Region 2, rather than white-tailed deer persisting at continually low numbers in the presence of wolves.

9. In some areas of Region 2, there have been some elk population declines with limited evidence that wolves may have played a role in limiting numbers or affecting elk distribution. In other areas aerial counts of elk have increased while harvest has decreased, with little apparent influence of wolves.

10. Consistent, long-term survey data indicate that elk in the Bitteroot Valley increased steadily until 2006, when planned reductions in elk numbers resulted from increases in harvest. The environment and conditions in the western portion of this valley suggest that wolves may affect elk numbers at some point, so close monitoring of this elk herd should continue.

11. At this time, there is little wolf presence in Administrative Regions 4 and 5, so chances of wolf impacts on ungulate populations in these areas are minimal at present.

12. It appears that some areas in Montana are unsuitable to wolves because livestock depredations continually lead to wolf removals, preventing wolves from increasing to densities that are seen in protected areas. In these areas, wolves are probably less likely to limit ungulate populations than in areas where depredation removals do not limit wolf survival and population growth.

13. The federally funded budget for wolf monitoring and management has increased by 8% since 2005, while the MFWP budget for all big game monitoring, including but not limited to all of the ungulate species, has declined by 15% since 2006. Currently, the wolf program budget is approximately 2/3 the size of the budget for the big game program. If wolves are removed from the endangered species list, and federal funding for the wolf program declines or is eliminated, our knowledge of either wolf or ungulate populations, or both, will decline under the current budget scenario.

14. Routine ungulate monitoring programs in Montana may only be powerful enough to detect large changes in ungulate numbers over a series of years, and power will be even lower in areas where harvest indices are used to monitor populations instead of aerial surveys. No routine surveys of ungulates in Montana are likely to be powerful enough to assign causes to declines in every case. This is apparently not always possible even in areas with intensive monitoring and research projects, because substantial debates concerning causes of declines and the role that predation plays in declines still persist in many of these areas.

# INTRODUCTION

Montana Fish, Wildlife, and Parks (MFWP) and the Ecology Department of Montana State University – Bozeman (MSU) initiated a cooperative investigation focusing on wolf-ungulate population interactions in the Greater Yellowstone Area (GYA) of southwestern Montana in 2001. Private landowners, the National Park Service (NPS), and the U. S. Fish and Wildlife Service (USFWS) were also important partners in this effort. Here, we summarize results of these investigations.

We also discuss MFWPs more extensive, but less intensive monitoring of wolf and ungulate population characteristics throughout Montana in relation to GYA studies. Throughout, we discuss findings in relation to other work done regionally on wolves and ungulates.

Within the GYA, wolves (*Canis lupus*) subsist on an elk (*Cervus elaphus*) economy. That is, elk are the main prey (~ 85-90% of winter prey) of wolves in the GYA, other ungulates such as white-tailed deer (*Odocoileus virginianus*), mule deer (*Odocoileus hemionus*), pronghorn (*Antilocapra americana*), and moose (*Alces alces*) make up little of the wolves prey base (Smith et al. 2004a, Hamlin 2006). The elk herds of the Yellowstone, Gallatin, Madison and the Gravelly-Snowcrest complex represent a highly valued resource. The re-introduced and expanding wolf populations in the same Greater Yellowstone Area (GYA), likewise, command national and statewide attention. The potential impact of wolf predation on ungulate populations is a highly controversial issue, both within the general public and the scientific community. Our investigations monitored trends in population parameters for these elk herds and newly established wolf packs across a range of geographic sites and different environmental conditions.

The best estimate as of December 2007 is that there were 1,513 wolves in at least 107 breeding packs in Montana, Idaho and Wyoming (Sime et al. 2008). This is the 8th consecutive year with more than 30 breeding packs for this area. The total included an estimated 453 wolves in the Greater Yellowstone Recovery area and an estimated minimum of 422 wolves (73 packs) and 39 breeding packs within the State boundaries of Montana (Sime et al. 2008). In the southern Montana experimental area, there were 37 packs (209 wolves); 16 packs met the breeding pair criteria. In northwestern Montana, there were 36 packs (213 wolves); 23 packs met the breeding pair criteria (Sime et al. 2008). Wolves have long since reached the numerical and distributional goals for recovery, but de-listing has not occurred and management options are limited.

Wolves are well established within Yellowstone National Park (YNP) and have been dispersing from the Park and establishing new packs in adjacent areas. Elk populations are a highly valued resource in this area and MFWP has collected data on these elk populations going back in some cases to the 1920s. FWP administrative Region 3, surrounding YNP, provides approximately 50% of Montana elk harvest and hunter days of recreation. Land ownership, land use, vegetation communities, and environmental conditions vary across this area. Elk harvest management strategies also vary and reflect different migratory patterns, harvest availability, and habitat of these elk herds. Our study approach allowed comparisons to be made among the demographics of elk herds subjected to wolf predation, but no hunting, herds affected by both wolf predation and hunting, and elk herds affected by hunting but little or no wolf predation.

It also was important to document ungulate population size, trend, and characteristics for areas without wolves prior to wolves becoming established. Expansion of study outside the GYA was necessary to find areas with no impact by wolf predation. By working in areas with differing ecological characteristics, we could make comparisons to identify factors that most impact wolf-elk dynamics. For comparative purposes, it is also important that wolves have been present in northwestern Montana, near Glacier National Park since 1979 and breeding pairs have been present there since about 1985-86. Because MFWP has historical data on elk and other ungulates, we can make pre- and post-wolf comparisons among sites. Within the broader, statewide perspective, other ungulates such as white-tailed deer and moose become more important prey species for wolves (Kunkel and Pletscher 1999), especially within MFWP Regions 1 and 2 and analyses include these ungulates.

It is also important to remember that the restoration of wolves occurred within an environment that included a rich component of other effective natural predators of ungulates. Grizzly bear (*Ursus arctos*), black bear (*Ursus americanus*), cougar (*Puma concolor*), coyotes (*Canis latrans*) are the most important, but other smaller predators are also present. Little is known about numbers/density of these predators.

The objectives of this report are to: 1) summarize findings of research to date on wolf-ungulate interactions in the GYA funded and conducted by this project and cooperators; 2) incorporate more extensive findings of research in the GYA by other projects for comparative purposes and; 3) incorporate extensive data throughout Montana on wolves, other predators, and ungulates for comparative purposes and to help determine data needs for further research and monitoring.

A summary publication on wolf-ungulate interactions in the Greater Yellowstone Area through 2007 was completed earlier (Hamlin et al. 2008).

## SUMMARY OF GYA AND SOUTHWESTERN MONTANA

### Study Areas

In the Greater Yellowstone Area, the main study areas for this project were the Lower Madison and Gallatin Canyon areas (Fig. 1). However, this project and cooperators also collected information on the Wall Creek Wildlife Management Area, Blacktail-Robb-Ledford WMAs, Yellowstone Valley, Northern Yellowstone, and Madison Headwaters areas (Fig. 1). For some comparisons within the GYA, we also used information collected in the entire Gravelly-Snowcrest Mountains, Tobacco Root Mountains, Crazy Mountains, and Absaroka-Beartooth Mountains.

For statewide perspectives, we used information on wolves and ungulates collected by MFWP biologists and wildlife specialists throughout MFWP Administrative Regions 1-5.

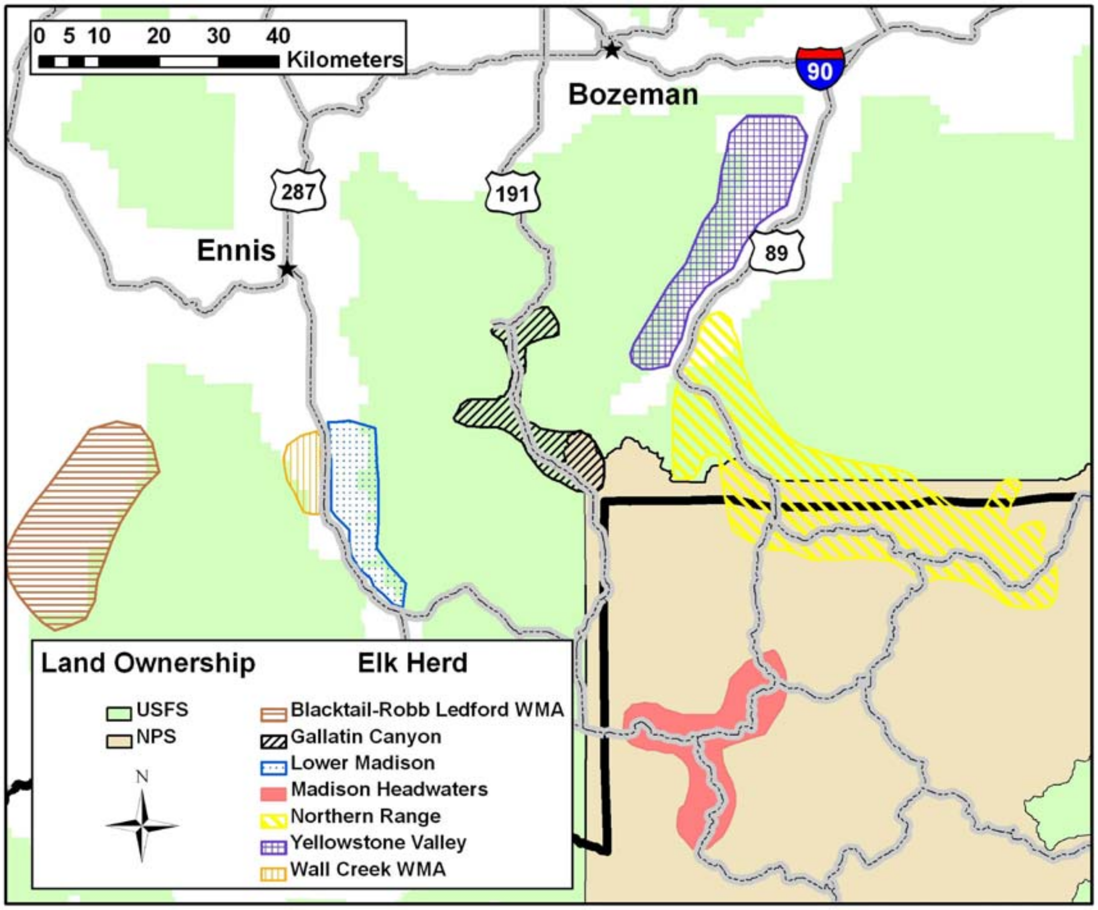


Figure 1. Winter ranges of elk herds monitored for the Wolf-Ungulate project within the Greater Yellowstone study area.

## Wolf Numbers

Wolves have been present in the North West Montana Endangered Area (NWMT) since at least 1979 and in the Greater Yellowstone Experimental Area (GYA) and Central Idaho Experimental Area (CID) since restoration in 1995 (Fig. 2). An estimated minimum 1,513 wolves were present in the 3 states of Montana, Idaho, and Wyoming as of December 2007 (Sime et al. 2008). Since restoration in 1995, estimated annual wolf population growth rate has been greatest in the CID (r = 0.293, λ = 1.34), slightly lower in the GYA (r = 0.224, λ = 1.251), and slowest in NWMT (r = 0.0.094, λ = 1.098).

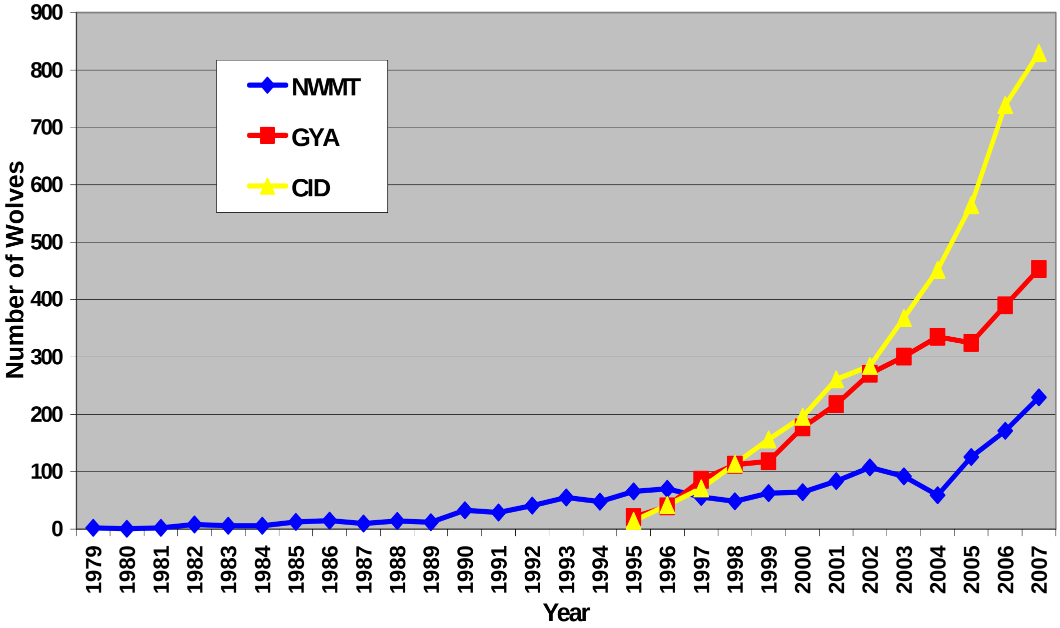


Figure 2. Estimated number of wolves by recovery area, Northwest Montana (NWMT), Greater Yellowstone Area (GYA), and Central Idaho Area (CID), 1979-2007.

Within the state boundaries of Montana, there were an estimated 422 wolves in 73 packs, which included 39 breeding pairs as of December 2007 (Sime et al. 2008, Fig. 3). Since 2000 (Fig. 4), annual wolf population growth rate was highest in the Montana portion of CID (r = 0.361, λ = 1.435) and lower, but relatively equal in NWMT (r = 0.143, λ = 1.153), and the Montana portion of GYA (r = 0.168, λ = 1.183). Rate of increase has been even greater after 2004 in MT portions of CID and NWMT (Figs. 3 and 4). A substantial increase in the number of wolves and wolf packs in the Bitterroot Valley area during the last 3 years accounts for much of the increased growth rate in the Montana portion of the CID.

Number of wolves associated with the Northern Range elk herd (including those within the Montana portion) increased substantially from 21 to 106 through 2003, declined in 2004 and recovered to 108 in 2007 (Fig. 5).

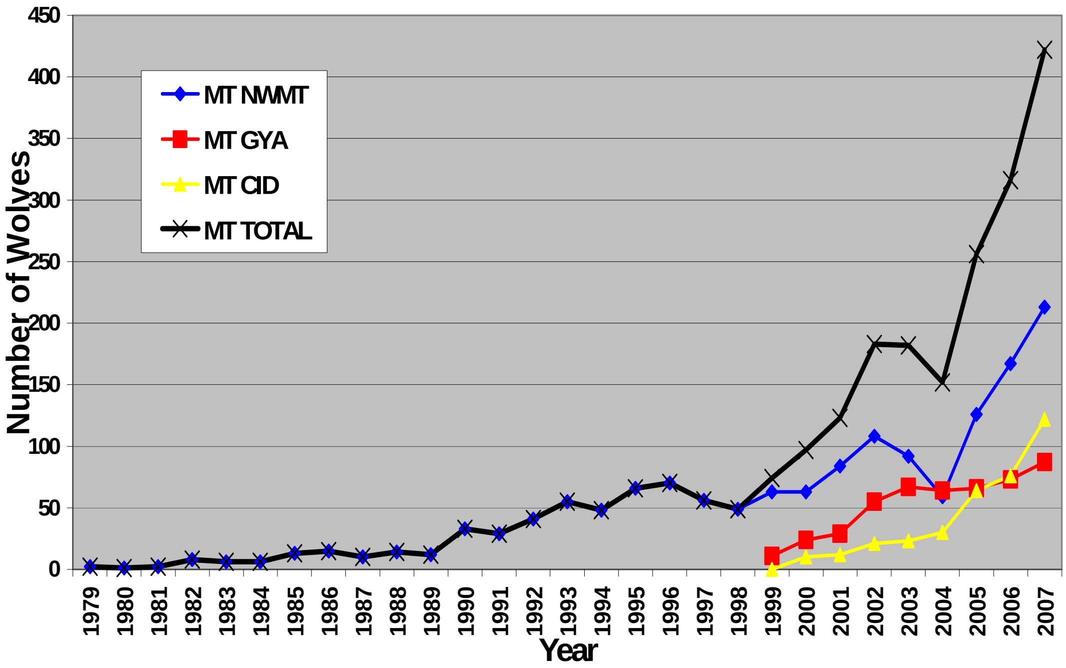


Figure 3. Number of Wolves in Montana by recovery area, 1979-2007.

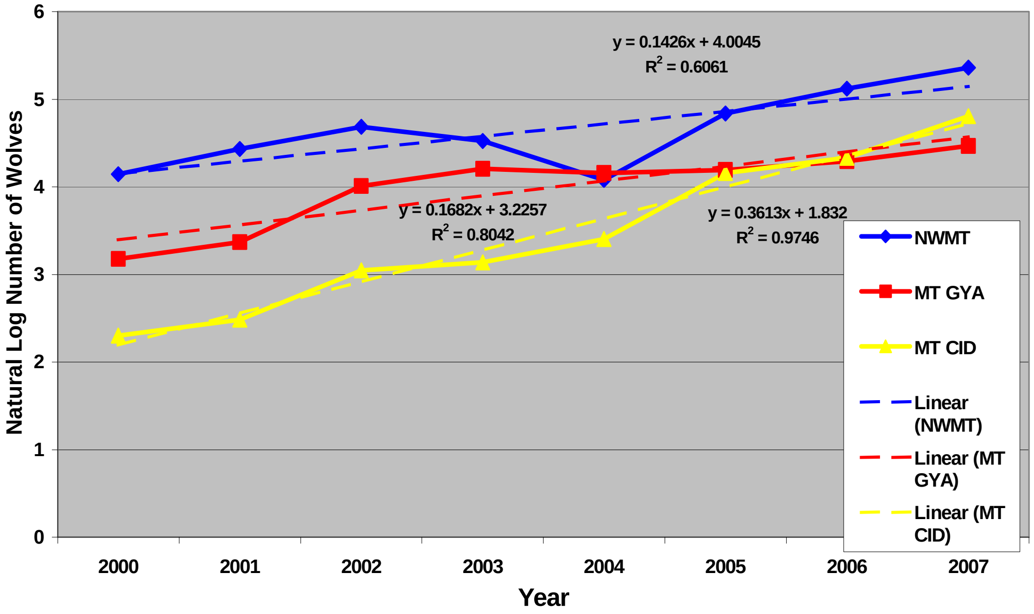


Figure 4. Rate of increase of wolves in Northwest Montana Endangered Area, Montana portion of GYA Experimental Area, and Montana portion of Central Idaho Experimental Area, 2000-2007.

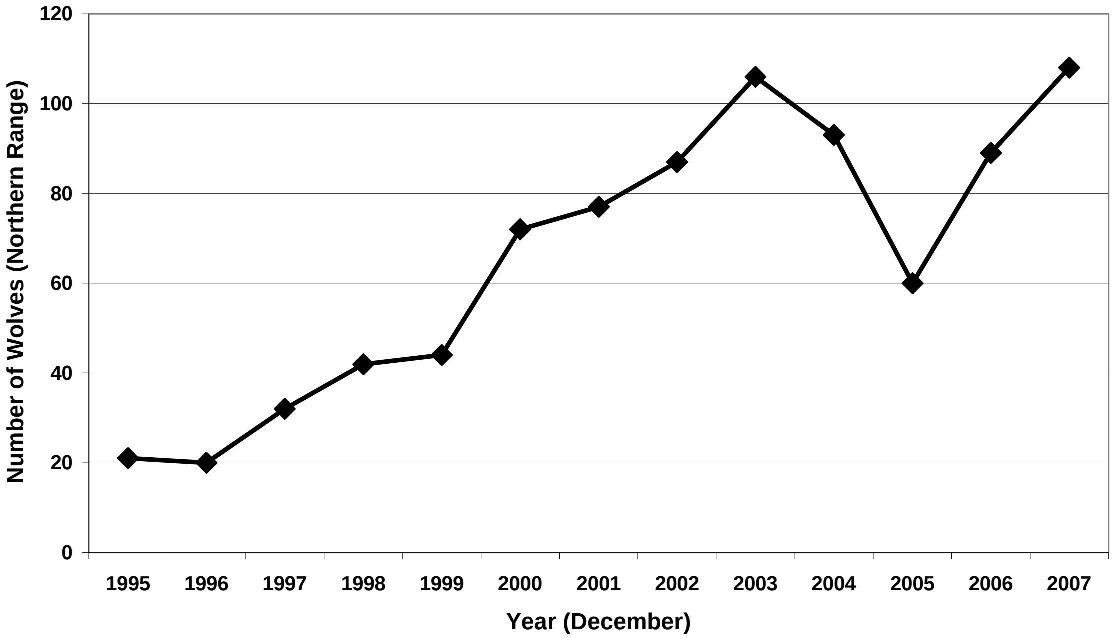


Figure 5. Number of wolves (December) within the area used by the Northern Range elk herd (including Montana portions), 1995-2007.

## Prey Selection by Wolves

Species of Kill

In southwestern Montana and the Greater Yellowstone area, elk are clearly the dominant natural prey species for wolves. For 118 wolf kills documented in the Gallatin Canyon during winters 2000-06 (J. Winnie, Jr. and D. Christianson, pers. comm.), 114 (97%) were elk and 4 (3%) were moose. In the Madison Valley study area (Gude and Garrott 2003, Fuller and Garrott 2004, Grigg and Garrott 2005, Hamlin 2006), 87% of 234 wolf kills were elk, 9% were mule deer, and 3% were pronghorn. In the Northern Yellowstone area (Smith et al. 2004a, Smith et al. 2001-2008), composition of more than 2,500 wolf-killed prey indicated 87% elk, 5% bison (*Bison bison*), 2 % moose, and 1% deer. Atwood et al. (2007) found that elk comprised 70%, white-tailed deer 26%, and mule deer 4% of wolf kills on a site on the north end of the Madison Mountains, within the GYA.

In contrast, in northwestern Montana, near Glacier National Park, Kunkel et al. (1999) found that white-tailed deer comprised 83% of wolf prey, elk 14%, and moose 3%. Thus we might expect that in MFWP Region 1 and the northern portions of Region 2, white-tailed deer are the main prey species for wolves and that for most of the rest of Montana, elk are the main prey species for wolves.

Little work has been accomplished regionally on wolf prey selection outside the winter period. Recently (Smith et al. 2007), investigations began of wolf prey selection and kill rates during summer. Although GPS radio-telemetry will form the basis for much of future knowledge on this project, wolf scat collection is the basis for current knowledge. Data from these summer-collected wolf scats indicated lower occurrence of elk, and higher occurrence of deer and moose in summer scats than the proportions of observed kill by species during winter (Smith et al. 2007).

Sex/Age Selection of Elk

Winnie and Creel (2007) reported that in the Gallatin Canyon, wolves killed adult female elk one-third as often as expected by chance, while bulls and calves were killed 2.2-fold and 2.5-fold more often than expected by chance, respectively. However, Hamlin (2006) reported that the home range of the Chief Joseph wolf pack overlapped and centered on the major bull elk wintering area in the Daly-Tepee-Lodgepole drainages of the Gallatin Canyon, which likely contributed to a sex/age ratio of kill skewed toward bulls. For the entire Gallatin Canyon study area, of 114 known sex/age elk killed by wolves, 54% were bulls, 30% calves, and 16% cows.

We partitioned wolf kill by sex and age class into those that occurred in the Daly-Tepee-Lodgepole (DTL) drainages (bull elk wintering area and wolf den site area) and those that occurred in the Porcupine and Taylor Fork (PTF) drainage areas. We also summarized sex/age classifications of elk in these 2 areas from early and late winter helicopter classifications over the same period, 2001-2006. Observed kill was distributed differently by sex/age class than expected (proportional to live population) kill in both the PTF ($\chi^2 = 92.6$, $P < 0.00001$) and DTL ($\chi^2 = 49.5$, $P < 0.00001$) areas. For the PTF area, 86% of the $\chi^2$ value was explained by the disproportionate selection for calves. Calves were killed at 5 times the expected proportional rate, bulls were killed similar to expected rates and cows were killed at 40% of the expected proportional rate. Observed sex/age class of the elk kill in PTF (57% calves, 34% cows, and 9 % bulls) was similar to that reported in the Madison Valley (68% calves, 26% cows, and 6% bulls, summarized by Hamlin 2006). For the DTL area, 53% of the $\chi^2$ value was explained by many fewer cows killed than proportionally expected and 34% of the $\chi^2$ value was explained by more bulls killed than expected. Cows were killed at about 10% of the expected rate and bulls were killed at about 1.7 times the expected rate. Calves were killed about 2-fold more than expected, but few calves were observed in the area and few total calves were killed there. Observed sex/age class of the elk kill in DTL (13% calves, 4% cows, and 83% bulls) was much more skewed toward bulls than observed elsewhere.

On the Madison Valley study area, of 204 known sex/age elk killed by wolves, 68% were calves, 26% cows, and 6% bulls (Gude and Garrott 2001-2003, Fuller and Garrott 2004, Grigg and Garrott 2005, Hamlin 2006). Observed kill was distributed differently by sex/age class than expected (proportional to live population) kill ($\chi^2 = 444.8$, $P < 0.00001$). Calves were killed at about 4.5 times the expected rate, cows at about one-third, and bulls at one-half of the expected rates based on proportions in the live population. Selection for calves accounted for about 85% of $\chi^2$ value.

Data from Smith et al. (2004a) and Smith et al. (2001-07) indicated that on the Northern

Yellowstone Range from 1995-2007, about 38% of elk killed by wolves during winter were calves, 32% cows, and 30% bulls. The proportion of wolf-kill that was calves has generally declined and the proportion bulls increased over the period. Overall, both calves and bulls were disproportionately selected, but an increasing trend toward selection of bulls has occurred.

Atwood et al. (2007) found that wolves killed more bull elk (64%) and fewer adult female elk (18%) than expected, but that calves (18%) were killed in proportion to their availability on the north end of the Madison Range. Although similar to the upper Gallatin Canyon (DTL) in high availability of bulls compared to most populations, here also, wolves clearly selected bulls.

Although wolves consistently tended to select young-of-the-year among elk in most areas, data reported in the GYA (Smith et al. 2004a, Hamlin 2006, Winnie and Creel 2007, Atwood et al. 2007, Smith et al. 2008, and Gude, Fuller, Grigg, Garrott, pers. comm.) indicated that sex/age class kill of elk by wolves can vary substantially among areas, year, and even sub-areas within areas (see above), depending on locations of wolf pack territory, social distribution of elk, habitat, composition of the prey population, and other factors. In some areas and situations, wolves clearly select bull elk disproportionately, which may relate to their relatively poorer condition during winter and habitats occupied (Winnie and Creel 2007, Atwood et al. 2007, Smith et al. 2008).

### Winter Predation Rate

In the Gallatin Canyon study area, estimated wolf kill rates were determined only for a 3-month period during winter 2000-01 (J. Winnie, Jr., pers. comm.). An estimated 0.085 elk kills per wolf-day were recorded. This was equivalent to 15 elk killed per wolf per 181 day winter period (November-April).

In the Madison Valley, Gude and Garrott (2003) reported wolf-kill rates of 0.112 elk kills per wolf-day during winter 2001-02 and 0.138 elk kills per wolf-day during winter 2002-03. The average of these rates (0.125 elk kills per wolf-day) was equivalent to 23 elk killed per wolf during November-April.

For the Northern Yellowstone Range, Smith et al. (2004a) estimated about 0.061 elk killed per wolf-day, but in more recent years, kill rate has declined to about 0.0373 elk killed per wolf-day (estimated from Smith et al. 2005-2008). These rates are equivalent to about 11 and 7 elk killed per wolf during November through April.

Estimated kill rates for Central Yellowstone (Becker et al. 2008, Garrott, pers. comm.) were similar to earlier rates for Northern Yellowstone (0.060 elk kills per wolf-day, or 11 elk killed per wolf per winter).

Combined evidence indicated that kill rates varied substantially (0.037 – 0.138 elk kills per wolf day, 7 – 23 elk killed per wolf/winter) across areas and among years within areas. Numerous factors such as winter conditions, availability of alternate prey, distribution of prey, and wolf pack size may play a role in this variation.

## Other Predators

Because information from a variety of regional studies (Schlegel 1976, Kunkel et al. 1999, Smith et al. 2006, Harris 2007, Atwood et al. 2007, Zager et al. 2007, Hamlin et al. 2008) indicated that bears, especially grizzly bear, as well as other predators such as cougar are important predators of both newborn and older elk, we also discuss predators other than wolves. Many Montana environments are multi-predator systems, where combined predator : prey ratios may be high and results and conclusions different than for single predator/prey systems.

Little is known about varying densities of grizzly bear, black bears, cougars, and coyotes across ecosystems and areas of Montana. Dusek et al. (2006) indicated that in much of Montana, cougars reached a peak in numbers during the mid-late-1990s. They also reported that annual rate of adult white-tailed deer mortality due to cougar predation was correlated to a 1-year lag in cougar harvest in the Salish Mountains of northwestern Montana. Cougar numbers apparently declined from highs after the late-1990s (especially after declines in ungulate numbers following the severe winter of 1996-97), but may have increased recently. However, there is no information to estimate cougar numbers by area and year across Montana. Similarly, Mace (pers. comm.) has determined estimates of black bear density across several areas of Montana, but these are “point-in-time” estimates. We have assumed that cougars, black bear, and coyotes occur at relatively similar densities at the same times across most of our ungulate study populations.

Estimates of grizzly bear numbers are made for the GYA (Haroldson 2008) which indicate that grizzly bears numbers have been increasing since 1987 (Fig. 6) and may be about 3.5 times higher in 2008 than in 1987. An estimated 571 grizzly bears were present in the GYA in 2007 (Haroldson 2008) and 596 in 2008 (Schwartz et al. 2009 *in press,* Fig. 6).

We used data provided in Inter Agency Grizzly Bear Committee annual reports (e.g. Haroldson et al. 2006 and 2007) to construct annual estimates for grizzly bear in 4 areas of the GYA coinciding with Montana elk populations (Fig. 7). These methods were based on numbers and distribution of observed females with COY and smoothed with a 3-year running average (see Hamlin et al. 2008 for methods). This information indicated that grizzly bear numbers increased during the post-wolf period in all 4 areas we examined, the Northern Yellowstone, Gallatin Canyon, southern Madison-Gallatin Range, and Madison-Firehole (Fig. 7). Although estimated numbers of grizzly bears were highest in the Northern Yellowstone, the numbers of bears per 1,000 elk was greatest in the Gallatin Canyon and Madison-Firehole (Hamlin et al. 2008).

An estimated 765 grizzly bears inhabit the Northern Continental Divide Ecosystem (NCDE) in Montana (http://www.nrmsc.usgs.gov/research/NCDEbeardna.htm, Accessed 1/16/09)**.** Annual estimates of grizzly bear numbers are unavailable, however substantial numbers of grizzly bear are available to prey on elk and other ungulates in the NCDE.

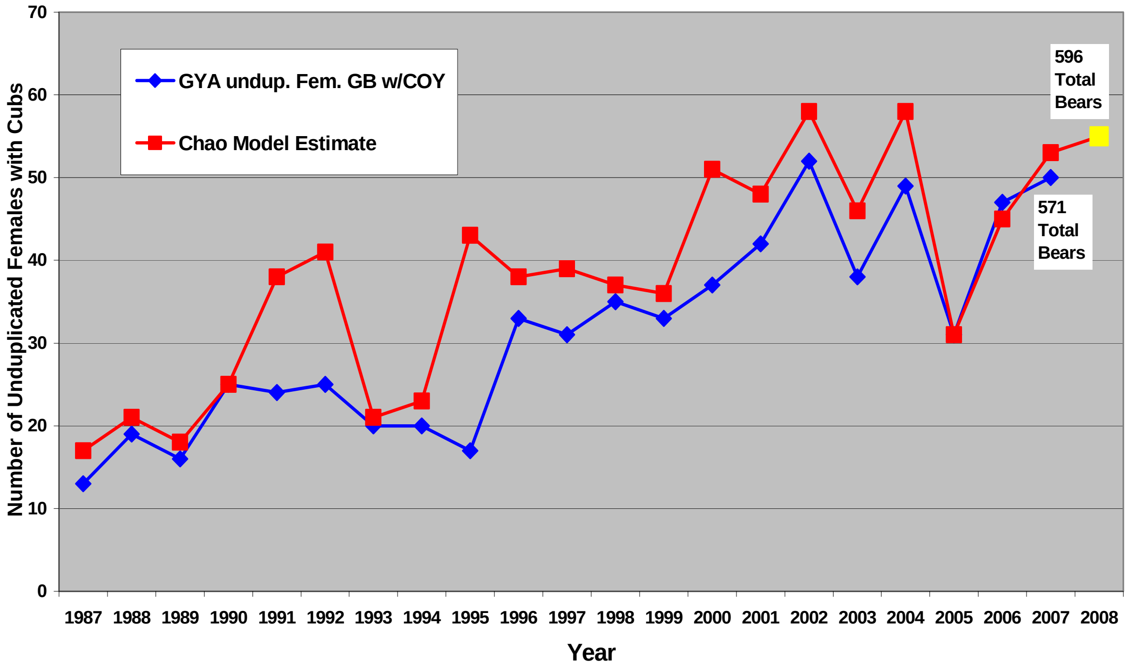


Figure 6. Minimum number of female grizzly bear with cubs-of-the-year (COY) observed and Chao model estimate for females with COY in the GYA (Haroldson 2008). Estimated Total number of grizzly bears provided for 2007 and 2008 (Yellow square = projected).

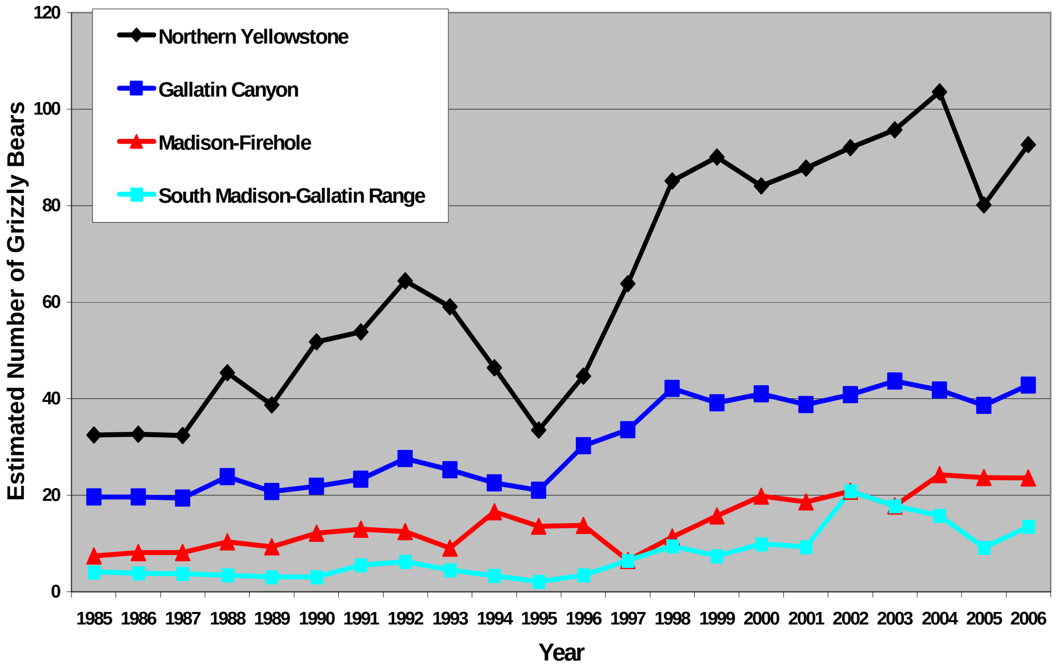


Figure 7. Three-year running average estimate for total grizzly bears within the range of the Northern Yellowstone, Gallatin Canyon, Madison-Firehole, and South Madison-Gallatin elk herds. See Hamlin et al. (2008) for method of estimation.

## Elk Vital Rates

### Pregnancy

Creel et al. (2007), using average progesterone concentrations in fecal samples, argued that elk pregnancy rates decreased with increasing ratios of wolves to elk. However, Hamlin et al. (2008) found no effect of wolf: elk ratios in the GYA on directly observed pregnancy rates or pregnancy rate determined by blood serum concentrations of pregnancy specific protein B (PSPB) for three elk winter ranges. Further, Hamlin et al. (2008) reported that post-wolf pregnancy rates in the GYA were equal to or higher than average pre-wolf pregnancy rates from seven elk herds across Montana (Hamlin and Ross 2002).

To provide additional insights into discussions surrounding these seemingly conflicting results, we also focused effort on detailed data collection and analysis for determining factors that affect elk pregnancy rates on the Northern Yellowstone elk herd. Hunters reported pregnancy status (PREG) of cow elk every year of the Gardiner Late hunt. We used only PREG data from elk age 2.5 and older because yearlings have a lower and more variable pregnancy rate than adults, and samples of yearlings were small in later years. Although hunter reports were, on average, lower than independent estimates of pregnancy derived from pregnancy-specific protein B assays in the same herd (Hamlin et al. 2008) it is reasonable to assume that under-reporting of pregnancy by hunters would be similar and consistent among years, so we could model the variation in reported pregnancy rates among years.

To determine what influences PREG, we considered multiple factors in a modeling exercise. Average age of the Northern Yellowstone elk herd has been increasing (Tom Lemke, MFWP unpublished data), and as elk become senescent, their pregnancy rates and lactation rates may decrease, so we considered average age of the elk herd (excluding calves) determined by eruption and wear (Quimby and Gaab 1957) at harvest as a covariate (AGE). We considered 2 warm-season weather covariates: a locally-measured precipitation index (PREC) and a regional drought index (Palmer Drought Severity Index [PDSI]; Palmer 1968), because local and regional weather patterns can influence ungulate vital rates. We measured PREC as the May-June precipitation recorded at the Tower weather station, and we measured PDSI from the average of Wyoming Region 1. We considered 2 cold-season weather covariates: cumulative snowfall over 1 November through 30 April (SNOW) measured at the Tower weather station, and a cumulative snow-moisture measure (SWE, Garrott et al. 2003). We also considered the effects of varying wolf and grizzly bear numbers on elk calf production and survival (Barber-Meyer et al. 2008). Covariate WOLF:ELK represented the number of wolves per elk on the Northern Yellowstone Range at the end of December (inside and outside YNP; e.g. Smith et al. 2007, Sime et al. 2008), and covariate GRIZ:ELK represented estimated grizzly bear per elk (a 3-year running average of an index of grizzly bear numbers associated with the distribution of Northern Range elk as calculated by Hamlin et al. 2008). This index was calculated from annual observations and locations of female grizzly bear with cubs-of-the-year (COY) reported in Interagency Grizzly Bear Committee annual reports (e.g. Schwartz et al. 2008). We used a 3-year running average because of the long reproductive cycle of grizzly bears (2-3 years), and because females with COY is generally a small number with high annual fluctuation. We also used lagged covariates for modeling (e.g. LWOLF:ELK represented wolves per elk present during the winter of pregnancy whereas WOLF:ELK represented the wolf covariate after calves were born).

We created a model suite that contained additive and interactive combinations of covariates based on *a priori* hypotheses described above. However, we knew several of the predictor variables were highly correlated, so we did not include variables with an $R^2 > 0.30$ in the same model to prevent complications of correlated predictors. We used the logit-transform of PREG for each year, and then examined multiple linear regression models. Total annual sample sizes used to estimate PREG ranged from 42 to 1,505, with a median of 528. For the one year when no yearlings were harvested, we imputed a value of 0.5, a small non-zero value that allowed the logit link but that prevented an outlying data point. For analysis, we centered and scaled all covariates (based on the years included in the analysis) to facilitate comparison of relative effect size among predictors. The SNOW and SWE covariates were each missing a singular value (2005 and 2007, respectively), which we interpolated using the average of the values in the data set (i.e., when centered and scaled, this value = 0).

We obtained 14,066 records of PREG during 1985-2007. Of 26 candidate models for to explain variation in PREG, 7 models were within 2 $\Delta AIC_c$ units, including the baseline (null) pregnancy rate model and six main-effects models (Table 1). No model explained more than 13% of the variation in pregnancy rate and model averaging suggested no covariates we examined significantly affected pregnancy rate. The model averaged coefficient value for wolf:elk ratio was –0.13 (95% C.I. = -0.29, 0.04), and –0.12 (95% C.I. –0.29, 0.05) for the lagged wolf:elk ratio, however both confidence intervals overlapped zero.

In large mammals, pregnancy is considered a stable vital rate unlikely to decline substantially except under extremely severe conditions (Fowler 1981, Gaillard et al. 1998, Eberhardt 2002). Our results from the Northern Yellowstone elk herd corroborated those expectations because no variable we examined had a significant influence on variation in pregnancy rate. Pregnancy rates have not significantly changed over the period 1986-2007 and change in pregnancy rate is apparently not a clear explanation for declining calf survival and population decline for the Northern Yellowstone elk herd (also see Hamlin et al. 2008).

Table 1: Model selection results for pregnancy in Northern Yellowstone elk, 1985-2007.

| MODEL | K | $\Delta$ $AIC_c$ | $AIC_c$ | $W_i$ | $R^2$ |
|---|---|---|---|---|---|
| PWOLF:ELK | 3 | 0.00 | 22.56 | 0.14 | 0.13 |
| P1 (NULL) | 2 | 0.33 | 22.89 | 0.12 | NA |
| PLWOLF:ELK | 3 | 0.49 | 23.06 | 0.11 | 0.11 |
| PPDSI | 3 | 0.73 | 23.29 | 0.10 | 0.10 |
| PPREC | 3 | 1.25 | 23.82 | 0.08 | 0.08 |
| PAGE | 3 | 1.65 | 24.21 | 0.06 | 0.06 |
| PSNOW | 3 | 1.80 | 24.37 | 0.06 | 0.05 |
| PWOLF:ELK+PREC | 4 | 2.64 | 25.20 | 0.04 | |
| PLWOLF:ELK+PREC | 4 | 2.67 | 25.24 | 0.04 | |
| PSWE | 3 | 2.85 | 25.42 | 0.03 | |
| PWOLF:ELK+SNOW | 4 | 2.92 | 25.49 | 0.03 | |
| PLWOLF:ELK+SNOW | 4 | 2.93 | 25.49 | 0.03 | |
| PWOLF:ELK+SWE | 4 | 3.16 | 25.72 | 0.03 | |
| PLWOLF:ELK+SWE | 4 | 3.46 | 26.02 | 0.02 | |
| PSNOW+AGE | 4 | 3.88 | 26.44 | 0.02 | |
| PPREC+AGE | 4 | 3.96 | 26.53 | 0.02 | |
| PSWE+AGE | 4 | 4.51 | 27.07 | 0.01 | |
| PWOLF:ELKXSNOW | 5 | 5.25 | 27.82 | 0.01 | |
| PLWOLF:ELKXSNOW | 5 | 5.38 | 27.94 | 0.01 | |
| PWOLF:ELKXPREC | 5 | 5.72 | 28.28 | 0.01 | |
| PLWOLF:ELKXPREC | 5 | 6.20 | 28.77 | 0.01 | |
| PWOLF:ELKXSWE | 5 | 6.23 | 28.79 | 0.01 | |
| PLWOLF:ELKXSWE | 5 | 6.59 | 29.15 | 0.01 | |
| PSNOWxAGE | 5 | 7.19 | 29.75 | 0.00 | |
| PPRECxAGE | 5 | 7.28 | 29.84 | 0.00 | |
| PSWExAGE | 5 | 7.75 | 30.32 | 0.00 | |

## Calf Survival

Adult female survival is generally ranked higher than calf survival in its effect on population growth. However, modeling by Raithel et al. (2007) indicated that because of its greater variance within and among populations, elk calf survival explained about 5 times more of the variation in population growth rates than did adult female mortality.

We used classifications of elk, including mid-to-late July classifications, to help determine timing of elk calf mortality. For some areas, mid-summer classifications were available in pre-wolf years, for most areas, they began in 2002.

Of 5 southwestern Montana elk populations with both pre- and post-wolf data for mid-summer elk classifications (Fig. 8), only the Gallatin-Madison and Northern Yellowstone areas showed substantial reductions in mid-summer calf:100 cow ratios during the post-wolf period. No pre-wolf mid-summer data were available for the Northern Yellowstone area, but calf : 100 cow ratios were lower there recently in mid-summer than in March (after an additional 7 months of mortality) during the pre-wolf period (Fig. 8). Declines of about 50% in calf survival in the Gallatin-Madison and Northern Yellowstone areas coincide with pre- and post-wolf periods, but do not necessarily imply causation. Other potentially influencing factors in these areas have co-varied with increases in wolf numbers, for example increased drought and increased numbers of grizzly bears (Hamlin et al. 2008).

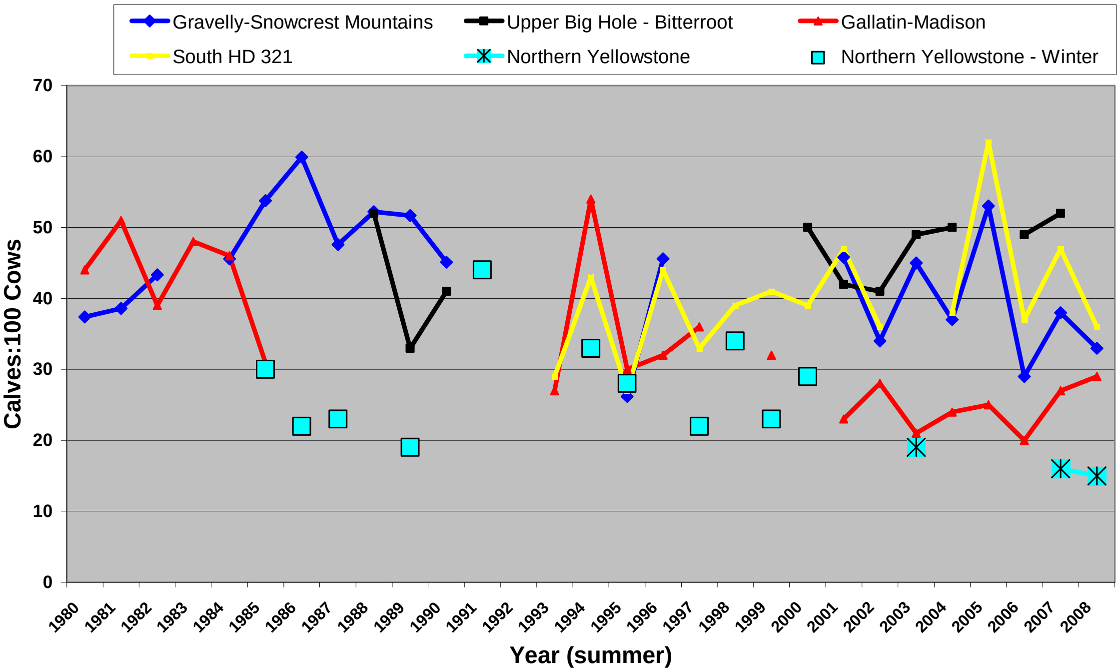


Figure 8. Mid-summer elk calf:100 cow ratios (March ratios for Northern Yellowstone prior to 2001) among southwestern Montana areas with long-term data.

We obtained mid-summer calf : 100 cow classifications from additional areas in Montana during 2001 through 2008 (Fig. 9). These data indicated that except for the Gallatin-Madison and Northern Yellowstone herds, mid-summer calf : 100 cow ratios were within historical norms during the period. Mid-summer calf : 100 cow ratios were about half of historically "normal" levels in the Gallatin-Madison and Northern Yellowstone herds. For the 2001-2008 period, areas with no wolves or grizzly bears (or only transitory presence) averaged 39 calves : 100 cows during mid-summer, areas with low numbers of wolves and no grizzly bears averaged 45 calves : 100 cows, and the Gallatin-Madison and Northern Yellowstone areas, with high numbers of both wolves and grizzly bears, averaged 21 calves : 100 cows.

An investigation of mortality rates and causes for newborn elk calves on the Northern Yellowstone Range was conducted during 1987-1990 (Singer et al. 1997) prior to wolf restoration and a follow-up study began in 2003 (Barber-Meyer et al. 2008).

Elk calf mortality during summer (birth through October) averaged twice as high during 2003-2005 than during pre-wolf years of 1987-90 (Barber-Meyer et al. 2008, Table 2). Winter mortality rates during the recent period were half that during 1987-1990 (Table 2) but the combination resulted in annual mortality rates of calves about 50% higher during 2003-2005 than during 1987-1990 (Table 2).

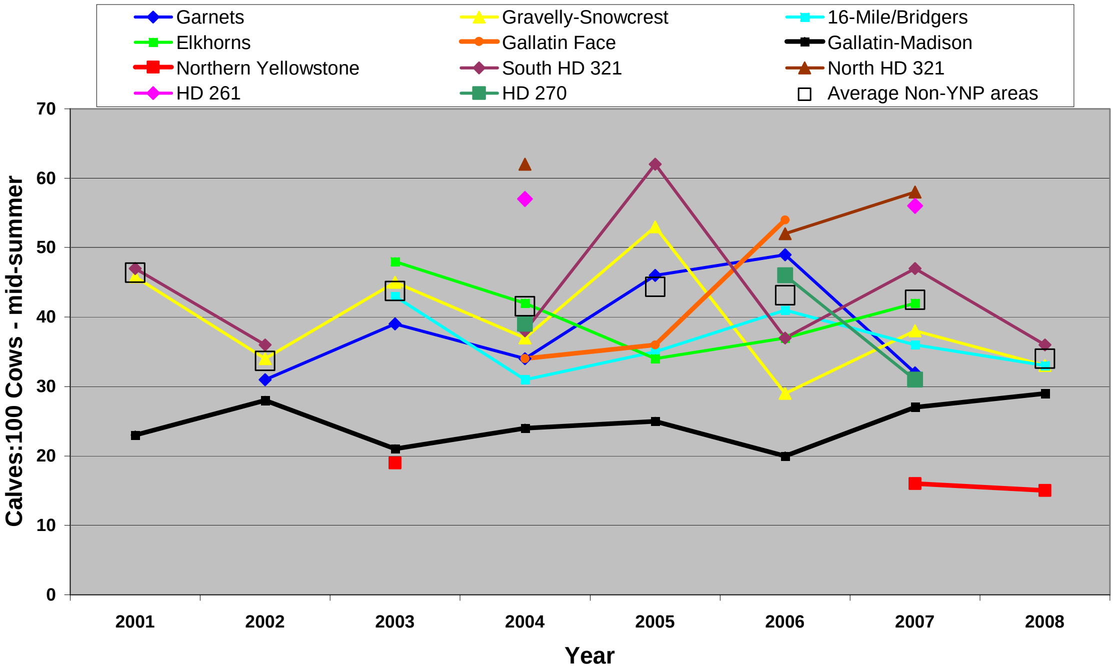


Figure 9. Mid-summer elk calf:100 cow ratios in southwestern Montana elk populations, 2001-2008.

The known causes of summer mortality averaged 95% predation during 2003-2005 compared to 72% during 1987-90. The increase in summer mortality appeared to be related to an increase in mortality caused by bears of both species (Table 3, 55% grizzly bear, 35% black bear, and 10% unknown bear species). Wolf predation on elk calves during summer was relatively minor, not totally offsetting a decline in mortality caused by coyotes from levels observed during 1987-90 (Table 3). Winter mortality rates of elk calves were lower during the post-wolf period. However, winter-kill/starvation loss associated with the fires of 1988 and following severe winter contributed to the high mortality observed for the earlier period. Excluding 1988-89, elk calf mortality during winter was low and similar for the pre- and post-wolf periods, but causes of winter mortality averaged 75% predation during 2003-2005 compared to 3% during 1987-1990 (Table 3).

Table 2. Mortality rate (%) of newborn elk calves, Northern Yellowstone Range, 1987-1990 and 2003-2005.

| | | Mortality Rate (%) | | |
|---|---|---|---|---|
| Year[a] | No. Marked | Summer [b] | Winter [c] | Annual |
| 1987[d] | 30 | 44 | 14 | 52 |
| 1988[d] | 29 | 15 | 84 | 86 |
| 1989[d] | 36 | 32 | 8 | 38 |
| 1990[d] | 32 | 50 | 6 | 53 |
| **TOTAL[d]** | **127** | **35** | **28** | **57** |
| | | | | |
| 2003[e] | 51 | 69 | 13 | 73 |
| 2004[e] | 44 | 73 | 9 | 77 |
| 2005 [e] | 56 | 75 | 8 | 79 |
| **TOTAL [e]** | **151** | **72** | **10** | **76** |

[a] Year = year of birth; [b] Summer = mid-May (birth) through October; [c] Winter = November – May; [d] from Singer et al. 1997;[e] from Barber-Meyer et al. 2008.

Table 3. Cause of mortality (%) for radio-transmitter marked newborn elk calves, Northern Range, 1987-90 (Singer et al. 1997) and 2003-2005 (Barber-Meyer et al. 2008) (**Known causes only used for percentages**).

| Cause of Mortality | 1987-1990 Summer | | 2003-05 Summer | | 1987-90 Winter | | 2003-06 Winter | |
|---|---|---|---|---|---|---|---|---|
| Wolf | | | 14 | | | | 25 | |
| Bear (both species) | 39 | | 60 | | | | | |
| Wolf or Bear | | | 2 | | | | | |
| Coyote | 28 | | 9 | | | | 25 | |
| Wolf or Coyote | | | | | | | 25 | |
| Eagle | 3 | | 1 | | | | | |
| Cougar | | | 3 | | 3 | | | |
| Wolverine | | | 1 | | | | | |
| Unknown Predator | 3 | | 5 | | | | | |
| **TOTAL PREDATION** | **72** | | **95** | | **3** | | **75** | |
| Starvation | 3 | | | | 58 | | | |
| Disease | 8 | | | | 3 | | | |
| Hunter Harvest | | | | | 15 | | 25 | |
| Accident | 6 | | | | 3 | | | |
| Unknown/Natural[a] | 13 | | 5[a] | | 15 | | | |
| **TOTAL OTHER** | **28** | | **5[a]** | | **97** | | **25** | |

[a] 2003-2005 – 1 likely drowning, 1 excess fluoride, 1 non-fully expanded lungs, 1 exposure (snowstorm), and 1 pneumonia.

Rates and causes of summer mortality of newborn elk calves (Table 4) were also determined recently in the Gallatin Canyon (2005, n =29, D. Christianson pers. comm.) and the Garnet Mountains (2003-2006, Harris 2007). Summer mortality rate was 52% and bears (identified bears were grizzly bear) accounted for 80% of elk calf summer mortality in the Gallatin Canyon (Table 4). A coyote or domestic dog killed one calf and 2 mortalities were of unknown cause. In the Garnet Mountains, mortality rates of telemetry–marked calves were much higher in 2002 than rates imputed from subsequent population surveys. Because of concerns about possible effects of capture techniques and other factors on survival of telemetry marked calves in 2002 (Harris 2007), we excluded 2002 data from our summaries (Table 4). Summer mortality rate of elk calves was substantially lower (15%) in the Garnet Mountains (Table 4) than for other areas, but predation accounted for 65% of known causes of mortality. Except for a few transients in the last year, no wolves or grizzly bears were in the Garnet study area. Black bear and cougar each accounted for 19% of elk calf mortalities, coyotes 4% and unidentified predators 23% of mortality. Malnutrition/starvation, likely from abandonment, accounted for 19% of mortality.

During 1984-88, a 17% summer mortality rate for telemetry-marked elk calves was recorded in the Gravelly-Snowcrest Mountains of southwestern Montana (Hamlin and Ross 2002). At that time, the Gravelly-Snowcrest Mountains had no wolves and rare transitory grizzly bear presence. Eighty-two percent of elk calf deaths were attributed to starvation due to abandonment and 18% of summer deaths were due to black bear predation (Hamlin and Ross 2002).

Elk calf survival to near recruitment as indexed by calf:100 cow ratios observed during late-winter/spring has been recorded for many years and populations in the GYA (Fig. 10). For most populations, calf survival has remained near long-term averages during the post-wolf and severe drought period (Fig. 10). However, calf recruitment has declined for the Northern Yellowstone, Gallatin Canyon, and Madison-Firehole populations, all of which have relatively high populations of both wolves and grizzly bear (Hamlin et al. 2008).

Drought has been considered as contributing to reduced elk calf survival in the past (Singer et al. 1997) as well as to recent reductions in calf survival (Vucetich et al. 2005). Reduced calf survival would presumably operate through a reduction in nutritional level, making calves less thrifty and more vulnerable to all forms of mortality. However, Hamlin et al. (2008) found that on the Northern Range, weights of calves harvested in January were at or above the long-term average during the drought period of 1998-2005. Regionally, across 7 elk populations in southwestern Montana and YNP, data presented by Hamlin et al. (2008) indicated that recruitment increased by about 6 calves:100 cows from the highest level of drought (measured by PDSI) to the most moist conditions. However, the same data indicated that recruitment averaged 22 calves:100 cows higher across the areas where wolves and grizzly bear were < 4:1000 elk (usually much less or none) compared to areas where there were > 4 wolves/grizzly bear:1000 elk (Hamlin et al. 2008). Thus, potential drought effects were minor compared to the effect potentially related to predation.

Table 4. Summer (birth – 31 August) mortality rates (%) and causes (%) of telemetry-marked elk calves, Northern Yellowstone Range 1987-90 and 2003-05, Gallatin Canyon 2005, and Garnet Mountains 2003-06.

| | Northern Range[a] | | Gallatin Canyon[b] | Garnets[c] |
|---|---|---|---|---|
| Years | 1987-90 | 2003-05 | 2005 | 2003-06 |
| Mortality Rate | **35%** | **71%** | **52%** | **15%** |
| CAUSE | | | | |
| Wolf | | 14 | | |
| Bear (both species) | 39 | 60 | 80 | 19 |
| Wolf or Bear | | 2 | | |
| Coyote | 28 | 9 | 7[d] | 4 |
| Eagle | 3 | 1 | | |
| Cougar | | 3 | | 19 |
| Wolverine | | 1 | | |
| Unknown Predator | 3 | 5 | | 23 |
| TOTAL PREDATION | **72** | **95** | **87** | **65** |
| | | | | |
| Starvation | 3 | | | 19 |
| Disease | 8 | | | 4 |
| Accident | 6 | | | 8 |
| Unknown | 13 | 5 | 13 | 4 |
| TOTAL OTHER | **28** | **5** | **13** | **35** |
| GRAND TOTAL | 100 | 100 | 100 | 100 |

[a] Data from Singer et al. 1997 and Evans et al. 2008.
[b] Data from D. Christianson, pers. comm.
[c] Data from Harris (2007), excluding 2002.
[d] Coyote or domestic dog.

Steve Ard photo

Ken Hamlin photo

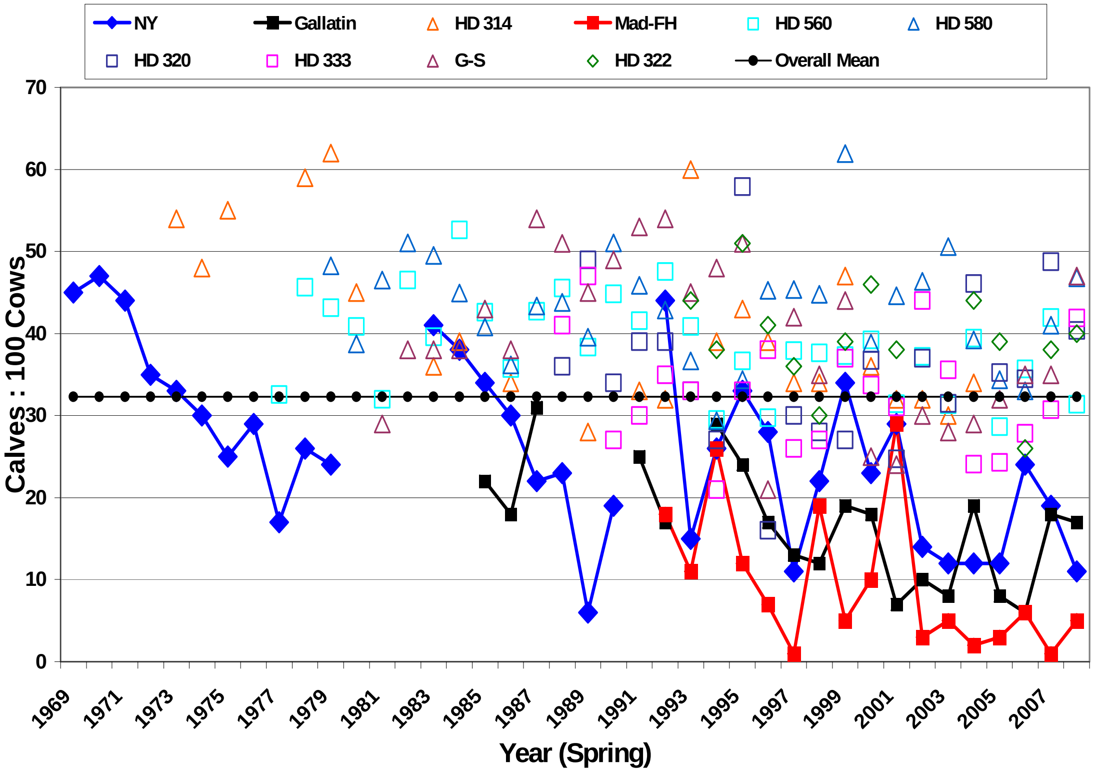


Figure 10. Elk calf:100 cow ratios observed during late-winter/spring in the GYA, 1969-2008.

Index data collected for Northern Yellowstone elk during the Gardiner late hunt also indicate that bear and wolf predation combine to affect elk calf survival. We used hunter-reported cow elk lactation status for elk harvested during January in the Gardiner late hunt as an index of early-season calf survival (ESCS). Although lactation generally ceases within 72 hours of cessation of suckling in most species of mammalian females, milk may remain in the mammary glands for a time afterward. However, milk is seldom present in mammary glands 2 months after lactation ceases (J. Berardinelli, Montana State University, personal communication). We defined ESCS as a calf surviving through October to account for this period of milk retained in mammary glands. We derived lactation rates only from elk age 3.5 and older, because 2.5 year olds would have bred as yearlings and would therefore have a lower and more variable lactation rate. We limited data to those collected in January so that all years' samples were consistent and because overall lactation rates normally decline from December through February due to weaning.

We indexed annual calf survival (ACS), survival through the first winter of life, from a ratio of harvested yearlings to cow elk, time-lagged appropriately to reference the year as calves. We used yearling (1.5 years) harvest rather than calf (0.5 years) harvest because hunters may differentially select for or against calves in different years with different hunting conditions, but hunters are less likely to differentiate a yearling cow from an adult cow. Furthermore, once elk calves survive their first winter, their survival rates are generally high and constant (Hamlin and Ross 2002). Thus, the number of yearling females taken in the hunt at year *t+1*, adjusted for the 60:40 ratio of female to male elk by age 8 months (Cunningham et al. *in press*, J. Cunningham, Montana Fish, Wildlife and Parks unpublished data) and divided by the number of females ≥ 2.5 years at *t+1*, provided an estimate of the calf:cow ratio for time *t*. The resulting variable (ACS) indexed cumulative effects from pregnancy through survival to the yearling age class. The ratio of ACS to ESCS represented the late-season survival (LSCS) of elk from age 6 months to 1.5 years. The ratio represented survival in that, if 50% of the cows were lactating at time *t*, then 50% of cows had a calf that survived the early season, and ACS/0.5 reflected the proportion of calves surviving to 1.5 years. This ratio is bounded between 0 and 1, where 1 suggests each calf born that survived the early-season also survived the late-season to become a yearling. We expected LSCS to be more sensitive to individual covariates than ACS, which represented cumulative effects from pregnancy through yearling age.

To determine which factors affect ESCS, LSCS, and ACS, we considered several potential predictor variables. We considered the average age of harvested elk (AGE), May-June precipitation recorded at the Tower weather station (PREC), the regional Palmer Drought Severity Index (PDSI), cumulative snowfall over 1 November through 30 April at the Tower weather station (SNOW), cumulative snow water equivalent at the Tower weather station (SWE), the number of wolves per elk on the Northern Yellowstone Range at the end of December (WOLF:ELK, and lagged by one year as LWOLF:ELK), and a 3-year running average of an index of grizzly bear numbers to elk numbers on the Northern Range, as calculated by Hamlin et al. (2008) (GRIZ:ELK, lagged one year as LGRIZ:ELK). These predictor variables were measured as described in the "Elk Vital Rates: Pregnancy" section above.

For each response variable, we created a model suite that contained additive and interactive combinations of covariates based on *a priori* hypotheses described above. However, we knew several of the predictor variables were highly correlated, so we did not include variables with an $R^2 > 0.30$ in the same model to prevent complications of correlated predictors. We used the logit-transform on ESCS, LSCS, and ACS for each year, and then examined multiple linear regression models. Total annual sample sizes used to estimate ESCS ranged from 32 to 808, median 278, and ranged from 65 to 1,754, median 654 for ACS. For the one year when no yearlings were harvested, we imputed a value of 0.05, a small non-zero value that allowed the logit link but that prevented an outlying data point. For LSCS, we recognized the comparison of two sources of ratio data could amplify sampling error, but most years in the Gardiner late hunt database contained high sample sizes resulting in high precision of estimates. The LSCS ratio focused more directly on variables influencing mortality during only age 6 months to 1.5 years and should eliminate the variation due to pregnancy and neonatal loss included in ACS. For analysis, we centered and scaled all covariates (based on the years included in the analysis) to facilitate comparison of relative effect size among predictors. The SNOW and SWE covariates were each missing a singular value (2005 and 2007, respectively), which we interpolated using the average of the values in the data set (i.e., when centered and scaled, this value = 0).

We obtained 7,342 records of lactation status for elk age 3.5 and older. Of 22 candidate models for early-season calf survival (ESCS) as indexed by lactation rate, the top model (> 2 $\Delta AIC_c$ units, $R^2 = 0.35$) contained the lagged grizzly bear:elk ratio (prior to calf birth), with an additive snow effect (Table 5; Fig. 11). The model-averaged coefficient estimates across all models with $W_i \geq 0.01$ suggested the lagged grizzly:elk ratio was negatively correlated with logit lactation rates (-0.11, 95% C.I. = -0.31, -0.01) and that snowfall during pregnancy also was related negatively to lactation rates (-0.11, 95% C.I. = -0.21, -0.03).

The model containing WOLF:ELK ratios and SNOW was most supported ($W_i = 0.65$, $R^2 = 0.52$) as influential to late-season calf survival (LSCS, Table 6, Fig. 12). The model-averaged coefficient estimates across all models with $W_i \geq 0.01$ suggested the wolf:elk ratio was negatively correlated with logit late-season calf survival (-0.91, 95% C.I. = -1.41, -0.41), and snowfall was also negatively correlated with late-season calf survival (-0.78, 95% C.I. –1.27, -0.28). Although not among the top models, grizzly bear to elk ratios were also negatively correlated with late-season survival (-0.83, 95% C.I. = -1.37, -0.30).

We modeled annual calf survival from a total harvested sample of 1,904 yearlings and 18,484 cows ≥ 2.5 years. Two models of a suite of 19 for total annual survival for calves (ACS) were within 2 $\Delta AIC_c$: those including the wolf:elk ratio and snow, and the grizzly:elk ratio and snow (Table 7, Fig. 13). These models received 46% and 21% (respectively) of the AIC weight, with $R^2 = 0.63$ and 0.60. The model-averaged coefficient estimates across all models with $W_i \geq 0.01$ suggested the wolf:elk ratio was negatively correlated with logit annual calf survival (-0.52, 95% C.I. = -0.73, -0.31), snowfall was negatively correlated with logit annual calf survival (-0.54, 95% C.I. –0.55, -0.14), and grizzly bear to elk ratios also were negatively correlated with logit annual calf survival (-0.50, 95% C.I. = -0.71, -0.29).

The predicted and observed negative correlation between early season calf survival and GRIZ:ELK is corroboration of the documented increase in early-season predation of grizzly bears on neonate calves (Singer et al. 1997, Barber-Meyer et al. 2008). Also as expected, SNOW the winter prior to birth influenced ESCS as indexed by lactation. Severe winters deplete the fat reserves of cow elk, which may affect the viability of the fetus, the neonatal calf, and the cow’s ability to provide milk to the calf (Verme 1969, Singer et al. 1997).

As expected, LSCS and ACS and were negatively associated with both WOLF:ELK and SNOW. Both wolves and severe winters are well-documented proximal causes of elk calf mortality on the Northern Range (see earlier). The appearance of GRIZ:ELK + SNOW as the second ranked model for annual calf survival could reflect the embedded cumulative effect of early-season calf survival within the annual calf survival metric. Although grizzly bear do predate some elk after emerging from hibernation, the importance of GRIZ:ELK to late-season calf survival may only be a reflection of the covariance of wolf:elk and grizzly bear:elk ratios ($R^2 = 0.94$).

Elk calf survival appears to be the vital rate most influential in recent elk population trends in the GYA (Hamlin et al. 2008). Our modeling results corroborate recently published information on causes and timing of elk calf mortality in the GYA (Barber-Meyer et al. 2008, Hamlin et al. 2008) and highlight the importance of total predation on calf survival.

Table 5: Model selection results for lactation, as an index of early-season calf survival, in Northern Yellowstone elk.

| **MODEL** | **K** | **$\Delta$ AIC$_c$** | **AIC$_c$** | **n** | **Wi** | **R$^2$** |
|---|---|---|---|---|---|---|
| **LGRIZ:ELK+SNOW** | **4** | **0.00** | **2.85** | **22** | **0.34** | **0.35** |
| LWOLF:ELK+SNOW | 4 | 2.60 | 5.45 | 22 | 0.09 | 0.26 |
| LGRIZ:ELKxSNOW | 5 | 2.93 | 5.78 | 22 | 0.08 | 0.36 |
| LGRIZ:ELK | 3 | 2.95 | 5.80 | 22 | 0.08 | 0.14 |
| LSNOW | 3 | 3.15 | 6.01 | 22 | 0.07 | 0.13 |
| L1 | 2 | 3.63 | 6.48 | 22 | 0.05 | NA |
| LGRIZ:ELK+SWE | 4 | 3.81 | 6.67 | 22 | 0.05 | 0.22 |
| LWOLF:ELK | 3 | 4.40 | 7.25 | 22 | 0.04 | 0.08 |
| LSWE | 3 | 4.40 | 7.26 | 22 | 0.04 | 0.08 |
| LWOLF:ELKXSNOW | 5 | 4.83 | 7.68 | 22 | 0.03 | 0.26 |
| LAGE | 3 | 5.00 | 7.85 | 22 | 0.03 | 0.06 |
| LWOLF:ELK+SWE | 4 | 5.28 | 8.14 | 22 | 0.02 | 0.17 |
| LGRIZ:ELK+PREC | 4 | 5.97 | 8.82 | 22 | 0.02 | 0.14 |
| LPREC | 3 | 6.17 | 9.02 | 22 | 0.02 | 0.01 |
| LPDSI | 3 | 6.27 | 9.12 | 22 | 0.01 | 0.00 |
| LGRIZ:ELKxSWE | 5 | 6.32 | 9.17 | 22 | 0.01 | 0.25 |
| LWOLF:ELKPREC | 4 | 7.41 | 10.27 | 22 | 0.01 | 0.08 |
| LWOLF:ELKXSWE | 5 | 7.82 | 10.68 | 22 | 0.01 | 0.20 |
| LPRECAGE | 4 | 8.02 | 10.87 | 22 | 0.01 | 0.06 |
| LGRIZ:ELKxPREC | 5 | 8.42 | 11.27 | 22 | 0.00 | 0.18 |
| LWOLF:ELKXPREC | 5 | 10.34 | 13.19 | 22 | 0.00 | 0.10 |
| LPRECxAGE | 5 | 10.92 | 13.77 | 22 | 0.00 | 0.08 |

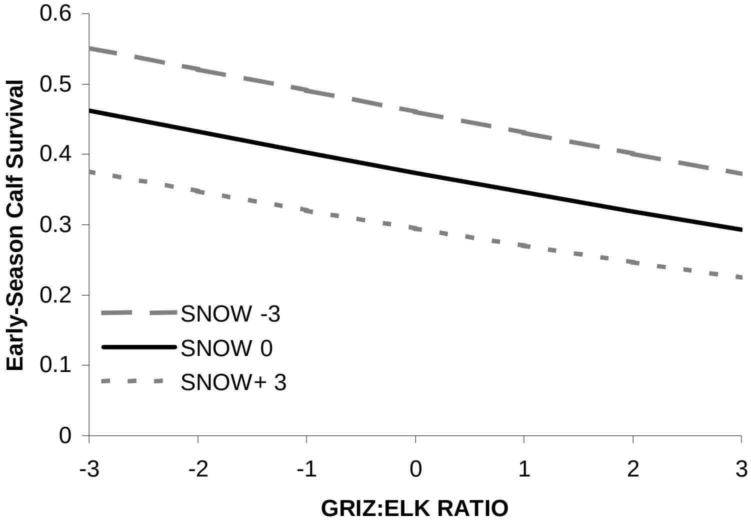


Figure 11. Early season calf survival as indexed by centered and scaled grizzly bear: elk ratios and snow.

Table 6: Model selection results for late-season calf survival in the Northern Yellowstone elk herd.

| MODEL | K | Δ $AIC_c$ | $AIC_c$ | n | Wi | R^2 |
|---|---|---|---|---|---|---|
| **SWOLF:ELK+snow** | **4** | **0.00** | **69.13** | **22** | **0.65** | **0.52** |
| SGRIZ:ELK+snow | 4 | 3.23 | 72.36 | 22 | 0.13 | 0.44 |
| SWOLF:ELKXsnow | 5 | 3.39 | 72.52 | 22 | 0.12 | 0.52 |
| SGRIZ:ELKxsnow | 5 | 6.60 | 75.73 | 22 | 0.02 | 0.44 |
| SWOLF:ELK | 3 | 7.12 | 76.26 | 22 | 0.02 | 0.23 |
| SWOLF:ELK+SWE | 4 | 7.73 | 76.86 | 22 | 0.01 | 0.31 |
| SPDSI | 3 | 7.89 | 77.02 | 22 | 0.01 | 0.20 |
| SGRIZ:ELK | 3 | 8.73 | 77.86 | 22 | 0.01 | 0.17 |
| SGRIZ:ELK+SWE | 4 | 9.56 | 78.70 | 22 | 0.01 | 0.25 |
| SWOLF:ELK+PREC | 4 | 9.81 | 78.94 | 22 | 0.00 | 0.24 |
| S1 | 2 | 10.22 | 79.35 | 22 | 0.00 | |
| Ssnow | 3 | 10.59 | 79.73 | 22 | 0.00 | 0.10 |
| SWOLF:ELKXSWE | 5 | 11.11 | 80.25 | 22 | 0.00 | 0.31 |
| SSWE | 3 | 11.51 | 80.64 | 22 | 0.00 | 0.06 |
| SGRIZ:ELK+PREC | 4 | 11.71 | 80.84 | 22 | 0.00 | 0.17 |
| SWOLF:ELKXPREC | 5 | 12.82 | 81.95 | 22 | 0.00 | 0.26 |
| SPREC | 3 | 12.83 | 81.96 | 22 | 0.00 | 0.00 |
| SGRIZ:ELKxSWE | 5 | 12.87 | 82.01 | 22 | 0.00 | 0.25 |
| SGRIZ:ELKxPREC | 5 | 14.97 | 84.10 | 22 | 0.00 | 0.18 |

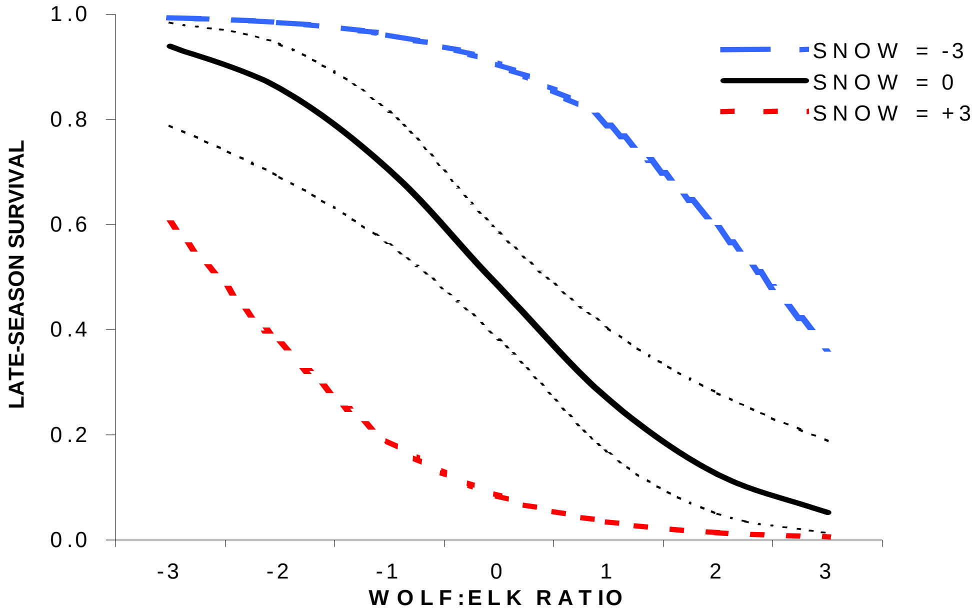
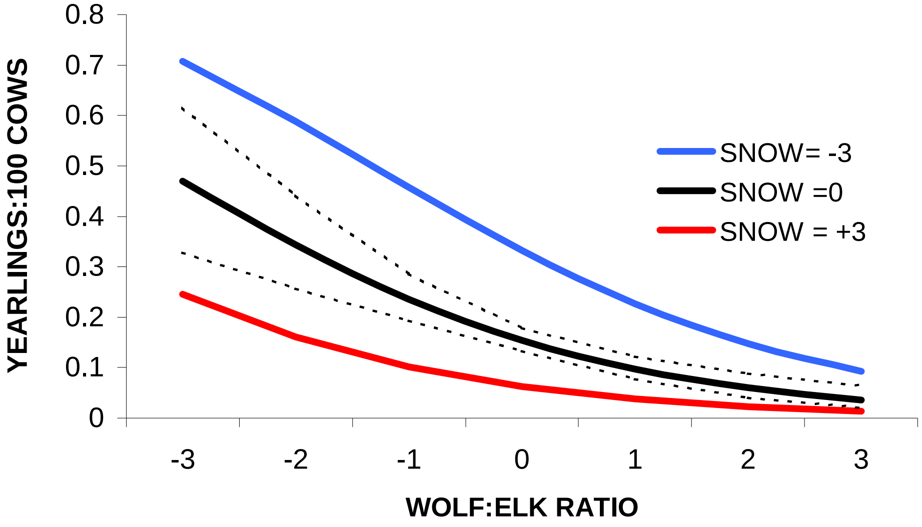


Figure 12. Late-season calf survival as indexed by centered and scaled wolf:elk ratio and snow. Dashed black lines represent 95% confidence intervals around SNOW = 0 (mean).

Table 7. Model selection results for total annual survival of Northern Yellowstone elk calves as indexed by yearling:100 cow ratios in year *t+1*.

| MODEL | K | Δ AIC$_c$ | AIC$_c$ | n | W$_i$ | R$^2$ |
|---|---|---|---|---|---|---|
| **YWOLF:ELK+snow** | **4** | **0.00** | **30.50** | **22** | **0.46** | **0.63** |
| YGRIZ:ELK+snow | 4 | 1.57 | 32.07 | 22 | 0.21 | 0.60 |
| YWOLF:ELKXsnow | 5 | 3.00 | 33.50 | 22 | 0.10 | 0.63 |
| YWOLF:ELK+SWE | 4 | 3.27 | 33.77 | 22 | 0.09 | 0.57 |
| YGRIZ:ELK+SWE | 4 | 4.69 | 35.19 | 22 | 0.04 | 0.54 |
| YGRIZ:ELKxsnow | 5 | 4.90 | 35.40 | 22 | 0.04 | 0.60 |
| YWOLF:ELKXSWE | 5 | 6.38 | 36.88 | 22 | 0.02 | 0.57 |
| YWOLF:ELK | 3 | 7.72 | 38.22 | 22 | 0.01 | 0.39 |
| YGRIZ:ELKxSWE | 5 | 8.00 | 38.51 | 22 | 0.01 | 0.54 |
| YGRIZ:ELK | 3 | 8.74 | 39.24 | 22 | 0.01 | 0.37 |
| YWOLF:ELK+PREC | 4 | 9.09 | 39.60 | 22 | 0.00 | 0.44 |
| YGRIZ:ELK+PREC | 4 | 11.15 | 41.66 | 22 | 0.00 | 0.38 |
| YWOLF:ELKXPREC | 5 | 11.84 | 42.35 | 22 | 0.00 | 0.45 |
| YPDSI | 3 | 12.54 | 43.04 | 22 | 0.00 | 0.25 |
| YGRIZ:ELKxPREC | 5 | 14.17 | 44.67 | 22 | 0.00 | 0.39 |
| YSWE | 3 | 15.43 | 45.93 | 22 | 0.00 | 0.14 |
| Y1 | 2 | 16.04 | 46.55 | 22 | 0.00 | |
| Ysnow | 3 | 17.68 | 48.19 | 22 | 0.00 | 0.05 |
| YPREC | 3 | 18.74 | 49.24 | 22 | 0.00 | 0.00 |

13a



13b

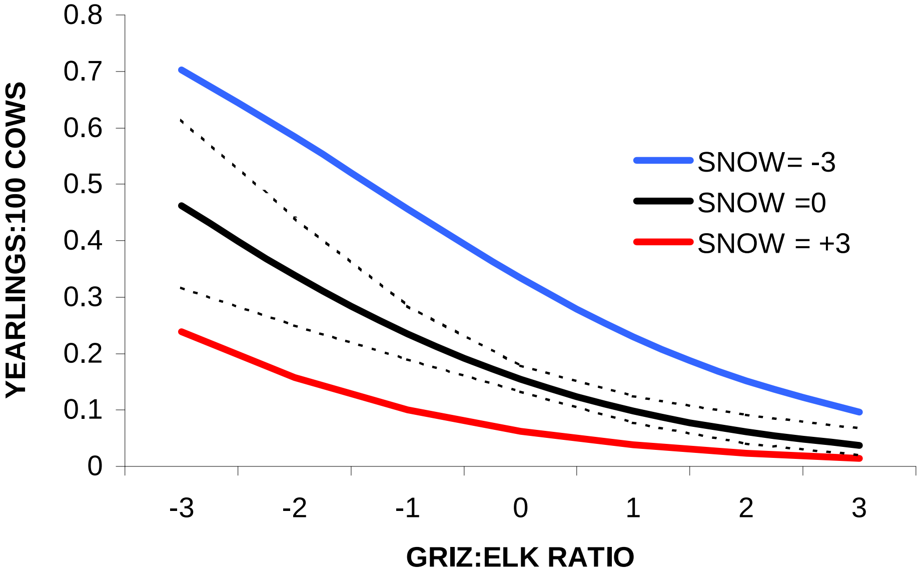


Figure 13. Annual calf survival as indexed by centered and scaled wolf:elk ratios (a) and grizzly:elk ratios (b) and snow. Dotted lines represent 95% confidence intervals around SNOW = 0 (average).

Adult Elk Survival/Mortality

Fifty-one adult female and 13 adult male elk marked with telemetry collars provided information for determination of binomial monthly survival/mortality rates in the Gallatin Canyon study area from 1 March 2002 through 31 May 2007. Elk that died within a week of capture or those for which the transmitter did not function were excluded. Also, for elk captured in the Gallatin drainage that wintered in the Madison drainage subsequent to capture, we recorded survival in Madison Valley calculations rather than for the Gallatin Canyon. Because 26 elk were equipped with GPS collars with programmed "drop-off" dates, annual samples by year were problematic. We used average monthly mortality rates, which we multiplied to estimate average annual rates over the period (Table 8). The months of March-December are based on 6 years and January and February are based on 5 years of data.

Wolf predation was the cause of 2 of 13 mortalities (Table 9). Our relatively small samples indicated about 1% and 5% annualized mortality due to wolf predation for adult females and adult males, respectively. Bear predation accounted for about 3% annualized mortality of adult females. Hunter harvest accounted for about 1% annualized mortality of adult females and 21% annualized mortality of adult males.

Table 8. Annualized monthly survival/mortality rates for adult elk, Gallatin Canyon study, 2002-2007.

| Month | Ad. Female Mean S/M(E. M.)[a] | Ad. Male Mean S/M(E. M.)[a] |
|---|---|---|
| June | 1.00 / 0.00 (102) | 1.00 / 0.00 (21) |
| July | 1.00 / 0.00 (95) | 1.00 / 0.00 (20) |
| August | 1.00 / 0.00 (89) | 1.00 / 0.00 (18) |
| September | 1.00 / 0.00 (89) | 1.00 / 0.00 (16) |
| October | 1.00 / 0.00 (87) | 0.938 / 0.063 (16) |
| November | 0.988 / 0.012 (86) | 0.813 / 0.187 (16) |
| December | 1.00 / 0.00 (86) | 1.00 / 0.00 (13) |
| January | 0.987 / 0.014 (74) | 1.00 / 0.00 (13) |
| February | 1.00 / 0.00 (77) | 1.00 / 0.00 (13) |
| March | 1.00 / 0.00 (120) | 1.00 / 0.00 (26) |
| April | 0.975 / 0.025 (118) | 1.00 / 0.00 (26) |
| May | 0.974 / 0.026 (115) | 0.963 / 0.037 (22) |
| **Mean Annual Survival / Mortality** | **0.925 / 0.075** | **0.734 / 0.266** |

[a] Mean Survival/Mortality (Elk Months)

Table 9. Causes of mortality of radio-collared adult elk on the Gallatin Canyon study area, 2002-2007.

| **Cause of Mortality** | **Adult Females** | **Adult Males** | **Total** |
|---|---|---|---|
| Hunter-kill archery | | 1 | 1 |
| Hunter-kill general season | 1 | 3 | 4 |
| Wolf-kill | 1 | 1 | 2 |
| Grizzly bear-kill | 1 | | 1 |
| Unknown spp. Bear-kill | 2 | | 2 |
| Natural/Broken leg | 1 | | 1 |
| Vehicle Collision | 1 | | 1 |
| Unknown | 1 | | 1 |
| Hunting | **1 (12.5%)** | **4 (80%)** | **5 (38.5%)** |
| **Predation** | **4 (50.0%)** | **1 (20%)** | **5 (38.5%)** |
| Other and Natural | **3 (37.5%)** | | **3 (23.0%)** |

To calculate binomial monthly survival/mortality rates for Madison Valley elk, we included 9 adult females and 1 male captured in the Gallatin Canyon 2002-2004 that subsequently wintered in the Madison Valley. However, the majority of the sample was 32 females and 4 males in 2005 and 29 females and 2 males in 2006 captured in HD 362 in the Madison Valley. Annualized survival for the small, limited samples in the Madison Valley (Table 10) of about 90% for females and 77% for males was very similar to that observed in the Gallatin Canyon (Table 8).

Annualized rates of survival for telemetry-collared adults in both the Gallatin Canyon and Madison Valley were both relatively high compared to survival observed during pre-wolf reintroduction years in the adjacent Gravelly-Snowcrest elk population (Adult females, S = 0.82; Adult Males, S = 0.25, Hamlin and Ross 2002), where almost all mortality was hunting related.

Annual survival of adult females estimated by the relatively small samples of radio-telemetry collars (Tables 8 and 10) was similar to survival estimated by age structure during the same period (about 88%) for the Madison Valley, but much higher than estimated by age structure (about 78%) for the Gallatin Canyon (Hamlin et al. 2008). This high rate of mortality for adult females in the Gallatin Canyon during 2001-2006 estimated by age structure is greater than for earlier periods with much greater hunter caused mortality (Hamlin et al. 2008).

Table 10. Annualized monthly survival/mortality rates for adult elk, Madison Valley study, 2002-2007.

| Month | Ad. Female Mean S/M(E. M.)[a] | Ad. Male Mean S/M(E. M.)[a] |
|---|---|---|
| June | 1.00/0.00 (90) | 1.00/0.00 (8) |
| July | 1.00/0.00 (90) | 1.00/0.00 (8) |
| August | 1.00/0.00 (89) | 1.00/0.00 (8) |
| September | 1.00/0.00 (89) | 1.00/0.00 (8) |
| October | 0.966/0.034 (87) | 0.875/0.125 (8) |
| November | 1.00/0.00 (84) | 0.875/0.125 (7) |
| December | 1.00/0.00 (83) | 1.00/0.00 (6) |
| January | 0.976 / 0.024 (83) | 1.00 / 0.00 (6) |
| February | 0.962 / 0.038 (52) | 1.00 / 0.00 (7) |
| March | 1.00 / 0.00 (110) | 1.00 / 0.00 (13) |
| April | 1.00 / 0.00 (110) | 1.00 / 0.00 (13) |
| May | 0.991 / 0.009 (110) | 1.00 / 0.00 (12) |
| **Mean Annual Survival / Mortality** | **0.898 / 0.102** | **0.766 / 0.234** |

[a] Mean Survival/Mortality (Elk Months)

Table 11. Causes of mortality of radio-collared adult elk on the Madison Valley study area, 2002-2007.

| Cause of Mortality | Adult Females | Adult Males | Total |
|---|---|---|---|
| Hunter-kill general season | 2 | 2 | 4 |
| Hunter-kill late season | 4 | | 4 |
| Wolf-kill | 1 (probable) | | 1 |
| Unknown | 1 | | 1 |
| Hunting | **6 (75%)** | **2 (100%)** | **8 (80%)** |
| **Predation** | **1 (12.5%)** | | **1 (10%)** |
| Other and Natural | **1 (12.5%)** | | **1 (10%)** |

Almost all mortality observed for radio-telemetry collared elk in the Madison Valley was hunting-related (Table 11). Only 1 of 10 mortalities recorded was suspected to be a wolf-kill (Table 11).

For the Northern Yellowstone elk population, annual survival of adult females was estimated as 0.99 during 1969-1975, after reduction and before the late hunts began in 1976 (Evans et al. 2006, Eberhardt 2002, Houston 1982). Vore (1990) reported 12 mortalities of adult females over 56 elk-years during 1984-86, which was equivalent to 0.79 survival (0.21 mortality). Of the mortalities Vore reported, 83% of deaths were due to hunting, 8.5% winter-kill, and 8.5% unknown/natural causes. During a similar period (1983-88), Hamlin et al. (2008) estimated survival of adult females as 0.84 based on age-structure of hunter-harvested elk. Similarly, Hamlin et al. (2008) also estimated survival of adult females in the Northern Range as 0.83 during 1989-96, 0.76 during 1997-2000, and 0.81 during 2001-06. In comparison with the latter period, Evans et al. (2006) based on telemetry, estimated a similar survival rate for adult females of 0.77-0.80 during March 2000 – February 2004. Predation accounted for 42%, hunting 33%, winter-kill 6%, and unknown causes 18% of telemetry-determined mortalities during 2000-04 (Evans et al. 2006).

Adjusting these data to a July – June period and including data through June 2008 (P. J. White, NPS unpublished data), average annual survival of adult female elk captured within YNP ranged from 0.78 to 0.90 and averaged 0.82 during 2000-08. From these data we estimated survival as 0.80 during 1 July 2007 – 30 June 2008. In contrast, for a small sample (13 after censoring) of adult females captured outside YNP on the Dome Mountain Wildlife Management area survival was 0.92 during 2007-08. One female died as a result of bear predation during October 2007. This sample was small, however, there have been no mortalities through October 2008 for an additional 29 adult females captured in February 2008. These data are preliminary, incomplete, and sample size is small, but it appears that there is a possibility that with little late hunt mortality since 2005, mortality of adult females wintering outside YNP may be lower than for those wintering primarily inside YNP.

## Elk Population Trends

Elk population trends in the GYA portrayed by Hamlin et al. (2008) have continued in the same directions with addition of 1 more year of information (Fig. 14). Elk population declines continued in areas with the highest predator : prey ratios (Madison headwaters, Northern Yellowstone, and Gallatin Canyon), while increasing, remaining stable, or slightly declining in the populations with the heaviest human harvest and lowest predator: prey ratios.

From 1994-2008, and more recently (2000-08) rate of population decline was $r = -0.078$ ($-0.105$)/ $\lambda = 0.925$ (0.901) for the Northern Yellowstone; $r = -0.094$ ($-0.122$)/ $\lambda = 0.910$ (0,886) for the Gallatin Canyon; and $r = -0.128$ ($-0.239$)/ $\lambda = 0.880$ (0.787) for the Madison headwaters. For 11 other southwestern Montana elk populations (Fig. 15), rate of increase/decline ranged from $r = 0.003$ to 0.078 ($\lambda = 1.003 – 1.081$) during 1994-2008 and $r = -0.031$to 0.078 ($\lambda = 0.969 – 1.081$) during 2002-2008. Most of these other southwestern Montana elk populations (Fig. 15) have maintained positive growth during the wolf restoration period, however the 2 Gravelly-Snowcrest elk populations (HD 323 and 324) and also HD 520 have experienced moderate population decline since 2002, r = -0.030, -0.031, and –0.007, respectively.

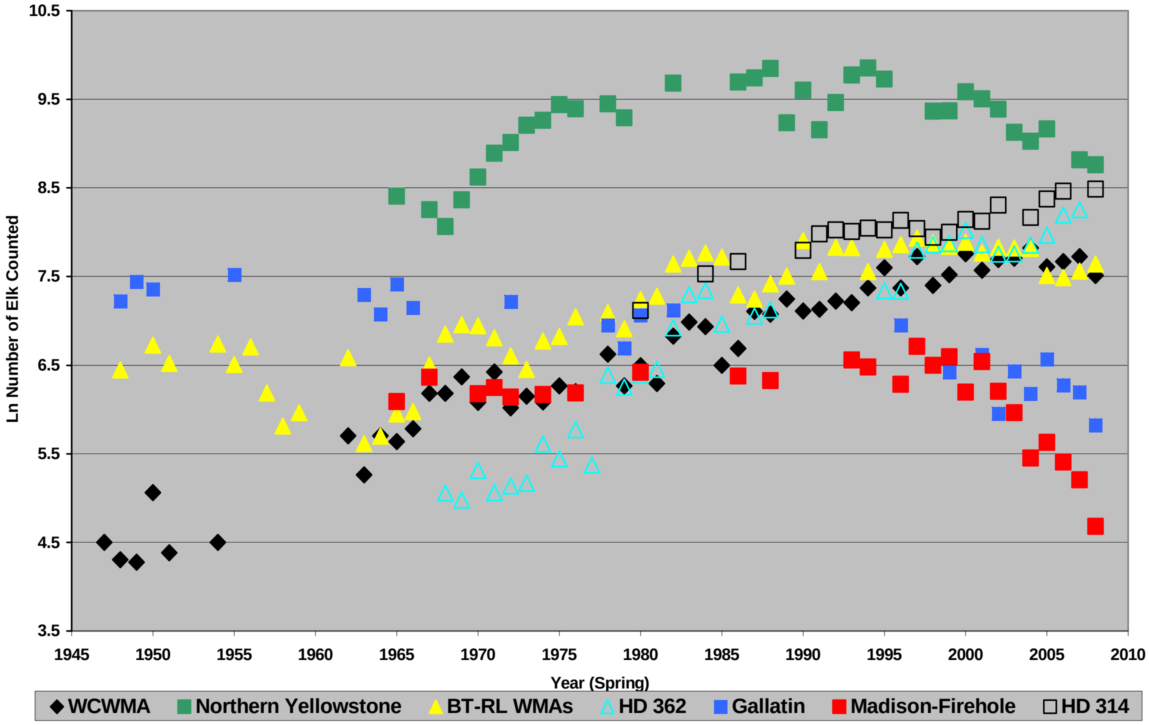


Figure 14. Elk population trend expressed as natural log of counts for the Wall Creek WMA, Northern Range, Blacktail-Robb-Ledford WMA, Hunting District 362, Gallatin Canyon, Madison-Firehole, and HD 314 populations.

The elk population declines have occurred with no human hunting in the Madison headwaters and declines have continued in the Northern Yellowstone and Gallatin Canyon with harvest of about 2% of preseason adult females since 2005. For most areas, at least some level of population growth has continued since 2002, but small recent population declines in HDs 323 (WCWMA), 324 (BT-RL WMAs), and HD 520 may be of concern because these declines have occurred despite what is, historically (Hamlin and Ross 2002), relatively light hunter harvest since 2001. Also, during the past year, the number of wolf packs in the Gravelly-Snowcrest Mountains has increased, which may contribute to increased elk mortality. The greatest elk population increases have occurred in areas with relatively few predators (to this time) and with greater private land hunting access that has resulted in low-to-moderate hunter harvest.

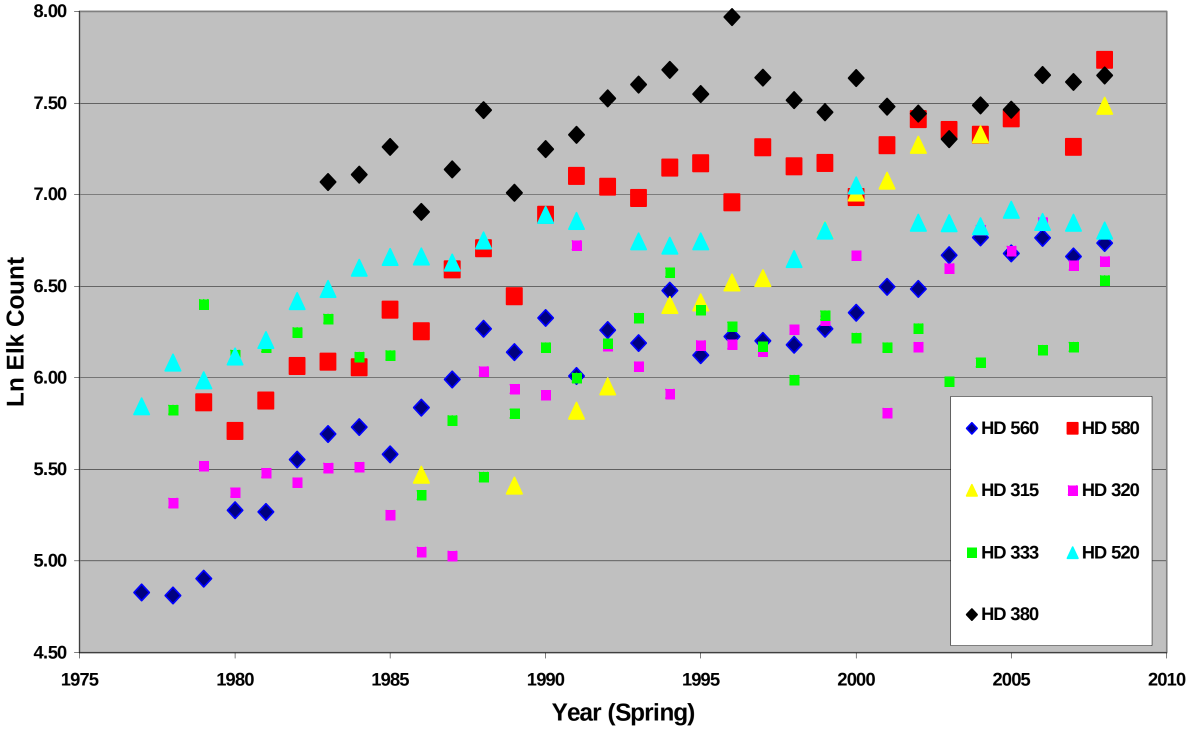
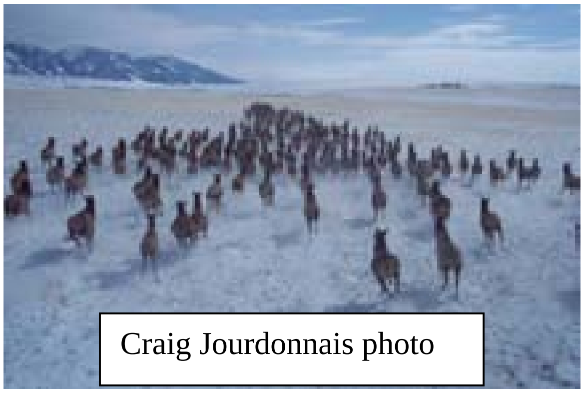


Figure 15. Elk population trend expressed as natural log of counts for populations in HDs 315, 320, 333, 380, 520, 560, and 580.

For population level displayed as natural log of counts (Figs. 14 and 15), degree of change relative to each other is more easily seen, but number changes are obscured. Therefore, we also present changes in numbers counted (Table 12) for those more comfortable with this presentation. Exceptionally good or bad counting conditions in the chosen "cutoff" years may affect results (Table 12), but similar conclusions as to the limited areas of severe elk population declines can be seen in either presentation.



Craig Jourdonnais photo

Table 12. Changes in number of elk counted in selected Greater Yellowstone Area elk populations, 1994-2008.

| **Area** | **Elk Count** | | | **Percent increase or decrease** | | |
|---|---|---|---|---|---|---|
| | 1994 | 2001 | 2008 | 1994-2008 | 1994-2001 | 2001-2008 |
| Northern Yellowstone | 19045 | 13400 | 6382 | - 67% | - 30% | - 52% |
| Gallatin Canyon | 1048 | 749 | 338 | - 68% | -29% | -55% |
| Madison – Firehole[a] | "700" | 577 | 108 | "- 85%" | "-18%" | -81% |
| HD 314 | 3118 | 3375 | 4852 | 56% | 8% | 44% |
| HD 315 | 600 | 1183 | 1780 | 197% | 97% | 50% |
| HD 320 | 370 | 333 | 763 | 106% | -10% | 129% |
| HD 323[b] | 1591 | 1994 | 1829 | 15% | 25% | -8% |
| HD 324[c] | 1919 | 2357 | 2086 | 9% | 23% | -11% |
| HD 333 | 717 | 476 | 687 | -4% | -34% | 44% |
| HDs 360/362 | 1816 | 3713 | 6178 | 240% | 104% | 66% |
| HD 380 | 2166 | 1774 | 2101 | -3% | -18% | 18% |
| HD 520 | 830 | | 901 | 9% | | |
| HD 560 | 830 | 663 | 842 | 1% | -20% | 27% |
| HD 580 | 1271 | 1435 | 2290 | 80% | 13% | 60% |

[a] 1994 spring numbers **roughly** estimated from pre-winter counts.

[b] Wall Creek Wildlife Management Area.

[c] Blacktail and Robb-Ledford Wildlife Management Areas.

Garrott et al. (2008) provide a summary of the causes of decline in the Madison-Firehole elk herd, the detail of which goes beyond what is possible with the data available to explain declines in other herds. However, coarse scale data along with more limited research data are available and may provide some insights into causes of declines in some other areas. Below, we provide further insights and data summaries for numbers and distribution, offtake by hunters and wolves, and demography of the Northern Yellowstone elk herd, in order to add to the discussion surrounding this well-known herd. The number of elk counted on cooperative Northern Range aerial counts has declined by about 70% since their peak in 1994 (Fig. 16, Table 12). Consequently, local, national, and international attention has focused on potential effects of wolf restoration on Northern Range elk populations, and this decline has been controversial. Fortunately, more consistently collected long-term information is available for the Northern Range than for most other areas of wolf restoration. Agreement about effects, causes, consequences, and future directions in this herd has remained elusive (Smith 2005, White et al. 2005, Vucetich et al. 2005, White and Garrott 2005, Varley and Boyce 2006, Eberhardt et al. 2007). Ultimate consequences of environmental perturbations (such as wolf restoration) may take many years to be fully recognized and early conclusions and predictions may be faulty (White et al. 2005). Nevertheless, with the end of our project at 13 years after wolf restoration to the GYA, we present our own conclusions, recognizing their limitations. Compared to earlier analyses, our analyses benefit from severely reduced elk harvest since 2005 (Fig. 16).

Numbers and Distribution of Elk on the Northern Range

Total elk counted and elk counted within YNP have declined significantly since 2000, but the number of elk counted outside YNP and north of Dome Mountain has remained the same (Fig. 17). More elk were counted outside than inside YNP in February 2008 (Fig. 17). The proportion of Northern Yellowstone elk wintering outside YNP has varied annually (Fig. 16), traditionally increasing during more severe winters. Similarly, prior to 2005, late hunt harvest increased with winter severity and the increased number of vulnerable elk outside YNP (Fig. 16). In the series of relatively mild winters since 1996-97, the number of elk counted and wintering outside YNP subject to late hunt harvest has been low, but relatively stable (Figs. 16 and 17). Conversely, the number and proportion of elk counted within YNP has declined (Fig. 17).

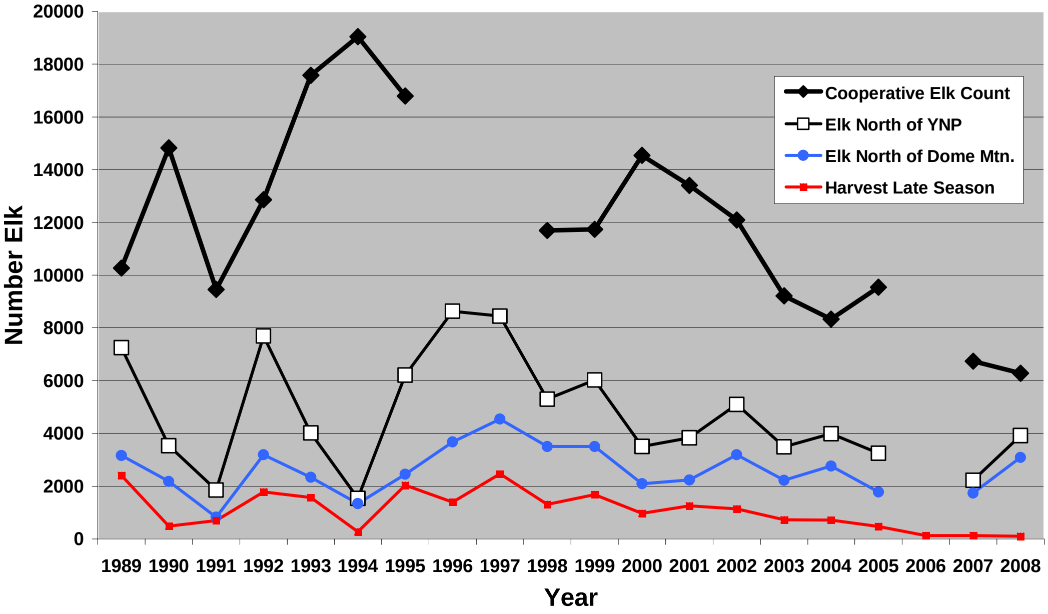


Figure 16. Cooperative elk counts for the Northern Range partitioned by area and late season elk harvest, 1989-2008.

Gardiner, Montana, 1948 – Ken Hamlin collection

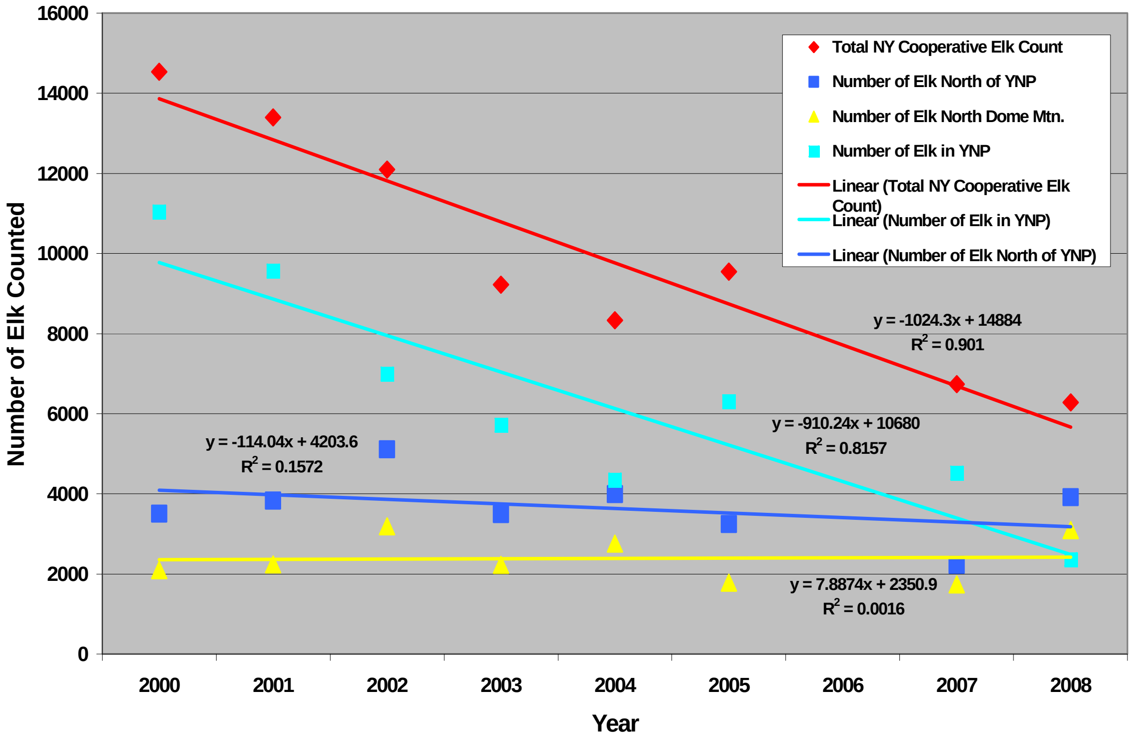


Figure 17. Changes in numbers and distribution of elk counted during the cooperative Northern Range elk count, 2000-2008.

Hamlin (2006) speculated that the Northern elk herd may be comprised of elk that winter outside YNP every year and are vulnerable to harvest during late hunts, elk that winter inside YNP every year and are not vulnerable to late hunt harvest, and elk that may variably winter either outside or inside YNP depending on weather conditions or other factors. Thus elk wintering in different areas are subject to different levels of mortality from different causes (human hunting, wolf predation, winter-kill). However, to this time, there is no evidence of fixed population segments in these categories.

For elk captured and marked with telemetry collars on northern winter ranges within YNP during 2000-04, there was no evidence that they had substantially changed migration routes or areas of use in the post-wolf restoration period (P. J. White, pers. comm.). Generally, most of these elk remained within YNP and were not vulnerable to hunter harvest, but some moved outside YNP during early winter and were harvested. During this study period, slightly more elk captured within YNP were killed by hunters than by wolves, but total natural predation loss was equal to hunter harvest (P. J. White, pers. comm.). Though most elk movements and areas of use were traditional from year-to-year, there was some evidence of individual flexibility with conditions (P. J. White, pers. comm.).

During February 2007 we captured 15 and in February 2008, 31 adult female Northern Range elk outside YNP and marked them with GPS telemetry collars. Data collection for

2008 elk will not be complete until February 2009, when the GPS collars are retrieved. Information to date (Fig. 18) indicates that migration and summer range is similar to that of elk marked by Vore (1990) during 1984-86 at comparable locations and also similar to elk marked within YNP during 2000-04 (P. J. White, pers. comm.). However, among the 41 females for which we maintained contact, we did not detect a segment of elk that was resident yearlong to areas outside YNP (northern blue dots in National Forest in Montana, Fig. 18) as reported by Vore (1990).

Information collected through 9 December 2008 indicates that all 2007 elk were outside YNP and "technically" vulnerable to harvest (depending on specific location) prior to opening of the late hunt and as of 9 December, 57% of 2008 elk were outside YNP with the remainder on or near the border (Cunningham, unpubl. data). Pending locations of elk at the start of the late hunt on 2 January 2009, it is likely that the large majority of elk we marked on the Northern Range outside YNP are subject to hunter harvest, but experience reduced wolf predation pressure compared to elk wintering within YNP.

At this time, we cannot determine if there are relatively "fixed segments" of the Northern Yellowstone elk herd in relation to winter range location. However, individual elk wintering in different areas experience or have experienced differing levels of hunter and wolf predation pressure. The number of elk wintering and counted within YNP (subject to the greatest natural predation pressure) has declined dramatically since 2000 (Fig. 17) compared to elk wintering and counted outside YNP (subject to greater hunter harvest and lower natural predation pressure). Since 2005, however, hunter harvest was insignificant for all Northern Range elk but wolf numbers and predation have increased.

Earlier, many harvested elk were shipped home by train from the Gardiner, Montana depot. Ken Hamlin collection

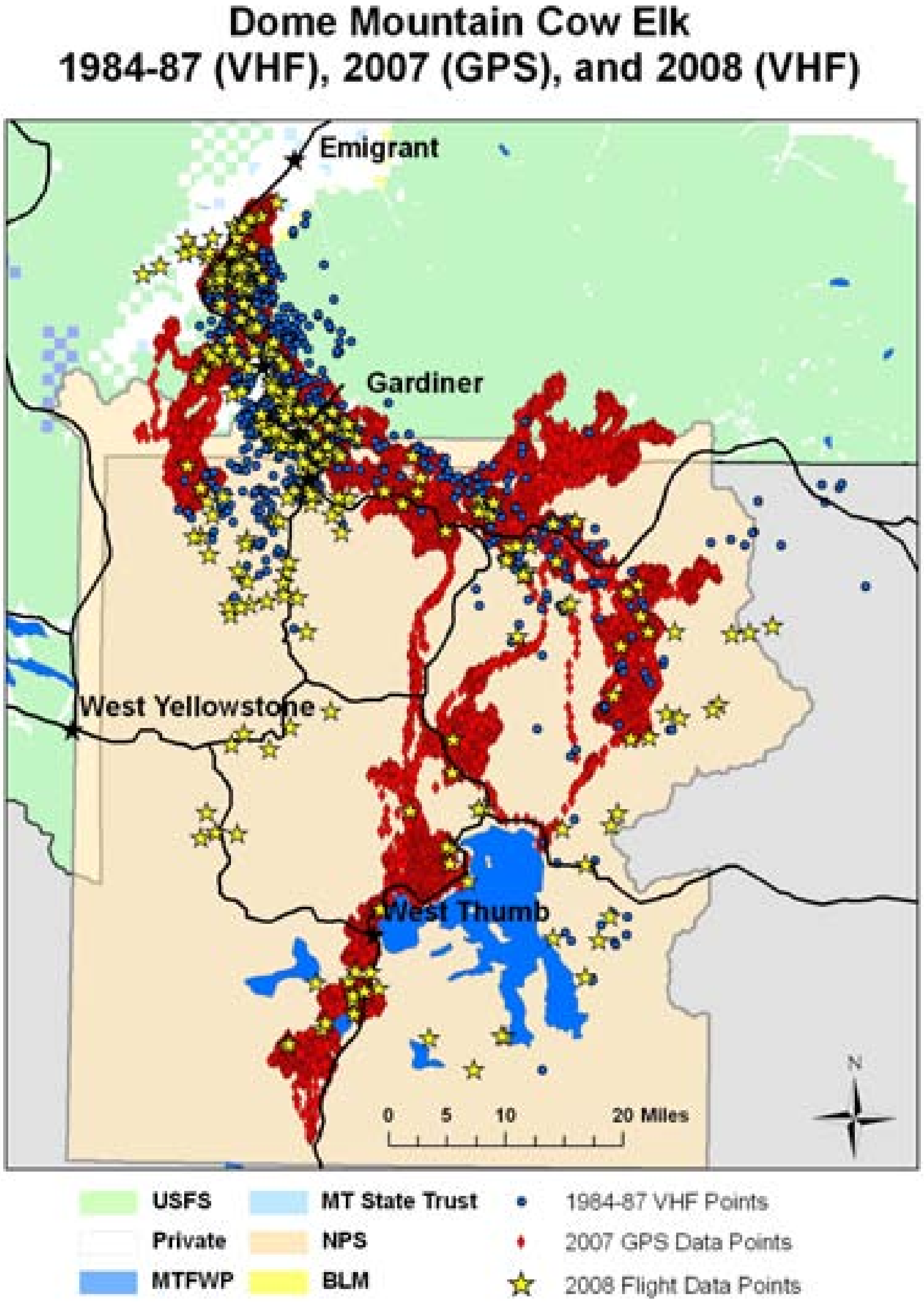


Figure 18. Yearlong distribution of 42 cow elk captured on the Northern Range outside YNP, 2007-08 (red diamonds and yellow stars) and 28 cow elk captured and marked in the same areas during 1984-86 (blue dots).

## Estimated Elk Offtake by Hunters and Wolves on the Northern Range

Relative changes in both elk numbers and distribution in the Northern Range since 2000 (Fig. 17) along with other data previously presented suggest that bear predation of neonates and wolf predation of elk during autumn through winter may be playing an increasing role in elk population trends.

Following, we present our estimates of relative contributions of wolf predation and hunter harvest to elk population trends in the Northern Yellowstone elk population. Others have made similar estimates (White et al. 2003, White and Garrott 2005 and Vucetich et al. 2005); however some of our assumptions/estimates are different. Most other estimates (White and Garrott 2005, Vucetich et al. 2005) have used unadjusted elk counts as the base from which to estimate offtake. We estimate actual pre-season elk numbers in all areas by adjusting counts based on available data (Singer et al. 1997, Hamlin and Ross 2002) including observability estimates, sightability, population modeling, and hunter harvest (FWP annual harvest surveys). For some years, this included using averages or ranges based on observing conditions during flights. Although any estimates are subject to question and interpretation, we believe it is important to use estimated pre-season elk numbers so that offtake estimates are not higher than reality.

We used wolf kill-rates of elk and sex/age composition of that kill from the literature for the Northern Range in calculations. The following wolf kill rates of elk on the Northern Range during winter were used for calculations: 0.061elk kills/wolf day (1995-2000); 0.0373 elk kills/wolf day (2001-2005); 0.046 elk kills/wolf day for 2005-06; and 0.373 elk kills/wolf day (2006-2008) (Smith et al. 2004a, Smith et al. 2004b, Smith et al. 2005-2008). We partitioned sex and age of kills by observed selection (Smith et al. 2004a, Smith et al. 2004b, Smith et al. 2005-2008). Other estimates used a winter period of October-May (White and Garrott 2005) and a summer (June-September) kill rate of 70% of the kill rate during winter based on estimates by Messier (1994). We used a winter period of November-April and a more conservative kill rate of 50% of the winter rate (Geode pack – summer, Smith 2004b) for the period of May-October.

Numbers of wolves using the area were based on published reports and modified based on personal communications with field researchers (Smith et al. 2004a, Smith et al. 2004b, USFWS et al. 1999-2007). We included wolves using the northern portion of the range in Montana omitted from later Yellowstone Wolf Project annual reports (e. g. Smith et al. 2008).

Total wolf-kill estimates (Appendix Table 1) do NOT include calves from birth through September. Estimated kill was calculated by multiplying kill rate (kills/wolf day) partitioned into sex and age classes and partitioned into time period times number of wolves using the area.

We estimated general and late season hunter harvest based on Montana's hunter harvest survey. In contrast to most other estimates, we incorporated estimates of crippling loss in the total using reduced estimates from Hamlin and Ross (2002). Total harvest including crippling loss was 1.1 times reported harvest for females and 1.05 times reported harvest for males.

Estimates of offtake in Appendix Table 1 are dependent on published/unpublished estimates of the individual component data. Given the incorporation of estimated "true" elk population size and hunter crippling loss, we believe the estimates to be relatively accurate. Compared to other published estimates, our estimates probably are inherently biased a little high for hunter offtake and a little low for wolf offtake.

For the Northern Range, estimated wolf numbers were 32, 42, 44, 72, 77, 87, 106, 93, 60, 89, and 108 wolves for 1997-98 through 2007-08. The results indicating offtake by wolves (Appendix Table 1) are highly influenced by these numbers because they change annually in the calculations but also by the changes in estimated kill rate and sex/age composition described above. The recent information presented on distribution of Northern Range elk during summer and fall (Fig. 17, P.J. White, pers. comm.) indicates that our estimates for wolf kill of elk during summer may be conservative. Rather than the wolf numbers presented above and used in calculations, Northern Range elk may be preyed upon by virtually all YNP wolves during summer and fall.

For all elk > 5 months-old, estimated hunter-kill has been declining, while estimated wolf-kill has increased throughout the period after restoration (Fig. 19, Appendix Table 1). This, and the following estimates are for only elk killed by hunters or wolves and do not include other sources of elk mortality.

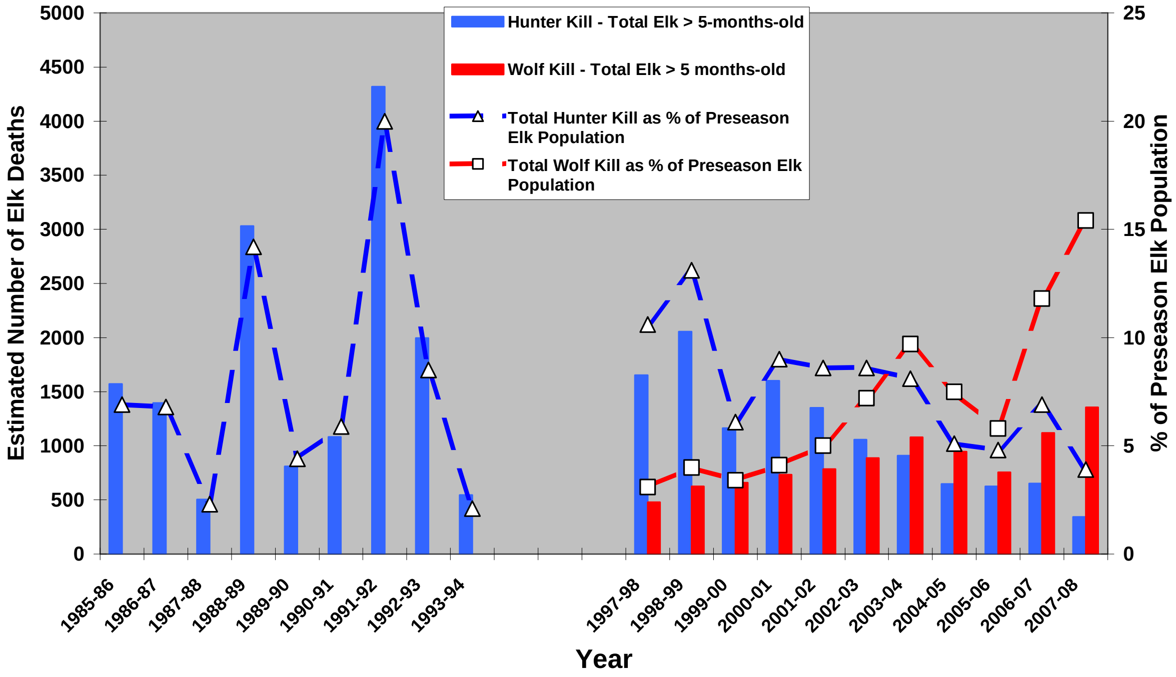


Figure 19. Estimated total hunter-kill and wolf-kill of Northern Range elk, 1986-87 through 2007-08 (fall – spring).

We estimate that wolves killed more female elk (Fig. 20) than were killed by hunters after 2005-06 and that wolves killed more male elk than hunters killed after 2001-02 (Fig. 21). Hunters kill few female elk during the general season and the reduction in late-season permits after 2003-04 has resulted in hunter harvest of only about 2% of estimated pre-season numbers of females since 2005-06 (Fig. 20). Thus, even with reduced numbers of wolves during 2005-06, estimated wolf-kill of females exceeded estimated hunter-kill. During 2003-04, 2006-07, and 2007-08, estimated wolf-kill of female elk also exceeded average pre-wolf hunter-kill as a percent of the pre-season population (Appendix Table 1). With the low rate of recruitment observed since 2002 (mean = 15 calves:100 cows), estimated level of wolf-kill of female elk during 2006-08, by itself, is enough to keep the elk population from growing. Any mortality of females in addition to that caused by wolves results in a declining population. Low recruitment has also resulted in the elk population comprised of disproportionately older females, increasingly subject to death from all causes such that current rates of mortality due to wolves, other predators, and other natural causes, even with no hunting mortality will likely guarantee elk population decline for the near future.

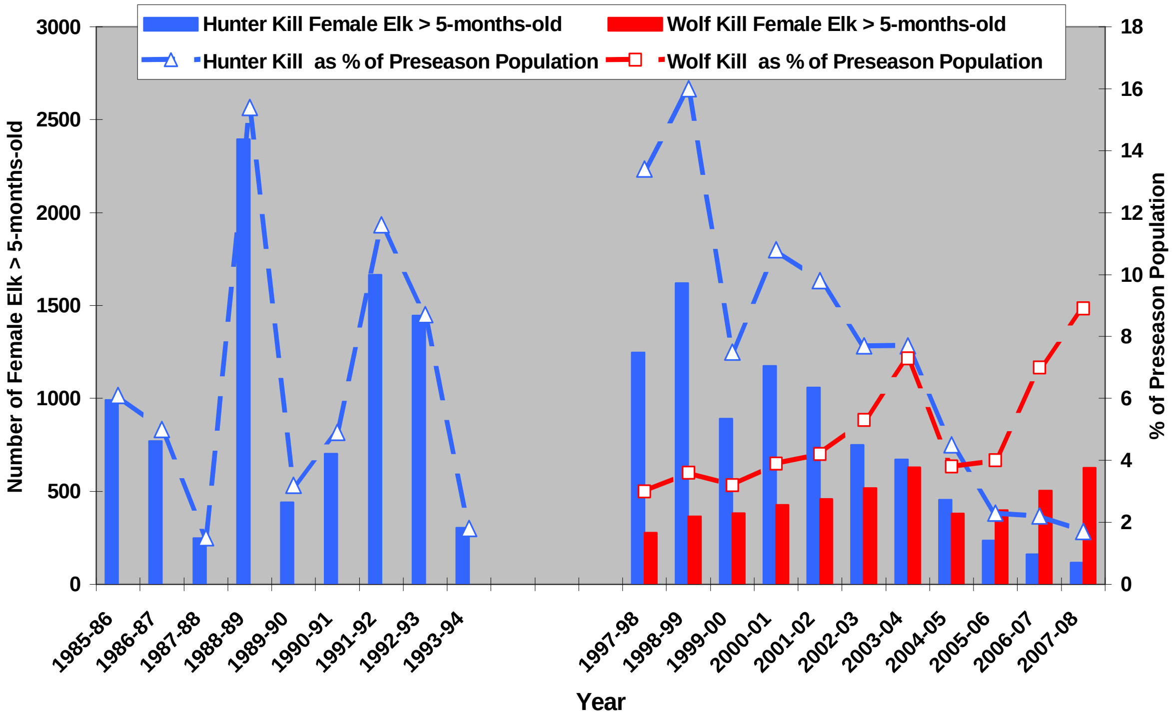


Figure 20. Estimated hunter-kill and wolf-kill of female (> 5-months-old) Northern Range elk, 1986-87 through 2007-08 (fall – spring).

Because adult males comprise a smaller portion of the population than females, reduced recruitment and increased mortality affect their relative population size to a greater degree than females. Also, wolves have been preying on males to a greater degree recently (Smith et al. 2008). Thus, although wolves have been proportionally killing more male elk than hunters since 2001-02, the proportion of the pre-season population taken by hunters also has increased as a function of the declining elk population (Fig. 21). Apparently, bull elk available to hunters have declined as well. The harvest of bulls in HD 316 during the general season has declined by 90% since 1994.

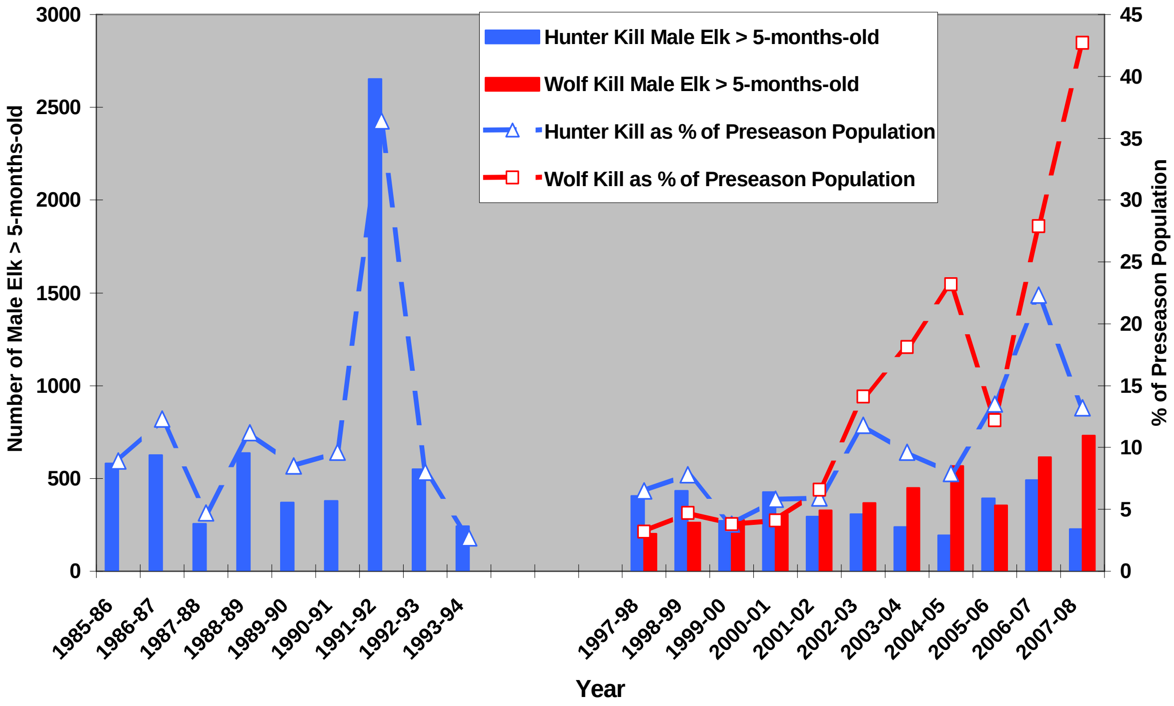
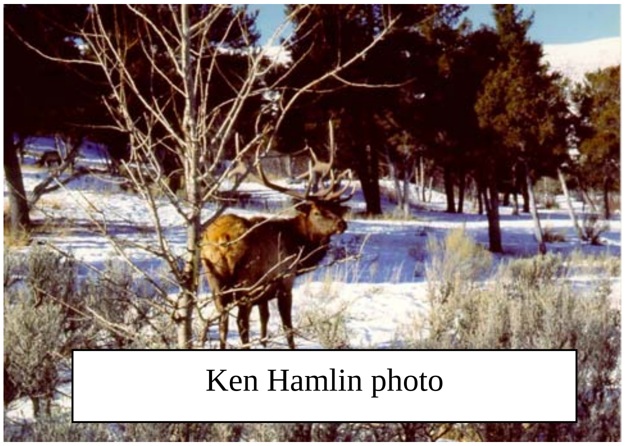


Figure 21. Estimated hunter-kill and wolf-kill of male (> 5-months-old) Northern Range elk, 1986-87 through 2007-08 (fall – spring).



Ken Hamlin photo

## Northern Range Elk Demography and Future Projections

A recent investigation (Wright et al. 2006) used hunter harvest data to provide a thorough demographic analysis of the Northern Yellowstone elk herd and its component vital rates, but the data set spanned 1995-2001, did not include juvenile survival, and many significant ecological changes have occurred since that time. The number of cow elk hunting permits for the portion of the Northern Yellowstone elk population that winters outside YNP, as well as antlerless harvest, has decreased substantially after 2000 (Fig. 16). Secondly, a recent elk-calf mortality investigation (2003-2006) demonstrated a significantly lower juvenile survival rates (summer survival of 0.29 and annual survival of 0.22; Barber-Meyer 2008) than had been estimated (summer survival of 0.65 and annual survival of 0.43) over 1987-1990 (Singer et al. 1997). Finally, estimated wolf populations on the Northern Range have averaged 88.6/year during 2001-2008 compared to an average of 38.5/year during 1995-2000. We suggest that these changed dynamics influence Northern Yellowstone elk population dynamics. To investigate this, we 1) estimated average values of age-specific pregnancy and survival rates, 2) estimated the rate of population change (λ) from these vital rates, and determined the expected population trajectory given the recently-decreased human hunting pressure, and 3) analyzed age-specific, reproductive and survival elasticity, sensitivity, and reproductive values to determine which parameters may most influence the population trend of Northern Yellowstone elk.

To estimate age-specific vital rates, we used data collected at the mandatory hunter check station for the Gardiner late hunt. At this check station, hunters were asked to report pregnancy status of harvested cow elk. We tested the assumption that hunters accurately reported pregnancy rates in elk by using trained MFWP personnel to examine a sub-sample of 871 viscera from field-dressed cow elk. Of 871 pregnancies evaluated by MFWP personnel, hunters had identified 13 as non-pregnant, for an error rate of 0.0149. We also could account for possible change in intra-uterine survival that may occur due to brucellosis. *Brucella abortus*, a bacteria known to cause late-term abortions, exists in this population at a seroprevalence of 0.03 - 0.05 (Atkinson et al. 2007, Anderson et al. 2008). We assumed that half the elk testing seropositive for *Brucella* actively carry the infection (i.e., half will be culture positive, N. Anderson, pers. comm.) and will abort, slightly reducing inter uterine survival and thus the birth rate. Hunter under-reporting would result in increasing pregnancy rates by 0.015, and brucellosis seroprevalence would result in decreasing pregnancy rates by 0.015-0.025. Therefore, we did not adjust pregnancy rates from hunter reports. Wright et al. (2006) similarly presented unadjusted, hunter-reported pregnancy rates. Hamlin et al. (2008) indicated that pregnancy rates determined directly from blood assays in this herd were higher than and were more accurate than hunter reports, but we decided to use unadjusted hunter-reported pregnancy rates to make our results comparable with Wright et al. (2006). To estimate age-specific pregnancy rates, incisors were extracted from harvested elk age 2.5 or older for *cementum annuli* analysis (Hamlin et al. 2000). Yearling elk are reliably identified in the field by tooth eruption patterns (Quimby and Gaab 1957, Hamlin et al. 2000), and were not aged by *cementum annuli* at the check station.

We separately estimated yearling pregnancy and adult pregnancy rates. Elk may first conceive at age 15 months, and the pregnancy rate associated with this age class may be highly variable and influenced by many factors (Eberhardt 2002, Hamlin and Ross 2002). We used 705 yearling records from 2002-2008 to estimate the overall yearling pregnancy rate and its variance. We compared this rate to 135 yearling harvest records from 1995-2002 using a pairwise proportional test in the statistics software package R 2.4.1 (R Development Core Team, 2006). Yearling pregnancy rate did not significantly differ between the time periods ($p$=0.20). Over 1995-2002, 54 out of 705 yearling cow elk were reported to be pregnant (0.077). During 2002-2008, 17 of 135 yearling cow elk were reported to be pregnant (0.11). We therefore pooled all 840 records from 1995-2008 for a total yearling pregnancy rate of 0.082, or 0.041 for female fetuses given a 50:50 sex ratio at birth (Cunningham et al. *in press*).

We estimated age-specific pregnancy rates for elk age 2.5 and older using 6,937 pregnancy records with matching cementum annuli age (Hamlin et al. 2000) over 1989-2008. We pooled all years for this analysis because adult elk pregnancy rates were constant among years in a previous analysis (see Elk Vital Rates: Pregnancy section above). We described the age-specific pregnancy rate with a second-order polynomial because we expected pregnancy rates would be lower at young ages when cows are just reaching full body size, peak at a prime age, and decrease for older ages because reproductive capacity may decline as body condition declines. This function fit the data very well ($R^2$ = 0.97), with the maximum of the function equal to 0.70 at 7.6 years old (Fig. 22).

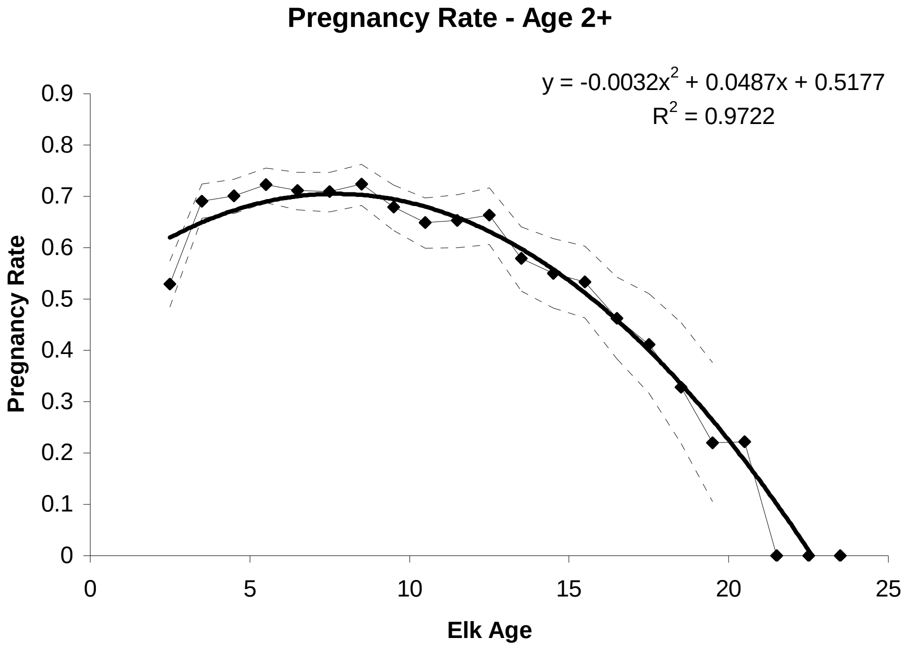


Figure 22. Age-specific hunter-reported pregnancy rates for Northern Yellowstone elk, 1989-2008. Dashed line represents a 95% confidence interval.

We used the 2002-2008 Gardiner late hunt hunter check station data and cementum annuli records to describe the proportion of adult cow elk in each age class ($S_x$), calculated survivorship ($l_x$) as $S_x/S_0$, and the age-specific survival probability ($g_x$) as $l_{(x+1)}/l_x$ (Gotelli 1998). Adult elk survival rates, as calculated from lifetable reconstruction methods, were similar to those previously reported (Wright et al. 2006, Fig. 23). There was an increase in g(x) for the 4-8 year old age category, and the average g(x) from 0 to age 15.5 was 0.83, compared with 0.81for previous estimates (Wright et al. 2006). Hamlin et al. (2008) estimated adult female survival from age structure as 0.81 from 2001-2006. Evans et al. (2006), from telemetry marked adult female elk, estimated survival as 0.80 for all females and 0.83 for females ages 1-15 during March 2000 – February 2004. Extending telemetry data through June 2008 (P. J. White, pers. comm.) and computing for a July – June annual period, we estimate that annual survival averaged 0.82 during 2000-2008. In combination, these data indicate little change in adult female survival (perhaps a maximum of 0.02 or 2.5%) after the elimination (for practical purposes) of hunting mortality in more recent years.

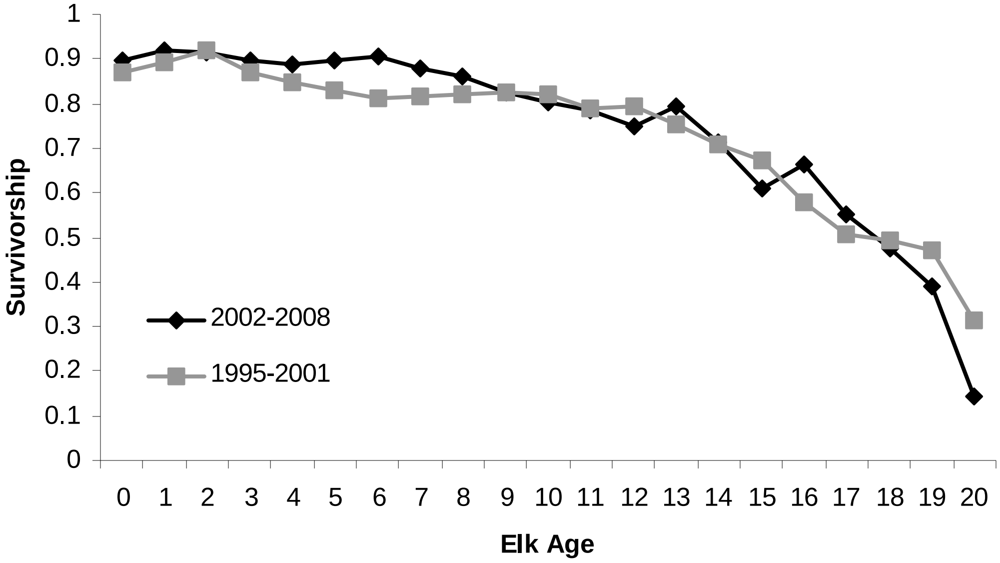


Figure 23. Age-specific survival of female Northern Yellowstone elk for 1995-2001 and 2002-2008 from life table reconstruction.

Annual calf elk survival has declined from an estimated rate of 0.43 over 1987-1990 (Singer et al. 1997) to 0.22 over 2003-2006 (Barber-Meyer et al. 2008). Although calf survival during summer differed by area in the NY, elk harvested in the Gardiner late hunt may calve across YNP (Cunningham et al. 2007, Cunningham and Hamlin unpublished data), and we used the pooled (all-area) summertime NY elk calf survival rate of 0.29 (Barber-Meyer et al. 2008).

Using the above estimated vital rates**,** we parameterized a 23 x 23 female-only, pre-birth pulse Leslie matrix model using the data sources described above. In the Greater

Yellowstone area, elk breed during the last 2 weeks of September and first week in October (Hamlin and Ross 2002, Cunningham et al. *in press*, MFWP unpublished data), with the birth period encompassing 15 May through 15 June. Thus, by the January late hunting season, calves were 6 to 7 months old. In a pre-birth pulse Leslie matrix model, the top row represents fecundity: the product of pregnancy rate, intra-uterine survival, and neonate survival to enter the first age class. In this female-based model, we multiplied the pregnancy rate by 0.5 because NY elk demonstrate a 50:50 sex ratio at birth (Cunningham et al. 2009, *in press*).

Output from the Leslie matrix model suggested a decreasing population, with a deterministic $\lambda = 0.93$. This compares with $\lambda = 0.91$, estimated from log-linear population count data over 2002-2008. Reproductive values were highest for elk age 1.5, and showed a general decline thereafter (Fig. 24). Survival elasticity was highest for elk age 0.5, with a general decline thereafter, whereas reproductive elasticity was generally quite low (<0.02) for all ages (Fig. 25).

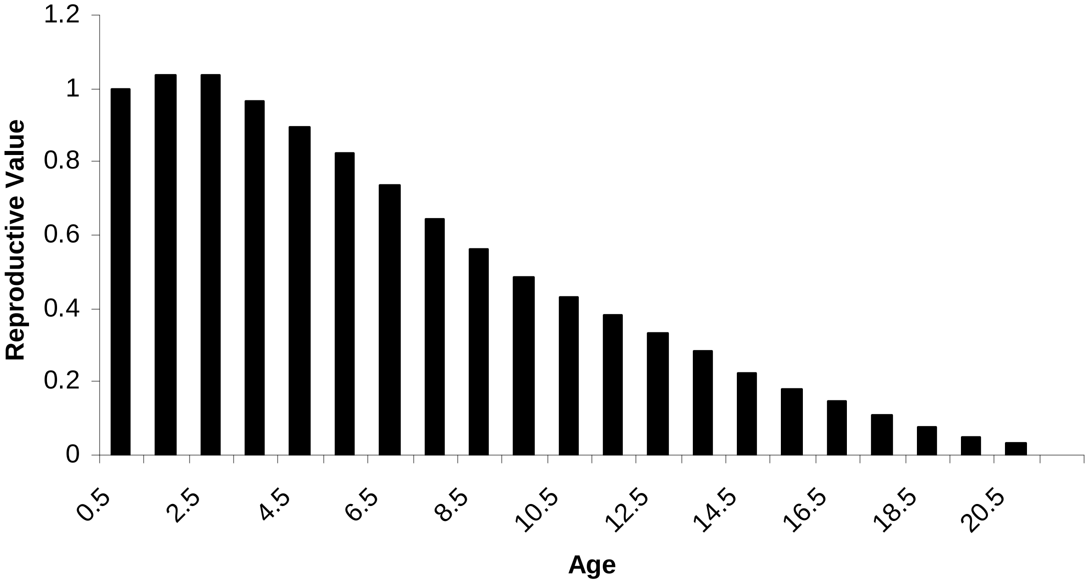


Figure 24. Age-specific reproductive values for female Northern Yellowstone elk.

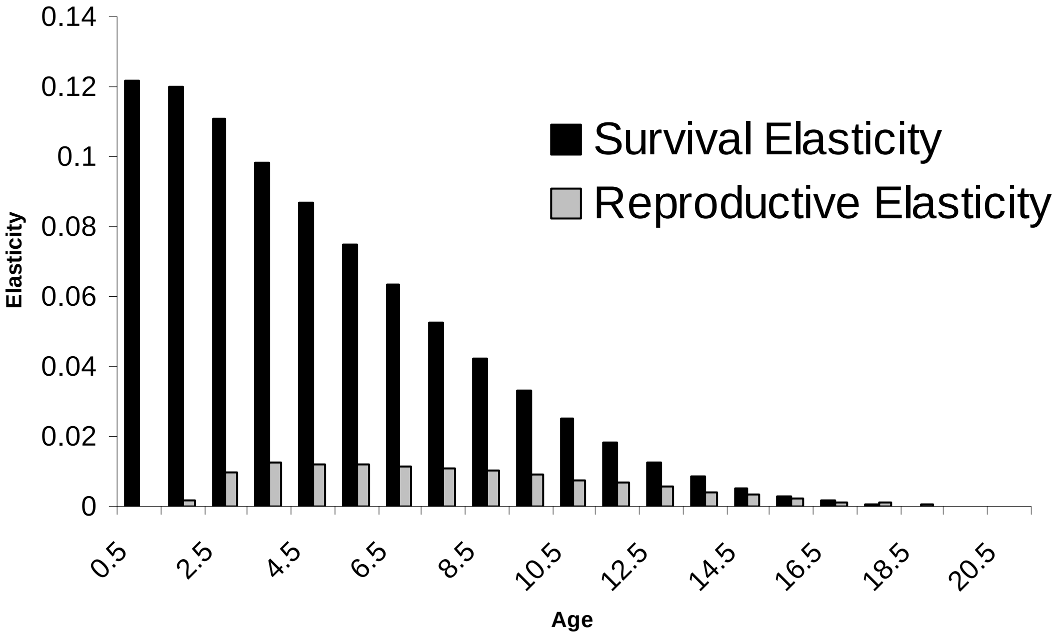


Figure 25. Relative survival and reproductive elasticity for female Northern Yellowstone elk.

Given the low value of λ, we performed some experimental manipulations on the matrix model. We increased all survival rates (age 0.5 and up) by 5% and by 10% to determine whether continued hunting reductions could ever increase λ in Northern Yellowstone elk. At a 5% increase in age-specific survival rates, the resulting λ = 0.97, still represented a declining population. At a 10% increase in age-specific survival rates (at which 2 survival rates had to be capped at 1), we found λ = 1.01, representing a slightly increasing population. Eliminating the approximately 100-150 deaths of antlerless elk now occurring due to hunting (2% of preseason female elk ≥ 5-months-of- age) cannot increase adult survival rates by 10%. An annual calf survival of about 0.55 (approximately 44 calves:100 cows) would be necessary to result in an increasing population given no increase in adult female survival. Thus, survival of elk calves would have to increase to rates higher than Singer et al. (1997) observed for the population trend to be positive. Concurrent increases in adult female survival would reduce the calf survival rate necessary for population increase. However, adult female survival probably cannot be further increased markedly by MFWP actions and the increasing age of the population (T. Lemke, MFWP unpublished data) makes it susceptible to increasing natural mortality, even without predation.

Our inferences concerning future trends in the Northern Yellowstone elk herd are tied to the estimates of elk vital rates that we used to populate the matrix model. Each of these vital rates was estimated using methods that contain assumptions, and those assumptions are being evaluated as we continue to refine this analysis. At this point, the combination of information suggests that the Northern Range elk population will continue to decline in numbers until natural changes reduce predation pressure on elk by bears and wolves primarily, but also by other predators.

## Indirect Effects of Wolves on Ungulates

In addition to the more commonly studied direct effects (killing) of wolves on prey, changes in prey behavior that occur to avoid predation may result in potentially negative indirect effects on prey and for some human values. Some of these behavioral changes such as increased vigilance (Liley and Creel 2008), reduced foraging time (Hughes and Ward 1993), and changes in habitat use (Creel et al. 2005) and forage selection could alter the nutritional status of the prey and reduce survival in some circumstances. Morgantini and Hudson (1985) found that human hunters (predators) caused changes in elk habitat use and foraging switched from grazing to browsing. Whether these changes ultimately affected elk survival has not been determined. Human recreation and economies also could potentially be impacted. If wolf predation pressure caused elk, for example, to alter habitat use and distribution, this could impact the success of human hunters or hunting outfitters, or change the relative amount of elk grazing pressure on private agricultural lands and adjacent public lands (and possibly, brucellosis exposure).

Research by this project and cooperating projects found varying indirect impacts of wolf predation pressure on elk. No effects seem substantial except in the Madison headwaters and perhaps the Gallatin Canyon. Grouping responses (larger or smaller group sizes) of elk to wolf predation pressure appeared to be habitat dependent (Proffitt et al. 2009), with some disaggregation (breaking-up) of large groups of elk in open habitats (Creel and Winnie 2005, Proffitt et al. 2009) in response to wolf predation risk. However, in the more complex grassland hills habitat of Madison Valley winter range (Proffitt et al. 2009) and in small heterogeneous wintering areas of the Madison-Firehole (Gower et al. 2008a), elk aggregated (formed larger groups) when wolves were present.

In the Gallatin Canyon, which has forested winter ranges with small meadow openings, Creel et al. (2005) found that when wolves were present, elk selected for conifer forest over grassland habitat. However Mao et al. (2005) found that on the Northern Range of YNP, elk selected more open habitats during winter post-wolf restoration than selected during the pre-wolf period. During summer, elk appeared to select areas and habitats that allowed them to avoid wolves (Mao et al. 2005).

Using GPS collars on both elk (30 minute interval locations) and wolves (3 hr interval locations), Proffitt et al. (2009) found that within the Madison Valley winter range, elk movement rate increased in response to threats of predation from both wolves and human hunters, corroborating conclusions presented in Gude et al. (2006). The movement response of elk to human hunters was much greater than response to wolves, but neither hunters nor wolves accounted for the majority of variation in elk movement rate. Prior to the late hunt period, the average movement rate of elk was 0.73 km (0.45 miles) per 4-hr period when wolves were greater than 10 km (6.2 miles) away and 1.04 km (0.64 miles) per 4-hr period when wolves were < 0.25 km (275 yards) distant, a difference of 0.31 km (0.2 miles) per 4-hr period. During the late hunt period, when hunters were also present, elk movement rates per 4-hr period increased by about 2.5 times when wolves were < 0.5 km (0.3 miles) distant. This average increase in movements was 1.23 km (0.8 miles) per 4-hr period. Thus, increased average movements of elk related to close presence of wolves (and hunters) in the Madison Valley even though statistically significant, were very short distance movements. The observed small increases in movement rates entail increased vigilance, "milling around", and small movement away from wolves, but not elk "leaving the country", or even the grassland flats. This may theoretically imply some loss of feeding and resting time for elk, however Gower et al. (2008b) and White et al. (2008a, 2008b) found minimal effects on elk food acquisition or nutrition by these small changes due to wolves.

Information from a GPS collar (3-hr location interval) on the Freezeout wolf pack from August 2005 through August 2006 (Fig. 26) indicated that wolves followed elk in their normal migratory pattern (Hamlin and Ross 2002) rather than altering that pattern. This wolf pack moved within a portion of Gravelly-Snowcrest elk summer fall range throughout June through 18 December and then spent winter moving between Basin-Sage, Blacktail, and Robb-Ledford elk winter ranges (Fig. 26). We had no telemetry collars on elk concurrent with the wolf collar. Therefore, it is possible there could have been some elk distribution changes within summer range and within winter range compared to the pre-wolf period (Hamlin and Ross 2002), but there was no change in landscape scale elk migratory patterns or their timing.

While conducting collections of elk urine in snow, we have observed much less elk use of the Blacktail WMA during the post-wolf period than during the pre-wolf period. Much elk use that formerly occurred on the Blacktail WMA now is occurring to the north of both the BTWMA and the Robb-Ledford WMA. Most wolf use occurred in the Basin-Sage Creek winter range and along the west Snowcrest range face, but wolves also used the area where "Blacktail elk" are now spending more time (Fig. 26). Reasons for the observed shift in elk winter use from the BTWMA are unclear. These "Blacktail elk" have not "escaped" predation pressure from wolves by moving, but may face reduced pressure in the open grasslands to the north of the WMAs (Fig. 26).

Although recent data from telemetry is unfortunately lacking, there is anecdotal evidence from the senior author's long-term personal observations in the Gravelly-Snowcrest area (Hamlin and Ross 2002) and from long-time hunters and others considered reliable observers, that at least local changes in elk behavior and distribution have occurred during the post-wolf period (also see discussion of BTWMA elk above). A small traditional elk calving area associated with the Freezeout wolf packs denning area (dense areas of blue dots south-central Fig. 26) has essentially been abandoned by elk. Also, hunters are having great difficulty finding elk during hunting season in the southern portion of the Gravelly and Snowcrest Mountains, which previously supplied much harvest (Hamlin and Ross 2002). Substantial declines in hunter harvest in the Gravelly-Snowcrest Mountains in recent years disproportionate to elk population changes (Fig. 14) and despite liberalized regulations also indicate behavioral and local distribution changes for elk affecting hunter harvest. Average annual winter elk counts for the WCWMA, BTWMA, and RLWMA actually increased by 3% for the 2001-2007 period compared to

1991-2000. Average counts decreased by only 4% for 2005-2007 compared to 1991-2000. Average annual harvest of antlerless elk declined by 29% from 1991-2000 to 2001-2007 and by 44% from 1991-2000 to 2005-2007. Average annual bull harvest declined by 19% from 1991-2000 and by 26% from 1991-2000 to 2005-2007. The combination of elk population and hunter harvest trend along with reliable anecdotal evidence, suggest that at least local elk behavioral and distributional changes have occurred in the Gravelly-Snowcrest Mountains during the post-wolf period that may have reduced hunter success.

We make similar landscape scale conclusions about elk and wolf movements in the southeast Madison Valley where both elk and wolves were marked with GPS collars. During summer, the distribution of the wolf pack was centered on elk distribution (Fig. 27). We have not yet analyzed summer movement interactions of elk and wolves as we have for winter (Proffitt et al. 2009), however, visual examination of simultaneous summer locations of wolves and elk does not indicate major effects. Telemetry-collared elk remained within the same drainage and area when wolves moved into those drainages during summer. Summer distribution of elk is the same as during the 1976-86 pre-wolf period (MFWP unpublished data, Cunningham et al. *in prep.*). More localized behavioral and distributional responses of elk to wolves, however, cannot be ruled out without more detailed examination of the data.

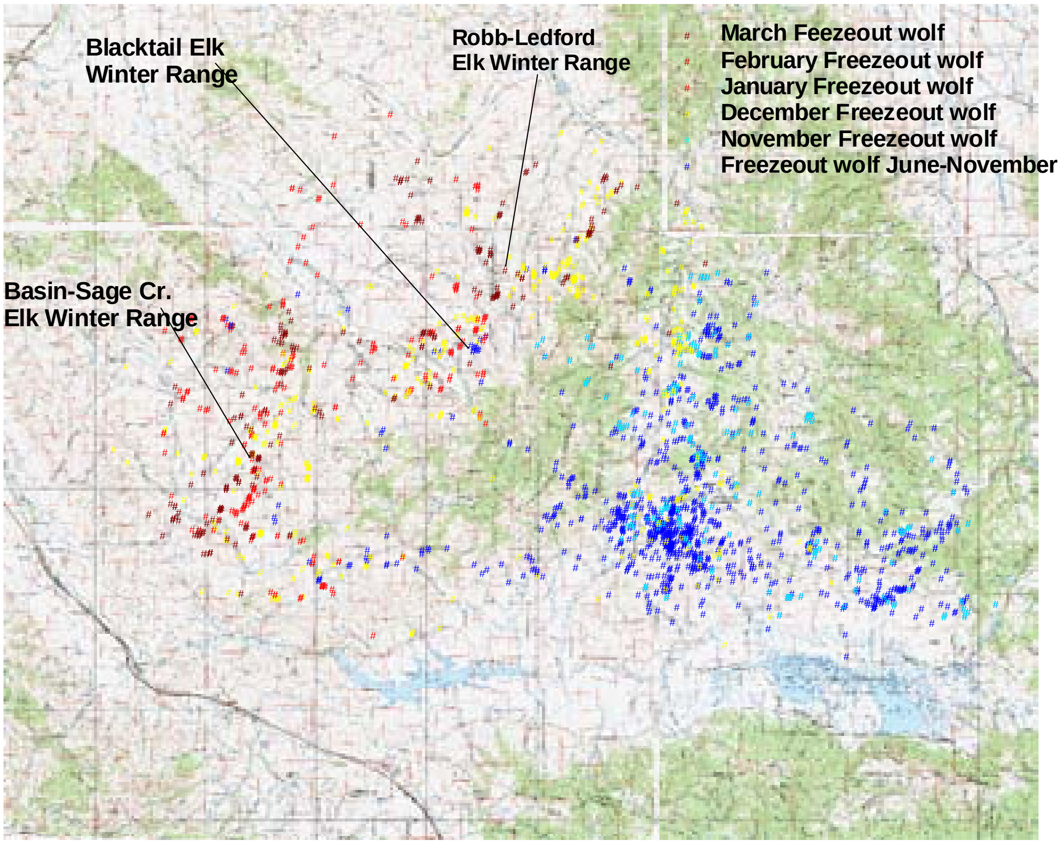


Figure 26. Freezeout wolf pack home range and locations (every 3 hours), August 2005–August 2006 in relation to major elk winter ranges.

In contrast to the Gravelly-Snowcrest Mountains, elk are moving to east Madison Valley winter ranges earlier in fall than during 1976-86. In October, prior to the general rifle season, substantial numbers of elk have moved to winter range and wolves follow them (Fig. 28). By the first week of the general hunting season, most elk have moved to winter range areas where hunting by the general public is precluded and the wolves have followed them (Fig. 29). During November of the general hunting season, distribution of both elk and wolves is centered on lands where hunting by the general public is precluded (Fig. 30). During November in 1976-86, when these winter range lands were more open to general public hunting, elk were much more widely distributed across the National Forest and more available to hunters (Fig. 31) than they are today.

The more recent early movement of elk to winter range areas is a result of establishment of "refuges" from human hunting, not a result of avoidance of wolf predation. Wolves follow the elk and are present and killing elk on these hunting "refuges".

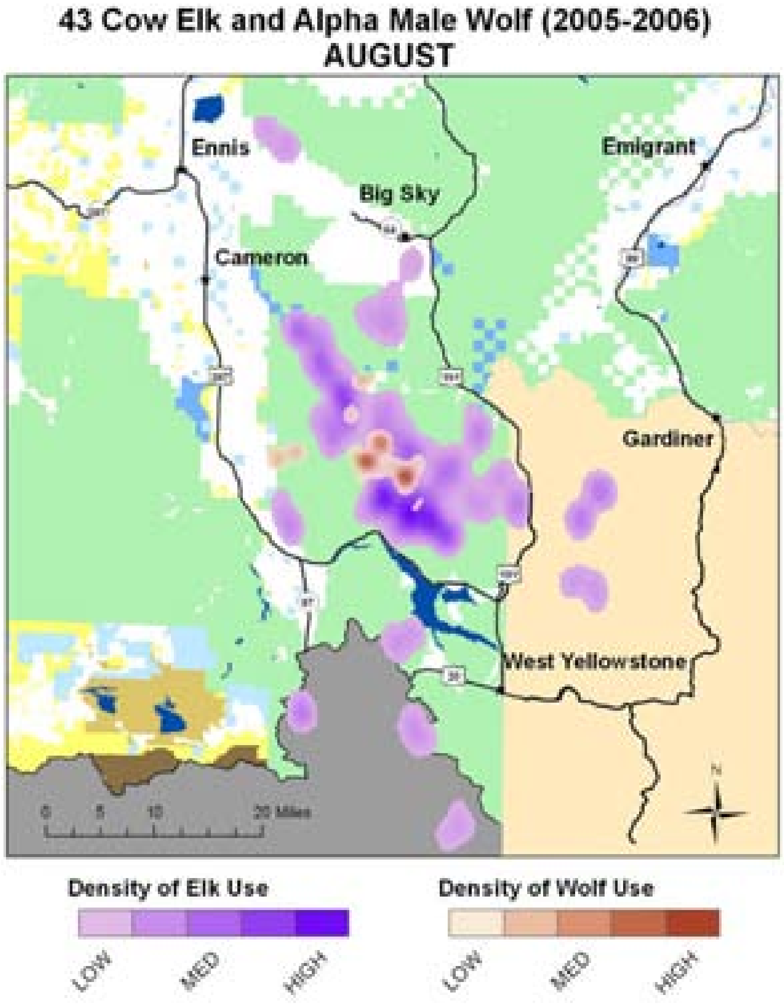


Figure 27. Density distribution of 43 cow elk and the alpha male of the wolf pack during August.

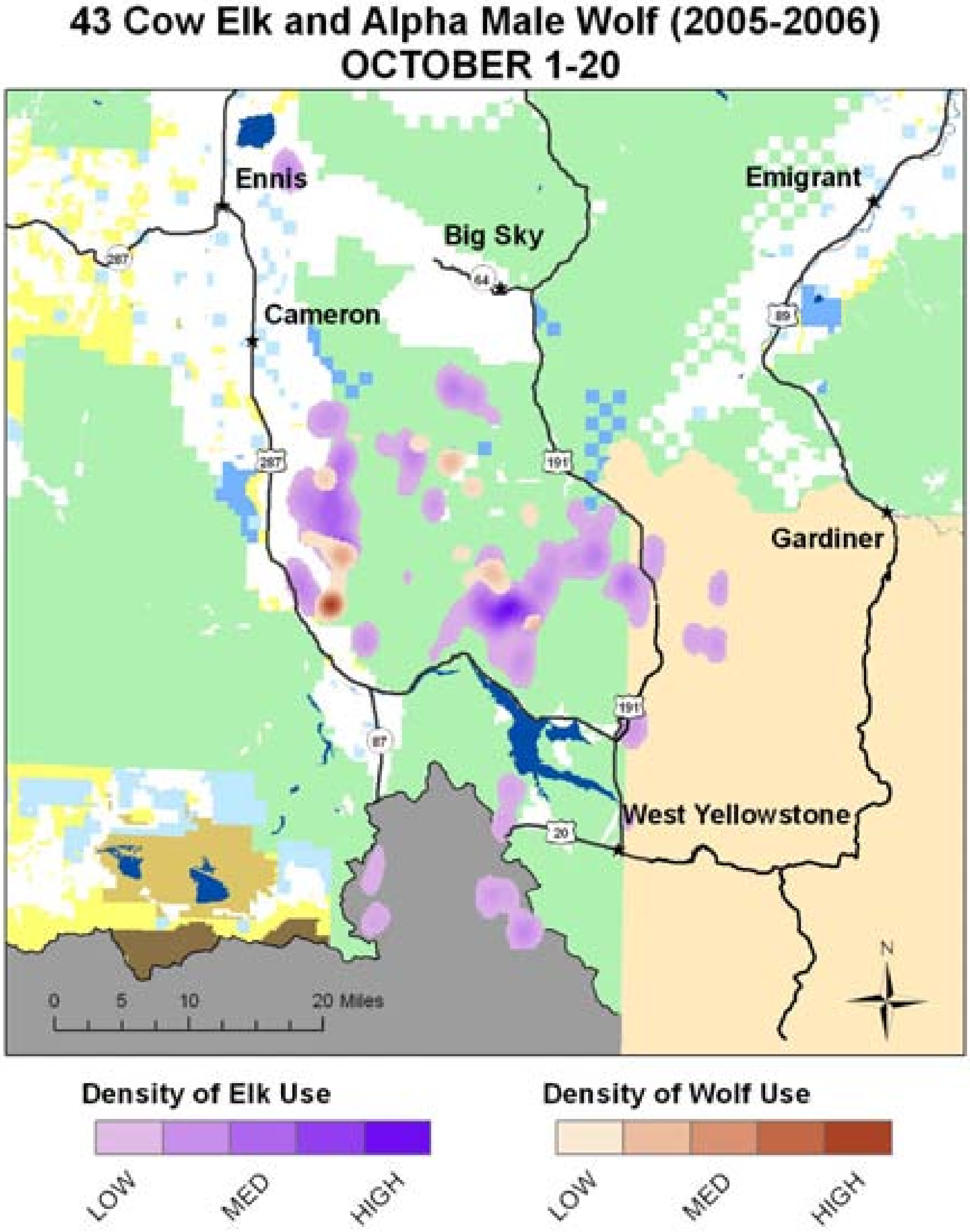


Figure 28. Density distribution of 43 cow elk and the alpha male of the wolf pack during October prior to general hunting season.

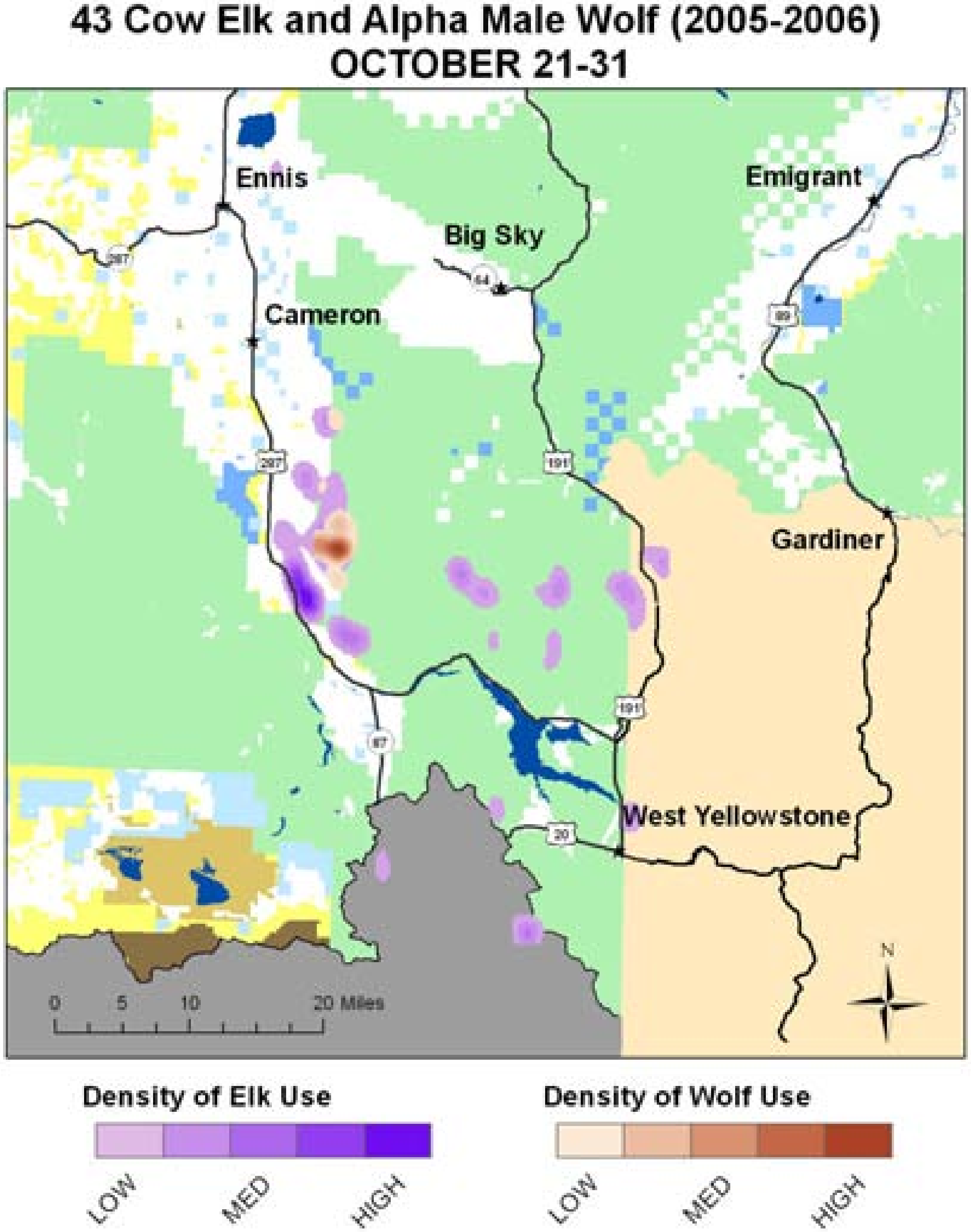


Figure 29. Density distribution of 43 cow elk and the alpha male of the wolf pack during the first week of the general hunting season.

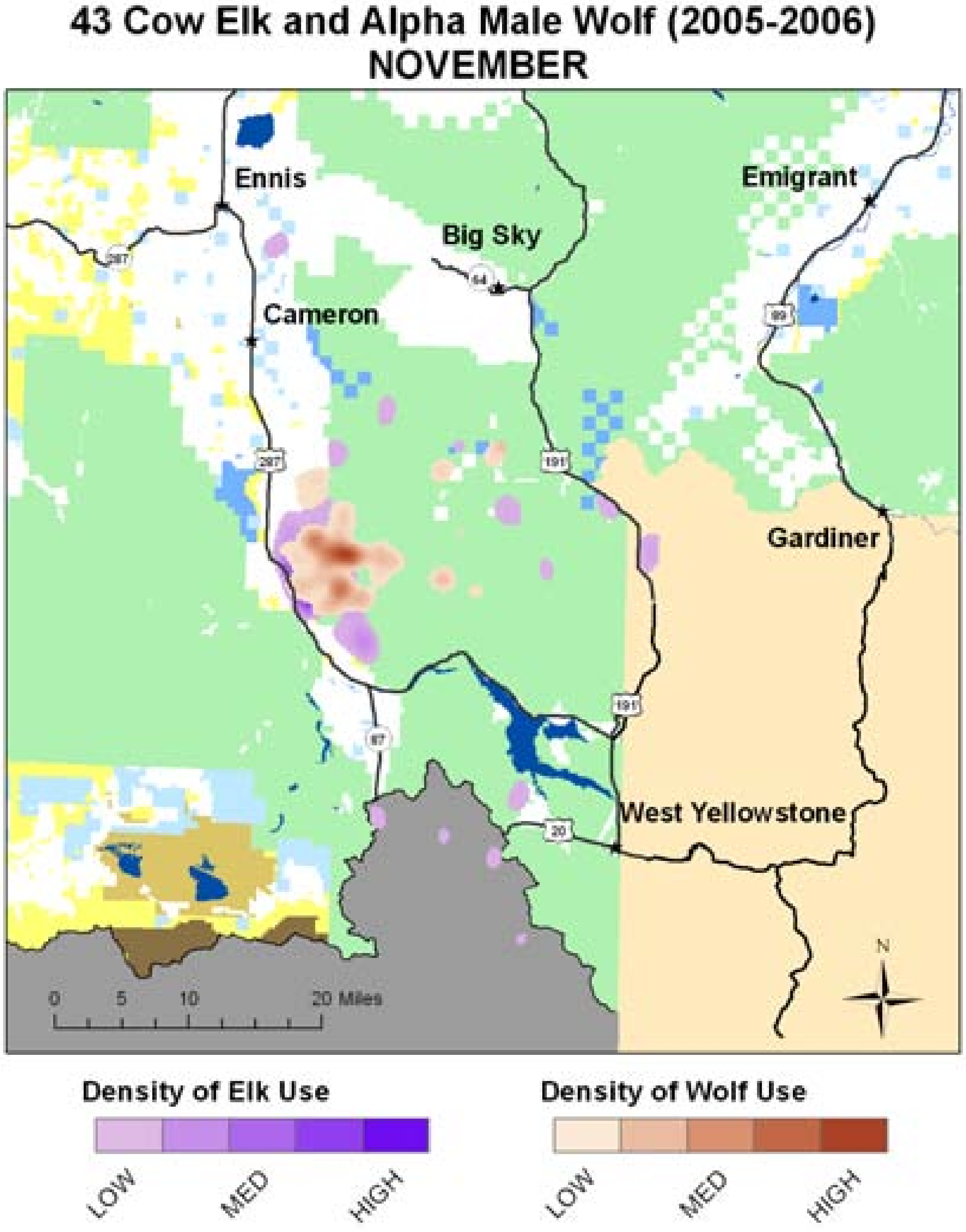
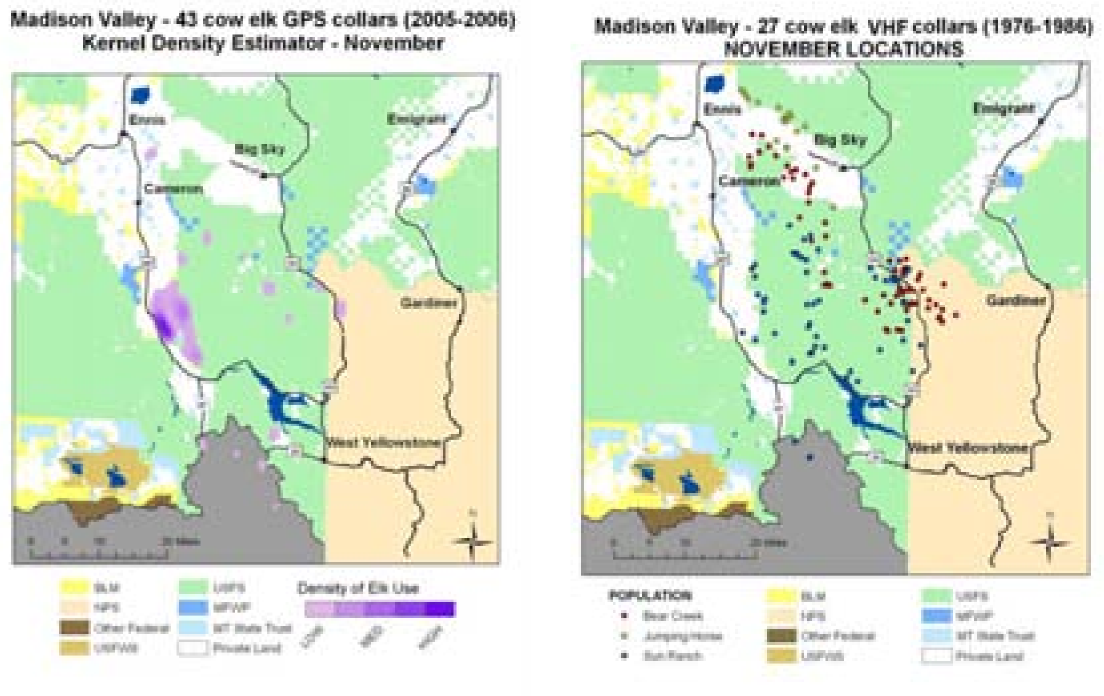


Figure 30. Density distribution of 43 cow elk and the alpha male of the wolf pack during November of the general hunting season.



**A.** **B.**

Figure 31. Density distribution of 43 adult female elk during November of the general hunting seasons of 2005 and 2006 (A.) and VHF locations of 27 adult female elk during the general hunting seasons of 1976-86 (B.).

Landscape scale changes in elk movements and distribution have been observed in the Madison headwaters area of YNP (Gower et al. 2008c). Because of deep snow during winter, elk habitat is limited primarily to thermal areas and areas near the rivers. Prior to wolf restoration, all marked elk remained within the Madison headwaters drainages (Gower et al. 2008c). After substantial wolf presence was established, about 19% of the traditionally non-migratory elk became migratory or permanently dispersed after wolf restoration, no longer wintering within the Madison-Firehole-Gibbon drainages (Gower et al. 2008c). No collared elk vacated the Madison drainage, which had the least wolf presence of the 3 drainages (Gower et al. 2008c). Elk that remained within the Madison headwaters area during winter made moderate increases in movements and home range, but this was constrained by the relative lack of options provided in this deep snow environment.

A similar increased pattern of elk movement to different wintering areas could be occurring in the Gallatin Canyon. There, the decline in elk counted is more severe than estimated mortality from hunters and wolves combined would explain. Although not as severe as in the Madison headwaters, snow is deeper and adequate wintering sites are more limited in size and number in the Gallatin Canyon than in most of southwestern Montana. A portion of elk summering in the Gallatin drainage have always moved through the Gallatin during early winter and over the Madison Range to winter on the east side of the Madison Valley. It is possible that an increasing proportion of elk have followed this migratory pattern after wolf restoration due to lower wolf predation pressure in the Madison Valley compared to the Gallatin Canyon. However, we do not have the intensity of marking over the entire pre- and post-wolf period to document changes in proportions of elk remaining in the Gallatin Canyon to winter versus moving to the Madison Valley and therefore potential changes in elk movement patterns remain speculative.

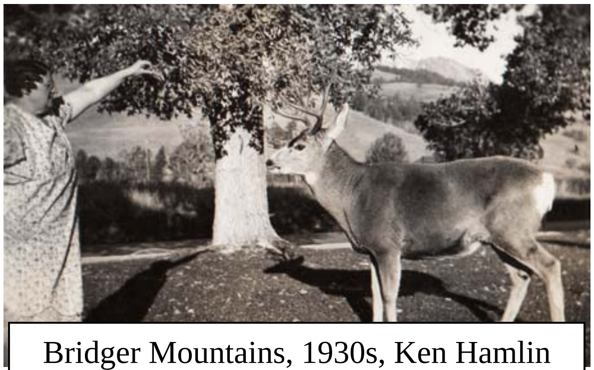
Potential relationships among wolves, ungulates and diseases such as Hydatid disease (*Echinococcus granulosis*) and brucellosis (*Brucella abortus*) transmission should be investigated in the future as any changes in disease occurrence may be an indirect impact of wolf restoration.

## Other Ungulates

Although elk are the major prey of wolves in southwestern Montana, other species of ungulates are of interest either as “control species” (mule deer) or in the case of moose, because they occur in limited numbers and may be impacted if preyed upon by high wolf numbers sustained by large elk populations.

Mule deer are rarely preyed upon by wolves in southwestern Montana (see earlier), but because their distribution overlaps elk and wolves and their recruitment and population dynamics are very susceptible to drought (Hamlin and Mackie 1989), they serve as a good “control species” for comparison with sympatric elk population dynamics.

Elk calf recruitment in the Northern Range of YNP and mule deer recruitment in HD 313 at the northern end of elk winter range followed the same annual pattern of change until spring 1999 (Fig. 32). Since spring 1995, mule deer recruitment has increased while elk calf recruitment has declined (Figs. 32 and 33). Mule deer on the Northern Range have faced the same degree of drought as elk since 2000, but less predation pressure from wolves and bear. Except for a non-significant decline in HD 392, mule deer recruitment in other portions of southwestern Montana also has shown an increasing trend since 1995 and through the drought period (Fig. 34).



Bridger Mountains, 1930s, Ken Hamlin collection

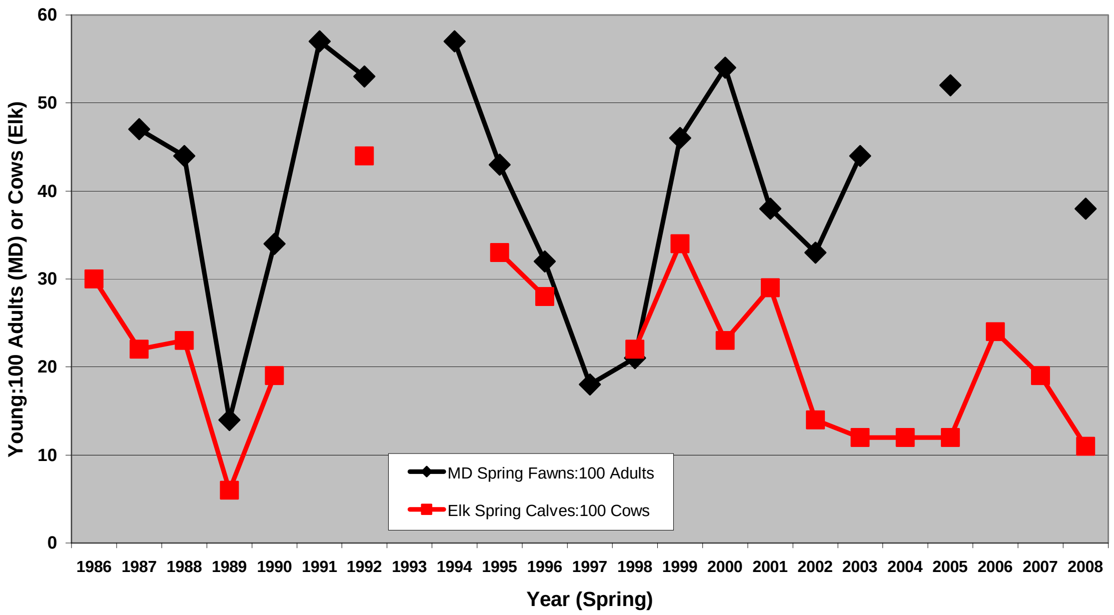


Figure 32. Spring recruitment of elk calves and mule deer fawns on the Northern Yellowstone Range, 1985-86 through 2007-08.

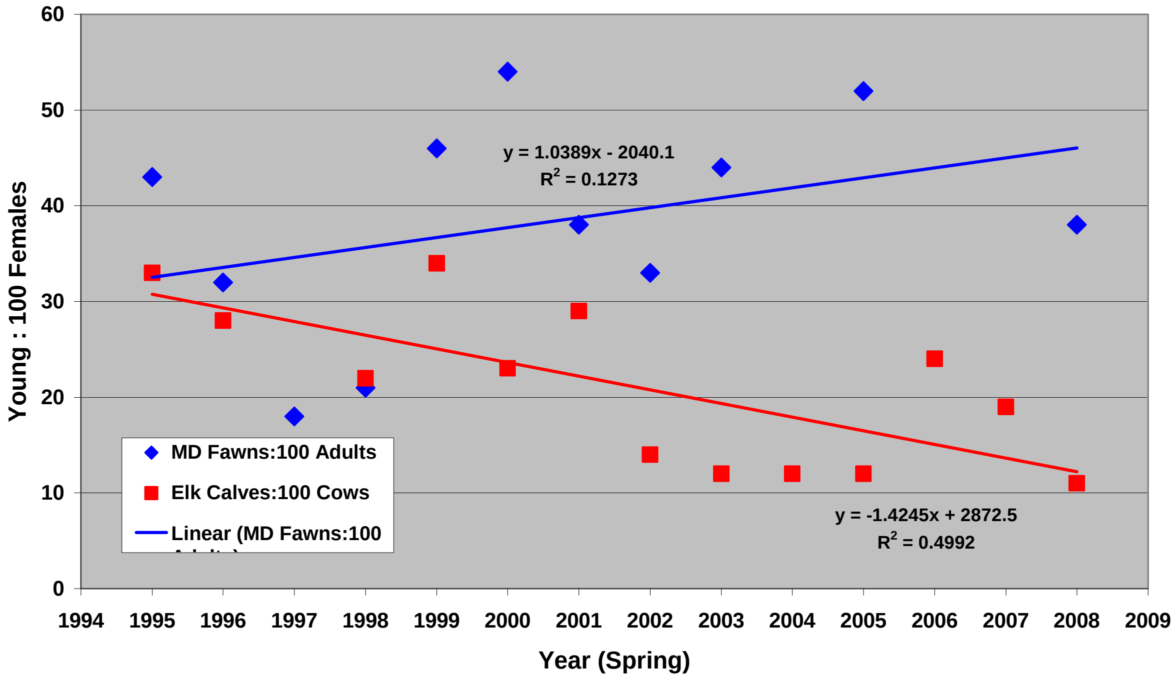


Figure 33. Trend in recruitment of elk calves and mule deer fawns during the post-wolf period on the Northern Yellowstone Range, 1995-2008.

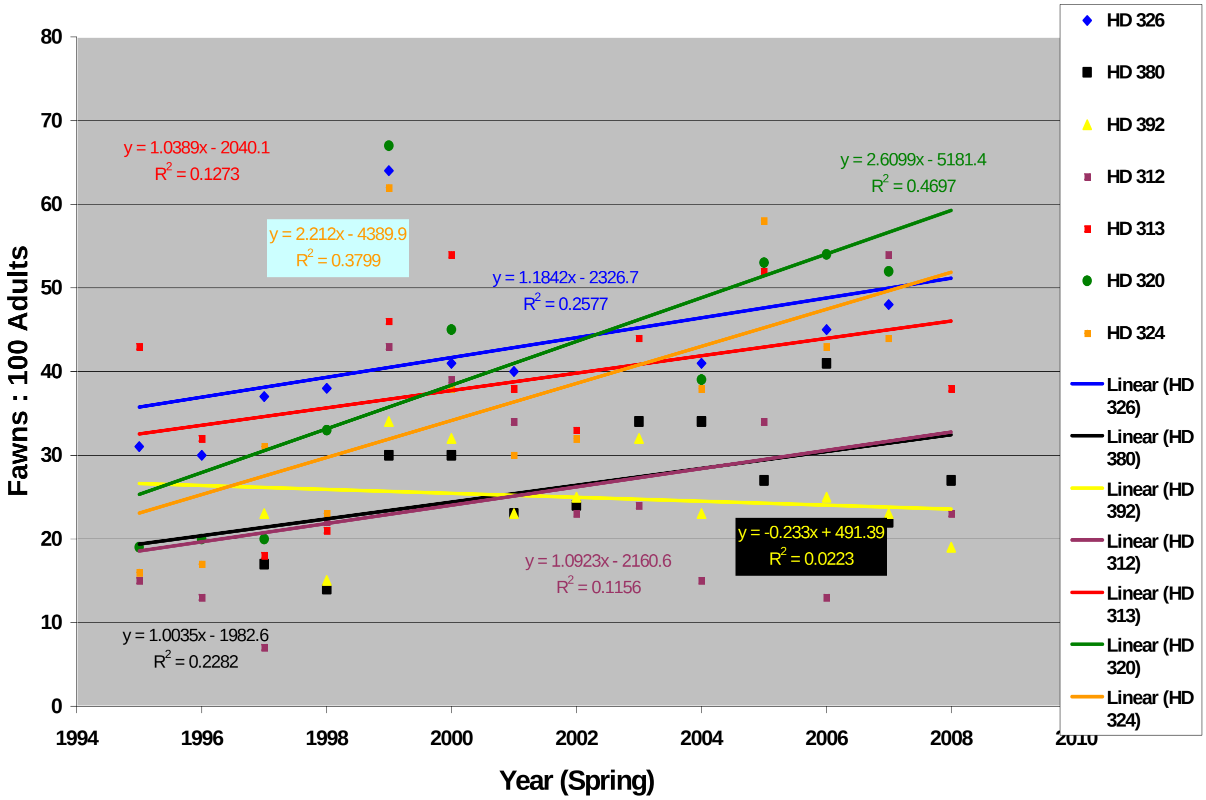


Figure 34. Trend in recruitment of mule deer fawns in 6 southwestern Montana populations, 1995-2008.

The number of moose counted around Red Rocks National Wildlife Refuge (HD 334) has continued to increase through 2008 (Fig. 35). Total number of moose calves recruited has remained about the same since 1978 because although recruitment rate has declined (an average of about 23 calves:100 adults since 1997 compared to an average of about 36 calves:100 adults prior to 1997), the number of cows producing calves has increased (Fig. 35). To this time, there is no evidence that wolf restoration has impacted this moose population. During 2005-2006, even though the den area of the Freezeout wolf pack was near wintering areas of this moose population, the wolf use locations indicated no overlap with HD 334 moose during winter (Fig. 26).

Numbers of moose counted and calf recruitment have declined in Big Hole hunting districts, but those declines began in the mid-to-late-1980s, prior to wolf restoration (Figs. 36 and 37). Because they continually commit depredations of livestock, wolves are heavily controlled in this area. However, due to declining recruitment and numbers of moose (from whatever cause), moose in this area should be closely monitored.

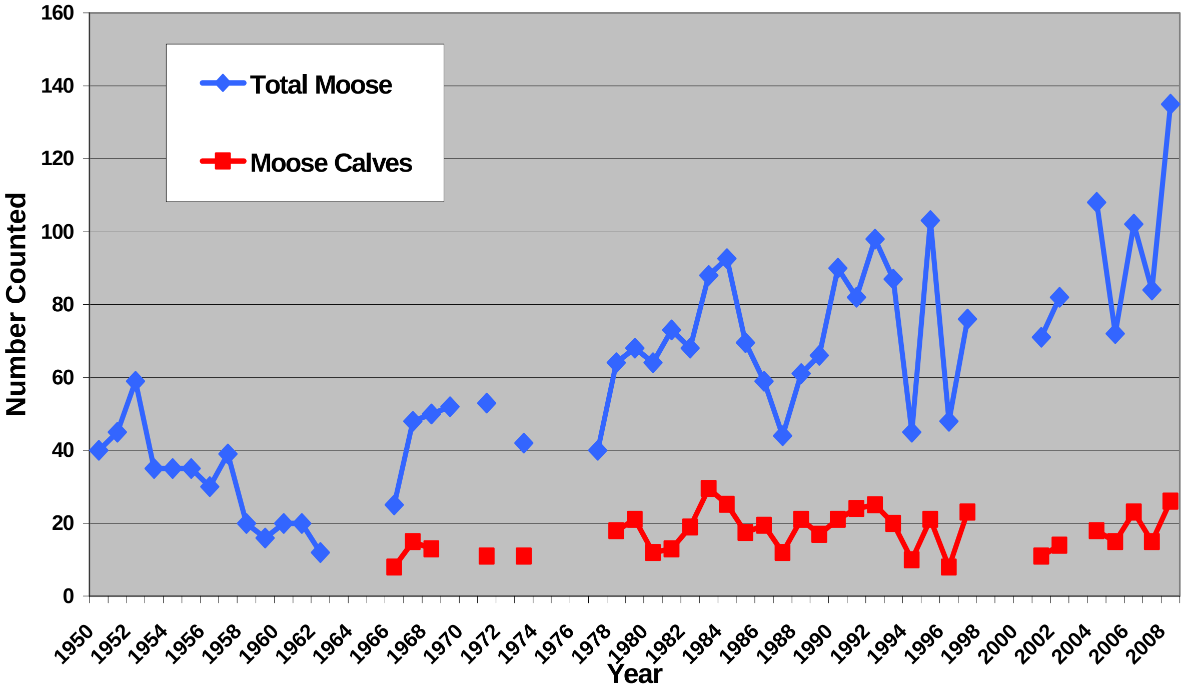


Figure 35. Moose population trends in the Red Rocks National Wildlife Refuge Area, HDs 334 and southern portion of HD 330.

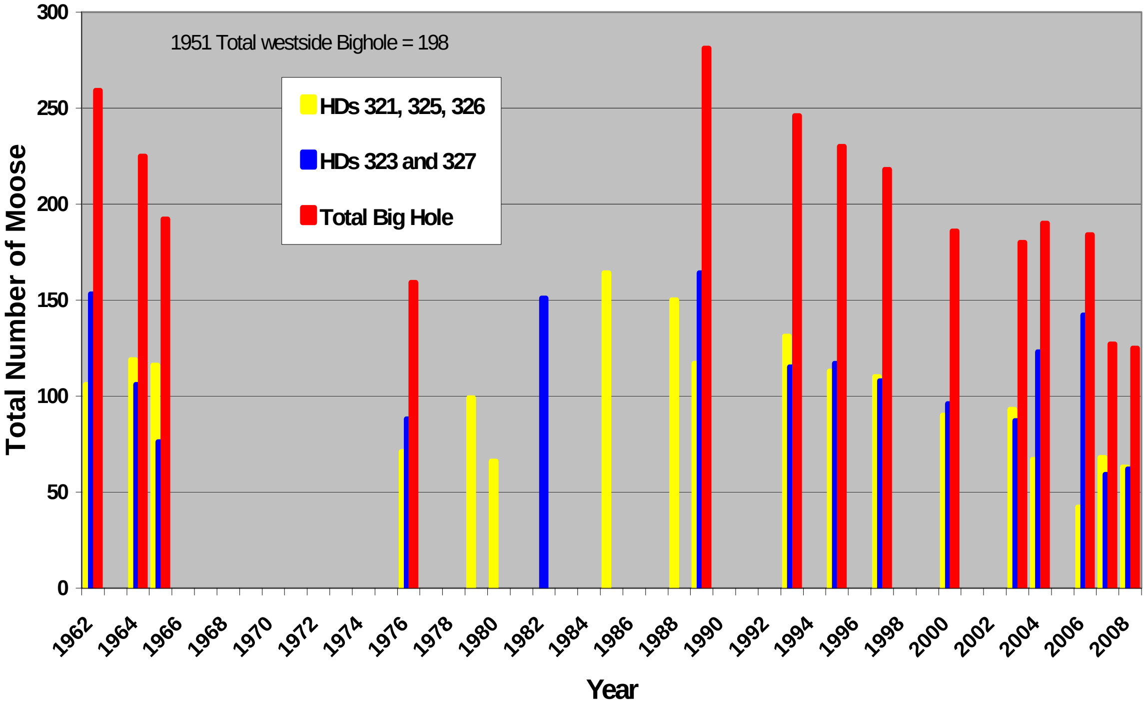


Figure 36. Number of moose counted in Big Hole hunting districts, 1962-2008.

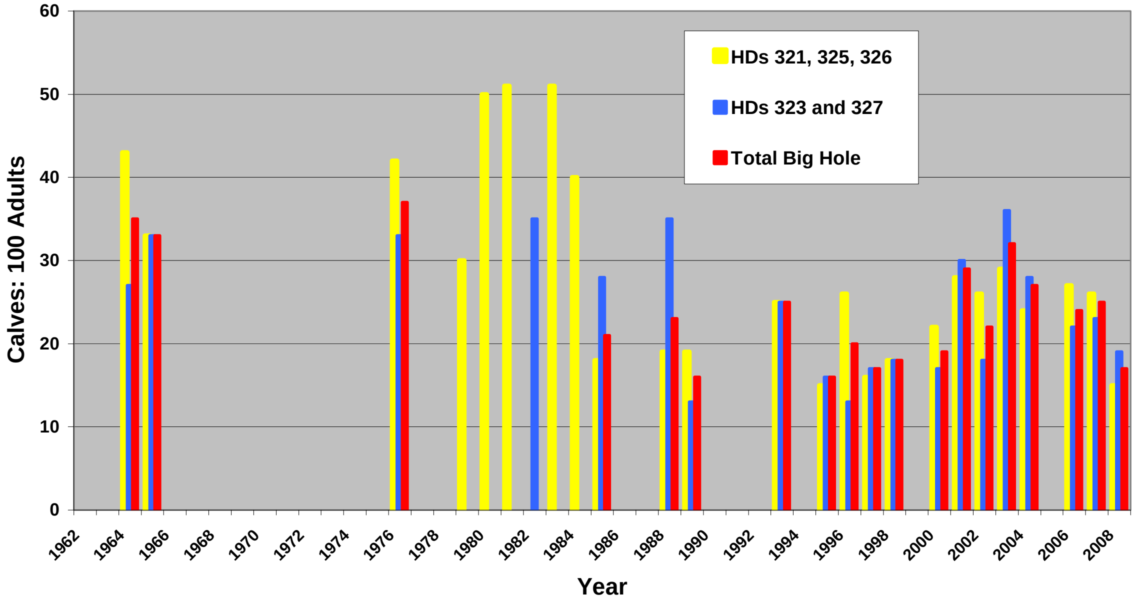


Figure 37. Recruitment of moose calves in Big Hole hunting districts, 1964-2008.

Data collection for moose in the Gallatin Canyon has been inconsistent. Records of all species observed while conducting radio-relocation and classification flights for elk were recorded during 1972-1977 and 2001-2007 in the Gallatin-Madison Ranges. Data from flights conducted during May through July (Table 13) indicated about half the moose and 6 times more grizzly bear observed during 2001-2007 compared to 1972-1977. Number of black bear observed was similar for the 2 periods. Wolves were not observed in the earlier period, but an average 0.43 wolves/flight was observed during 2001-2007.

Table 13. Numbers of moose, grizzly bear, and black bear observed during May-July aerial radio-relocation flights for elk in the Gallatin-Madison Ranges, 1972-77 and 2001-07.

| | Moose | | Grizzly Bear | | Black Bear | |
|---|---|---|---|---|---|---|
| | Number Moose (Flights) | Moose/Flight[a] | Number Grizzly.Bear (Flights) | Grizzly Bear/Flight[a] | Number Black Bear (Flights) | Black Bear/Flight[a] |
| 1972-1977 | 138(31) | 4.36 | 15 (31) | 0.47 | 37 (31) | 1.31 |
| 2001-2007 | 54 (23) | 1.96 | 68 (23) | 2.81 | 30 (23) | 1.23 |

[a] Averages for each month were weighted equally to determine average number per flight for the 2 periods.

Surveys conducted from the ground by vehicle in the Gallatin Canyon during December 1980 and 1981 recorded 61 and 81 moose, respectively. During December 2007, we observed 18 moose in the same area. The same number of moose (18) was recorded on a fixed-wing flight the same morning within area covered by the survey from the ground. The simultaneous ground and aerial surveys each missed and observed 2 moose the other survey did not. Thus, there were at least 20 moose within the area surveyed. Mid-summer classification flights for elk recorded an average of 28.7 moose per flight in 1980, 1983, and 1984. During mid-summer 1994 and 1995 an average 48 moose were observed and during 2001-2007, an average of 5 moose per flight was recorded.

Sporadic (1968, 1970, 1971, 1979-81, 1984, and 1994) early winter classifications of moose during the pre-wolf period indicated 18-28 calves:100 adults (60 calves/254 adults, average = 23.6 calves:100 adults). During 2003-04 through 2007-08, we observed 10 moose calves and 114 adult moose (8.8 calves:100 adults) during early winter.

This information in combination indicates that moose numbers and calf recruitment have declined in the Gallatin Canyon, but timing and degree of decline are unclear. Moose data from the Gallatin Canyon are inconsistently collected and of marginal quality. The data are insufficient to assign cause of declines, but are sufficient to indicate concern about moose population trend and any source of moose mortality.

Data collection for moose in Gravelly-Snowcrest hunting districts 331 and 332 has been too sporadic to present population trend information. The available data for trend in calf recruitment in HD 331 is concerning, however. Moose calves per 100 adults ranged from 19 – 50 and averaged 31 calves:100 adults during 1967 – 2004 (177 calves, 571 adults total). Classifications for most years were near the mean of 31:100. Classifications for 2005, 2006, and 2008 were 7.7, 13.4, and 10.9 calves:100 adults, respectively, averaging 11.7 moose calves:100 adults (18 calves, 154 adults total). Monitoring of moose in Gravelly-Snowcrest hunting districts should be intensified.

## MONTANA OUTSIDE THE GYA

As a focus of this project, we had originally intended to thoroughly examine the routine ungulate population data collected by MFWP outside the GYA to look for changes subsequent to wolf restoration and/or determine if the data is sufficient to detect changes in a timely manner. However, with the assignment of additional duties during the past year we could not do a credible job of achieving this goal. Therefore, we confine the section below to general and cautionary observations, data strengths, weaknesses, and opportunities for analyses and for change.

Consistently conducted aerial trend surveys have been best for monitoring ungulate populations in Montana (MFWP Mule Deer Adaptive Harvest Management, 2001: D. Pac, R. Mule, S. Stewart, editors, Elk Management Plan, Wildlife Division, 2005). However, in heavily timbered portions of the state, aerial surveys are difficult and results variable. Also, budgetary constraints, weather conditions, and pilot availability limit aerial surveys. Because of this, we look to other types of collected information to examine or index ungulate population trend in most areas.

As long as any hunter with a license can harvest an adult male, trend in harvest of males may be a general indicator of population level (Hamlin and Ross 2002, Dusek et al. 2006). This indicator may not be useful as an annual indicator, only as a general or long-term indicator, because weather conditions during the hunting season often overrides population level in influencing annual harvest (Hamlin and Ross 2002). Thus, in hindsight, we might be able to determine that an ungulate population likely started declining 3 years ago, but cannot be confident that it changed significantly from the previous year. Also, trends in male harvest are not comparable across periods of regulation change such as from any bull legal to brow-tined bull only legal, thus shortening the historical period of comparability. Lastly, changes in some HD boundaries during the period precluded their use in analysis.

Survival trends of young can be useful in predicting population trend (Hamlin and Mackie 1989, MFWP Mule Deer Adaptive Harvest Management 2001: D. Pac, R. Mule, S. Stewart, editors). Age ratios determined from spring classifications (young/adult), or with a one-year-delay, from check station age ratios (yearling/older) can indicate survival trends for young ungulates. Reduced survival of vulnerable young can result from many causes, including severe winter, drought, and increased predation. Increased predation, however, does not necessarily result in obviously declining young/adult ratios. As we described earlier, sex/age selection by wolves is variable by area and year and fawns/calves may not always selected at a differential rate great enough to produce substantive changes in young/female or young/adult ratios. Where cougars, an ambushing predator, are also present, little age selection may occur in the kill, especially for deer. Kunkel and Pletscher (1999) found that both wolves and cougars readily killed prime-aged deer in relatively good condition. Thus, use of ungulate age ratios alone as an indicator of a potentially declining population or of increased predation is problematic. At this time, in most areas we are limited to a cursory examination of adult male harvest and age ratios as indicators of population change and our conclusions are limited.

## Focus Areas

Most of southwest Montana and the GYA is encompassed by MFWP Administrative Region 3. For extensive analyses, we therefore focused on MFWP Administrative Regions 1, 2, 4, and 5 (Figure 38). For smaller scale summaries, we make use of data collected during routine monitoring surveys by MFWP wildlife biologists and managers in deer and elk hunting districts 101, 109, 110, 121, 123, 124, 201, 202, 204, 240, 250, 261, and 270, as well as more general data from all of western Montana (Figure 38).

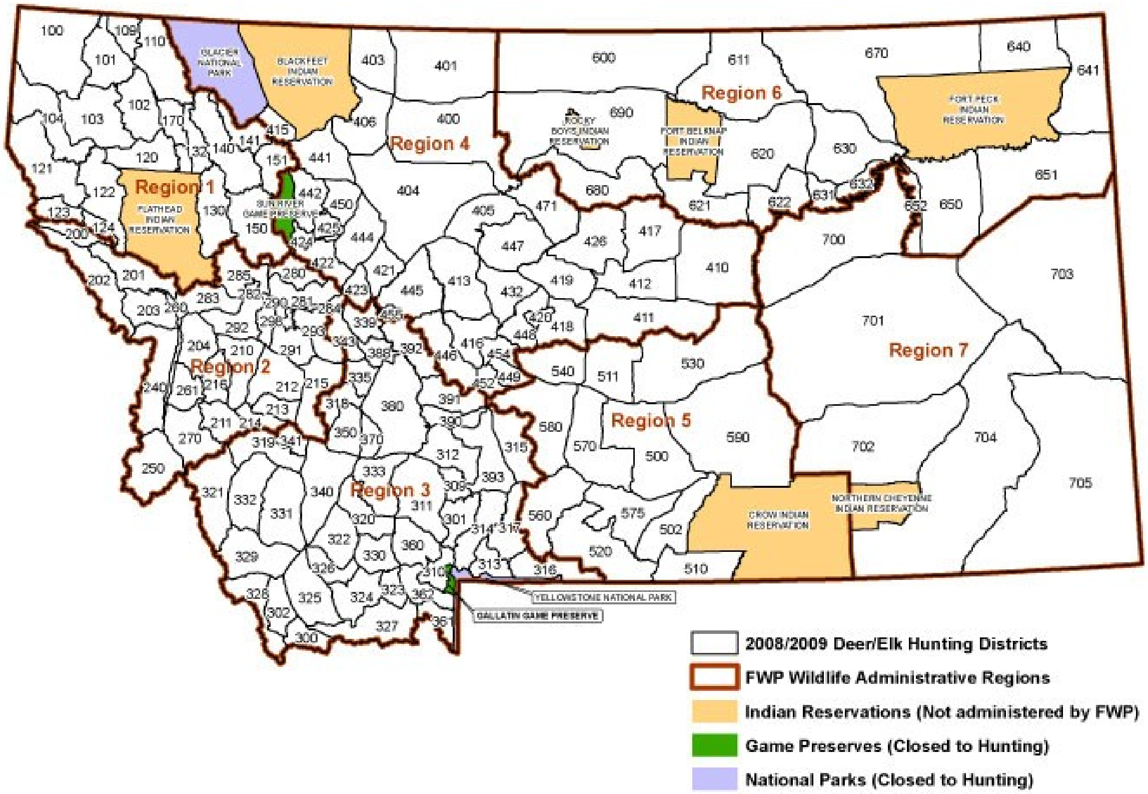


Figure 38. MFWP Administrative Regions and Deer/ Elk Hunting Districts.

## MFWP Administrative Region 1

Region 1 is heavily timbered and aerial surveys are difficult. Some aerial trend surveys are conducted for elk, but none for white-tailed deer, the species most likely to be impacted by wolf predation in MFWP Region 1 (Kunkel and Pletscher 1999). Most aerial trend surveys for elk are small trend areas of recent origin where substantial variation in counts occurs. Also, budgetary or other factors result in less than consistent annual surveys. The exception is for HDs 121, 123, and 124, where consistent long-term annual aerial counts of elk occur (Fig. 39). Few wolves have established within these HDs to this time and the elk count trends there serve as a "control area" for the Region. There are no adequate aerial trend count data for elk in areas with established wolf packs in Region 1 to compare with that for HDs 121, 123, and 124. Elk trend counts in HD 121, especially, have increased from a low in 1997 to the present, perhaps stabilizing since 2003 (Fig. 39).

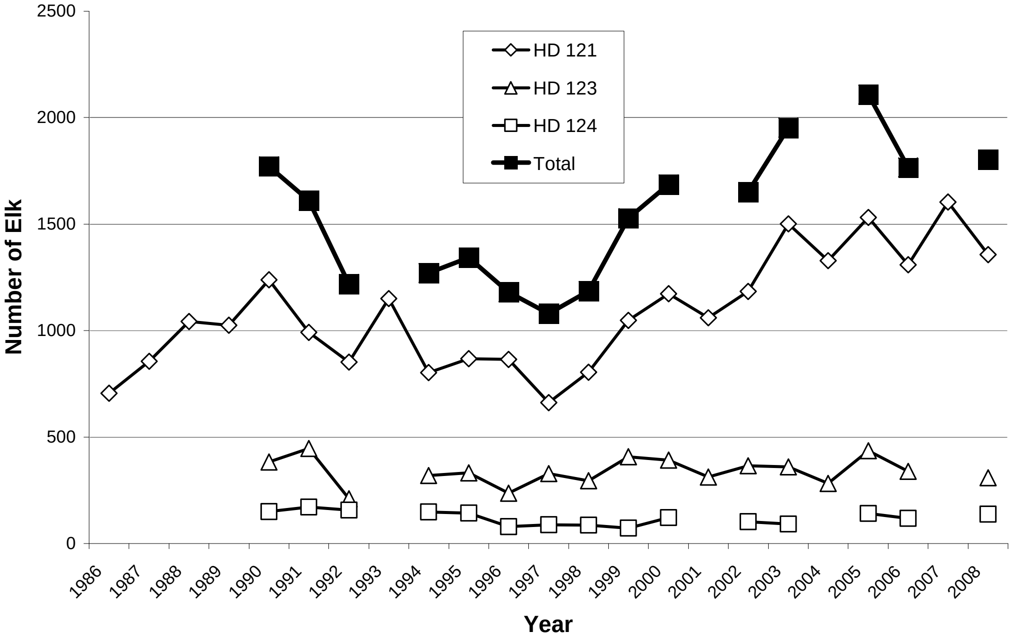


Figure 39. Aerial trend counts for elk in hunting districts 121, 123, and 124, 1986-2008.

One moose hunting district (HD 105) in Region 1 has a history of adequate aerial surveys to draw inferences about long-term trends. Few wolves have established within this HD thus far. Survey conditions are variable enough that even within this consistently flown area, annual changes are suspect (Fig. 40) and only long-term trends are adequate for interpretation. Thus, it is likely that the decline in moose counted from 114 in 2001 to 46 in 2002 resulted from poor counting conditions in 2002 rather than representing a real decline in the population (Fig. 40). There is no evidence that this moose population is either declining or increasing. Unfortunately, a least 2-3 years trend is likely necessary to detect "real" changes in this moose population. There are no adequate aerial surveys for moose in Region 1 within areas of relatively high wolf numbers to draw inferences about long-term trends.

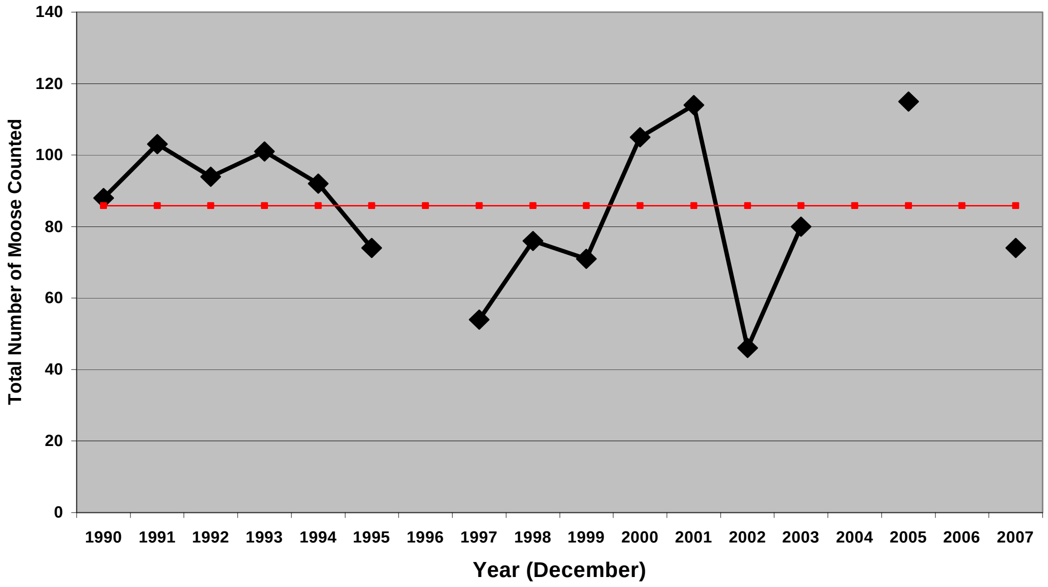


Figure 40. Helicopter counts of moose in HD 105, December 1990-2007. Red line equals mean for all counts.

With little aerial trend count information for any species, and none for white-tailed deer, the species of most concern, we look to hunter harvest of males to examine or index ungulate population trend in MFWP Region 1.

White-tailed deer buck harvest (and presumably the total population) increased in Region 1 from a low after the winter of 1996-97 until 2006 (Fig. 41). The recent highs reached were slightly under previous highs, but occurred within a period of increasing wolf numbers. Declines in buck harvest that occurred starting in 1994 and 2006 also coincided with increasing antlerless harvests (Fig. 41) and it is likely that increased antlerless harvest contributed to population declines (as intended). However, antlerless/antlered ratios of the harvest averaged 0.53 during 1986-1994 and 0.35 during 1998-2006 and thus the buck harvest (and possibly population) did not reach previous levels despite relatively lower antlerless harvest during the latter period. Factors other than antlerless harvest level are likely also involved the reduced population recovery after 1997.

Hunting district 110, encompassing the North Fork of the Flathead River, has had wolves present since 1979, and breeding pairs since 1985-86. There, Kunkel et al. (1999) found that white-tailed deer were the primary prey of both wolves (83%) and cougars (87%). White-tailed deer buck harvest (and likely population level) began declining in 1989 in HD 110 compared to 1994 for the rest of Region 1 (Fig. 42). A more recent decline also began earlier in HD 110, starting in 2004-05 compared to 2006-07 for the rest of the Region. White-tailed deer buck harvest declined about the same amount (60%) in both areas, but the declining phase occurred over 11 years in HD 110 compared to 3 years for the rest of Region 1 (Fig. 42). Recovery to pre-decline level occurred after 15 years in HD 110, but harvest for the rest of the Region did not quite recover to 1991-94 levels.

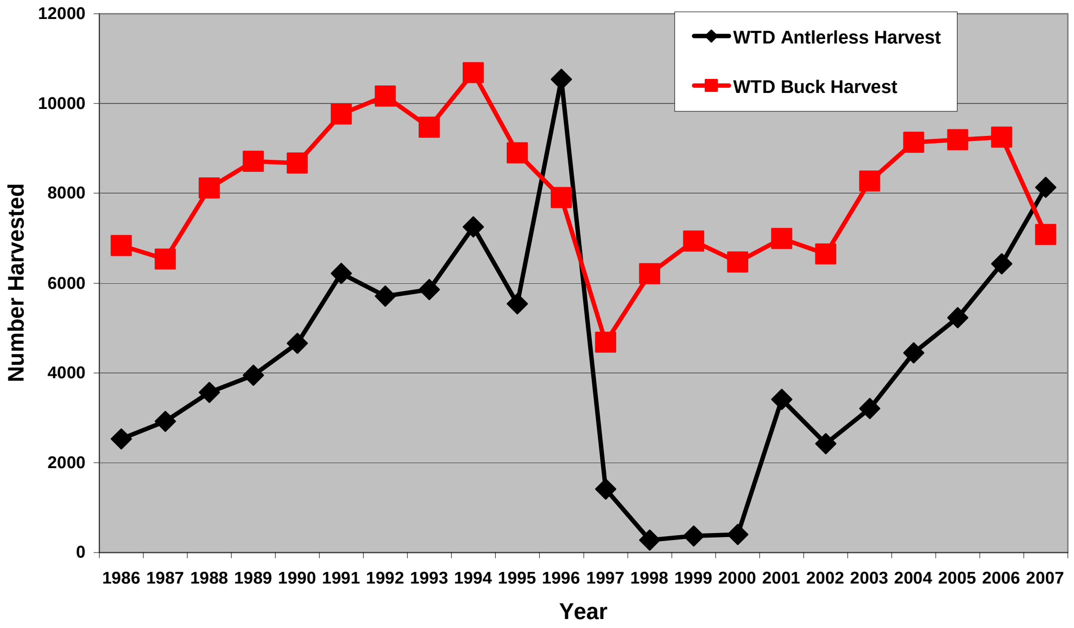


Figure 41. White-tailed deer antlerless and buck harvest for MFWP Region 1, 1986-2007.

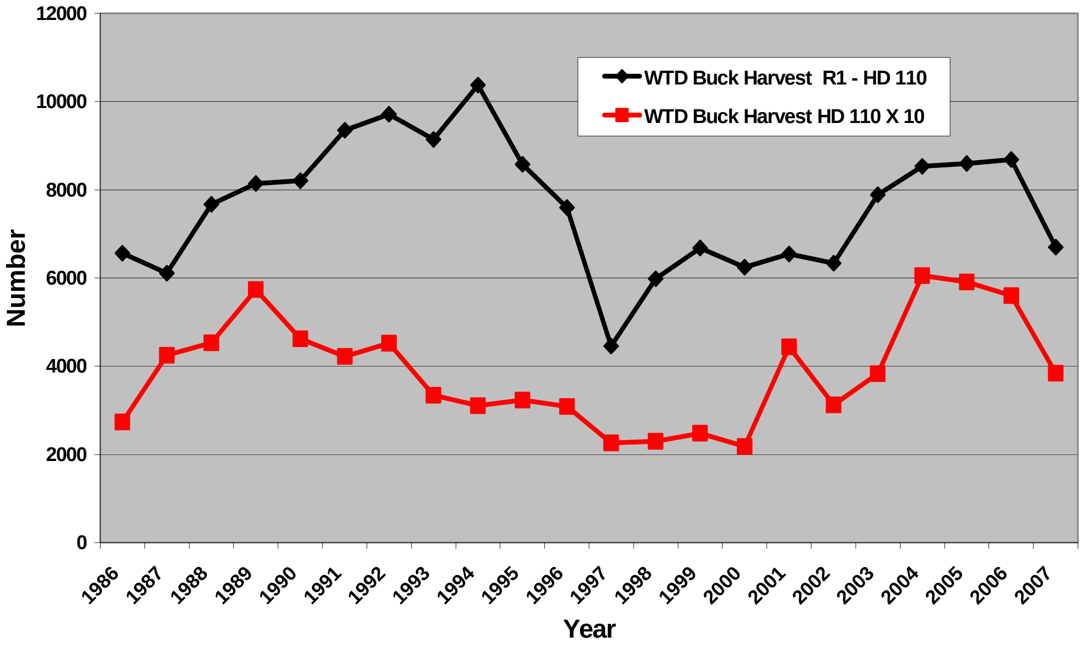


Figure 42. Trend in WTD buck harvest compared between Region 1 as a whole (without HD 110) and HD 110 (harvest displayed as times 10 for scale), 1986-2007.

During the mid-1990s, Kunkel et al. (1999) estimated that about 10 wolves, 70 cougars, 64 grizzly bears, and 200 black bears per 1,000 km$^2$ occurred in the North Fork basin, which included much of HD 110. This high complement of large predators likely contributes to observed white-tailed deer, elk and moose dynamics (Kunkel 1997, Kunkel and Pletscher 1999). Similarly, combined prey population levels relative to wolf numbers were very high (Kunkel and Pletscher 1999). If white-tailed deer buck harvest level represents overall WTD population trend, it appears that cycles of predator and prey abundance may develop in environments such as occurs in HD 110. In HD 110, white-tailed deer numbers declined for 15 years after addition of wolves to the predator mix, but then apparently recovered to previous highs (Fig. 42). Cause and effect are very difficult to establish in these complex ecological environments, but it appears that in HD 110, total predation impacts may have reduced average white-tailed deer “standing crop”. However, predator numbers also fluctuated, and predation did not “hold” prey numbers permanently at lower levels.

Dusek et al. (2006) reported that combined predation of cougars and wolves probably had some impact on observed white-tailed deer population dynamics in HD 101/109. Cougars were more important than wolves in documented mortality at that time. Harvest trends suggest that the white-tailed deer population may have declined by at least 25% from 1992, before effects of the severe winter of 1996-97 (Fig. 43). Because antlerless harvest was relatively low during 1992-1995, any effects of predation likely occurred during this period. From 1997, white-tailed deer buck harvest level recovered to previous highs by 2006. Antlerless harvest in 2006 and 2007 was at levels that could impact future population trend (Fig. 43). Similar to HD 110, combined predation of WTD by multiple predators within HDs 101/109 may, in combination with other factors, initiate and/or lengthen population declines, but did not maintain the population at permanently lower levels than historically observed.

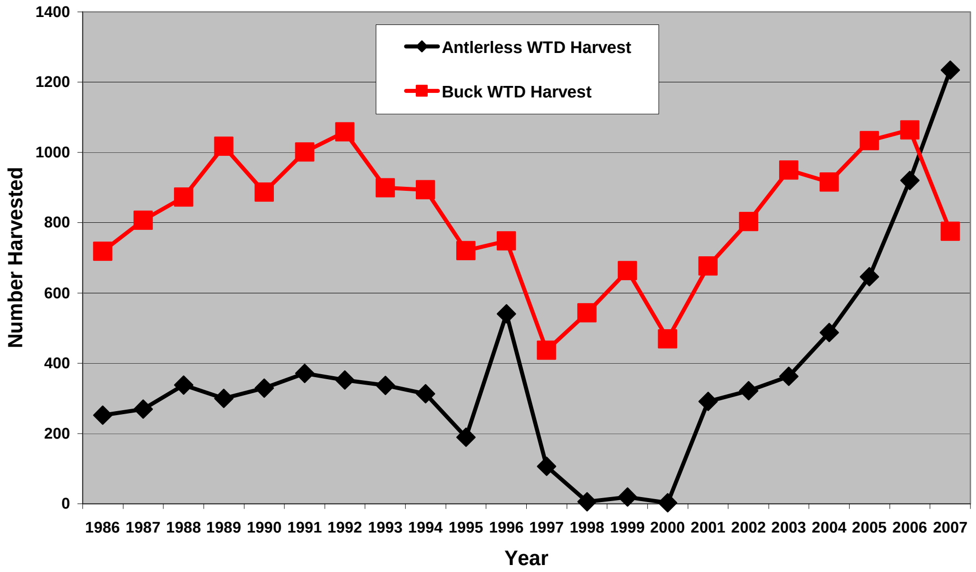


Figure 43. White-tailed deer buck and antlerless harvests in HDs 101/109, 1986-2007.

## MFWP Administrative Region 2

For the northern portions of MFWP Region 2, white-tailed deer are likely the primary prey of wolves, but elk will be significant prey also. For the southern portions of Region 2, the relative portions of wolf prey are likely reversed. Throughout Region 2, cougars coyotes, and for newborns, black bear are additional important predators of ungulates. Grizzly bear are included in the mix of predators in the northeast portion of Region 2. Wolves have been present in the Nine Mile area (HD 201) since about 1990 and wolves began to appear just west of there in HD 202 shortly after.

Similar to Region 1, there are no aerial surveys of white-tailed deer in areas where wolves currently have a substantial presence. There are aerial surveys for elk throughout much of Region 2, however. White-tailed deer buck harvest was relatively stable in Region 2 as a whole from 1988 – 2006(Fig. 44). High antlerless harvests and the severe winter of 1996-97 likely contributed to a decline in harvest in 1997 and high antlerless harvests may have contributed to a decline in harvest in 2007 (Fig. 44). Most individual hunting districts had stable or increasing white-tailed deer buck harvests after 1997 (Fig. 45), but there were exceptions such as HDs 201 and 202 (Figs. 46 and 47). In these 2 HDs, white-tailed deer buck harvest began declining about the time wolf packs established (1990-91) and have never recovered to previous highs. However, during portions of the early decline and during the current further decline, antlerless harvest also has been high. Cause and effect cannot be established with this type of data/analyses, however we have not seen this degree of long-term decline in WTD buck harvest in other Region 2 hunting districts.

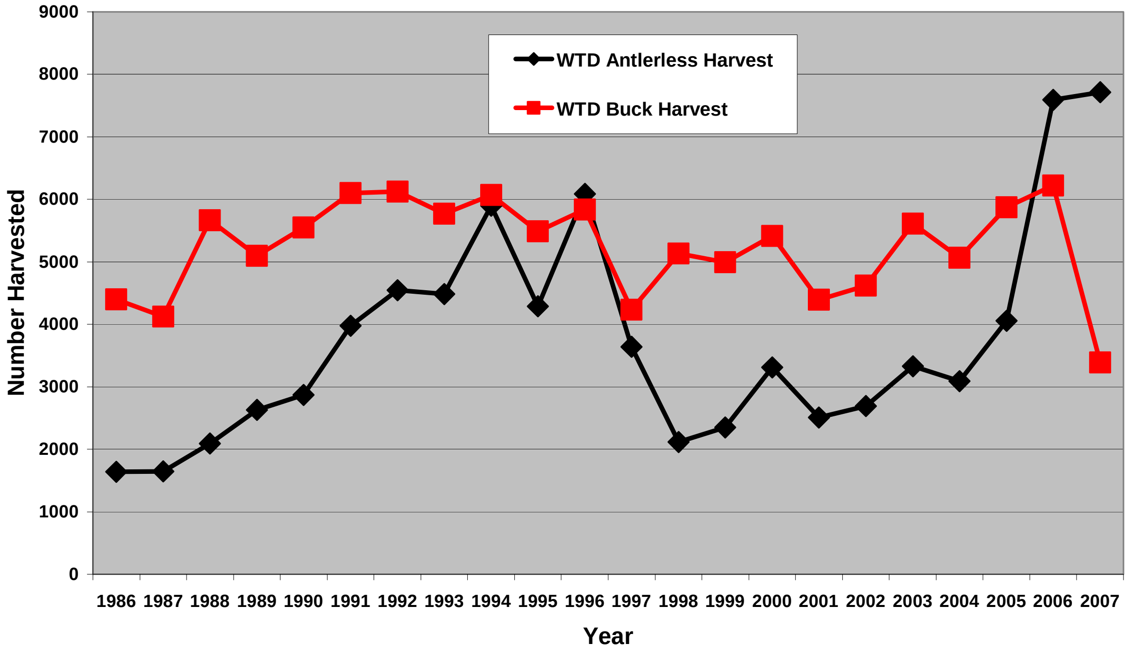


Figure 44. White-tailed deer harvest in Region 2, 1986-2007.

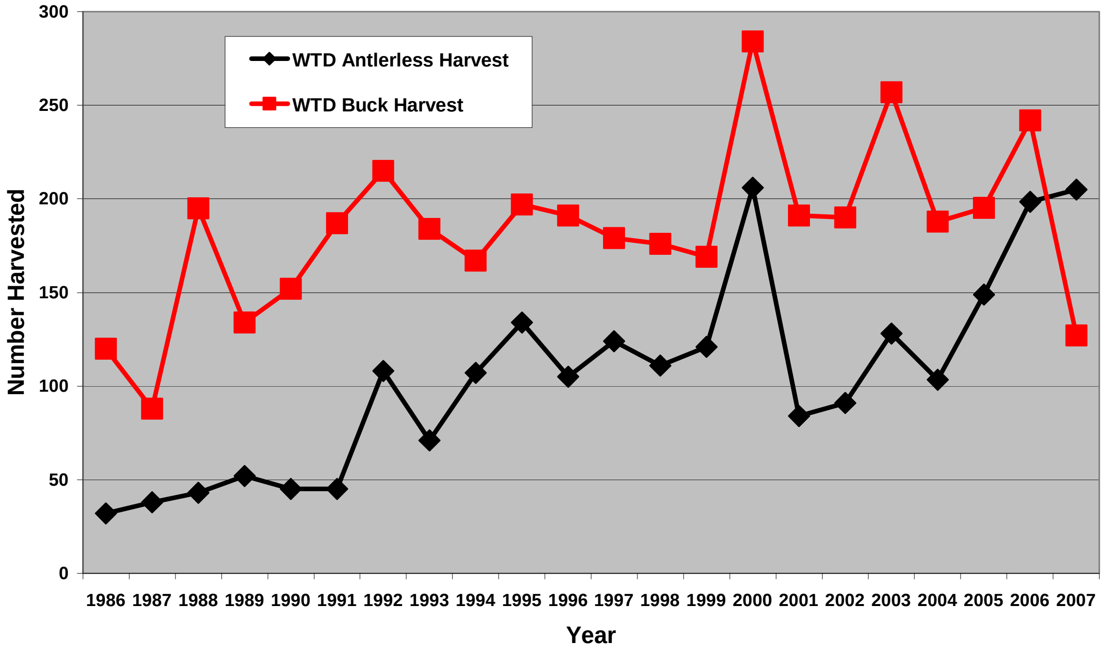


Figure 45. White-tailed deer harvest in HD 270, 1986-2007.

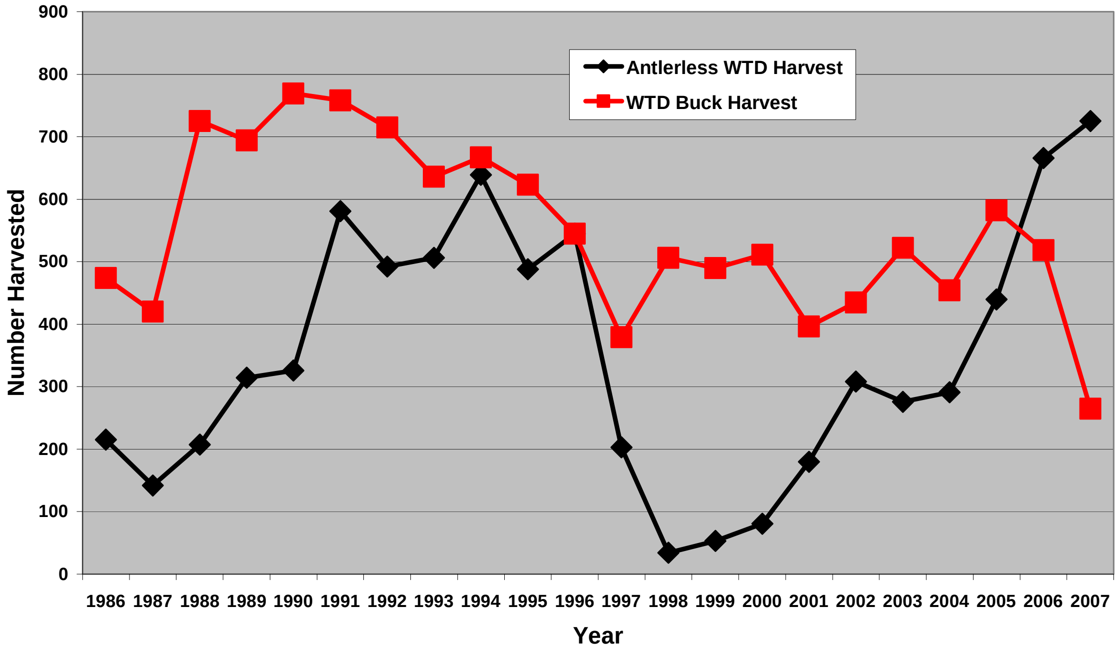


Figure 46. White-tailed deer harvest in HD 201, 1986-2007.

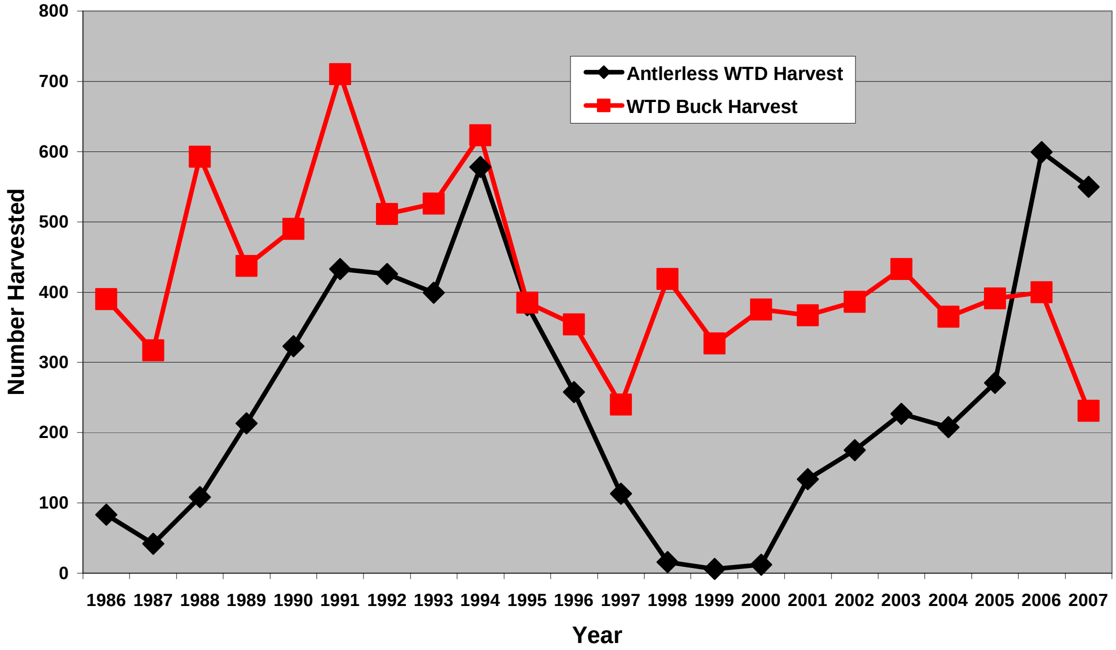


Figure 47. White-tailed deer harvest in HD 202, 1986-2007.

Use of bull elk harvest trends as an index of population trends is more difficult because regulations changed from antlered bull to brow-tined bull during the period examined and also at different times (1991 and 1996) in different hunting districts.

Bull elk harvest declined in HD 201 through 1996 (antlered bull regulation) during the post-wolf period, but antlerless harvests were high also (Fig. 48). After winter 1996-97 and implementation of brow-tined bull regulations (1996), bull harvest increased through 2006, but did not reach previous highs. Aerial counts followed similar trends as harvest during 1986-1996. However, subsequent to 1997 aerial trend counts indicated that the elk population recovered to higher levels than previously observed (Fig. 49). Thus, the recent lower levels in bull elk harvest in HD 201 appears unrelated to actual population level and no numerical effect of wolves on elk numbers in HD 201 is apparent.

A similar pattern occurred in HD 202 except that there, recent aerial counts have declined along with bull harvest (Figs. 50 and 51). The North Fish Creek segment is a small portion of HD 202, but elk numbers have declined the most there. Whether this is the result of an actual decline in elk numbers or a shift in distribution related to wolf presence is unknown (B. Henderson, pers. comm.). Number of elk counted has also declined in other portions of HD 202 such that numbers counted currently are about half previous highs.

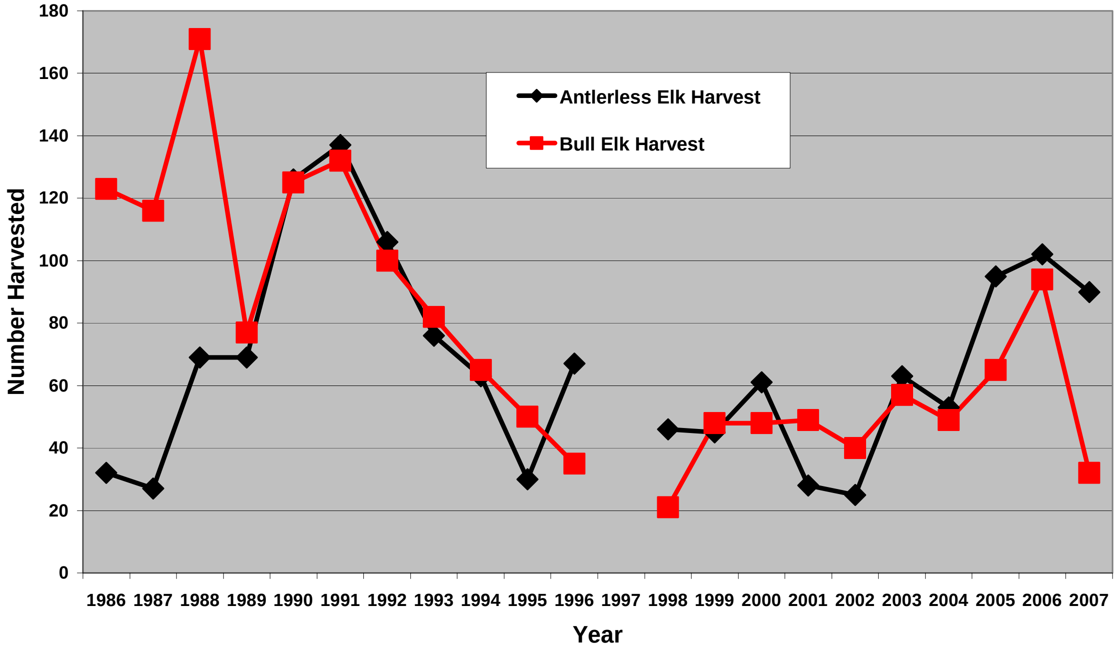


Figure 48. Elk harvest in HD 201, 1986-2007.

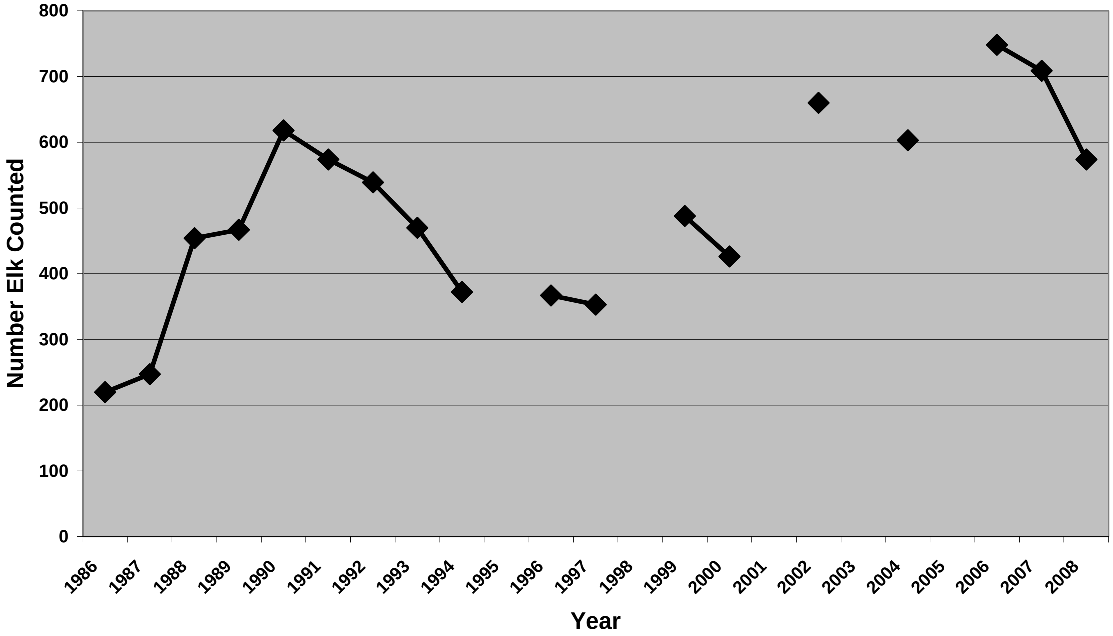


Figure 49. Aerial counts of elk in HD 201, 1986-2008.

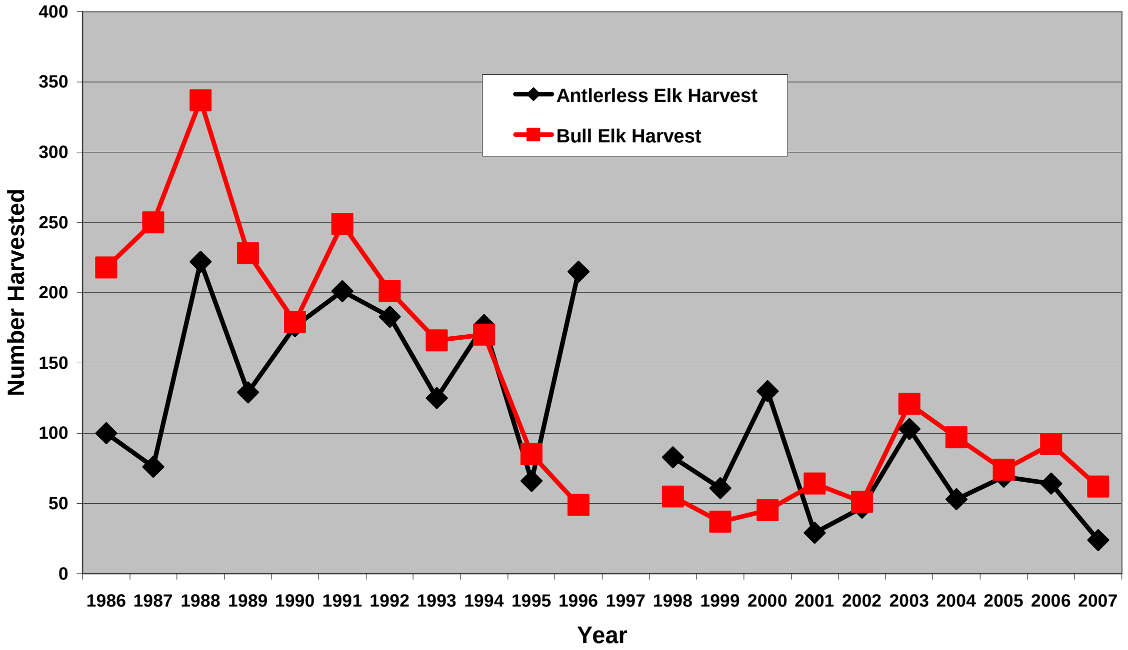


Figure 50. Elk harvest in HD 202, 1986-2007.

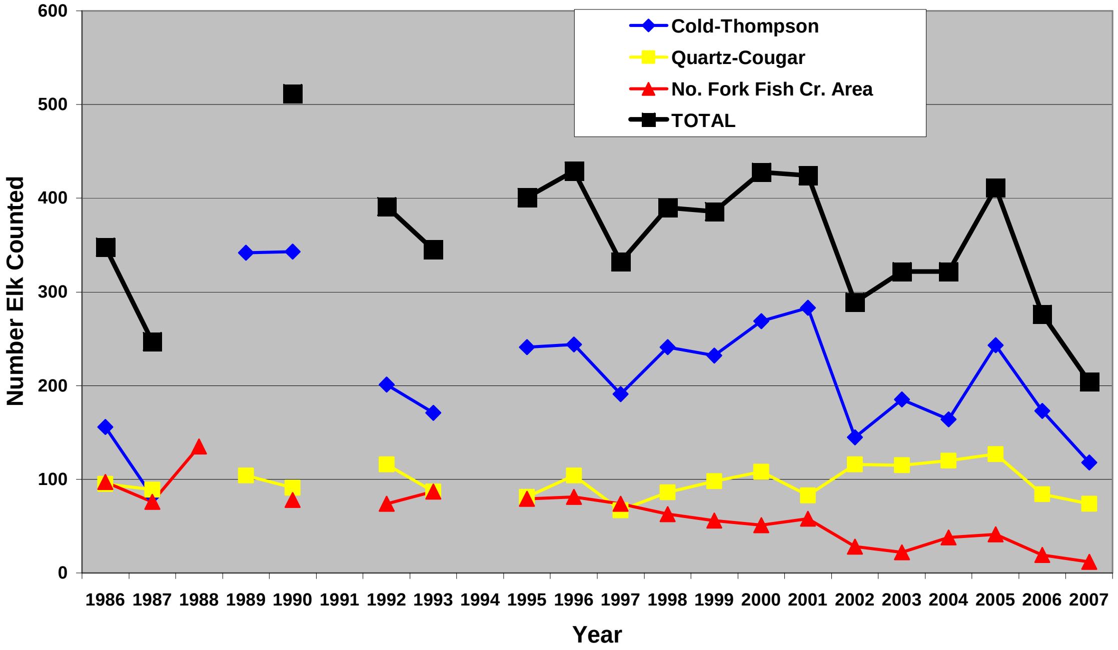


Figure 51. Aerial counts of elk in portions of HD 202, 1986-2007.

One of the best series of long-term elk counts anywhere occurs for populations in the Bitterroot Valley (Fig. 52). After a long, steady increase in elk numbers since the mid-1960s, numbers counted have declined since 2003-05. Recent antlerless harvests have been high in an attempt to reduce numbers and there is no evidence that wolves or combined predator numbers have much to do with the decline in elk counted through 2008. The decline thus far is likely primarily due to increased antlerless harvests achieving a planned management reduction.

The Bitterroot area, however, is one in which wolf numbers have increased at a high rate recently. Increasing wolf numbers and possibly increasing cougar numbers along with the type of elk wintering habitat (Bergman et al. 2006, Hamlin et al. 2008) in hunting districts along the Idaho border suggest that white-tailed deer and elk populations should be monitored closely for declines beyond those intended in these areas (HDs 202, 240, 250).

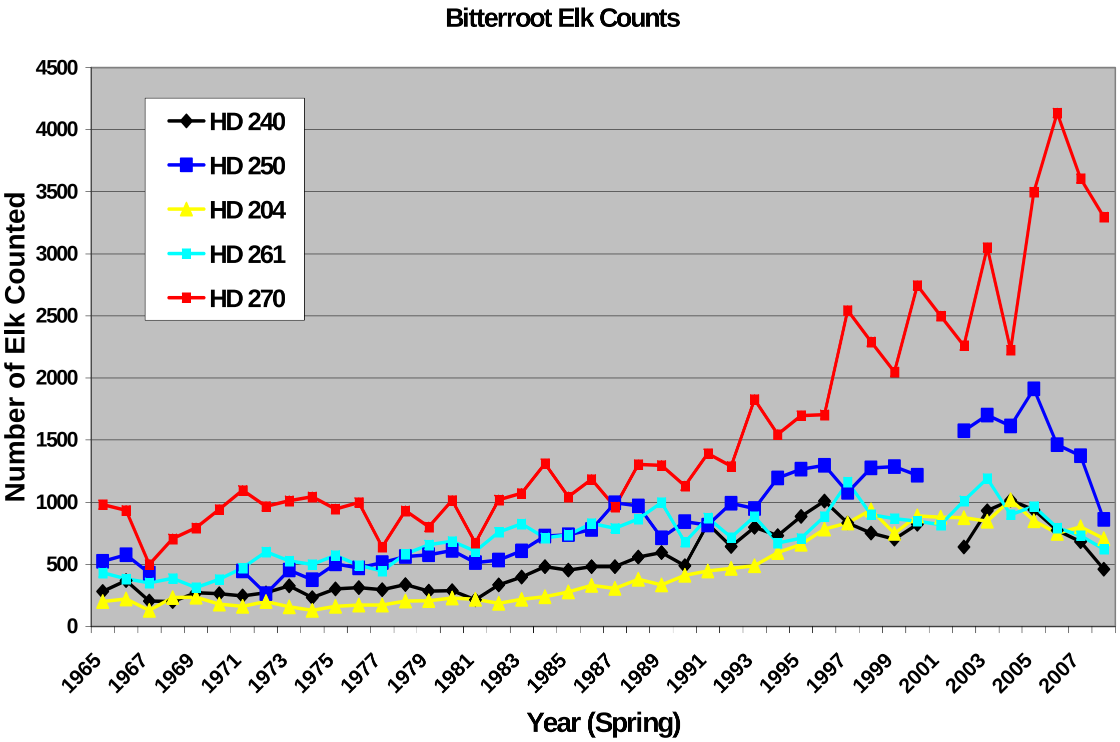


Figure 52. Aerial counts of elk in Bitterroot hunting districts, 204, 240, 250, 261, and 270, 1965-2008.

## MFWP Administrative Regions 4 and 5

There is little wolf presence in most of MFWP Regions 4 and 5 at this time. Areas in Region 5 with wolves were covered under the GYA/southwestern Montana section of this report. Wolf presence in Region 4 at this time is primarily along the Rocky Mountain Front and associated summer range. Adequate aerial elk counts occur in this area to monitor population changes. Wolf numbers relative to elk numbers are low enough at this time that we expect little impact to have occurred. Little Belt Mountain hunting districts will serve as good “pre-wolf control areas”, due to consistent surveys in these areas, for comparisons in the future.

## Larger-Scale Patterns

### Wolf Distribution, Depredations, and Implications to Ungulates

Hamlin et al. (2008) concluded that in areas where wolf depredations consistently occurred, wolves were controlled and did not reach numbers/ predator:prey ratios where population impacts on ungulates were detected. Wolves commit depredations on livestock and dogs throughout most of their distribution in Montana (Fig. 53). Information presented in Figure 53 covers the period 1999-2007, includes 373 wolf pack locations (as of 31 December each year) and does not include 20 packs totally removed prior to the end of a year. Some locations are nearly the same for each year and do not show in the scale of Figure 53. Number of packs and depredations increased in 2008 (Fig. 54), but are not displayed in Figure 52 because GPS locations were not available at the time of this report. Only in far northwest Montana (deer/elk HD 100), Glacier Park/Bob Marshall Wilderness area, areas of the Bitterroot (up to 2007 - changing) and along the Idaho border, and Yellowstone National Park interior have depredations been lacking or minimal (Fig. 53). These areas without depredations are where wolf numbers and predator: prey ratios have the greatest likelihood of increasing to levels where ungulate populations might be measurably impacted, if the pattern of higher wolf survival in areas without livestock depredations holds.

The clusters of red dots (Fig. 53) indicate that depredation-related wolf control actions have not and are unlikely to prevent certain areas from sustaining recurring depredations by wolves (known 2008 depredation locations continue the “red cluster pattern”). If these areas continue to be unsuitable for wolf survival due to recurring livestock depredations, ungulate populations in these areas might reflect the relatively low wolf:elk ratios over time. Depredations, staff time, and expense of wolf control will likely continue in these unsuitable areas, but wolves are unlikely to significantly impact ungulate populations over the long-term in these “red cluster areas”.

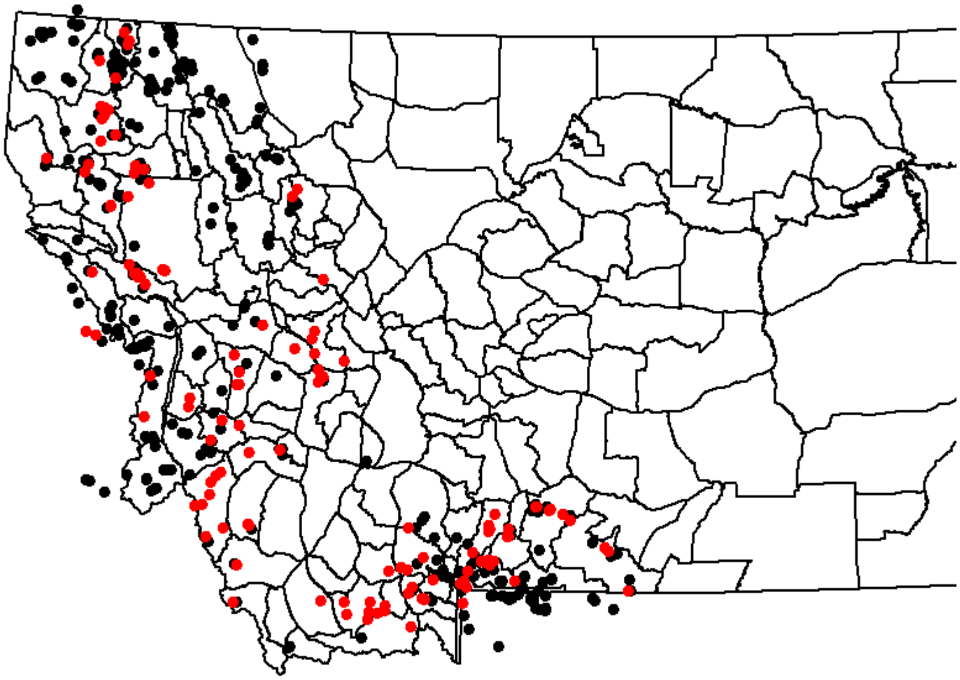


Figure 53. Wolf pack locations relative to Montana deer/elk hunting districts, 1999-2007. Red dots = packs that depredated on livestock/dogs (including non-fatal).

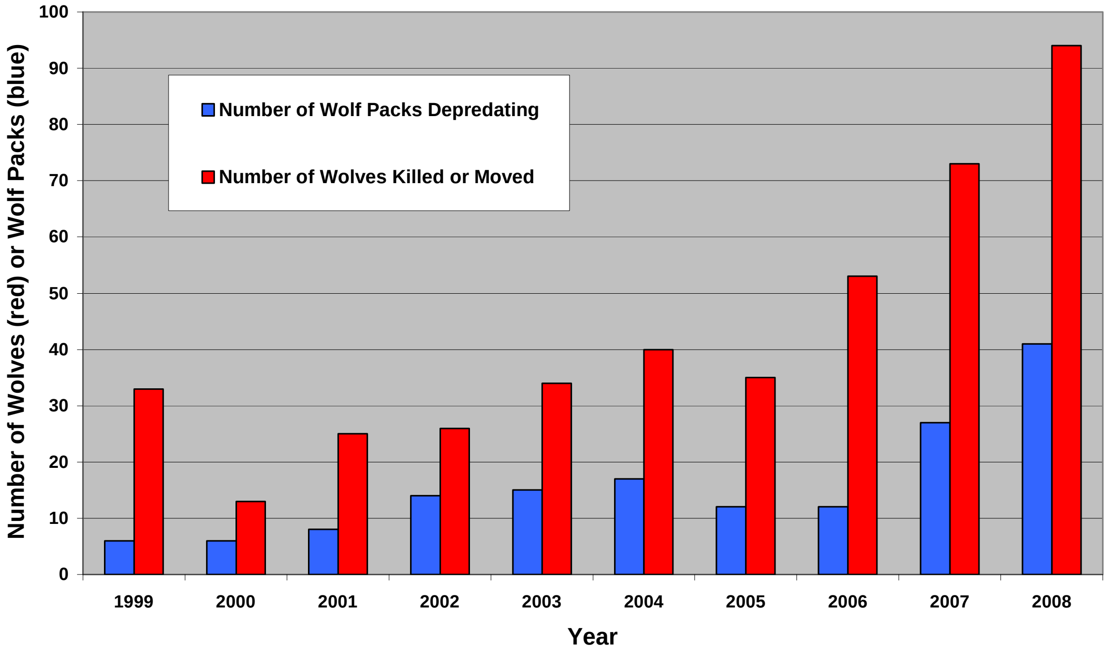


Figure 54. Number of Montana wolf packs depredating (including non-fatal) and number of wolves moved or killed because of depredations, 1999-2008. Data for 2008 from Wolf Weeklies through 19 December 2008 (final 2008 numbers may vary).

Additional Potential Indirect Effect of Wolves on Ungulates

To this time, with wolves remaining protected under the Federal Endangered Species Act, the USFWS provides federal money to operate Montana’s Wolf Management Program. This agreement is effective through June 2010, or until the wolf population in Montana is removed from the federal list of threatened or endangered species. Should wolves be delisted, it is distinctly possible that federal monetary contributions for wolf management in Montana will cease. This sum, currently over $500,000 dollars annually including some, but not all, costs of control, will represent a large additional cost to MFWP and Montana hunters unless new sources of funding are found. Wolf Program annual expenditures are currently about two-thirds of the current annual expenditures (Fig. 55) for operations (non-personnel/salary) of Montana’s Big Game Survey and Inventory budget (money spent for flying aerial surveys of deer, elk, antelope, moose, bighorn sheep, and mountain goats, conducting hunter check stations, conducting classifications from the ground, processing biological samples in the laboratory, etc.).

Expenditures for Big Game Survey and Inventory declined by 15% from FY 2006 through 2008 while expenditures for the Wolf Management Program increased by 8% during the same period. If Montana’s Survey and Inventory Program is expected to provide funding for the Wolf Management Program upon delisting, monitoring of Montana’s ungulate populations will decline substantially from the minimal baseline that now exists.

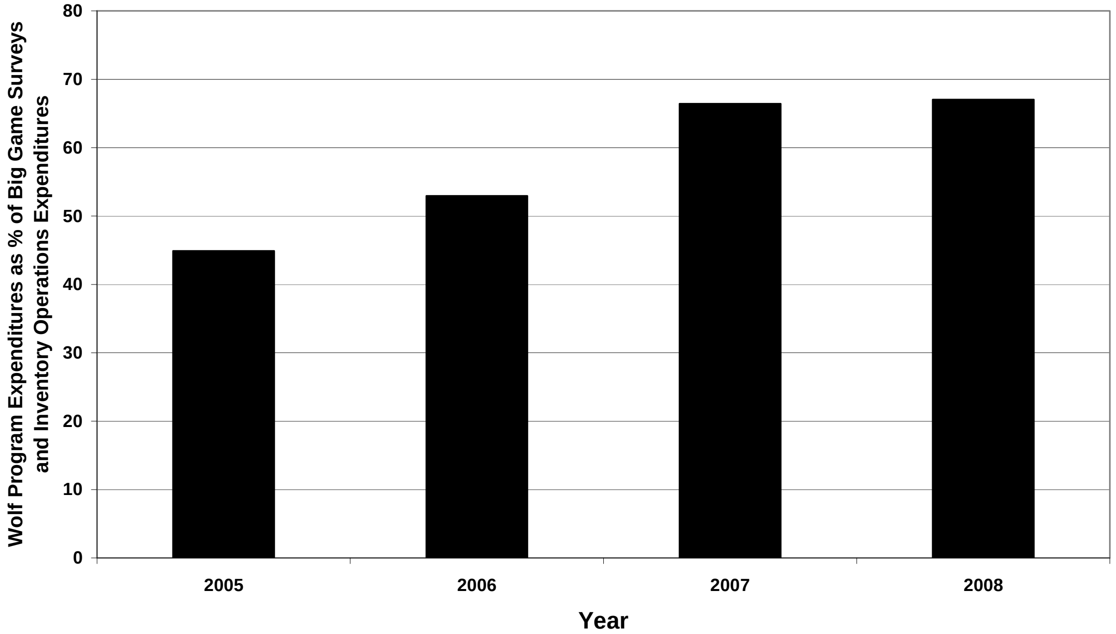


Figure 55. Expenditures of Montana’s Wolf Management Program (including partial control costs) as a percentage of operations expenditures for Montana’s Big Game Survey and Inventory Program.

# CONCLUSION

Even where intensive data has been collected, there has been scientific and public debate concerning the impacts of wolf restoration on ungulate populations. Disagreement generally does not occur about the fact of declines in numbers of some ungulate populations, but disagreement about cause(s) or proportional shares of cause continues to exist. Data collected during intensive research for this project indicate that predation can affect elk population dynamics. This seems to occur when high ratios of predators to elk are reached, which has occurred most often in areas where both grizzly bears and wolves have increased rapidly in recent years in southwest Montana and the GYA. This has not occurred in all areas in southwest Montana and the GYA, and some elk populations are stable or increasing in the presence of predators. Data collected during intensive efforts in this research project also indicate that wolves affect elk distribution and behavior on small scales within seasonal ranges, but at larger scales wolves appear to have some effects in some areas and evidence remains equivocal about the strength and types of effects.

Given this history from intensive research projects and monitoring programs in high-profile areas, are Montana's routine ungulate management monitoring surveys "good enough"? Where they exist, most long-term aerial trend counts are adequate to document changes. However, substantial changes in counts (>40%) for several years (along with coincident declines in hunter harvest of males) may be necessary to convince some of the reality of any declines. For white-tailed deer, the species most likely to be impacted in Region 1 and much of Region 2, only the index of hunter harvest of bucks is available for population trend. This should also be combined with an index of yearling/adult in harvest data to document whether recruitment is declining simultaneously. These indexes will be less sensitive than direct counts and certainty of declines will take longer.

Nowhere are data adequate to "scientifically" assign cause(s) for any declines that may occur. This is true because assignment of cause remains controversial even where substantially more data than routine MFWP aerial surveys are collected. "Control areas and circumstantial evidence" will be the primary justifications for proposed management actions relative to predators. Lest some construe this as a criticism, it is not. Montana has more widespread counts of ungulates on an annual basis across a larger area than any other state and cannot do more with existing budgets and personnel. Realistic expectations and openness to monitored experimentation will be key to adaptive management of Montana's ungulates, bears, cougars, and wolves.

Appendix Table 1. Estimated number and percentage of pre-season (15 Oct.) Northern Yellowstone elk population harvested by hunters and killed by wolves, 1985-1994 and 1997-2008. Male column includes 0.40 of calves and female column includes 0.60 of calves ages > 5 months. Does not include newborn calves, birth - 15 October.

| Year | Est. No. Elk Pre-season[a] | ♂♂- Hunter Harvest[b,d] | ♂♂- Wolf-kill[c,d] | ♀♀ - Hunter Harvest [b,d] | ♀♀ - Wolf-kill[c,d] | Total Hunter Harvest[d] | Total Wolf-kill[d] | Total HK+WK[d] |
|---|---|---|---|---|---|---|---|---|
| 1985-86 | 22,662 | 581 (8.9) | - | 991 (6.1) | - | 1,572 (6.9) | - | 1,572 (6.9) |
| 1986-87 | 20,398 | 625 (12.3) | - | 771(5.0) | - | 1,396 (6.8) | - | 1,396 (6.8) |
| 1987-88 | 21,852 | 256 (4.7) | - | 249 (1.5) | - | 505 (2.3) | - | 505 (2.3) |
| 1988-89 | 21,299 | 637 (11.2) | - | 2,395 (15.4) | - | 3,032 (14.2) | - | 3,032 (14.2) |
| 1989-90 | 18,241 | 369 (8.5) | - | 441 (3.2) | - | 810 (4.4) | - | 810 (4.4) |
| 1990-91 | 18,336 | 378 (9.6) | - | 704 (4.9) | - | 1,082 (5.9) | - | 1,082 (5.9) |
| 1991-92 | 21,625 | 2,653 (36.4) | - | 1,666 (11.6) | - | 4,319 (20.0) | - | 4,319 (20.0) |
| 1992-93 | 23,587 | 550 (8.0) | - | 1,447 (8.7) | - | 1,997 (8.5) | - | 1,997 (8.5) |
| 1993-94 | 25,432 | 241 (2.7) | - | 305 (1.8) | - | 546 (2.1) | - | 546 (2.1) |
| **Pre-wolf Mean** | **21,492** | **699 (11.4)** | | **997 (6.5)** | | **1,695 (7.9)** | | **1,695 (7.9)** |
| | | | | | | | | |
| 1997-98 | 15,574 | 406 (6.5) | 201 (3.2) | 1,248 (13.4) | 278 (3.0) | 1,654 (10.6) | 479 (3.1) | 2,133 (13.7) |
| 1998-99 | 15,676 | 432 (7.8) | 262 (4.7) | 1,621 (16.0) | 365 (3.6) | 2,053 (13.1) | 627 (4.0) | 2,680 (17.1) |
| 1999-00 | 19,103 | 272 (3.8) | 275 (3.8) | 890 (7.5) | 383 (3.2) | 1,162 (6.1) | 658 (3.4) | 1,820 (9.5) |
| 2000-01 | 17,782 | 425 (5.8) | 305 (4.1) | 1,176 (10.8) | 428 (3.9) | 1,601 (9.0) | 733 (4.1) | 2,334 (13.1) |
| 2001-02 | 15,793 | 294 (5.9) | 327 (6.6) | 1,058 (9.8) | 458 (4.2) | 1,352 (8.6) | 785 (5.0) | 2,137 (13.5) |
| 2002-03 | 12,306 | 306 (11.8) | 368 (14.1) | 750 (7.7) | 518 (5.3) | 1,056 (8.6) | 886 (7.2) | 1,942 (15.8) |
| 2003-04 | 11,160 | 237 (9.6) | 449 (18.1) | 671 (7.7) | 630 (7.3) | 908 (8.1) | 1, 079 (9.7) | 1,987 (17.8) |
| 2004-05 | 12,586 | 193 (7.9) | 566 (23.2) | 455 (4.5) | 381 (3.8) | 648 (5.1) | 947 (7.5) | 1,595 (12.7) |
| 2005-06 | 12,998 | 393 (13.5) | 355 (12.2) | 234 (2.3) | 399 (4.0) | 627 (4.8) | 754 (5.8) | 1,381 (10.6) |
| 2006-07 | 9,439 | 491 (22.3) | 614 (27.9) | 162 (2.2) | 504 (7.0) | 653 (6.9) | 1,118 (11.8) | 1,771 (18.8) |
| 2007-08 | 8,783 | 226 (13.2) | 730 (42.7) | 117 (1.7) | 626 (8.9) | 343 (3.9) | 1,356 (15.4) | 1,699 (19.3) |
| **Post-wolf Mean** | **12,473** | **334 (9.8)** | **405 (25.8)** | **762 (7.6)** | **452 (4.9)** | **1,096 (8.8)** | **857 (6.9)** | **1,953 (15.7)** |

[a] Estimated based on population reconstruction, sightability, and harvests. Data from Singer et al. (1997) used and also applied to counts from 1997-2008. When counts were not made, estimates extrapolated from existing data. Population estimate = 1.322x count for good conditions and 1.863x count for poor conditions.

[b] Hunter harvest estimates from Statewide harvest questionnaire, check station and also includes estimates for crippling loss- data from Hamlin and Ross (2002) reduced by half because of more open terrain & controlled hunt. Total harvest including crippling loss = 1.1x reported harvest for females and 1.05x reported harvest for males. Male and Female columns each include 0.40 males and 0.60 females for calves 5-months & older.

[c] Wolf kill estimates based on reported wolf numbers on the Northern Range, published kill rates partitioned among adult males, adult females, and calves as observed, and partitioned among 2 time periods (see description in text)

[d] Number (percent of estimated pre-season population).

Ken Hamlin receiving lessons on graphics and analytical software from his grandchildren, Destry and Devin Brandal.

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